Chapter 2: Depth distribution and breeding patterns of the demersal species most commonly caught by trawling in the South West Arm of Lake Malawi

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Introduction

Given the tremendous diversity of Malawi cichlids, very few studies have been carried out on their breeding biology so far. Earlier studies focused on some species in the north (Jackson et al. 1963) and central part of the lake (zooplanctivorous *Utaka*: Iles 1960, 1971). A comprehensive work highlighted the reproductive seasonality of ten rock frequenting species (Marsh et al. 1986). A recent survey of the pelagic zone provided information about the breeding of *Copadichromis quadrimaculatus*, *Diplotaxodon limnothrissa* and *'big eye'* and *Rhamphochromis longiceps* (Thompson et al. 1996). Despite the fact they hold an economically important commercial fishery, very few species apart from *chambo* (Lowe 1953, McKaye & Stauffer 1988, Turner et al. 1991) have been studied in the south of the lake, where the commercial fisheries take place. Maturity and fecundity were estimated for *Copadichromis* ("*Haplochromis*") *mloto*, *Lethrinops parvidens* , *L. longipinnis*, *Mylochromis* ("*Haplochromis*") *anaphyrmus* and *Otopharynx* ("*Haplochromis*") *intermedius* (Tweddle & Turner 1977), while breeding season and maturity were detailed for three *Lethrinops* species, *microdon*, *'species A'* and *gossei* by Lewis & Tweddle (1990). McKaye (1983) reported marked seasonal variations in nest numbers for *Cyrtocara eucinostomus*.
Although the information is incomplete for some species, our study describes the breeding biology of about 40 of the most important trawled species in the SWA.

It is important to remember that the sampling period was June 1998 to May 1999. However, all the information related to catches are based on the period from July 1998 to May 1999 for the reasons explained in the previous chapter. Owing to inter species variability of occurrence in the catches and therefore to sample size, the results presented in this chapter will be of irregular quality, the information being complete and reliable for some species and more indicative for the rarer ones. For the reader's convenience, information about the species is delivered per genera, which are ordered alphabetically. For each species, whenever possible, the following information is displayed: size range (SL), depth distribution, occurrence and abundance over the full sampling period, breeding season, age and size at maturity, fecundity and egg size.
For the breeding season, priority will always be given to the females pattern. Most of the time in cichlids, males are sexually active for longer periods than females; a way to always be 'ready' probably. As a consequence, determination of the breeding season is more accurate when based upon female data. However, when the sample sizes are not optimum for females, information about males may be useful. On the other hand, as most Malawi cichlids form breeding leks to attract females (Konings 1995, Turner 1996), priority will be given to ripe males distribution for estimation of spawning depth. The weight of individuals was not taken on board, but only in the lab on ripe females, except for the nine target species (*Alticorpus macrocleithrum*, *Alticorpus mentale*, *Copadichromis virginalis*, *Diplotaxodon limnothrissa*, *Diplotaxodon macrops*, *Lethrinops argenteus*, *Lethrinops gossei*, *Mylochromis anaphyrmus* and *Taeniolethrinops praeorbitalis*), for which all the females were weighed. Most of the

length-weight relationships are then based on data for ripe females, which explain their low sample size sometimes.

Material and methods

All the fish analysed were collected during the monthly trawl catches in the north of the South West Arm (see Chapter 1 for details).

The comparisons of CPUE per depth for each species with those reported in Tómasson & Banda (1996) are based on the values given in Appendix 3, but pooled per depth category (shallow zone = 0-50 m, deep zone = 51-100 m, very deep zone = >100 m) and reported to 30 min pulls (instead of 20 min in our case) to be comparable with Tómasson & Banda (1996) values.

The maturity stage of female gonads was macroscopically determined using the slightly modified scale of Legendre & Ecoutin (1989) (Duponchelle 1997).

Stage 1: immature. The gonad looks like two short transparent cylinders. No oocytes are visible to the naked eyes. As a comparison, immature testicle is much longer and thinner, like two long tinny silver filaments.

Stage 2: beginning maturation. The ovaries are slightly larger and little whitish oocytes and apparent.

Stage 3: maturing. The ovaries continue to grow in length and thickness and are full of yellowish oocytes in early vitellogenesis.

Stage 4: final maturation. The ovaries occupy a large part of the abdominal cavity and are full of large uniform sized oocytes in late vitellogenesis.

Stage 5: ripe. Ovulation occurred, oocytes can be expelled by a gentle pressure on the abdomen. This stage is ephemera.

Stage 6: spent. The ovaries look like large bloody empty bags with remaining large sized atretic follicles. Small whitish oocytes are visible.

Stage 6-2: resting. The general aspect of the gonad recall a stage 2, but the ovarian wall is thicker, the gonad is larger, often reddish with an aspect of empty bag. This stage is distinctive of resting females, which have spawned during the past breeding season.

Stage 6-3: recovering post-spawning females. The general aspect of the gonad is like a stage 3 but with empty rooms, remaining large-sized atretic follicles and the blood vessels are still well apparent. This stage is characteristic of post-spawning females initiating another cycle of vitellogenesis.

Males were only recorded as being either in "breeding colour" or not.

For each species, all the stage 4 and 5 females were preserved in 10 % formalin for later examination.

Nine target species were selected according to their relative abundance, depth distribution and basic ecological characteristics (benthic or pellagic habits, broad trophic category) (Tómasson and Banda 1996, Turner 1996). These were *Lethrinops gossei* Burgess & Axelrod, *Lethrinops argenteus* Ahl (= *L. longipinnis 'orange head'*), *Diplotaxodon limnothrissa* Turner, *Diplotaxodon macrops* Turner & Stauffer, *Copadichromis virginalis* Iles, *Mylochromis anaphyrmus* Burgess & Axelrod, *Alticorpus mentale* Stauffer & McKaye, *Alticorpus macrocleithrum* Stauffer & McKaye and *Taeniolethrinops praeorbitalis* Regan.

For these species, all the females from each haul were preserved in formalin for later examination.

All fish preserved in formalin were measured (SL) to the nearest mm and weighed to the nearest 0.1 g. Their maturity stage was determined and the gonads in stage 4 were weighed for Gonado-Somatic Index (GSI) calculation (gonad weight/total body weight × 100) then preserved in 5% formalin for fecundity and mean oocyte weight calculation.

The breeding season was determined from the monthly proportions (in %) of the different stages of sexual maturation (Legendre & Ecoutin 1989, Duponchelle et al. 1999). In order to eliminate the small immature females, which would give a biased weight to the immature stages (1 and 2), and to define more precisely the spawning season, only females which size was greater than or equal to the size at first sexual maturity were considered in analysis.

The average size at first maturation (L_{50}) is defined as the standard length at which 50% of the females are at an advanced stage of the first sexual cycle during the breeding season. In practice, this is the size at which 50% of the females have reached the stage 3 of the maturity scale (Legendre & Ecoutin 1996, Duponchelle & Panfili 1998). For the estimation of L_{50}, only the fish sampled during the height of the breeding season were considered.

Age at maturity was calculated from the Von Bertalanffy Growth Curve (VBGC) equation:

$$L_t = L\infty\ (1-\exp\ (-K\ (t-t_0))) \qquad (2)$$

Where L_t is the mean length at age t, $L\infty$ is the asymptotic length K the growth coefficient and t_0 the size at age 0. This equation can be written:

$$t = (-\ln\ (1-\ (L_t\ /\ L\infty))\ /\ K) + t_0$$

Replacing L_t by the mean size at maturity (L_{50}), age at maturity (A_{50}) is then:

$$A_{50} = (-\ln\ (1-\ (L_{50}\ /\ L\infty))\ /\ K) + t_0$$

$L\infty$ and K were obtained from length frequency distribution analysis and are provided in the Chapter "Growth" for twenty three of the species. The size at age 0 was considered null.

Fecundity is defined here as the number of oocytes to be released at the next spawn, and correspond to the absolute fecundity. It is estimated, from gonads in the final maturation stage (stage 4), by the number of oocytes belonging to the largest diameter modal group. This oocyte group is clearly separated from the rest of the oocytes to the naked eye and corresponds approximately to oocytes that are going to be released (Duponchelle 1997, Duponchelle *et al*. 2000).

Oocyte weight measurements were all carried out on samples preserved in 5% formalin. The average oocyte weight per female, was determined by weighing 50 oocytes (Peters 1963) belonging to those considered for fecundity estimates.

In order to compare mean oocyte weight and diameter among the different species, the measurements need to be made on oocytes in a similar vitellogenic stage, then on oocytes whose growth is completed. A simplified version of the method applied by Duponchelle (1997) was used to determine the GSI threshold above which the oocyte weight do no longer increase significantly. For each species, the individual oocyte weights were plotted against the GSI. The GSI corresponded to the beginning of the asymptotic part of the curve was visually determined and the fish whose GSI was inferior to the defined GSI were removed. The final GSI threshold was reached when no correlation subsisted between the mean oocyte weight and the GSI.

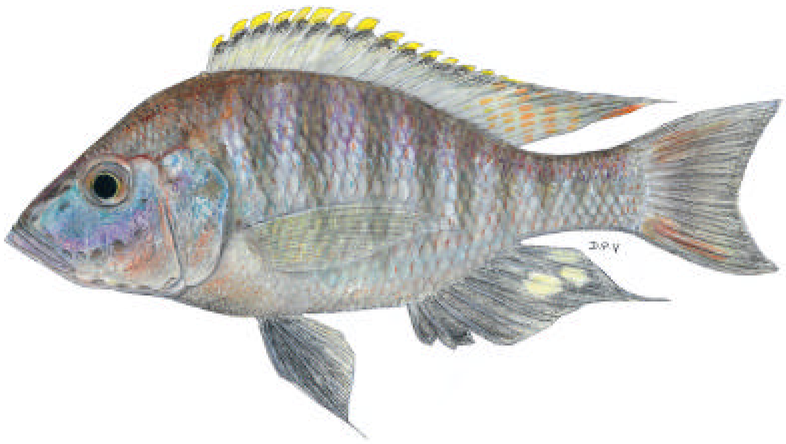

Plate 1. *Alticorpus 'geoffreyi'* (by Dave Voorvelt).

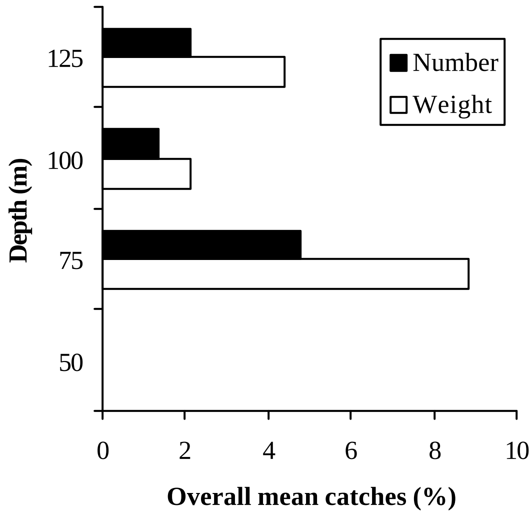

Figure 2-1. Mean occurrence and abundance in the catches per depth of *Alticorpus 'geoffreyi'* in the SWA between July 1998 and May 1999.

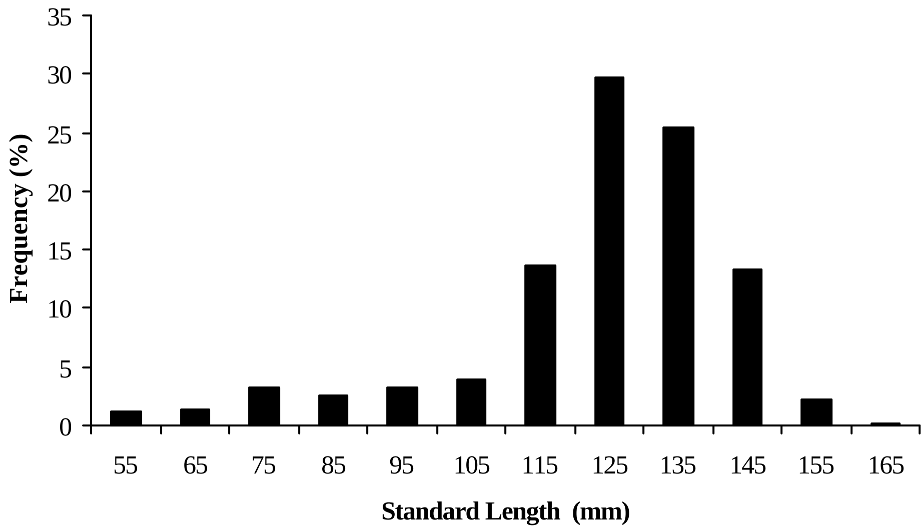

Figure 2-2. Size range and frequencies of *Alticorpus 'geoffreyi'* caught in the SWA between July 1998 and May 1999.

Results

Alticorpus spp.

***Alticorpus 'geoffreyi'* (Plate 1)**

721 females and 845 males were analysed. *A. 'geoffreyi'* is a deep water species rarely encountered at 50m. In our sampling it was most abundant at 75m and still well represented at 125m. (Figure 2-1). It constituted in average between 2 and 9% of the catches in weight and between 1 and 5% in number, depending upon depth, but was more abundant at 75 m. The mean CPUE per depth category was 0.3 kg for the shallow zone, 37.4 in the deep zone, and 9.1 in the very deep zone, which differed markedly with the values reported by Tómasson & Banda (1996) for the shallow (9.3 kg) and deep (11.4 kg) zones, but matched in the very deep zone (9.0 kg). They also observed *A. 'geoffreyi'* from 20 m depth downwards in the SWA, whereas we never encountered it before 50 m. This might explain the difference in CPUE in the shallow zone. Specimens caught ranged between 55 and 165 mm with a mode from 110 to 150 mm (Figure 2-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

The breeding season for females occurred from March to October with a maximum activity between May and August (Figure 2-3a). The proportion of males in breeding colour was much higher than the proportion of ripe females, but basically confirmed the position of the breeding season (Figure 2-3b). Ripe females were mostly found at 75 and 100 m whereas males in breeding colour were much more abundant at 75m, suggesting that breeding could occur around 75 m depth (Table 2-1). The size at maturity of female was about 90mm (Figure 2-4) and was reached at 14 months old.

Table 2-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Alticorpus geoffreyi* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
50 m	0.5	0	0	0.5	
75 m	54.1	38.7	40.2	84.4	78.8
100 m	13.5	42.7	16.7	3.9	15.2
125 m	31.9	18.6	43.1	11.2	6

The length-weight and fecundity-weight relationships are given in Figure 2-5 and 2-6, respectively. Fecundity ranged from 86 to 231 for females weighing between 33 and 94 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3.7% (Figure 2-7) and the mean oocyte weight was 17.70 mg (± 2.48 SD, N= 26).

