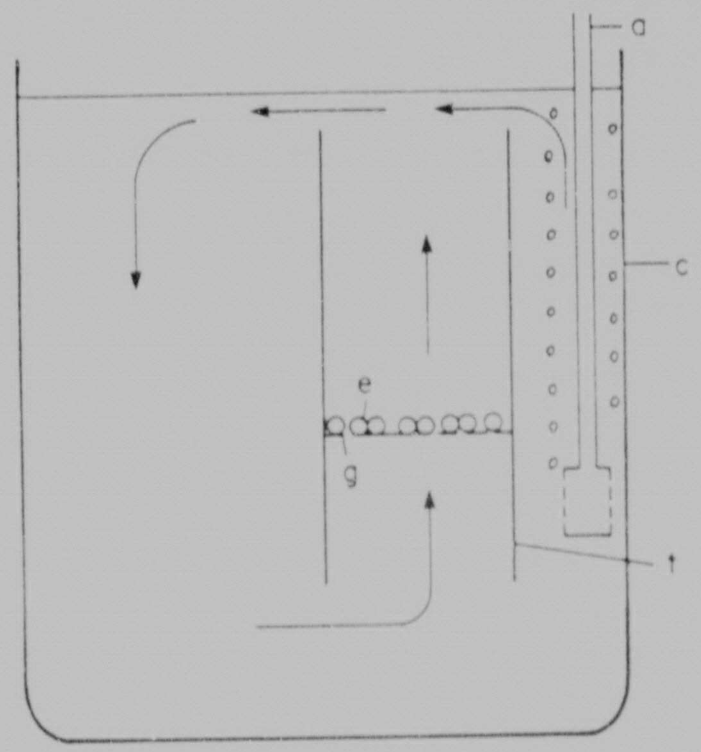

Fig. 6.2. Apparatus used for rearing O. *mossambicus* eggs in the laboratory. a = aerator, c = 5 ℓ container, e = eggs, g = mosquito gauze, t = 5 cm diameter PVC tube. Arrows indicate approximate direction of water flow induced by aeration.

Table 6.2. Mean number of eggs per gram and standard error from randomly selected examples of *O. mossambicus*, *C. carpio* and *C. gariepinus* ovaries. In each case six sub-samples were taken, for *O. mossambicus* each sub-sample weighed approximately 0.5 g and for the other two species approximately 0.25 g . % SE = standard error as a percentage of the mean.

SPECIES								
O. mossambicus			*C. carpio*			*C. gariepinus*		
Mean eggs.g^{-1}	SE	%SE	Mean eggs.g^{-1}	SE	%SE	Mean eggs.g^{-1}	SE	%SE
275.3	4.31	1.6	2089	13.20	0.6	779.9	26.15	3.4
310.3	3.66	1.2	2046	14.20	0.7	665.8	15.20	2.3
299.0	4.67	1.6	1735	25.72	1.5	577.6	11.53	2.0
285.9	4.23	1.5	1697	26.52	1.6	840.6	12.81	1.5
287.0	10.04	3.5	967	14.40	1.5	828.6	27.85	3.4

larvae from each brood was measured every two days. There was little within-sample variance and five lengths yielded a standard error of less than 3% of the mean. Only three replicates could be undertaken as mouth-brooding females could not be obtained in February and March 1984, after the initial trial. A sample of 189 females collected on the 17th March 1984 did not contain a single mouth-brooding fish.

The percentage of females mouth-brooding was determined from samples obtained with a seine net in October and November 1982. Fish caught in gill nets were found to spit out fry and eggs and could not be used.

6.2.3 Mortality

Total mortality of an exploited fish population is made up of losses due to fishing and losses due to all other causes such as predation and disease. This may be described as,

Total mortality = Fishing mortality rate + natural mortality rate

which in turn may be expressed as (Ricker, 1975):

$$A = u + v$$

where A = annual expectation of mortality

u = expectation of capture by man

v = expectation of natural death

or, $Z = F + M$

where Z = instantaneous rate of total mortality

F = instantaneous rate of fishing mortality

M = instantaneous rate of natural mortality.

Independent estimates of M are rare and are generally obtained during periods of negligible fishing mortality (Cushing, 1981). The most common method of separating F and M is by relating total mortality to changes in fishing effort. A plot of total mortality on fishing effort results in a linear relationship with the y-intercept providing an estimate of natural mortality (Gulland, 1983). Implicit in this method are the assumptions, usually made in mortality estimates (Robson & Spangler, 1978), that F is proportional to fishing effort and that M is constant over time. These assumptions are major limitations and a major problem associated with the use of the relationship $Z = F + M$ is that F and M are related to each other but the functional form of the dependence is not known (Robson & Spangler, 1978). Cushing (1981) stated that precise separation of F and M remains inaccessible and is one of the central problems in fisheries research.

In this study, the assumption that M and v remain constant with time was made and the rates were derived from knowledge of the total and fishing mortality rates. This assumption should hold for the range of conditions, particularly the rate of exploitation, measured during the study but changes in natural mortality rate could be anticipated if there were major increases or reductions in fishing pressure.

A further problem associated with determination of natural mortality is changes in natural mortality with increasing age. In general, death rate is greatest in the juvenile stages, lowest in early and middle adulthood and increases with old age (Cushing, 1981). Increased mortality with old age has been ascribed to decreased relative cruising speed with age, resulting from increased water resistance and changes in muscle structure in larger and older fish, which decreases feeding efficiency and increases the risk of predation (Cushing, 1981). It has also been suggested that older fish are more susceptible to disease (Gulland, 1983). However, there is little evidence of fish dying of old age (Gulland, 1983) and predation is probably the major component of natural mortality (Cushing, 1981).

In Hartbeespoort Dam, adult fish of the three major species are not exposed to predation as there are no large predators in the system (Section 6.4.3). In addition moderate to severe fishing mortality prevented significant numbers of fish reaching an age at which senescence is likely (Section 6.3.3.3). Therefore the lives of the three species were divided into two stages, the first year or part of the first year, when natural mortality is high (Section 6.2.3.4) and the older stages when natural mortality is lower and assumed to remain constant for all age classes and over time. It is again probable that a large reduction in fishing effort could invalidate the assumption of constant natural mortality for all older age classes of a given species, as the potential life span of the population would increase and the older fish could suffer higher natural mortality.

6.2.3.1 Fishing mortality

In calculating fishing mortality it was necessary to calculate the mean catch per unit effort by anglers and the total number of anglers using the dam.

The Division of Nature Conservation (DNC) has a voluntary angling return system operating at two of their recreational sites, Oberon and Kommandonek (Fig. 2.1). Anglers weigh their catches on departure and record and return the total number and mass of each species caught. Individual fish masses are not recorded. From these returns the total number of anglers reflected on returns and the total number and mass of each species caught per month were obtained and this permitted the calculation of a mean catch per unit effort (CPUE) per month.

