

*The persistence of two
introduced tilapia species in
Lake Naivasha, Kenya, in
the face of environmental
variability and fishing pressure*

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14.1 INTRODUCTION

Unlike most of the small lakes in the Rift Valley, Lake Naivasha is fresh despite the absence of an exit river. The most likely reason is that the dissolved substances in the input are dilute, biochemical and chemical processes are in place to remove ions such as sulphates and carbonates and there is seepage from the lake bottom (Harper *et al.*, 1990). Because the lake is fresh, there might be an expectation of a rich fish fauna, in line with the diversity found in other lakes such as Victoria and Malaŵi. It comes as a surprise to many that the fish fauna is sparse and contains mostly introduced species. In the past, these have died out after only a few years. A clue to the low fish diversity, and to the frequent extinctions, may lie in the variability that is characteristic of the water level, the abundance of the aquatic macrophytes and the limnological conditions. In the face of this variability, three fish species and a crayfish form the basis of a commercial fishery that has lasted for 30 years.

Why did the three fish species, largemouth bass, *Micropterus salmoides*, and two tilapias, *Tilapia zillii* and *Oreochromis leucostictus*, establish themselves in the lake and then persist in the face of exploitation? Not much will be said in this chapter about the bass, but data will be presented that suggest a reason why the tilapia species have survived. Initially, we will outline recent changes in the lake and describe the history of the fishery. Some comment will be made at the end on Lake Naivasha as a place in which to study the role of environmental variability in determining extinction rates and persistence of species.

14.2 VARIABILITY OF THE LAKE NAIVASHA ECOSYSTEM

The recent history of the Lake Naivasha ecosystem has been described by Harper *et al.* (1990), Muchiri and Hickley (1991) and Harper (1992). Variability in water level has been a strong influence on the littoral habitat for as long as the lake has been studied scientifically. Oral histories by the Masai tell of the lake drying out shortly before the European immigration into the area. The lake was also much bigger about 10 000 to 12 000 years ago. In the last 100 years the lake level has had a high of 1896 m a.s.l. in 1895 and a low of 1882 m a.s.l. in the 1945–1955 period (Harper *et al.*, 1990). Changes like this alter the greatest depth of water in the lake, but the most important ecological effect is on the littoral. The lake is shallow around its edges (Chapter 1). A drawdown of 14 m would change drastically the area of shallow water available for macrophytes. If water levels fluctuate rapidly, there could be an important influence on the abundance and diversity of organisms living in the littoral, including fish which may use the area as a spawning and feeding ground. The reduction of diversity is true for storage reservoirs that have heavy drawdown.

Since 1970, there have been marked changes in the abundance and distribution of the floating and submerged macrophytes. The reasons for the changes may be several (Harper *et al.*, 1990) and are not well understood but may include changes in water levels, predation by coypu, *Myocaster coypus*, and by red swamp crayfish, *Procambarus clarkii* Girard. The changes in macrophytes have been grouped into three periods by Harper (1992). From 1930 up to the late 1970s the shallow-water macrophyte community had 25 species, 10 submerged, 8 floating and 7 associated with floating vegetation (Gaudet, 1977). This period is regarded by Harper (1992) as a 'normal' condition.

From 1975 to 1983 no submerged or floating-leaved aquatic vegetation was found in the main lake. Floating vegetation was dominated by the introduced *Salvinia molesta*, which was often associated with large floating rafts of papyrus, *Cyperus papyrus*. These drifted around the lake, driven by

the wind, eventually becoming beached when the water levels fell to their lowest for the period in 1987 and early 1988. From about 1986, submerged macrophytes began to return to the littoral. Recolonization began on the eastern shores of the lake, around Crescent Island and near the Safariland Lodge (map, Fig. 14.7). This recolonization was accompanied in the latter part of 1988 by increasing water levels.

During the period of rapid change, the clarity of the water decreased and phytoplankton abundance increased. This was accompanied by an increase in gross primary production in the upper layers of the lake (Harper, 1992). The benthic fauna of the lake is discussed by Clark *et al.* (1989).

14.3 THE FISH COMMUNITY: SPECIES AND THEIR CHANGES

Some of the introduced fish species have been mentioned already. A list of fish species that have been recorded from the lake is given in Table 14.1. Only *Aplocheilichthys antinorii* and *Barbus amphigramma* have arrived in the lake without human intervention. Lakes Nakuru and Elmenteita, once part of the same lake as Naivasha, have no endemic species (Richardson and Richardson, 1972). The remaining nine species or species groups have been introduced and several of them, such as largemouth bass and the rainbow trout, *Oncorhynchus mykiss*, are originally from outside Africa. The average persistence time is 36.9 ± 29.7 years for the ten species in Table 14.1 for

Table 14.1 A history of the fish community in Lake Naivasha since the beginning of the 20th century (from Muchiri and Hickley, 1991)

Species	Date of introduction/disappearance
Endemic	
<i>Aplocheilichthys antinorii</i>	Last reported 1962
Introduced	
Failed	
<i>Oreochromis spirulus niger</i>	1925
<i>O. leucostictus</i> × <i>O. s. niger</i> hybrid	Gone by 1972
<i>O. niloticus</i>	1967
Still present	
<i>Micropterus salmoides</i>	1929, 1940s and 1951
<i>Tilapia zillii</i>	1956
<i>Oreochromis leucostictus</i>	1956
<i>Gambusia</i> sp. and <i>Poecilia</i> sp.	Date unknown
<i>Lebistes reticulata</i>	Date unknown
<i>Oncorhynchus mykiss</i>	R. Malewa, date unknown
<i>Barbus amphigramma</i>	1982 (rivers)

which the start and end of their presence can be deduced with any certainty. In the case of the only known endemic, it is assumed that the fish had been present for 100 years before extinction in 1962. This would take account of the waterless lake just prior to the arrival of Europeans, when the fish was presumably absent. The reciprocal of the persistence time, 0.027, can be regarded as an extinction rate (Schoener and Spiller, 1992). Over recorded history, five out of eleven species have become extinct which is 45% of the fish that have been known to live in the lake. This appears to be a poor record.

