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The dynamics and ecology of exotic tropical species in floating plant mats: Lake Naivasha, Kenya

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Abstract

The floating water fern *Salvinia molesta* has occurred in Lake Naivasha since the early 1960s and during this period has obstructed fishing activities and navigation. In recent years the extent of *Salvinia* has declined markedly. Since 1988, a second floating weed, *Eichhornia crassipes* (water hyacinth), has colonised the lake. *Salvinia* formed large mats around the edges, bays and lagoons and had very few plant or invertebrate species associated with it. Mats of *E. crassipes*, however, support a greater abundance and variety of animal and plant species, which shows a relationship with mat size. This seems to have facilitated plant succession but without a zonation typical of the classic hydroseral sequence for the lake.

Introduction

Lake Naivasha is a shallow, endorheic, freshwater lake situated in warm and semi-arid conditions in the eastern Rift Valley of Kenya, lying within an enclosed basin at an altitude of approximately 1890 m (Fig. 1). Rainfall is bimodal with peaks during April and October but shows inter-annual irregularity and an annual evapotranspiration rate that exceeds local rainfall (Harper et al., 1995) as a consequence of long-term climatic changes that affect the catchment (Vincent et al., 1979). The lake as a result of this has a surface area that fluctuates between 100 and 150 km^2, which influences its productivity (Harper, 1991). Its limnology and productivity have also been affected more recently by human intervention. Intensive horticultural development in the last two decades has accelerated papyrus clearance (Boar et al., 1999), drainage and application of fertilizers. This has come on top of exotic species introductions and arrivals between 1926 and 1988. The lake is now considered moderately eutrophic (Kitaka, 2000) because of agricultural developments in its catchment as well as its lakeshore. These changes have affected the aquatic plant species composition and abundance (Harper, 1992) as well as phytoplankton biomass (Hubble & Harper, 2001).

Three main rivers flow into the northern section of Lake Naivasha and transport suspended sediments from upstream erosion during rainfall events. The River Malewa is the largest and flows continually with a watershed area of 1730 km^2 (Gaudet & Melack, 1981). The rivers Gilgil and Karati are seasonal depending on rains and their volumes of flow are much smaller. The area of river inflow was formerly a swamp consisting of river channels flowing into the lake through a marshy area dominated by papyrus (*Cyperus papyrus*). Up to 30 years ago this area was a genuine papyrus swamp (Gaudet, 1977; Gouder et al., 1998) but the area of *C. papyrus* is now only a fragment of its former area (Johnson et al., 1998).

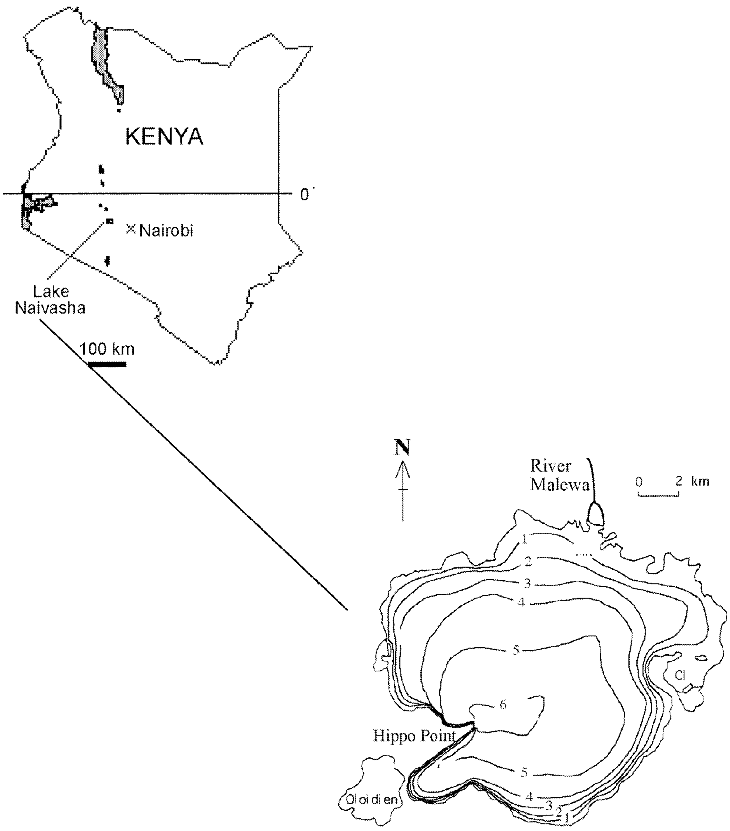

Figure 1. Location map of Lake Naivasha.

