Chapter 20

Fish community and habitat changes in the artificially stocked fishery of Lake Naivasha, Kenya

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Abstract

Lake Naivasha is a freshwater lake with 'Ramsar' status lying in a chain of lakes situated in the eastern rift valley of Kenya. Only five species of fish are present, all of which have been introduced. Three species, largemouth bass, *Micropterus salmoides* Lacépède, *Oreochromis leucostictus* (Trewewas) and *Tilapia zillii* (Gervais), form the basis of an important gill net fishery and the bass is also taken by rod and line for sport. Also introduced and exploited commercially is *Procambarus clarkii* (Girard). Some of the mechanisms underlying the principal ecological changes that have been observed in recent times are described. Fish and crayfish catches are examined in relation to changes in water level and aquatic macrophyte abundance. Catches of *O. leucostictus* increased with rise in water level whereas those of *T. zillii* decreased. Bass appeared not to be influenced by water level but had a positive relation with crayfish catch. Submerged macrophytes disappeared between 1987 and 1999 and possible causes are considered, the hypothesis being that grazing by crayfish was responsible. Using the importance of food items in bass stomachs as an indicator of prey species availability, an inverse relationship was demonstrated for crayfish abundance against area of submerged water plant cover.

Keywords: aquatic macrophytes, commercial fisheries, introduced species.

20.1 Introduction

Lake Naivasha is a shallow (3–6 m deep), freshwater lake, approximately 160 km^2 in area, situated in the eastern rift valley of Kenya about 100 km north of Nairobi. It lies in a closed basin at an altitude of 1890 m above sea level, receives 90% of its water from the perennial River Malewa and is subject to considerable fluctuations in water level. Dominant vegetation types are marginal papyrus, *Cyperus papyrus* L., submerged *Naias pectinata* (Parl.), and floating *Salvinia molesta* Mitch. and *Eichhornia crassipes* (Mart.). The abundance of all these aquatic macrophytes is, however, in a continual state of flux. An overview of the lake and its changing ecology can be found in Harper, Mavuti & Muchiri (1990).

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When Lake Naivasha was first studied (*ca*. 1900) only one species of fish was present, the endemic *Aplocheilichthys antinorii* (Vinc.) which was last recorded in 1962 (Elder, Garrod & Whitehead 1971). Since 1925 various fish introductions have been made, some successful and some not (Muchiri & Hickley 1991). Present today are *Oreochromis leucostictus* (Trewewas), *Tilapia zillii* (Gervais), the largemouth bass, *Micropterus salmoides* Lacépède, *Barbus amphigramma* Blgr. and the guppy, *Poecilia reticulata* Peters. Since 1959 the two tilapias and bass have formed an important fishery (Muchiri & Hickley 1991) with all three species being commercially exploited using gill nets, and bass also being taken by rod and line for sport.

The Louisiana red swamp crayfish, *Procambarus clarkii* (Girard), was introduced into Lake Naivasha in 1970 with a view to establishing a commercial fishery (Parker 1974). When Lowery & Mendes (1977) recorded its increasing numbers and distribution from 1974 to 1976 it was an important organism in the eastern basin, but since then has spread throughout the lake. Initially opened in 1975, the crayfish fishery at the outset produced several hundred metric tonnes annually for export, mainly to Europe, but since 1983 much lower catches have supplied only the local, mostly tourist, market (Harper *et al*. 1990).

Hickley, Bailey, Harper, Kundu, Mucheri, North & Taylor (in press) examined the status and future of the Lake Naivasha fishery. They:

1. identified three phases in its development – an initial ‘boom and bust’ (1959–1973), a period of stability (1974–1988) and, currently, a poorly performing fishery with low reported catches;
2. concluded that the annual yield could be enhanced – a prospect based upon the mean theoretical yield (about 900 t year^{-1}) being considerably higher than the overall maximum sustainable yield (about 650 t year^{-1}) as computed from catch per unit effort (CPUE) figures; and
3. proposed that the introduction of additional, appropriate fish species should be seriously considered, albeit only in association with improved enforcement and stock conservation regimes.

This chapter describes some of the mechanisms underlying the principal ecological changes that have been observed in recent times (since 1987) by Harper, Adams & Mavuti (1995) and Hickley *et al*. (in press). Various key inter-relationships are considered, in particular those of fish catches and the influence of water level, largemouth bass catches compared with those of crayfish and, finally, the impact of crayfish density upon submerged macrophytes. The supposed improvement in understanding of these components of the Lake Naivasha ecosystem are used to draft selected recommendations for the better management of the aquatic resources.