Only a small percentage of anglers filled in survey forms and hence an estimate of total number of anglers had to be obtained. Monthly figures on the total number of visitors to the sites at Oberon and Kommandonek were obtainable from the DNC. In order to extrapolate these figures to the entire lake, the relationship between the sum of anglers at the two sites, and the total number of anglers on the lake per day was determined by undertaking five angler counts. These were performed from a boat on five separate occasions, covering conditions from peak usage on a public-holiday in mid-summer to a minimum on a Tuesday in winter.

It was frequently difficult to determine who was actually angling as many fisherman left their rods unattended, thus the number of rods with lines in the water was counted. Wherever people were clearly engaged in angling, the number of fisherman and the number of rods were counted, which permitted the calculation of a mean number of rods per fisherman. The legal limit in the Transvaal was two rods per fisherman. Rod counts were recorded for the recreational sites at Oberon and Kommandonek and for the total lake. A plot of the sum of the rods for Oberon and Kommandonek against the total rods in the lake produced a linear relationship of the form

$$y = 67.78 + 3.35\,x \quad (n=5,\ r^2 = 0.97)$$

where y = number of rods in the whole lake per day

x = number of rods at Oberon and Kommandonek

The mean number of rods per fisherman over the period was 1.49 (2SE=0.04). Hofmeyr (1978) reported that at least 90% of the visitors to DNC sites went there for angling. Therefore the total number of anglers per month was calculated as follows,

(a) the number of visitors to Oberon and Kommandonek was multiplied by 0.9 to estimate the number who were fishing, and divided by the days in the month to obtain a mean number per day

(b) the result from (a) was multiplied by 1.49 to estimate the number of rods

(c) the result from (b) was substituted into the regression equation to calculate the total number of rods per day

(d) the total number of rods per day was multiplied by the number of days in the month and divided by 1.49 to estimate the number of anglers per month.

Hofmeyr (1978) pointed out that some visitors stayed at the dam overnight but did not estimate the proportion who did this. The assumption was made that this proportion was negligible. Therefore the CPUE obtained from the DNC was assumed to be catch per angler day and the calculated total number of anglers to be the number of angler days per month spent at the dam. These two figures were used to calculate the total monthly catch.

The biomass estimates obtained in Section 5.3 and the mean annual catch were used to calculate u (rate of exploitation) and F was derived from the formula (Ricker, 1975),

$u = FA/Z$

where F = instantaneous rate of fishing mortality

A = annual expectation of death

Z = instantaneous rate of total mortality

The nature of the DNC returns prevented determination of age or size at recruitment to the population susceptible to angling of the three species. Therefore an appeal was made through a South African magazine, Tight Lines/Stywe Lyne, for angling returns to be completed by enthusiastic, regular anglers on Hartbeespoort Dam (Cochrane, 1983). Respondents were provided with forms and encouraged to complete these as thoroughly and regularly as was possible. The response was poor with returns being submitted on behalf of 19 anglers with varying frequency, but sufficient data were obtained to assess age at recruitment and angler selectivity. Respondents provided individual masses of their catches and these were converted to standard length and age from the relationships and growth curves given in Section 4.2 and

Section 6.3.1. Returns were obtained from August to December 1983 after which no further returns were received despite repeated contact with the respondents.

6.2.3.2 Total mortality

Youngs and Robson (1978) list three general methods for estimating survival in freshwater fish populations.

(a) The survival rate derived from the ratio of the number of fish at the end of a time period to the number which were alive at the beginning. It is assumed that the group is closed except for mortality.

(b) The Chapman-Robson method which can be used when recruitment and survival are relatively constant and the population may be assumed to be stable on an annual basis. The method requires unbiased estimates of age class frequencies up to, at least, some age greater than the first fully recruited age.

(c) A tag-recapture method which requires several years marking-recapture data with serially numbered tags.

Different methods were used to determine adult mortality (and hence survival) for the three species. Mortality rates in *O. mossambicus* and *C. carpio* are based on the first general method of Youngs and Robson but, as the frequency and confidence limits of standing stock estimates were not suitable, CPUE was used as an estimate of abundance. The CPUE of *C. gariepinus* in both research and angling catches was low and therefore a modification of the Chapman-Robson method, using length (age) frequency and assuming a stable population, was used.

The *O. mossambicus* population experiences variable winter mortality of 0+ fish thus the age class structure does not remain constant from year to year and varied considerably over the period studied (Section 6.3.3.5). Angler catches gave the larger return but, as they were obtained as monthly totals, could not be broken up into age-classes and no portion of the population could be identified and considered closed to recruitment. Therefore CPUE of the research gill net fleet was used as a measure of change in *O. mossambicus* abundance. The catch was split into two classes, recruits from spawning in the summer of 1981/82 and recruits from earlier spawnings. The second class was used to determine adult mortality. It consisted of fish spawned in the seasons from 1975/76 to 1977/78 (Table 6.28). The intermediate age classes were absent as a result of winter mortality in their first year (Section 6.3.3.5). The mean CPUE for each month was calculated from gill net catches from Stations 4, 16 and 17. The marked changes in water level would have influenced density of the fish population and thus the CPUE was corrected by multiplying actual CPUE by the proportion of full supply volume for each month (Section 5.2.2b). An exponential relationship of the form,

$$\text{CPUE} = a\,e^{bt}$$

where a and b are fitted constants
t = time in months,

was fitted to the data.

The best fit line was then used to calculate total mortality over one year.

The same method was used for carp but, in the absence of suitable gill netting data, the TPA angler returns were used to calculate monthly CPUE. *C. carpio* did not spawn in the summer of 1982/83 and the fry spawned in November 1981/82 were considered fully recruited to the population susceptible to angling by March 1982 (Section 5.2). Therefore the population could be considered closed except to mortality from March 1982 to March 1984. Effort dropped to very low levels in winter 1982 (Table 6.17) and the CPUE for this period was considered unreliable. Rising water levels and the establishment of large stands of aquatic vegetation in the summer of 1983/84 (Section 2.0) would have influenced catchability of *C. carpio*. Therefore CPUE over the period March 1982 to April 1983 inclusive was used to determine total mortality. An exponential relationship was fitted to the data, as for *O. mossambicus*, corrected for volume.

Analyses of the length frequency structure of the *C. gariepinus* population, as determined from mark and recapture samples, were used to estimate mortality under the assumption of uniform recruitment over the time period represented by the sample. The length frequencies of the samples did not show clear age class peaks, even when separated according to sex. This prevented the splitting up of the sample into age classes by graphical methods or the statistical breaking up of the polymodal curve into its constituent normal distributions. Therefore discriminant analysis was used. From the data used for growth rate determination, the mean and variance of length at age of *C. gariepinus* was calculated, separately for males and females. Using this information the fish of known length and unknown age were classified into age classes using the formula (Fatti *et al.*, 1982):

$$V_i(x) \quad = \quad x(x_i/S_p^2) - 0.5\,(x_i^2/S_p^2) + \ln\,(P_i)$$

where x = standard length of the fish (cm)

$V_i(x)$ = discriminant function

x_i = mean length of age group i years

S_p = pooled variance

P_i = estimated proportion of the population in the i th age group

$V_i(x)$ was calculated for each age group for each fish of known length and the fish was assigned to the age class for which $V_i(x)$ was the greatest. P_i was held constant and the same for all age groups and the analysis was done iteratively, recalculating x_i and S_p after each iteration until there was no further change in the number of fish allocated to each age class. The analysis was undertaken by a FORTRAN V programme written by the author (Appendix 1). The results of the analysis yielded numbers of fish in each age class and the fully recruited age classes were then used to calculate total mortality using Heincke's estimate (Ricker, 1975).

$$A = N_o/N$$

where A = annual expectation of death

N_o = frequency of fully recruited age class

N = sum of frequencies of all age classes older than and including N_o.