In the past 40 years, two highly productive and damaging exotic floating plants have appeared in the lake; 'Kariba weed', the aquatic fern, *Salvinia molesta* D.S. Mitchell [*S. auriculata*] (Salviniaceae) in the late 1960s and the Water Hyacinth, *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae) in 1988. Both these plants formed dense mats, which out-compete less vigorous water plants for both light and space. Both weeds reproduce vegetatively and are distributed to new areas by winds and water currents. *E. crassipes* remains the world's most problematic water weed despite widespread and various approaches to its control (Heard & Winterton, 2000). In the last decade, control at Naivasha has focused upon biological control measures with the introduction of the Salvinia weevil, *Cyrtobagus salvinia*, in the early 1990s, and an Eichhornia weevil (*Neochetina* sp.) in the late 1990s.

S. molesta was abundant up to the end of the 1980s, occupying up to 25% of the lake surface in mobile mats (Johnson et al., 1998). In the 1990s, however, many small floating mats (based on *C. papyrus* and *E. crassipes*) formed when parts of the fringing vegetation broke off and floated due to a combination of wind action and changes in lake level. These mats were temporary in both form and location as they moved with the wind, and may have either split further, coalesced or rejoined the fringing vegetation. Such mats or islands have been reported from a number of wetlands around the world (e.g., Little, 1969), but there has been little ecological study since their initial description (Sahni, 1927 and citations below).

Because of their size and integrity, floating mats offer a colonisation opportunity for other herbaceous plants and shrubs usually found in the littoral zone of lakes. Such plants, if they reproduce by seed, germinate and may complete their life cycles on floating mats. In Lake Kariba, *Salvinia* provided a substratum stable enough for the growth of a number of emergent aquatic and semi-aquatic plants such as *Ludwigia* sp., *Phragmites* sp., *Typha* sp. and *Scirpus* sp. with a total of 40 plant species recorded (Boughey, 1963). Over a period of 10 years, Penfound & Earle (1948) found 63 species: 33 aquatic; 21 wetland and 9 terrestrial, growing on mats of *E. crassipes* in Louisiana in the southern United States. Floating islands may also provide a local habitat for invertebrates and juvenile fish (Oliver & McKaye, 1982; Sazima, 1985; IUCN 1986; Gopal, 1987; Dibble et al., 1996). The invertebrates can be both aquatic species associated with roots (Schramm et al., 1987) or terrestrial species in the aerial vegetation parts (Toft unpublished).

E. crassipes has an ability to root in damp mud (which *S. molesta* cannot do for more than a few days) and so in Naivasha, as in other locations that it has colonized, the littoral zone is overwhelmingly dominated by both floating plants of *E. crassipes* in the shallow water and rooted plants on the shore edge. The dominance has a physical stability, for, as water level changes, rooted plants can float and *vice versa*. It is thus possible that the classic zonation of vascular plants from land to the open water, described for Naivasha by Gaudet (1977), has been be altered. Gaudet classified 108 plant species in a primary successional sequence from lake edge to dry land after a period of naturally low water levels that occurred between 1971 and 1973. The zones were: the seedling zone dominated by *Nymphaea nouchali* seedlings that did not survive further drying; the sedge zone dominated by *Cyperus papyrus*, *C. digitatus* and *C. immensus* and, further inland, the Composite Zone dominated by *Conyza*, *Gnaphalium* and *Sphaeranthus* (Fig. 2).