20.2 Methods

Catch data were obtained from the Fisheries Department of the Kenya Government. Finfish are taken with multifilament gill nets (>50 mm bar mesh) set from canoes and the crayfish are caught with traps. All fish must be landed at approved locations where Fisheries Department personnel record the catches. Data collection commenced in 1963. From 1987 annual sampling of the fish population was carried out using survey gill nets. The CPUE for the commercial fishery was calculated as kg per canoe. The CPUE measure for the survey nets was the catch converted to numbers of fish per standard gill net per hour, where a standard gill net comprised five 30-m sections, being one each of 11, 15, 20, 24 and 35 mm bar mesh.

Bass stomach contents were analysed as described by Hickley, North, Muchiri & Harper (1994), i.e. the number of guts in which each food item occurred was recorded and expressed as % Occurrence, and the % Abundance of different foods in individual guts was calculated as the count of a food item expressed as a percentage of the total count for all food items. To assess the relative importance of each dietary item consumed, a prominence value (PV) (Wilhm 1967 as adopted by Hickley & Bailey 1987) was calculated from the product of its % Abundance and the square root of its % Occurrence.

20.3 Results

20.3.1 *Fish catches*

It appears that annual catches of *O. leucostictus* follow a similar trend to the fluctuations in water level, with increases in catch associated with an increase in water level (Fig. 20.1). For the bass, *T. zillii* and crayfish such subjective appraisal is more difficult. Annual reported catches in the second half of the period were very low, the exception being the 1998–1999 increase following the 1997–1998 rise in water level.

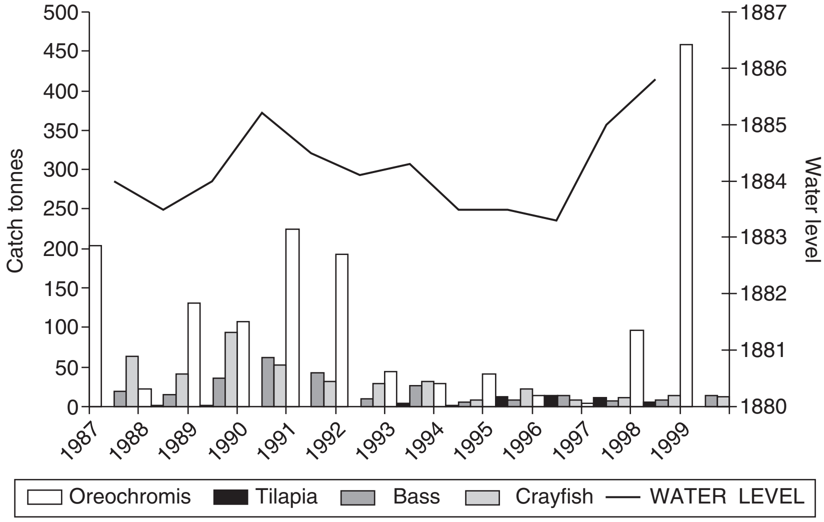

Figure 20.1 Annual fish catches taken by commercial gill nets, annual crayfish catches taken by commercial traps and mean annual water level since 1987

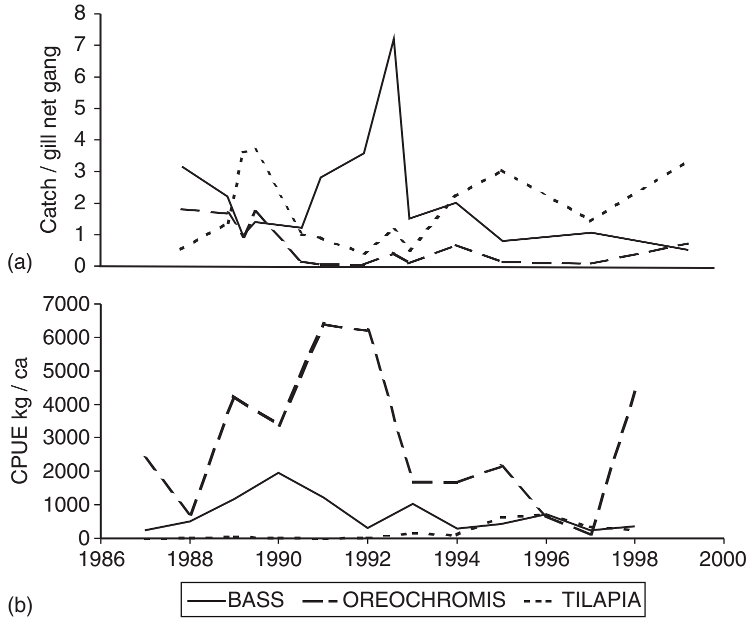

Figure 20.2 Annual CPUE for: (a) survey gill nets, expressed as number of fish per standard gill net gang per hour; (b) commercial gill nets, expressed as kg total annual catch per canoe