6.2.3.3 Natural mortality

Estimates of Z and F were made (Section 6.2.3.1 and 6.2.3.2) and this permitted the derivation of M, the natural mortality. This was obtained directly from the relationship,

$$Z = F + M \text{ (Ricker, 1975)}$$

assuming constant M (Section 6.2.3)

The annual expectation of natural death, v, was computed from

$$v = MA/Z$$

6.2.3.4 0+ mortality

Mortality in the early stages of life is usually very high and small changes can lead to a severe total effect (Bagenal & Braum, 1978). Backiel and Le Cren (1978) stated that density dependent mortality in the early stages of life has the major impact on variations in production.

(a) Methods of determination

C. carpio young of the year were assumed to be vulnerable to fishing mortality when they had reached a mass of 150 g which occurred at an age of six months (Section 5.2.2 and Table 6.18). In contrast *O. mossambicus* reached a mass of approximately 25 g after one year and *C. gariepinus* a mass of approximately 125 g . Therefore the assumption was made that no fishing mortality occurred in the first year for these two species.

O. mossambicus in Hartbeespoort Dam spawned continuously from October to March and the fry were easily captured. Therefore 0+ mortality was studied in this species by fitting catch curves to length frequencies of samples (Ricker, 1975) obtained from January to April in 1982-1984. From a knowledge of the growth rate during the first six months of life, the length data were converted to age frequencies and thus the survival rate obtained. Three such curves were calculated for each year and a mean survival rate obtained.

The young of the year of *C. carpio* and *C. gariepinus* were rarely caught by seine or gill nets and no information on changes in abundance during the first year could be obtained. Therefore the total mortality rate during this year was obtained from a Leslie matrix (Emlen, 1973; Vaughan & Saila, 1976) using age specific mortality and fecundity data (Table 6.3). This method relies on the assumption of a stable population and therefore the accuracy or validity of the estimates of survival in the first year are dependent on the fecundity and survival data being representative of long term trends. It is possible that total mortality was abnormally high during the study period due to increased fishing mortality resulting from the drought (Section 6.4.3). This would result in an overestimate of first year survival. The validity of the results obtained using the Leslie matrix are assessed in Sections 6.4.3 and 7.3.3.

The longevity of both species was taken as a maximum of ten years (Table 6.3). The survival rates used in the Leslie matrices would reduce the age class strength at one year old by 99.95% after four years (*C. carpio*) and 95% after ten years (*C. gariepinus*).

A second approximation of 0+ mortality rates was obtained from the results of the littoral poisoning undertaken in January 1984 and estimates of the population fecundity (Section 5.3.2 and Section 6.3.2 respectively). The population estimates obtained from littoral poisoning were based on three samples and were thus only approximate but the mortality rates so obtained provided a means of checking the first estimates, particularly those obtained using the Leslie matrix.

Table 6.3. Parameter estimates (Section 6.3.2 and 6.3.3.3) used in construction of Leslie matrices for the determination of 0+ mortality in a) *C. carpio* and b) *C. gariepinus* in Hartbeespoort Dam

	a) *C. carpio*		b) *C. gariepinus*	
Year class	M_x	P_x	M_x	P_x
1	64144	0.15	0	0.91
2	329015	0.15	22958	0.89
3	602521	0.15	47907	0.85
4	788244	0.15	77662	0.85
5	895390	0.15	108668	0.80
6	953013	0.15	138604	0.72
7	982506	0.15	167166	0.72
8	997498	0.15	191537	0.61
9	1005358	0.15	213062	0.61
10	1009001	0.15	230021	0.61

where M_x = age specific fecundity of individual of age x
P_x = probability of individual of age x surviving to age x + 1

(b) Density dependent mortality in the first year

The problem of density dependence in fish stocks has been widely discussed (Ricker, 1975; Backiel & Le Cren, 1978; Cushing, 1981). It is a concept which should be included in any model attempting to predict fish yields under different harvesting pressures but is still poorly understood. The greatest problem in determining density dependent effects is separating the influence of density dependence from that of environmental changes in observed data (Ricker, 1975).

Density dependence is inherent in the logistic population growth curve, in which a population will tend to increase towards a maximum biomass or carrying capacity (Ricker, 1975) and this curve has been widely used by fisheries biologists (Ricker, 1975). In its simplest form there is no need to understand the regulation mechanism and a parabolic curve is simply fitted to observed relationships, such as yield and stock (Ricker, 1975). A greater knowledge of the density dependent mechanism is implicit in the use of stock:recruit relationships

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a) $R = a\,Pe^{-bP}$

b) $R = 1/(a+b/P)$

where a and b are constants

P = size of parental stock

R = number of recruits

According to Ricker (1975) the former relationship is more applicable when cannibalism plays a significant role in regulation, when increased density delays the time necessary for fish to grow through a vulnerable stage or when there is a time lag in the response of predators or parasites to the abundance of fish. The latter is more appropriate when available food is the limiting factor or when the response of predators or parasites to changes in fish abundance is immediate.

The mechanisms causing density dependent production include the response of mortality and growth to density. A third possible mechanism is a change in fecundity but this is considered to be of minor importance in relation to growth and mortality in density dependent mechanisms (Cushing, 1981). Backiel and Le Cren (1978) stated that the life span of a fish could be divided into 2 stages

a) the early stages when mortality responds to changes in density and growth responses can be ignored and

b) later stages when mortality changes can be ignored but growth varies with density.

However, they also state that variations in growth rate are likely to be insignificant in relation to the impact of variations in survival rates. The major impact of growth rates on population size is a decrease in growth rate increasing the period of maximum vulnerability (Ricker, 1975; Backiel and Le Cren, 1978; Cushing, 1981) and thus it will be manifested in higher mortality.

In view of the recognised importance of juvenile mortality to population size, it was decided to incorporate density dependence into the yield models of Hartbeespoort Dam in the form of density dependent mortality in juveniles.

Shepherd (1982) has suggested a single curve which can have the characteristics of either the Ricker or Beverton and Holt curves, depending on the selection of parameters. The suggested curve is

R = $aP/(1 + (P/K)^b)$ where R and P as previously defined

a = constant, representing the slope of the curve at the origin

b = constant, expressing the degree of compensation involved. Therefore $b = 1$ has exact compensation

K = threshold biomass, biomass above which density dependent effects dominate

Shepherd states that in the common absence of sufficient data to determine the constants, their value should be assumed and then K determined to fit the predicted to observed data. He suggested, for example, that b should normally lie between 0.5 and 2, and be greater than 1 only when cannibalism is significant.