The present study had the overall objective of examining whether these two exotic species, forming floating mats, were influencing the richness of flora and fauna in Lake Naivasha. This paper describes the changes in the distribution of *E. crassipes* and *S. molesta* which have occurred in the lake since 1988, documents species of plant and invertebrate recorded on them and analyses aspects of the composition of different-sized floating islands of *E. crassipes.*

Methods

The percentage cover of all plants in 4 × 2 m quadrats placed at random in 155 sites on the floating swamp at the edge of the lake was recorded at intervals over the period 1988 to 1998. GPS co-ordinates of each site were recorded on first visit. Sub-sets of the same sites were sampled on later visits. Where *C. papyrus* was present, quadrats were positioned on floating mats at its the lakeward edge. Plants were identified to species as far as possible mainly using Agnew & Agnew (1994) and a composite list compiled.

Samples for invertebrates were collected from individual *E. crassipes* which were taken into a net and later taken apart by hand. Invertebrates were removed by pooter or directly into sample tubes by pipette and preserved in 70% ethanol. A portion of plant was taken back to the laboratory where it was placed into traditional Tullgren funnels, and the extracted fauna collected prior to subsequent microscope examination.

Islands were sampled on a transect stretching from the south-west of the lake at Hippo point to the north, adjacent to the entry of the Malewa river (Fig. 1). Mat size was measured across the largest dimension and at right angles to that and area estimated from this, assuming a rectangle. Plant and animals were counted as 'Recognisable Taxonomic Units' (RTU).

Results

E. crassipes arrived in 1988, where it was recorded as isolated plants in the northern shallows. In 1989, 81% of the 155 sites surveyed around the lake had a percentage cover of more than 75% *S. molesta*. By 1993, when 132 sites were surveyed, only 5% of the sites supported the same high density. However, by this time *E. crassipes* had reached in excess of 75% cover in 63% of sites (Fig. 3). Present-day *S. molesta* cover is negligible and cover by *E. crassipes* has remained relatively stable. It usually forms a narrow fringe 0–5 m wide around much of the lake. Larger mats occur in sheltered bays and inlets.

Fifty-one species of plants were recorded on or in floating mats of *E. crassipes* and *S. molesta* between 1988 and 1998 (Tables 1 and 2), including submerged plants. Figure 4 shows plants apportioned between mat-forming species, grass and sedge species, herbs and shrub species. *Cyperus pectinatus* was the most frequent grass or sedge, and appeared to have an important role in binding the *E. crassipes* mat, facilitating colonisation by other species.

Since 1993, the species richness of herbaceous colonisers of the mats appears to have increased with a peak of 23 species found in August 1997. This was coincident with the first records of colonization of floating mats by the shrubby species *Hibiscus* sp. and *Sesbania* sp. It was thus 5 years after the first appear-

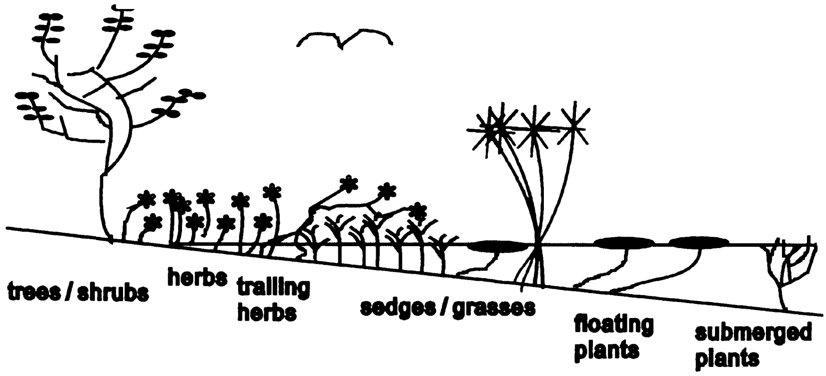

Figure 2. Hydroseral succession of plant species around the shore of Lake Naivasha in the 1970s. After Gaudet (1977).