The overall species composition differed noticeably between the commercial nets, which took adult fish, and the survey nets, which caught juveniles (Fig. 20.2). In the commercial catches *O. leucostictus* averaged 67% of the catch, bass 22.2% and *T. zillii* 10.2%. In contrast, survey catch composition was *O. leucostictus* 12.4%, bass 46.5%, *T. zillii* 38.7% and *B. amphigramma* 2.4%. Notwithstanding these percentages being gravimetric for the commercial nets and numeric for the survey nets, the differences in catch composition probably reflect capture efficiency of the two types of gear relative to the target species. Nevertheless, there is a tendency for the tilapia and bass catches to deviate in opposite directions to each other, or at least not to follow the same pattern against time (Fig. 20.2).

20.3.2 *Fish catch and water level*

Figure 20.3 shows catches against lake water level for all species combined, *O. leucostictus*, *T. zillii* and bass, respectively. Water level was plotted as the average for the calendar year preceding that during which the catches were made, so as to guarantee that all catches used in determining the mean value were made subsequent to, rather than prior to, the water level measurements. Fish catch for all species combined increased with increase in water level ($P < 0.01$). Split into the component species, the relationships with increasing water level were direct for *O. leucostictus* ($P < 0.01$), inverse for *T. zillii* ($P < 0.05$) and absent for largemouth bass. It is assumed that the

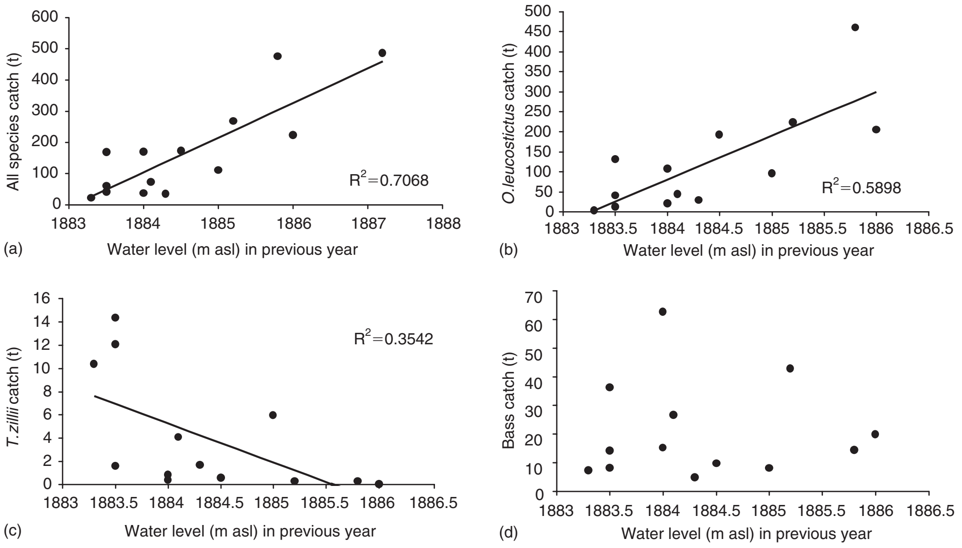

Figure 20.3 Relationship between annual mean fish catches for the period 1987–1999 and annual mean water level in previous year: (a) all species combined; (b) *O. leucostictus*, (c) *T. zillii*, (d) *M. salmoides*

predominance of *O. leucostictus* in the overall catch influenced the similarity of the respective regression lines.

20.3.3 *Bass and crayfish*

A simplified food web was presented by Muchiri, Hickley, Harper & North (1994) in which crayfish were placed both as the principal consumer of submerged macrophytes and also as the main prey of the bass. Hickley *et al.* (1994) described largemouth bass in Lake Naivasha as a generalised macro-predator. The most important invertebrate prey organisms for the juvenile bass (<260 mm fork length) were *Micronecta scutellaris* (Stal.) and dipteran pupae. For larger bass (>260 mm fork length), the crayfish, *P. clarkii*, was the preferred food.

The analysis of bass stomach contents ($n=1991$) showed noticeable changes from year to year in the prominence of the different food items (Table 20.1). For example, for large bass, *Xenopus* toads ranked first in 1987 compared with *P. clarkii* from 1990 onwards. For small bass, whilst *M. scutellaris* ranked first in most years, the status of some other invertebrates changed dramatically. A case in point was the appearance of conchostracans in the 1991/1992 samples.

