



Feeding of the exotic Louisiana red swamp crayfish, *Procambarus clarkii* (Crustacea, Decapoda), in an African tropical lake: Lake Naivasha, Kenya

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Abstract

The Louisiana red swamp crayfish, *Procambarus clarkii*, has had a major impact on aquatic ecosystems in Europe and America where it has been introduced for human consumption. In Lake Naivasha, where it was introduced in 1970, it is suspected of causing the complete disappearance of native floating-leaved and submerged plants by 1982 and again by 1996; recovery of submerged plants occurred in between, concurrent with a decline in *P. clarkii*. Examination of the feeding of *P. clarkii* by microscopic analysis of gut contents collected from the lake confirmed information from both its native and exotic ranges; that it is an omnivore with green plants and insects the predominant items recognised. Feeding experiments confirmed this omnivory, with a preference from herbivory over carnivory. They further showed the importance of native plants as opposed to exotic water hyacinth *Eichhornia crassipes*. It is concluded that *P. clarkii* could well have accounted for the observed elimination of native plant species in Lake Naivasha; the cyclical nature of populations of submerged plant species and of *P. clarkii* in inverse proportion to each other lead us to hypothesise that *P. clarkii* is a 'keystone' species in the lake ecosystem.

Introduction

The feeding behaviour of the Louisiana red swamp crayfish, *Procambarus clarkii* (Girard, 1852), has been widely studied, principally because of concern over its wide distribution outside its native range (the southern United States of America and northern Mexico) (Hobbs et al., 1989; Correia & Costa, 1994). Lowery & Mendes (1977b) noted that the water lily *Nymphaea nouchalii* var. *caerulea* had declined in Naivasha after *P. clarkii* introduction and suggested that it was feeding on this plant, a suggestion supported by Hofkin et al. (1991) following experiments. *P. clarkii* can exist on decomposing plant matter (Sommer & Goldman, 1983), or on detritic plant material and associated 'microbiota' (Morshiri & Goldman, 1969; Mason, 1975; Avault et al., 1983; Wiernicki,

1984; Avault & Brunson, 1990). Adults tend towards herbivory (Mason, 1975; Olsen et al., 1991; Ilhéu & Bernardo, 1993a) while juvenile crayfish are carnivorous or omnivorous. Other authors have shown that it is carnivorous and even cannibalistic (Lorman & Magnuson, 1978; Ilhéu & Bernardo, 1993a). Hofkin et al. (1992), found experimental evidence that *P. clarkii* are active predators of snails. Other experimental studies have identified predation of snail egg masses and a significant negative association between *P. clarkii* presence and snails in the field (Hofkin et al., 1991). Benthic macro-invertebrates with reduced escape reactions (Odonata, Ephemeroptera larvae and planorbid snails) were selected in laboratory trials of various crayfish (Rickett, 1974; Matthews et al., 1993; Ilhéu & Bernardo, 1993a). Schoener (1971) and Ilhéu & Bernardo (1993b) argue that adult crayfish prefer

animal food but switch to phyto/detritophageous feeding when predation efficiency is low. *P. clarkii* is known to predate *Biomphalaria pfeifferi* and *B. glabrata*, the molluscan intermediate hosts of human schistosomiasis in Kenya (Hofkin et al., 1991; Hofkin et al., 1992). Ilhéu & Bernardo (1993a) found that adults in an introduced population in Portugal take invertebrates when vegetation is not readily available and that animal food can make up 85% of the diet. However, *P. clarkii* will eat plant detritus if no animals are present and plant detritus in preference to plant material (Ilhéu & Bernardo, 1995). *P. clarkii* therefore has a diverse diet, feeding on green plants, animal or plant detritus, periphyton, benthos, plankton, agriculture by-products or microbially enriched detritus (Huner, 1983). The preferences appear to switch according to availability of food items. Plant detritic material is also the main component of the stomach contents of several other crayfish species, together with aquatic macroinvertebrates, particularly insect larvae (Prins, 1968; Dean, 1969; Rickett, 1974; Mason, 1975; Covich, 1977; Abrahamsson, 1996).

There are no indigenous species of crayfish on mainland Africa, but expanding populations of *P. clarkii* can now be found in Kenya, Uganda and Zambia (Arrignon et al., 1990). Its introduction into new areas has caused the reduction or even disappearance of several indigenous aquatic plants and damaged shores through tunnelling (Sommer & Goldman, 1983). *P. clarkii* was introduced to Lake Naivasha in 1970 when 300 individuals were released into the lake (Oluoch, 1990). It was first harvested in 1975 producing a yield of several hundred metric tonnes per annum until exports ceased in 1983 (Harper et al., 1990). Now approximately 40 metric tonnes are caught annually for local consumption (mainly tourism). It is the main prey item in the diet of black bass (*Micropterus salmoides*) over 260 mm in size (Hickley et al., 1994), which is one of three fin-fish species exploited commercially in the lake.

Field observations made upon Lake Naivasha over the past two decades have suggested that *P. clarkii* has been responsible for the complete disappearance of the floating-leaved and submerged native plant species (Harper, 1991; Harper et al., 1995; Hickley & Harper, 2002). This has happened twice; first in 1982 when they were totally absent from Naivasha but present in Lake Ololdien and then in 1996 when they were absent from both. The submerged plants reappeared, in abundance, between 1987 and 1993

but with only limited spatial or temporal reappearance of the once-widespread *Nymphaea nouchalii* var. *caerulea* (Harper et al., 1995; Gouder et al., 1998). The inverse correlation between *P. clarkii* abundance in the lake (sampled as importance value in the diet of large-mouthed bass *Micropterus salmoides* Lacépède) and the area covered by submerged plant beds (Hickley & Harper, 2002) led us to the belief that the abundance of the former was directly responsible for the decline and disappearance of the latter.

The present paper describes observations and experiments that are part of a wider study, one objective of which is to test the hypothesis that the exotic *P. clarkii* has become a keystone species in this lake because of the consequence for the remainder of the ecosystem of native plant species loss. The null hypothesis tested here is that *P. clarkii* does not have a dietary preference for green plant material.

