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Distribution and abundance of the Louisiana red swamp crayfish *Procambarus clarkii* Girard at Lake Naivasha, Kenya between 1987 and 1999

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Abstract

The abundance and habitat distribution of *Procambarus clarkii*, an exotic herbivore at Lake Naivasha, Kenya, was studied between 1987 and 1999. Its growth and morphometrics were similar to other locations in the world where the species have been studied. *P. clarkii* was found primarily amongst the floating, exotic vegetation where it achieved densities of over 500 m^{-2} by the end of the study. It is suggested that these densities became possible because the habitat offers protection against predation and an adequate food supply of bacterial-enriched detritus exists in the absence of green plant material. Both adults and juveniles forage on the lake bed at night.

Introduction

Crayfish are well known, on the one hand, to be important members of aquatic food webs (Mathews et al., 1993; Lodge et al., 1994) and on the other hand, to create havoc as exotic species in modified food webs (Lodge et al., 1998). The Lousiana crayfish, *Procambarus clarkii* Girard is now the dominant invertebrate in the littoral habitats of Lake Naivasha. It was introduced to the lake in 1970 when 300 individuals were released and transferred to various sites around the margins (Oluoch, 1990). It was first harvested in 1975, initially as an export crop. In latter years it has been mainly for local consumption, yielding a few thousand kg per annum.

Lowery & Mendes (1977a) identified densities of up to four adults m^{-2} in 1973. They, and then Olouch (1990), found that the Naivasha population showed continuous egg production, with 60% of males sexually active throughout the year, unlike the U.S. populations where reproduction is seasonal. In the U.S., Burras et al. (1995) found that *P. clarkii* produced tertiary burrows (a 'pipe' with end chamber) of median depth 3.3 m; median diameter 6.4 cm and median volume of 4000 cm^3. In Naivasha, burrows of indeterminate shape and volume appeared at low lake levels (Lowery & Mendes, 1977a). Males guard females in their burrows when the latter are 'berried' (Olouch, 1990). Adults mature at a larger size (males 40, females 42 mm; Oluoch 1990) than either its native Louisiana (males 31 mm, females 32 mm; Penn, 1943) or other exotic locations such as the Azores (males 36.4 mm, females 36.2 mm; Correia & Costa 1994). Other studies have shown temperature and food availability to influence size at maturity (Huner & Romaine, 1978) and Naivasha, although equatorial, is less-warm than much of the southern U.S. in summer, because of its altitude (1890 m).

The distribution of crayfish around Naivasha was first shown by Lowery & Mendes (1977b) to be concentrated on the east and north east of the lake. Factors influencing distribution were suggested to include the fishing effort (concentrated near Naivasha); and availability of vegetation and detrital food (more in the shallow areas). Changes in the ecology of Lake Naivasha over the last 30 years have been dramatic. The native aquatic vegetation has been subjected to pressures from fluctuating lake levels and the exotic floating species *Salvinia molesta* and *Eichhornia crassipes* (Harper et al., 1995; Gouder et al., 1998). *P. clarkii* is now considered the major factor that reduced submerged and floating plant species. Studies of diet choice lend support to this belief (Smart et al., 2002).

The maximum commercial exploitation of *P. clarkii* was recorded in 1983 (Harper et al., 1995). An 8-week intensive survey of aquatic plants of the lake at that time (December 1982–January 1983) found no floating-leaved native or any submerged plants in the main basin or Crescent Island lagoon (Rich & Harper 1984). In the adjacent Oloidien lake (which was then (under high water level; Becht & Harper, 2002) connected through *Cyperus papyrus* swamp to the main lake but whose conductivity was three times higher (ca. 800 μS cm^{-1}), a clear zonation of submerged plants occurred between 0.5 and 3 m depth (Harper & Rich, 1984). *P. clarkii* was noted during the plant survey to be very abundant in the main lake and absent from Oloidien, but regrettably its density was not then systematically recorded.