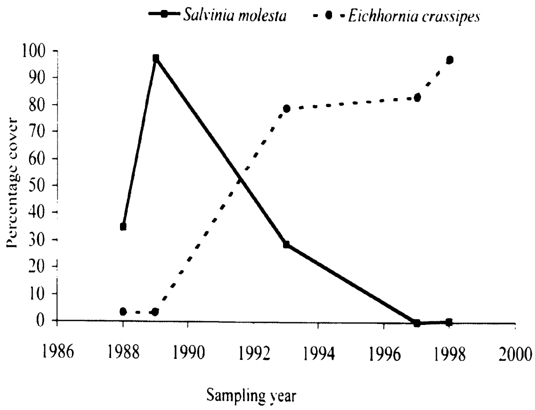

Figure 3. Changes in cover of open water by floating plants of *Salvinia molesta* and *Eichhornia crassipes* in Lake Naivasha between 1988 and 1999.

ance of *E. crassipes* in the lake that mats became colonised with species usually associated with shoreline communities and 8 years before shrubs appeared.

The fauna associated with mats was concentrated in the layer between the leaves and the aquatic roots of the plants. The major groups of invertebrates found in this layer were Oligochaeta (mainly *Alma emini*), Insecta and Arachnida (both aquatic and terrestrial). Within this zone, dead plant material is continuously being broken down and wind-blown dust accreted in a soil-forming process, in which the earthworm *A. emini* appears to be very important. Young individuals of *Procambarus clarkii* and *Micronecta scutellaris* are common in and amongst the roots in *E. crassipes*. In contrast, *S. molesta* mats harbour a very limited fauna, both in species diversity and number of individuals. To date (2001), no individuals of the introduced weevils, *Cyrtobagus salviniae and Neochetina* sp., have been identified in any floating vegetation.

Table 1. Species list of all plants recorded on floating mats of *Salvinia molesta* and *Eichhornia crassipes* in Lake Naivasha, compiled over the period 1988–1999

Floating species	Herbaceous species
Azolla africana	*Basella alba*
Eichhornia crassipes	*Bidens pilosa*
Pistia stratiotes	*Circium arvense*
Salvinia molesta	*Callitriche truncata*
Wolffia arrhiza	*Commelina benghalensis*
	Conyza sp.
Sedges	*Crassocephalum picridifolium*
Cyperus dives (immensus)	*Crotalaria barkae*
C. flavescens	*Crassula schimperi*
C. marginatus	*Diplanche fusca*
C. papyrus	*Enydra fluctuans*
C. pectinatus	*Epilobium hirsutum*
C. rigidifolius	*Gnaphalium luteo-album*
	Hydrocotyle sp.
Grasses	*Ipomoea cairica*
Acroceras zizanioides	*Iris* sp.
Agrostis stolonifera	*Ludwigia stolonifera*
Miscanthidium sp.	*Lythrum rotundifolium*
Pennicetum clandestinum	*Polygonum salicifolium*
Setaria veristicelata	*P. senegalense*
Typha latifolia	*Pycnostachys coerulae*
	P. deflexifolia
	Senecio sp.
Submerged species	*Sphaeranthus napierae*
Najas horrida	*Tagetes minuta*
Nymphaea nouchali	*Veronica* sp.

There was an increase in RTU number with increasing island size. The upper limit for plant richness was reached before that for invertebrates, as the rich-

Table 2. Taxonomic list of invertebrates recorded on *Eichhornia crassipes* at Naivasha

Turbellaria		
	Dugesia sp.	
Oligochaetaea		
	Alma emeni	
	Brachiura sowerbyi	
	Potamothrix sp.	
Mollusca		
	Bulinus sp.	
	Physa acuta	
Diplura (terrestrial)		
Aranaea		
	Hydracarina	
	Arachnida (terrestrial)	
Crustacea		
	Procambarus clarkii	
	Ostracoda	
	Copepoda	
Insecta (terrestrial)		
	Collembola	
	Thysanoptera	
	Orthoptera	
	Dermaptera	
	Cicadoidea	
	Staphylinidae	
	Formicidae	
Insecta (aquatic)		
	Coleoptera	
		Hydaticus sp.
		Rhantus sp.
		Cybister sp.
		Helochares sp.
		Berosus sp.
		Eochrus sp.
		Canthyrus sp.
		Hydrovatus sp.
		Methles sp.
		Synchortus sp.
		Bidessus sp.
		Helodidae
Hemiptera		
	Micronecta sp.	
	Plea sp.	
	Mesoveliidae	
	Lygaiedae	
Diptera		
	Culicidae	
	Ceratopogonidae	
	Chironomidae	
	Tipulidae	
	Sciomyzidae	
Odonata		
	Enallagma sp.	
Ephemeroptera		
	Cioeon sp.	
Trichoptera		
	Ecnomus sp.	