The present fish fauna is composed of five species: largemouth bass, the two cichlids, *Barbus* and the guppy. The first three form the basis of the commercial fishery for which records exist since 1963. The crayfish, introduced in 1970, is also fished for commercially, but we will not discuss its fishery further. The commercial catch of tilapias declined through the 1970s. At the same time crayfish populations were increasing, eventually reaching about 4 m^{-2} in the littoral. This increase has been suggested as a possible contributor to the decline in macrophyte populations (Harper *et al.*, 1990), a decline which possibly contributed to the decrease of the cichlid stocks. The crayfish increase may have led to a gradual recovery of the bass populations towards the end of the 1970s because crayfish form an important part of the bass diet. Possibly as a result of a 10 cm minimum mesh size rule in the fishery and a return of the macrophytes, the cichlid catches began to increase towards the end of the 1970s. By the end of the 1980s the crayfish population had fallen back to about 0.25 m^{-2} , a change possibly coupled with the fall in the bass catch at the same time. Tilapia catches had stabilized at around 200 t (tonnes) a year.

14.4 THE FISHERY FOR TILAPIA

Commercial fishing is mostly by gill nets set from glass-fibre or wooden canoes (Muchiri and Hickley, 1991). These are powered by sail, oars or outboard motor. Each fisherman is permitted to use 10 multifilament gill nets, each of 100 m. The mesh must be no less than 100 mm. The catch must be landed at a point on the eastern shore near the town of Naivasha where inspectors from the Fisheries Department of the Kenya Government record the weight of the catch from each vessel. Records began in 1963 and the catch was separated into bass and 'tilapia' from 1974 on. Landings were not separated into *T. zillii* and *O. leucostictus* until 1987. Bass are caught by both commercial and sport fishermen, the latter using rod and line. The only other species caught commercially is *B. amphigramma*, which is caught using scoop nets as it attempts to ascend the River Malewa to spawn.

The total catch in tonnes from 1963 to 1989 is shown in Fig. 14.1 (from Muchiri, 1990). This also shows the number of canoes in the fishing fleet

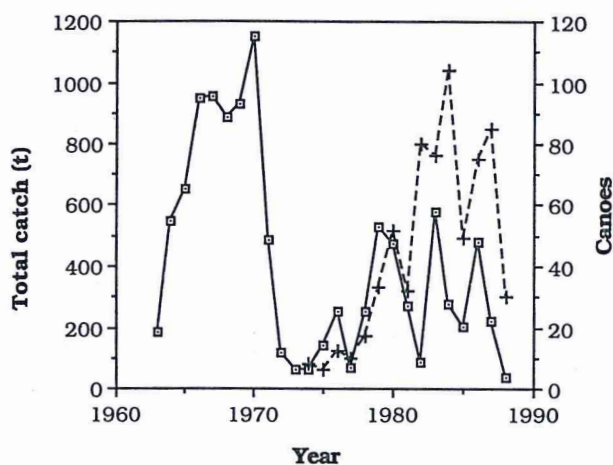


Fig. 14.1 The combined catch (solid line) of *T. zillii*, *O. leucostictus* and *M. salmoides* in Lake Naivasha between 1963 and 1989 together with the number of canoes in the fishery from 1974 (dashed line).

from 1974 onwards. The total catch and the lake water levels are plotted together in Fig. 14.2. The catch increased rapidly in the early years to a high of 1150t. The early effort, the effects of which were made worse by the use

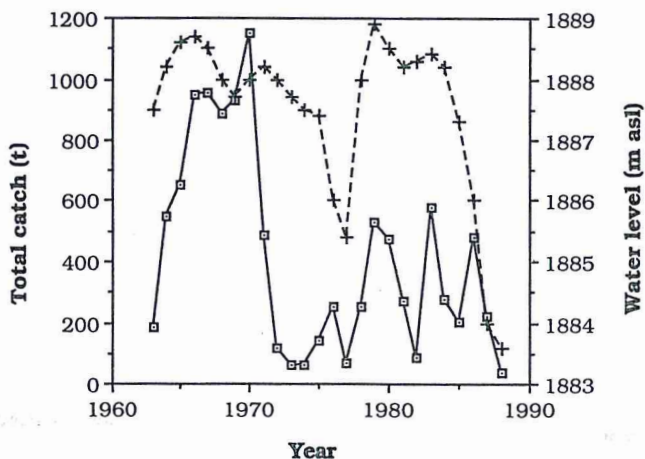


Fig. 14.2 The combined catch of *T. zillii*, *O. leucostictus* and *M. salmoides* in Lake Naivasha between 1963 and 1989 (solid line) together with the water levels (dashed line).

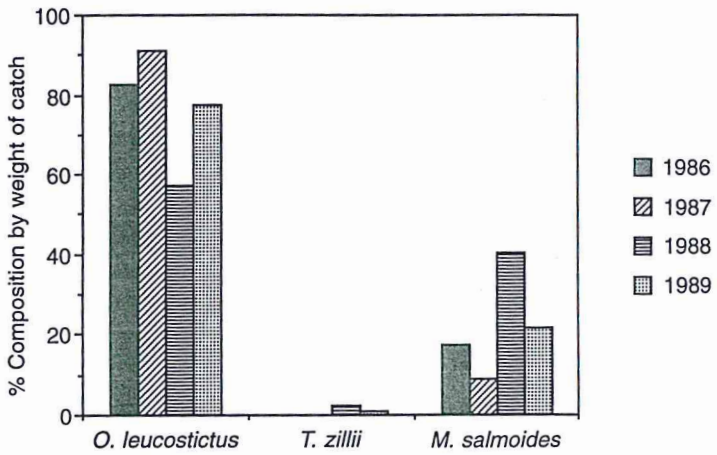


Fig. 14.3 Histograms showing the species composition of the catch for the last 4 years of the period under study.