Figure 20.4 shows annual catch of bass from the commercial gill nets plotted against annual catch of crayfish from the crayfish trap fishery. The resultant regression line ($P < 0.01$) suggests that, in keeping with the seeming importance of crayfish as bass prey, there could be a possible relationship between the bass and crayfish population sizes.

Table 20.1 The ranked importance of food items found in stomachs of *M. salmoides* based on PV for the years 1987–1998 inclusive for all habitats combined where the food item ranked fifth or higher in any year

	Rank of food item in given year									
Food item	1987	1988	1989	1990	1991	1992	1993	1994	1996	1998
Small bass										
M. scutellaris	1	1	1	1	1	1	1	3	1	2
Chironomid pupae	2	3	2	2	2	2	2	1	2	
P. clarkii	3		5	3			5	2	3	1
Cladocera	4		3	4	4	3	4			
Chironomid larvae		4	4	5	5	5	3		4	
Conchostraca					3	4				
Fish	5							4		5
Anisops		2						5		3
Trichopteran larvae		5							5	
Ostracoda										4
Large bass										
P. clarkii	2	2	2	1	1	1	1	1	1	1
M. scutellaris		1	1	2		2				3
Xenopus	1									
Fish	3	3		3			2	2		2
Chironomid pupae			3							
Frogs		4	5	4						
Chironomid larvae			4							
Coleoptera										4
Lepidoptera								3		
Laccocorris		5								

Section (a) is small bass, 60–260 mm fork length ($n = 1799$) and section (b) is large bass, 260–500 mm fork length ($n = 192$).

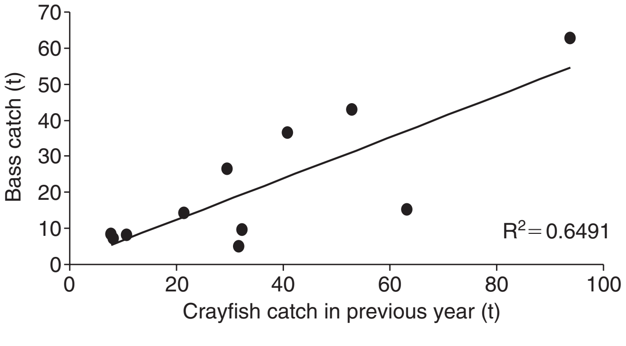

Figure 20.4 Relationship between annual catch of bass taken by commercial gill nets and annual catch of crayfish taken by commercial traps in the previous year

20.3.4 *Aquatic plants and crayfish*

Maps published by Gouder de Beauregard, Harper, Malaisse & Symoens (1998) showed the changes that have taken place in the submerged macrophyte beds of Lake Naivasha. Since 1987, the trend was one of reduction in overall coverage. Although suspecting such reduction could be due to grazing by crayfish Harper *et al*. (1995) concluded that there was no clear coincidence of high crayfish catch returns and low plant cover, believing that the catch returns did not adequately reflect the crayfish population in the lake but rather the performance of the trap fishery.

The variation in importance of bass food types in different years (Table 20.1) suggests a similar opportunism of bass feeding habit in Lake Naivasha, as has been observed elsewhere (Hodgson & Kitchell 1987). Accordingly, it is feasible to adopt the PV of prey species in bass stomachs as an indicator of the abundance and availability of such species. Table 20.2 shows approximate areas of Lake Naivasha occupied by submerged aquatic macrophytes in different years (after Gouder de Beauregard *et al.* 1998; Harper *et al.* 1995) compared with the abundance of crayfish as represented by their PV in bass stomach contents. Submerged macrophyte abundance was significantly ($P < 0.001$) inversely correlated against the PV of crayfish (Fig. 20.5).

20.4 Discussion

20.4.1 *Fish catches*

Muchiri & Hickley (1991) attributed some of the observed fluctuations in fish catches to fishing pressure, changing lake levels and the loss of submerged macrophytes.

Table 20.2 Approximate areas of Lake Naivasha occupied by submerged aquatic macrophytes in different years (after Gouder de Beauregard *et al*. 1998; Harper *et al*. 1995) compared with the abundance of crayfish as represented by their importance in bass stomachs (assessed as PV)

	Submerged macrophyte	~~Importance of crayfish in bass diet PV~~			~~Sample size *n*~~	
Year	(ha)	Small bass	Large bass	All bass	Small bass	Large bass
1987	1900	80.1	257.0	168.5	127	21
1988	2600	0.0	130.1	65.0	139	36
1989	2300	28.8	183.4	106.1	235	24
1990	900	68.1	612.6	340.3	321	16
1991	650	8.5	1000.0	504.35	264	37
1992		9.8	844.0	426.9	244	29
1993		11.9	875.0	443.5	110	5
1994		198.1	670.0	434.0	126	10
1995	350					
1996	80	32.0	1000.0	516.0	154	2
1997						
1998	(0)	758.4	527.0	642.7	79	12

The nominal zero value for 1998 represents the fact that no submerged macrophytes could be located during the survey period of that year.