This inverse distribution of *P. clarkii*, and aquatic plants, together with evidence of crayfish diets in their natural range (e.g., Penn, 1943), subsequently led to the hypothesis that, in Lake Naivasha, a high density of *P. clarkii* was responsible for the elimination of floating-leaved and submerged aquatic plants. The area covered by plants was mapped each year (Harper et al., 1995; Gouder et al., 1998); and this showed that the area occupied by submerged plants increased from zero at the beginning of 1983 to 20 km^2 in 1987, then decreased almost to zero again by 1995. An inverse correlation between plant area in the lake and crayfish abundance was highly significant when the measure of abundance used was the proportion of crayfish in the diets of large-mouthed bass, *Micropterus salmoides* (Hickley & Harper, 2002).

The aquatic plants involved in this dynamic inverse relationship during the 1990s were submerged species with very little contribution from the single native floating-leaved species, *Nymphaea nouchalii* var. *caerulea*. This latter had been an abundant, characteristic species at Lake Naivasha throughout the 20th Century, regardless of lake level. A bank of viable seeds has built up in lake sediments, which results in rapid germination when soils are newly flooded by water rises following earlier heavy rains. The last record of extensive natural beds of *N. nouchalii* var. *caerulea* was in September 1974, when a hot air balloon was filmed dragging its basket through lily beds in *C. papyrus*-fringed lagoons (Root & Root, 1976). The underside of the lily leaves was 'dripping' with *P. clarkii*. By September 1977 *N. nouchalii* var. *caerulea* had completely disappeared from the lake (J. Root, pers comm.) and between 1988 and 2000 isolated clumps were only recorded occasionally in small areas and for a short time. The longest period of occurrence was inside Crescent Island lagoon, where a continuous thin belt (2 m wide, which corresponded to depths of 0.5 and 2 m, approximately) existed between 1987 and 1992.

A second hypothesis was formulated; that *P. clarkii* had eliminated the *N. nouchalii* var. *caerulea* in Lake Naivasha in the late 1970s and it only reappeared from germination briefly when and where *P. clarkii* was not able to graze it. No published records of *N. nouchalii* var. *caerulea* in Naivasha since 1977 exist and there are only five brief occasions when the species has been observed: (i) Crescent Island lagoon, 1987–92, where no crayfish were recorded until they rafted in on wind-blown *E. crassipes* floating mats; (ii & iii) in May 1988 and again November 1997 when rapid water level rise flooded new shallow lagoons on northern and eastern edges of the lake for a few months; (iv) a small bed (1 m $\times$ 5 m) was recorded in 1992 on the south east shoreline in front of horticultural land, where the *C. papyrus* had recently been cleared and the floating exotic vegetation was absent; and (v) for a period of about a year in 1993–4 when a stranded *C. papyrus/E. crassipes* island in the western edge of the lake (vicinity of Korongo Farm) created a 1–2-m deep lagoon about 200 m long off the fixed fringing *C. papyrus*, within which submerged native submerged and floating-leaved aquatic plants germinated. *N. nouchalii* var. *caerulea* has also existed continuously to the present day, adjacent to the lake in one horticultural irrigation pond maintained behind the *C. papyrus* fringe to provide a constant head of water for pumps. The virtual absence of *N. nouchalii* var. *caerulea* from the lake (except in unpredictable areas and periods) meant that testing the hypothesis was limited to laboratory experiments (Smart et al., 2002). These supported the hypothesis, as have other published experiments (Hofkin et al., 1991).

A deduction from the hypotheses is that the abundance of crayfish, as grazers on native aquatic plants (Smart et al, 2002), is inversely proportional to the abundance of native plants. The study examines the density of crayfish in the decade 1987 to 1999 and aspects of its spatial distribution in the lake as part of the testing of this hypothesis.

Study site

Lake Naivasha (0° 45′ S, 36° 20′ E) lies in the Eastern Rift Valley at 1890 m above sea level, approximately 100 km north west of Nairobi. The lake is freshwater with two rivers draining into the north of the lake and a subterranean inflow and outflow (Ase, 1987; Becht & Harper, 2002). The recent biological history of the lake is reviewed by Harper et al. (1990). *P. clarkii* now occurs in the main lake (approximately 100 m^2 area) and in the Crescent Island lagoon. It has not been recorded since 1982 in Oloidien Lake, which is slightly saline with an alkalinity by the late 1990s of around 2000 $\mu S\ cm^{-1}$ (Fig. 1).