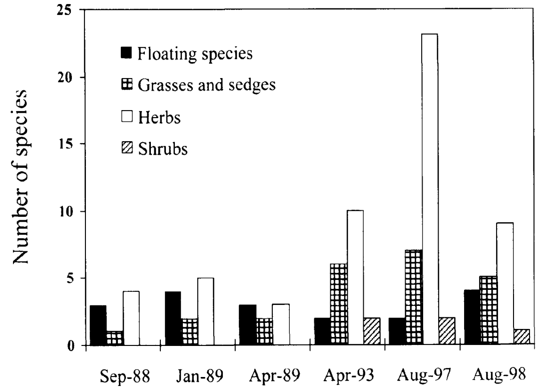

Figure 4. The species richness of groups of plants found growing on floating mats of *Eichhornia crassipes* in Lake Naivasha over the period 1988–1999.

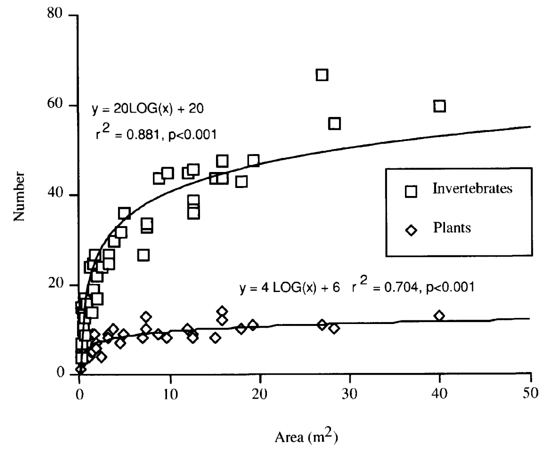

Figure 5. Change in plant and invertebrate species numbers with change in island size.

ness of the latter continued to increase with island size (Fig. 5).

Invertebrate density decreased with island size in a power relationship, with density more or less constant for islands above approximately 10 m^2 in area (Fig. 6). No similar relationship was evident for plants.

As plant species richness increased, so did invertebrate richness (Fig. 7).

Discussion

S. molesta had been first recorded in Lake Naivasha in 1962, inside the lagoons that were common inside the lake's fringing papyrus. Measures to control the spread of the weed involved herbicide applications and phys-

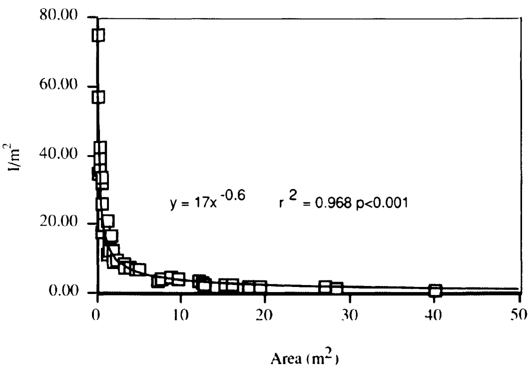

Figure 6. Changes in invertebrate density with increasing island area.

