The biology and impacts of *Oreochromis niloticus* and *Limnothrissa miodon* introduced in Lake Kariba
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Developing a sustainable pelagic fishery in an African reservoir: trends in the catches of the introduced freshwater sardine *Limnothrissa miodon* and associated species in Lake Kariba, Zimbabwe

Portia C. Chifamba
Han Olff
Abstract
The formation of reservoirs in former tropical riverine ecosystems is associated with introductions of pelagic species to develop fisheries, but with varying long-term success and unclear impact on native inshore (formerly riverine) species. The freshwater sardine, Limnothrissa miodon was introduced into the Lake Kariba reservoir in the late 1960s to develop a pelagic fishery in this reservoir. Fishing started in 1974 and catches peaked in 1990 but declined steadily thereafter, and with that also the socio-economic benefits from the fishery in this lake. This paper examines the trends in catch and temperature data in order to understand these trends and better manage this fishery. A multiple regression analysis shows that fishing effort and lake level explains the variation in the total catch whilst fishing effort and maximum temperature explained variation in catch per unit effort (as indicator of biomass). As the catches were at and above estimated Maximum Sustainable Yield (MSY), the collapse of the sardine fishery may be explained by overfishing. A combination of high fishing pressure with less suitable ecological conditions due to warmer water may together explain the declining harvest. Understanding the life-history characteristics of L. miodon highlights aspects of its vulnerability to fishing. Limnothrissa miodon inhabits both the pelagic and inshore areas. Juveniles are found in the marginal area only, while adults use both the pelagic and shallow areas. Large sardines caught in waters less than 30 m deep may stay close to the margin to feed on their own juveniles, perhaps also to breed. Overexploitation of young adult fish by the fishery might be compromising recruitment by reducing the number of breeding fish, and the number of large fish that carry relatively larger numbers of eggs compared to the young adults. The temporal rise and fall of the L. miodon catch was synchronous with that of its predator, the tigerfish Hydrocynus vittatus. Other inshore fish in addition to tigerfish are caught in the sardine fishery, indicating their tendency to venture into deep water to feed. Bycatch of juveniles of inshore species of commercially importance was low (0.85% in weight), hence capture was unlikely to have a large impact on the gill-net fishery on these species. To ensure sustainability of the sardine fishery both fishing effort and environment need to be considered in the management of the sardine fishery. Fishing effort needs to be reduced to sustainable levels through constant monitoring of the size of the sardine population. It is also critical that a detailed ecosystem production model of Lake Kariba is developed that can inform sustainable fisheries.
Introduction

The formation of reservoirs for hydroelectricity, irrigation and drinking water in areas where previously rivers were the main freshwater habitat, has major consequences for their fish fauna. In general, riverine species will not be adapted to the deep waters of such reservoirs, leaving open niches (Fernando & Holčík 1991; van Zwieten et al. 2011), limiting opportunities to also use reservoirs for fishing. In several cases, this has led to species introductions to develop new fisheries in newly formed reservoirs (De Silva & Sirisena 1987; van Zwieten et al. 2011). However, such introductions have varied in success, calling for more insight in the processes underlying changing catches (Fernando & Holčík 1991).

The Lake Kariba dam on the Zambezi River was completed in 1958 and the lake filled to capacity in 1963. At 5 820 km$^2$ surface area it was then the largest man-made reservoir (Coche 1974). It is made up of five hydrological basins separated by narrows or chains of islands (Figure 6.1). Uppermost basins, the Mlibizi and Binga basins are small and narrow and the Zambezi River influences the characteristics of these basins. They have riverine conditions for most of the year. The other three basins, Sengwa, Chalala and Sanyati, or Kariba basins, are more lacustrine (Coche 1974).

Figure 6.1 Map of Lake Kariba showing the Lake basins.
Before the formation of the lake, the Middle Zambezi River was inhabited by at least 31 riverine fish species (Jackson 1961; Bell-Cross 1972). The native riverine species were not able to colonize the deep open water after the lake formed and were restricted to water not more than 15 m depth with the highest catches between 2 and 10 m (Coke 1968; Balon 1972; Sanyanga et al. 1995). To improve fisheries in the lake, *Limnothrissa miodon*, a freshwater sardine locally known as ‘kapenta’ was introduced into Lake Kariba from Lake Tanganyika between 1967 and 1968 to fill the deep water pelagic ecological niche (Bell-Cross & Bell-Cross 1971). Experimental fishing using different gears and an echo sounder revealed that by 1973 the population of *L. miodon* was large enough to support commercial fishing (Begg 1974). The *L. miodon* fishery, also referred to as the ‘sardine’ or ‘pelagic’ fishery, started in the middle of 1974. Fishing takes place at night using lights to attract the fish which are then caught using a lift net with a mesh size of 8 mm. In the early 1970s purse seines were also used for fishing.

Catches in the *L. miodon* fishery increased initially. After reaching a peak of nearly 22,000 tonnes, landed in Zimbabwe in 1990, they started to decrease. Marshall (2012a) attributed the decline to overexploitation, whilst Magadza (2011) suggested climate change to be the cause. Both fishing and environment factors are likely important because biomass of *L. miodon* was high in the beginning of the fishery and decreased as fishing effort increased (Marshall 1988a). The environment is important because low river flow into the lake, and drought, are associated with poor catches of *L. miodon* (Marshall 1988b). In addition, climatic factors such as rainfall and maximum temperature had the highest correlation with Catch per unit Effort (CPUE) compared to the hydrological factors ‘river inflows’ and ‘lake level’ (Chifamba 2000). Both human and environmental, often together are involved in the collapse of many fisheries worldwide (Dekker 2003; Daskalov et al. 2007; Ruiz et al. 2009). For example, the collapse of Anchovy kilka (*Clupeonella engrauliformis*) fishery in the Caspian Sea was attributed to recruitment failure caused by the introduced predator ctenophore (*Mnemiopsis leidyi*) and overfishing (Daskalov et al. 2007). A holistic approach in the analysis of the causes is recommended (Botsford et al. 1997; Starkie 2003; Borja et al. 2008). This approach was adopted by Ruiz et al. (2009) investigating the impact of large-scale climatic patterns, turbulence, upwelling and river flow on the recruitment and catches of anchovy in the Bay of Biscay, Spain. In the same way, a multivariable approach is needed in the assessment of the causes of collapse of the sardine fishery of Lake Kariba, where both the environment and fishing appear to play a part.

