

## The aquatic plant communities of the Lake Naivasha wetland, Kenya: pattern, dynamics and conservation

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### Abstract

The spatial and temporal patterns of the wetland plant communities at Lake Naivasha over the past decade, and the past five years in particular, are discussed in relation to the major controlling factors. The four communities are:- the emergent swamp, dominated by *Cyperus* species; the floating raft, dominated by the aliens *Salvinia molesta* and *Eichhornia crassipes*; the floating-leaved plants, represented only by *Nymphaea caerulea*; and the submerged angiosperms, consisting of three species of *Potamogetons* – *P. pectinatus*, *P. schweinfurthii*, *P. octandrus* – together with *Najas pectinata*. The major factors affecting their dynamics are:- water level changes which influence agricultural clearance, introduced crayfish *Procambarus clarkii*, and interactions between communities such as the physical effects of mobile floating rafts. The value of the different communities to the ecological and economic value of the lake is highlighted, and the possible damage from future activities discussed.

### Introduction

The ecology of the papyrus swamps and the fringing vegetation of the freshwater Lake Naivasha (located in the eastern Rift Valley of Kenya) has been well studied by Gaudet (1977, 1979). Less well studied have been the communities of submerged and floating plants or the fauna associated with these littoral plant habitats at the lake. An understanding of the role of all the plant communities is now essential, because major changes have occurred over the last decade in both water quality parameters and in the species and distribution of both the emergent swamp and the submerged plant beds (Harper, Mavuti & Muchiri 1990).

Harper (1992) described the recent state of the lake's aquatic vegetation in terms of three phases: a 'normal' phase to 1975, a 'reduced' phase to 1983, and a 'recovery' phase thereafter. This paper concerns itself with greater detail of the 'recovery' phase, which is seen as a sequence of interconnected changes, with possible explanations for species shifts and predictions about the future stability of the plant communities.

### Methods

Plant specimens were collected from a boat or wading in shallow water between 1983 and 1991 by hand collection if they were floating or emergent, and by grapnel if they were submerged. The relative abundance of submerged plant species was estimated from their proportions in replicate grapnel hauls at sites along transects radiating out from shore and recorded by both distance from the shore and lake depth. Distance and depth measurements were made using a marked polypropylene rope. Sediment samples were taken by Ekman grab and particle composition visually estimated in subsamples examined at 100 x magnification under a compound microscope. The relative abundance of floating plants was estimated in replicate 1 m<sup>2</sup> quadrat frames placed on the vegetation surface from the side of a boat. The distance from one plant or clump of *Eichhornia* to the nearest was recorded (twenty replicates at each station) as an indication of the species' frequency in floating mats and shoreline strandings. The total areal cover of plants together with lakeside land use was estimated by

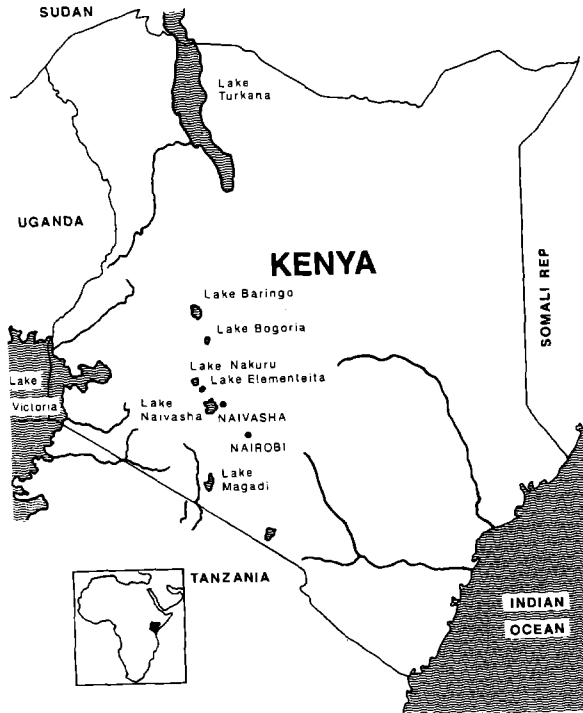


Fig. 1. The location of Lake Naivasha in the chain of lakes forming the Eastern Rift Valley which runs through Kenya.

aerial photographs taken from a light airplane and plotted onto a 1:50,000 map.

### The physical background

Lake Naivasha and its history is described more fully in Harper, Mavuti & Muchiri (1990); its geography and location are shown in Figures 1 and 2. The lake occupies a closed basin in the floor of the Rift Valley at approximately 1890 m altitude, with an inflow predominantly from the Nyandarua mountains rising to 3,960 m to the north and east. These mountains are within the range of the Intertropical Convergence Zone. The inter-annual rainfall is irregular. The local rainfall around Naivasha is exceeded by annual evapotranspiration. This instability gives the lake an area that fluctuates with inflow. It is always shallow; apart from a small deep crater known as Crescent Island lagoon (Fig. 3) with a depth exceeding 20 m, the main body of the lake has a maximum depth of around 10 m and a mean depth of around 5 m. Water levels have fluctu-

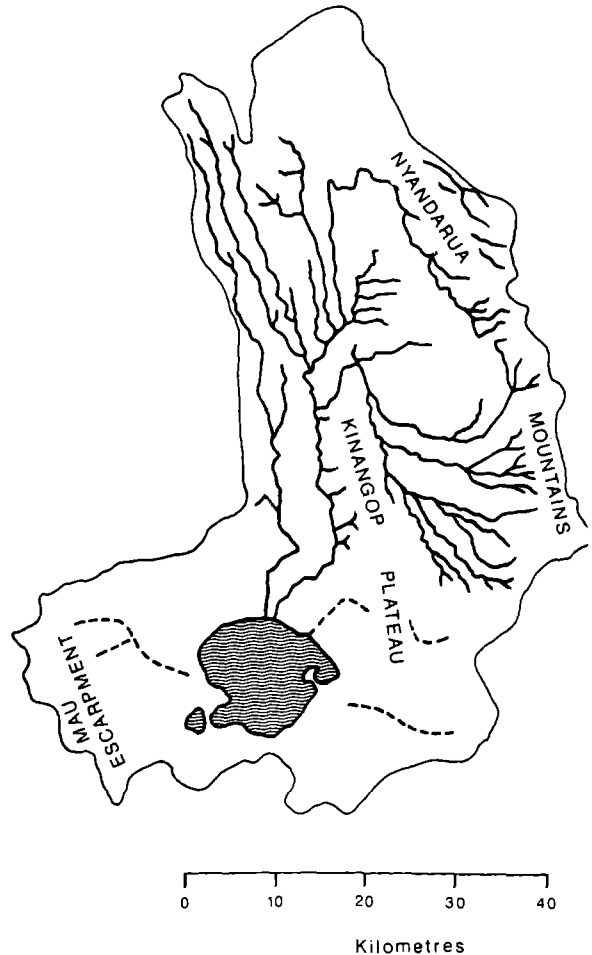


Fig. 2. The catchment area of Lake Naivasha in the Nyandarua mountains.

ated by about 7 vertical m this century (Harper, Mavuti & Muchiri 1990) and by 4 m in the past decade (Fig. 4). The lake area is approximately 140 km<sup>2</sup>; a third of this area is shallower than 3 m and potentially capable of supporting submerged plant growth.