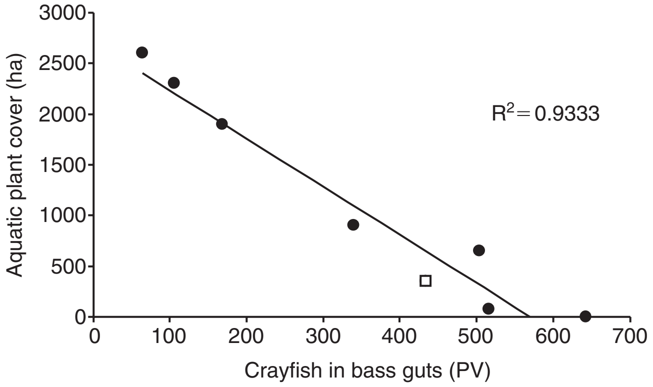

Figure 20.5 Relationship between area covered by submerged macrophytes and PV of crayfish in bass guts 1987–1998. Closed circles are for the same year; open square is 1995 macrophyte cover (ha) against 1994 crayfish PV

Overall fish catches appeared to be related to trends in water level changes with a rise in lake level generally followed by increased catches and a fall in level followed by a corresponding decline in fish catch. This supposition was confirmed for *O. leucostictus* and *T. zillii* (Fig. 20.3). The reasons why the two tilapias responded differently is not clear. *T. zillii* is found in deeper water than *O. leucostictus,* which shows a greater tendency to frequent the margins (Muchiri 1990). Thus, for *O. leucostictus* (increased catch with increased water level), it could be that as the water rises the areas close to the marginal vegetation become more accessible to the commercial nets, whereas for *T. zillii* (increased capture with reduced water level) it is possible that as the water level goes down the deeper water can be sampled more efficiently by the nets.

For bass, the catches of which did not seem to be influenced by water level, it would appear that crayfish abundance is the more likely influencing factor (Fig. 20.4). Such bass and crayfish interactions have been recognised elsewhere. In achieving a 98% reduction in a population of papershell crayfish, *Orconectes immunis* (Hagen), in a fish rearing impoundment in Wisconsin, using traps and stocking largemouth bass, Rach & Bills (1989) found that it was predation by the bass which was the major factor. Similarly, Taub (1972) reported that largemouth bass reduced populations of *Cambarus diogenes* Girard to the extent that insufficient crayfish could be caught to make population estimates.

A reduced presence of submerged macrophytes could also have affected recruitment of new individuals to sustain the bass fishery by disrupting the availability of shelter from predators, including birds such as cormorants, *Phalacrocorax* spp., grebes, *Podiceps* spp., gulls, Laridae, and terns, Sternidae (Henderson & Harper 1992). Bettolli, Maceina, Noble & Betsill (1992) showed that habitat complexity, as mediated by vegetation abundance, was the principal factor regulating piscivory by largemouth bass in the littoral zone of Lake Conroe, Texas, and Miranda & Hubbard (1994) found that 0-group bass depend on vegetation for cover. Bass may also be influenced in other ways by loss of macrophytes. In Lake Baldwin, Florida, grass carp, *Ctenopharyngodon idella* (Val.), were used to eradicate all submerged macrophytes whereupon one component of the bass population sought locations with other forms of underwater structures and another moved to open waters devoid of structures and made little use of the inshore regions (Pothoven & Vondracek 1999). Colle, Cailteux & Shireman (1989) showed that following mechanical harvesting used to reduce *Myriophyllum spicatum* L. in Fish Lake, Wisconsin, growth rates for younger bass increased and for older bass declined. In two Minnesota lakes, after herbicide treatment, enhanced growth of largemouth bass was observed, probably related to improved opportunity for piscivory (Unmuth & Hansen 1999).

Absence of vegetation would be unlikely to affect directly spawning site availability for the finfish because nest excavation in the substratum is used by both bass (McClane 1978) and *T. zillii* (Greenwood 1966), and *O. leucostictus* is a female mouth-brooder (Greenwood 1966). Also, it is unlikely that the loss of macrophyte beds as a feeding area or as a food, would have a noticeable effect. Both *T. zillii* and *O. leucostictus* have high proportions of detritus in their diet. Detritus is an unlimited food item which has allowed the two tilapia species to co-exist (Muchiri, Hart & Harper 1995).