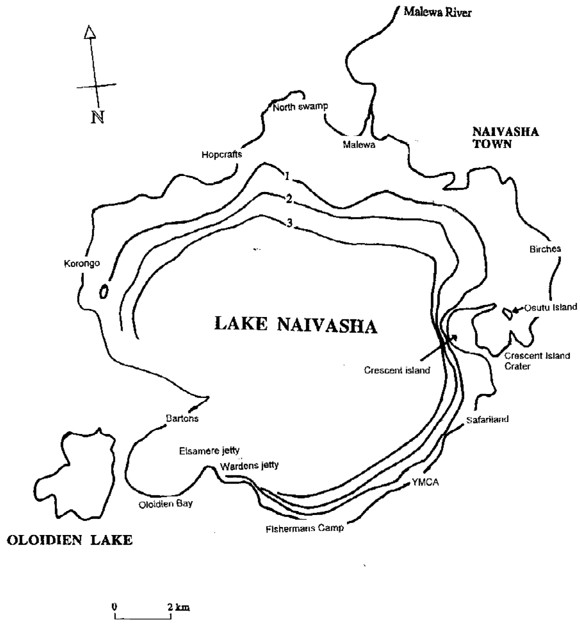

Figure 1. Map of Lake Naivasha showing depth contours (metres) and sample sites. After Hickley et al. (2002).

Methods

Four methods of sampling for crayfish have been used to estimate population abundance during April and August each year. The first was trapping from the sediment, which is not a density measure (and has additional sampling problems which were not addressed (Westman et al., 1978; Brown & Brewiss, 1978). The other three were used for density measures in the shallow littoral zone of floating exotic vegetation species, from a minimum of five locations, covering the four compass quadrants of the lake each year. These different methods were developed of necessity as the vegetation changed over the decade and the previous method became impractical.

1. *Traps.* In water deeper than 1 m, or on the lakeward side of the fringing plant mat, *P. clarkii* was sampled using baited traps of the same design used by commercial fishermen on the lake. A cylindrical wire frame of approximately 50 cm length and 20 cm diameter was covered with plastic 1 cm mesh, with inward-facing funnel openings at either end and a rectangular 20 × 10 flap opening, held shut by a catch. The trap was baited, usually with fish and then sunk, to lie on the bottom for a fixed length of time, usually for half an hour. *P. clarkii* entered by crawling in at either funnel end, was unable to crawl out, and when the trap was raised were removed by hand through the rectangular opening for processing. Density measures were not possible with this trapping and although mark-recapture was tried several times with batteries of traps, at no time were enough marked individuals re-caught. The mesh size of these traps did not reliably hold juveniles. Overnight trapping was carried out in 1992 and 1994 using micromesh fish traps, which did.
2. *Cage.* A wire mesh cube cage of 1 m^3 volume, open at the top and bottom, was used between 1987 and 1990. The floating vegetation of the littoral during this time consisted only of scattered *S. molesta* (and a few other aquatic species; Adams et al., this volume). The vegetation offered no physical impediment to sampling and the cage was dropped to the lake bed in depths of up to 1 m, randomly from a boat. The invertebrate contents of the 1 m^3 water volume enclosed and its sediment were then removed by successive sweeps with a standard macroinvertebrate hand net until no further individuals could be found. This collected *P.*

clarkii from both the sediment and the floating vegetation.