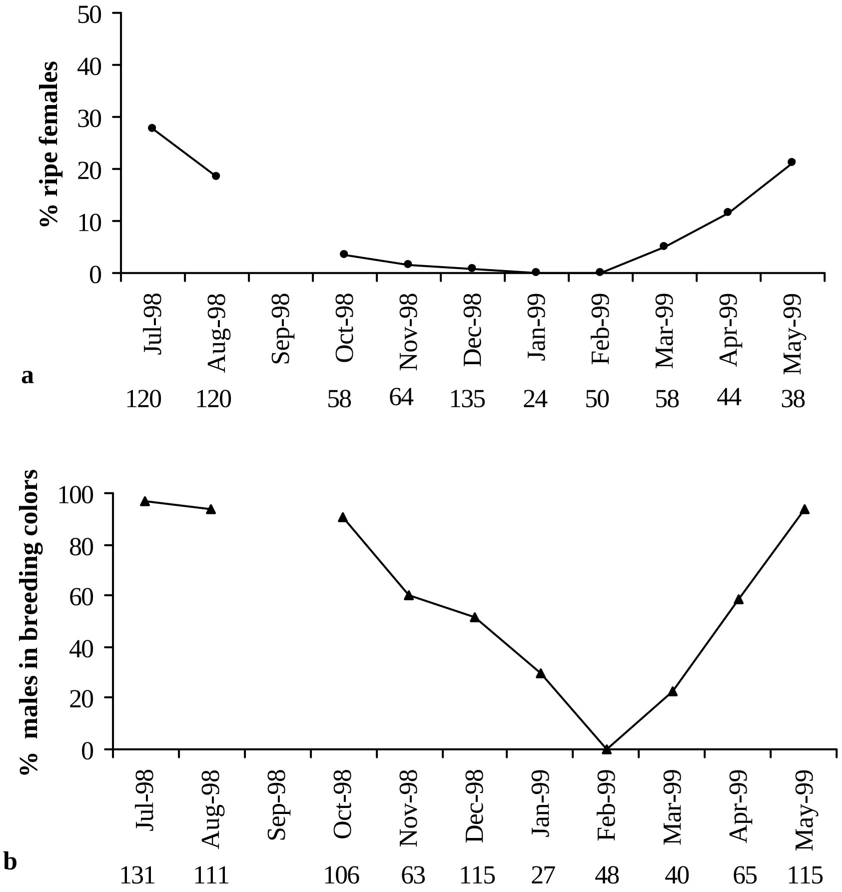

Figure 2-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Alticorpus 'geoffreyi'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

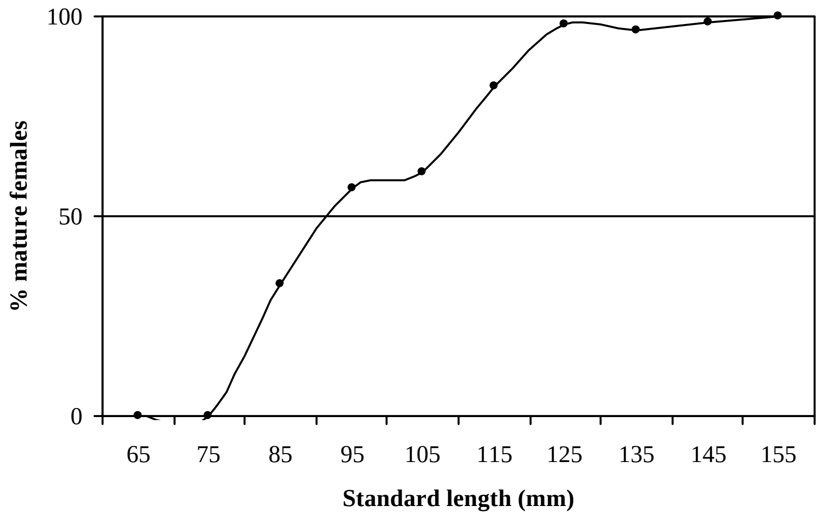

Figure 2-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Alticorpus 'geoffreyi'* in the SWA.

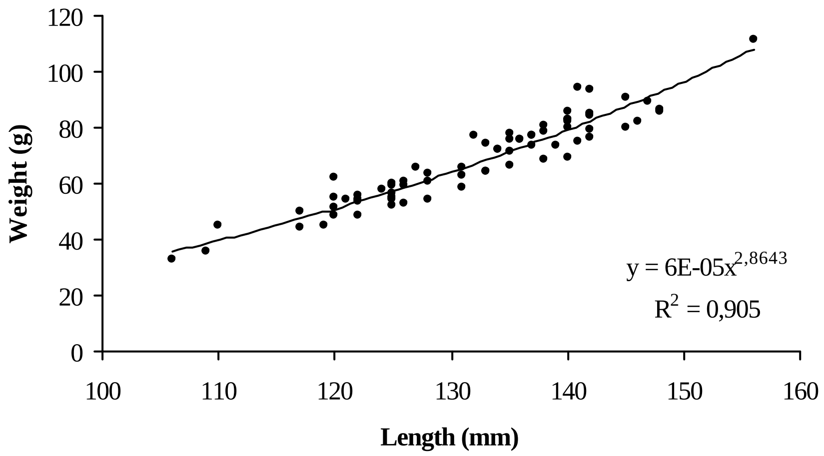

Figure 2-5. Length-weight relationship for *Alticorpus geoffreyi* females in the SWA. (R^2 = determination coefficient).

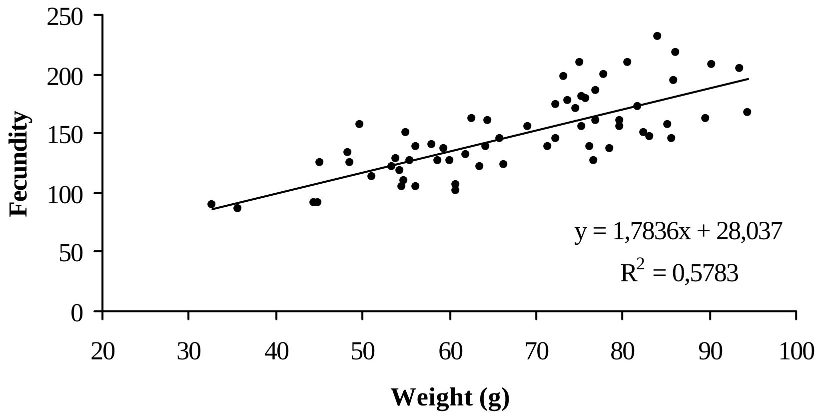

Figure 2-6. Fecundity-weight relationship for *Alticorpus geoffreyi* females in the SWA. (R^2 = determination coefficient).

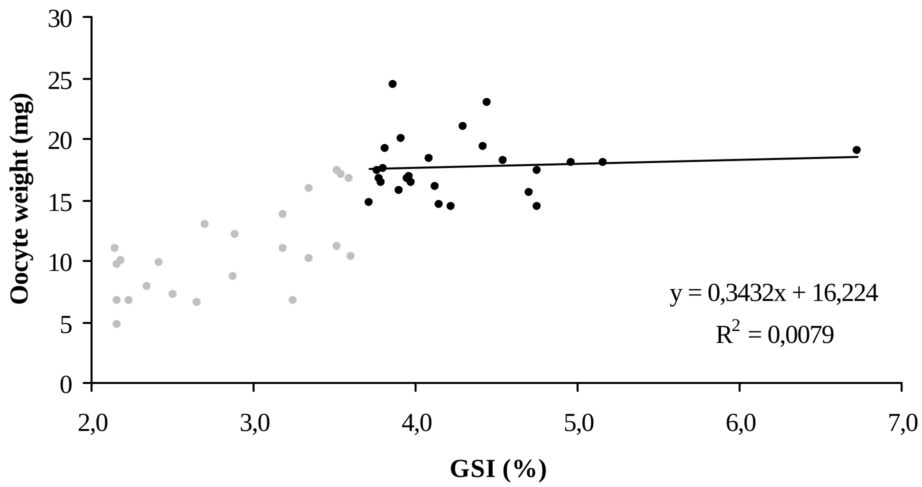

Figure 2-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Alticorpus geoffreyi*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3.7 %. (R^2 = determination coefficient)

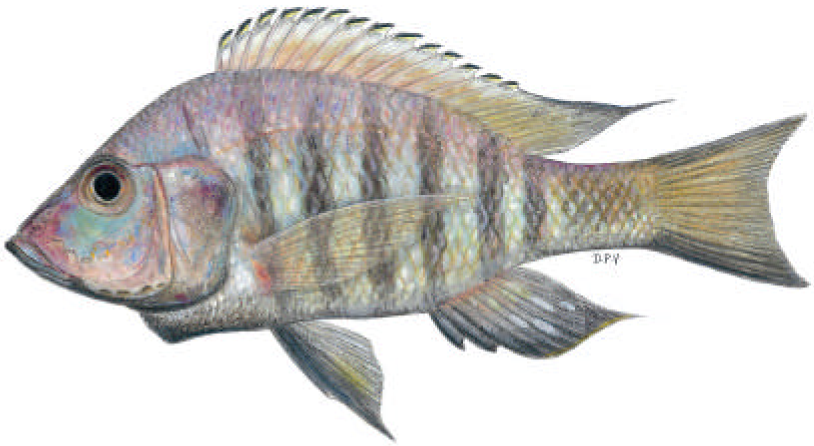

Plate 2. *Alticorpus macrocleithrum* (by Dave Voorvelt).

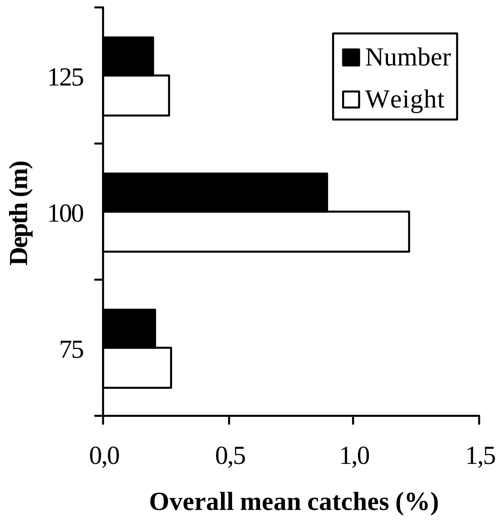

Figure 3-1. Mean occurrence and abundance in the catches per depth of *Alticorpus macrocleithrum* in the SWA between July 1998 and May 1999.

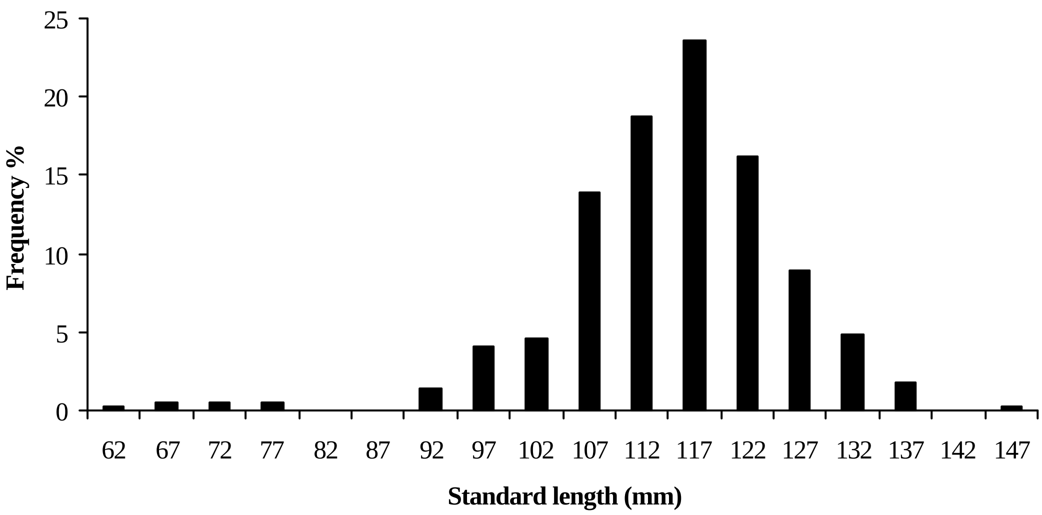

Figure 3-2. Size range and frequencies of *Alticorpus macrocleithrum* caught in the SWA between July 1998 and May 1999.

Alticorpus macrocleithrum (Stauffer & McKaye) (Plate 2)

317 females and 153 males were analysed. *A. macrocleithrum* is a deep water species encountered between 75 m and 125 m, but more abundant at 100 m (Figure 3-1). It is not an abundant species, always constituting less than 1.5% of the catches both in weight and number. The mean CPUE per depth category was 5.1 kg in the deep zone and 0.6 kg in the very deep zone, which is about twice the values reported in Tómasson & Banda (1996) for the deep zone (2.7 kg), but 8 times less in the very deep zone (5 kg). As for *A. 'geoffreyi'*, the depth distribution we found was more restricted than that observed by Tómasson & Banda (1996), who found *A. macrocleithrum* from 40 m downwards. Specimens caught ranged between 60 and 148 mm with a mode from 105 to 130 mm (Figure 3-2). The sex ratio observed over the full sampling period was F/M 0.7/0.3.

Owing to weak sample number at some months both for females and males, the breeding season is difficult to determine with certainty (Figure 3-3a and b). It seemed from female data (Figure 3-3a) that breeding season occurred between April and August. Despite high fluctuations from 0 to 100% due to very low sample size at some months (June, October, April and May), the data for males supported by correct sample size tended to confirm that breeding season. However, the low sample size for females in September–October and in March do not allow us to exclude the possibility that breeding season might be a bit protracted, beginning a bit earlier and finishing a bit later than observed on those graphs (March to September ?). All the breeding females, nearly all (97%) the males in breeding colour (Table 3-1) were found are 100 m, suggesting that spawning might occur at that depth. Maturity was reached early in their second year at 18 months old at a mean size of 100 mm for females (Figure 3-4). However, size at maturity has to be determined at the height of the breeding season to be accurate but owing to the low sample size we had to consider every data available. As a consequence, it is likely that L_{50} was overestimated.

Table 3-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Alticorpus macrocleithrum* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	29.7				
100 m	64.4	100	83.3	96.6	88
125 m	5.9		16.7	3.4	12

The length-weight and fecundity-weight relationships are given in Figure 3-5 and 3-6, respectively. Fecundity ranged from 96 to 304 for females weighing between 26 and 76 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 4.5% (Figure 3-7) and the mean oocyte weight was 12.73 mg (± 2.6 SD, N= 24).

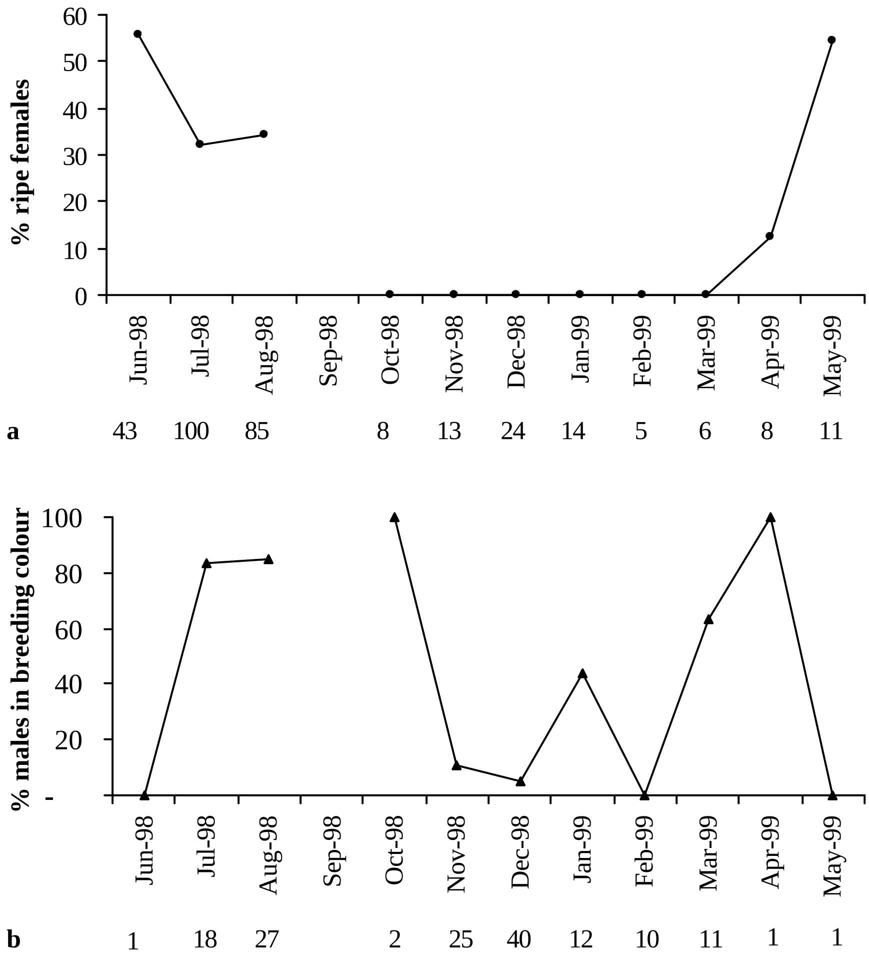

Figure 3-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Alticorpus macrocleithrum* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

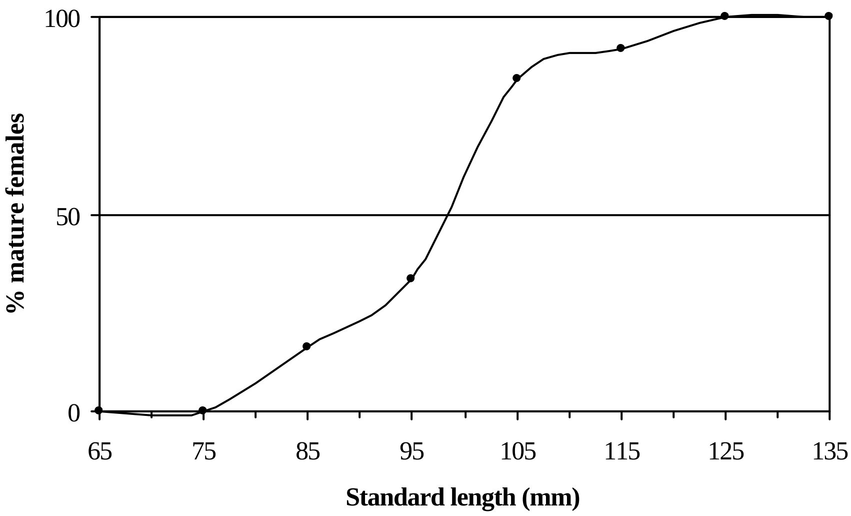

Figure 3-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Alticorpus macrocleithrum* in the SWA.