The shallowest part of the lake with the most gentle gradient is the northern part, but the depth contours in Figure 3 indicate that the depth is suitable for submerged and emergent plant colonization over large areas of the east and west portions of the northern half. A substantial difference in substrate composition exists, however, with the north-eastern parts of the lake being dominated by loose flocculent organic matter derived from *Cyperus papyrus* and *Salvinia molesta* debris. The western

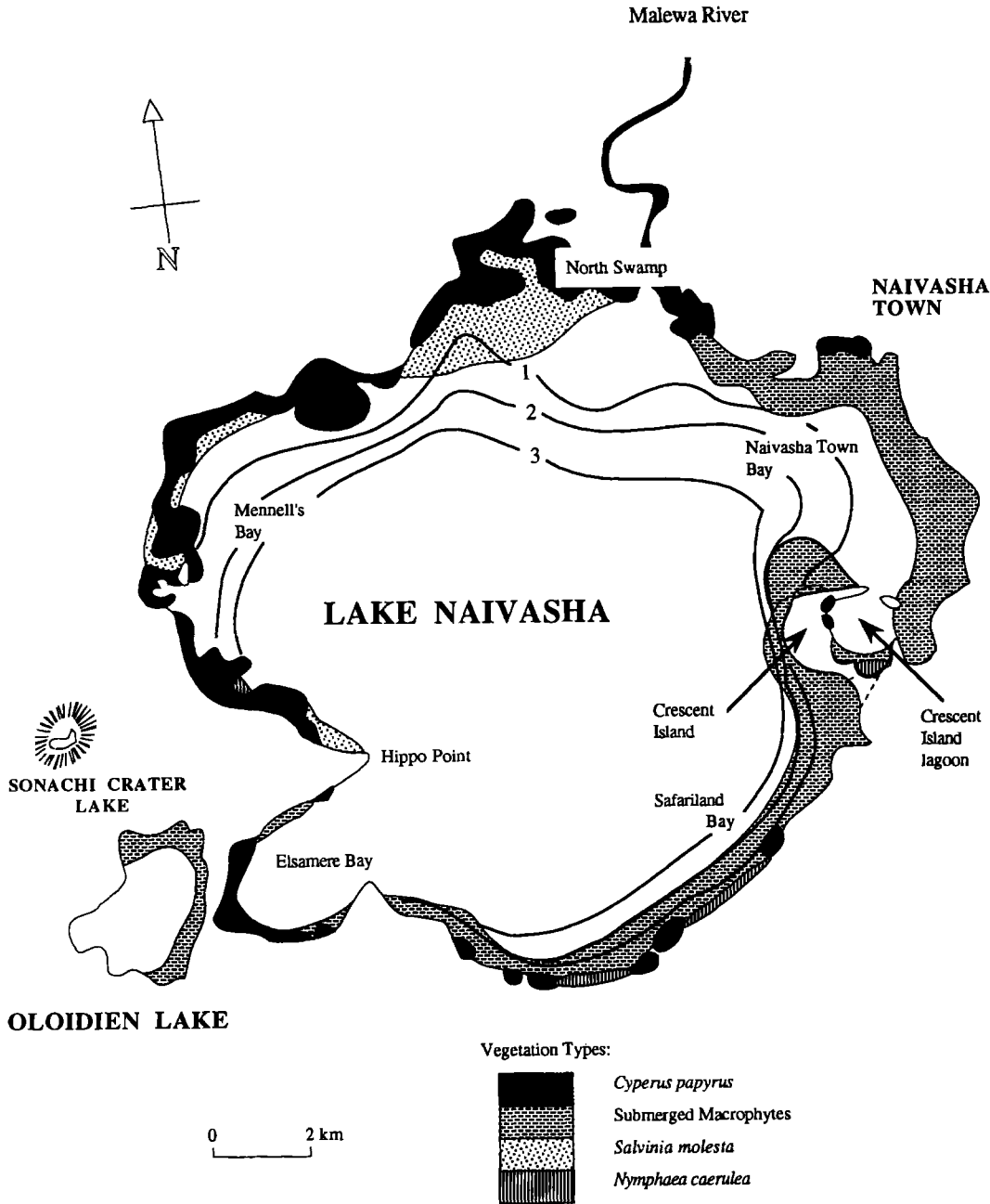


Fig. 3. Lake Naivasha and its two associated lakes, Oloidien and Sonachi Crater. The lake outline, depth contours and major plant communities represent conditions in 1987. The plant communities are not drawn to scale. The maximum depth of the main lake is reached just off Hippo Point, at 7m.

half, by contrast, contains more sand and fine inorganic particles; the lake lies in a volcanically active area and most of the surrounding soils are sandy soils of volcanic origin (Fig. 5). Most work was carried out in Safariland Bay, where the gradient was

0.4% and the 3 m depth contour lay about 500 m from the inner edge of wetland vegetation (Fig. 6). The gradient in the north is <0.1% and inside Crescent Island Lagoon >2%.