The use of the above curve is still, essentially, empirical and is best fitted to a number of years observed data, which are not available for Hartbeespoort Dam. In addition, the curve incorporates both growth and loss from the population. In the yield models for Hartbeespoort Dam, growth, in numbers and mass, and mortality are computed directly and what was required was a relationship which would permit the incorporation of density dependence in the models. For this purpose, the Shepherd (1982) curve was rearranged.

The relationship of Shepherd (1982) can be split into a growth and a loss component,

$$\ln R = \ln (aP) - \ln(1+(P/K)^b)$$

aP = gross recruitment = number of recruits at time 0 (R_o),

R = net recruitment = number of recruits at time 1 (R_1),

$S = R_1/R_o$

Therefore, from the equation of Shepherd (1982),

$$R_1 = R_o/(1 + (P/K)^b)$$

Therefore $S = 1/(1+(P/K)^b)$

This relationship, incorporating biomass and the constants K and b, was used to simulate density dependent mortality in the Hartbeespoort Dam yield models. Values of b were selected for each species on the basis of qualitative knowledge of regulation of the species in Hartbeespoort Dam and K determined so as to fit observed values of S and P.

6.2.3.5 Winter mortality of 0+ *O. mossambicus*

O. mossambicus is known to be sensitive to prolonged exposure to temperatures below approximately 13°C (Allanson *et al.*, 1962) and cold-induced mortality has been recorded from several localities in Natal, the Transvaal and Eastern Cape (Cochrane, 1984). Cold-induced mortality was observed on Hartbeespoort Dam in 1981 and resulted in the almost complete extinction of the 0+ year class of the 1980/81 spawning season (Cochrane, 1984). Mortality was also observed in June/July of 1982, 1983 and 1984 but to a less severe degree. The obvious importance of this source of mortality to potential yield from the population necessitated its incorporation into the yield models. Therefore, the frequency and extent of winter mortality in the population was investigated.

In June/July 1982 an attempt was made to estimate, directly, the number of fish killed over the period.

In 1982 the first reports of winter mortality were received on the 29th June and a survey was undertaken on the following two days. Seventeen sites around the shoreline were sampled and the number of dead fish at each site estimated by undertaking six transects of 12 - 15 metres along the water's edge at each site. Where visibility was good enough transects were also made from the shore into the water, at right angles to the shoreline. Dead fish were counted in a band 1.5 m wide from the shore to the point at which fish on the bottom could no longer be seen. The maximum depth at which fish could still be seen was usually approximately one metre but counts were frequently prevented by the presence of *Microcystis aeruginosa* scums.

A further sampling trip was made on the 7th July and it was apparent that more fish had died. Where the density of fish was too great to use transects, the number of fish in 20 - 30 circular quadrats of 0.082 m^2 at each locality were counted. Twenty random measurements of the width of the band of dead fish at the high fish-density sites were also made which permitted the calculation of number of fish per metre of shoreline. Further transects were made to determine the number of submerged dead fish. Statistical examination of the results did not show a decrease in the number with increasing depth. However, both dead and live fish were concentrated in certain littoral areas where they were associated with *Microcystis* scums. This was due to the fish, in a chill coma, being blown by the wind and accumulating on leeward shores. Therefore the assumption was made that, at each locality, submerged fish were randomly distributed in the littoral zone, and the total of the number of fish on the shore and the number submerged in water up to two metres deep were calculated per metre of shore at each site. Four sites were sampled on this occasion.

Comatose live fish were caught with a seine net at several localities. The fish were inactive and total mass caught was used as an estimate of biomass. The area seined was calculated, total mass of fish caught determined and a sub-sample of fish taken. Length and mass of fish in the sub-sample were subsequently measured.

On the 13th and 20th July sampling trips were undertaken but there had been no more deaths.

This method gave an estimate of the number of dead fish washed ashore which could be used as an indicator of the relative severity of winter kills over a number of years. However, the method as a whole was considered impractical because,

(a) while a large number of dead fish were washed ashore, the number sinking to the bottom could not be accurately determined

(b) the period of mortality on this occasion ultimately extended over two weeks but there was no means of predicting when it would cease, which would have necessitated extensive field work and required continuous monitoring. This effort was not justified in view of the potential errors described in a).

The winter mortality of 0+ *O. mossambicus* was monitored in 1983. A max/min thermometer was located near Station 17 (Fig. 2.1) 10 cm below the water surface and read weekly. At first there was no indication of mortality despite low temperatures. However, in August 1982 large numbers of *O. mossambicus* fry were observed beneath a thick algal scum at the dam-wall. On the 17-08-83 samples were taken from the lake-bottom, beneath the scum, with a van Veen grab. Dead fish were collected in these samples, indicating that mortality had taken place. However, the number of dead fish trapped in the scum, which was up to 0.75 m thick (Segev pers. comm.), and the number of dead and comatose fish which had been carried out through the canal outflows could not be estimated. The increased difficulties associated with direct estimation of the extent of mortality experienced in 1983 confirmed that monitoring of the strength of the one year age class provided the more practical means of determining the severity of the previous winter mortality. The association of comatose fish with a *Microcystis* scum again in 1983 demonstrated that the sites of accumulation of fish are determined by wind-induced currents.

No historical record of temperatures in the lake existed but meteorological data were obtained from a site 15 km north of the dam. This provided daily maximum and minimum air-temperatures from 1968 and these data were used to determine the probable frequency of severe *O. mossambicus* mortality in Hartbeespoort Dam.

6.3 Results

6.3.1 Growth rates

(a) *O. mossambicus*

The results for time of ring formation in this species showed some variation. In 1981, when sampling started, the *O. mossambicus* population consisted mainly of fish with six or more scale rings (Fig. 6.3) with the other age classes absent as a result of winter mortality (Cochrane, 1984 and Fig. 6.19). The number of marginal circuli in scales with more than two rings were recorded and analysed, but data from younger fish was not included as this would have resulted in large variability, as a result of the faster growth rate, and hence larger number of marginal circuli, in younger fish. Analysis of marginal circuli showed two clear minima, in April and October 1982 (Fig. 6.4), showing that rings were formed at this time, co-inciding with the end of spawning (March/April) when rapid growth would occur, and a further growth spurt (September/October) when temperatures rose and prior to the onset of breeding. The marginal circuli counts in the older fish did not show clear trends after November 1982 as the fish approached their growth asymptote and growth became very slow.