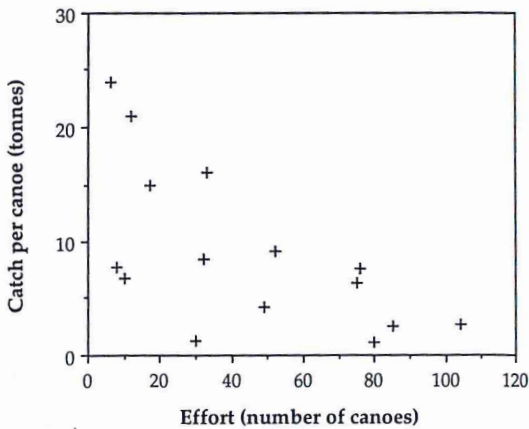


Fig. 14.4 Catch per unit effort, expressed as tonnes caught per canoe, plotted against the total effort expressed as the number of canoes. These data form the basis of the stock assessment given in the text.

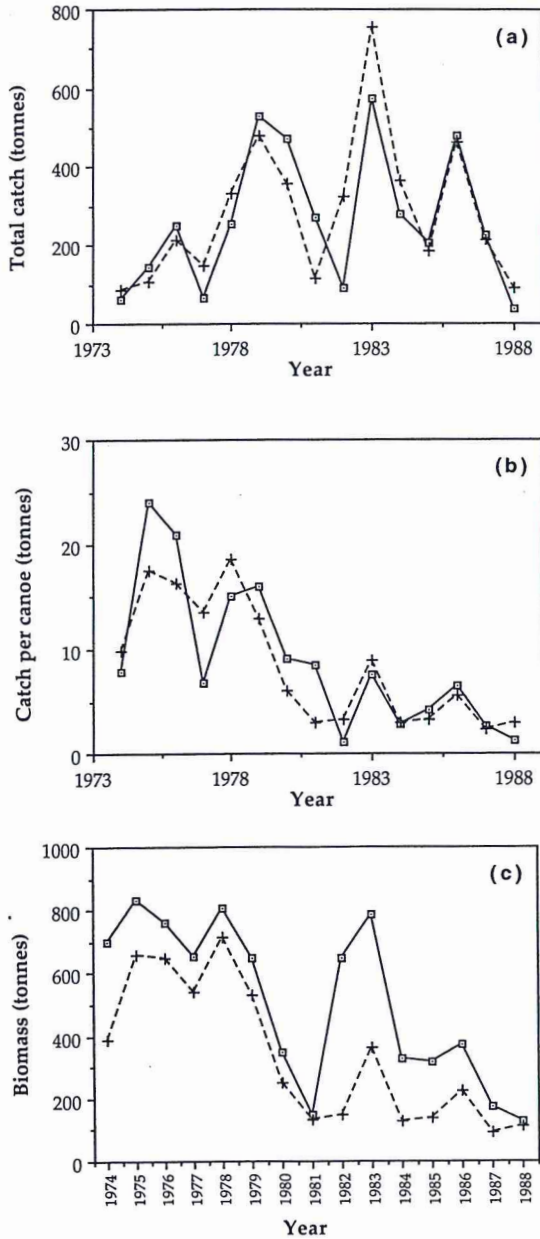


Fig. 14.5 Fit of the Gulland–Fox model to total catch from Lake Naivasha. (a) Actual (solid line) and predicted catch (dashed line), 1974–1988. (b) Actual (solid line) and predicted (dashed line) catch per unit effort for the same period. (c) Biomass estimates (solid line) for the 15 year period. This panel also shows biomass as calculated from the Schaeffer logistic model of population growth (dashed line).

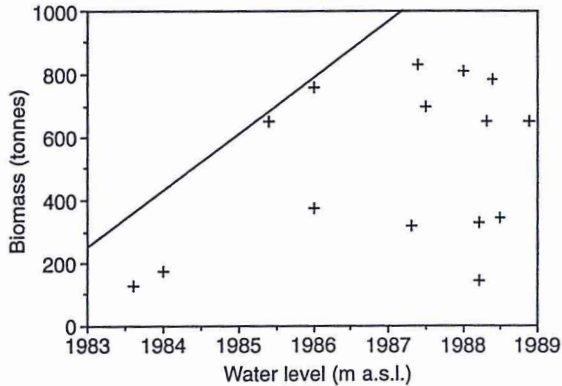


Fig. 14.6 Biomass of all three species plotted against the water levels over the period 1974 to 1988. The curve defines the empty area above which no biomass/water level combinations occur.

of small-mesh nets, led to a sharp decline in the early 1970s. The limnological changes already described may also have had an effect. Following the introduction of a 100 mm minimum mesh size in the early 1970s, the catch increased from a low of about 60 t to between 200 and 500 t, values which remained until the 1988 season when the catch fell to an all-time low for the period of 37 t.

The species composition of the catch between 1986 and 1989 is shown in Fig. 14.3. *O. leucostictus* dominated the fishery during this period. The fishery is mainly executed in shallow water less than 3 m deep. Survey gill netting showed that *O. leucostictus* occurs mostly in water of less than 3 m whilst *T. zillii* is more abundant in water deeper than 3 m (Muchiri, 1990).