Fishing can impact the fish population through selection of a particular size group, thereby affecting level of reproduction and recruitment into the fishery. This tendency is linked to the exponential relationship between the fish size and the number of eggs in its ovary as well as differences in the quality of these eggs (Birkeland & Dayton 2005; Arlinghaus et al. 2010). To avoid capture of juveniles...
that inhabit the shallow water, the sardine fishery is permitted only in deep water (≥ 20 m). Cochrane (1984) reported that Limnothrissa miodon are found at all depths, with the juveniles and inhabiting the shallow marginal areas and the size increasing with depth. In Lake Kivu, the juveniles (10 – 35 mm) and the large fish (85 – 110 mm) were always found in the littoral area. The largest were caught close to the margin, whilst the medium sized (65 – 90 and 85 – 110 mm) were pelagic (de Iongh et al. 1983). The Lake Kivu study shows that the sardine moved into deeper water as they grew up to a point, and then moved back into shallower water at a large size. This had not been observed in Lake Kariba, when the current study on the distribution of sardines by depth was started to determine how they utilize space and what stages would interact with the inshore fishes.

Though the introduction of L. miodon (a pelagic fish) was not expected to have impact on inshore fish, it changed the habit of a top predator, the tigerfish Hydrocynus vittatus, and it may have indirect impact on other species. The former riverine H. vittatus, which was first confined to the inshore lake, entered the pelagic area to forage on L. miodon and is caught as bycatch of the sardine fishery (Marshall 1987b). From April 1969 to March 1970, only 1.5% of the stomach content of H. vittatus consisted of sardines, whereas from April 1970 to March 1971 the amount had risen to 41.4% and in samples from 1994 – 1997 it was more than 45% (Kenmuir 1973; Mhlanga 2003). A record of the H. vittatus catch was kept since the beginning of the L. miodon fishery in 1974. It is interesting to know how the catch of this species responded to the changes in the catch of L. miodon.

The other fish species caught in the sardine fishery are not routinely recorded because of low representation in catch and small size that make them difficult to separate from the rest of the catch. Even so, the cumulative catch in number of these small fish was thought to be large. It was observed that these fish included juveniles of the gill-net fish species. Lack of information on the other components of the bycatch that was not recorded, prompted the collection on the data aimed to evaluate the impact of this fishery on the inshore fished through the capture of undersize fishes.

In this paper, we investigate the causes of the decline in the pelagic catches by analysing the relationships between catches of L. miodon, fishing effort and several key environmental variables: air temperature and hydrological factors (rainfall, river flow and lake level). The effect of depth on fish size and fish catches was assessed to understand the distribution of L. miodon particularly with regard to the large fish largely missing from the fishery. Trends in H. vittatus catches in the pelagic area were examined to detect the response of the fish to the decrease in the catches of L. miodon. The impact of the L. miodon fishery on the inshore fish species through the capture of juvenile of inshore fish species, was evaluated by quantifying and determining the species composition of bycatch.
Materials and methods

Relationship between catches, fishing effort and environment variables

Catch and effort data for the *L. miodon* fishery from 1974 to 2011 were obtained from the Lake Kariba Fisheries Research Institute and hydrology and weather data from Zambezi River Authority. One unit of effort is one fishing boat, fishing one night, and catch per boat per night was taken as the catch per unit effort (CPUE). The environmental variables ‘rainfall’, ‘river inflow’, ‘maximum temperature’, ‘minimum temperature’ and ‘fishing effort’ were all entered into a Generalized Linear Model to test which of the variables explained the variation in *L. miodon* catch and CPUE.

The relationship between catch and effort, based on the combined data from Zimbabwe and Zambia for the period 1974 – 2011 (Kinadjian 2012), was used to estimate maximum sustainable yield (MSY) using the Schaefer and Fox Surplus Yield models (Pitcher & Hart 1982):

\[ Y_e = U_\infty F - b F^2 \]  
\[ Y_e = F U_\infty e^{-F(q/k)} \]

where \( Y_e \) = yield or catches, \( F \) = fishing effort, \( U_\infty \) = CPUE at infinity; \( q \) = catchability coefficient; \( k \) = rate of increase of biomass, and \( b \) = a constant.

Effect of depth on *L. miodon*

Data from two projects carried out in the Sanyati Basin of Lake Kariba were used for this analysis. The first project was done in 2001 – 2002. Monthly samples, taken at depths of 2 to 55 m, were collected in November and December 2001, and in January, March, April, May and June 2002. Fish were caught at night on a fishing rig, using a 4-m diameter lift net of 8 mm stretched mesh size, lined with a 1-mm stretched mesh net. A site was sampled twice, first without light, to measure fish density, then with light. Three 2800 lumens (80W) mercury vapour light bulbs were used, of which two provided surface lighting and one was used for underwater lighting. The net was set for 30 minutes each time.

In the second project, done in March 2013, samples were taken at depths of between 20 and 55 m. Sampling was carried out for 10 days, using a commercial fishing rig with a net of 7.5 m diameter. Three light intensities, 2 800 (80 W), 11 500 (250 W) and 20 000 (400 W) lumens, were used for lighting, because the main objective of this study was to measure the effect of light intensity on catches. As in the 2001 - 2002 study, the fish were captured with and without light. When fishing without light, the net was set for 30 minutes as before but for 2 hours when using light.

Catch of each species from each setting was recorded in the field. About 200 g of *L. miodon* was subsampled and all the fish longer than 7 cm were selected for
determination of length, weight, mouth gape, body height, sex, gonad weight, number of eggs, stomach content and stomach content weight. The body height and mouth gape were measured using a vernier caliper. The mouth gape was measured in the dorso-ventral plane with the mouth fully open. Catches taken without light were used to calculate the density of the fish using the swept area method such that:

\[
\text{Fish density} = \frac{\text{Catch from one setting without light}}{\text{Area of net opening}}.
\]

The surface area of the net opening was 12.6 m² in 2001 – 2002, and 44.2 m² in 2013. This method of estimating biomass was also used by Cochrane (1978) and Marshall (1985) to estimate the density of *L. miodon* in Lake Kariba. Data was analysed using regression analysis to test the effect of depth gradient on fish length, catch and density.