The year classes spawned in 1981782 and 82/83 could be identified on the basis of length, and times of ring formation were observed in these classes. The former class formed rings in August/September in 1982 and 1983. None of the fish observed in this age class formed rings in March/April 1983 or 1984. Similarly the 1982/83 year class formed their first ring in August/September 1983 and did not form a ring in the following March/April. Therefore it is suggested that *O. mossambicus* in Hartbeespoort Dam form one ring per year, at the beginning of summer, until they reach full sexual maturity when two rings are formed per year. However, the age of full sexual maturity varies according to population density (Section 6.3.2) and this would influence the age at which two rings are formed and hence the relationship between the number of rings and age. During this study a second ring was not formed in a single year in fish less than three

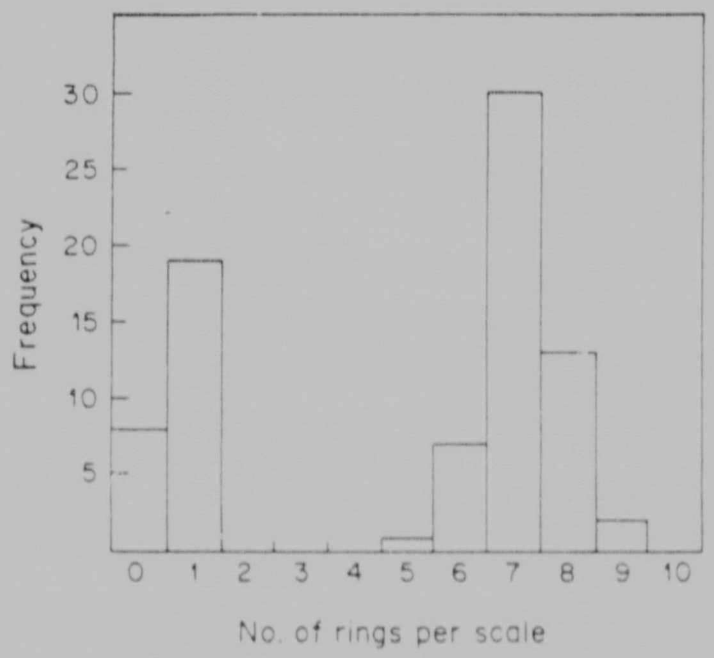

Fig. 6.3. *O. mossambicus* scale ring frequency (October to December 1981). n = 80.

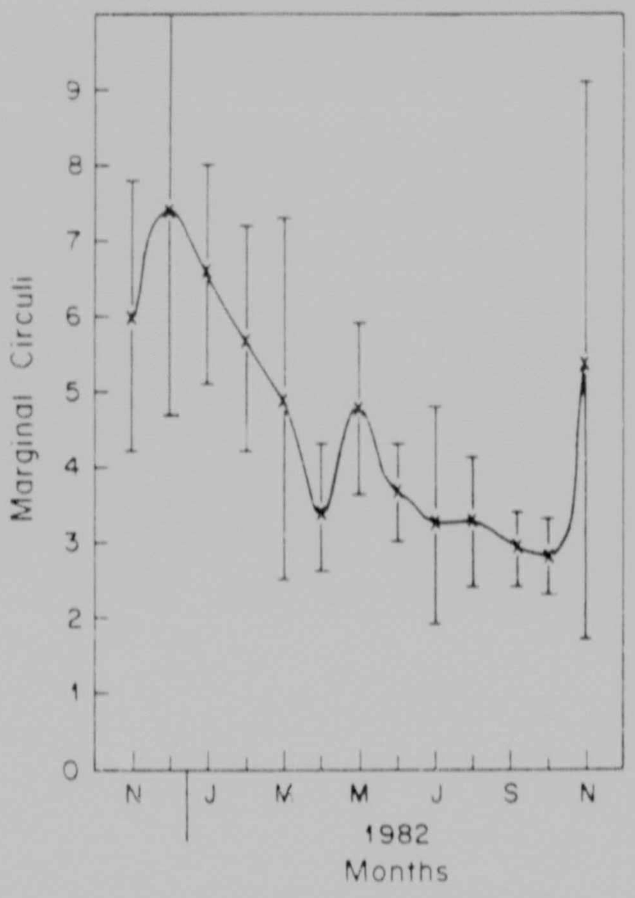

Fig. 6.4. Mean number of marginal circuli per *O. mossambicus* scale with six or more rings (November 1981 to November 1982). Bar = 95% CI.

years old. Therefore the following relationship between number of scale rings and age was used;

Number of rings	Age
0	0+
1	1+
2	2+
3	3+ (September)
4	3+ (March/April)
5	4+ (September)
6	4+ (March/April)
etc	

where the transition from one age group to the next is assumed to occur in September, with the onset of summer.

The relationship between standard length and scale radius was computed from all scales read and combined for both sexes. The relationship was,

$$SL = 1.70 + 42.58\ SR \quad (n=656,\ r^2=0.94)$$

where SL = standard length (cm)

SR = scale radius (cm)

The y-intercept of 1.70 was then used in the calculation of the length of each fish at the time of each ring formation and the mean length at formation of each ring calculated for the complete sample of each sex (Table 6.4).

Table 6.4. The age and standard length of *O. mossambicus* at the time of scale ring formation with 95% confidence limits (CI) of length and the annual growth increment derived from standard lengths

Scale ring	Age	Male			Female		
	(yr)	SL(cm)	95% CI	Incr(cm)	SL(cm)	95%CI	Incr(cm)
1	1	8.90	8.61- 9.20	10.23	9.03	8.80- 9.26	8.85
2	2	19.13	18.52-19.73	4.52	17.88	17.59-18.17	4.95
3	3	23.65	22.75-24.55	5.39	22.83	22.63-23.03	3.51
5	4	29.04	28.18-29.91	3.16	26.34	26.16-26.53	1.70
7	5	32.20	31.33-33.06	1.60	28.04	27.87-28.22	1.16
9	6	33.80	31.21-36.38	-	29.20	28.86-29.55	-

A von Bertalanffy growth curve was fitted to the above data and the resulting equations were

a) Males $l_t = 37.19\ (1 - e^{-0.42(t - 0.36)})$

b) Females $l_t = 30.86\ (1 - e^{-0.51(t - 0.30)})$

where l_t = standard length at age t years

Predictions of length at age from these equations corresponded closely to the observed data (Fig. 6.5).

The growth of *O. mossambicus* recruits in the three summers studied showed clear differences (Fig. 6.6). The growth rate of the 1982/83 recruits, when the lake level was low and aquatic vegetation was absent, was lower than the other two year classes. Even after two summers, the mean length of this class was less than that of the 1981/82 class at the same age. The 1983/84 class showed the same mean growth rate, after six months, as that of the 1981/82 group, despite much higher densities occurring in their first summer. The high populations of emergent and submerged macrophytes, supporting high epiphytic populations, probably resulted in the rapid growth rate. These differences in growth in the first year demonstrate the variability which occurs as a result of environmental change.