Study site

Lake Naivasha is an endorheic freshwater lake lying in the eastern part of the Rift Valley about 80 km south of the equator and 100 km north west of Nairobi (0° 45' S, 36° 20' E). The lake, at 1890 m altitude, is the highest of the Kenyan Rift Valley lakes (Harper et al., 1990; LNROA, 1993). It has a surface area of between 100 and 150 km² caused by fluctuating lake volume that is itself a major influence on the macrophyte and animal communities (Gaudet, 1977; Gaudet, 1979; Vincent et al., 1979; Harper, 1991; Verschuren et al., 2000) (Fig. 1). Some water characteristics vary over time as a consequence, conductivity between 250 and 400 $\mu\text{S cm}^{-1}$ for example. Short-term changes relate more to climate; surface temperature varies between 18 and 26.5 °C for example but the diurnal variation is greater than the seasonal (unpublished data). The water is rich in carbonates, with Na⁺ and Ca²⁺ as major cations; mean pH value is 8.5 (Litterick et al., 1979; Gaudet & Melack, 1981; Burgis & Mavuti, 1987; Harper et al., 1995). Its water, fish and ecosystem form important resources for local people, horticulture and tourism (Harper, 1992; Harper et al., 1995). As well as *P. clarkii*, the lake harbours several exotic species with a significant impact (Harper et al., 1990). Two exotic floating plants arrived unintentionally; the water fern *Salvinia molesta* in the late 1960s and the water hyacinth, *Eichhornia crassipes*, in 1988 (Harper et al., 1995). Observations had shown that *P. clarkii* used *E. crassipes* plants extensively for shelter.

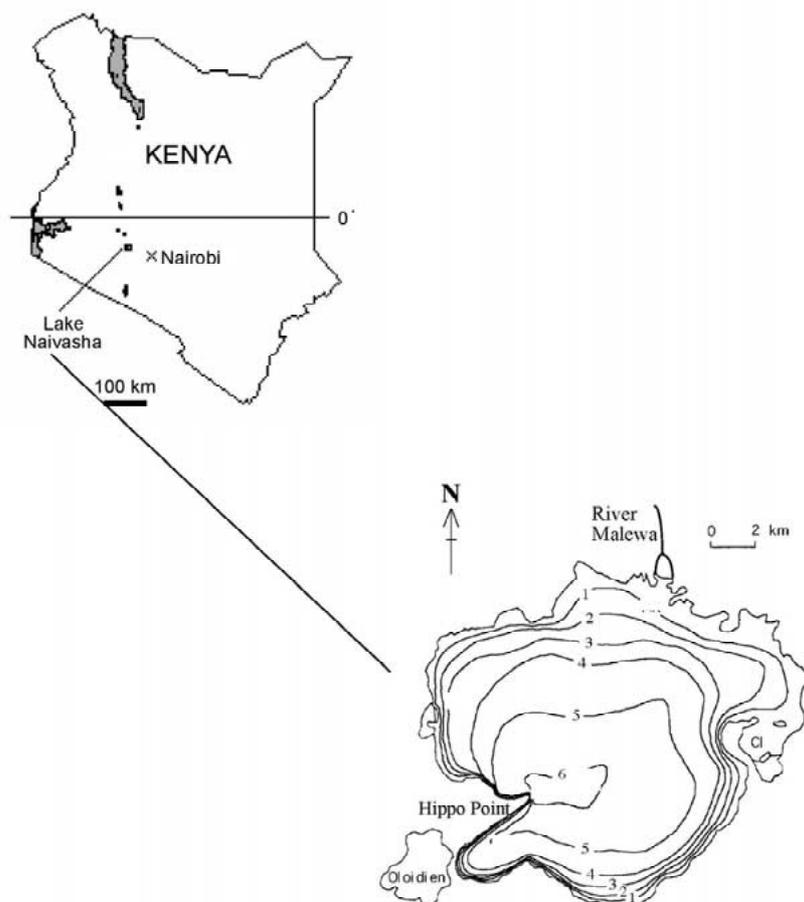


Figure 1. Location Map of Lake Naivasha, Kenya. After Hickley et al. (2002).

Ecology of the experimental animal and plants

Louisiana red swamp crayfish

P. clarkii has a mean size of 100 mm and large individuals can reach a length of 200 mm (Arrignon et al., 1990; Arrignon, 1996). Sexual maturity is generally reached at 11 months (Oluoch, 1990) and seems to be dependent on water levels (Gutiérrez-Yurrita & Montes, 1999). Life span at low latitudes does not exceed 3 years but can reach 5 years in higher latitudes. *P. clarkii* is extremely tolerant of poor water quality (Arrignon et al., 1990): oxygen >3 ppm; alkalinity >50 ppm (in CaCO₃); pH of 6.5–8.5; salinity <15‰ and temperature of 22–25 °C. Open water with light penetration of less than 40 cm appear to be the preferred habitat; it copes well with alternatively inundated and dry areas through burrowing (inundation periods allow the proliferation of the macrophyte

components of its diet and many of its predators are eliminated during the dry periods). Among macrophytes identified in Louisiana as preferential habitat of *P. clarkii* are *E. crassipes* and several *Cyperus* spp. (Arrignon et al., 1990), also present in Lake Naivasha. At Naivasha, *P. clarkii* is an important component of the diet of *M. salmoides* (Hickley et al., 1994; Hickley & Harper, 2002) and heron, egrets, ibis, fish eagle, marsh mongoose and otter are above-water predators (pers. obs.).

Eichhornia crassipes

Water hyacinth, *Eichhornia crassipes* (Mart.) Solms, is an indigenous monocotyledonous species of tropical South America (François, 1969) that has become a widespread exotic pest of tropical zones (Blackburn et al., 1969; MacDonald & Wolverton, 1979; De Parcevaux, 1980). An attractive plant in flower, it has been widely cultivated as an ornamental pond

plant, which has facilitated its spread. *E. crassipes* is semi-amphibious and usually floats but can also survive rooted in wet margins. The main root, which may be several meters long, supports dense (up to 70 cm^{-1}) lateral roots. The plant has rosette characteristic leaves and a lilac white inflorescence (François, 1969; Bruynseels & Lawalrée, 1981). The fruit is a dehiscent capsule containing 3–364 seeds. The total production per plant varies from a few seeds to more than 5000. Seeds sink to the bottom of water when mature and remain viable for at least 15 years (Blackburn et al., 1969). *E. crassipes* lives in stagnant freshwaters or in slow currents; is a megatherm species with its optimum growth in a temperature between 25 and 30 °C. The plant can not survive more than 5 weeks when the temperature exceeds 34 °C and growth is almost stopped below 10 °C (De Parcevaux, 1980). The species tolerates extreme pH within a range of 4–10 although its growth optimum seems to correspond to 7. A pH value of 4.2 appears to be a limiting factor in Africa (Berg, 1959; Gopal, 1986; Tabuti et al., 1998). The species is now well established on the shore of Naivasha and forms floating mats. Plants are only of moderate size because the water temperature is below optimum for growth. The root system of *E. crassipes* shelters a large number of macro-invertebrate species (Bailey & Litterick, 1993), and in Naivasha the worm *Alma emini* Mich is particularly common (Adams et al., 2002).