For the crayfish, reduced lake depth could increase reproductive opportunity. Olouch (1990) described *P. clarkii* in Lake Naivasha as breeding not only inside burrows but also on the sediment in shallow water at a depth between 0.5 and 4 m and concluded that reproduction is very much a lake edge activity. In recent times, however, much more of the lake has become <4 m deep. In 1991 the average depth was 3.35 m (Hickley, in press), 1.75 m less than in 1983 (Åse, Sernbo & Syren 1986).

20.4.2 *Aquatic plant abundance*

With regard to the fluctuations in aquatic plant abundance (Gouder de Beauregard *et al.* 1998; Harper *et al.* 1995), several factors need to be taken into account, namely water depth, water quality and consumption. Change in water depth seems to have more influence on aquatic species present than total macrophyte abundance (Gouder de Beauregard 1998). Water quality changes are likely to have an impact but relationships with aquatic plant density could be complex and reciprocal. Furthermore submerged plant beds have been shown to influence their own light regime, creating a micro-environment of calm water with reduced phytoplankton (Harper 1992), whereas during the recent period of reduced macrophyte occurrence, very high chlorophyll a values ($178\,\mu g\,L^{-1}$) were recorded (Mbogo, personal communication). It should be noted, however, that although the overall demise of the submerged vegetation might or might not be linked to the detrimental change in lake water quality, the situation has undoubtedly been exacerbated by a parallel decline in the fringing *C. papyrus* stands (Boar, Harper & Adams 1999). In addition, Smart (1990) suggested that macrophytes can provide alternative grazing for hippopotamuses, *Hippopotamus amphibius* L. This is on the basis that the changing lake environment and increasing agriculture around the lake has resulted in both habitat loss and restricted access to nocturnal grazing areas due to electric fences. Hippopotamuses were observed eating in the water, taking both *Naias* and *Potamogeton*.

The crayfish, *P. clarkii*, is generally assumed to be herbivorous (Penn 1943). In this context, according to Harper *et al.* (1990), it is likely that the disappearance of blue water lilies, *Nymphaea nouchali* Burm.f., which was more or less complete by the end of the 1970s, was a result of the combined grazing pressure of coypu, *Myocastor coypus* (Molina), and crayfish. Once the lilies had gone the crayfish would have had a more substantial grazing effect upon submerged vegetation, which in turn had disappeared from the lake by 1983. With no macrophytes the crayfish could only subsist as detritivores and the population, as observed subjectively by local residents, seemingly declined. Between 1984 and 1987 the aquatic vegetation returned during a period of water level decline. Harper *et al.* (1990) concluded that the reappearance of submerged plants after a 10-year period of absence from the lake was almost certainly a result of the disappearance of coypu and the population decline of crayfish.

For the second extirpation of submerged macrophytes, which occurred from 1987 onwards, Gouder de Beauregard *et al.* (1998) concluded that, although more than one factor should be considered, crayfish were primarily responsible for the reduction in submerged macrophytes, similar to this study (Fig. 20.5).

This argument is supported by other studies where crayfish, *P. clarkii*, were shown to exert a considerable ecological impact, affecting species composition, diversity and biomass of plants (Andres 1977; Feminella & Resh 1986; Ilheu & Bernado 1995; Gutierrez-Gurrita, Sancho, Bravo, Baltanas & Montes 1998).

20.4.3 *Future management of Lake Naivasha*

Implementation of management proposals based upon scientific findings can sometimes prove difficult, so care in communication is paramount if integration and acceptability of actions is to be achieved (Hickley & Apprahamian 2000). Accordingly, the riparian owners of Lake Naivasha have developed a comprehensive management plan to assist this process (LNRA 1999). With respect to the fishery, it has already been recommended by Hickley *et al.* (in press) that the overall lake management package should include conservation measures based on sound ecology (such as refuge areas and close times), appropriate legislation and the enforcement thereof (such as minimum mesh sizes and a ban on trading in undersized fish), education of all parties and the addressing of associated social issues. In addition, from the results presented here, there are two principal conclusions that should be taken into account.

Firstly, water level fluctuations affect fish catches and thus the stability and predictability of the commercial fishery performance. A number of water usage measures are identified in the Lake Naivasha Management Plan (LNRA 1999) which, if implemented, could ameliorate some of the fluctuations in water level.

Recommendation 1: Water usage should be managed with a view to stabilising lake level fluctuations.