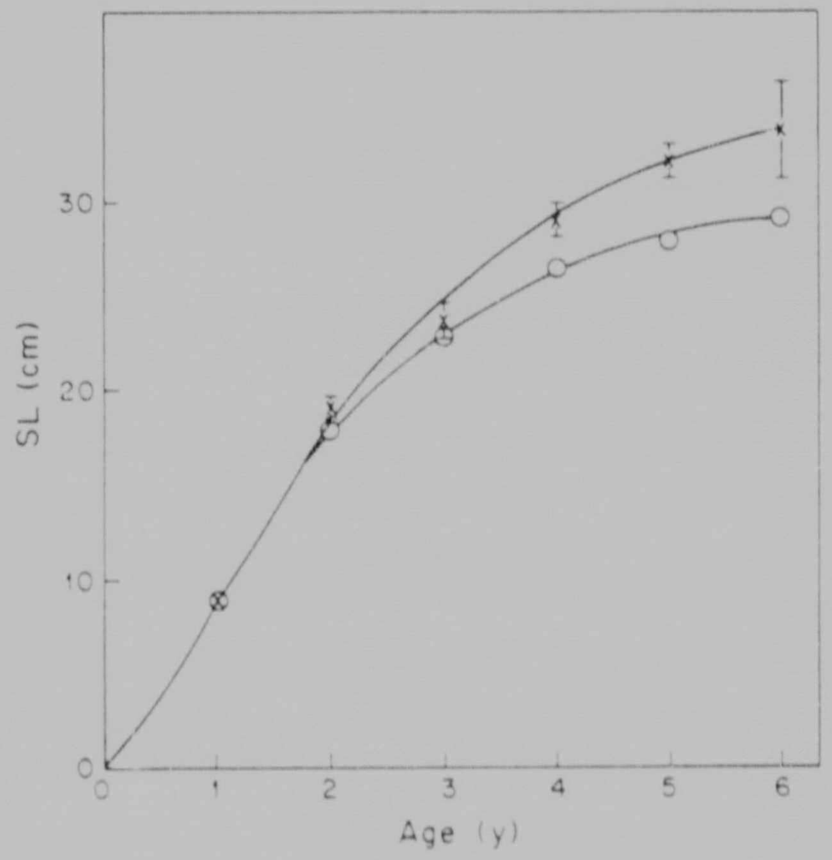

Fig. 6.5. Length at age and fitted growth curves of male (x) and female (o) *O. mossambicus*. ⊢⊣ = 95% CI of male length at age. In all cases female 95% CI fell within point marker (o).

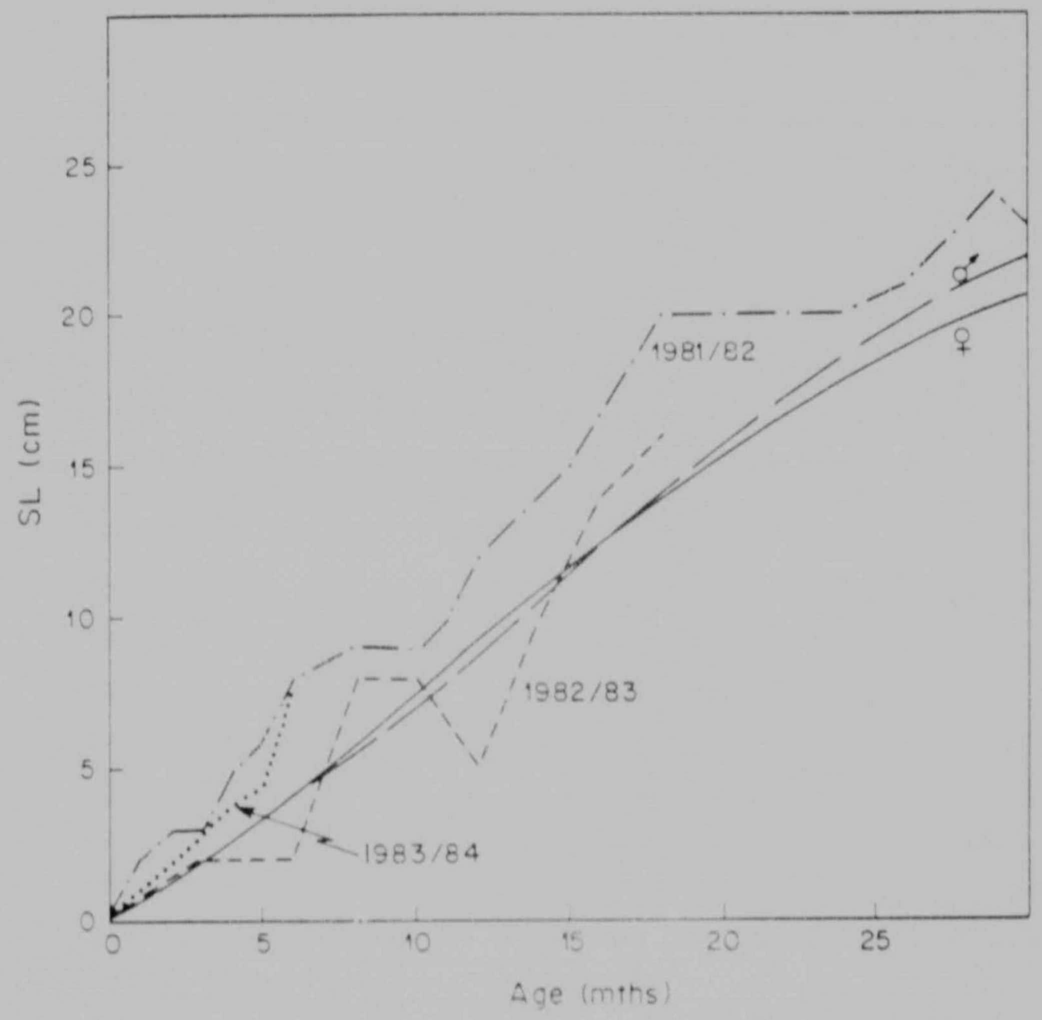

Fig. 6.6. Growth of *O. mossambicus* spawned in 1981/82, 1982/83 and 1983/84, up to April 1984, as shown by modes of length frequencies. ♂ = male growth curve and ♀ = female growth curve as determined from scales.

The growth curves calculated from scales underestimated the growth rates determined by Petersen analysis for the first two years for the 1981/82 recruits, but approximated the length achieved by them after 2.5 years (Fig. 6.6). The length predicted from the growth curve underestimated the observed lengths in this age class at 2.5 years by only 4% (males) and 10% (females). This shows that the hypothesis formulated on the time of ring formation resulted in the derivation of realistic growth curves which could be used to model the potential yield.

(b) *C. carpio*

i) Preliminary growth curve from the Petersen method.

Time of ring formation on carp vertebrae could not be determined by examination of mean marginal width and the Petersen method had to be used (Section 6.2.1b). The three samples obtained during the initial survey and October/November mark and recapture exercises were used and normal distributions fitted to the polymodal length frequencies (Fig. 6.7). The differences between the predicted and observed frequencies were significant in all cases (Table 6.5), as a result of differences in growth rate between male and female. This difference meant that the age class length frequencies were in fact bimodal but it was felt that the potential errors in separating two similar normal distributions for each age class, and the resulting reduction in sample size, would decrease the accuracy of this method. Therefore, the curves fitted to total age class were used to estimate age class mode.