**Quality and species composition of bycatch**

Records of *L. miodon* and *H. vittatus* catches, kept since the beginning of the pelagic fishery, were used to analyse the relationships between the *L. miodon* and *H. vittatus* catches. For the incidental catches that were not routinely recorded, catch data was obtained from fishing companies operating in the Mlibizi and Binga, Sengwa, Chalala and Sanyati basins on the Zimbabwean side of Lake Kariba (Figure 6.1) from April 1993 to June 1994. Additional data was obtained from experimental mid-water trawling in the Sanyati basin in June 1993. The trawl net was operated during the day between 10 and 30 m depth, shot 7 times and towed for 1 hour.

Daily landing of bycatch was recorded on specifically designed forms. The bycatch was split into the following groups for easy identification; *H. vittatus*, cichlids, *Synodontis* spp, *Schilbe intermedius*, *Brycinus lateralis* and others. A subsample was collected from commercial companies fishing in the Sanyati basin in June 1993, to determine species composition of the cichlid group and size of the fish.

**Results**

**Relationship between catches, fishing effort and environmental variables**

The total annual catches of *L. miodon* rose from the time the fishery started in 1974 to a peak in 1990, and thereafter declined steadily till 2011 (Figure 6.2a). Fishing effort increased throughout the whole period except from 1992 to 2000, when it was more or less constant. Catch per boat per night decreased throughout the whole period except for a more constant period between 1980 and 1990, suggesting a deterioration of conditions for the fish.

The MSY estimated from combined Zimbabwean and Zambian catch and effort data from 1974 to 2011, is 23 185 (Schaefer model) and 22 355 (Fox model) tons per annum, and the estimated effort \( (F_{msy}) \) used to catch the MSY is 10 867 (Schaefer) and 11 226 (Fox) boat nights (Figure 6.2b). The estimates of MSY and effort were...
Figure 6.2 Changes in the a) catch, fishing effort and CPUE and b) catch and effort regression in the \( L.\ miodon \) fishery of Lake Kariba. The regression lines are fitted with the Schaefer \( (R^2 = 0.79; \ p < 0.0001) \) and Fox \( (R^2 = 0.76; \ p < 0.0001) \) Surplus Yield models.

used to make inference on the sustainability of the fishery. The maximum fish landing of 30 000 tons of sardines were higher than the value of MSY.

To explore the potential cause of this, we related CPUE to temperature. The pattern in the CPUE mirrors that of mean maximum air temperature (Figure 6.3a). Regression
Figure 6.3 Relationship between CPUE and maximum temperature in the *L. miodon* fishery of Lake Kariba in a) trends in CPUE and temperature (1974 to 2011) b) regression of temperature and CPUE (fitted with an exponential model CPUE = 33.3380.6 exp(-0.04496 × temperature); \( R^2 = 0.80; p < 0.0001 \)).

Analysis confirms a strong statistically significant negative exponential relationship with the fitted function (Figure 6.3b). Both fishing effort and temperature explain a significant amount of the variation in CPUE (Table 6.1). In contrast, the total catch is correlated with total fishing effort and lake level but not with mean maximum air temperature (Table 6.1).
Table 6.1 The $\chi^2$ and $p$ values from the Generalized Linear Model testing the relationship between fishing effort, rainfall, lake level, mean maximum and minimum air temperature and both catch and CPUE.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Catch Wald $\chi^2$</th>
<th>$p$</th>
<th>CPUE Wald $\chi^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>16.54</td>
<td>0.000</td>
<td>8.34</td>
<td>0.004</td>
</tr>
<tr>
<td>Fishing effort</td>
<td>37.11</td>
<td>0.000</td>
<td>15.84</td>
<td>0.000</td>
</tr>
<tr>
<td>Rainfall</td>
<td>1.63</td>
<td>0.200</td>
<td>2.00</td>
<td>0.160</td>
</tr>
<tr>
<td>Lake level</td>
<td>15.95</td>
<td>0.001</td>
<td>3.83</td>
<td>0.051</td>
</tr>
<tr>
<td>Maximum temperature</td>
<td>3.23</td>
<td>0.072</td>
<td>14.87</td>
<td>0.000</td>
</tr>
</tbody>
</table>

Depth distribution of fish

Estimates of fish density were $24.8 \pm 12.2$ and $38.8 \pm 6.2$ kg/ha for 2001 – 2002 ($\geq 20$ m; pelagic) and 2013, respectively. The 10-day survey carried out in March 2013 showed a depth gradient in the catches of all species. The catch per set of *L. miodon* ($R^2 = 0.191$; $F = 8.99$; $p = 0.0048$, *H. vittatus* ($R^2 = 0.136$), and *Synodontis* spp ($R^2 = 0.139$), and the catch without light of *L. miodon* ($R^2 = 0.145$) were highest in shallower water ($< 30$ m) compared to deep water ($> 40$ m), even though the amount of variation explained by a linear relationship with depth was rather low ($p < 0.05$, Regression analysis; $n = 40$) (Figure 6.4). The other species, which included *Tilapia rendalli*, *O. niloticus*, a 1.25 kg *O. mortimeri*, and small cichlid species, were caught only at Site 1 ($< 30$ m deep).

Samples from the period November 2001 to June 2002 showed variations in mean fish length and catch size with depth (Figure 6.5). Figure 6.5a-b shows that the mean length increased significantly with depth, both in samples taken without ($R^2 = 0.276$; $F = 10.29$; $p = 0.003$; $n = 30$; regression analysis) and with light attraction ($R^2 = 0.313$; $F = 12.78$; $p = 0.001$; $n = 30$; regression analysis). The mean size of fish taken using light attraction ($3.5 \pm 1.73$ cm) was significantly larger than that of fish taken without light ($2.29 \pm 1.37$ cm) ($F = 6.99$; $p = 0.011$; $n = 59$; ANOVA). Large fish ($> 10$ cm) were present especially when fishing with light.