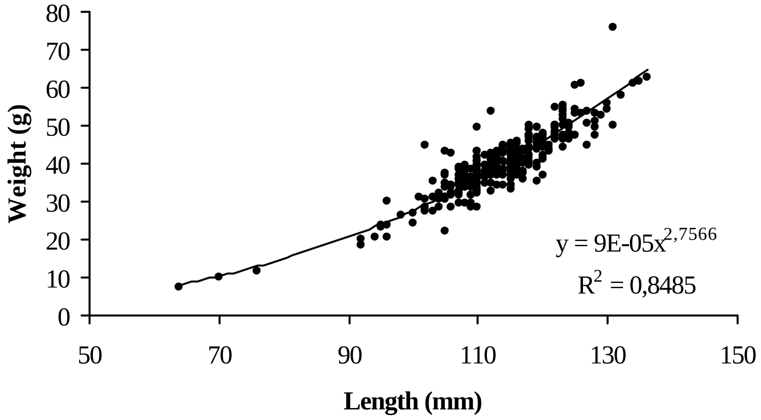

Figure 3-5. Length-weight relationship for *Alticorpus macrocleithrum* females in the SWA. (R^2 = determination coefficient).

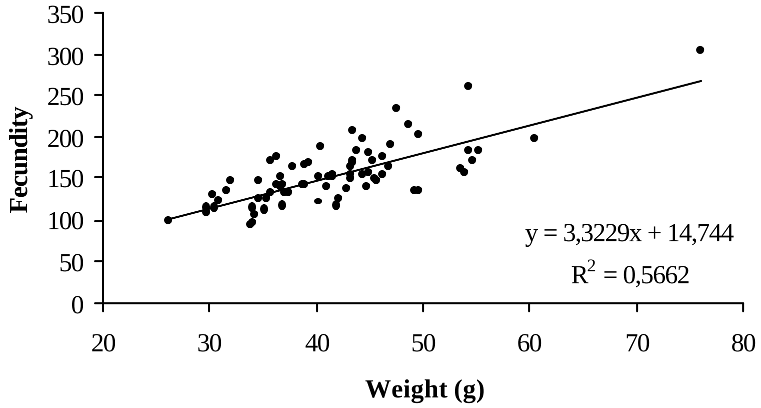

Figure 3-6. Fecundity-weight relationship for *Alticorpus macrocleithrum* females in the SWA. (R^2 = determination coefficient).

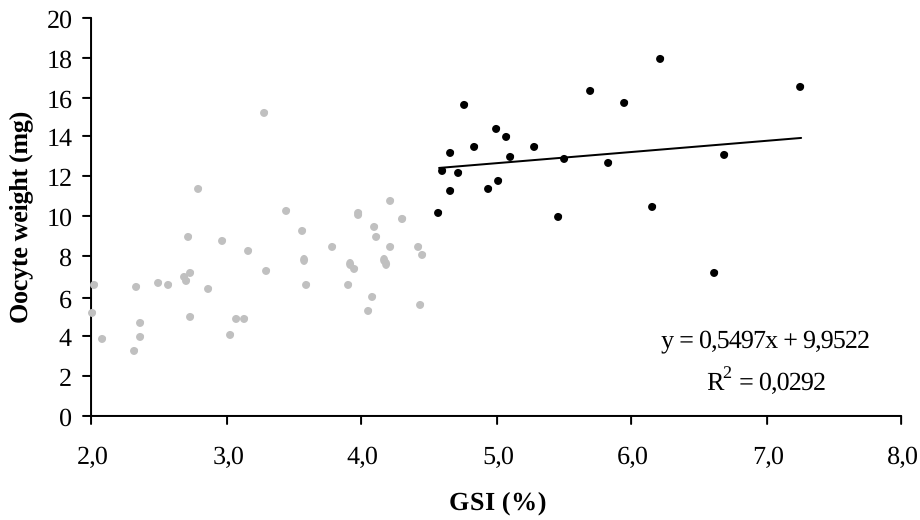

Figure 3-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Alticorpus macrocleithrum*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 4.5%. (R^2 = determination coefficient)

Plate 3. *Alticorpus mentale* (by Dave Voorvelt).

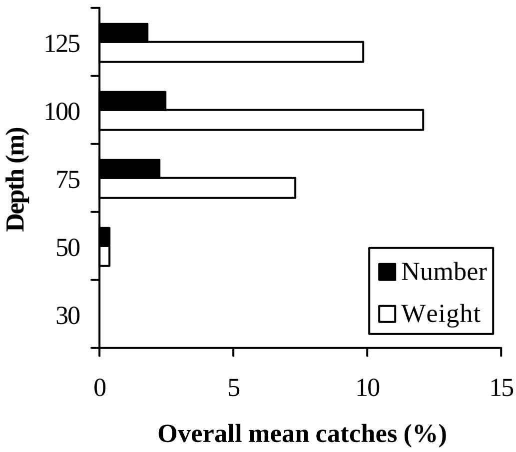

Figure 4-1. Mean occurrence and abundance in the catches per depth of *Alticorpus mentale* in the SWA between July 1998 and May 1999.

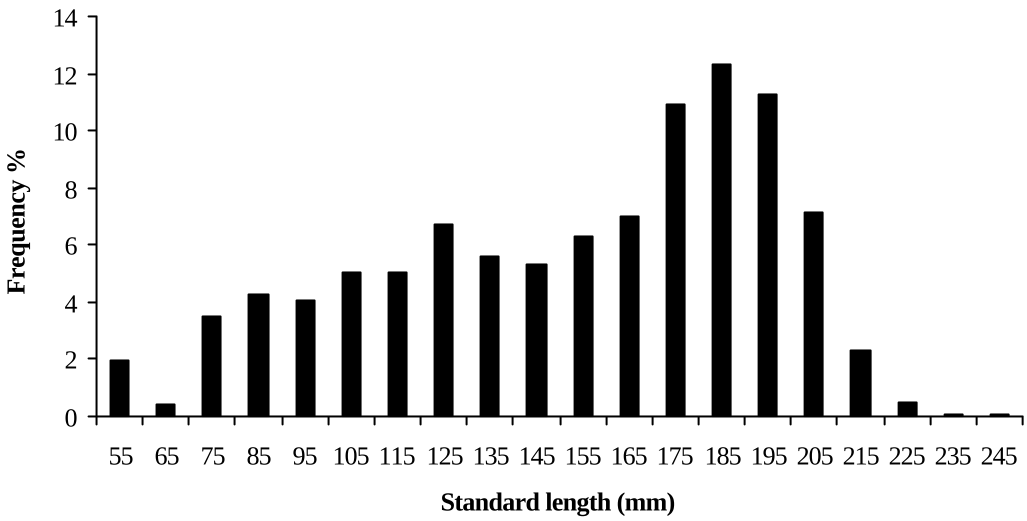

Figure 4-2. Size range and frequencies of *Alticorpus mentale* caught in the SWA between July 1998 and May 1999.

Alticorpus mentale (Stauffer & McKaye) (Plate 3)

1011 females and 959 males were analysed. *A. mentale* is a deep water species that can be encountered from 30 m but becomes abundant from 75 m downwards (Figure 4-1). It is an abundant fish always constituting between 7 and 13% of the catches in weight and a bit less in number (about 3%) due to its large size. The mean CPUE per depth category was 1.1 kg in the shallow zone, 51.1 kg in the deep zone and 20.1 kg in the very deep zone, which is about twice as much as reported in Tómasson & Banda (1996) for the deep and very deep zones (11.4 and 12.7 kg, respectively), but 2 times less in the shallow zone (2.3 kg). The depth distribution we found corresponded with that observed by Tómasson & Banda (1996). Specimens caught ranged between 53 and 245 mm (Figure 4-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Unlike *A. 'geoffreyi'* and *A. macrocleithrum*, *A. mentale* breeds throughout the year with a peak in November and another one in January-February and a marked decrease of activity in December and May (Figure 4-3a). Males in breeding colour were also found at each month even thought peaks of activity did not necessarily match those of females (Figure 4-3b). It is interesting to note that the period from November to March is the period when *Aulonocara 'minutus'*, frequently found as the dominant prey items in *A. mentale* stomach contents (see Chapter "Diet"), was most abundant in the catches. Ripe females were more abundant at 75 and 100 m whereas males in breeding colour were preferentially found at 100 m and 125 m in a lesser extent (Table 4-1). Immature individuals were mostly found at 75 m but were reasonably abundant at 100 and 125 m. *A. mentale* seems able to spawn at any depth between 75 and 125 m. Maturity was reached early in their second year at 16 months old at a mean size of 160 mm for females (Figure 4-4).

Table 4-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Alticorpus mentale* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
30 m	0.2	0	0	0	0
50 m	1	0	2.6	0.5	4.7
75 m	39	41.8	4.3	9.4	54.3
100 m	26.9	44.5	25	68.5	19.6
125 m	32.8	13.6	29.1	21.6	21.5

The length-weight and fecundity-weight relationships are given in Figure 4-5 and 4-6, respectively. Fecundity ranged from 92 to 356 for females weighing between 49 and 307 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 4-7) and the mean oocyte weight was 24.36 mg (± 4.18 SD, N= 31).

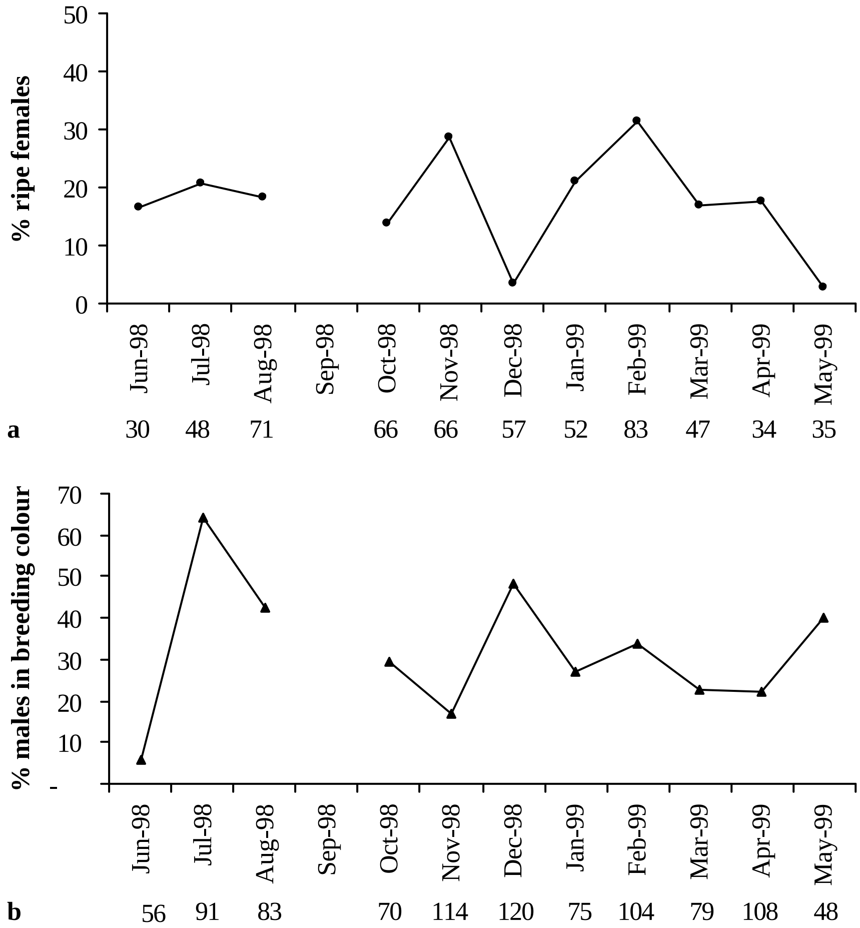

Figure 4-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Alticorpus mentale* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

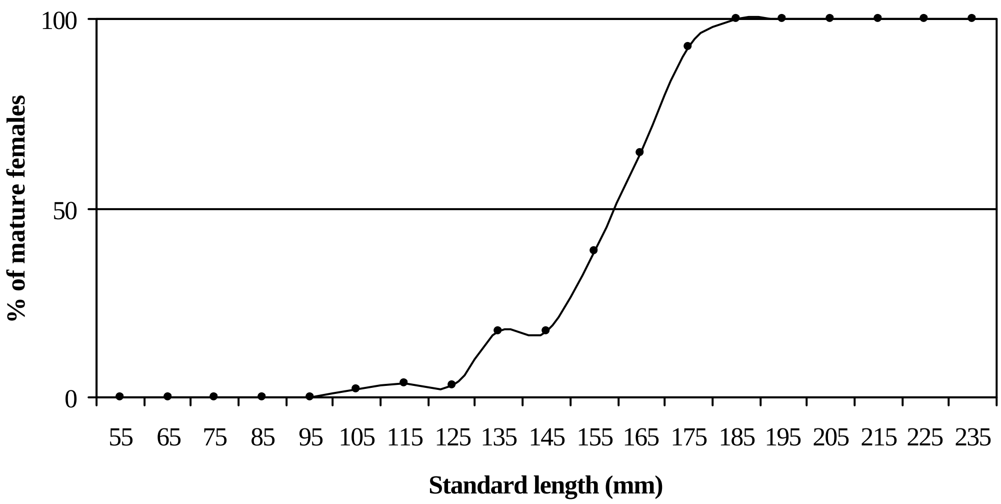

Figure 4-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Alticorpus mentale* in the SWA.

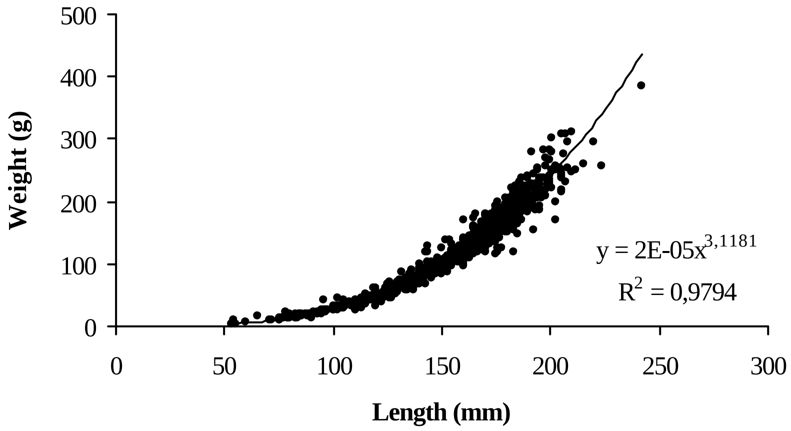

Figure 4-5. Length-weight relationship for *Alticorpus mentale* females in the SWA. (R^2 = determination coefficient).