The age class represented by a particular mode was determined strictly by counting from the left hand side of the distribution. The shift in mode from one year to the next in the three samples was then determined (Fig. 6.7) which gave an estimate of annual increment. The two peaks at 55 and 58 cm in the 1983 sample were not included as these age classes had not been well represented in the previous two samples.

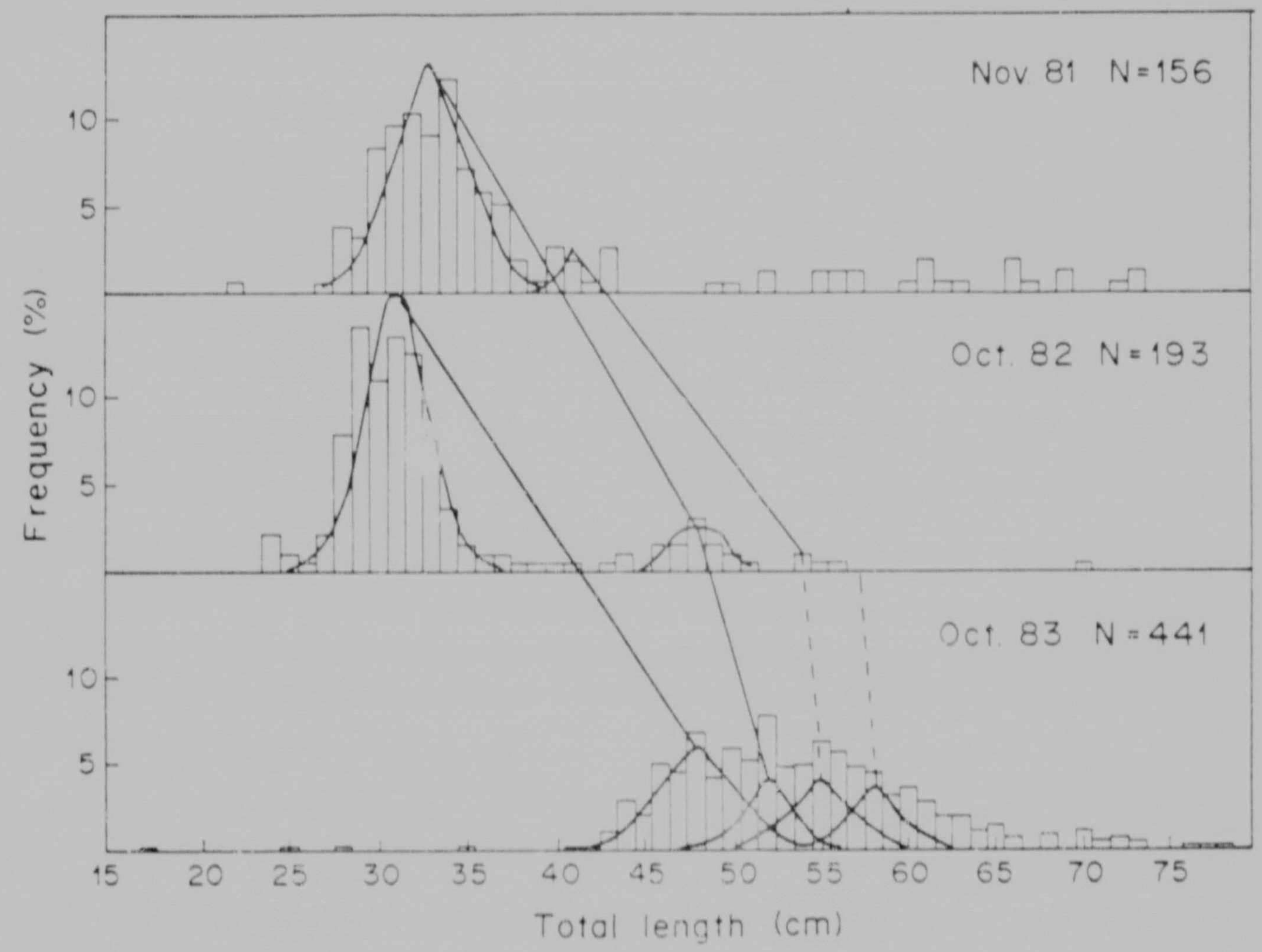

Fig. 6.7. Length frequencies of *C. carpio* with fitted normal distributions to indicate age classes within samples taken in November 1981 and October 1982 and 1983. Lines linking modes in successive years show growth in length for different age classes.

Table 6.5. Modes and goodness of fit of normal distributions fitted to observed length frequencies of *C. carpio*.

Date of sample	Mode(s) (cm)	n	Chi-squared	Significance
Nov. 1981	33.5; 41.5	11	26.5	> 0.001
Nov. 1982	31.5	11	19.4	> 0.025
Oct. 1982	48.5	5	2.05	> 0.50
Oct. 1983	48.5; 52.5; 55.5; 58.5	19	15.57	> 0.50

The total length (TL) data were converted to standard length (SL) from the calculated relationship,

$$TL = 0.64 + 1.09SL \quad (n=27,\ r^2=1.0)$$

and the initial length : annual increment data were used to calculate a von Bertalanffy growth curve. The relationship between these two parameters was,

$$\text{Increment} = 29.6 - 0.53(IL) \ (r^2=0.97,\ n=6)$$

where IL = initial length

and the growth equation

$$l_t = 55.81\ (1 - e^{-0.76\ (t - 0.02)})$$

where l_t = standard length at age t years

The estimated asymptotic length of 55.8 cm was less than the observed maximum length of greater than 75 cm total length or 68 cm standard length (Fig. 6.7) indicating some error in the fitting of normal distributions or assigning age classes to the normal distributions to calculate the growth increment. The latter could have been done by a more subjective assignment of age classes, but this was considered to be equivalent to seeking those points which would best produce the desired result. The curve was therefore used in its calculated form.

(ii) Verification and use of vertebral growth rings.

The relationship between standard length and vertebral radius was described by the equation -

$$SL = 15.53 + 55.43\ VR\ (n=102,\ r^2 = 0.87)$$

where SL = standard length (cm)
VR = vertebral radius (cm)

The intercept, 15.53, was used as a correction factor in the equation to calculate standard length at time of ring formation (Section 6.2.1(a)). The mean length at the time of ring formation was computed for the combined sample of male and female *C. carpio* and, using the above growth equation and assuming spawning at the beginning of November, the month each ring was formed was estimated (Table 6.6).

Table 6.6. Mean length at time of vertebral ring formation in a combined sample of male and female *C. carpio*, and the age and month of ring formation computed from the length frequency derived growth curve. Month of formation assumes spawning at the beginning of November

Ring	Standard length (cm)	n	95% CI	Age (mths)	Month of formation
1	27.68	102	26.79-28.58	11	October
2	40.69	83	39.38-42.00	21	August
3	45.78	60	44.51-47.05	27	February
4	49.45	45	48.03-50.90	35	October
5	51.63	41	50.18-53.07	41	April
6	53.12	33	51.58-54.66	48	November
7	54.23	24	52.49-55.97	57	July

After the seventh ring, confidence limits became too broad for meaningful predictions of age. The first and second rings were formed at the beginning of summer, at approximately one and two years of age respectively (Table 6.6). Thereafter, two rings were formed per year, at the beginning and end of summer. Rings in skeletal structures are formed at times of slow growth (Quick & Bruton, 1984). The early summer growth check would be a result of utilisation of energy and food for formation of gametes and for spawning.