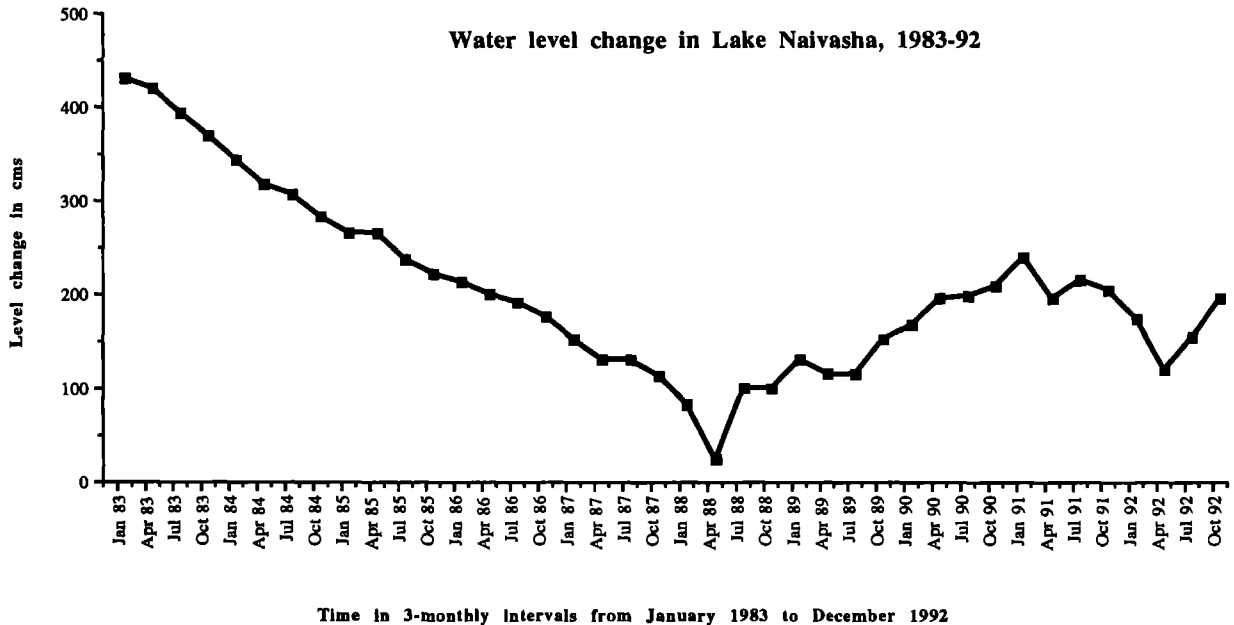


Fig. 4. The depth changes of Lake Naivasha in the decade 1983-1992.

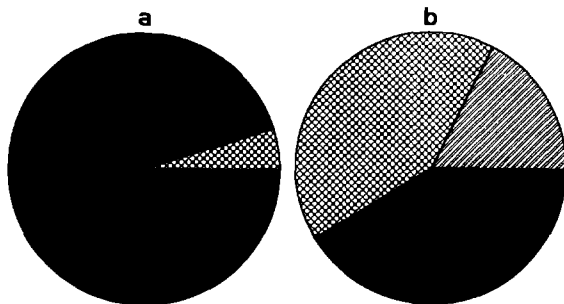


Fig. 5. Pie diagrams of the percentage composition (estimated by microscopic examination) of substrate samples collected with an Ekman grab in shallow water off: a) the western shore, and b) the eastern shore.

■ organic matter; ▨ silt/clay; ▩ very fine sand

## Results

### Emergent and swamp plants

#### Spatial distribution

The dominant visual feature of the lake in the early 1980s had been a high water level that lifted large *Cyperus papyrus* clumps from their original location so that they formed numerous floating islands, intermingled with an extensive *S. molesta* raft. Most

of the lake shoreline was fringed with *C. papyrus* and other *Cyperus* species. As the water level receded 3 m vertically between 1983 and 1987, a broad drawdown zone became established, similar to that described by Gaudet (1977), that was dominated naturally by grasses (*Cynodon* spp.) and *Polygonum* spp. Much of the *Cyperus* and drawdown vegetation was cleared for arable agriculture that followed the receding water line all around the lake such that, by the end of 1987, only an estimated 2 km<sup>2</sup> papyrus swamp remained around Naivasha. In May 1988, following heavy rains, a rapid rise of 1 m in water level led to the new germination of *C. papyrus* and *C. dives* seedlings in the band of soil suddenly re-flooded.

The swamp that rapidly developed persisted through subsequent small rises and falls of water level to the present day. Its outer edge frequently lifted from the sediments in about 1-2 m water depth, but its integrity was largely maintained. Some few islands have floated free and many more small clumps germinated in *S. molesta* or *E. crassipes* rafts. Its area is now (1992) estimated to be 11-12 km<sup>2</sup>, mostly in the north, but it forms a continuous band around perhaps 80-90% of the lake edge. At Safariland Bay its width is around 200 m and it is largely unbroken, and with few lagoons.