Figure 6.5a-b shows that the minimal mean length of fish increased stronger with depth than the maximum mean length. A similar increase in the size of the smallest fish was also found in the samples taken in March 2013. This means that larger fish also went deeper, whilst smaller fish remained shallower. Fish of all sizes could be found in the shallow area, though the small fish ($< 2$ cm) were restricted to the shallow area ($< 20$ m deep). Monthly variations in the trends were observed. There is no clear pattern of catch with depth, though catches are always low at the shallowest sites and highest at medium depths (Figure 6.5c-d).
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Figure 6.4 Changes in catch per set of a) *L. miodon* catch in the dark, b) *L. miodon* catch with light, c) *H. vittatus* and d) *Synodontis*, along the depth gradient in March 2013 (fitted with linear regression line).

Figure 6.5 Depth and a) the mean length of fish caught with light b) mean length of fish caught without light c) caught with light d) catch without light.
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Figure 6.6 Length frequency distribution of the bulk of the catch, the large specimen and fish found in the stomachs of 5.9 to 10.5 cm long fish (diet fish) from experimental fishing in March 2014.

Catches from Site 1 in March 2013 included some large fish between 8 and 12 cm total length, though the bulk of the catch were between 2.5 and 6.5 cm with a mode at 4 cm (Figure 6.6). Most of the large fish had food in the stomach and all of them had eaten small sardines (1.9 to 3.0 cm total length) (Figures 6.6 and 6.7a). The ingestible size range for large sardines of a given length is determined by the ratio of mouth gape over body height as a function of fish length. The body-height increase with increasing length is larger than that of the mouth gape (Figure 6.7b). Considering the size of their mouth gape, the large *L. miodon* had eaten *L. miodon* smaller than they potentially could swallow. The large fish that could be sexed, were all sexually active, judged from their enlarged gonads as well as the size of the eggs in females. Gonad size increased exponentially with body size in females, but there was no significant trend in males (Figure 6.7c). The relationship between female gonad size and fish length is given by the function: Gonad weight (g) = 0.0066 exp (0.3825 × fish length (cm)) ($R^2 = 0.336; p = 0.0047; n = 22$). The number of eggs increased exponentially with female size (Figure 6.8) and can be expressed by the function: Number of eggs = 199.0030 exp (0.0344 × fish length (mm)) ($R^2 = 0.6755; F = 158.1882; p = 0.0000; n = 77$). The size of fish caught in the fishery is much smaller than the fish that had the highest fecundity expressed by the number of eggs.

*Relationship between pelagic H. vittatus and L. miodon*

When the fishery began in 1974, the CPUE of *H. vittatus* was high and rose to a peak in 1977, but subsequently fell together with the CPUE of *L miodon* (Figure 6.9a). The relationship between CPUE of *H. vittatus* and *L. miodon* can be described by a power relationship in the function: tigerfish CPUE = 0.0862 × sardine CPUE $^{3.7845}$ ($R^2 = 0.65; p < 0.001; df = 37$), illustrated in the logarithmic plot (Figure 6.9b).
Figure 6.7 The relationships between the length of *L. miodon* caught in March 2013 and a) weight of *L. miodon* found in their stomachs b) mouth gape and body height c) gonad weight for females and males and d) weight.

Figure 6.8 The relationship between the number of eggs and the size of *L. miodon* caught in the Sanyati basin of Lake Kariba. Size range and modal length caught in the commercial fishery are represented by the shaded area and the vertical line, respectively.
Figure 6.9 The relationship between a) *L. miodon* and *H. vittatus* (pelagic and inshore) CPUE (tons/boat/night) from 1974 to 2011, b) regression of logarithmic scale (base 10): *L. miodon* and pelagic *H. vittatus* CPUE (kg/boat/night).
Quality and species composition of bycatch

The survey covered all basins of Lake Kariba and 26 out of 62 Zimbabwean fishing companies participated. Catches of the sardine fishery contained very small quantities (0.32%) of other species. From May 1993 to June 1994, 69.2 tons of bycatch were landed compared to 21,370 tons of *L. miodon*. Bycatch was also small compared to catches from the inshore fishery, where 1,281 and 987 tons were landed in 1993 and 1994, respectively.

Of the total bycatch, 93.8% comprised of 3 fish species, *Schilbe intermedius* (42.2%), *H. vittatus* (37.1%) and *Brycinus lateralis* (14.5%) by weight. Catches of cichlids (2.0%) and *Synodontis* spp (4.2%) were low. The cichlid group consisted of *Pharyngochromis acuticeps*, *Pseudocrenilabrus philander*, *Serranochromis macrocephalus*, *Tilapia rendalli* and *Oreochromis mortimeri*. *Synodontis* species caught were *Synodontis zambezensis* and *Synodontis nebulosus*. Negligible quantities of *Serranochromis robustus*, *Labeo altivelis* and *Mormyrops deliciosus* were also caught.

In the bycatch from the experimental mid-water trawling, only three species were caught: *S. zambezensis*, *S. nebulosus* and *P. acuticeps*. They constituted 2.47% of the total catch. In the March 2013 survey, the bycatch was 0.85% (14.0 kg) of the total fish catch. Most of the bycatch was *H. vittatus* (86.1%), and the rest was *Synodontis* spp (5.3%) and cichlids (8.6%).

The bycatch consists of small fish of species that make up the bulk of the inshore fishery catch, but also a portion that do not. Two of the important species in the bycatch, *S. intermedius* and *B. lateralis*, are not caught in the gill-net fishery because of their small size. The cichlid group also includes smaller species that are not exploited in the inshore gillnet fishery. The inshore fishery species caught in measurable amounts in the bycatch were *H. vittatus* and the cichlids *S. macrocephalus*, *T. rendalli* and *O. mortimeri*. Of these, only *H. vittatus* was caught in relatively large amounts. The catches of *H. vittatus* in the sardine fishery were 7.6% and 8.9% of the gill-net fishery in 1993 and 1994, respectively.