The late summer growth check coincided with turnover of the lake in March or April and thus could be related to food stress induced by decreased food availability, resulting from the rising oxycline prior to over-turn, or by environmental stress at and following over-turn when oxygen concentrations can become very low (Robarts *et al.*, 1982).

The first, second, fourth, sixth etc. rings therefore coincide with age classes and may be taken as annual rings. The lengths at time of formation of these rings (Table 6.7) were used to calculate separate von Bertalanffy growth curves for males and females. The relationships between initial length and annual growth increment were,

i) males

$$\text{Incr} = 24.60 - 0.43\ \text{IL}\ (n=6,\ r^2 = 0.96)$$

ii) females

$$\text{Incr} = 29.67 - 0.50\ \text{IL}\ (n=5,\ r^2 = 0.88)$$

where Incr = annual increment

IL = initial length

The growth curves were,

i) males

$$l_t = 57.56\ (1 - e^{-0.56\ (t + 0.15)})$$

ii) females

$$l_t = 59.49\ (1 - e^{-0.69\ (t - 0.14)})$$

where l_t = std length at age t years.

The estimated asymptotic lengths of 58 cm (male) and 59 cm (female) again underestimated the 68 cm observed in the actual population (Fig. 6.7) but provided an accurate fit to length at age data (Fig. 6.8). The calculated growth curves were therefore considered sufficiently accurate to use in the yield models.

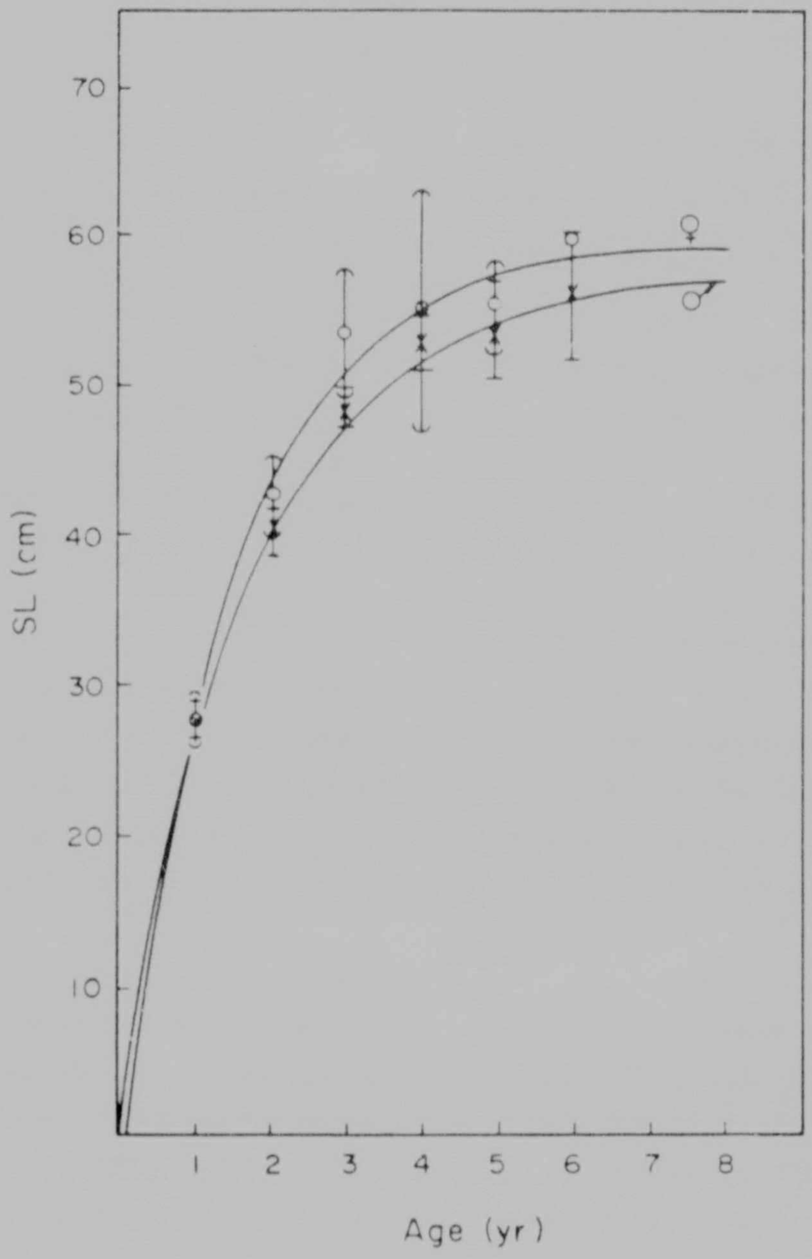

Fig. 6.8. Length at age and fitted growth curves of male (x) and female (o) *C. carpio*. ⊢⊣ = 95% CI of male length at age and (—) = 95% CI of female length at age.

Table 6.7. Mean length at time of vertebral ring formation in male and female *C. carpio*. CI = confidence intervals.

Ring	Age	Males				Females			
	(yr)	n	SL (cm)	95% CI	Incr. (cm)	n	SL (cm)	95% CI	Incr. (cm)
1	1	68	27.63	26.53-28.73	12.27	34	27.79	26.17-29.41	14.73
2	2	58	39.90	38.45-41.34	8.38	25	42.52	39.75-45.30	11.09
4	3	35	48.28	47.01-49.56	4.55	10	53.61	49.36-57.86	1.13
6	4	28	52.83	51.31-54.35	0.67	5	54.74	46.62-62.85	0.46
8	5	9	53.50	50.27-56.73	2.18	2	55.20	52.06-58.35	4.30
10	6	6	55.68	51.40-59.96	-	1	59.50		

(c) *C. gariepinus*

A comparison of standard length at capture and number of spine rings present, showed an increase in length with increasing number of rings (Table 6.8). The wide variation in length for each number of rings is to be expected as the interval between ring formation and time of capture would vary widely. The data indicate the validity of the rings for use in growth structures.

The time of ring formation in the pectoral spines of *C. gariepinus* could not be demonstrated conclusively. The mean marginal width of the spines showed minima in July 1982, from October 1982 to March 1983 and in August 1983 with a fourth forming in February 1984 (Fig. 6.9). The significance of the two winter minima, each based on a single point is dubious, and the prolonged period of reduced marginal width in the summer of 1982/83 may have been the only genuine indication of ring formation in the data set. The unusual conditions, with falling lake level, failure of the species to spawn in the summer of 1982/83 and major changes in macrophyte abundance probably influenced the time of ring formation, preventing its usual seasonal pattern.

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