Periods of water rise occurring after 1988 have

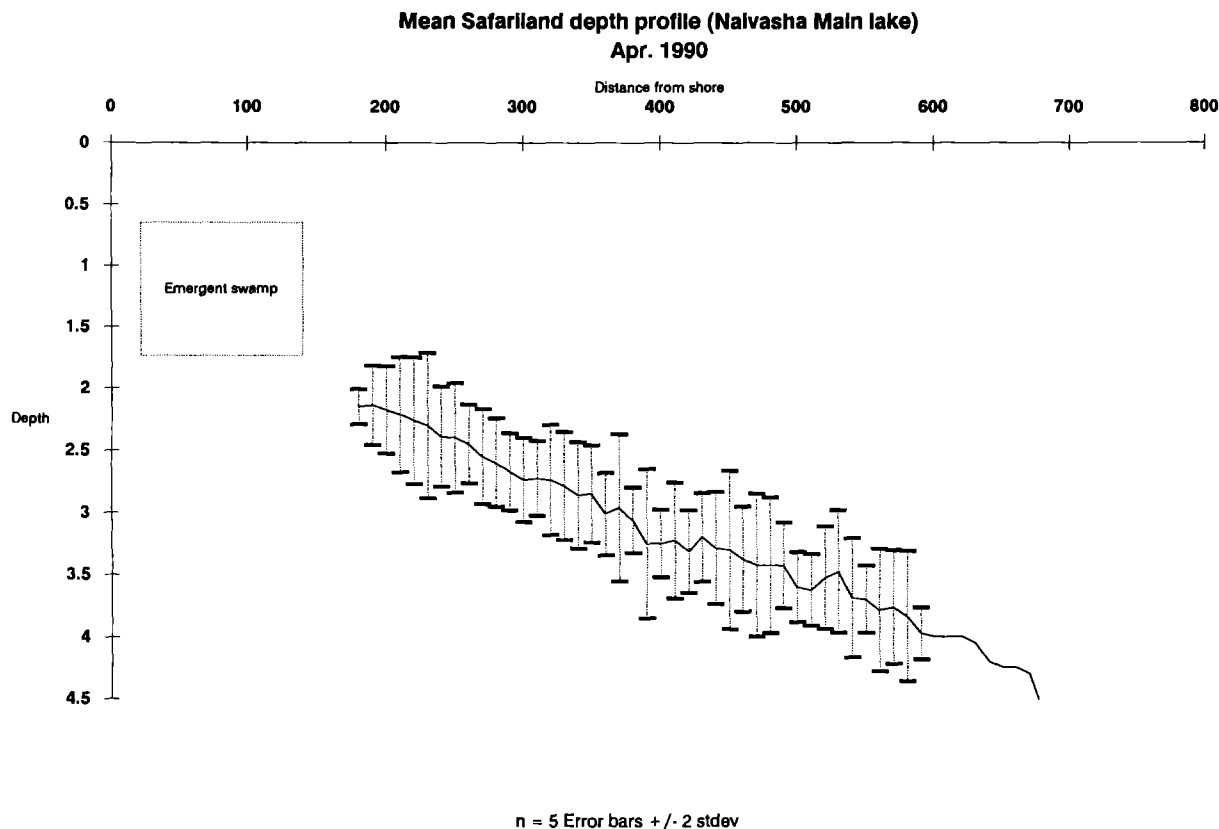


Fig. 6. Profile of the littoral zone at Safariland Bay.

not been followed by extensive new *Cyperus* germination, but have resulted instead in the formation of shallow lagoons of flooded grassland on the landward edge of the 1988 *Cyperus* swamp.

#### Species composition

The swamps are largely stands of the two *Cyperus* species, but colonized by smaller wetland plants and climbers where they can root in the bases. Table 1 shows the composition and frequency of occurrence in the swamp at Safariland one year after its development.

#### Floating-leaved plants

#### Species composition and spatial distribution

The only floating-leaved plant in the lake is *Nymphaea caerulea*, which has experienced consid-

Table 1. Frequency of occurrence (%) of plant species in emergent swamp one year after its formation, January 1989.

<i>Cyperus dives</i>	100
<i>Polygonum spp.</i>	84
<i>Cyperus papyrus</i>	70
<i>Salvinia molesta</i>	64
<i>Conyza spp.</i>	39
<i>Cynodon aethiopicus</i>	20
<i>Circium arvense</i>	16
<i>Nymphaea caerulea</i>	11
<i>Ludwigia stolonifera</i>	9
<i>Epilobium hirsutum</i>	5
<i>Crassocephalum picridifolium</i>	5
<i>Enhydra fluctans</i>	2
<i>Sesbania sesban</i>	2
Compositae indet.	14
<i>Cyperus</i> indet.	11
Graminae indet.	57

erable fluctuations in its abundance and distribution. It was completely absent from the lake in 1983. By 1987 it had developed a dense zone 10 m wide

on the inside of Crescent Island and occurred in frequent clumps in shallow water <1 m depth elsewhere. The Crescent Island beds disappeared by 1988, but in that year scattered plants could be found throughout the lake amongst the newly-germinated emergent swamp. By 1989 very few plants could be found again anywhere in the lake. In 1990, newly germinated seedlings became common in the shallow lagoons that formed over grassland inside the papyrus fringe after the slight water level rise of that year. In 1991 a bed of *N. caerulea* began to develop off the edge of the *Cyperus* in Mennell's Bay, on the inside of a raft of floating vegetation that had become semi-permanently stuck over the outer edge of the submerged macrophyte bed.

### Floating raft

#### Species composition

The dominant species of floating plant community are the aliens *Salvinia molesta* and *Eichhornia crassipes*. The former has been present in the lake for twenty years and the latter first appeared in 1988. The raft may be associated with islands of *Cyperus* species when the fringing swamp is older (>3-5 years) and pieces break free from the outer edge. *E. crassipes*, in particular, but *S. molesta* to a lesser extent (see Taylor & Harper 1984) also form a stable platform of their own upon which detritus can build up and swamp plants germinate. The most common species of the floating raft are shown in Table 2.

#### Spatial and temporal distribution

Floating rafts were a dominant feature of the lake around 1980 to 1983, but declined in extent through to 1987 as the water receded and stranded them on shore where they dried. The rapid rise in lake level in 1988 was followed by the development of a new raft of *S. molesta* with scattered plants of *E. crassipes*. This raft remained a large feature of the lake for the next year before breaking up on a slight fall in water level. A similar sequence of raft formation and decline occurred after the less rapid water level rise in 1990.

*E. crassipes* had first been observed in Naivasha

Table 2. Frequency of occurrence (%) of floating raft community, January 1989.

<i>Eichhornia crassipes</i>	63
<i>Salvinia molesta</i>	61
<i>Pistia stratioides</i>	34
<i>Hydrocotyle ranunculoides</i>	16
<i>Ludwigia stolonifera</i>	11
<i>Cyperus papyrus</i>	6
<i>Enhydra fluctans</i>	4
<i>Polygonum senegalense</i>	2
<i>Cyperus dives</i>	1
<i>Polygonum pulchrum</i>	1
<i>Polygonum salicifolium</i>	<1
<i>Crassocephalum picridifolium</i>	<1
<i>Scirpus inclinatus</i>	<1
<i>Sesbania sesban</i>	<1
<i>Wolfia arhiza</i>	<1

in August 1988, as a few plants among a *S. molesta* raft trapped by a south wind against the *Cyperus* edge in the north of the lake near the Malewa river inflow. It spread slowly, considering that changes in wind direction occur almost throughout 360° with season (Ase, Sernbo & Syrén 1986); by January 1989 it could be found in *S. molesta* rafts or against the lake edge throughout the western half of the lake from the Malewa inflow round to the shore adjacent to Oloidien lake (but not in Oloidien itself, a water of higher alkalinity). It was ubiquitous throughout the lake edge and rafts by April 1990. Nearest neighbor comparison of plant abundance in floating rafts showed a substantial decrease from 3.6 in 1989 to 0.5 m in 1991; it became completely dominant plant in the floating rafts by 1992 as *S. molesta* declined rapidly in abundance following introduction of the biological control agent *Cyrtobagus salviniae*. In 1992 it was rooted along all shorelines and shallow water, associated with emergent *Cyperus* swamp, floating rafts and exposed beaches. Large plants are associated with sheltered edges, such as the North swamp area, whilst smaller plants are found in the floating rafts and exposed beaches.