The mean sizes of fish caught in the sardine fishery were small compared to those from the inshore gill-nets (Table 6.2). Because of the small size of the cichlids in the bycatch, their quantity in numbers may be of larger significance than the weight may portray. Using the species composition to partition the cichlid bycatch, the estimated numbers of *T. rendalli*, *O. mortimeri* and *S. macrocephalus* caught during the survey in the whole lake were 41,327, 98,129, and 27,677, respectively. The overall picture masks the temporal and spatial differences that can be important to management. There are spatial variations in the quantity and species composition of the bycatch (Table 6.3). The Sengwa basin had the lowest CPUE, Binga and Mlibizi basins the highest.
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**Table 6.2** Mean weight (g) of individual specimens from incidental catch in Kariba, the gill-net fishery, and the maximum size caught in Lake Kariba (Kenmuir 1983).

<table>
<thead>
<tr>
<th>Species</th>
<th>Incidental (g)</th>
<th>Gill net (g)</th>
<th>Maximum (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. vittatus</em></td>
<td>92.2</td>
<td>1 970.8</td>
<td>15 500</td>
</tr>
<tr>
<td><em>O. mortimeri</em></td>
<td>4.4</td>
<td>664.1</td>
<td>3 500</td>
</tr>
<tr>
<td><em>S. macrocephalus</em></td>
<td>10.2</td>
<td>370.9</td>
<td>1 500</td>
</tr>
<tr>
<td><em>T. rendalli</em></td>
<td>7.3</td>
<td>658.8</td>
<td>2 100</td>
</tr>
<tr>
<td><em>P. acuticeps</em></td>
<td>3.1</td>
<td>Nil</td>
<td>23</td>
</tr>
<tr>
<td><em>P. philander</em></td>
<td>2.1</td>
<td>Nil</td>
<td>8</td>
</tr>
<tr>
<td><em>B. lateralis</em></td>
<td>2.6</td>
<td>Nil</td>
<td>11.9</td>
</tr>
<tr>
<td><em>S. zambezensis</em></td>
<td>28.0</td>
<td>no record</td>
<td>900</td>
</tr>
<tr>
<td><em>S. nebulosus</em></td>
<td>3.4</td>
<td>no record</td>
<td>90</td>
</tr>
<tr>
<td><em>S. intermedius</em></td>
<td>no record</td>
<td>no record</td>
<td>770</td>
</tr>
</tbody>
</table>

**Table 6.3** The estimated catches (metric tons) from the sardine fishery by species and basins from May 1993 to June 1994.

<table>
<thead>
<tr>
<th>Species</th>
<th>Binga &amp; Mlibizi</th>
<th>Sengwa</th>
<th>Chalala</th>
<th>Sanyati</th>
<th>Total (tons)</th>
<th>Corrected total</th>
<th>% in bycatch</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. vittatus</em></td>
<td>5.08</td>
<td>1.77</td>
<td>2.40</td>
<td>16.42</td>
<td>25.67</td>
<td>22.1</td>
<td>31.1</td>
</tr>
<tr>
<td><em>S. intermedius</em></td>
<td>0.59</td>
<td>0.01</td>
<td>13.79</td>
<td>14.79</td>
<td>29.18</td>
<td>25.1</td>
<td>42.2</td>
</tr>
<tr>
<td><em>B. lateralis</em></td>
<td>2.21</td>
<td>0.00</td>
<td>2.40</td>
<td>5.46</td>
<td>10.07</td>
<td>8.7</td>
<td>14.5</td>
</tr>
<tr>
<td><em>Cichlids</em></td>
<td>0.26</td>
<td>0.04</td>
<td>0.86</td>
<td>0.23</td>
<td>1.38</td>
<td>1.2</td>
<td>2.0</td>
</tr>
<tr>
<td><em>Synodontis spp</em></td>
<td>0.40</td>
<td>0.02</td>
<td>1.00</td>
<td>1.49</td>
<td>2.91</td>
<td>2.5</td>
<td>4.2</td>
</tr>
<tr>
<td><em>L. miodon</em></td>
<td>2377.03</td>
<td>2048.14</td>
<td>7579.33</td>
<td>12838.74</td>
<td>24843.24</td>
<td>21369.9</td>
<td></td>
</tr>
<tr>
<td><strong>Total catch</strong></td>
<td>2379.89</td>
<td>2048.20</td>
<td>7583.59</td>
<td>12845.92</td>
<td>24857.60</td>
<td>21429.4</td>
<td></td>
</tr>
<tr>
<td><strong>Bycatch</strong></td>
<td>8.53</td>
<td>1.84</td>
<td>20.45</td>
<td>38.39</td>
<td>69.21</td>
<td>59.5</td>
<td></td>
</tr>
<tr>
<td><strong>% in bycatch</strong></td>
<td>0.36</td>
<td>0.09</td>
<td>0.27</td>
<td>0.30</td>
<td>0.28</td>
<td>0.28</td>
<td></td>
</tr>
</tbody>
</table>

**Discussion**

We found that the initial increase in catch of *L. miodon* in Lake Kariba, could not be sustained after 1990 and the CPUE decreased throughout the whole period, reducing profitability. Increased temperatures were associated with the decline of CPUE (as an indicator of stocks), indicating declining ecologically favourable conditions for *L. miodon*, especially in the first two decades of the study (1970 – 1980; Figure 6.2). Fishing effort that subsequently increased strongly (1980 – 1990), was another factor
strongly affecting CPUE, and fishing effort beyond $F_{\text{msy}}$ may have caused the collapse of the sardine fishery. *Hydrocynus vittatus* responded to the decrease in sardine CPUE. Catches and CPUE of *H. vittatus* were high when the sardine fishery started, then decreased simultaneously with sardine CPUE. *Hydrocynus vittatus* and other inshore fish species also utilize the deep pelagic water and were caught in the pelagic fishery as incidental or bycatch. *Limnothrissa miodon* occurred in high numbers and biomass in all depth zones and fish size increased with depth, with juveniles confined to inshore areas. However, the largest specimens of *L. miodon* were caught below 30 m depth, overlapping with the conspecific juveniles they fed upon. These large fish have a higher fecundity compared to the size caught in the fishery.