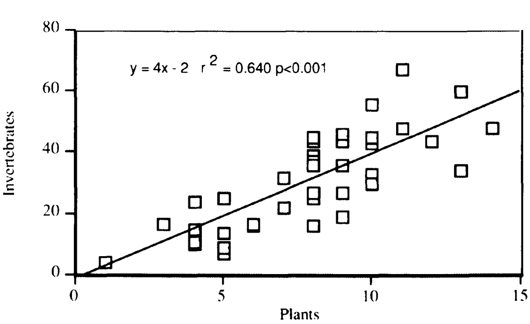

Figure 7. Correlation between numbers of plant and invertebrate species on islands.

ical removal but these were unsuccessful. However, experiments conducted during these times showed that *S. molesta* exposed to the windy and choppy conditions of the open lake quickly perished. However, reproduction in the more sheltered and shaded lagoons resulted in plants being pushed out so that, between 1975 and 1983, floating mats covered large areas of the northern and western open water of the lake (Harper, 1992). When lake level receded in the late 1980s, the sheltered lagoons almost totally disappeared and this resulted in a dramatic decline (Tarras-Wahlberg, 1986; Harper et al., 1990). At present, *S. molesta* is found only in the wetland at the lower reaches of the Gilgil river. In this area, the Gilgil river flows only gently, and the area is sheltered from the exposed conditions of the open lake (Everard et al., this volume). These conditions are similar to those of the former sheltered lagoons and hence are a likely explanation why *S. molesta* has survived only in this part of the lake system. The lack of records of the introduced weevil implies that it has had a limited part in the disappearance of *S. molesta* and that instead the loss of suitable habitat from the lake is a more likely cause of the plant's decline. Additional evidence for this is that no *S. molesta* is to be found in the lower reaches of the Malewa river (except during high water levels of the 1999 'El Nino' rains when extensive lagoons were once again formed in the river mouth at the northern end of the lake).

E. crassipes has colonised the full extent of Lake Naivasha shoreline in only a few years but the rate of its growth is small compared with its invasion and persistence in Lake Victoria, the Sudd and elsewhere throughout the tropics and sub-tropics. Interesting features of *E. crassipes* in Lake Naivasha are that individual plant biomass is low and that the plant has not colonised the open lake in large mats. High exposure to winds and relatively low water temperature may have constrained its spreading. Water hyacinth is at its most productive when maintained at water temperatures of around 28 °C (Bock, 1969). The annual mean water temperature in Lake Naivasha, (at an altitude of 1890 m) is around 21°C (Muthuri et al., 1989) and is thus rather low for tropical waters. A genetic basis for differences between productivity of particular clones of *E. crassipes* may also exist (Geber et al., 1992).

The absence of individuals of the weevil *Neochetina* in any of the *E. crassipes* samples investigated to date, implies that the introduction of the weevil has not (or not yet) significantly affected the spread of the water hyacinth. The largest floating mats occur in the north of the lake around the inflow of the River Malewa, which may advantage the plant with a nutrient supply as well as shelter (prevailing winds for most of the year push floating plants to the north (Litterick et al., 1979)).

The plant species richness of the islands of *E. crassipes*, although not reaching the total recorded by Gaudet (1977) indicate from this study that this floating exotic plant is unlikely to be reducing the biodiversity of semi-aquatic plants in Naivasha. The results also indicate that the islands represent an extension of the swamp and so partially replace its loss to agriculture at declining water levels. The recent evidence of shrub species indicate that the islands are also undergoing successional processes as described on land (Kaul & Zutshi, 1966; Gaudet, 1977). This is aided by the accumulation of suspended organic matter and the activities of wet soil animals such as *A. emini* which encourages further colonization (Trivedy et al., 1978). The nature of this succession though is to dissemble the spatial zonation of plants described by Gaudet (1977) with a temporal succession of species occurring on the mats themselves.

The invertebrate richness cannot be compared directly with other habitats, but the aquatic part of the taxonomic list represents a broad cross-section of the full list for the lake from the 1980s published by Clark et al. (1989). The terrestrial component is not identified adequately for meaningful interpretation but represents aerial dispersal and indicates the availability of arthropod prey for birds such as plovers, ibises, gulls and terns which are common on *E. crassipes* mats (Henderson & Harper, 1992). The increase in richness with island size is likely to represent the increased probability of colonization, whilst the reduced density with island size probably reflects a less suitable environment in the middle of islands (Gopal, 1987; Bailey & Litterick, 1993).

Acknowledgements

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