### Submerged macrophytes

#### Species composition

Four species of submerged plant occurred in Naivasha – *Potamogeton pectinatus*, *P. octandrus*,

*P. schweinfurthii* and *Najas pectinata*. Occasional specimens of a charophyte were collected in 1987-8.

#### Spatial and temporal distribution of submerged plant beds

Submerged macrophyte beds, completely absent from the lake in 1983 and sparse in 1984, developed between 1984 and 1987 to cover >20 km<sup>2</sup> of lake. The beds were confined to four main littoral areas – Safariland Bay, the north side of Crescent Island, Naivasha town Bay and Elsamere Bay, all on the east side of the lake, as shown in Figure 3. The Naivasha town and Elsamere beds declined through 1988 and 1989, whilst the Crescent Island beds extended westwards. A further decline between 1990-91 left only the Crescent Island beds of any significance, together with a new development in the west side of the lake in Mennell's Bay for a total coverage of <10 km<sup>2</sup>. In 1992 macrophyte beds were confined to Mennell's bay and Elsamere Bay, covering an area of about 5 km<sup>2</sup>. Submerged plants have been recorded to around 4 m depth (see below), which meant that less than 50% of the lake area potentially colonisable was inhabited by submerged plants at any time.

#### Spatial and temporal distribution of submerged plant species

Initially all four species were present in approximately equal abundance, measured as frequency of occurrence. As time went on, first *P. octandrus* and then *P. schweinfurthii* became less frequent and by 1991 the former species was no longer found. At the same time *Najas pectinata* became the dominant species throughout the remaining beds and the depth distribution of the two dominant species changed from shallow water <2m, to deeper water > 2m, leaving a clear zone outside the emergent swamp (Fig. 7).

#### Oloidien Lake

Throughout the decade 1983-1992 the submerged plant beds of Oloidien Lake remained intact. Oloidien (Fig. 3) is a closed crater lake with water of higher conductivity than Naivasha, although the two appear hydrologically connected because they

experience similar level fluctuations. No papyrus swamp or floating rafts exist at Oloidien because of the higher ionic concentration of the water. The area covered by the submerged plants at Oloidien has remained constant; a relatively narrow band around the lake. These beds consisted of the three common species of the main lake, although dominated by *Potamogeton pectinatus*. *Najas pectinata* has progressively disappeared over the past five years (Fig. 8).

## Discussion

### *Water level fluctuations*

It seems clear that water level fluctuations were the driving force behind swamp development and decline. Decline followed water level decrease or stability, when farmers were able to follow the water down with burning and cultivation or grazing. Any period of water level rise provides greater uncertainty over crop loss from waterlogging, so that a partial recovery of the natural vegetation follows. The major event of *Cyperus* species germination was the particular period of a rapid water level decline (hence soil and seed drying) followed by a rapid rise. This re-flooded a band of bare soil that had barely had time to be colonized by terrestrial plants. Evidently, from the precise boundaries of the new swamp, these were the ideal conditions for *Cyperus* spp. germination, which require damp, nutrient-rich soils (Thompson 1985). Any period of water rise subsequent to May 1988 has not followed a rapid decline; thus the newly flooded soils have been grass-covered rather than bare, and any germination was not followed by seedling success.

Water level fluctuations are probably also responsible for the spread and recession of the floating raft. A period of water level fall strands portions of the raft whenever they are blown to shore by wind; *S. molesta* quickly dries up although other species such as *Cyperus* and *E. crassipes* can root in waterlogged soil. A period of water level rise releases nutrients from re-flooded soils which were previously dried and oxidized. We have observed that *S. molesta* is rarely in a state of vegetative reproduction in the floating rafts, where it appears brown and moribund. In the littoral zone it is green with divid-