3. *Hand net.* The floating vegetation developed from the early 1990s into a more substantial physical habitat as a result of the spread in the lake of *E. crassipes* (first seen in 1988). It became apparent that *P. clarkii* was burrowing into the mat. *S. molesta* was the dominant species in 1991, with increasing density (of initially small plants) of *E. crassipes* from then onwards, (Adams et al., this volume). The vegetation was not tightly packed and so it was most easily sampled by using a hand net (0.0625 m^2) from beside the boat, inserting it vertically under the plant mat, turning the net to a horizontal position and then raising it through the mat. The vegetation thus collected was placed in a domestic bowl in the boat and carefully examined by hand to remove all crayfish. The sediment below was scraped with the net for approximately 0.0625 m^2 and any crayfish added. The location of net samples was randomised by the selection of compass bearings from the boat centre. The hand net was also used to collect crayfish from the submerged rhizomes on the outside of floating clumps of *C. papyrus*; here the net was scraped vertically upwards for 25 cm to give a similar-sized sample.
4. *Quadrat.* The floating vegetation after 1995 progressively became composed of *E. crassipes* plants (with other swamp colonist species of minor importance to the physical structure). Individual plants were larger than a single hand net and matted together so that it became no longer practical to collect a net sample of 1 m^2. A wooden square quadrat of 1 m^2 was placed on the vegetation surface (at random bearings on the side of the boat driven into the middle of the fringing mat), and then all plants within the quadrat were lifted by hand into a bowl held adjacent, holding the hand net under to collect any *P. clarkii* which fell from the plants. The sediment below was also scraped with the net for approximately 1 m^2 and any crayfish added to the bowl.

The density figures obtained from methods 2–4 are used here to give a continuous picture of change over the decade, even though it has never been possible to compare them directly. Both types of sample method – littoral density and catch per unit effort (catch per trap per hour) – were used independently to compare locations within the lake at the same time, or the whole lake at different times.

The length of the carapace of all animals collected as above was measured using callipers or mm ruler. Four hundred animals during 1994 were weighed (using a 0–30- or 0–100-g spring balance) and measured (using callipers) to establish the relationship between weight, carapace length, full length and total length (defined in Oluoch, 1990). A number of animals across the sampled size ranges were killed and the tail was removed and weighed to examine the incidence of crayfish muscle-wasting disease (Lowery & Mendes, 1977b).

Results

There was a significant linear relationship ($r^2 = 0.97$) between carapace length and total length for *P. clarkii* (Fig. 2) with a relationship TL (total length) = 2.15 + 1.91CL (carapace length). No apparent variation existed between males and females. A strong relationship ($r^2 = 0.76$) existed between carapace length and weight (W) (Fig. 3), as $\log W = -4.45 + 2.93 \log \mathrm{CL}$ (Fig. 3).

There was a greater variation in weight in animals over 40 mm carapace length, indicating the probability that a number of animals are suffering from 'tail-wasting' disease. Figure 4 suggests that animals over 20 g in weight (approximately 40 mm carapace length) may be suffering from the disease.

The density of *P. clarkii* in littoral floating vegetation increased between 1987 and 1996 but with quite wide confidence limits and without statistical significance (Fig. 5). The densities in this habitat were quite high nevertheless, ranging from 6 to 77 m^{-2}. The majority of these were always juveniles (Fig. 6) with the mean carapace length varying between 8 and 18 mm during this time (Fig. 7). In 1996 the proportion of adults jumped to over one-third of the population in

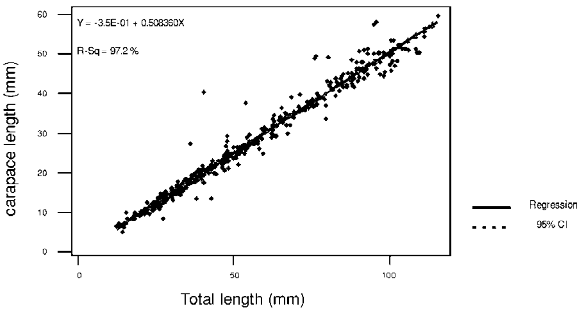

Figure 2. Relationship between carapace length and total length in *Procambarus clarkii* at Lake Naivasha.