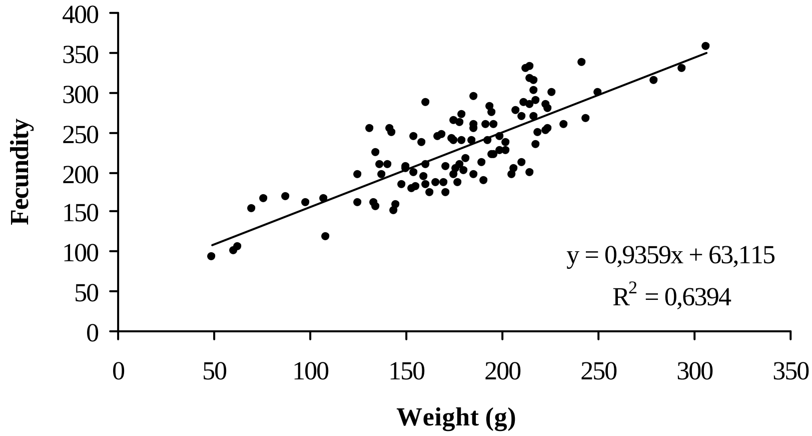

Figure 4-6. Fecundity-weight relationship for *Alticorpus mentale* females in the SWA. (R^2 = determination coefficient).

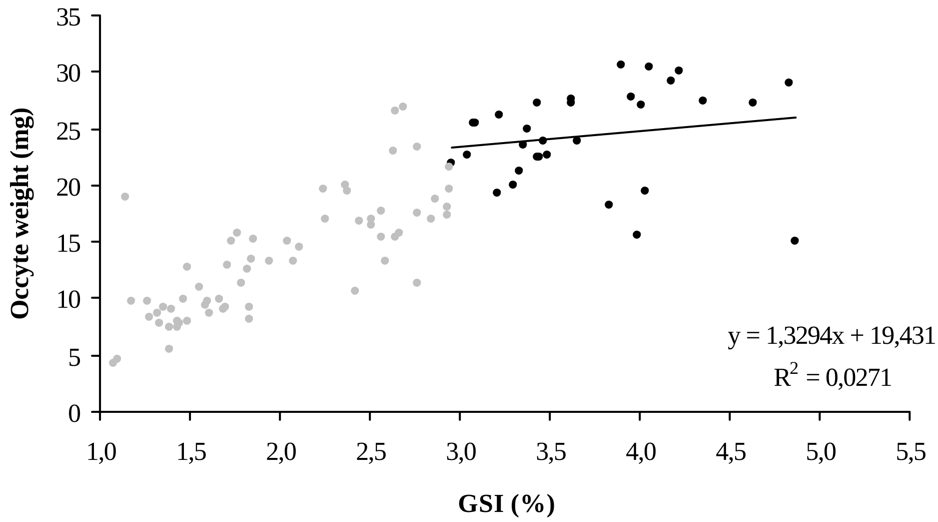

Figure 4-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Alticorpus mentale*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient)

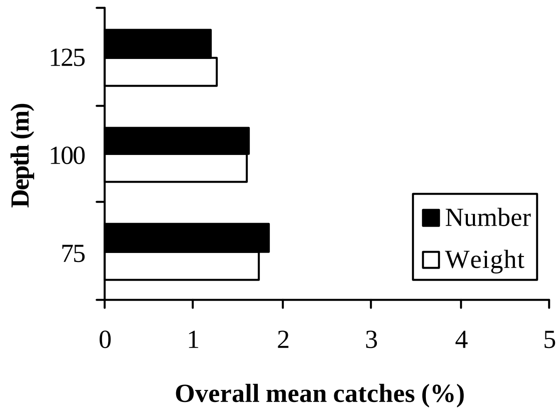

Figure 5-1. Mean occurrence and abundance in the catches per depth of *Alticorpus pectinatum* in the SWA between July 1998 and May 1999.

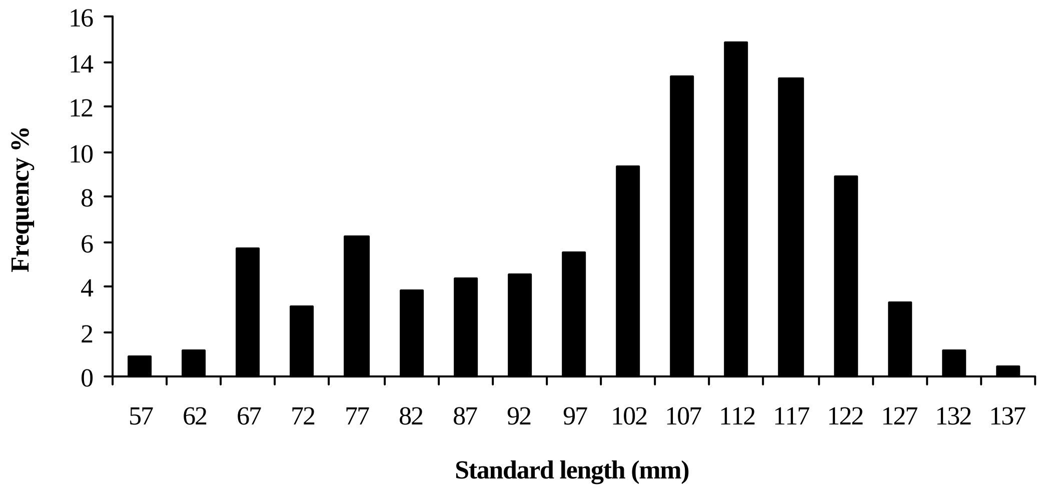

Figure 5-2. Size range and frequencies of *Alticorpus pectinatum* caught in the SWA between July 1998 and May 1999.

Alticorpus pectinatum (Stauffer & McKaye)

259 females and 375 males were analysed. *A. pectinatum* is a deep water fish evenly distributed between 75 m and 125 m (Figure 5-1). It is not an abundant species, always constituting between 1 and 2% of the catches both in weight and number. The mean CPUE per depth category was 8.4 kg in the deep zone and 2.6 kg in the very deep zone, which is about twice as much as the values reported in Tómasson & Banda (1996) for the deep zone (3.8 kg), but about 4 times less in the very deep zone (8.9 kg). As for *A. 'geoffreyi'* and *A. macrocleithrum*, the depth distribution we found was more restricted than that observed by Tómasson & Banda (1996), who found *A. pectinatum* from 45 m downwards. Specimens caught ranged between 55 and 140 mm with a mode from 100 to 125 mm (Figure 5-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

The breeding season occurred from November to May with an increased activity in January-February (Figure 5-3a). The monthly progression of males in breeding colour indicated the same pattern and suggested that breeding season could be protracted, occurring also in June, when all the males (43) were in breeding colour (Figure 5-3b). About three quarter of the breeding females were found at 100 m and the other quarter at 75 m, whereas males in breeding colour and immature individuals were more evenly distributed at 75 and 100 m (Table 5-1). Spawning might occur mostly at 100 m although males and immature distribution does not confirm it firmly. Maturity was reached early in their second year at 12 months old at a mean size of 70 mm for females (Figure 5-4).

Table 5-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Alticorpus pectinatum* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	37.6	24.1	53.3	47	42.3
100 m	40.2	72.4	19.2	30.5	50
125 m	22.3	3.4	27.5	22.5	7.7

The length-weight and fecundity-weight relationships are given in Figure 5-5 and 5-6, respectively. Fecundity ranged from 38 to 181 for females weighing between 7 and 44 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 4% (Figure 5-7) and the mean oocyte weight was 15.29 mg (± 2.8 SD, N= 3).

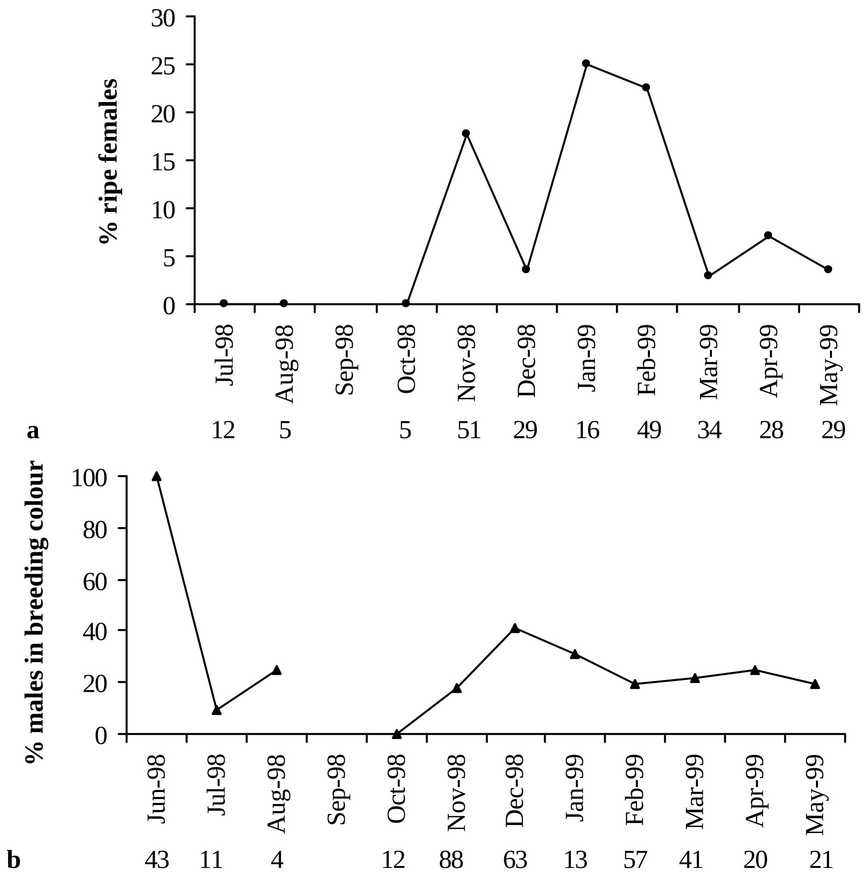

Figure 5-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Alticorpus pectinatum* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

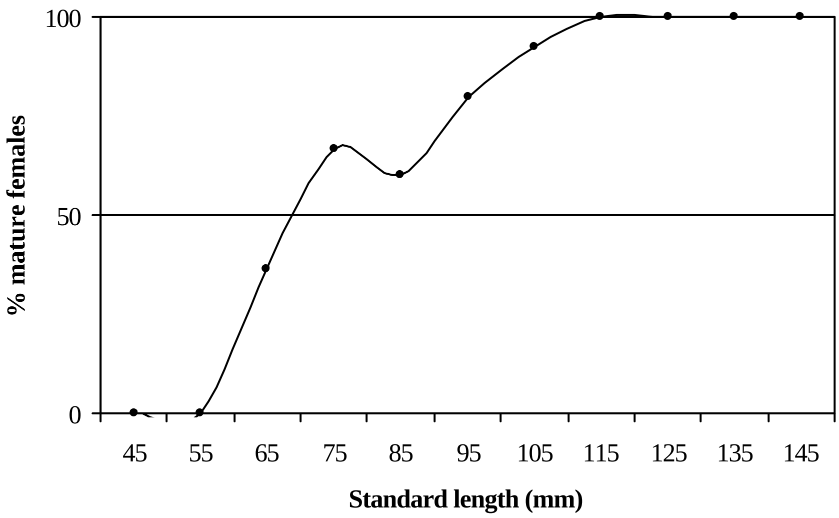

Figure 5-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Alticorpus pectinatum* in the SWA.

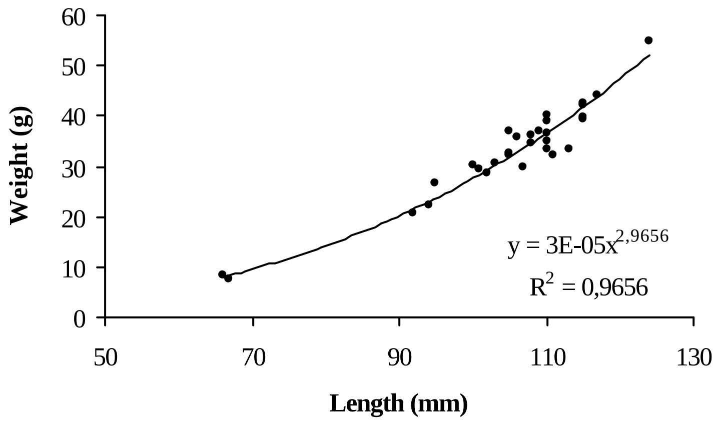

Figure 5-5. Length-weight relationship for *Alticorpus pectinatum* females in the SWA. (R^2 = determination coefficient).

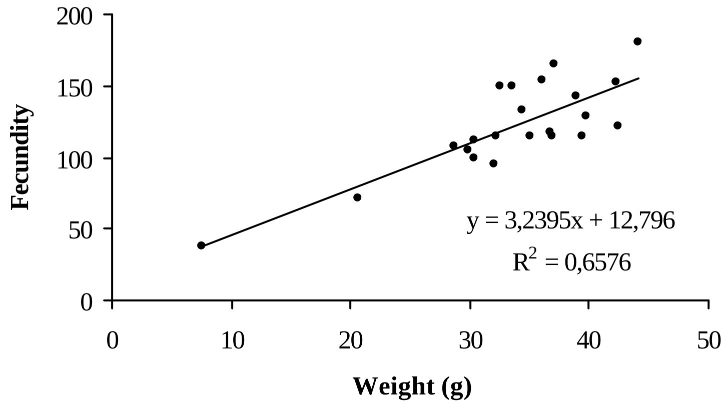

Figure 5-6. Fecundity-weight relationship for *Alticorpus pectinatum* females in the SWA. (R^2 = determination coefficient).

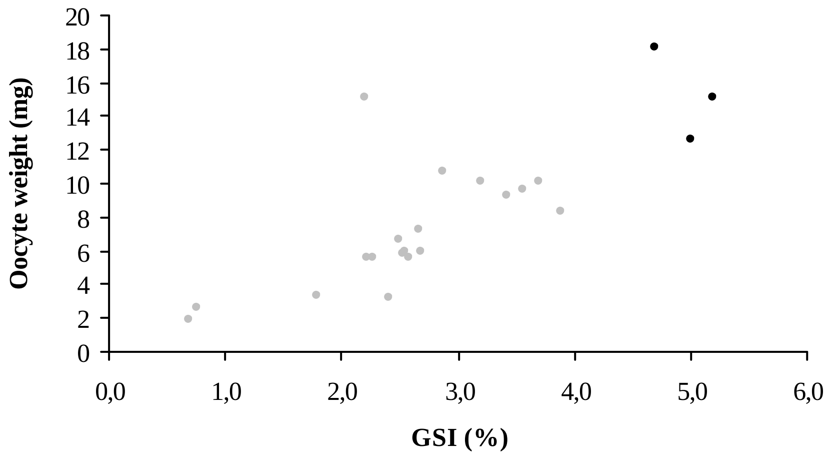

Figure 5-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Alticorpus pectinatum*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 4%. (R^2 = determination coefficient)

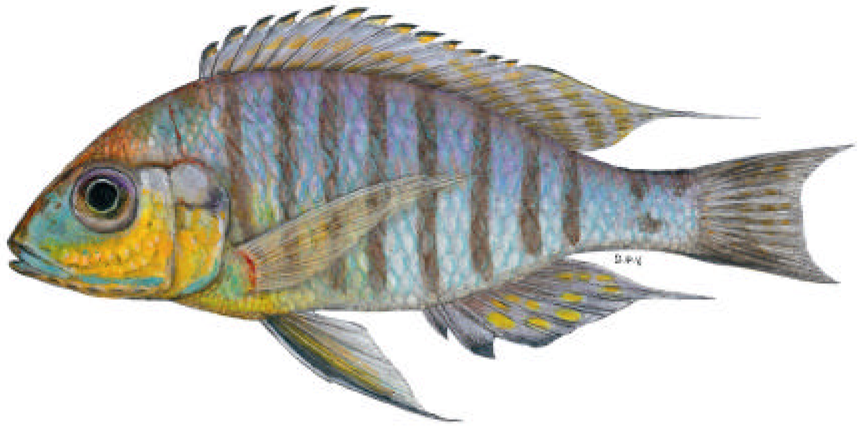

Plate 4. *Aulonocara 'blue orange'* (by Dave Voorvelt).

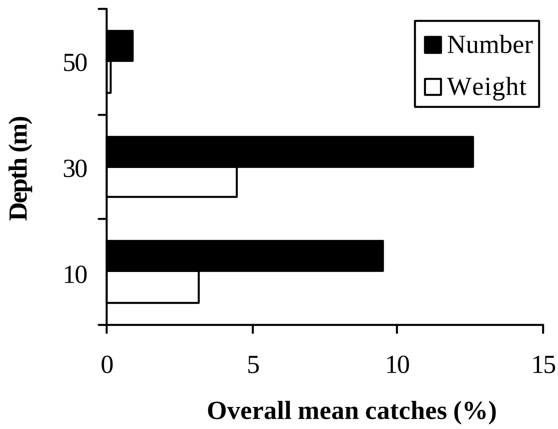

Figure 6-1. Mean occurrence and abundance in the catches per depth of *Aulonocara 'blue orange'* in the SWA between July 1998 and May 1999.