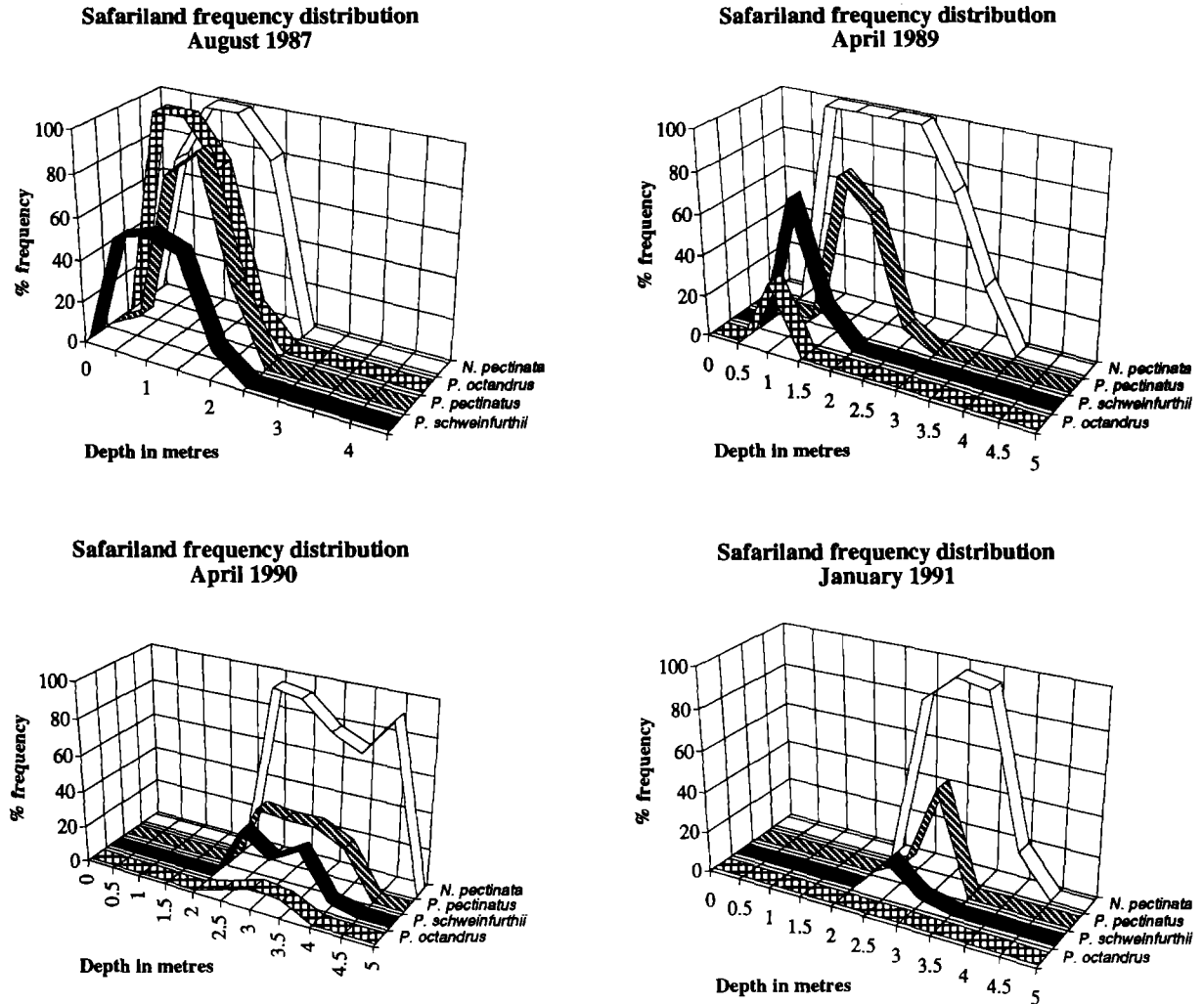


Fig. 7. The frequency distribution of submerged plants at Safariland Bay, 1987-1991.

ing ramets, so we hypothesize that rapid growth occurs with the flush of nutrients and new plants are pushed out into the lake and picked up by the wind. It is unlikely that *S. molesta* can grow rapidly in conditions of open water – bright sunlight, daily wind disturbance and low night-time temperatures (air temperatures down to 10°C). On two occasions, about a year following periods of water level rise (1989, 1991), the rafts have progressively declined in coverage on the lake, probably due to death and sinking of moribund *S. molesta*.

*E. crassipes* has spread unexpectedly slowly since its first appearance in 1988, compared to experience of its dynamics elsewhere in the tropics (e.g., the Nile in Sudan). This rate of colonization is

probably because the temperature regime at Naivasha is below the optimum for the plant; Naivasha water temperatures fluctuate between 28-18°C. Four years after its arrival however, it is ubiquitous both in the floating rafts and along the littoral. We anticipate that, because of its substantial root system and above-water architecture, it will form the base for a more substantial floating raft than previously, especially since *S. molesta* has been reduced by the March 1991 introduction of *Cyrtobagus salviniae*.



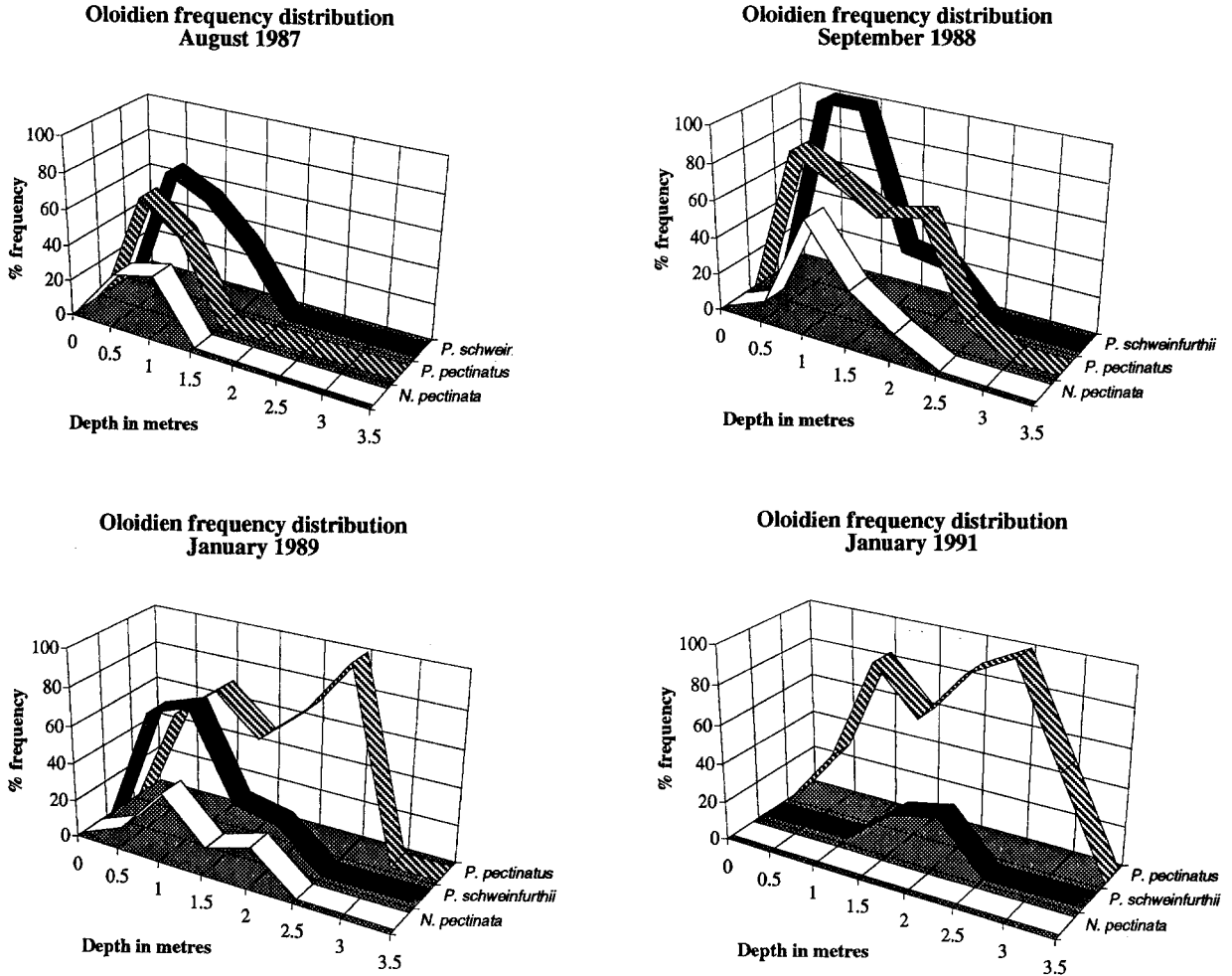


Fig. 8. The frequency distribution of submerged plants at Oloidien Lake, 1987-1991.