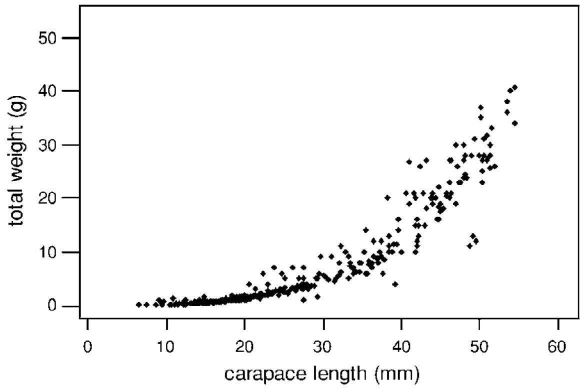

Figure 3. Relationship between carapace length and total weight in *Procambarus clarkii* at Lake Naivasha.

the littoral vegetation (mean size 30±14 mm) but in the following 2 years fell back within the limits of the preceding years and could not be explained by any concurrent environmental measurements. In 1999 the population density increased dramatically reaching over 500 individuals m^{-2} in early 2000; the majority juvenile (mean size 14±5.6 mm with only 2% of the population sexually mature in April 2000).

The abundance of trapped crayfish from the sediments each year to 1996 never exceed three individuals $trap^{-1}$ h^{-1} with no statistical difference between years. The catch in 1999 and early 2000, was three times higher than previously (9.5 and 11, respectively, individuals $trap^{-1}$ h^{-1}).

Adults dominated all the trap returns in daytime throughout the 1990s, whilst juveniles dominated the floating vegetation. A comparison of returns from traps during daytime (1992 mean size 45±5 mm; 1994 mean size 46±11 m) confirmed this ((ANOVA and Tukey test $p < 0.001$; F=189.7; Fig. 8). Trapping overnight captured a full size range of individuals (mean size 1992 35±9 and 1994 32±12 mm).

The vegetation in 1992 consisted of both *S. molesta* and *E. crassipes*, containing a similar density of individuals. These were significantly larger in *E. crassipes* (mean carapace length 22 mm) than in *S. molesta* (mean carapace length 13.2 mm) (ANOVA; $p < 0.01$). Comparison was not possible after 1994, as *S. molesta* became an insignificant part of the vegetation. The only other species from then on to the present contributing, structurally to the littoral vegetation was *C. papyrus*. Where it occurred stranded on the lakebed, its rhizomes supported abundant juvenile *P. clarkii*, marginally but not significantly smaller than *E. crassipes* (e.g., 11.9 mm compared to 14.7 mm in April 1995) Where the *C. papyrus* formed a continuous floating fringe at the edge of the lake, however (usually on the landward edge of a thick *E. crassipes* mat), few *P. clarkii* could be found. *C. papyrus* islands (a dominant landscape feature of the lake up to the early 1980s) were rare with few *P. clarkii* clinging to them.

A significantly higher density of crayfish was found in vegetation around the southern quarter of the lake (Kruskal–Wallis $p <$ df 18) but the catch in traps showed the opposite pattern (Kruskal–Wallis, $p < 0.99$, df 16) with higher catches in the north and west (Table 1). Crayfish trapped from the sediment surface were found in significantly higher numbers at depths between 1 and 2 m with fewer (and many zero catches) in either shallower or deeper water (7.7±2.1 individuals $trap^{-1}$ h^{-1} compared to 1.6±0.8 and 2±1.2, $n = 42$) (Table 2).

Discussion

P. clarkii grows well in Naivasha (corresponding to growth found elsewhere, such as in Portugal and Spain (Correia, 1993; Romaine et al., 1977)) but its economic value is influenced to an unknown extent by tail-wasting disease, which had been reported shortly after the introduction of the species (Lowery & Mendes, 1977a) with tail weights reduced to 10% of normal due to the disease. This is not extreme; Mikkola (1979) estimated reductions to 37% (male) and 27% (female) of normal tail weight. and suggested the accumulation of bacterial growth on gills leading to hypoxia and starvation to be its cause (Lindquist & Mikkola, 1979).