The data on catch and number of canoes (Fig. 14.1) have been used to calculate catch per canoe as an index of abundance. Catch per canoe is plotted against the number of canoes in Fig. 14.4. The best fit to these data, using the CIDA software package (MRAG, 1992) is achieved with an exponential curve ($r^2 = 0.7$) and a Gulland-Fox model for population growth (Ricker, 1975). Using this, $B_\infty = 719$ t (90% confidence limits: 539–1040 t), maximum sustainable yield is 365 t and the number of canoes yielding this would be 37. The fit of the model to the data is shown in Fig. 14.5 (a, b, c).

Fitting a straight line to the catch per unit effort and effort plot (Fig. 14.4) leads to a logistic or Schaeffer model of population growth. Using this yields an estimate of $B_\infty = 892$ t, with an MSY of 446 t. For both these fits it should be remembered that the analysis assumes that fish population and fishery are in equilibrium, which they are probably not. The fit is also made to data aggregated from three species.

The estimate of biomass for the 15 years between 1974 to 1988 (Fig. 14.5(c)) has been plotted against water level in Fig. 14.6. The correlation of the two is not significant but it is interesting to note, as highlighted by the curve added to the figure, that high biomass never co-occurred with low water levels. The mechanisms determining this relationship are not clear, but there is a hint that low water levels reduce the areas available for spawning to the *Tilapia* and *Oreochromis* populations. At high water levels other mechanisms, such as increased fishing pressure, would have greater influence on biomass. It should also be remembered that this analysis is applied to the total catch of three species, each with its own population dynamics. The conclusions can only be preliminary.

14.5 WHY HAVE THE TILAPIA SPECIES PERSISTED IN THE FACE OF HEAVY FISHING PRESSURE AND HABITAT CHANGE?

Many species introduced into the lake have become extinct. The two tilapia species and the largemouth bass have persisted despite being the subject of fishing pressure. Lake Naivasha was not necessarily the most appropriate habitat for some of the introduced species and this may explain why they failed to establish themselves. A research programme was begun in 1987 to investigate aspects of the feeding ecology of the two tilapias. The results of the work (Muchiri, 1990) provide an insight into aspects of the trophic ecology of the two species that could explain their persistence in the face of a fluctuating environment and heavy fishing mortality. The results on the feeding habits of *T. zillii* and *O. leucostictus* will be summarized so that the reasons for persistence may be examined.

14.6 TROPHIC ECOLOGY OF THE TILAPIAS

Collection of fish samples

Fleets of multifilament gill nets of five mesh sizes (40, 48, 70, 100 and 125 mm stretched mesh) were used to collect monthly fish samples from three sampling sites (Fig. 14.7) from June 1987. Two sites were located at the main lake: (i) off Crescent Island, which at the beginning of sampling was devoid of submerged macrophytes, and (ii) off Safariland Lodge where, in contrast to the Crescent Island area, there was an extensive cover of submerged macrophytes. Sampling continued until June and July 1988 at sites (i) and (ii) respectively. The third site was in Oloidien Lake, which was confluent with Lake Naivasha before 1984 during high water. Sampling in Oloidien Lake started in August 1987 and continued until May 1988.

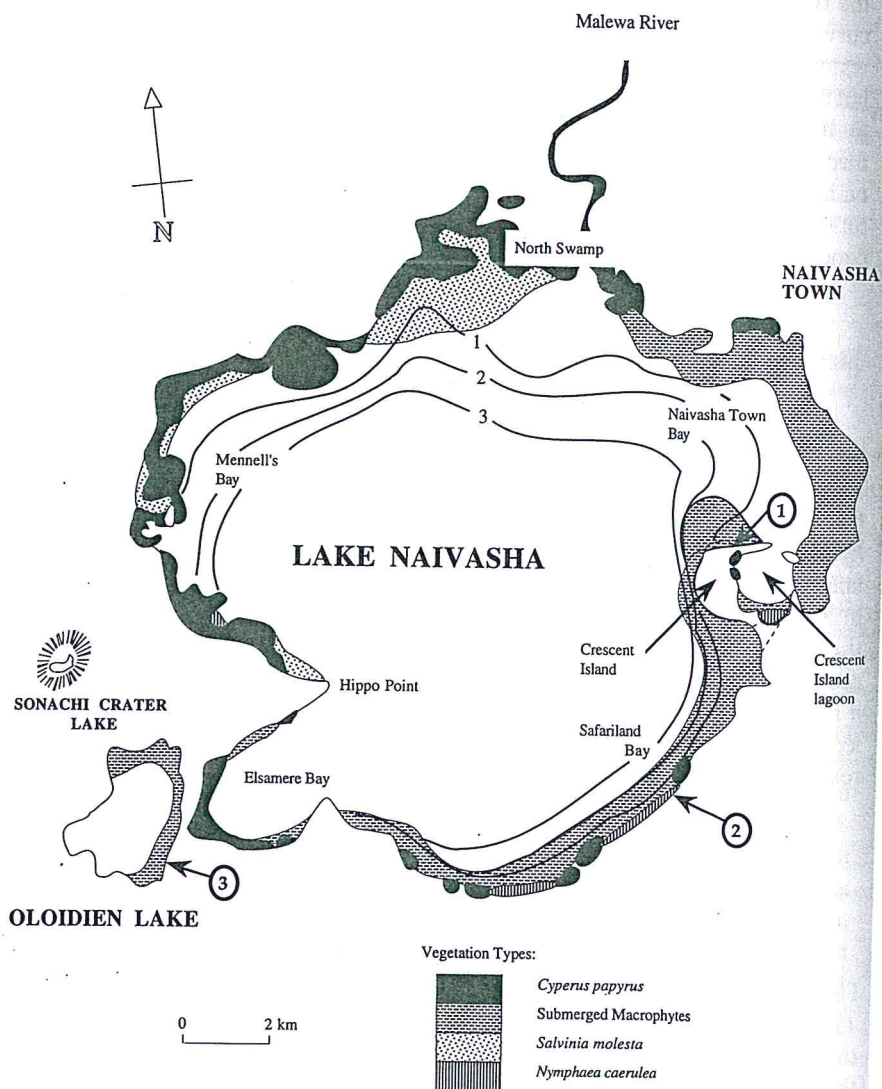


Fig. 14.7 Map of Lake Naivasha to show the sites (encircled numbers) used for sampling the populations of *O. leuostictus* and *T. zillii*: 1, Crescent Island; 2, Safariland Lodge; 3, Oloidien Lake. Additional information and other sites are mentioned in the text. Depth contours in m.