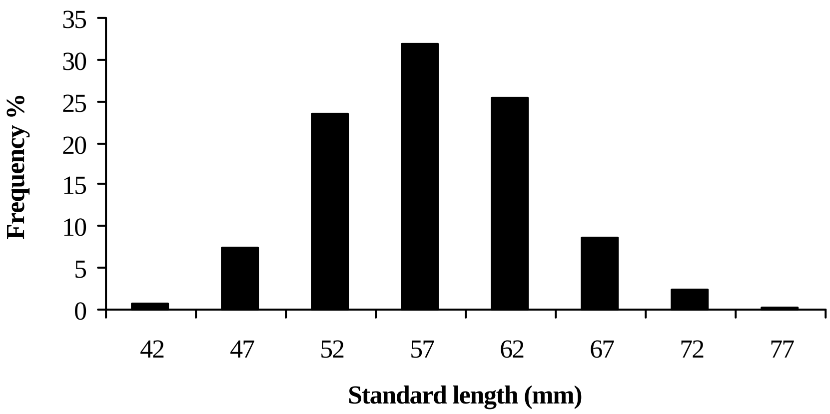

Figure 6-2. Size range and frequencies of *Aulonocara 'blue orange'* caught in the SWA between July 1998 and May 1999.

Aulonocara spp.

Aulonocara 'blue orange' (Plate 4)

244 females and 485 males were analysed. *A. 'blue orange'* is a small fish encountered in shallow water between 10 and 50 m but only abundant at 10 and 30 m, where it constituted 9.5 and 12.6% of the catches in number, respectively and 3.2 and 4.5% in weight (Figure 6-1). It was found only once at 75 m in November 98. The mean CPUE per depth category was higher (17.6 kg in the shallow zone) than that reported in Tómasson & Banda (1996). The depth distribution was much more restricted in our case than the 10 to 130 m depth range they reported. Specimens caught ranged between 40 and 80 mm with a mode from 50 to 65 mm (Figure 6-2). The sex ratio observed over the full sampling period was F/M 0.3/0.7.

Owing to identification uncertainty, data from June and July 1998 were not included in the analyses. The breeding season seemed to occur between July-August and February (Figure 6-3a and b). However, due to the very low sample size in March and April and the high percentage of males in breeding colour in April and May, it can't be excluded that *A. 'blue orange*' might breed throughout the year. More than three quarter of the ripe females were sampled at 10 m and the other quarter at 30 m (Table 6-1). Males in breeding colour were evenly distributed between 10 and 30 m and most of the immature individuals were found at 30 m. If *A. 'blue orange*' does spawn at a precise depth, it does not reflect clearly in breeding males and immature distribution. However, the results suggest that spawning would occur around 10 m. Maturity was reached in their first year at 9 months old at a mean size of 48 mm for females (Figure 6-4).

Table 6-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Aulonocara 'blue orange'* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	47.3	76	60.9	45.5	34.2
30 m	47.9	24	36.6	48.5	61.8
50 m	4.8	0	2.6	6.1	3.9

The length-weight and fecundity-weight relationships are given in Figure 6-5 and 6-6, respectively. Fecundity ranged from 9 to 41 for females weighing between 2 and 7g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 2.5% (Figure 6-7) and the mean oocyte weight was 4.46 mg (± 0.89 SD, N= 16).

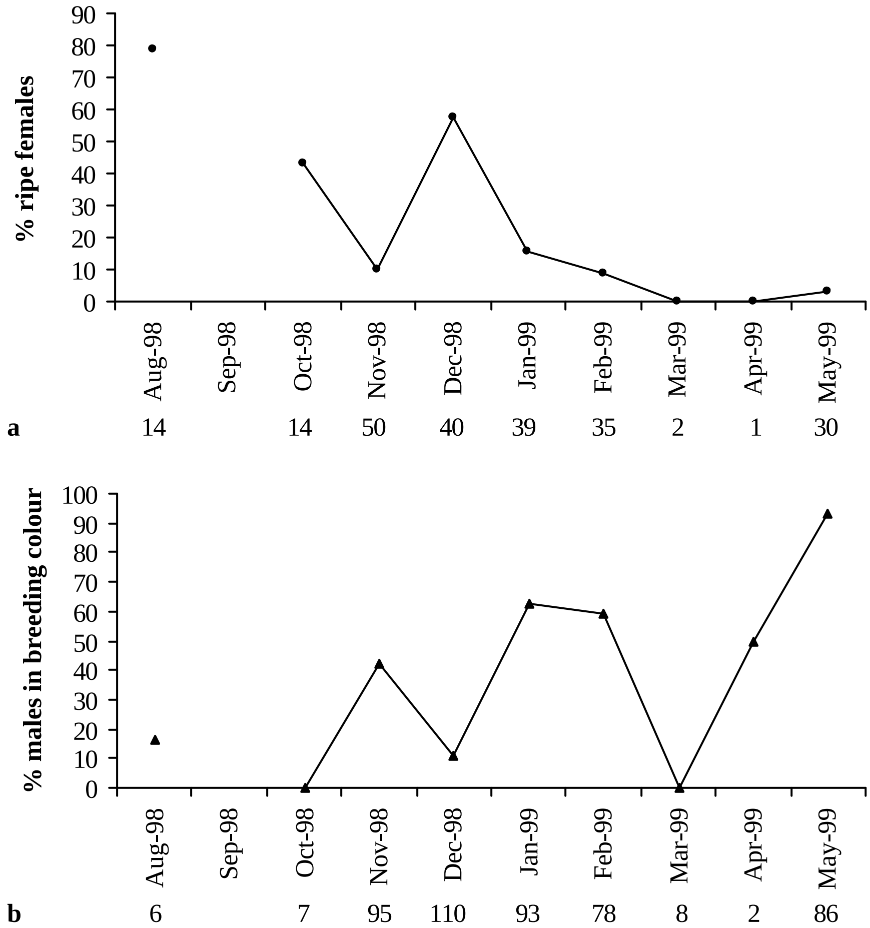

Figure 6-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Aulonocara 'blue orange'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

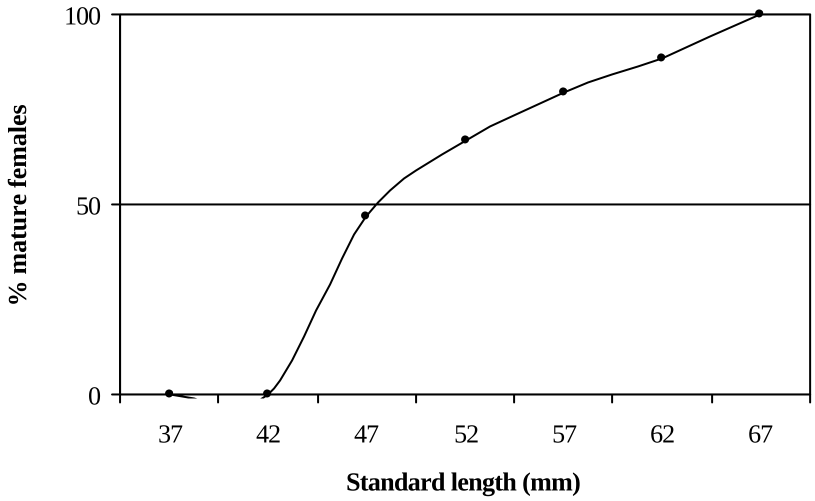

Figure 6-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Aulonocara 'blue orange'* in the SWA.

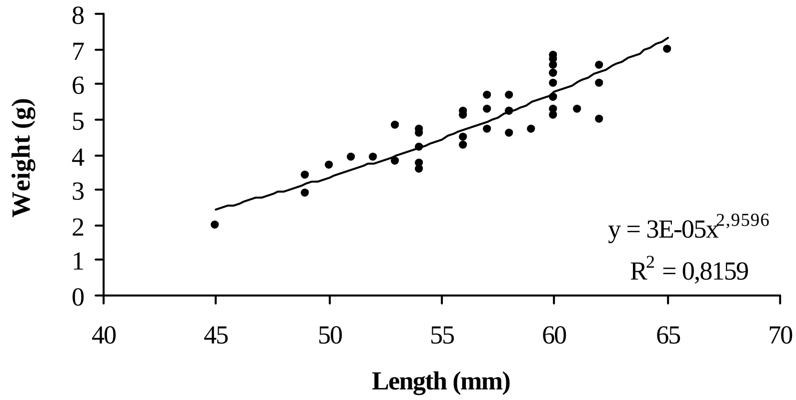

Figure 6-5. Length-weight relationship for *Aulonocara 'blue orange'* females in the SWA. (R^2 = determination coefficient).

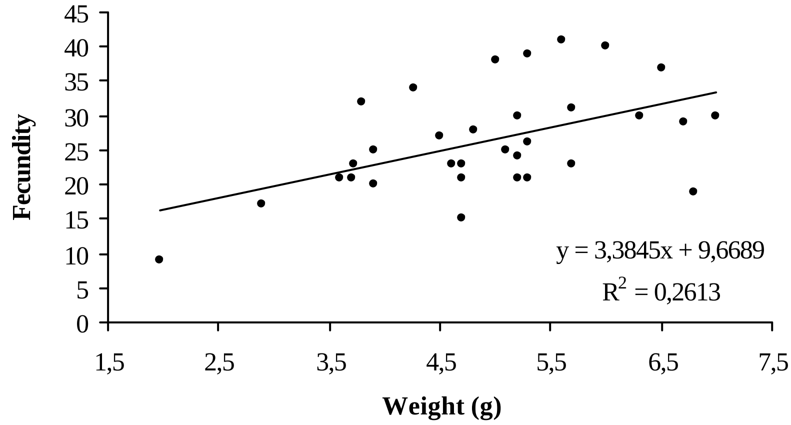

Figure 6-6. Fecundity-weight relationship for *Aulonocara 'blue orange'* females in the SWA. (R^2 = determination coefficient).

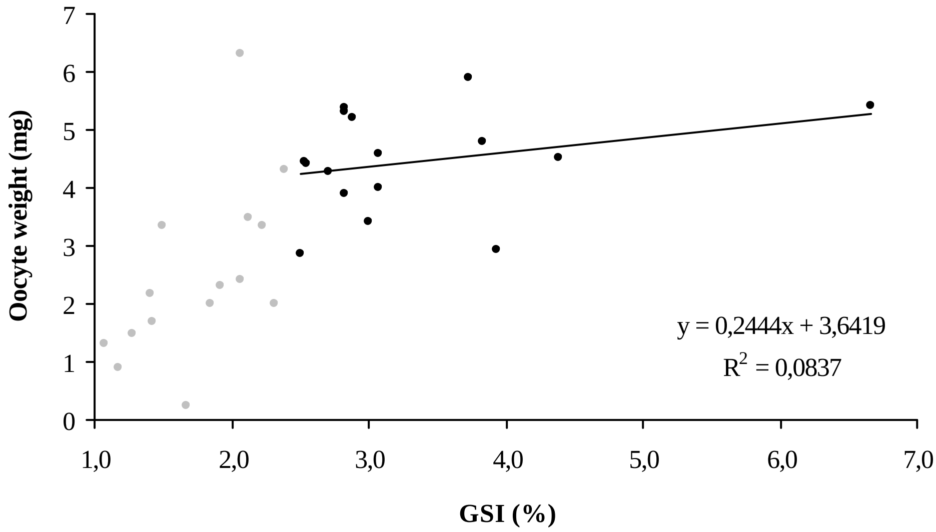

Figure 6-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Aulonocara 'blue orange'*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 2.5%. (R^2 = determination coefficient).

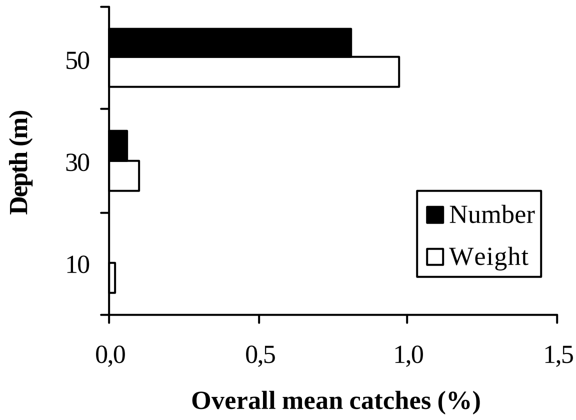

Figure 7-1. Mean occurrence and abundance in the catches per depth of *Aulonocara 'cf. macrochir'* in the SWA between July 1998 and May 1999.

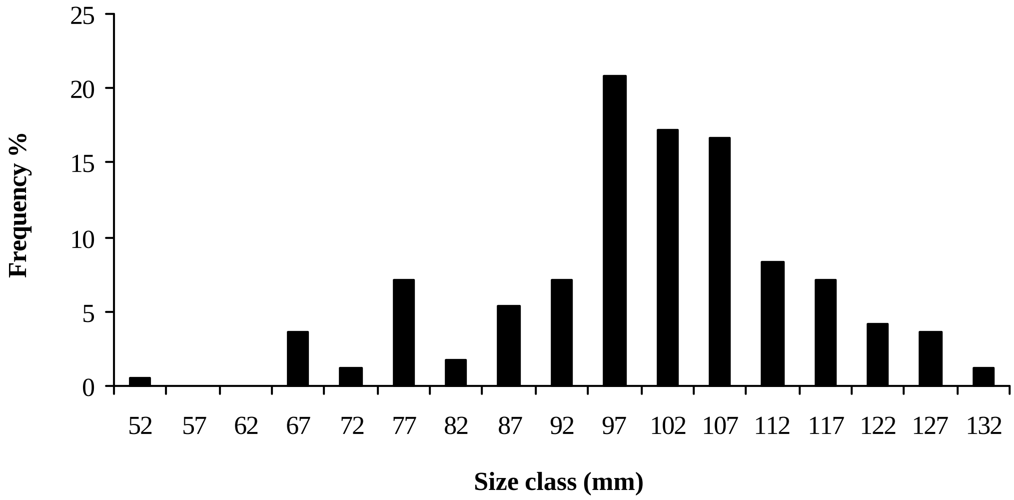

Figure 7-2. Size range and frequencies of *Aulonocara 'cf. macrochir'* caught in the SWA between July 1998 and May 1999.

Aulonocara 'cf. macrochir'

74 females and 90 males were analysed. *A. 'cf. macrochir'* was a relatively rare fish encountered from 10 m to 50 m but more abundant at 50 m where it constituted 1% and 0.8% of the catches in weight and number, respectively (Figure 7-1). The mean CPUE per depth category (2.7 kg in the shallow zone) matched that reported in Tómasson & Banda (1996). The depth distribution was much more restricted in our case than the 8 to 150 m depth range that they reported. Specimens caught ranged between 50 and 135 mm with a mode from 95 to 110 mm (Figure 7-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

As *A. 'cf. macrochir'* is a relatively rare species, the following information about life history traits is based on low sample size and can not be considered as very reliable but rather as indicative. A breeding activity was observed from August to October and from December to March (Figure 7-3a and b). Taking into account the sparse information available about both females and males, it can be hypothesised that this species might breed most of the year, with reduced activity in June and July. As most specimens were caught at 50 m the percentages of ripe females (62.5%), males in breeding colour (100%) and immature individuals (87%) at this depth suggested that spawning probably occurs at 50 m. Maturity was reached at about 100 mm for females (Figure 7-4). Again, owing to low sample size, L_{50} was probably overestimated and is likely to be closer to 90 mm.

The length-weight and fecundity-weight relationships are given in Figure 7-5 and 7-6, respectively. Fecundity ranged from 50 to 134 for females weighing between 16 and 60 g. No relationship was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was impossible to assess due to the low sample size. However, as no relationship was found between oocyte weight and GSI from the data available (Figure 7-7), the mean oocyte weight was estimated from all the available data and was 4.82 mg (± 1.13 SD, N= 8).