Secondly, the crayfish, *P. clarkii,* has a detrimental effect upon the submerged macrophyte beds of Lake Naivasha. The first time that the crayfish induced the disappearance of these water plants a decline in the crayfish population followed, thus facilitating the return of the vegetation. With the present absence of submerged plants it remains to be seen whether the crayfish population will decline as in the past, thus enabling the macrophytes to recover. Already in December 2000 (2 years after the disappearance of the plants), however, there has been a noticeable reduction in crayfish numbers (Foster & Mbogo, personal communication). Nonetheless, given that crayfish are not currently exploited to the same degree as previously (Fig. 20.1), and taking into account the environmental perturbations that are superimposed this time around, measures to control crayfish density should be incorporated into the overall management package to assist the re-establishment of submerged plants.

Recommendation 2: Attempts should be made to control the crayfish population by:

- encouraging the reinstatement of a high level of commercial trapping,
- protecting the bass population using net mesh size enforcement in the commercial fishery and the release of catch in the recreational fishery.

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References

Andres L.A. (1977) The economics of biological control of weeds. *Aquatic Botany* **3**, 111–123.

Åse L.E., Sernbo K. & Syren P. (1986) Studies of Lake Naivasha, Kenya, and its drainage area. *Naturgeografiska Institutionen Stockholms Universitet, Forsningsrapport* **63**, 1–75.

Bettolli P.W., Maceina M.J., Noble R.L. & Betsill R.K. (1992) Piscivory in largemouth bass as a function of aquatic vegetation abundance. *North American Journal of Fisheries Management* **12**, 509–516.

Boar R.R., Harper D.M. & Adams C.S. (1999) Biomass allocation in *Cyperus papyrus* in a tropical wetland, Lake Naivasha, Kenya. *Biotropica* **31**, 411–421.

Colle D.E., Cailteux R.L. & Shireman J.V. (1989) Distribution of Florida largemouth bass in a lake after elimination of all submerged aquatic vegetation. *North American Journal of Fisheries Management* **9**, 213–218.

Elder H.Y., Garrod D.T. & Whitehead P.J.P. (1971) Natural hybrids of the African cichlid fishes *Tilapia spirulus nigra* and *T. leucosticta*, a case of hybrid introgression. *Biological Journal of the Linnean Society* **3**, 103–146.

Feminella J.W. & Resh V.H. (1986) Effects of crayfish grazing on mosquito habitat at Coyote Hills Marsh. *Proceedings and Papers of the Annual Conference of the California Mosquito and Vector Control Association* **54**, 101–104.

Gouder de Beauregard A.-C., Harper D.M., Malaisse F. & Symoens J.-J. (1998) Dynamique récente et cartographie de la végétation aquatique (1960–1996) du lac Naivasha (Rift Valley, Kenya). *Mededelingen der Zittingen, Koninklijke Acdemie voor Overzeese Wetenscaappen, Bulletin des Seances, Academie Royale des Sciences d'Outre-Mer* **44**, 373–389.

Greenwood P.H. (1966) *The Fishes of Uganda*. Kampala: The Uganda Society, 131 pp.

Gutierrez-Gurrita P.J., Sancho G., Bravo M.A., Baltanas A. & Montes C. (1998) Diet of the red swamp crayfish *Procambarus clarkii* in natural ecosystems of the Donana National Park temporary fresh-water marsh (Spain). *Journal of Crustacean Biology* **18**, 120–127.

Harper D.M. (1992) The ecological relationships of aquatic plants at Lake Naivasha, Kenya. *Hydrobiologia* **232**, 65–71.

Harper D.M., Adams C. & Mavuti K. (1995) The aquatic plant communities of the Lake Naivasha wetland, Kenya: pattern, dynamics and conservation. *Wetlands Ecology and Management* **3**, 111–123.

Harper D.M., Mavuti K.M. & Muchiri S.M. (1990) Ecology and management of Lake Naivasha, Kenya, in relation to climatic change, alien species introductions and agricultural development. *Environmental Conservation* **17**, 328–336.

Henderson I.G. & Harper D.M. (1992) Bird distribution and habitat structure on Lake Naivasha, Kenya. *African Journal of Ecology* **30**, 223–232.

Hickley P. & Bailey R.G. (1987) Food and feeding relationships of fish in the Sudd swamps (River Nile, southern Sudan). *Journal of Fish Biology* **30**, 147–159.

Hickley P., Bailey R.G., Harper D.M., Kundu R., Mucheri S.M., North R. & Taylor A. The status and future of the Lake Naivasha fishery, Kenya. *Proceedings of Symposium on Science and Sustainable Management of Tropical Waters, Naivasha, Kenya, April 1999* (in press).

