There was an apparent marked rise in CPUE from May 1983 to September 1983 but this was considered unreliable as it was based on a very small number of returns (14 and 15 in July and August respectively.) Therefore the analysis was carried out for the period March 1982 to April 1983. Spawning of *C. carpio* did occur in October/November 1981 and by March 1982 these recruits would have attained a mass of approximately 150 g and were assumed to be recruited to the fishable stock. The absence of any sustained increase in CPUE during the period of analysis, indicative of no further recruitment, supported this assumption. Therefore the population susceptible to angling was considered closed from March 1982 to March 1984 when recruitment from the November 1983 spawning may have occurred. As a result of the unreliable CPUE from May 1983, analyses were undertaken on the CPUE from March 1982 to April 1983.

Over this period natural mortality would have depleted the population and this would result in an underestimate of population size by Leslie's method (Ricker, 1975), with the bias being directly related to the contribution of natural mortality to total mortality. However, this method was the only one available for *C. carpio* and thus the assumption that adult natural mortality was insignificant during the period had to be made. The absence of large piscivores, and of disease or parasite epidemics supported this assumption. In addition, the rapid decline in age class strength and normal dominance of the population by the 1+ age class (Fig. 6.7), in a species with a longevity of between 9 and 15 years (Brown, 1957), showed that fishing mortality was having the major impact on total mortality and thus that Leslie's method would give a realistic estimate of standing stock.

Abundance is related to CPUE by the equation (Gulland, 1983),

$$N = (1/q)*u$$

where N = mean abundance
q = catchability
u = mean CPUE.

During the period March 1982 to April 1983 the dam volume fell from 90% to 37%. This would have increased the density of fish and thus affected q, the catchability. In order to correct for changes in stock density induced by lake level changes, the catchability, q, was assumed to be inversely related to density. Therefore CPUE was corrected for changes in lake volume by multiplying it by the proportional volume of the lake. Catch already taken was computed from the mean uncorrected CPUE and the estimated total number of anglers (Section 6.2.3.1). Regression was undertaken by least squares analysis and the 95% confidence limits of the X-intercept according to the method of Ricker (1975).

(c) Littoral poisoning

Two littoral poisoning exercises were held, in March 1982 and in January 1984. In 1983 the falling water level resulted in an absence of marginal vegetation in the lake. In the absence of shelter, fry moved into deeper water which could not be sampled by poisoning. Poisoning experiments were therefore not undertaken in that year. Poisoning in March 1982 showed very low littoral populations as fry had already started to move offshore as water temperatures declined. In 1984 the exercise was held earlier in the year, in January.

In each year, three sites were sampled. In 1982 one was on the northern Magalies shore and one each on the southern Magalies and Crocodile shores (Fig. 5.2). In 1984 the shoreline was markedly different, because of lower dam volume, and suitable sites were selected on the southern Magalies shore and two on the north-eastern shore (Fig. 5.2). In 1982 a net measuring 100 x 3 m of 35 mm stretch mesh and in 1984 a net measuring 50 x 3 m of 13 mm stretch mesh were used to close off the sampling areas.

In 1982, St. 4 was enclosed at 9.30 am but, after the low fish returns in this sample, the other two sites were closed at 12h00, as were the 1984 sites. The net was laid out, ready to close, approximately one hour before closing. It was left until 12h00 and then rapidly drawn across the sides of the site. The

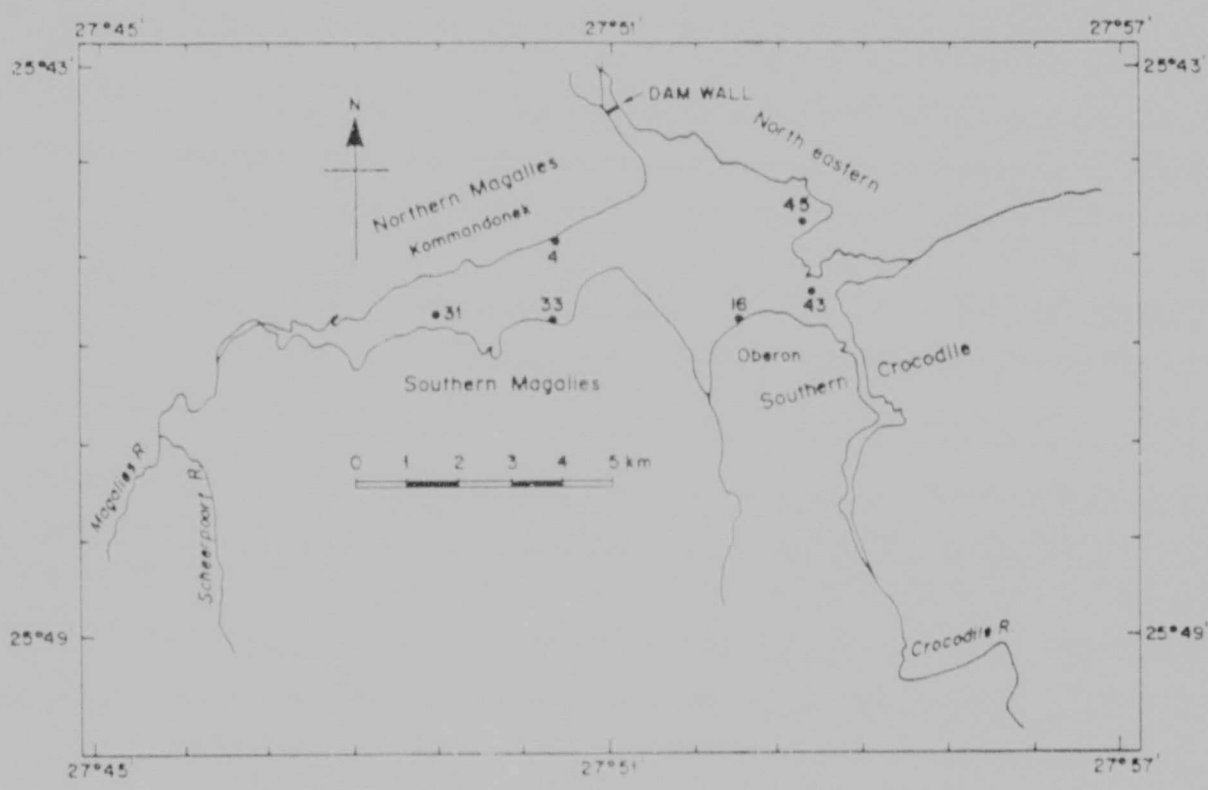

Fig. 5.2. Hartbeespoort Dam at full supply with location of littoral poisoning sites.

sites were immediately poisoned with a concentration of 2 mg.ℓ^{-1} of 5% rotenone wettable powder. This compares with 3 mg.ℓ^{-1} (Marshall & Lockett, 1976) and a minimum of 1 mg.ℓ^{-1} (Mitchell, 1976). On some occasions wind-generated currents washed treated water out of the enclosure and in these cases the applied concentration was increased to 5 mg.ℓ^{-1} to ensure a complete kill. A suspension of the powder was applied through a weighted hose-pipe, two metres long with outlets every 30 cm along its length. The poison was applied initially along the netted side to reduce the chance of escape of smaller fish through the net. Thereafter it was applied in two series of transects, at right angles to each other, parallel to the major axes of the site. Parts of St. 43, in 1984, were too deep to apply the poison manually and the outboard motor of the boat was run slowly, within the site, to ensure mixing and distribution of the poison to these areas.