It has, for the last decade, existed primarily in floating exotic vegetation at the edge of the lake where it has achieved a higher density than recorded in other locations outside artificial culture (Huner, 2002). The evidence presented here indicates that adults forage on the lake bed during the day and juveniles also do at night. This suggests that *E. crassipes* does not provide adequate food (confirmed by Smart et al., 2002) but does provide adequate shelter from predation. *P. clarkii* is an important component of the diet of *M. salmoides* in this lake (Hickley & Harper, 2002) and is also fed upon by cormorants (Childress et al., 2002) fish eagles (Harper et al., 2002) as well as other wading birds such as ibises and mammals such as marsh mongoose (pers. obs.). The refuge provided by *E. crassipes* is probably essential to the

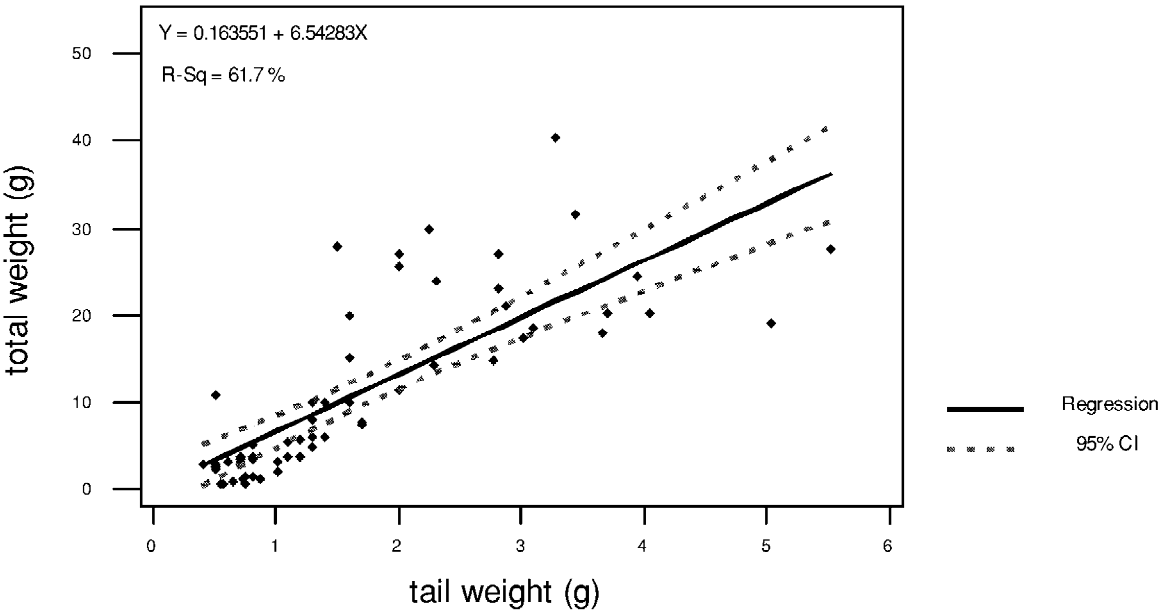

Figure 4. Relationship between tail weight and total weight of *Procambarus clarkii* at Lake Naivasha.