In 1989 further fish collection was done in January, March and April. In addition to the Oloidien site, gill netting was done in four habitat types in Lake Naivasha. These were: macrophyte zone, rocky shore, North Swamp and the open water. During the 1989 sampling sessions two smaller mesh sizes (22 and 30 mm stretched mesh) were introduced to sample the smaller fish sizes.

Description of the sampling sites

(i) *Crescent Island* At the beginning of sampling in June 1987 the Crescent Island site was devoid of submerged macrophytes and due to continued recession of the shoreline that began in March 1984, swamp vegetation was not established. The bottom substrate in this area was hard in the nearshore, gradually becoming soft flocculent mud along a transect line from Crescent Island towards the mouth of the River Malewa, on the north-east shore. A greater part of this area was less than 3 m in depth. By November 1987 submerged vegetation (mainly of *Potamogeton schweinfurthii*, *P. pectinatus* and *Najas pectinata*) was abundant. As the lake level began to rise again in the latter part of 1988 a fringing swamp of mainly *Cyperus* spp. formed along the shoreline.

(ii) *Safariland site* In contrast to the Crescent Island site, this station had beds of submerged vegetation up to 1000 m wide to a depth of 4 m. The shoreline had a thin cover of *Cyperus papyrus* swamp. As the lake level rose by about 1 m in early 1989, the swamps increased with lagoons forming behind them.

(iii) *Oloidien Lake* This is a small, saline, basin-shaped lake with a rim of water less than 3 m in depth stretching 200 m offshore, with a deeper central area going down to a maximum depth of about 6 m. Oloidien did not experience any loss of submerged plants (Harper, 1992). The substratum of the shallow zone of this lake has only a thin layer of organic mud and in some areas the bottom is hard and covered with volcanic gravel. The deeper parts of the lake have a flocculent iron-rich silt bottom.

(iv) *Rocky shore* Rocks are found only along the south-western shore of Lake Naivasha and the inner rim of Crescent Island. The shoreline of the south-western shore contains no submerged plants and falls steeply only a few metres offshore to 6 m, the deepest part of the lake.

(v) *North swamp* This is the northern part of the lake most influenced by fringing papyrus swamps and the inflowing rivers, which are often laden with silt and rotting organic debris brought in from the catchment area. It

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is a shallow area (<3 m deep) with a detritus-rich substrate and sparse vegetation cover.

(vi) *Open water* The open water is the most extensive of the habitats available to fish in Lake Naivasha, covering over 60% of the total surface area of the lake.

Laboratory treatment of fish samples

Fish caught in the gill nets were measured and weighed before being opened to remove their stomachs. The fish stomachs were preserved separately in 10% formaldehyde solution. The stomach contents were later examined with a low-power microscope. The larger food items were identified and their volumes estimated.

Because all the examined stomachs contained food items that were too small to be examined sufficiently under the low-power magnification, the stomach contents were mixed thoroughly to form a homogeneous mixture. Small amounts of this mixture were pipetted onto a microscope slide and examined under high-power magnification (up to $\times 400$) using a Nikon compound microscope.

In both cases visual estimates of relative volumes were made by comparing the area occupied by each food item in the field of view. This meant that larger items contributed greater proportions (and therefore volume) of the stomach contents. The estimated volumes were allotted numbers between 1 and 10; 10 was allotted where the whole stomach content was made up of only one food item and 1 where a food item was estimated to constitute 10% of the contents.

The numbers of guts of each species in which a food item occurred were added up and expressed as a percentage (% occurrence) of the sum total of the non-empty stomachs for each of the food items. The proportion and occurrences were then used to estimate the relative importance of each food item consumed by employing Wilhm's (1967) prominence values (PV):

$$PV = \% \text{ proportion} \times (\% \text{ occurrence})^{\frac{1}{2}} \quad (14.1)$$

PVs range between 0.0 and 1000.0; 0.0 where a food item is not consumed at all and 1000.0 for a food item where only that one item is taken. This method was adopted by Hickley and Bailey (1987) in their analysis of the diets of fishes of the Sudd swamps of the River Nile.

The data on diet were analysed with two aims in mind: to examine the degree of diet overlap and to determine the food webs supporting each of the tilapia species. Dietary overlap was quantified by following Wilhm (1967) who used the PVs to calculate coefficients of similarity in populations of benthic organisms from different sampling stations. The scheme was employed

in this study to examine similarity of food items eaten and hence diet overlap among the two tilapia species. The coefficient of similarity index, C , was calculated as follows:

$$C = 2 \times (\sum PV_{(\text{low})}) / \sum PV_1 + \sum PV_2 \quad (14.2)$$

where $PV_{(\text{low})}$ is the lower prominence value calculated for each of the food items taken in common by the two species to be compared, and PV_1 and PV_2 are the prominence values of each food item for species 1 and 2 respectively. C ranges between 0.0 and 1.0, where 0.0 shows no sharing of any food items and 1.0 occurs where there is total overlap in feeding. A 60% ($C = 0.6$) cut-off value was adopted in this study to imply competition in feeding: i.e. where 60% or more of the scores of food items eaten were shared by the two species as indicated by the coefficients of similarity, then competition for food would be a possibility (Zaret and Rand, 1971; Mathus, 1977, as quoted by Wallace, 1981).