#### *Water quality and transparency changes*

Water quality is linked to water level in several ways. Directly, river input is a major source of nutrients. Quality is moderated by the presence of swamp vegetation at the inflows (Gaudet 1979), which tends to retain sediment and nutrients and thus smooth out seasonal fluctuations. Lake level rise provides further nutrient influx from flooded soils whilst lake level fall results in concentration of nutrients (Harper et al., 1993). Land use probably also affects the extent to which runoff influences the lake directly, and also the nutrient content of flooded soils. There is no evidence for a direct effect of water quality and transparency upon plant com-

munities, because the greatest extent of underwater plant growth occurred during the periods of lowest transparency in 1987-88. Oloidien Lake, with very high algal biomass and low transparency (Secchi disc extinction is about 50 cm), has always retained its submerged plant beds.

#### *Floating plant raft*

The extent of the floating plant raft has already been linked to water level changes. It is possible that the raft itself influences submerged and floating-leaved plants, since periods of high floating raft occurrence (up to 1983, 1989 and 1991) are coincident with

submerged plant absence or decline. The possibility of a major effect upon submerged plants was however discounted by Harper (1992), because in 1983 no submerged plants grew in shallow lagoons free from the effects of floating plant rafts at localities (western littoral, Mennel's Bay) where submerged plants had later become abundant (by 1991). Elsewhere, the floating raft is mobile and has not stayed long enough in any part of the lake for an absence of submerged plants to be attributed to its effect. The location where the raft is most persistent, the North Swamp, is also the area of most flocculent substrata and this latter effect is probably more important in restricting submerged plant establishment. In several locations, parts of the floating raft (including islands of *Cyperus*) have become 'grounded' on top of submerged plant beds. This phenomenon happened in 1989-91 in the beds of the northern shore of Crescent Island and in 1991-2 on the beds in Mennel's Bay. The relative persistence of these stranded islands (at least a year in the same exact location) indicates a minimal effect upon the submerged beds.

It is probable however, that the floating raft has been the major influence upon the distribution and persistence of the water lily *Nymphaea caerulea* over the past five years. This plant grew in a dense zone between 0.5-2 m depth inside Crescent Island Lagoon in 1987, when the lagoon was free of floating raft. The zone had disappeared by 1988, coincident with a water level rise high enough to allow access of wind-blown floating rafts over the shallow rim of the Crescent Island crater; once inside the Lagoon they became 'locked' within it due to its relatively sheltered position from prevailing winds. Elsewhere throughout the lake in 1988, germination of the new emergent swamp was also associated with germination of *N. caerulea* plants: but by 1990 the swamp had closed in with the growth of the main *Cyperus* species and all free water surfaces within the swamp were completely covered by *S. molesta* and *E. crassipes*. In 1991-92, the only area of *N. caerulea* in the lake was a zone of 0.8-2 m depth in a small (about 1 ha) area of submerged plant bed in Mennel's Bay. This was also the only area of the submerged bed to be unaffected by periodic floating rafts as it was protected by the build up of a semi-permanent 'reef' of *E. crassipes* and *Cyperus*-dominated raft which at that time was

'grounded' on top of the dense bed of submerged plants. Shallow lagoons around the lake, on the inside of the papyrus swamp, have periodically between 1989 and 1992 developed prolific seedlings of *N. caerulea*; the presence of the swamp makes these lagoons free of dense *Salvinia* for several months after their formation. This set of circumstantial evidence points to continual germination success of *N. caerulea* from a seedbank throughout the sediment, but success to flowering only in locations free of floating raft vegetation.

### *Crayfish populations*

The Louisiana swamp crayfish *Procambarus clarkii* was introduced to the lake in the 1970s in a program to diversify the commercial fishery, and initially this was successful. The official catch returns are shown in Figure 9. Crayfish population rise and decline has been the factor linked most firmly to the success of both submerged and floating-leaved macrophytes, because of their known effects upon plant populations in lakes in the United States (Harper, Mavuti and Muchiri 1990, Harper 1992). Figure 9 shows however, that there was no clear coincidence of high crayfish catch returns and low plant cover. We believe however, that these catch returns do not adequately reflect the crayfish population in the lake; rather they reflect the availability of large crayfish for trapping. Samples of all invertebrates collected in the littoral zone (<0.5 m depth) by 1 m<sup>2</sup> quadrat cylinders in 1987 and in 1990 and 1991 showed a crayfish density rising from 0.25 adults m<sup>-2</sup> in 1987 to up to 200 (mainly young individuals) m<sup>-2</sup> in 1991, and although these data do not allow an accurate population density estimate because of the limited depths of sampling, they do indicate dynamic fluctuations in crayfish not reflected in official catch returns. A further line of evidence comes from the importance of crayfish as a food item in the diet of bass (*Micropterus salmoides*) over 260 mm length, which increased from a small amount in 1987 to a substantial proportion in 1991 (100% occurrence in examined stomachs in 1991 which is equivalent to a 'Prominence Value' of this dietary item of 1000; (Hickley et al., 1994), Fig. 9).

We thus believe that the instability of submerged plant cover in this lake is related, at least in part, to