Najas horrida

Najas horrida A. Br. Ex Magn. syn. *Najas pectinata* auct. Afr. Non (Parl.) Magnus is a tropical submerged annual aquatic herb with roots. Thin, ramified stems carry simple sessile leaves (3.2–20.0 mm long). Isolated flowers are located at the stems' node, and produce achenes (Triest & Symoens, 1983). It is frequently found in deep waters (in Naivasha from 0.8 to 2.2 m depth, with an average of 1.36 m), anchored on hard bottom or rocks (Gouder et al., 1998).

Potamogeton octandrus

Potamogeton octandrus Poiret is an aquatic herb with underground rhizomes and roots, with an entirely or nearly submerged habit. Thin, ramified stems support floating and submerged leaves (20–45 mm long, 1 mm width). Paired green flowers produce small fruits (2.0 mm long, 1.5 mm width) (Lisowski et al., 1978). A rare plant in Kenya, it is considered a pioneer species in shallow locations (0.60 m depth in average,

from 0.40 to 0.90 m). In Naivasha its appearance and spread is sudden and fast but it declines or disappears under competition from other plant species (Gouder et al., 1998).

Potamogeton pectinatus

Potamogeton pectinatus L. is a cosmopolitan submerged perennial aquatic herb, with underground roots and ramified rhizomes. The stems, cylindrical and thin, reach up to 3 m long and carry threadlike and submerged leaves (4–12 cm length, 1–2 mm width), which vary according to the depth (Lisowski et al., 1978). The spike inflorescences produce ovoid seeds (3–4 mm) up to 11.500 per square metre in some areas of Lake Naivasha. It occurs here at an average depth of 1.20 m (amplitude: 0.65–1.70 m, Gouder et al., 1998). *P. pectinatus* is widespread in alkaline waters (pH 7.0–9.0 in average) and has a large temperature and a tolerance to polluted and turbid waters (Kantrud, 1990). It is adapted to currents and water level fluctuations but it is not resistant to wave action. This species is well adapted in Naivasha as water movements are a common feature, as well as a fluctuating transparency. It was present with other species in the adjacent Lake Oloidien in the 1980s but the latter lake became increasingly saline to the present day as a consequence of evaporation of water maintained by groundwater input from Naivasha (the two lakes had been connected by surface water only between 1979 and 1981). Species died out as salinity increased and *P. pectinatus* was the last to disappear at a conductivity of $1800\ \mu\text{S cm}^{-1}$ in 1996.

Potamogeton schweinfurthii

Potamogeton schweinfurthii A. Benn is a submerged perennial aquatic herb, with underground rhizomes and roots. The stems, up to three metres long, supports broad leaves (11–25 cm length, 9–30 mm width), the upper sometimes floating (Lisowski et al., 1978). The spike inflorescences, up to 10 cm long, are held above the water. It is a dynamic species with mainly vegetative reproduction through stolons (runners) but can produce 500–12 000 seeds m^{-2} (Gouder et al., 1998).

Methods

Collection of P. clarkii from the lake

Large crayfish (carapace length greater than or equal to 40 mm) were removed from the lake using traps

while medium (carapace length 20–40 mm) and small crayfish (carapace length below 20 mm) were collected from floating *E. crassipes* using methods described in Harper et al. (2002).

Examination of gut contents

Animals were placed in a refrigerator to slow down their metabolism and then killed by freezing. They were removed from the freezer and allowed to thaw before dissection. Juvenile animals were dissected by removing a dorsal section of the carapace exposing the stomach. The pyloric and cardiac sections were removed intact by severing the gut, then reaching beneath the stomach with forceps to sever the oesophagus. Connective tissue generally broke away as the stomachs were removed. Adult animals were dissected by removing a section of the lateral body wall and lifting to expose the pyloric and cardiac stomachs. Stomachs were removed by severing the connection to the gut and the oesophagus and cutting connective tissue as the two parts were lifted away. Attempts to lift adult stomachs directly from a dorsal incision frequently led to rupture and loss of material. Stomachs were preserved in 70% Industrial Methylated Spirits or 4% Formalin for later examination. Examination was made on a Leica Zoom Stereo-Microscope at $\times 5$ to $\times 30$ magnification. Stomach contents were emptied into a Petri-dish and sorted to separate vegetation and detritus from identifiable animal fragments. Stomachs were inverted to ensure all material was examined. Five slides were made of samples of material from each gut to recognise oligochaete chaetae. One hundred and seventy eight guts were examined in this way.

Experiments

All experiments were undertaken in a laboratory located on the south-west shore of Lake Naivasha. Water, plant and animal material used in the experiments were all taken from the lake. *P. clarkii* were kept in opaque basins or tanks (9 l; 1 l or 300 ml; depending on size category) with a refuge tube and a piece of plastic mesh for cover. Animals were starved for 24 h before the beginning of the experiments. Where possible, the lighting regime followed natural conditions but occasionally lights were on for a short time after sunset. Regularly oxygenated lake water was used which was renewed every 2 or 3 days to minimise variations of oxygen and ensure clean and odourless

water. In laboratory conditions the physical and chemical parameters of water were: 24 °C, 2.5–4.0 mg.l⁻¹ O₂, 0.35 mS cm⁻¹ conductivity.

Ex situ herbivory of water hyacinth

In the laboratory, 32 crayfish (8 blocks) were fed four treatments of water hyacinth: leaves, floats (petioles), roots (containing *Alma eminii*), roots where *Alma* was removed. One crayfish was placed in each basin and received one of the four food types. Food in the system was weighed every 3 days over a period of 24 days by removing the crayfish; filtering the water and removing any plant material for weighing; then replacing all plant material and crayfish in the basins.

Ex situ herbivory of submerged plant species

Crayfish of each size category were presented with a known wet weight of a submerged plant species over a set period of time. The quantity of macrophyte remaining after the time period was measured and recorded. Trials were set up using two or three crayfish of each size category for either 24 h or 5 days (without disturbance, measuring *Najas horrida*, *Potamogeton pectinatus*, *P. schweinfurthii* at the end of the trial); and using one crayfish of large and medium size categories over 19 days (measuring the quantity of *Najas horrida*, *Potamogeton octandrus*, *P. pectinatus*, *P. schweinfurthii* remaining every 2 or 3 days). The initial trials (with no disturbance) were replicated twice, while the latter (19 day) experiment was set up in 8 blocks with 4 treatments and controls.