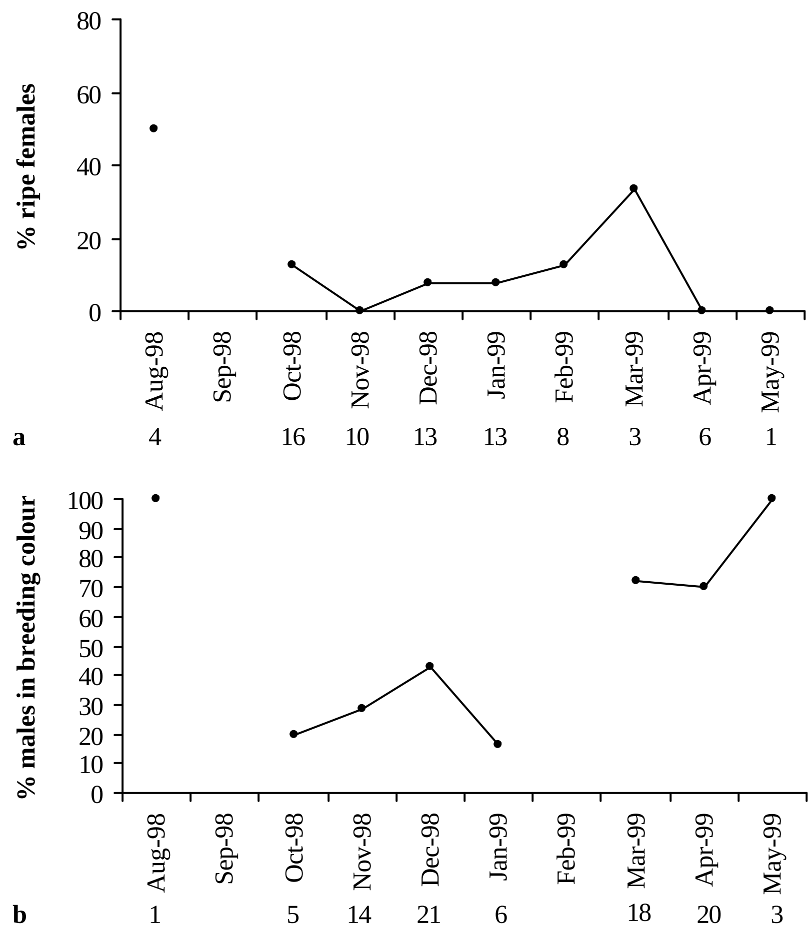

Figure 7-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Aulonocara 'cf. macrochir'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

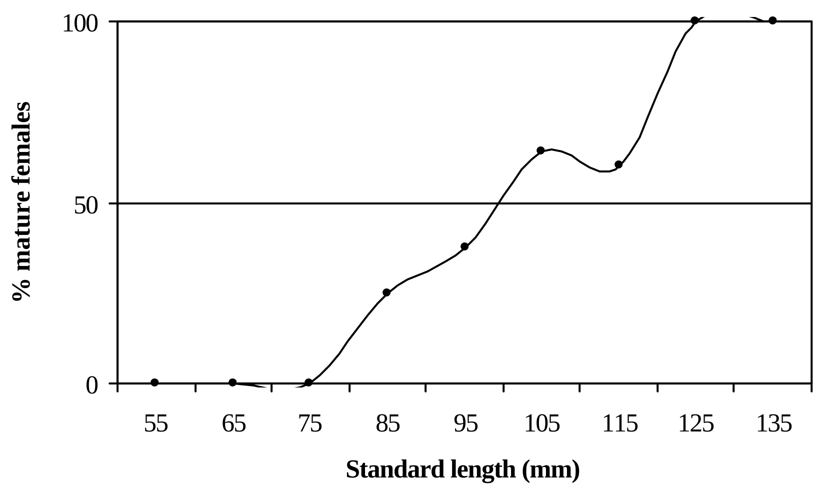

Figure 7-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Aulonocara 'cf. macrochir'* in the SWA.

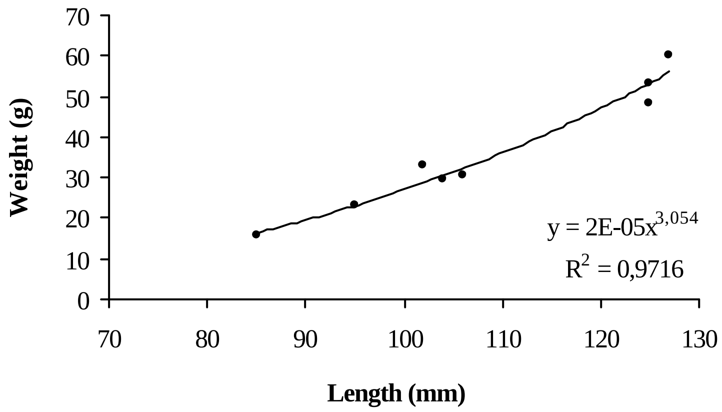

Figure 7-5. Length-weight relationship for *Aulonocara 'cf. macrochir'* females in the SWA. (R^2 = determination coefficient).

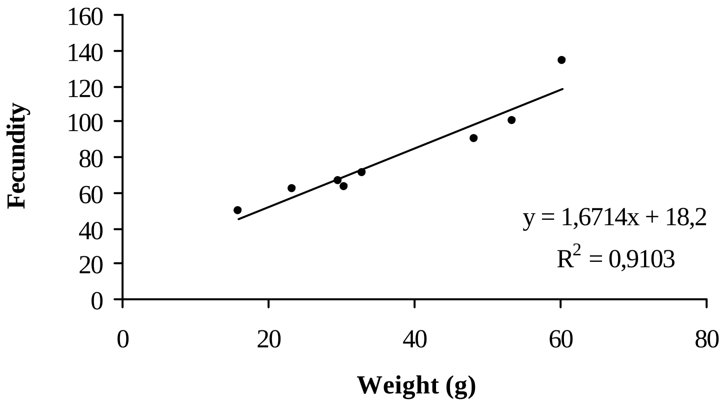

Figure 7-6. Fecundity-weight relationship for *Aulonocara 'cf. macrochir'* females in the SWA. (R^2 = determination coefficient).

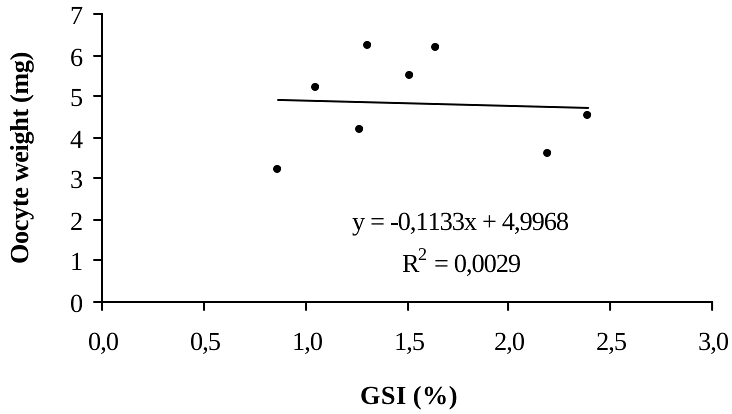

Figure 7-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Aulonocara 'cf. macrochir'*. (R^2 = determination coefficient).

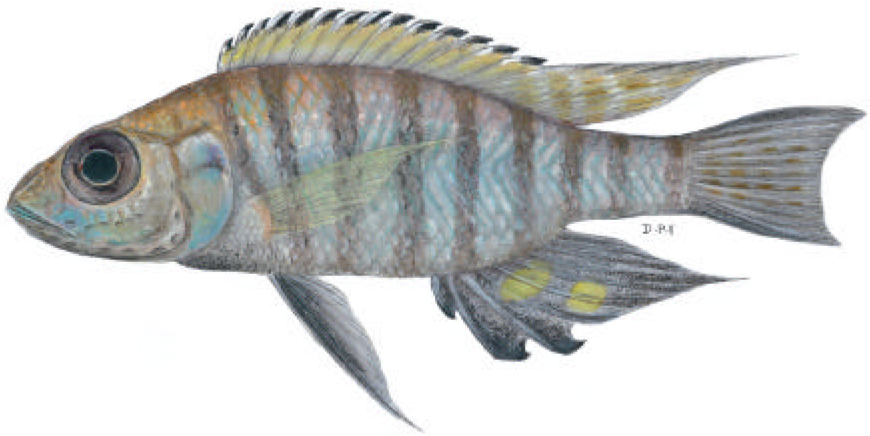

Plate 5. *Aulonocara 'minutus'* (by Dave Voorvelt).

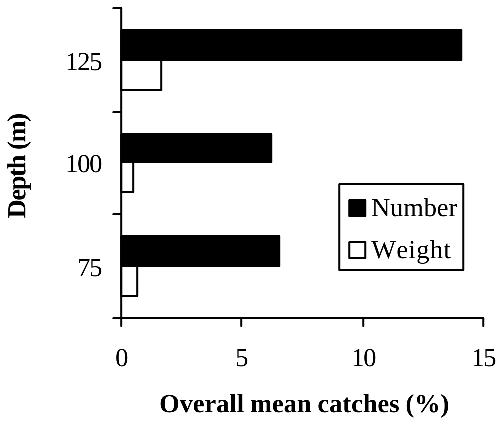

Figure 8-1. Mean occurrence and abundance in the catches per depth of *Aulonocara 'minutus'* in the SWA between July 1998 and May 1999.

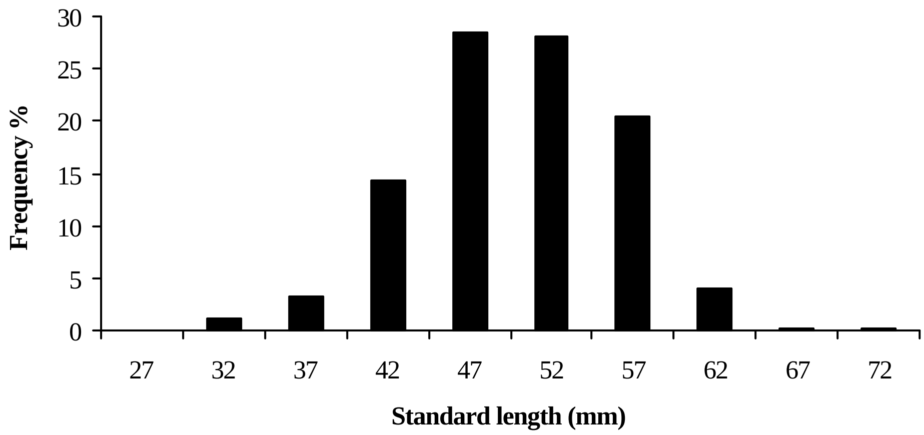

Figure 8-2. Size range and frequencies of *Aulonocara 'minutus'* caught in the SWA between July 1998 and May 1999.

Aulonocara 'minutus' (Plate 5)

573 females and 781 males were analysed. *A. 'minutus'* is a deep water fish caught from 75 to 125 m depth (Figure 8-1). It was much more abundant at 125 m, where it constituted up to 14% of the catches in number and only 1.7% in weight owing to its very small size. *A. 'minutus'* is one of the smallest demersal species of Lake Malawi. Specimens collected ranged between 25 and 75 mm with a mode from 40 to 60 mm (Figure 8-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6. The mean CPUE per depth category was 3.5 kg in the deep zone and 2.6 kg in the very deep zone, which is about two times less than the values reported in Tómasson & Banda (1996) for the deep zone (7.3 kg), and about 4 times less in the very deep zone (11.3 kg). As for *A. 'cf. macrochir'* and *A. 'blue orange'*, the depth distribution we found was much more restricted than that observed by Tómasson & Banda (1996), who found *A. 'minutus'* from 10 to 130 m.

Unlike *A. 'cf. macrochir'* and *A. 'blue orange'*, *A. 'minutus'* was found to breed throughout the year with an increased activity in June and February (Figure 8-3a and b). About 50% of non breeding females and males as well as immature individuals were found at 125 m, the other half being evenly distributed between 75 and 100m (Table 8-1). On the other hand, about 50% of the ripe females and males in breeding colour were caught at 100 m, whereas the other half were evenly distributed at 75 and 125. This suggested that spawning might occur at 100 m. Maturity was reached in their first year at 7 months at a mean size of 42 mm for females (Figure 8-4).

Table 8-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Aulonocara 'minutus'* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	24.2	18.7	15.7	20.9	18.1
100 m	27.7	53.8	28.6	48.1	32.2
125 m	48.1	27.5	55.7	31	49.7

The length-weight and fecundity-weight relationships are given in Figure 8-5 and 8-6, respectively. Fecundity ranged from 50 to 134 for females weighing between 16 and 60 g and was not significantly correlated to female body weight (r = 0.26). No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 2% (Figure 8-7) and the mean oocyte weight was 3.82 mg (± 1.13 SD, N= 29).

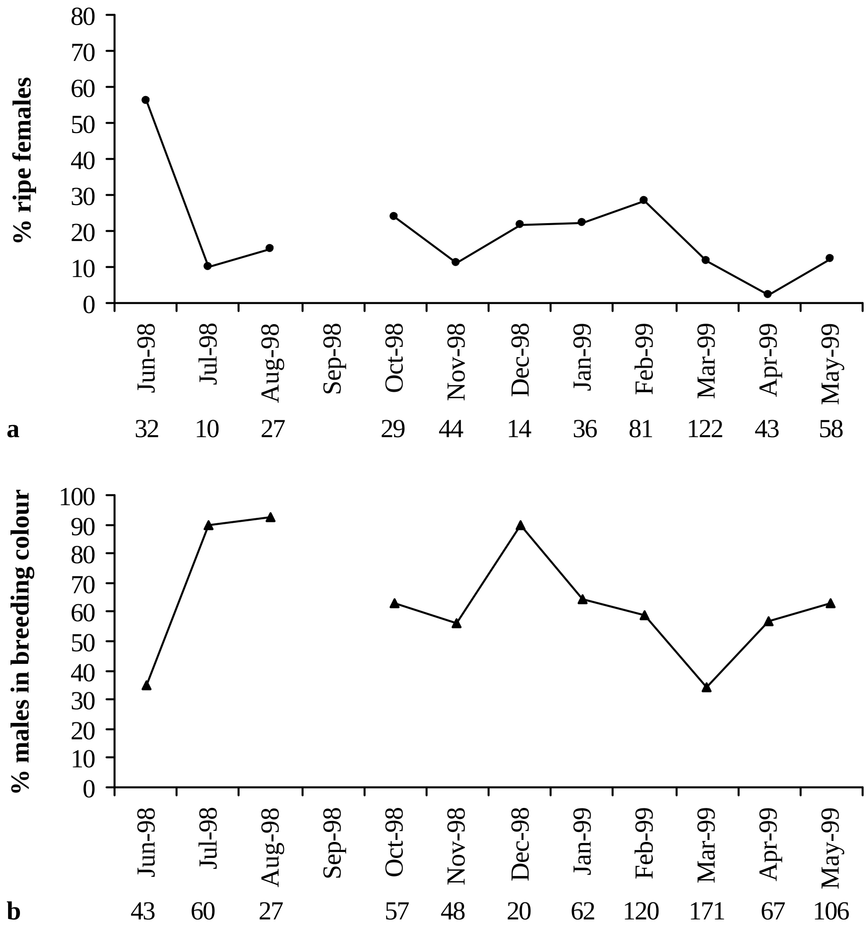

Figure 8-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Aulonocara 'minutus'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

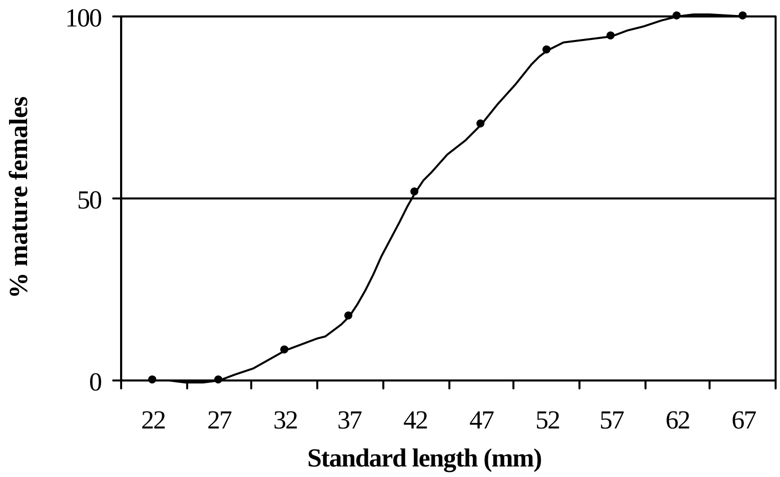

Figure 8-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Aulonocara 'minutus'* in the SWA.