The diet of *O. leucostictus*

Detailed results of stomach content examination for *O. leucostictus* during the sampling period 1987–88 and 1989 respectively are given in Muchiri (1990). Only the main features are summarized in this chapter. Throughout the sampling periods, detritus constituted the highest proportion in the diet of *O. leucostictus*. Detritus found in the guts of fish during the first few months of sampling in Lake Naivasha and in all sampling occasions in Ololdien Lake was mainly of coarse rotting material, in most cases associated with grit. This suggested bottom feeding. In later months the detritus found in the guts was generally of material that had a finer particle size.

Phytoplankton also constituted significant proportions of the gut contents collected from the Lake Naivasha sampling stations. *Closterium* spp., *Botryococcus* sp., and *Microcystis* spp. were the dominant species, in that order. Occasionally, in some stomach samples examined the filamentous diatom *Melosira* sp. constituted significant proportions. Other phytoplankton found in the stomachs of *O. leucostictus* included the bluegreen alga *Spirulina* sp., *Merismopedia* sp., *Ceratium* sp., *Pediastrum* sp., and *Chlorococcus* sp. During 1988 and 1989 phytoplankton constituted smaller proportions of the gut contents of *O. leucostictus*. This was particularly evident where there was extensive cover of submerged macrophytes.

Macroinvertebrates were also consumed, albeit in small proportions. In the guts of some individual fish, macroinvertebrates constituted significant proportions of the diet. This was particularly true for insects (mainly *Micronecta*) which are large food items and are therefore more prominent than other items.

Benthic macroinvertebrates are less significant, except in two habitat types

in Lake Naivasha (macrophyte beds and rocky shore) in 1989, where oligochaete worms constituted notable proportions of the diet. It is, however, likely that fish picked up the worms which were attached to macrophytes and rocks rather than collecting them from the bottom mud. In Oloidien Lake, chironomid larvae were taken in significant proportions.

Zooplankton were consumed in very small quantities and were absent in most cases in both Lake Naivasha and Oloidien Lake.

The diet of *T. zillii*

Detailed results of the *T. zillii* stomach content analysis are given in Muchiri (1990). As with *O. leucostictus*, detritus constituted the most important food item in the diet of *T. zillii* in both Lake Naivasha and Oloidien Lake.

During the loss of submerged macrophytes in Lake Naivasha, *T. zillii* consumed mainly detritus and insects (dominated by the corixid *Micronecta scutellaris*). This was indicated by the feeding of *T. zillii* at the Crescent Island site during the months of August to November 1987. Macrophytes constituted the only other significant food item in Naivasha during the latter months of 1987 and 1988, while chironomid larvae were also consumed in significant proportions in Oloidien Lake.

In the habitat types sampled in 1989, chironomid larvae were consumed in significant proportions in the macrophyte zone whereas oligochaete worms were more significant in the rocky shore. It is unlikely that the detritus and macroinvertebrates consumed in Lake Naivasha this time were collected from the bottom because these items were not associated with grit (as they were in samples from Oloidien Lake). The detritus had a fine particle size and could have been of planktonic origin sedimented onto the macrophytes.

Other food items were found in small amounts in the guts of *T. zillii*, but these were presumably taken incidentally as fish fed on the preferred food items. Epiphytes and molluscs, for example, were ingested as the fish consumed macrophytes.

Feeding overlap

A summary of the feeding habits of the two tilapias in the main lake is given as Fig. 14.8. Coefficients of similarity calculated to assess the apparent sharing of food revealed a great deal of overlap in the diet of *O. leucostictus* and *T. zillii* in virtually all the habitats. By adopting 60% cut-off value to decide competitive sharing, the feeding overlap in the two species suggested competition for food. The coefficient of similarity at Crescent Island in 1988 was 0.60 while those of Safariland in 1987 and 1988 were 0.63 and 0.68 respectively. At Oloidien Lake the coefficients were 0.66 in 1987 and 0.63 in 1988. Out of the three habitats sampled in 1989, where sample sizes were

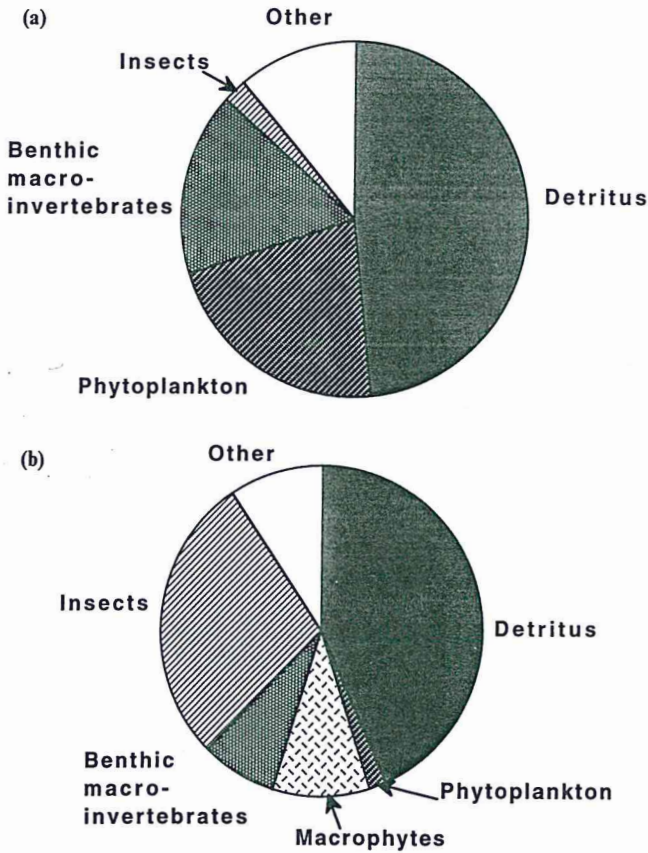


Fig. 14.8 Pie charts illustrating the diet composition for (a) *O. leucostictus* and (b) *T. zillii* in the main lake.

large enough for both aspects to be compared, two habitats, the macrophyte zone and rocky shore, had coefficients that suggested competition (0.67 and 0.60 respectively). Closer scrutiny of the data showed that the observed large coefficients of similarity were a result of the two tilapia species feeding on large amounts of detrital material. By recalculating the coefficients leaving out detritus, feeding overlap was shown to be very small in all habitats.