At St. 4 in 1982, the first station poisoned, the net was left in position for 48 h and fish collected at intervals over this period to assess the length of time required for all dead fish to float to the surface. At subsequent stations fish were collected for 24 h after application of the poison. All fish collected were identified, a subsample taken and preserved in 4% formaldehyde for later weighing and measuring, and the total mass per species of the remainder taken.

5.3 Results

5.3.1 Mark and recapture

The results of the four mark and recapture exercises are shown in Table 5.2. All results for May 1982 and the *C. gariepinus* estimates for October 1982 and March 1983 were considered unreliable because of bias caused by tagging mortality or fungal infections in *O. mossambicus* and the low number of recaptures.

In October 1982 and March 1983 separate estimates were made for 1+ *O. mossambicus* and the older age classes. In October 1+ fish were tagged with staples on the dorsal fin. Eight hundred and thirty six

Table 5.2. Mark and recapture results for four exercises undertaken between May 1982 and October 1983, M = no. marked, R = no. of recaptures, N = population estimate. Results for 1982 based on modified Petersen formula and for 1983 on Schnabel's formula. CI = confidence intervals.

Month	M	R	N	95% CI
a) *C. mossambicus*				
May 82	1 250	3	190 465	86 575 - 1 269 765
Oct 82	2 581	26	296 452	210 367 - 470 835
Oct 82*	836	0	-	729 579 - ∞
March 83	1 996	11	145 620	81 311 - 296 634
March 83*	3 199	4	1 569 865	615 633 - 6 279 461
Oct 83	6 935	31	861 803	607 199 - 1 272 226
b) *C. zanzibaricus*				
May 82	143	1	12 600	4 500 - 252 000
Oct 82	724	3	90 806	41 275 - 605 375
March 83	591	1	585 626	104 576 - 5 856 260
Oct 83	1 595	6	175 276	80 279 - 478 026
c) *C. carpio*				
May 82	88	-	-	-
Oct 82	165	-	-	-

*1+ fish only. All other *C. mossambicus* estimates for 2+ and older.

fish were tagged and 3 229 taken in the census sample but no tags were recovered and hence no population estimate could be made.

However, the occurrence of 1+ fish in gill net catches in comparison to older fish was calculated for a total of 11 settings of the nets at stations 4, 13, 16 and 17 from September - November 1982. This showed that 1+ fish accounted for a mean of 83.19% of the fish caught (95% confidence limits 45.69 - 120.69%). Using the estimate of 2+ and older fish obtained in October, the number of 1+ fish was estimated to be 1 467 000 (95% confidence limits 249 400 - infinity).

In March 1983 the 1+ age group (1981/82 spawning) was still much smaller than, and easily separable from, the older age classes. It was therefore treated separately although Floy-type tags were used for both size groups. In October 1983 the new 1+ age group (1982/83

spawning) was not included as these fish were still less than 10 cm standard length and were scarce in catches.

The length frequencies of *C. gariepinus* caught during mark and recapture excercises were approximately unimodal with the modes at lengths of nearly 70 cm or more. Smaller size classes were poorly represented in the catches (Fig. 5.3). The mean mass of the catch was thus biased towards the older and larger fish. This bias was overcome by using the calculated mortality rates (Section 6.3.3) of the population to determine the numerical age group structure of the populations, and, in combination with the mean age class individual masses, the total mass of each age class and the population biomass was calculated (Table 5.3). On this basis the population biomass estimate for October 1983 was 292 t (134 - 797).

The *C. mossambicus* and *C. carpio* populations were representatively sampled for the 1+ and older age groups in the mark and recapture and angling samples respectively and the bias towards older fish did not occur in their estimates. Therefore the mean mass of fish in the samples taken was used to calculate the biomass of these species (Table 5.4 and Section 5.3.2).

Table 5.3. Population structure and biomass of the different age classes of *C. gariepinus* from the population estimate of October 1983 (175 276), and assuming an overall sex ratio of 1:1. Prop. = number in age class, for each sex, as a proportion of total number of sex. Mass = mean individual mass for the age class.

	Males				Females				
Age	Mort.	Prop.	No.	Mass (g)	Mort.	Prop.	No.	Mass (g)	Class mass (t)
1	0.09	0.24	21033	140	0.09	0.20	17528	190	6.27
2	0.11	0.22	19280	620	0.11	0.18	15775	610	21.58
3	0.15	0.19	16651	1410	0.15	0.13	14022	1180	40.02
4	0.20	0.15	13146	2390	0.15	0.14	12269	1820	53.75
5	0.28	0.11	9640	3460	0.20	0.12	10517	2460	59.23
6	0.39	0.06	5259	4530	0.28	0.08	7011	3060	45.28
7	0.54	0.03	2629	5550	0.28	0.06	5258	3620	33.62
8	0.76	0.01	877	6480	0.39	0.04	3506	4090	20.02
9	-	-	-	-	0.39	0.02	1753	4500	7.89
10	-	-	-	-	0.39	0.01	876	4820	4.22
Total mass = 292t									