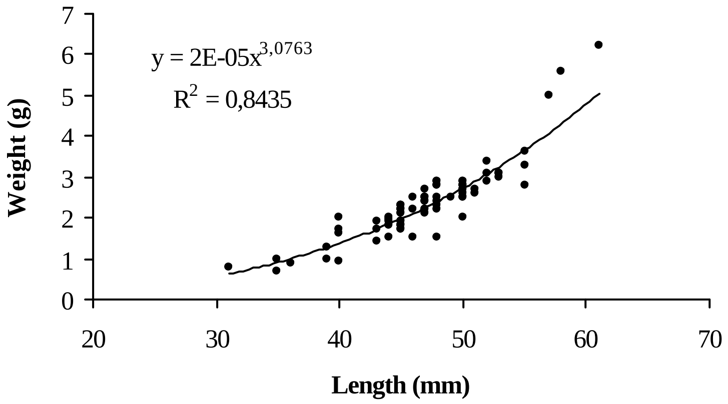

Figure 8-5. Length-weight relationship for *Aulonocara 'minutus'* females in the SWA. (R^2 = determination coefficient).

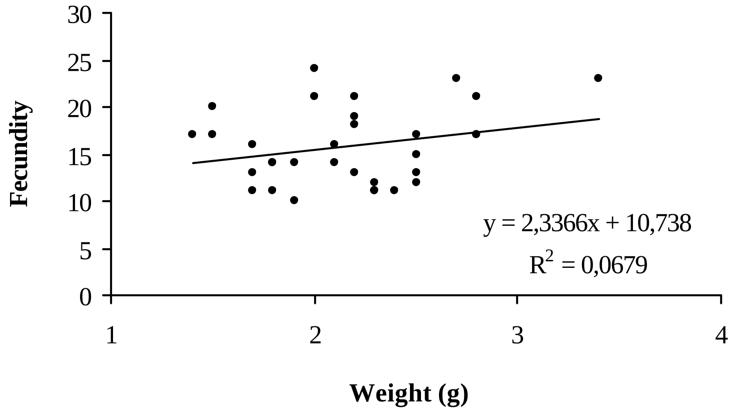

Figure 8-6. Fecundity-weight relationship for *Aulonocara 'minutus'* females in the SWA. (R^2 = determination coefficient).

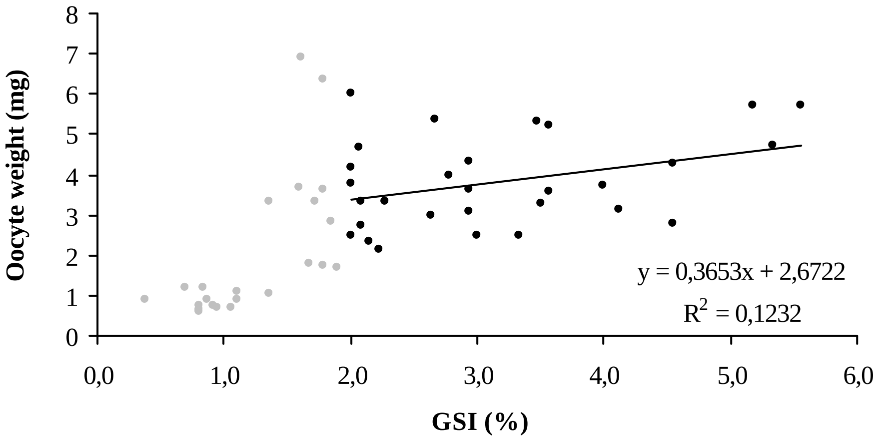

Figure 8-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Aulonocara 'minutus'*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 2%. (R^2 = determination coefficient).

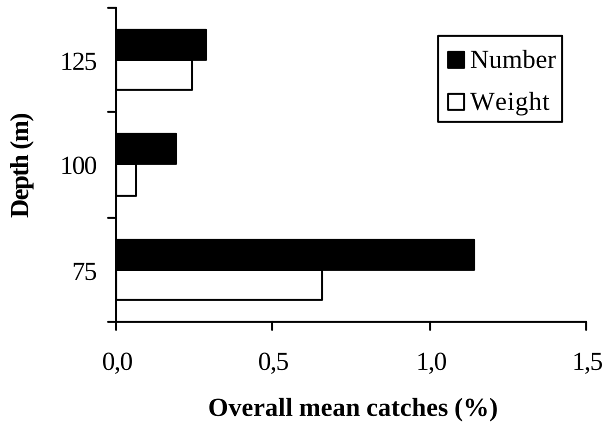

Figure 9-1. Mean occurrence and abundance in the catches per depth of *Aulonocara 'rostratum deep'* in the SWA between July 1998 and May 1999.

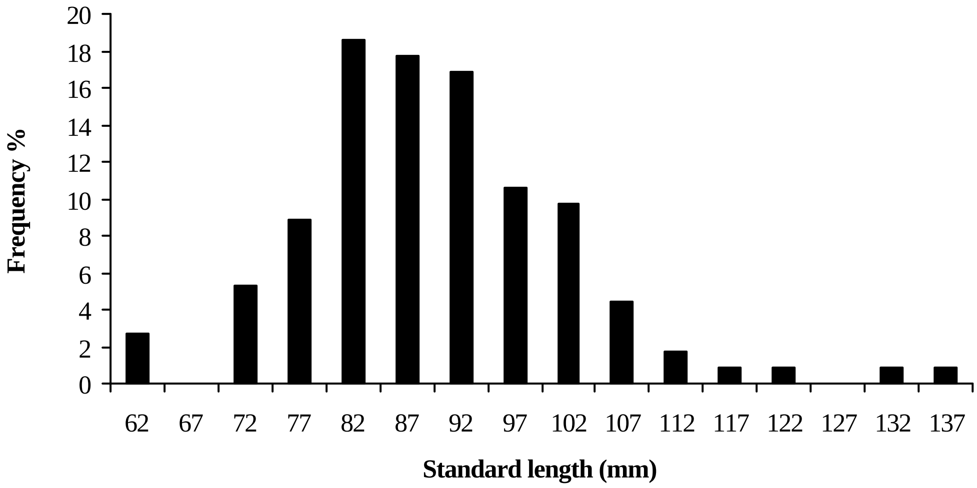

Figure 9-2. Size range and frequencies of *Aulonocara 'rostratum deep'* caught in the SWA between July 1998 and May 1999.

Aulonocara 'rostratum deep'

56 females and 57 males were analysed. *A. 'rostratum deep'* is a relatively rare fish found from 75 to 125 m depth but more frequent at 125 m (Figure 9-1). The mean CPUE per depth category was 1.7 kg in the deep zone and 0.5 kg in the very deep zone, which is about ten times less than the values reported in Tómasson & Banda (1996) for the deep zone (5.1 kg), and more than twenty times less in the very deep zone (13.2 kg). As for *A. 'cf. macrochir'* and *A. 'blue orange'* and A. *'minutus'*, the depth distribution we found was much more restricted than that observed by Tómasson & Banda (1996), who found *A. 'rostratum deep'* from 30 to 130 m. Specimens caught ranged between 60 and 140 mm with a mode from 80 to 105 mm (Figure 9-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

As *A. 'rostratum deep'* is a rare species, the following information about life history traits is based on low sample size and can not be considered as very reliable but rather as indicative. A breeding activity was observed in October, March and May (Figure 9-3a and b). From the few data available, ripe females and males in breeding colour were evenly distributed among depths. Maturity was reached at about 75 mm (Figure 9-4).

The length-weight and fecundity-weight relationships are given in Figure 9-5 and 9-6, respectively. Fecundity ranged from 41 to 167 for females weighing between 14 and 69 g. The mean oocyte weight was impossible to assess from the few data available on this species.

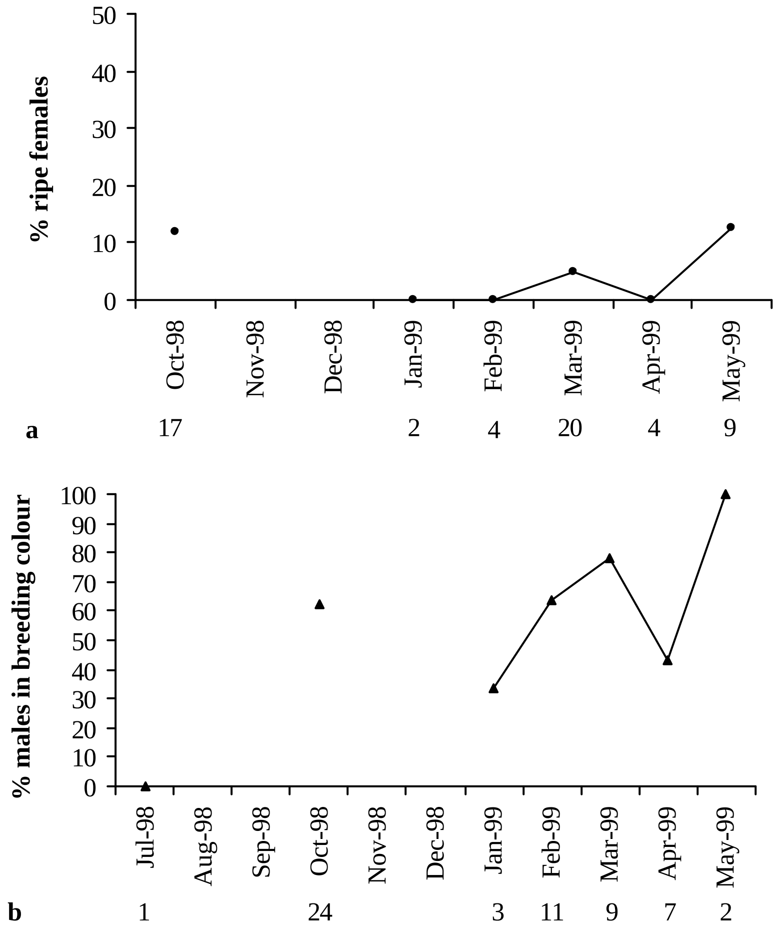

Figure 9-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Aulonocara 'rostratum deep'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

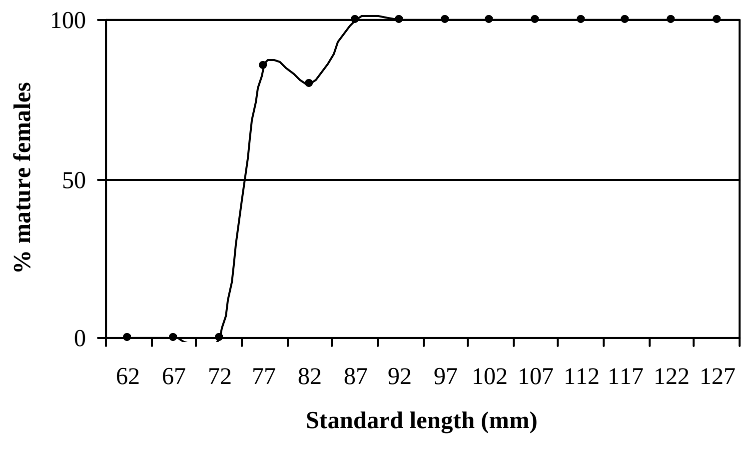

Figure 9-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Aulonocara 'rostratum deep'* in the SWA.

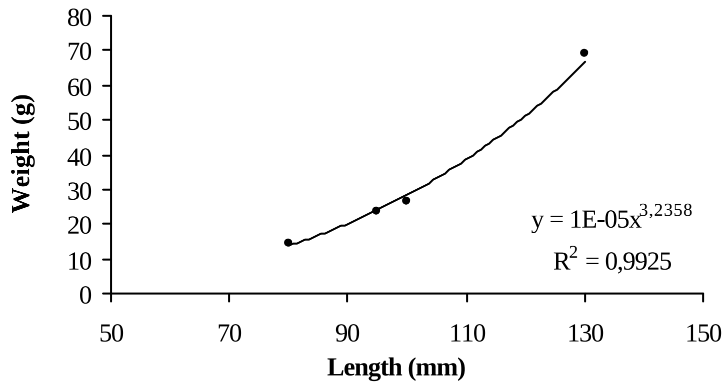

Figure 9-5. Length-weight relationship for *Aulonocara 'rostratum deep'* females in the SWA. (R^2 = determination coefficient).

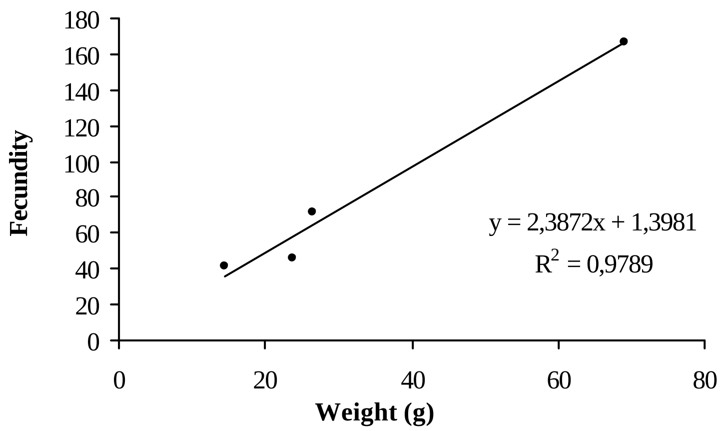

Figure 9-6. Fecundity-weight relationship for *Aulonocara 'rostratum deep'* females in the SWA. (R^2 = determination coefficient).

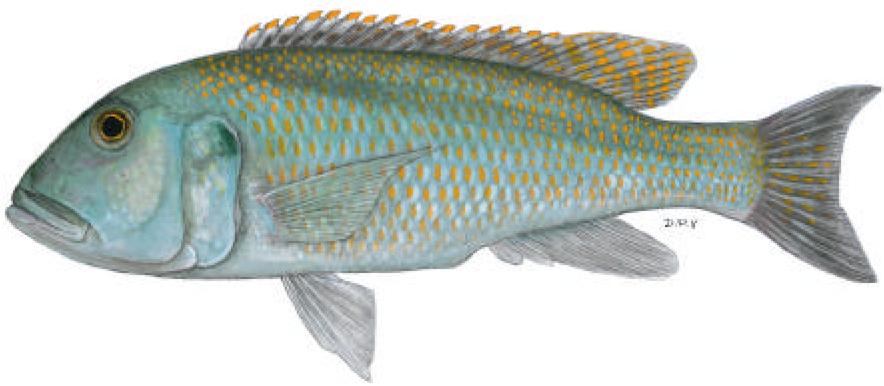

Plate 6. *Buccochromis lepturus* (by Dave Voorvelt).

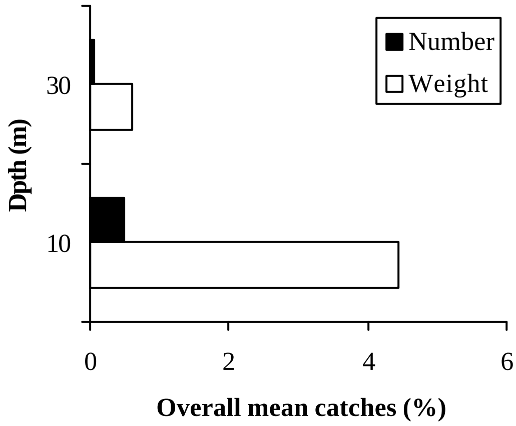

Figure 10-1. Mean occurrence and abundance in the catches per depth of *Buccochromis lepturus* in the SWA between July 1998 and May 1999.