**Spatial distribution of *L. miodon***

Different stages of fish are often spatially segregated to limit intraspecific completion and predation (Persson *et al.* 2000). For example, in Lake Kivu juvenile *L. miodon* (1.0 – 3.5 cm in length) were always caught in the margins, fish of 3.0 – 7.0 cm in the littoral and inshore areas, and the next larger size class (6.5 – 9.0 cm) in pelagic waters. Sardines of 8.5 – 11.0 cm were caught in all zones except the lake margins, whilst large fish (10.0 – 15.0 cm) were mainly caught in the margins (de Iongh *et al.* 1983; Spliethoff 1983). The sardines from the pelagic waters fed exclusively on plankton, whereas those in the inshore area fed on a mixture of plankton, a relatively large fraction of chironomid pupae, and juvenile clupeids. The largest sardines (> 100 mm, total length) were cannibals, just like in our study, and lived near the margins (de Iongh & Spliethoff 1983). In Lake Tanganyika, the larvae of *L. miodon* were predominantly present near the shore, immigrating towards sandy shores as they became larger (Tshibangu & Kinoshita 1995). The small pelagic cyprinid *Rastrineobola argentea* from Lake Victoria displays a similar behaviour of using the inshore areas for spawning and as a nursery area (Wanink 1999). This study confirms earlier studies showing that juvenile *Limnothrissa miodon* are always confined to the lake margins (Cochrane 1978), and reports that the large (> 8 cm) adults in Lake Kariba seem to utilize both the pelagic and the marginal shallow areas. This size distribution might partly explain the general scarcity of the largest size group in the deep waters. Comparable habitat segregation was found in 1+, 2+, and 3+ year old Eurasian Perch, *Perca fluviatilis* in Lake Abborrtjärn 3 in central Sweden. Year classes are segregated according to diet, with the planktivorous youngest in offshore and the oldest carnivores predominantly in the inshore area, where they feed entirely on macroinvertebrates (Persson *et al.* 2000). Absence of the large fish from the pelagic may be a consequence of their lower foraging efficiency compared to the smaller fish. Persson (1987) found that one year old and 1+ perch have a higher capture rate and a lower handling time than the two years old and 2+ perch. This means that the smaller fish have competitive advantage when feeding on pelagic zooplankton.
These mechanisms observed in other species, may be driving the segregation of the size classes in Lake Kariba and other lakes in which the sardine occurs.

Cannibalism of large individual fish on conspecific juveniles can be of ecological importance and can affect the dynamics of fish populations (van den Bosch & Gabriel 1997; Claessen et al. 2000; de Roos et al. 2003). Cannibalism of juveniles by large (> 8 cm) *L. miodon* was observed in Lake Kariba by Begg (1974). Other fish species, like *Haplochromis philander* and *Barbus* sp, have also been ingested. In Lake Kivu, large (> 10 cm) *L. miodon* were cannibalistic (de Iongh 1983). Cannibalism observed in large fish that were caught in deep water (> 30 m), is a normal feeding strategy of *L. miodon*. This suggests that the large fish migrate to the shallow area to feed on juveniles, which may not be necessarily their own species. This is probably a necessary diet shift to compensate for changes in energetic demands, due to somatic growth (Werner & Gilliam 1984). Cochrane (1984) suggests that fish in the pelagic area would be too large to be eaten by these large sardines. This idea is supported by our study on mouth gape and body height. The inshore movement of cannibalistic *L. miodon* is necessary to find suitably sized prey to optimize the energetic needs.

Cannibalism may have consequences on the population dynamics by controlling recruitment pulses. For example, the densities of perch ≥ 2 years old in the pelagic area determined the intensity of cannibalism on the one-year-old fish that inhabit the pelagic area (Persson et al. 2000). In lakes where the cannibal sized perch were reduced by a top predator (pike, *Esox lucius*), the abundance of the small perch (young-of-the-year and 1-year-old) were more abundant than in lakes were perch occurred alone. This suggests that cannibalism controlled the abundance of the small perch (Wahlström et al. 2000), which can have a stabilizing effect on the fish population (van den Bosch & Gabriel 1997; Claessen et al. 2000). Evolution might favour cannibalism because of the survival advantages in terms of provision of energy that can be directed to population growth through reproduction. Persson et al. (2000) observed that after a die-off that affected mostly the large fish, the surviving cannibalistic individuals gained substantial energy from cannibalism in years with strong recruitments, which increased both growth rate and per capita fecundity. Hence, the energy gained by the cannibals may be essential for the recovery of the population, as this energy is allocated into new recruits (van den Bosch et al. 1988; Persson et al. 2000). In the case of the sardines in Lake Kariba, the larger individuals that survive by cannibalism would benefit the population by being more fecund, which might increase recruitment.

*Interaction between Hydrocynus vittatus and its prey L. miodon*

The interactions between the sardines and tigerfish in Lake Kariba confirm that variation in the prey population affects the ecosystem (Marshall 1987b; Bakan et al. 2000; Smith et al. 2011; Essington et al. 2015). Removal of the prey through overfishing alters the abundance and composition of upwelling pelagic communities
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(Curry et al. 2000). The initial rise in *H. vittatus* catches in Lake Kariba, when the sardine fishery developed, seems to be typical of new reservoirs. For example, the increase of Nile perch (*Lates niloticus*) and *H. vittatus* in Lake Kainji (Nigeria) and Lake Volta (Ghana), and that of pike (*Esox lucius*) in Cimljansk Lake due to the abundance of prey species (Lelek & El Zarka 1973). Fishing removes sardines from the ecosystem, denying tigerfish this resource and causing a reduction in the number of predators in deep waters. Generally, the inshore tigerfish seem to be unaffected by the reduction in pelagic sardines because they utilize alternative prey, even though *L. miodon* remains an important prey item (Mhlanga 2003). Hence the decline in the sardine caused the decline of the pelagic tigerfish, which became more restricted to the inshore area where they supplement their sardine diet with alternative prey.