In situ herbivory of submerged plant species

Two *P. clarkii* (>40 mm) or 4 crayfish (20–40 mm) were enclosed in a metal cage of approximately 30 cm \times 30 cm \times 30 cm, with a 2 mm mesh on all surfaces, along with measured quantities of macrophyte. The cage was then submerged in the lake to a depth of 1–2 m, for 7 days. At the end of this period, the plant material was removed and wet weighed to determine the quantity removed by the crayfish.

Ex-situ herbivory of mixed submerged macrophytes

Known quantities of submerged macrophytes were presented to one, two or three *P. clarkii*, in the laboratory, for a period of 5 days. The quantity of plant material remaining at the end of the trial was wet weighed and the quantity presumed eaten determined.

Table 1. The percentage occurrence of identifiable food items in crayfish stomachs. Data separated by carapace length (mm) and year of examination. n. d. = species not determinable

| | 1992 | | 1994 | | 1999 | |
|-----------------------|--------|--------|--------|--------|-------|--------|
| | <35 mm | >35 mm | <35 mm | >35 mm | <35mm | >35 mm |
| Total examined | 12 | 8 | 30 | 40 | 38 | 20 |
| <i>Najas</i> | 33 | 50 | 33 | 27 | 0 | 0 |
| Green plant, n.d. | 0 | 0 | 15 | 70 | 68 | 30 |
| Plant detritus | 0 | 25 | 3 | 0 | 8 | 35 |
| <i>Micronecta</i> sp. | 83 | 37 | 27 | 36 | 16 | 10 |
| Chironomidae | 17 | 12 | 13 | 17 | 5 | 0 |
| <i>Ecnomus</i> sp. | 17 | 0 | 0 | 0 | 5 | 0 |
| <i>Alma eminii</i> | 0 | 0 | 0 | 5 | 0 | 0 |
| Coleoptera | 0 | 0 | 0 | 2 | 3 | 0 |
| Mosquito larvae | 0 | 0 | 0 | 7 | 0 | 0 |
| <i>P. clarkii</i> | 0 | 0 | 0 | 5 | 3 | 0 |
| Gastropoda | 0 | 0 | 0 | 2 | 0 | 5 |

Ex situ carnivory of macro-invertebrates and food preferences

P. clarkii of each size category were presented with known numbers of the same or two different types of macro-invertebrate over 24 h. Each crayfish was in a tank with a refuge and plastic mesh to act as an inedible substratum. Numbers (or length in the case of *A. eminii*) of animals remaining at the end of the trial were recorded.

Ex situ herbivory in the presence of animals and carrion

This was to establish the crayfish preferences between animal food (worms and fish) and vegetable food (submerged plants). Various densities and size categories of *P. clarkii* were placed into containers with macrophytes and *A. eminii* or macrophytes and fish carrion for a period of 3 days. The quantity of macrophyte eaten was compared with and without animal material.

Results

Analysis of gut contents

The food items were predominantly plant material, either as large amounts of detritus or small unidentified fragments (Table 1, Fig. 2). Approximately 60% of adults had empty stomachs in 1999 (when there were no submerged plants in the lake) compared to

1% in 1994 and 13% in 1992 (when there were). No evidence of oligochaete prey was found from examination of microscope slides. The three main dietary items were *Najas* or unidentified green plants, *Micronecta* and chironomid larvae; the two animal groups being those that were in high densities (Clark et al., 1989).

There were significant differences between adult and juvenile food items (χ^2 , $p < 0.001$ (Yates' correction)), apart from the invertebrates in 1994, which were equally distributed between adults and juveniles (Fig. 3). The overall dietary strategy of individuals (omnivory, carnivory and herbivory) between each year recorded was significantly different for adults (χ^2 , $p < 0.001$ between 1992 and 1994; and 1992 and 1999) but not juvenile diets in 1994 and 1999 (Fig. 4).

Ex situ herbivory of water hyacinth

During the 24 days when *P. clarkii* was offered only *E. crassipes* plant items, leaves (Fig. 5) were significantly removed compared to losses in the controls due to decay (Newman-Keuls test, $p < 0.05$). Bite marks were made on the decomposing edge of the leaves during the experiment. No significant differences existed between the treatment and control for petioles (Fig. 5). Significant differences between control and crayfish treatments appeared after 12 days in both experiments with roots (Fig. 5). Examination of the changes with time of the four alternates (Fig. 6) show that the leaf biomass eaten is greater but that this is only small (approx. $0.15 \text{ g crayfish}^{-1} \text{ d}^{-1}$).