Food webs

Food webs for both tilapia species are shown in Fig. 14.9 (a and b) and are based on data given in Muchiri (1990). The only difference between the two is that *O. leucostictus* did not make use of macrophytes.

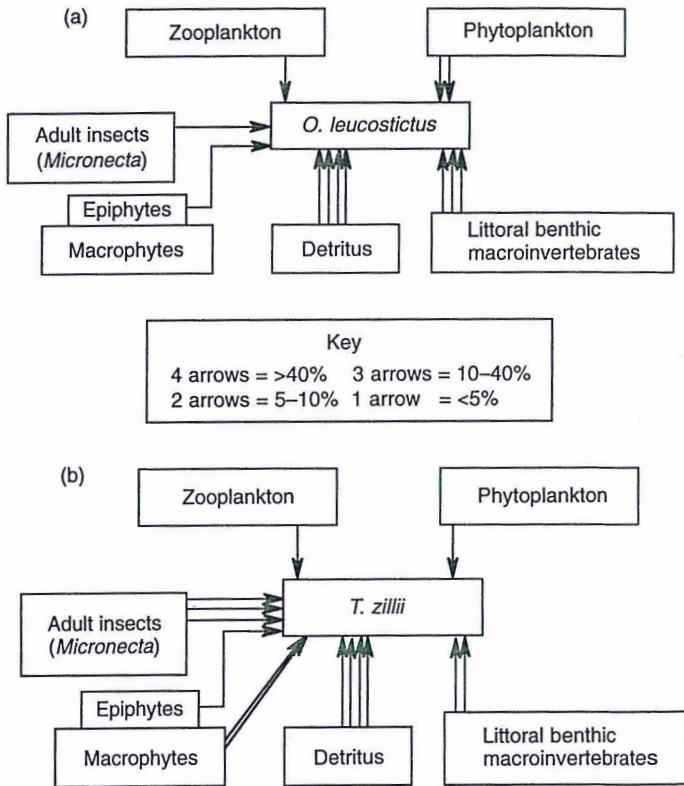


Fig. 14.9 Proposed food webs for the two tilapia species indicating the proportion of the diet, shown by the number of arrows, coming from the main sources of food. (a) *O. leucostictus*, (b) *T. zillii*.

14.7 DETRITUS AS A BUFFER AGAINST HABITAT VARIABILITY

Detritus was shown in this study to be the most important food item for both *O. leucostictus* and *T. zillii* in Lake Naivasha and the adjoining Oloiden Lake. In Lake Naivasha during the early phase of the study, sources of detritus were mainly from *Cyperus* spp. in the lake, from allochthonous organic material coming into the lake in river water, from surface run-off and from sedimenting plankton. Recovery of submerged macrophytes and rise in the lake level, thus flooding terrestrial vegetation in the drawdown zone, led to increased formation of detritus. The loss of submerged vegetation and the decline in the lake level did not therefore have great effects on the quantity of detritus. This meant that detritus was available at all times. The availability

of this almost unlimited food item allowed the two tilapia species to coexist with minimum competition for food.

The importance of detritus as food for tilapias has been discussed in detail by Fryer and Iles (1972) and Bowen (1979, 1982). Bowen (1982) pointed out that detritivory in fish ensures that food quantity does not become the limiting factor. This is particularly important in Lake Naivasha because some of the other food items consumed by the tilapias are also shared with other animals in the ecosystem, although the quantitative aspects of the overlap are not known. The tilapias share insects and chironomid larvae with juvenile largemouth bass (Hickley and North, unpublished data). *T. zillii* also shares submerged macrophytes with crayfish and the large numbers of coot, *Fulica cristata*, the yellow-billed ducks, *Anas andulata*, and the African pochard, *Aythia erythrophalma*.

It would be interesting to know more about the fitness of the two species in this regime compared with one in which a more varied selection of food types was available. The effect of more choice on *O. leucostictus* may not be so significant because the species commonly feeds on detritus in other habitats. Earlier studies in Lake Naivasha have also shown that detritus is important to the species. Malvestuto (1974) and Siddiqui (1977) reported the diet of *O. leucostictus* in Lake Naivasha to consist of mainly chironomid larvae and detritus. The diet of *T. zillii* was, however, reported in the past to be 67.7% macrophytes (Siddiqui, 1977). *T. zillii* has been known to feed on other foods in other habitats. Abdel-Malek (1972) and Spataru (1978) have reported *T. zillii* as feeding on benthos in Lake Quarun, Egypt, and Kinneret, Israel, respectively. In Kinneret they also consumed phytoplankton. In the Sudd swamps of the River Nile, Hickley and Bailey (1987) found the diet of *T. zillii* to be 61% periphyton. These results may indicate that *T. zillii* is feeding on a poorer diet than it would choose if greater prey diversity was available.

Analysing the trophic relationship between the two tilapia species is handicapped without a knowledge of their population sizes. From the fishery data, it could be concluded that *O. leucostictus* is very much more abundant than *T. zillii*. As *T. zillii* is more likely to be caught in deeper water than is *O. leucostictus* (Muchiri, 1990), it is possible that *T. zillii* is underrepresented in the fishery.