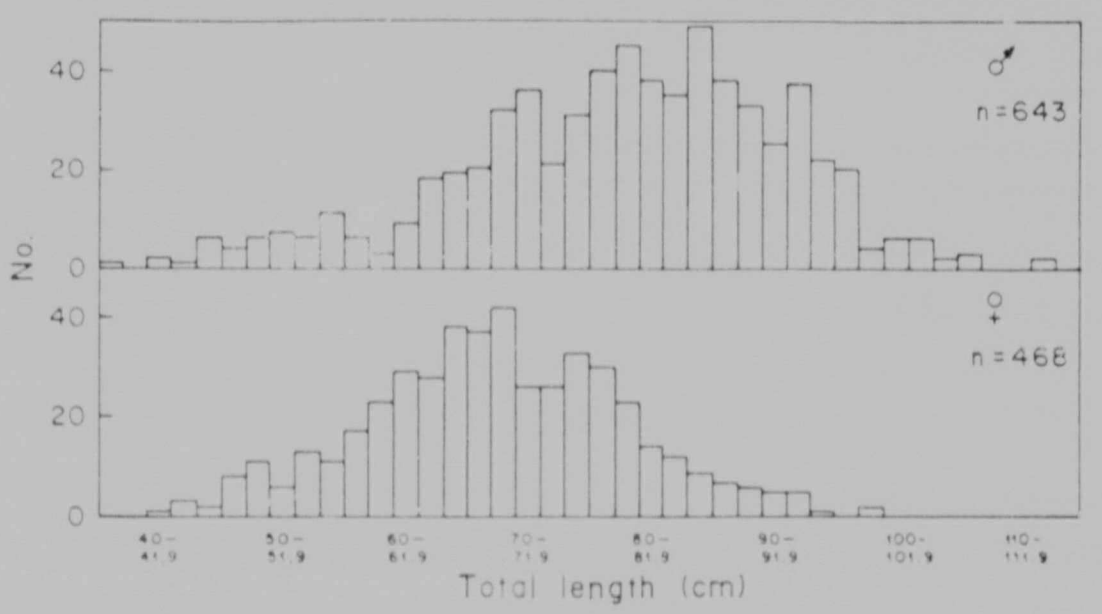

Fig. 5.3. Total length frequency of male and female *C. gariepinus* caught during mark and recapture exercise (October, 1982).

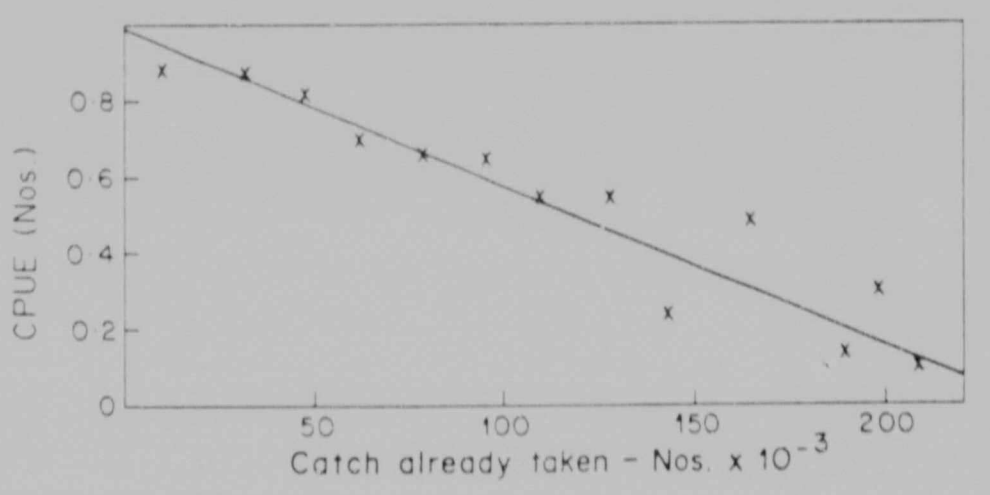

Fig. 5.4. Relationship between transformed angling success per angler day for *C. carpio* and catch already taken, with best-fit regression line.

Table 5.4. Population biomass estimates of *C. mossambicus* and *C. gariepinus* based on mark and recapture results. CI = confidence intervals.

Date	Population	Mean Mass (g)	n	Biomass (t)	95% CI
(a) *C. mossambicus*					
Oct 82	2+	940	296 452	279	198 - 443
	1+	30	1 467 000	44	7.0 - Infinity
	Total			323	-
Mar 83	2+	919	145 620	134	75 - 273
	1+	254	1 569 865	399	156 - 1595
	Total			533	-
Oct 83	2+	605	861 803	521	367 - 770
(b) *C. gariepinus*					
Oct 83	Total	1665	175 276	292	134 - 797

The *C. mossambicus* population grew from an estimated 323 t to 521 t from October 1982 to October 1983 (Table 5.4). This net growth was largely due to the strength of the 1981/82 class which experienced relatively mild winter mortality in its first year (Section 6.3.3.5). The only reliable estimate of *C. gariepinus* biomass was 292 t but this still had broad confidence limits (134 - 797). The large size of the lake and the limited effort which could be applied to estimating the population's sizes, meant that the number of recaptures was generally low. However, despite the wide confidence limits, the biomass estimates provided the best indication of population size for use in determining the potential yield and describing the species composition of the lake.

5.3.2 Leslie's method of biomass determination for *C. carpio*

The data and fitted regression line are shown in Figure 5.4. The best-fit equation was:

$$y = 0.98 - (4.04*10^{-6})\ x \qquad (n = 14,\ r^2 = 0.89)$$

where y = CPUE (kg.angler day^{-1}),
x = cumulative catch (kg).

This yielded a population estimate of 242 997 fish (95% CI = 217 247 - 281 278). The mean mass of fish caught during this period was 2.39 kg (range of monthly means was 0.69 - 3.22) which results in a biomass estimate of 580 t (519 - 672).

5.3.3 Littoral poisoning

The relative abundance of juveniles and the smaller species of fish was determined by littoral poisoning at six sites of differing characteristics (Table 5.5).

Table 5.5. Characteristics of sites at which littoral poisoning exercises were undertaken in March 1982 and January 1984

Site	Date poisoned	Water temp (°C)	Area (m^2)	Max depth (m)	Substrate & vegetation
4	9.3.82	25	737	1.1	Sand. 40% *Potamogeton pectinatus*, 5% *Panicum* sp.
16	15.3.82	24	831	1	80% sand, 20% rocks. 5% *P. pectinatus*, 5% *Panicum* sp.
33	17.3.82	24	609	1	Sand & silt 5% *P. pectinatus* 8% *Panicum* sp.
31	16.1.84	28	987	1	50% rock & pebbles, 50% sand. Thick *Panicum* sp., occassional *Polygonum* sp.
45	23.1.84	28	198	0.72	Sand & silt. Thick *Panicum* sp. On edge of thick *Polygonum* sp. belt.
43	30.1.84	24	370	1.5	Stones & shale. Predominantly *Polygonum* sp., some *Panicum* sp.

Table 5.6. Times of fish collection at St. 4 after poisoning, and the rate at which fish were collected.