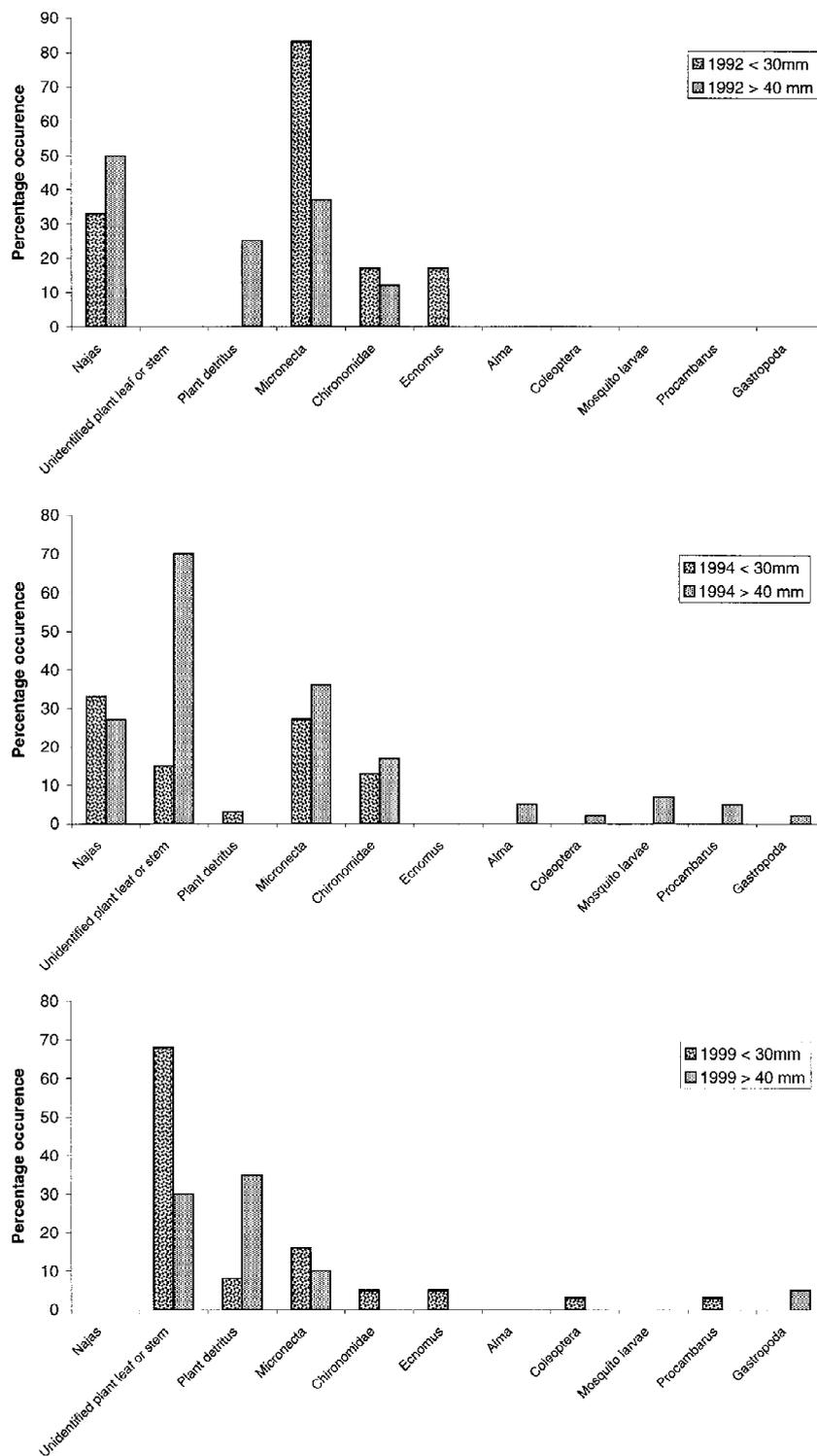


Figure 2. Mean percentage occurrence of identifiable food items in crayfish stomachs in each year of examination.

Ex situ herbivory of submerged plant species

The removal of *N. horrida*, *P. pectinatus* and *P. schweinfurthii* after 24 h (mean from 10 replicates) and 5 days (mean from 2 replicates) was not significant (χ^2 analysis). However, in all treatments, *P. pectinatus* was the macrophyte eaten the least, while *N. horrida* was consumed to the greatest extent in four of the five treatments (Fig. 6).

However, crayfish began eating *N. horrida*, *P. octandrus*, *P. pectinatus* and *P. schweinfurthii* from the beginning of the long term feeding trial (Fig. 7). The juvenile crayfish were the most voracious with an apparent preference for *N. horrida* (eaten in 10 days), then *P. octandrus* (16 days), *P. pectinatus* (5% remaining) and *P. schweinfurthii* (19% remaining after 19 days). Adult crayfish consumed less, with *P. octandrus* eaten most rapidly (6% remaining after 19 days). In all cases except *P. pectinatus*, the plant material deteriorated rapidly with controls losing up to 40% over the period of the trial. Newman–Kuels test showed that the differences between reduction of plant wet weight for all sizes of crayfish and the control were not significant for *N. horrida*, *P. octandrus* and *P. schweinfurthii*. *P. pectinatus* did show a significant reduction (Newman–Kuels test; $p < 0.05$) between the control (7.9% reduction in wet weight) and crayfish (52.2% reduction in wet weight) treatments. The mean quantity of all four plant species combined was significantly lower than the natural loss of the control plants for adults (Newman–Kuels test; $p < 0.05$) and juveniles ($p < 0.01$, Dunnett method).

In situ herbivory of submerged plant species

Over 7 days in the lake (Table 2) up to 10 g of plant per crayfish was eaten with an adult preference for *N. horrida* compared to *P. schweinfurthii*, although there was no statistical difference between juveniles and adults.

Ex-situ herbivory of mixed submerged macrophytes

There was significant loss of weight compared to controls when the four plant species were given together to crayfish (ANOVA, $p < 0.001$ all sizes and densities combined) (Fig. 8). The crayfish showed preferences for *P. octandrus* and *N. horrida*, followed by *P. schweinfurthii* and *P. pectinatus*. Only the upper leaves of *P. pectinatus* were grazed while the material from *P. schweinfurthii* consumed included decomposing leaves. An increase in the number of crayfish per

experiment increased the plant removal, with single crayfish consuming a significantly smaller proportion (55%) than two (70%) or three (75%) crayfish ($p < 0.01$). No significant interaction was found for different sizes with both size classes of crayfish apparently sharing the same feeding habits.

Ex situ carnivory of macro-invertebrates and food preference trails

Initial trial observations had confirmed that crayfish of all size categories can consume all of the prey items offered to them although large crayfish have difficulty catching *Micronecta* sp. and do not crush and digest the shell of gastropod molluscs to the same extent as the smaller size categories. The results (Table 3) confirm the observations with almost total removal of prey. The number of *Micronecta* sp. and gastropod shells taken was significantly lower by the adult crayfish (ANOVA & Tukey Test; $p < 0.001$).

When experiments were conducted with two different prey items, no significant preference (ANOVA) existed between any of the macro-invertebrates tested (Table 4).

Ex situ herbivory in the presence of animals and carrion

No significant difference in consumption occurred when worms and submerged plant material were offered together (Fig. 9). However, consumption of submerged macrophytes was significantly reduced in the presence of fish (*Tilapia* sp.) carrion ($p < 0.001$). Single crayfish gave a significant reduction of plant weight when it was offered with either worms or carrion but no difference was found when two or three individual crayfish were present ($p < 0.05$). Different size classes of crayfish showed no significant difference in the rate that they consumed plants or worms.