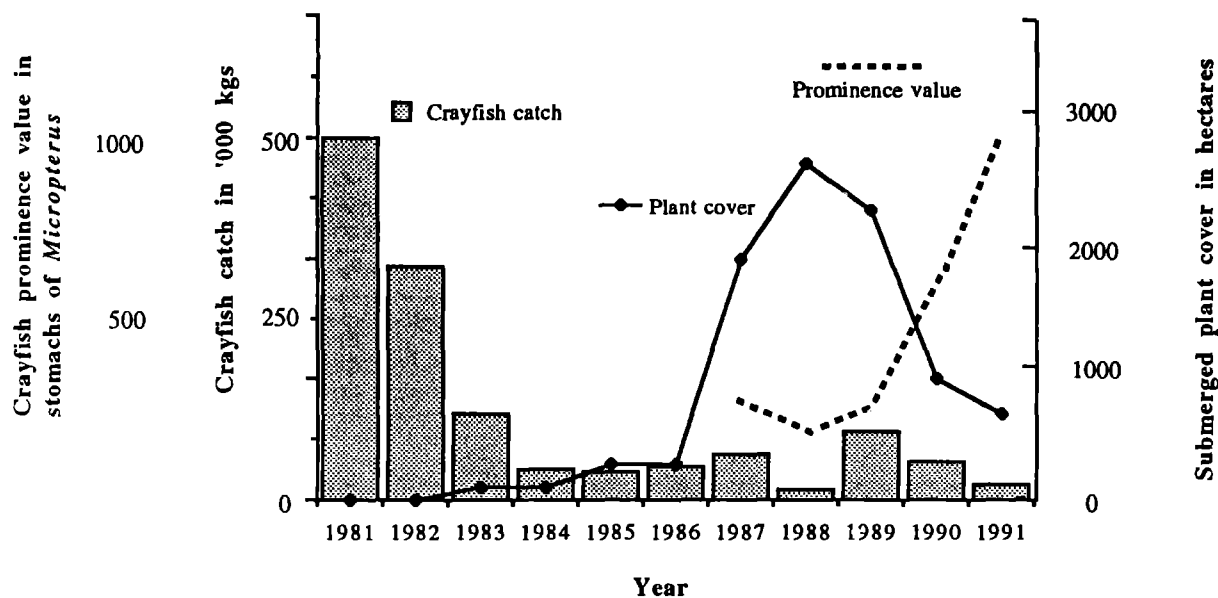


Figure 9. Changes in the commercial crayfish catch, the Prominence Value of crayfish in the diet of experimentally-caught *Micropterus salmoides* and the areal cover of submerged macrophyte beds.

crayfish grazing. No healthy crayfish have ever been found in Oloidien Lake, and the submerged plant cover there has hardly changed. It is clear from the recent decline in macrophyte cover in Naivasha that any recovery over the next 2-3 years coincident with a continued low catch of crayfish and decline of crayfish population indicators would strengthen this circumstantial evidence for crayfish-submerged plant cyclic interactions.

#### Other factors

The reasons for the changes in distribution of submerged plants around the lake, and in the changed frequency of submerged species, are unclear. Given that at the beginning of the 1980s there were no submerged plants, re-colonization must have come from seed germination in the period when low crayfish density is indicated by the rapidly declining commercial catch. It is probable that seedling establishment was more successful in the firmer sediments of the eastern half of the lake than the flocculent sediments of the west. However, once established in the west, mature macrophyte plants were capable of persisting through the anchoring capabilities of their roots.

The change in species frequency at one location probably reflects the environmental requirements (particularly light and response to grazing) of individual species and inter-specific competition between mature plants. The progressive disappearance of *P. octandrus*, a species rare elsewhere in Kenya, could be because it is a rapid colonizer but declines under competition from more robust species. It was the first colonizer of Naivasha (the only species that we found in 1984). *P. pectinatus* may have declined with decreasing ionic composition; the conductivity has fallen from around 500 to 250  $\mu\text{S}/\text{cm}$  since 1988 (Harper et al 1993). *P. schweinfurthii* seems to have more specific requirements; it is the only species to occur in monospecific stands within the plant beds in different sections of the lake; but we have no idea what these requirements are. There is a dearth of information about the specific requirements of submerged plants (Denny 1985b, c), but it appears that *Potamogeton pectinatus* has a higher light requirement than other species and is generally found in shallower waters. *P. schweinfurthii* is generally found in deeper water. This relationship, together with salinity, probably accounts for dominance of *P. pectinatus* in Oloidien Lake, where phytoplankton algal biomass is consistently high and the light gradient steep. In Oloidien, the progressive

decline and disappearance of *N. pectinata* may also be due to the increase in salinity over the decade, because in 1983 the water level of Naivasha was high enough for the two lakes to be connected on the surface. We do not have conductivity readings from Oloidien in 1983, but conductivity of Oloidien at the end of the decade was around 1000  $\mu\text{S}/\text{cm}$ .

#### *Ecological and conservation value of the plant communities*

A large number of studies have shown the importance of the different plant communities for the overall lake-based ecosystems and the humans who depend upon them. A variety of benefits are ascribed to fringing emergent plant wetlands, as runoff 'buffers' from surrounding agricultural land use, particularly for nutrient removal (Mitsch and Gosselink 1986, Denny 1985b).

In Naivasha, Muchiri & Hickley (1991) and Muchiri, Hart and Harper (1994), demonstrated the role of submerged plants in tilapia population success through both feeding and reproduction (and hence the success of the commercial fishery). Henderson & Harper (1992) showed that the different plant communities of the lake-edge each contributed to bird species richness and abundance; moreover they showed a significant relationship between the abundance of birds and the width of the submerged plant beds in 1987.

Submerged plant beds in Naivasha influence their own light regime. They create a micro-environment of calmed water within them that results in a reduction of phytoplankton by settlement and/or littoral zooplankton grazing (Harper 1992). The richness and abundance of littoral zooplankton and lentic invertebrates is considerably higher than in open littoral zones (unpublished data). We have observed them to be fed on extensively by *Hippopotamus amphibius* during the daytime, and swatches created through the beds by *H. amphibius* create open-water zones which appear to be more favored by fish.

The wetland plant communities thus have a direct benefit to human uses of the lake in fisheries and in conservation and tourism, and an indirect benefit because the lakeshore agriculture depends upon irrigation water of relatively low ionic composition.

#### *The future – lake environs and catchment land use*

Land use, particularly conversion of swamp to grazing and cultivation, clearly had a direct effect upon the emergent swamp vegetation in the mid-1980s. That effect is currently lessened due to the combined effect of an irregular (hence unpredictable) water level fluctuation and a voluntary agreement by the riparian owners (the Lake Naivasha Riparian Owners Association) to set the limit for cultivation to 50 m from the lake edge. In the future however, it is likely that land use in the wider environs of Lake Naivasha will have a dramatic effect upon lake level, quite apart from any indirect effects of nutrient or pesticide runoff about which we know very little. Agriculture is very intensive because the combined effects of an equatorial solar regime and rich volcanic soils make the land's productivity limited only by water because local evapo-transpiration greatly exceeds rainfall. Lake-water irrigation can overcome this limitation. By 1991, an analysis of aerial photographs indicated that a lake of area 140 km<sup>2</sup> was supporting irrigated agriculture over 105 km<sup>2</sup> of environs, (compared with about 11 km<sup>2</sup> of fringing *Cyperus* swamp). Added to this is the use of cooling water by the Hell's Gate Geothermal Power Station (Africa's first geothermal plant, due to treble its capacity in the next few years). These present demands, together with the construction of a water supply reservoir for the expanding town of Nakuru, that will export a substantial proportion of the flow of the main river, the Malewa, out of the upper catchment, will lead to substantial environmental impact upon the lake in the next decade.

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