Collection time (h after poisoning)	Fish collected ($g.h^{-1}$ since previous collection)	Cumulative %
6.5	110.8	60.9
8.0	27.5	64.3
20.0	14.8	79.3
24.0	25.2	87.9
26.0	18.2	90.9
29.5	0	90.9
46.0	6.5	100.0

The initial examination to determine the sampling time required to collect all fish after poisoning showed that after 24 hours, from the time of poisoning, approximately 88% of the total biomass of fish at St. 4 in 1982 had been collected (Table 5.6). However, the additional 9.1% collected after 46 hours was fish trapped in the net and retrieved when the net was pulled in. They would therefore have also been collected if the net had been pulled in after 24 hours. Thus 3.0% of the total sample would have been lost if collection had been terminated after 24 hours. This was considered to be negligible and the net was kept in position and fish collected for 24 hours after poisoning on all subsequent exercises.

In 1982 only three species were collected and the mean mass of fish was 29.7 $kg.ha^{-1}$ or 6 000 $fish.ha^{-1}$ (Table 5.7). Wind-induced currents prevented a complete kill at St. 33 and the mass recorded underestimates the true standing stock. In 1984 seven species of fish were collected and the mean mass of fish at the three stations was 267 $kg.ha^{-1}$ or 104 000 fry of the three dominant species per hectare (Table 5.7). Only 0+ fish were found in the 1982 experiments.

O. mossambicus was the dominant species accounting for 56 and 84% of the total mass of fry and small species collected in the two years (Table 5.7). The reason for the smaller contribution of *O. mossambicus* to the total sample in 1982 as well as the much lower total biomasses was related to the months of sampling. By March, water temperatures at the surface were 24-25°C compared to 24-28°C in January 1984. The low in 1984 was recorded on an overcast and windy day. Thus in March 1982 fish, particularly *O. mossambicus*, had moved away from the littoral regions and were not vulnerable to this type

Table 5.7. Mean biomass and percentage of total of the three samples of all species of fish collected in littoral poisoning programme. a) = March 1982, b1) = juveniles (January 1984) and b2) = adults (January 1984). X indicates occurrence of a species at the sampling site.

Species	Mass kg.ha^{-1}	2SE	%	Occurrence St. 4	St. 33	St. 16
a)						
C. mossambicus	17.2	13.2	56	X	X	X
C. flaviventris	11.7	11.7	38	X	X	X
C. carpio	1.6	-	5	X	-	-
b1)				St. 31	St. 43	St. 45
C. mossambicus	225.0	390.2	84.2	X	X	X
C. gariepinus	16.2	13	6.1	X	X	X
C. carpio	6.3	4.7	2.4	X	X	X
C. flaviventris	17.8	-	6.7	X	X	X
T. sparrmanii	0.6	-	0.2	-	-	X
B. unitaeniatus	1.0	-	0.4	-	-	X
P. philander	0.05	-	-	-	-	X
b2)						
C. mossambicus						
1+	55.3	-	14.5	-	-	X
2++	35.2	37.3	9.2	X	X	-
C. gariepinus	29.3	-	7.7	X	-	-
C. carpio	261.0	-	68.5	X	-	-

of sampling. The higher biomass and greater species diversity found in 1984 could also be related to the nature and extent of the aquatic vegetation. In 1982, the marginal emergent vegetation was limited to a band, one to two metres wide, around most of the shoreline. There were extensive beds of *Potamogeton pectinatus* in the littoral areas but the very thick growth of this species did not afford good shelter to fish. In contrast, in January 1984, approximately 20% of the lake bottom was covered with living emergent vegetation, particularly *Polygonum* and *Panicum* species which provided a protective and productive habitat for fish.

The much higher biomass of *C. carpio* and *C. gariepinus* juveniles in 1984 was also related to season and vegetation and to the shorter delay between the species spawning and sampling in 1984. The fish were therefore smaller at the time of sampling in 1984 and thus more likely to be confined to shallow water.

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C. gariepinus	16.2	13	6.1	X	X	X
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C. flaviventris	17.8	-	6.7	X	X	X
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B. unitaeniatus	1.0	-	0.4	-	-	X
P. philander	0.05	-	-	-	-	X
b2)						
O. mossambicus						
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Chetia flaviventris was the second most abundant species in 1982 and of the small species in 1984. However, the species is limited to inshore areas and thus the results for *C. flaviventris* include both adults and juveniles while those for the three dominant species (Table 5.7) include only the 0+ class. The relative abundance of this species is therefore exaggerated in this method of sampling. Nevertheless *C. flaviventris* must be recognised as a significant component of the population. Its diet included small fish (NIWR, 1985), and it would influence the populations of the three dominant species by preying on larvae and small fry.

The 1984 results can be used to give an indication of the abundance of 0+ fish of the three major species at that time. As only three samples were taken the standard errors were large and results from extrapolation to whole dam must be treated with caution. The absence of 0+ fish of all three species in gill net catches at this time indicated that they were confined to littoral regions and would have been most abundant in areas with macrophytes. Submerged and emergent vegetation was generally confined to water less than two metres deep which, at the time of poisoning, amounted to 206 ha. Extrapolating the mass per hectare of 0+ fish of the dominant species led to the following estimates of total abundance (2 x standard error in brackets). The dominance of *C. mossambicus* shown by mass estimates is supported by the estimates of fry numbers.

Species	No.	Mass (t)
C. mossambicus	20 844 996 (36 140 125)	46 (80)
C. carpio	123 436 (90 348)	1.3 (1.0)
C. gariepinus	375 436 (293 318)	3.3 (2.7)

5.4 DISCUSSION

Growth, recruitment and mortality ensure that standing stock is dynamic and that it changes on a daily basis as well as in the long term through changes in the carrying capacity of the environment. The drought and low water levels of 1982-84 would have affected this carrying capacity. However, the response to a decrease in carrying capacity is not normally instantaneous and occurs largely through

recruitment (Section 6.2.3.4). The biomass estimates made in 1982 and 1983 would not grossly underestimate the mean standing stock under stable, full supply conditions. These estimates were, to the nearest 10 tonnes.

O. mossambicus (1983)	520 t
C. carpio	580 t
C. gariepinus	290 t
TOTAL	1 390 t

No attempt was made to incorporate fry and adult biomass because of the small contribution of the fry to the total, the counter-acting influences of mortality and recruitment and the different times of sampling. The total standing stock of 1 390 t represented 695 $kg.ha^{-1}$ at full supply and accounted for more than 90% of the standing stock of all species (Section 4.3.1).