Discussion

P. clarkii at Lake Naivasha is opportunistic, and may even switch between diets depending on the most optimal feeding strategy at the time. In *in-situ* and *ex-situ* feeding experiments, it showed a preference for *P. octandrus* and *Najas*, followed by *P. schweinfurthii* and *P. pectinatus*. Crayfish removed from beds of submerged macrophytes dominated by a single species for

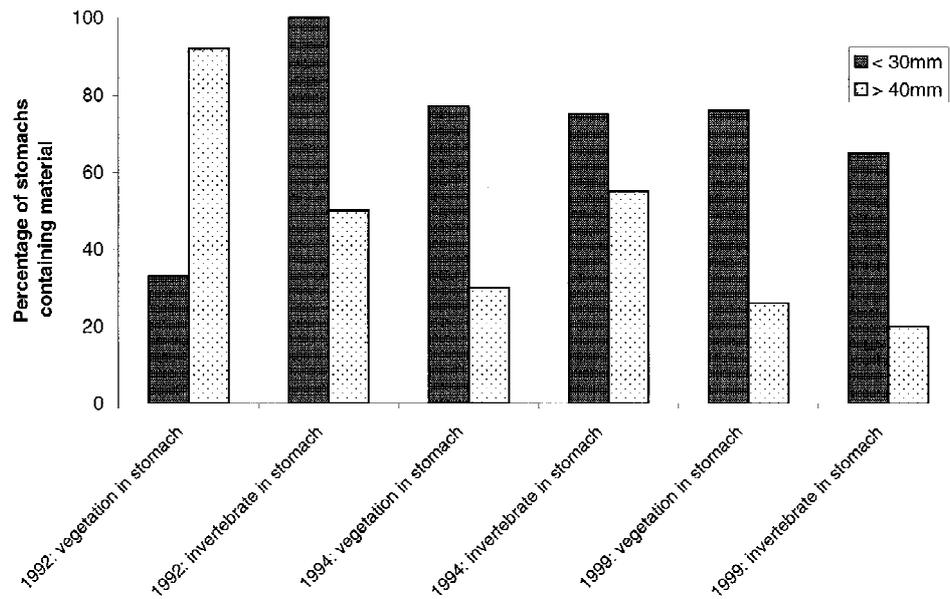


Figure 3. Mean percentage of animal and plant food items, in adult and juvenile crayfish in the three years of collection.

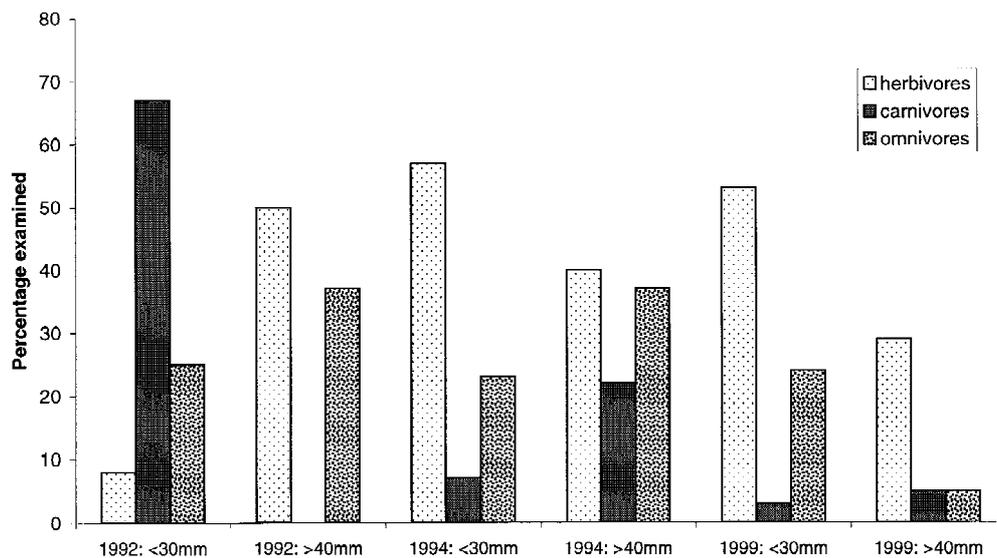


Figure 4. Mean percentage of *P. clarkii* individuals, which were herbivores, carnivores or omnivores in each year of collection.

experiments may have been habituated to feeding on that species and that may have affected results of these trials. However, the crayfish impact on the pioneer species, *P. octandrus*, could well influence the colonisation strategy of submerged vegetation and may impede the reappearance of that species. *P. clarkii*'s major way of feeding is by cutting (observations in the experiments) and so macrophytes are unlikely to

remain connected to their root systems in the presence of crayfish. Harper et al. (1990) and Hofkin et al. (1991) implied that the impact of this feeding strategy strongly implicated the crayfish as the main cause of the decline in abundance of *Nymphaea nouchalii* var. *caerulea* in Naivasha. *P. clarkii* showed little preference for different animal species in experimental conditions, eating whatever they came across.