Quality and species composition of incidental catch

Our results provide several additional insights on the importance of bycatch of the *L. miodon* fishery. The species caught as bycatch are mostly those species that favour deep water, they are either planktivores or piscivores. *Hydrocynus vittatus* and *Brycinus lateraris* are known to inhabit pelagic waters, and both species were caught in the initial experimental fishing for *L. miodon* (Balon 1971; Woodward 1974). One of the species in the bycatch was *Schilbe intermedius*. This small catfish is common in the inshore areas of Lake Victoria, but it was also found in the pelagic zone (Witte & van Densen 1995). The species is also common in the inshore areas of Lake Kariba but there has been no record of its occurrence in the open water (Kenmuir 1984; Sanyanga et al. 1995). The abundance of *Synodontis zambezensis* in the catches increased with depth, with the highest catch per unit effort at the maximum depth range sampled (12 – 20 m) between 1990 and 1993 (Sanyanga 1996). In Lake Kariba, *Pharyngochromis acuticeps* occurs in deep water and on both shelving and steep, eroding shores with no vegetation (Hustler & Marshall 1990; Mudenda 1992). *Oreochromis mortimeri, B. lateralis, P. acuticeps, Pseudocrenilabrus philander* and juvenile *Serranochromis macrocephalus* are all plankton feeders (Mhlanga 2000; Zengeya & Marshall 2007). Similarly, planktivorous juvenile European perch, *Perca fluviatilis* (8 – 19 mm) are predominant in the pelagic zone of an Australian reservoir, Lake Humme, where also planktivorous Australian smelt (*Retropinna semoni*) and climbing galaxid (*Galaxias brevipinnis*) occur (Matveev et al. 2002). Clearly, planktivorous and carnivorous fish species in Lake Kariba venture into deep water for feeding, where they are caught in the sardine fishery. Capture of non-target fish species, or bycatch, can have impacts on the ecosystem (Crowder & Murawski 1998). In Lake Kariba, the harvest of juveniles of other species in the sardine fishery is a potential problem. Though the sizes of fish caught in the sardine fishery are smaller than those caught in the inshore area, and the yield was also small, comprising 0.32% of the sardine catch by weight. Only in the trial trawl catches was it higher (2.47%). A large proportion (60.9%) of the bycatch consisted of *S. intermedius* (42.2%), *B.
lateralis (14.5%), and Synodontis spp (4.2%), species that are not important at all in the gillnet fishery. Hence, their capture in the sardine fishery can only be beneficial. Only a small proportion of the bycatch are cichlids, most of which are small species that are too small to be exploited in the gill net fishery. Hence, the bycatch had little impact on the inshore fishery through the capture of juvenile fish. The quantity of the bycatch is small, demonstrating that the current management of the Lake Kariba sardine fishery, that restricts fishing depth to water deeper than 20 m, limits the catch of non-target species.

Effect of fishing effort and environmental variables on catches
Various environmental changes can be responsible for the observed CPUE (as an indicator of the ecologically suitability of the lake) for L. miodon. Previous studies found that air temperature, rainfall and river flow were associated with catches of L. miodon in Lake Kariba (Marshall 1982; Chifamba 2000; Magadza 2010). Variation of L. miodon catches in Lake Kariba was found to be correlated to river inflow, with years of drought associated with low catches (Marshall 1982, 1988b). Maximum air temperature had the highest correlation with CPUE of L. miodon compared to other hydrological factors namely, rainfall, river flow and lake level (Chifamba 2000). The current analysis, using a much longer time series, shows that air temperature still accounts for the highest variation of L. miodon catches, with low temperatures associated with high catches, especially early in the study. In addition, rivers bring nutrients into the lake and temperature is important for internal cycling of these nutrients. Lake Kariba is monomictic and is stratified most of the year, during which time the epilimnion becomes depleted of nutrients and of oxygen. Turn-over occurs during winter, often in July. Then, nutrients from the hypolimnion become available in the photic zone. Hence, turn-over, rainfall and river mouths are associated with increased zooplankton production (Magadza 1980 Masundire 1989). Production cycles in Lake Kariba are thus driven mostly by temperature, causing a high correlation with sardine CPUE.

Temperature change can affect fish populations by modifying their environment and food resource (Beaugrand et al. 2003; Cohen et al. 2016). Rising temperature in Lake Kariba is thought to have caused changes in the plankton community, timing of stratification and the depth of the epilimnion (Magadza 2010; Mahere et al. 2014). Magadza (2011) observed that the phytoplankton in the lake is now dominated by Cyanophyceae, particularly Cylindrospermum raciborskii. This author also noticed that the breakpoints in the relationships of the sardine catch with air temperature and lake temperature were at 34.8 and 28.7 °C, respectively, occurring in 1987 – 1988. This was just before the peak catch in Zimbabwe in 1990. A similar consequence of warming was found in Lake Tanganyika, where warming has reduced water circulation and hence nutrient concentrations in the hypolimnion (Verburg 2003; O’Reilly et al. 2003). This is also found over longer time spans: an analysis of fish
fossils and temperature in Lake Tanganyika revealed a negative relationship between temperature and both fish and mollusc production in the last ∼150 years, which was associated with a decrease in diatom abundance, resulting from sustained warming during that period (Cohen et al. 2016).

Environmental factors are expected to affect fish populations through their effect on life history parameters (Gutiérrez et al. 2007; Takasuka et al. 2007; Itoh et al. 2009; Pörtner & Peck 2010). Beaugrand et al. (2003) reported that rising temperature induced changes in the occurrence of plankton species, and led to higher mortality rates in cod larvae, thus lowering recruitment. Effects of temperature could arise from a shift away from the optimum temperature for growth, as shown in the Japanese anchovy (Engraulis japonicus) and Japanese sardine (Sardinops melanostictus) larvae in the western North Pacific (Takasuka et al. 2007). A difference in the optimum temperature for growth of these two species is behind the shifts in the fishery between a warm anchovy regime and a cool sardine one. Small pelagic fish species (such as L. miodon with a life span of < 3 years; Chapter 7) are particularly vulnerable and react rapidly to environmental fluctuations and global change because of their short life span (Cury & Roy 1989). Hence, environmental change may explain part of the change in CPUE of the sardines in Lake Kariba. An understanding of how this factor affects CPUE is crucial in making decisions on how to manage the fishery to avoid overfishing.