Hickley P., North E., Muchiri S.M. & Harper D.M. (1994) The diet of largemouth bass, *Micropterus salmoides*, in Lake Naivasha, Kenya. *Journal of Fish Biology* **44**, 607–619.

Hickley P. & Aprahamian M. (2000) Fisheries science and the managerial imperative. In I.G. Cowx (ed.) *Management and Ecology of River Fisheries.* Oxford: Fishing News Books, Blackwell Science, pp. 346–360.

Hodgson J.R. & Kitchell J.F. (1987) Opportunistic foraging by largemouth bass (*Micropterus salmoides*). *American Midland Naturalist* **118**, 323–335.

Ilheu M. & Bernado J.M. (1995) Trophic ecology of red swamp crayfish *Procambarus clarkii* (Giraud) – preferences and digestibility of plant foods. In *Freshwater Crayfish 10. Tenth International Symposium of Astacology*. Baton Rouge, LA (USA): Louisiana State University, pp. 132–139.

LNRA (1999) *Lake Naivasha Management Plan.* Lake Naivasha Riparian Association, PO Box 1011 Naivasha, Kenya, 77 pp.

Lowery R.S. & Mendes A.J. (1977) *Procambarus clarkii* in Lake Naivasha, Kenya, and its effects on established and potential fisheries. *Aquaculture* **11**, 111–121.

McClane A.J. (1978) *Field Guide to Freshwater Fishes of North America*. New York: Henry Holt, 212 pp.

Miranda L.E. & Hubbard W.D. (1994) Winter survival of age-0 largemouth bass relative to size, predators, and shelter. *North American Journal of Fisheries Management* **14**, 790–796.

Muchiri S.M. (1990) *The feeding ecology of tilapias and the fishery of Lake Naivasha, Kenya*. PhD Thesis (unpublished), University of Leicester, UK, 233 pp.

Muchiri S.M. & Hickley P. (1991) The fishery of Lake Naivasha, Kenya. In I.G. Cowx (ed.) *Catch Effort Sampling Strategies: Their Application in Freshwater Fisheries Management.* Oxford: Fishing News Books, Blackwell Science, pp. 382–392.

Muchiri S.M., Hickley P., Harper D.M. & North E. (1994) The potential for enhancing the fishery of Lake Naivasha, Kenya. In I.G. Cowx (ed.) *Rehabilitation of Freshwater Fisheries*. Oxford: Fishing News Books, Blackwell Science, pp. 348–357.

Muchiri S.M., Hart J.B. & Harper D.M. (1995) The persistence of two introduced species in Lake Naivasha, Kenya, in the face of environmental variability and fishing pressure. In T.J. Pitcher and P.J.B. Hart (eds) *Impact of Species Change in African Lakes*. London: Chapman & Hall, pp. 299–319.

Olouch A.O. (1990) Breeding biology of the Louisiana red swamp crayfish *Procambarus clarkii* Giraud in Lake Naivasha Kenya. *Hydrobiologia* **208**, 85–92.

Parker I.S.C. (1974) *The Status of the Louisiana Red Swamp Crayfish in Lake Naivasha*. Nairobi, Kenya: I.S.C. Parker Wildlife Services, 45 pp.

Penn G.H. (1943) A study of the life history of the Louisiana Red Crayfish *Cambarus clarkii* Girard. *Ecology* **24**, 1–18.

Pothoven S.A. & Vondracek B. (1999) Effects of vegetation removal on bluegill and largemouth bass in two Minnesota lakes. *North American Journal of Fisheries Management* **19**, 748–757.

Rach J.J. & Bills T.D. (1989) Crayfish control with traps and largemouth bass. *The Progressive Fish-Culturist* **51**, 157–160.

Smart A.C. (1990) The density of *Hippopotamus amphibius* Linnaeus at Lake Naivasha, Kenya. *Tropical Freshwater Biology* **2**, 241–247.

Taub S.H. (1972) Exploitation of crayfish by largemouth bass in a small Ohio pond. *Progressive Fish-Culturalist* **34**, 55–58.

Unmuth J.M.L. & Hansen J.M. (1999) Effects of mechanical harvesting of Eurasian water milfoil on largemouth bass and bluegill populations in Fish Lake, Wisconsin. *North American Journal of Fisheries Management* **19**, 1089–1089.

Wilhm J.T. (1967) Comparison of some diversity indices applied to populations of benthic invertebrates in a stream receiving organic wastes. *Journal of Water Pollution Control Federation* **39**, 1673–1683.