Little information for comparison is available on fish standing stocks in southern African [illegible] bodies. Koch and Schoonbee (1980) used mark and recapture methods to estimate the number of large fish species in Boskop Dam in the Western Transvaal (approx. 150 ha). They calculated a total population of 311 000 fish but did not give a biomass estimate. Marshall *et al.*, (1982) reported biomass estimates for the marginal fish species of Lake Kariba of 33 $kg.ha^{-1}$ and for the pelagic species of between 9 and 23 $kg.ha^{-1}$. Coulter (1981) stated that the density of pelagic clupeids in Lake Tangayika was approximately 230 $kg.ha^{-1}$. He also gave standing stock estimates for North American lakes of between 143 and 170 $kg.ha^{-1}$ and a mean of 382 $kg.ha^{-1}$ for Oklahoma ponds. He cited unpublished estimates of standing stock for tropical African lakes at between 80 and 800 $kg.ha^{-1}$ with most being below 400 $kg.ha^{-1}$. The estimated 695 $kg.ha^{-1}$ for Hartbeespoort Dam, even considering the broad confidence li[illegible]s, is high in comparison to these results.

Hanson and Leggett (1982) described a significant relationship between standing stock of fish and the total phosphorus concentration of the water. The data set on which their model was based covered latitudes 0 to 56°N, total phosphorus concentrations from 10 to 557 $\mu g.\ell^{-1}$ and fish standing stocks from 2.6 - 859 $kg.ha^{-1}$. Their equation was:

$$\log (\text{fish standing stock}) \ (\text{kg.ha}^{-1}) = 0.708 \log TP + 0.774$$

where TP = total phosphorus ($\mu g.\ell^{-1}$).

The mean total phosphorus concentration of Hartbeespoort Dam from 1981/82 to 1983/84 was approximately 520 $\mu g\ \ell^{-1}$ (NIWR, 1985). With this value the model predicts a standing stock of 498 $kg.ha^{-1}$. While this estimate is lower than that of 695 $kg.ha^{-1}$ derived in this study, there were broad confidence limits about the mark and recapture estimates and the two results are not significantly different. The existence of this relationship and the general importance of phosphorus as a limiting nutrient in freshwater (Wetzel, 1975) suggest that the high phosphorus concentration in Hartbeespoort Dam is the major factor causing the high fish standing stock.

Robarts (1984) estimated the mean annual primary production as 1.47 kg $C.m^{-2}.y^{-1}$ in 1981/82 (Robarts, 1984) and as greater than 2.00 kg $C.m^{-2}.y^{-1}$ in 1983/84 (Robarts pers. comm.). The lake has been described as the most productive freshwater or saline lake studied (Robarts, 1984) and this high primary production is clearly leading to high fish standing stocks.

The standing stock estimates provide starting values for the yield models described in Chapter 7. The wide confidence limits, particularly for the *C. gariepinus* population, introduce error into yield predictions which would have to be considered in estimating potential yield. However, the high phosphorus concentration and primary production in the lake indicate that the high standing stocks estimated are likely to be realistic.

The effort required for precise standing stock determinations and the problems associated with obtaining unbiased results, even in a relatively small system such as Hartbeespoort Dam, demonstrate the need for simple, accurate means of determining standing stock and yield. In developing countries there is rarely the man-power available for intense studies of each fishery, and in southern Africa freshwater fisheries will become increasingly important with population growth. Relationships between biomass or yield and indicators such as phosphorus (Hanson & Leggett, 1982) and primary production

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(Melack, 1976; Oglesby, 1977a) will have to be investigated and, where possible, refined for particular geographical sets of lakes. These will provide at least first estimates of yield and permit initial development and management of a fishery.

The adverse effects of high primary production on the fish species composition of the lake have been discussed (Section 4.4).

CHAPTER 6

POPULATION GROWTH AND MORTALITY

6.1 Introduction

The overall aim of this chapter is to derive and present those parameters necessary to obtain yield estimates. Yield is dependent on population production, that is, the net effect of somatic growth, recruitment by way of breeding, and mortality. Production has been defined as the total elaboration of new tissue in a given time period by a population (Chapman, 1978). This includes the sum of growth increments for all population members alive at any time over a given period. By Chapman's definition growth increment is the net increase or decrease in the amount of tissue contained in bodies of all population members, regardless of the fate of the tissue.

Thus

$$P = B_1 - B_o + B_d \quad \text{(Chapman, 1978)}$$

where P = production

B_1 = biomass at time t_1

B_o = biomass at time t_o

B_d = sum of masses of fish which died during time Δt.

One of the more common models for assessing production is given by (Chapman, 1978) as

$$P = GB(e^{(G-Z)}-1)/(G-Z)$$

where G = instantaneous growth rate

Z = instantaneous mortality coefficient

B = biomass of the population.

However, this formula is dependent on exponential rates of growth and mortality which rarely apply over long periods of time. In addition, in order to account for immigration, emigration and recruitment of new age classes, growth and numbers must be assessed over short time intervals (Chapman, 1978). Such estimates of numbers are rarely practical.

A numerical method using similar data was used by Rudenko and Volkov (1974).

$$P_t = W_t * ((N_t + N_{(t+1)})/2)$$

where

W_t = weight increment of fishes per unit time

N_t and $N_{(t+1)}$ = abundance of fish at the beginning and end of unit time.

This model requires information on mean individual growth rate and abundance of fish at two separate times. Alternatively, from a single population estimate and knowledge of the recruitment and mortality rates, the change in standing stock per unit time could be determined.

An alternative method used in fisheries management is the determination of surplus production which is the sum of recruitment and growth, less natural mortality (Ricker, 1975). This and other yield models will be discussed in Chapter 7, which deals with the synthesis of parameters derived in this chapter to estimate yield.

In summary, production over extended periods can be determined from a knowledge of recruitment of new age classes to the stock, the average increase in individual body mass per unit time, the total population size and the total mortality rate. Population size was determined in Chapter 5 and the objectives of this chapter are to:

(a) quantify the individual growth rates of the major species

(b) establish population fecundity by describing the relationships between female size and fecundity, the age at first maturity of females of the three species and the breeding seasons and frequency of spawning

(c) establish total, fishing and natural mortality rates of adults of the three species

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(c) establish total, fishing and natural mortality rates of adults of the three species

(d) determine the total mortality rate of fish in their first year and

(e) assess the impact of cold-induced mortality on the *O. mossambicus* population.

6.2 Methods

6.2.1 Growth rates

The growth rate of fish may be determined by direct measurement of the growth increment per unit time of known age fish or, most commonly, by the calculation of growth increments from the known length or mass of fish at successive ages. Direct measurement of the growth rates of individual fish can be made either by marking or tagging of captured wild fish or fish in ponds. In using such a method it is essential to determine that the marking does not affect the growth rate or that the growth rate in any experimental enclosure does not differ from that of the population in its natural environment.