**Implication to management of the fishery**

Overfishing has caused the collapse of fisheries worldwide (Walters & Maguire 1996; Botsford 1997; Marshall 2012a; Watson 2013) At the time of its collapse, the Lake Kariba sardine harvest was within the range of the estimated potential yield and above the classic model estimates of MSY. Using a baseline lake where the species forms a successful fishery as a ‘predictor of ecology’, Pitcher (1995) estimated a potential yield of about 5.5 t km$^{-2}$ (range: 5 – 6.75 t km$^{-2}$), amounting to an annual yield of 27 000 – 36 000 t of sardines for Lake Kariba. Our MSY estimates from the Schaefer and the Fox models were 23 185 and 22 355 tons per annum, with an optimum effort $F_{msy}$ of 10 867 and 11 226 boat nights, respectively. One major shortcoming of using the classic models is that the MSY is estimated in retrospect. Therefore, other methods of estimating sustainable catches are strongly recommended. A management system that recognizes a catch limit based on the lake productivity, and that incorporates the variations in the fish abundance caused by environmental changes, would improve catches and profitability.

Changes in CPUE do not always reflect fish density, due to changes in fish catchability arising from environmental change, fish behaviour and technology creep, or changes in the efficiency of fishing vessels (Chifamba 1995; Rose & Kulka 2011; Marriott 2011). Shoaling fish are particularly vulnerable to capture even at
low fish density, because fishers can search for, and locate the fish shoals (MacCall 1975; Salthaug & Aanes 2003). A stable CPUE may also occur when fishing vessels concentrate on fish aggregates that have become confined to a smaller area (Rose & Kulka 2011; Kraus et al. 2015). Changes in fishing power of fishing vessels, or technology creep, can also change CPUE (Chifamba 1995). For example, an increased use of echo sounders for locating fish, radios for communicating and the replacement of mechanical with hydraulic winches for lifting sardine fishing nets, has increased the fishing efficiency of boats in Lake Kariba (Chifamba 1995). Another example of technology improvement that affected CPUE is the introduction of skewed hooks and swivel line in the haddock (Melanogrammus aeglefinus) and Atlantic cod (Gadus morhua) longline fisheries off the Faroe Islands resulted in an increase in catch per unit effort by about 51% and 26%, respectively (Eigaard et al. 2011). Hence, reliance on CPUE as a measure of fish density will introduce errors in judging the impact of fishing. Better methods of measuring fish abundance should be used in the long-term monitoring of sardine abundance.

Estimation of biomass of pelagic fish, using hydroacoustic surveys and other methods such as the swept area method, provides information on the fish stock (Jurvelius 1996; Nøttestad et al. 2014). Our study provides some estimates of L. miodon density in the Sanyati basin of Lake Kariba (24.8 and 38.8 kg/ha in 2001 – 2002 and 2013, respectively) that can be compared to those from earlier studies. The earliest estimates in the Sanyati basin were made in January (8.9 kg/ha) and April (23.1 kg/ha) 1976 (Cochrane 1978). These are lower than the estimates in our study. Estimates from a more comprehensive survey of the Sanyati basin by Marshall (1988a) were 90.5, 48.1 and 38.7 kg/ha in 1981, 1982 and 1983, respectively. Except for 1983, these values are higher than those in our study. Sanyati basin biomass estimates from a lake-wide hydroacoustic survey in September 1988 were between 16 and 44 kg/ha (Lindem 1988). Lake-wide surveys by Ngalande (1995) yielded 25.3, 35.4, 7.6 and 7.6 kg/ha in January 1992, November 1993, January 1994 and July 1994, respectively, for the Sanyati basin. Another lake-wide survey in August 2014 found approximately 60 kg/ha in the Sanyati basin (Mafuca 2014). These surveys showed temporal as well as within-and-among lake-basin variation in fish densities in Lake Kariba. Most density estimates for L. miodon in Lake Kariba are higher than the value of 23 kg/ha that was reported for Lake Kivu, a natural lake into which the species has been introduced (Guillard et al. 2012). Different methods used in making the estimates, and lack of continuous records of sardine densities make it impossible to determine long-term trends. Therefore, there is a need for extensive continuous surveys in order to understand the contribution of changes in sardine abundance on the fluctuations of the catches in Lake Kariba.

A reduced stock has implications for the sustainability of the fishery, resulting from reduced spawning stock biomass and recruitment. Daskalov (1999), reported a correlation between the recruitment of whiting (Merlangius merlangus) and anchovy
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(Engraulis encrasicolus) in the Black Sea, with stock biomass and the physical environment. Removal of large fish, which produce more eggs of better quality, may reduce recruitment (Birkeland & Dayton 2005; Arlinghaus et al. 2010). Fishing can also cause the evolution of traits, when the vulnerability to capture is positively correlated with fitness traits such as intensity of parental care, as reported for largemouth bass (Micropterus salmoides) by Sutter et al. (2012). In Lake Kariba, the heavy exploitation of small size sardines (< 7 cm) therefore may reduce the reproductive potential through having a small spawning stock biomass and a small number of large fish. This possible connection between heavy exploitation of the small fish and fecundity needs to be investigated further, for us to understand the mechanisms operating in the Lake Kariba sardine fish stock and its interactions with fishing.

Fisheries often collapse as a result of the combined pressures from fishing and the environment, which are difficult to separate (Ruiz et al. 2009). Our study is another example of this phenomenon. Therefore, the effects of both fishing and the environment on the catches should be incorporated in the management of a fishery, to avoid overfishing. There are many aspects of the sardine biology and ecology that we need to understand better before we will be able to soundly predict the environmental effects, particularly those of temperature, on the sardine abundance in Lake Kariba. Abundance and recruitment should be monitored and used to estimate total allowable catches, as is done in closely managed fisheries such as the anchovy fishery in South Africa (Cochrane & Hutchings 1995). A better understanding of the ecosystem production of Lake Kariba is essential, as it will inform us of the limits on fish catch to ensure sustainability and long-term profitability.

Acknowledgements

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*Limnothrissa miodon*: a large specimen was caught eating a small conspecific. The small fish was removed to compare the sizes.