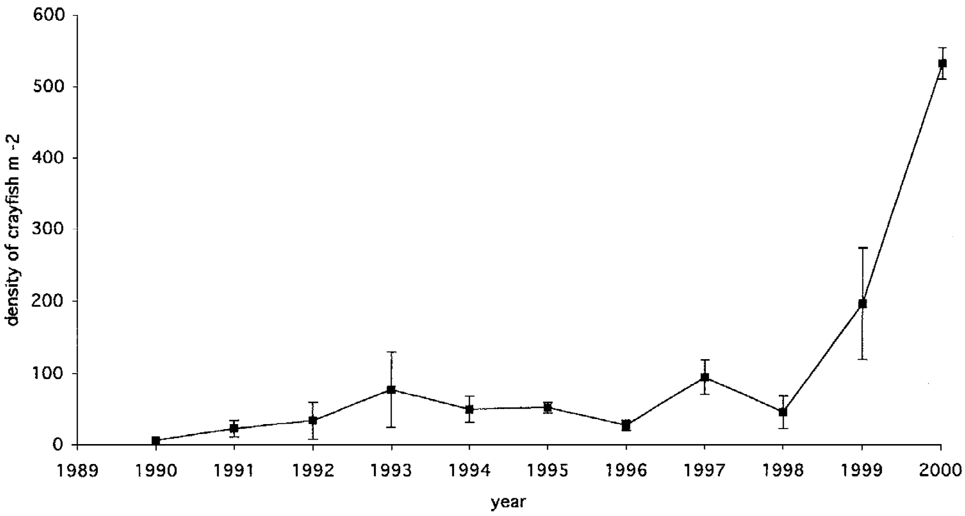

Figure 5. Density of *Procambarus clarkii* in littoral vegetation at Lake Naivasha, 1990–2000.

survival of *P. clarkii*. A prediction was made earlier (Harper et al., 1995) that the food chain in Naivasha of aquatic plants–*P. clarkii*–*M. salmoides* was inherently unstable, with the plants and the crayfish each in a cycle of about 10 years duration between maximum and minimum density. The plant cycle commenced with germination from the seed bank in the sediment when *P. clarkii* declined as a consequence of absence of food plus predation, which last happened around 1985. If the prediction had been correct, then the abundance of plants recorded in 1987 (Harper, 1992) would have been followed by their elimination shortly afterwards, closely followed by a crash in *P. clarkii* and the re-appearance of plants 5 years later. This did not happen however; the plants were eliminated in the early 1990s (Gouder et al., 1998) as predicted but *P. clarkii* remained abundant and prevented plant re-appearance for the remainder of that decade. The one large difference in the lake in the 1990s is the presence of *E. crassipes*. It has been recorded else-

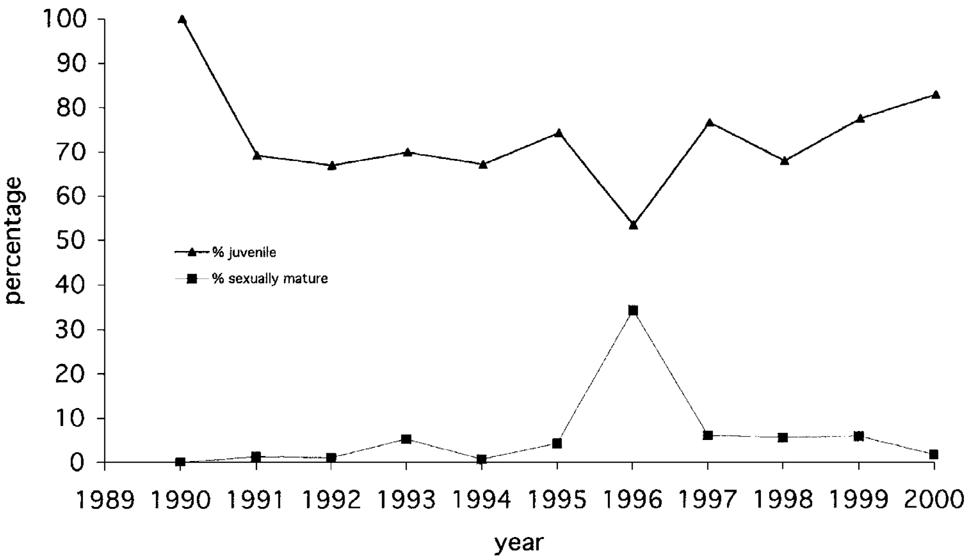

Figure 6. Percentage of *Procambarus clarkii* in littoral vegetation at Lake Naivasha composed of juvenile and sexually mature adults, 1990–2000.