Population stability of a species could be influenced by the complexity of the food web from which it is supplied (Pimm, 1991). In Lake Naivasha the dependence of both tilapia species on a large reservoir of organic detritus as their main food source seems to damp out the effect of any fluctuations in the populations of other food organisms. It is also the case that both species are dependent on nearly the same food web, so that both should be similarly affected by changes in food species. It is more likely that fluctuations in the populations result from reduced stocks of submerged plants diminishing the fish's breeding opportunities (Fig. 14.6). The nest-building *T. zillii* is most

likely to be affected by these changes. Fishing pressure would have added further perturbations to the populations (Muchiri and Hickley, 1991).

Several major sources of fish food in Lake Naivasha remain underutilized. These include the benthos, especially in the offshore zones, and the limnetic zooplankton and phytoplankton. This is because all the existing fish species in Lake Naivasha live in the shallow littoral zones. Analysis of fish yields in relation to the lake's primary productivity has shown that Lake Naivasha could have a capacity for higher yields than are now realized (Muchiri and Hickley, 1991). This has led to suggestion for careful consideration of further introductions of fish species that would use the unexploited resources, to diversify the species composition of the fish community and increase the yield for the fishery (Muchiri and Hickley, 1991).

14.8 HABITAT VARIABILITY AND EXTINCTION RATES IN THE FISH COMMUNITY

It has been assumed earlier that the recent variability of the lake ecosystem may be related to the sparseness of the lake's fish fauna. With only five fish species now present and only ten species (excluding hybrids) known over the past 100 years, the fauna is atypical of many tropical lakes (this volume). This situation is likely to be a result of a number of factors, mostly historical. Lake variability is probably not, on its own, a deciding factor.

Lake Naivasha is not well connected to other lakes and rivers so that it is hard for immigrants to find their way to it. With no surface outlet, fish from other lakes or river systems cannot get into Lake Naivasha. The inflowing rivers are short and not connected to any other lakes (map, Chapter 1, Fig. 1.1). The nearest lakes in the Rift Valley, such as Nakuru and Elmenteita, are soda lakes and unlikely to have fish species that would thrive if they arrived in the fresh water of Lake Naivasha. In addition, the instability of the lake level over the past 150 years would have made it difficult for immigrants to establish themselves.

These remarks still leave untested the assumption that even if individuals of an immigrant species do arrive at the lake, the species will not last long because of the variability of the ecosystem. This variability is likely to have strong effects on the population abundance of immigrants, making it fluctuate widely in unison with the habitat changes.

Early studies on extinction rates of immigrants on islands did not account for population variability (MacArthur and Wilson, 1967) and concluded that extinction rate would be inversely correlated with population size. In general, large populations would not go extinct. As the carrying capacity increased (K), time to extinction would become infinitely long. Recent theoretical work by Mangel and Tier (1993) and empirical work with birds (Pimm *et al.*, 1988;

Tracey and George, 1992) and spiders (Schoener and Spiller, 1992) has shown that the early ideas were faulty because they did not account for variability in population abundance. The theoretical study has shown that if catastrophes are included in the model that predicts time to extinction, then the very large values disappear. The study also shows that if there are catastrophes, even large populations can become extinct.

The empirical work has produced conflicting results. Pimm *et al.* (1988), working with birds on British islands, found that large populations were less likely to go extinct, but the risk of extinction was greater for species the populations of which varied greatly with time. Reanalysing the data, Tracey and George (1992) found that there was no evidence for this idea. Extinction rates of spiders on Caribbean islands showed an inverse relation with temporal variability in population size (Schoener and Spiller, 1992). Schoener and Spiller also found that the coefficient of variation of population size was directly proportional to population size; large populations were more variable. These relationships are explained by arguing that a small population invading an island and going extinct several times over a short time span, would never have the chance to build up temporal variability in population size. These small populations would become extinct for three reasons: (1) demographic – stochastic accidents under ‘normal’ or ‘average’ conditions, such as a series of deaths before sufficient births had occurred, would cause the population to die out; (2) islands might have very poor conditions, so that births and deaths would be substantially worse than normal; (3) females might fail to reproduce because they would not encounter a male in time. The second condition might describe the situation in Lake Naivasha. The environmental variability makes it difficult for a new species to establish itself. The tilapia species have persisted because they can exploit a resource that is not affected by changes in water level and reductions in macrophyte communities.

14.9 SUMMARY

The tilapias, *Oreochromis leucostictus* and *Tilapia zillii*, have been introduced into Lake Naivasha, Kenya and form the basis for a commercial fishery. Lake Naivasha is characterized by frequent changes in water level and varying amounts of submerged vegetation. Changes in the lake ecosystem tend to occur rapidly and have significant ecological consequences. The endemic fish community in the lake has been sparse during recent times. Human additions to the fish fauna have led to the present community which is dominated by largemouth bass, *O. leucostictus* and *T. zillii*. The persistence of the two tilapia species in the face of rapid ecological change and heavy fishing is an interesting challenge to our understanding. To elucidate the problem, a study of the diet of the tilapias was made over a 3 year period at three contrasting sites in

the lake. For each species, 40–50% of the food eaten was detritus. The rest of the diet of *O. leucostictus* was composed of 22% phytoplankton, 17% benthic macroinvertebrates and a small proportion of insects. Apart from detritus, the diet of *T. zillii* included 28% insects and then less than 10% each of macrophytes, benthic macroinvertebrates and non-specified material. The emphasis on detritus in both species indicates that competition for food between the two is unlikely. Their diets may also mean that changes in macrophyte or invertebrate abundances do not seriously influence the feeding ecology of the two fish species. The quantity of detritus is unlikely to change quickly in response to change in macrophytes and water levels, so damping out short-term ecosystem changes. Environmental variability is more likely to influence the fish populations by changing the availability of spawning habitat.

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