In this study, growth rate was calculated by determining growth increments from the length at age of fish. The most commonly used method of determining the age of fish is by analysis of growth marks or rings on the hard parts of fish (Bagenal & Tesch, 1978). Such marks are formed during periods of relatively rapid or slow growth or may be due to environmental influences such as temperature, seasonal variations in food supply or to physiological influences (Bagenal & Tesch, 1978). Hard parts commonly used to age fish are scales, otoliths and various bones (Ricker, 1975) including opercula, vertebrae and cross sections of spines and fin-rays (Bagenal & Tesch, 1978).

Bagenal and Tesch (1978) gave two criteria which should be satisfied if reliable estimates of age and growth are to be determined from growth rings:

(a) a recognizable pattern must be discernible and

(b) a regular time scale must be allocated to the visible pattern.

Attempts to describe growth rate without age validation have led to errors in yield estimates with major financial implications (Beamish & McFarlane, 1983). False annuli, which may be caused by starvation, unfavourable temperatures, disease, injury or other irregular stimuli, and which may result in gross errors in age determination do occur (Weatherley, 1978). Bagenal & Tesch (1978) listed five methods for age validation. These are, agreement with results obtained by Petersen's method, analysis of the edge of the ageing structure for a seasonal pattern, observation of year classes over a number of years, and marking or tank or pond experiments.

A second method of assessing growth rates is the Petersen method (Ricker, 1975; Bagenal & Tesch, 1978). This method utilises length-frequency data and, by identifying each age class mode in a distribution, permits estimation of annual increment. A variety of statistical, mathematical and computational methods have been developed to assist in the analysis of length frequencies (Ricker, 1975). The above techniques for ageing fish have all been validated (Ricker, 1975) and the choice of method depends on the species and population being investigated.

Different methods of age determination had to be used for each of the three species but all three methods relied on the examination of growth rings on hard parts of the body. In all cases the basic approach was to identify growth rings on the structure, to ascertain the frequency of formation of the rings and then, using lengths at age back-calculated from growth rings, to determine mean length at age, for the range of ages for each sex. The growth of all species was described by standard length (SL), which is the greatest length from the fishes anterior extremity to the base of the median tail fin rays (Lagler, 1978).

(a) *O. mossambicus*

The growth of *O. mossambicus* in South Africa has been widely studied and most studies have made use of scales (Hecht, 1980). Bruton and Allanson (1974) analysed the seasonal frequency of marginal circuli in *O. mossambicus* in Lake Sibaya, Kwazulu, and found that two rings per year were formed. The scale rings consisted of areas of widely spaced circuli which were formed in September/October and in January. Ring formation was ascribed to

pre- and post-spawning migrations into sheltered littoral areas where increased feeding and hence growth occurred.

Hecht (1980) studied growth of *O. mossambicus* in a Venda impoundment using both scales and otoliths. He also used the number of marginal circuli on the scales as a guide to time of ring formation and found that only one ring was formed, in February/March, at the end of the breeding season. By studying the margin of sagittal otoliths he found that two opaque bands were formed on these per year, one in February/March and the second in July/August. He did not attempt to explain the factors causing ring formation at these times. He found that scales and otoliths could be used for age determination up to four years old but thereafter scale rings became too crowded to read accurately. Otolith rings remained distinguishable throughout life.

Finally, le Roux (1961) studied growth in *O. mossambicus* in a number of Transvaal impoundments, excluding Hartbeespoort Dam, and found that a single ring was formed in August. He gave no explanation for the time of ring formation.

The differences in rate and seasonality of ring formation revealed in these studies, showed the need to verify the time of ring formation, in the determination of the growth rate of any previously unstudied population.

In this study scales and otoliths were initially examined for suitable growth rings. In both structures rings were clearly discernible even when up to ten rings were present. As otoliths were time-consuming to extract and prepare, it was decided to use scales. They were removed from the region between the operculum and the start of the dorsal fin, above the lateral line. Scales were washed in warm, soapy water, dried with paper tissue and three scales mounted between two microscope slides which were secured with masking tape. Material prepared in this manner has been stored at room temperature for up to three years with no sign of deterioration. Scales were read using a standard microfiche reader. All three scales were read and the results only accepted if rings on at least two were clear and the

numbers in agreement. Length, mass, sex, date, number of marginal circuli, the number and radius of each ring and the total scale radius, from focus to the central edge of the anterior field (Bruton & Allanson, 1974) were recorded for use in the growth rate determination.

Only rings which extended from one lateral field to the other and which consisted of widely spaced circuli were accepted. Scales were frequently encountered with a transparent central portion, lacking circuli, around the focus and covering an area varying from a few circuli to beyond the first ring. These clear areas may have resulted from scale regeneration after scales were lost in mid-winter through cold-stress or fungal infection, or may have resulted from scale resorption (Bagenal & Tesch, 1978). Such scales were not used for growth analysis.

Data were analysed by the method described by Bagenal and Tesch (1978). The relationship between standard length and scale radius was described by linear regression of length on scale radius. The y-intercept (a) was determined for use in the Fraser-Lee equation which is used for length determination when the relationship is linear but the regression line does not pass through the origin (Bagenal & Tesch, 1978).

$$l_n - a = (S_n/S)(l-a)$$

where l_n = length when annulus 'n' was formed

l = length of fish when scale sample was obtained

S_n = radius of annulus 'n'

S = total scale radius

a = y-intercept of standard length:scale radius relationship

This equation was used to determine the length of each fish at the time of formation of each annulus. The mean length at ring formation for the sample and 95% confidence limits of the mean were calculated separately for males and females for each ring.

Once these data had been obtained, von Bertalanffy growth curves were fitted to the data. While the use and form of growth curves is controversial, the von Bertalanffy growth curve

satisfies the functions of providing a reasonable fit to most data and of providing meaningful growth parameters which can be used in a model (Gulland, 1965).

Curves were fitted by plotting annual growth increment (cm) against initial standard length (cm) and fitting a straight line to the data. The x-intercept of this line provides an estimate of $L\infty$, the maximum theoretical length, while the slope of the line, b, is related to the Brody growth coefficient, K, (Ricker, 1975) by

$$b = -1 + e^{-K} \qquad \text{(Bagenal \& Tesch, 1978)}$$

The final parameter required for fitting the von Bertalanffy equation is the hypothetical age at which the fish would have had zero length, t_o, and is calculated from the equation (Gulland, 1965)

$$t_o = t + (1/K)(\ln((L\infty - l_t)/(l\infty)))$$

where l_t = length at age t

The value of t_o is calculated for all values of t for which l_t is known. The best estimates of t_o are obtained from younger but fully recruited age groups where errors in the calculated values of l_t will be smallest (Gulland, 1965).