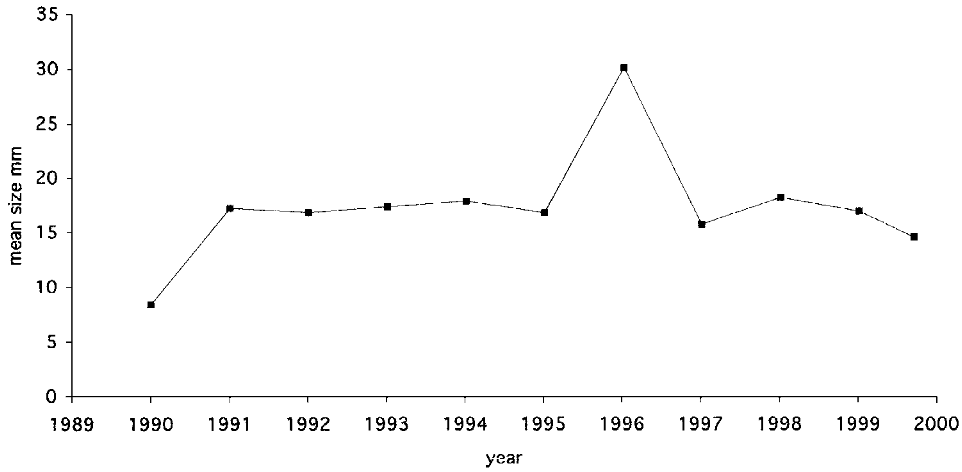

Figure 7. Mean carapace length of *Procambarus clarkii* in littoral vegetation at Lake Naivasha, 1990–2000.

where as holding an important faunal community of its own (Bailey & Litterick, 1992) and in Naivasha it provides the only structural habitat under the water surface, which for 5 years, 1995–2000 has, we suggest, prevented elimination of *P. clarkii*, by sheltering them from predation. The survival of the crayfish population requires not only shelter from predation but also an adequate food supply. This could have been provided by an abundance of bacteria-rich detritus on the lake bed, by the decomposition of an abundant supply of *S. molesta* and then *E. crassipes* plants. Whilst this may not be the most energy-rich, or even preferred food (Ilhéu & Bernardo, 1993) it is an important food for many other crayfish species (Nystrom, 2002). The two tilapia fish species introduced to Naivasha, which form the basis of the commercial fishery (Hickley et al., 2002) also utilise detritus as an important food buffer against habitat variability (Muchiri et al., 1995).

The ecological implications of *P. clarkii* in lake Naivasha are the elimination of aquatic plants; in that sense the effects can be predicted from the knowledge of lakes that have similarly lost their aquatic plant base as a consequence of eutrophication, compounded by the possibility that invertebrate species may also be directly eliminated by *P. clarkii* (Nystrom, 2002). This example of Lake Naivasha thus provides a counterbal-

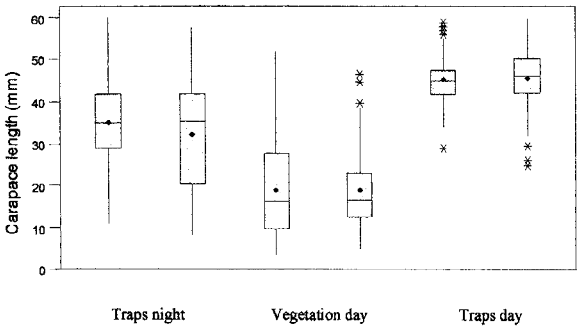

Figure 8. Mean carapace size of *Procambarus clarkii* from daytime traps, nightime traps and daytime littoral vegetation at Lake Naivasha, 1992 and 1994.

Table 1. Density of *P. clarkii* in the four compass quadrant of littoral vegetation at Lake Naivasha in 1995

	West	North	East	South
Density (m^{-2})	3.30	6.75	5.80	15.00
S.D.	0.89	6.91	5.27	7.18
Indiv $trap^{-1}$ h^{-1}	2.65	3.21	1.31	1.84
S.D.	3.04	3.91	1.20	1.67

Table 2. Catches in traps from different depths at Lake Naivasha, 1997

Depth (m)	Indiv. $trap^{-1}$ h^{-1}	S.D.	*n*
0–1	1.64	1.78	14
1–2	7.65	5.70	20
2 +	1.75	1.98	8

ance to suggestions that *P. clarkii* should be introduced as a biological control agent for the intermediary host molluscs of Schistosomiasis (Hofkin et al., 1991) and furthermore suggests, that *P. clarkii* is a 'keystone' species in this aquatic ecosystem.

Acknowledgements

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