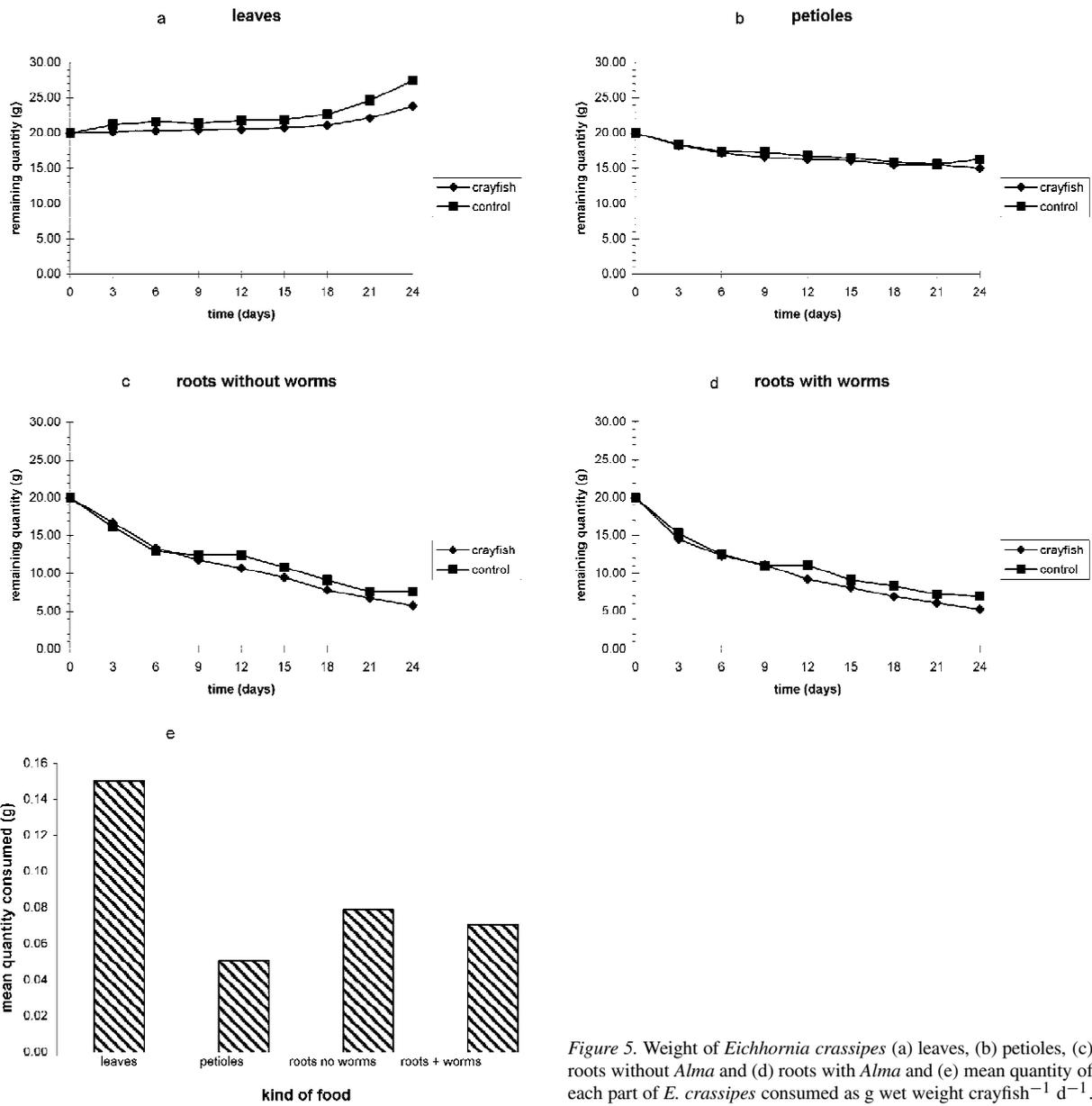


Figure 5. Weight of *Eichhornia crassipes* (a) leaves, (b) petioles, (c) roots without *Alma* and (d) roots with *Alma* and (e) mean quantity of each part of *E. crassipes* consumed as g wet weight crayfish⁻¹ d⁻¹.

Highly mobile species such as *Micronecta* sp., were less easily consumed by adult *P. clarkii*. There did not appear to be a preference for fish carrion over macro-invertebrates in the laboratory.

When the submerged plant populations collapsed in Naivasha (as at the beginning of the 1980s and in the mid-late 1990s) *P. clarkii* was left with only detritus and a reduced availability of invertebrates (because of the absence of submerged plant habitat) together with *E. crassipes* in the latter period. These results show

that no part of *E. crassipes* can compensate for the native plant food loss and suggest that the collapse of the *P. clarkii* population, which occurred following the first disappearances of submerged plants, may be a proximate consequence of food shortage. Food shortage may not be the ultimate cause of death, as predation on weakened individuals unprotected by the visual refuge of macrophyte beds in the lake or in the shallows is much more likely. The number of predators known to feed on crayfish in Naivasha is

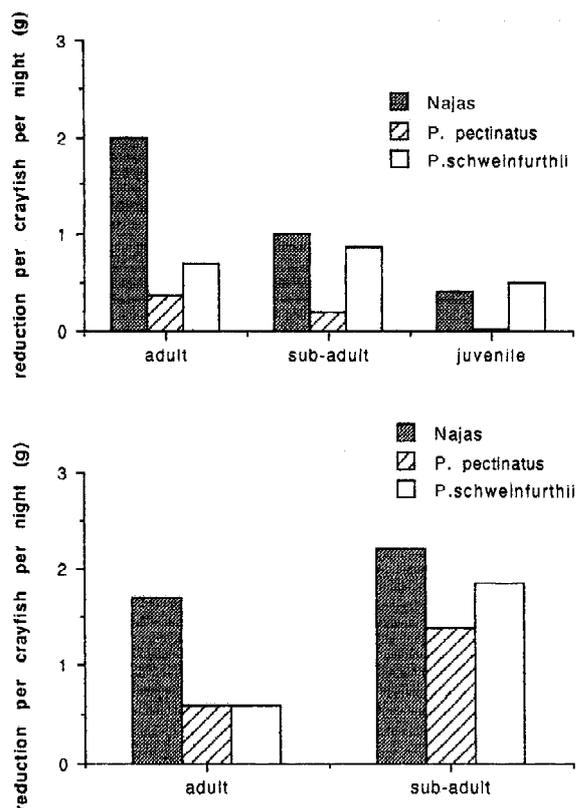


Figure 6. Reduction of submerged macrophyte wet weight by *P. clarkii* during 5 day feeding trials expressed as g wet weight crayfish⁻¹d⁻¹.

Table 2. Reduction in macrophyte wet weight crayfish⁻¹ d⁻¹ over 7 days feeding in the lake

| Plant species | <i>N. horrida</i> | <i>P. schweinfurthii</i> |
|-------------------------------------|-------------------|--------------------------|
| <i>P. clarkii</i> (carapace length) | | |
| >40 mm | 10.7 | 5.9 |
| <40 mm | 2.5 | 2.6 |

high (Fig. 10). Moreover, *P. clarkii* has in the past suffered from muscle-wasting disease, first recorded by Lowery & Mendes (1977a). They found this reduced tail weights at Naivasha to 10% of normal (Lowery & Mendes, 1977b) while Mikkola (1979) estimated reductions to 37% (male) and 27% (female). Lindquist & Mikkola (1979) identified the causes of this disease to be accumulation of material on gills, bacterial growth that leads to hypoxia and starvation.

Table 3. Mean number of potential prey items removed by *P. clarkii* where n (prey items) = 5 in each container with a single crayfish (unless otherwise indicated). Each crayfish size category was replicated ten times.

| | Crayfish carapace size | | |
|-----------------------------|------------------------|------------|------------------|
| | <20 mm | 20-40 mm | >40 mm |
| Oligochaeta | 4.4 | 5 | 5 |
| Chironomid larvae | 5 | 5 | 9.7 ($n = 10$) |
| <i>Micronecta</i> | 4.5 | 4.7 | 1.8 ($n = 10$) |
| Gastropods (tissue) | 4.9 | 4.6 | 4.8 |
| Gastropods (shells) | 4.1 | 4.6 | 2.3 |
| <i>Alma</i> (12-15 mm long) | No data | 84% length | 90% length |
| Ostracoda | 5 | 5 | 5 |

The dramatic impact of crayfish species, both native and exotic, on lentic ecosystems, is well known. Mathews et al. (1992, 1993) demonstrated by a combination of fieldwork, before and after crayfish elimination through plague, and enclosures into which crayfish were added, that the native *Austropotamobius pallipes* was important in regulating both lake vegetation by grazing and community structure by predation on otherwise-dominant invertebrate species such as *Gammarus* or chironomid larvae. Lodge et al. (1994) demonstrated by enclosure experiments that the exotic omnivorous crayfish *Orconectes rusticus*, controlled the abundance of macrophytes, snails as well as periphyton in the littoral zone of lakes in the northern United States. As a consequence of studies such as these, together with the detrimental effects on biodiversity that exotic introductions have, Lodge et al. (1998) have suggested that management of exotic species should be focussed on preventing introduction, because elimination is almost impossible once introduction has occurred. *P. clarkii* is the most introduced crayfish in the world (Correia & Ferreira, 1995) which is spreading widely in Kenya (Lowery & Mendes, 1977a). In many agricultural areas within its introduced range, it reaches pest status because its burrowing behaviour causes irrigation banks to leak and earth dams to collapse (Correia & Ferreira, 1995). Despite its agricultural damage risk as well as its known ecological disruption it has potential benefits as a biological control of snail species which are the intermediate host of schistosomiasis (Hofkin et al., 1991). In Kenya, at least, the benefits have to be evaluated against the disbenefits if any management strategy is considered.