The Petersen method was also used to calculate growth rates for the recruits of the 1981/82, 1982/83 and 1983/84 age groups which were readily identifiable on the basis of length. Results from these analyses were used for verification of the growth rate determined from scales.

(b) *C. carpio*

Scales have been found to be reliable for aging cyprinid fish (Crivelli, 1981) but most studies were undertaken in north-temperate areas. The use of eye lens weight was tested (Crivelli, 1980) but found to be unreliable for fish older than three years. No studies of growth rate of wild carp have been undertaken in southern Africa.

The carp population in Hartbeespoort Dam consisted of full- and half-scale carp. Scales and opercula were investigated but, although rings were apparent, there was no regularity in rate of ring formation or consistency in the clarity and nature of scale rings. Clear and apparently regular rings were found on the vertebrae. The vertebrae between the dorsal edge of the operculum and the first dorsal fin ray were collected from a number of fish between March 1983 and March 1984. These were removed, placed in boiling water for approximately 15 minutes, and then all flesh and cartilage removed from the individual vertebrae. The bones were placed in a 4% formaldehyde solution for 48-72 hours, which was found to prevent fungal attack of the bones. They were then dried and stored at room temperature.

Subsequently the bones were examined and the number of rings (transluscent) counted. The rings occurred on the concave surfaces forming the joints between individual vertebrae. The radius of each ring was measured in the plane at right angles to the original vertebral axis, from the vertebrae centre to the lateral edge. The total radius was also measured which permitted calculation of the marginal width from the last ring to the vertebral edge.

The mean marginal widths for the three-monthly samples collected from March 1983 - March 1984 were examined to determine times of ring formation, but no pattern was discernible. Therefore the Petersen method was used to calculate a growth curve which was then used to determine the times of ring formation. The samples of carp collected in the initial survey in November 1981 and the mark and recapture exercises in October 1982 and November 1983 were used. In order to identify the actual modes more accurately, normal distributions were fitted to the observed data by determining the expected from the observed frequencies (Zar, 1974) in each age class. The goodness of fit was tested using the chi-squared test. The shifts in the modal lengths of age classes from year to year were used to compute a von Bertalanffy growth curve. As the fish had not been sexed this curve was a mean curve for both sexes.

The mean lengths at time of ring formation on the vertebrae of the combined sample of males and females were then compared to the Petersen method growth curve and, assuming spawning at the beginning of November each year, the times of formation of each ring calculated. This showed clear trends in the times of ring formation (Table 6.6) and validated the rings as regularly laid down. The mean lengths at ring formation for each sex were then used to compute a von Bertalanffy growth curve for each sex, as for *O. mossambicus*, using the more accurate vertebral data

(c) *C. gariepinus*

C. gariepinus do not possess scales. The growth of the species has been widely studied, usually by using sections of the pectoral spines (van der Waal & Schoonbee, 1975; Bruton & Allanson, 1980; Clay, 1982 and Quick & Bruton, 1984). Pectoral spines were widely used to study growth in American catfishes (Clay, 1982). In view of the succesful results obtained by previous workers on the species, pectoral spines from *C. gariepinus* in Hartbeespoort Dam were examined for use in age and growth determination and found to have clear, regular growth rings.

Spines were removed from dead fish and placed in boiling water for 15 minutes to soften muscle and cartilaginous tissue which was then removed. A lateral section of the spine approximately two mm thick was then cut by hand from the spine. Bruton and Allanson (1980) referred to the problem of bone resorption in pectoral spines and overcame the problem by consistently cutting sections at the point 5/7 from the distal end of the spine. For the same reason, and to minimise variation in the spine diameter:length relationship, all sections were cut from this area in this study. Consequently bone resorption was not found to prevent use of spines except in a few of the largest fish.

Once sections had been removed, they were ground down by hand, using fine glass paper, until they were 0.5 - 1.0 mm thick and the rings were clearly visible under a light transmission microscope. Bruton and Allanson (1980) suggested staining the bone tissue with alizarin red in cases where rings were not clear. While this technique was attempted with success in this study, it was found to be unnecessary.

Bruton and Allanson (1980) measured spine diameter and ring diameter along the antero-lateral radius of the spine. In this study rings were found to be clearer in the region between the antero-lateral radius and the anterior edge. Therefore the radius at 45° to the antero-lateral radius, in the anterior segment, was used. In addition to spinal and ring diameter, fish standard length and sex were recorded, and the marginal width between last ring and the spine edge. As in previous species, the marginal width was recorded in order to ascertain time of ring formation. The length frequencies of even large samples of *C. garleppinus* did not show clear age class modes, either separated by sex or combined (Fig. 5.3), and could not be used for validation or growth rate determination.

The length at age and von Bertalanffy growth curves were computed as for the previous two species.

6.2.2 Fecundity, age at maturity and frequency of spawning

Knowledge of the number of recruits to the 0 year old age class (0+) was necessary to construct yield models for each population. This was estimated by determining the fecundity:size relationships, age at maturity, breeding seasons and frequency of spawning for each species.

Definitions of fecundity vary. In this study the definitions of Bagenal (1978) have been used:

> fecundity is the number of ripening eggs found in the female just prior to spawning
>
> population fecundity is the sum of the fecundities of all the breeding females.

Some work has been done on the relationship between fecundity and fertility, where fertility is the actual number of eggs shed by the female. In certain cases a large proportion of eggs has been found to be retained at spawning and later resorbed, but generally there are few residual eggs and fecundity is similar to fertility (Bagenal, 1978). In this study the number of ripening eggs in the female was

taken to be equal to fertility. The different stages of gonad development were not easily recognisable in the males and, as fertility was based on the number of eggs produced, the breeding seasons are described in terms of female gonad development. Similarly, only the female age at maturity was considered. The number of reproductively active males was considered not to limit spawning and recruitment.

Females of the fish collected in routine sampling were examined for gonad condition and classified into seven categories according to the scheme in Table 6.1, adapted from those of Kesteven and Nikolsky (Lagler, 1978). Both ovaries of females classified as active-ripe or ripe were removed, weighed and stored in Gilson's fluid (Bagenal & Braum, 1978) for from one to four weeks. Gilson's fluid breaks down the connective tissue of the ovary and liberates the eggs, facilitating counting.