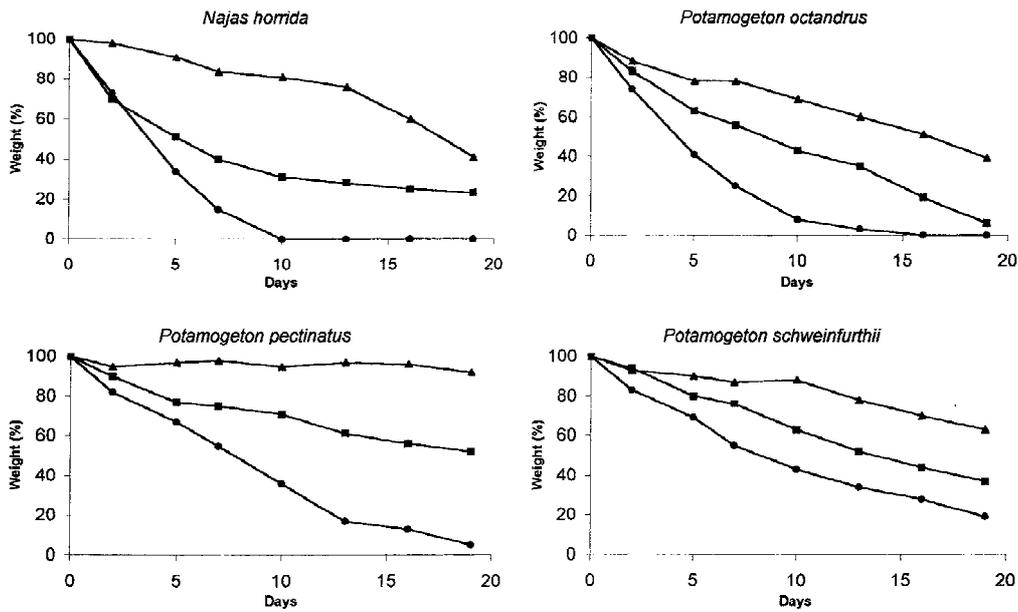


Figure 7. Reduction in wet weight of four submerged macrophyte species in the presence of *P. clarkii* during 19 day feeding trials expressed as a percentage of the original weight.

Table 4. Number of potential prey items removed by *P. clarkii* where initial density of prey items was 5 of each of two different taxa in each container with a single crayfish. Each crayfish size category was replicated 10 times

| | Crayfish carapace size | | | | | |
|-------------------------------|------------------------|-----------|-----------|-----------|-----------|-----------|
| | <20 mm | | 20–40 mm | | > 40 mm | |
| Prey species | Species A | Species B | Species A | Species B | Species A | Species B |
| <i>Micronecta</i> & Ostracoda | 4.5 | 4.6 | 5 | 5 | | |
| Chironomid larvae & Ostracoda | 5 | 5 | 5 | 5 | | |
| Oligochaeta & Ostracoda | 5 | 5 | 5 | 5 | | |
| <i>Micronecta</i> & Gastropod | 4.7 | 4.9 | | | | |
| <i>Alma eminii</i> & Snails | | | | | 4.7 | 3.5 |

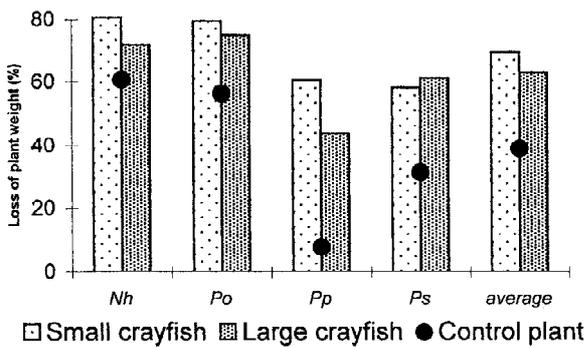


Figure 8. Total loss of plant wet weight as a percentage of the original weight compared with control loss for adult and juvenile crayfish.

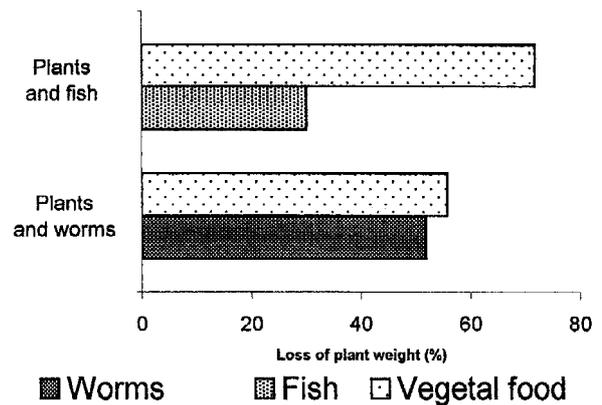


Figure 9. Reduction of submerged plant weight with and without the presence of animal food.

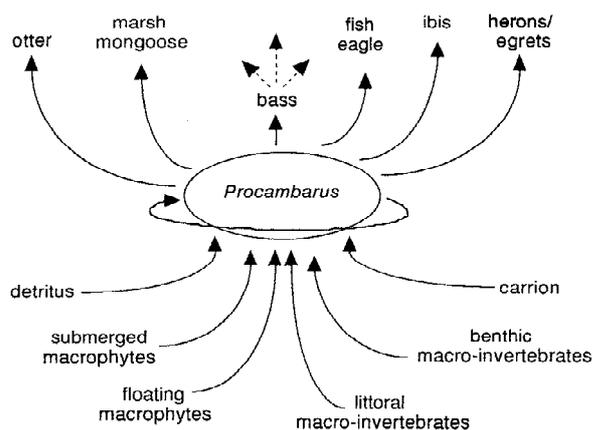


Figure 10. The position of *P. clarkii* in the Naivasha food web.

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