Table 6.1. Criteria for classification of fish gonad development adapted from Kesteven and Nikolsky (Lagler, 1978)

Stage	Characteristics
1. Inactive (I)	Small gonads, close to the vertebral column. Gonads transparent and grey.
2. Inactive - active (IA)	Testes and ovaries transluscent, grey-red. Single eggs just visible to the naked eye. Gonads extending most of the length of the ventral cavity.
3. Active (A)	Eggs visible to the naked eye. Gonads reddish with blood capillaries, filling 1/3 - 1/2 of the ventral cavity.
4. Active - ripe (AR)	Ovaries orange-red (except in *C. gariepinus* where gonads remain grey throughout development). Testes white with red blood vessels. No milt-drops appear under pressure. Eggs opaque.
5. Ripe (R)	Sexual products mature. Testes exude milt when pressure exerted. Eggs spherical.
6. Ripe-running (RR)	Eggs and milt run with slight pressure.
7. Spent (S)	Gonads have appearance of deflated sacs, reddish colour (except *C. gariepinus*). Occasional residual eggs and some milt.

After storing in Gilson's fluid, the bottle containing the fluid and ovarian tissue was vigorously shaken to complete separation of the eggs. Large pieces of connective tissue were removed and the remainder of the sample, consisting of separated eggs and fragments of connective tissue, weighed and stored in 10% formaldehyde solution until counting. In the case of small *O. mossambicus* ovaries (less than 3 - 4 g) the whole sample was counted but in all other cases sub-samples were taken, weighed and the number of mature eggs counted. It was found that six sub-samples of approximately 0.5 g for *O. mossambicus* and 0.25 g for the other two species was sufficient to result in a standard error of less than 5% of the mean (Table 6.2) and this number of sub-samples was used for all counts. The mean number of eggs per unit mass was then calculated and the total number of mature eggs estimated by proportion.

Mature eggs to be released at the next spawning were clearly distinguishable from immature eggs on the basis of size (Fig. 6.1), their spherical shape and colour.

O. mossambicus is a multiple spawner and mouth brooder and attempts were made to determine the frequency of spawning. 2+ Fish brought back to the laboratory did not breed, despite raising the temperature to 26°C . The male responded immediately to the presence of a female with colour display and nest building behaviour. However, the females, despite initial response to the male display, did not reach oviposition. After 1 - 2 hours of courtship the male became aggressive and attempted to kill the female if she was not removed. Both relocating females to a male tank and vice versa were attempted without success.

The frequency of spawning was therefore determined indirectly by calculating the mean length of time for which a female carried eggs or fry in her mouth, and the mean number of mouth-brooding females at any given time during the breeding season. By direct proportion, the total number of days spent mouth-brooding by a female could then be calculated and hence the number of spawnings per season.

To determine the time taken for a female to rear a single brood, eggs and larvae were brought back to the laboratory and reared in specially designed five litre containers (Fig. 6.2). Total length of five

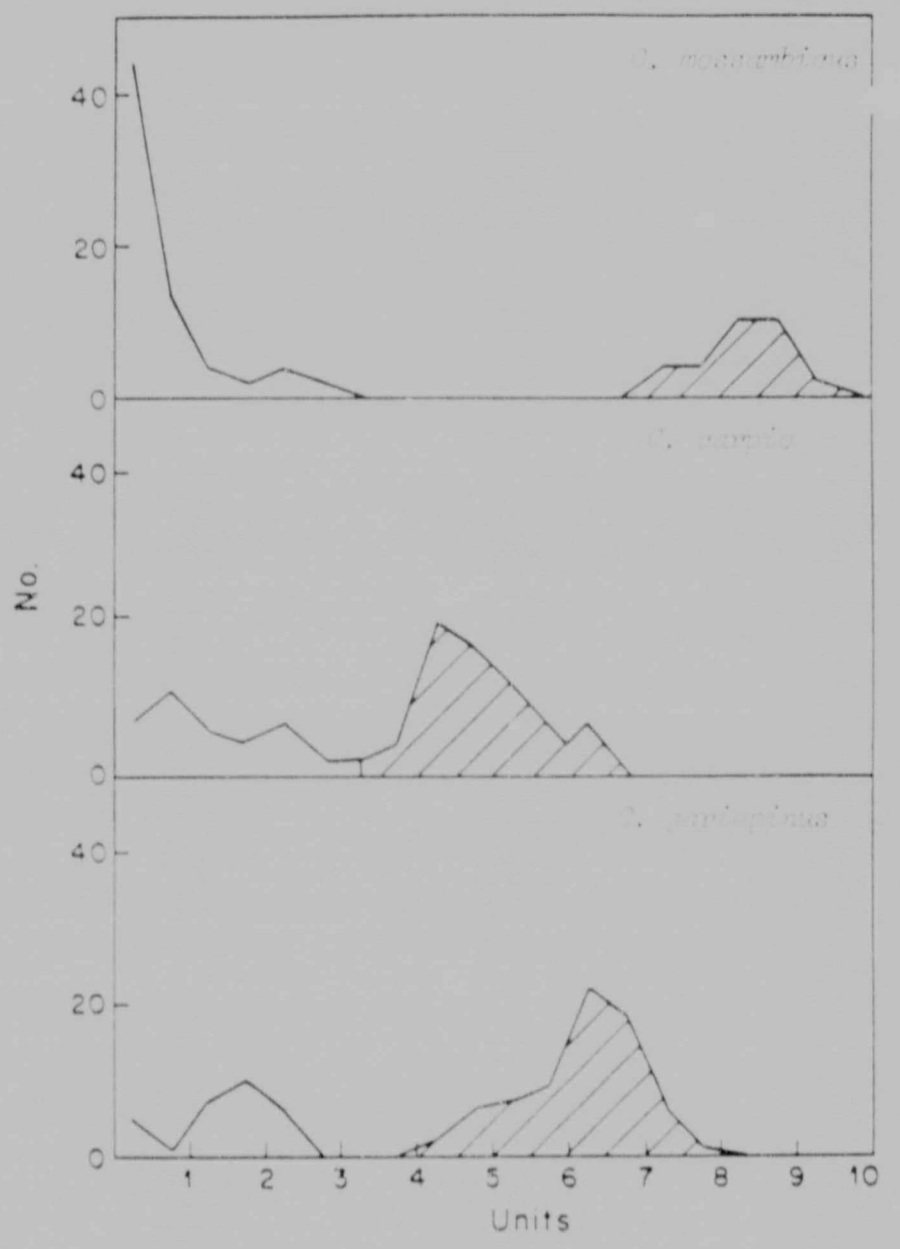

Fig. 6.1. Diameter of eggs, in microscope units, of the three major species in active-ripe and ripe ovaries of selected females. Shaded portions indicate mature eggs.