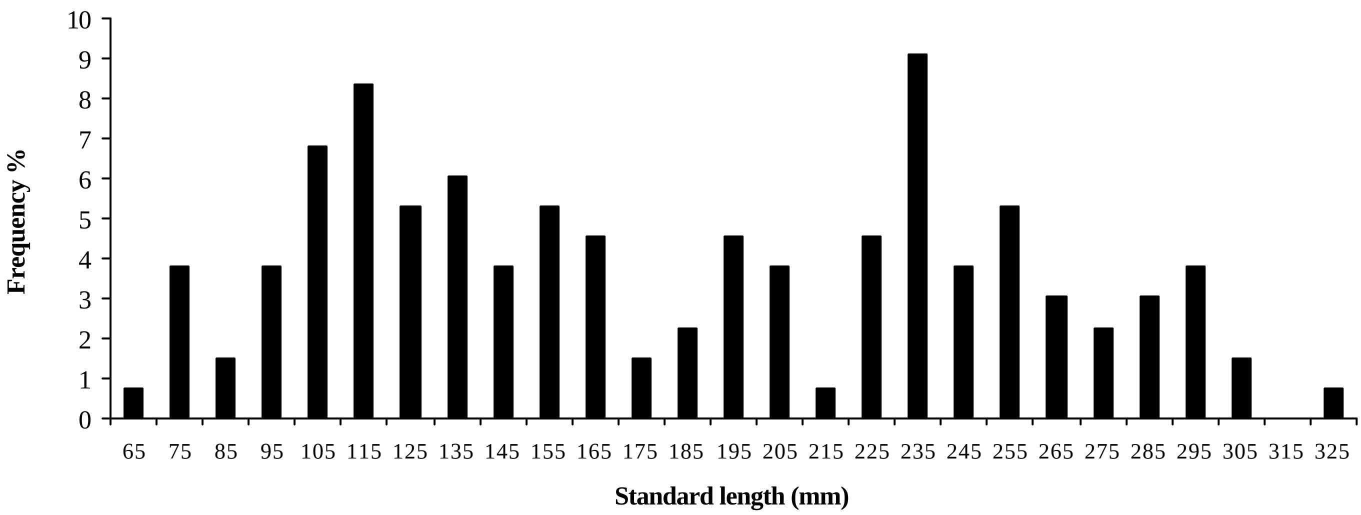

Figure 10-2. Size range and frequencies of *Buccochromis lepturus* caught in the SWA between July 1998 and May 1999.

Buccochromis spp.

***Buccochromis lepturus* (Regan) (Plate 6)**

74 females and 58 males were analysed. *B. lepturus* is a large shallow water fish essentially encountered at 10 m, where it constituted 4.5% of the catches in weight but only 0.5% in number owing to its large size (Figure 10-1). It was also found sometimes at 30 m. The mean CPUE per depth category was 6.5 kg in the shallow zone, which approximately matched the values reported in Tómasson & Banda (1996) (7.4 kg). The depth distribution observed in our study was more restricted than that of Tómasson & Banda (1996), who found *B. lepturus* down to 50m. Specimens caught ranged between 60 and 330 mm (Figure 10-2). The sex ratio observed over the full sampling period was F/M 0.6/0.4.

B. lepturus being an abundant species, the number of specimen caught at each sampling session was very low, which severely hampered the precise determination of breeding season and other life history traits. From the few data available, it seems that breeding season might occur between March-April and August (Figure 10-3a and b). The few ripe females or males in breeding colour were mostly found at 10 m, suggesting a rather shallow spawning. Maturity was reached at about 160 mm for females (Figure 10-4).

The length-weight and fecundity-weight relationships are given in Figure 10-5 and 10-6, respectively. Fecundity ranged from 267 to 627 for females weighing between 294 and 588 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was difficult to assess due to low sample size but was tentatively fixed at about 2% (Figure 10-7). The mean oocyte weight was 19.99 mg (± 1.88 SD, N= 4).

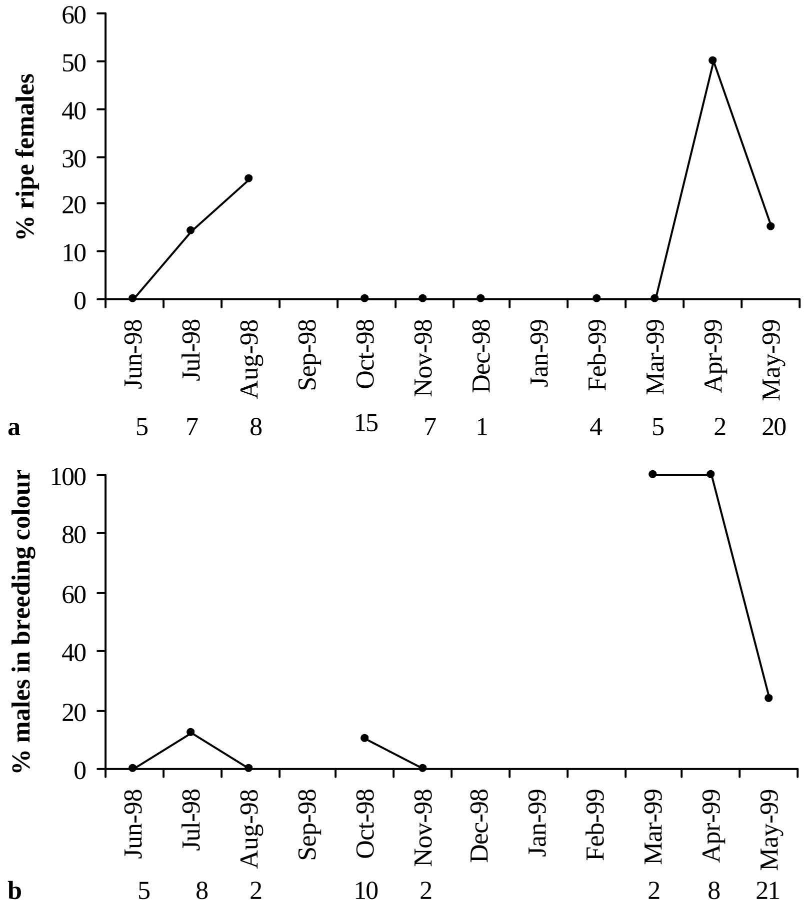

Figure 10-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Buccochromis lepturus* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

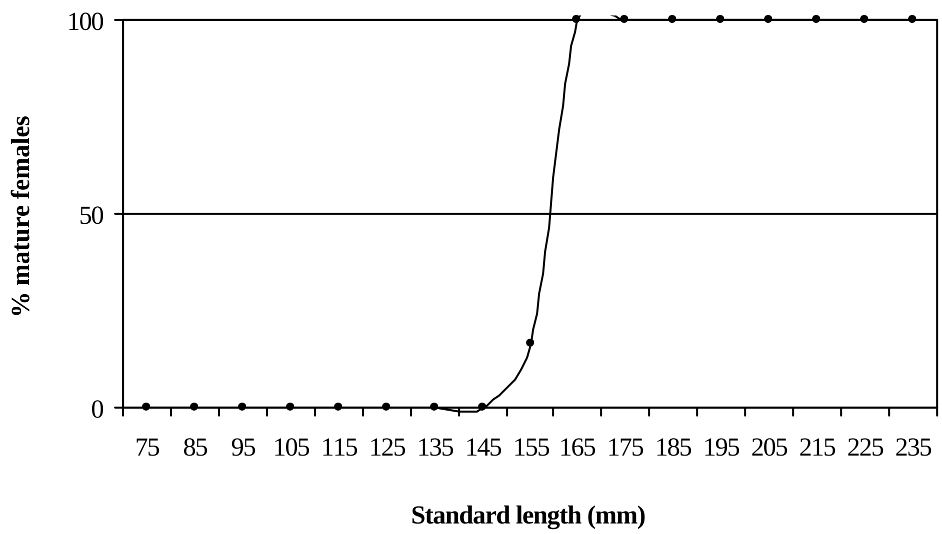

Figure 10-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Buccochromis lepturus* in the SWA.

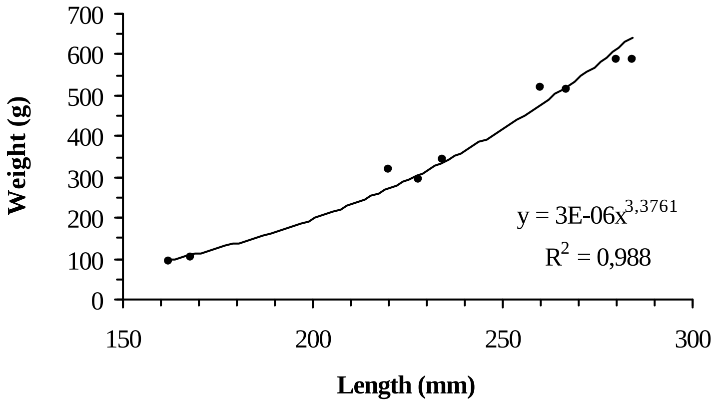

Figure 10-5. Length-weight relationship for *Buccochromis lepturus* females in the SWA. (R^2 = determination coefficient).

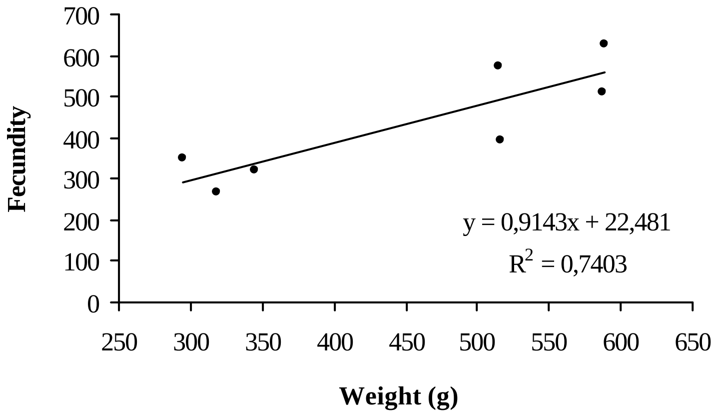

Figure 10-6. Fecundity-weight relationship for *Buccochromis lepturus* females in the SWA. (R^2 = determination coefficient).

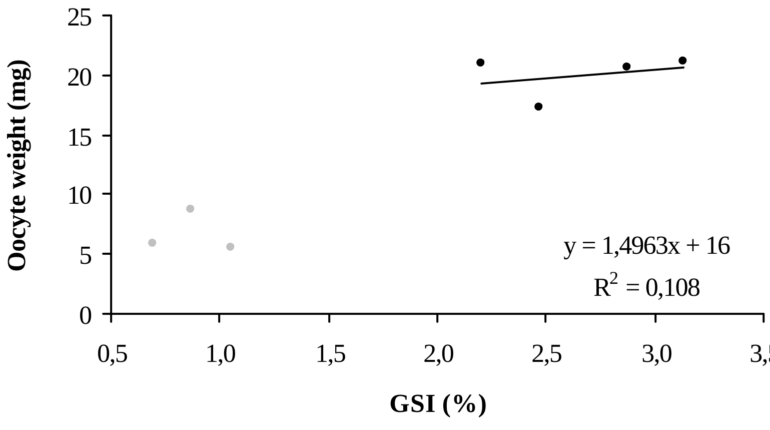

Figure 10-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Buccochromis lepturus*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 2%. (R^2 = determination coefficient).

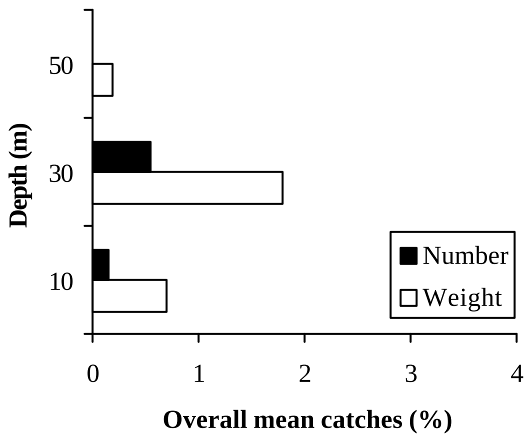

Figure 11-1. Mean occurrence and abundance in the catches per depth of *Buccochromis nototaenia* in the SWA between July 1998 and May 1999.

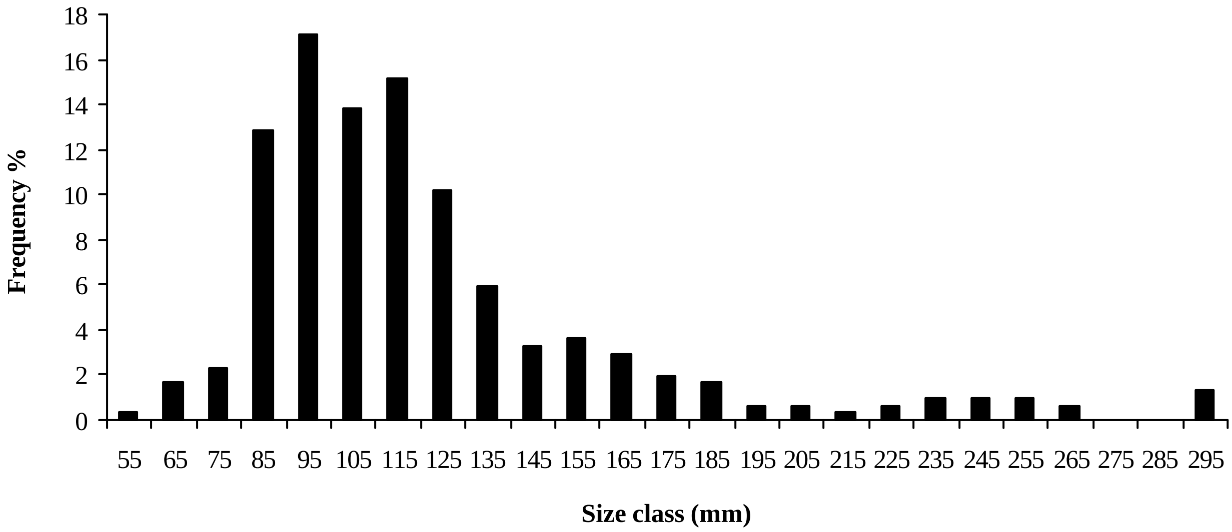

Figure 11-2. Size range and frequencies of *Buccochromis nototaenia* caught in the SWA between July 1998 and May 1999.

Buccochromis nototaenia (Boulenger)

122 females and 182 males were analysed. *B. nototaenia* is a large shallow water fish found between 10 and 50 m (Figure 11-1). It was more frequently encountered at 30 m, where it constituted about 2% of the catches in weight and 0.5% in number. The mean CPUE per depth category was 5.1 kg in the shallow zone, which was a bit more than the value reported in Tómasson & Banda (1996) (3.9 kg). The depth distribution observed in our study matched that of Tómasson & Banda (1996). Specimens caught ranged between 50 and 300 mm (Figure 11-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

As for *B. lepturus,* the low sample size hampered the precise determination of breeding season and other life history traits. All that can be said from females (Figure 11-3a) and males (Figure 11-3b) data is that we observed a breeding activity in April, July and August. However, it seems a weird behaviour for a Malawi cichlid to start breeding for one month then stop for two months and beginning again for two others months. Although there was no data to support it, it can be hypothesised that breeding season might occur between April and August as for *B. lepturus*. About 70% of the ripe females and males in breeding colour and 84% of the immature individuals were sampled at 30 m, suggesting that spawning could occur at this depth (Table 11-1). The plot of the percentage of ripe females against standard length did not give a proper sigmoïd curve (Figure 11-4). Size at maturity has to be determined at the height of the breeding season to be accurate but owing to the low sample size we had to consider all data available. As a consequence, females caught outside the breeding season were included in the analyses, even large resting females, which may explain the shape of the upper part of the curve. Nevertheless, small sized females are more informative than large ones and the size range between 100 mm and 130 mm was supported by the higher sample size (55 females), giving a relative "power" to this part of the curve. From the data available it can be estimated that maturity was reached around 115 mm for females. Maturity appears at a smaller size than anticipated given the large maximum observed length for this species and compared to *B. lepturus*.

Table 11-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Buccochromis nototaenia* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	20.9	28.6	17.6	16.7	14.6
30 m	79.1	71.4	80	66.7	84.4
50 m			2.4	16.7	1

The length-weight and fecundity-weight relationships are given in Figure 11-5 and 11-6, respectively. Fecundity ranged from 100 to 315 for females weighing between 40 and 250 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was difficult to assess due to low sample size but was tentatively fixed at about 2% (Figure 11-7). The mean oocyte weight was 11.70 mg (± 3.63 SD, N= 3).

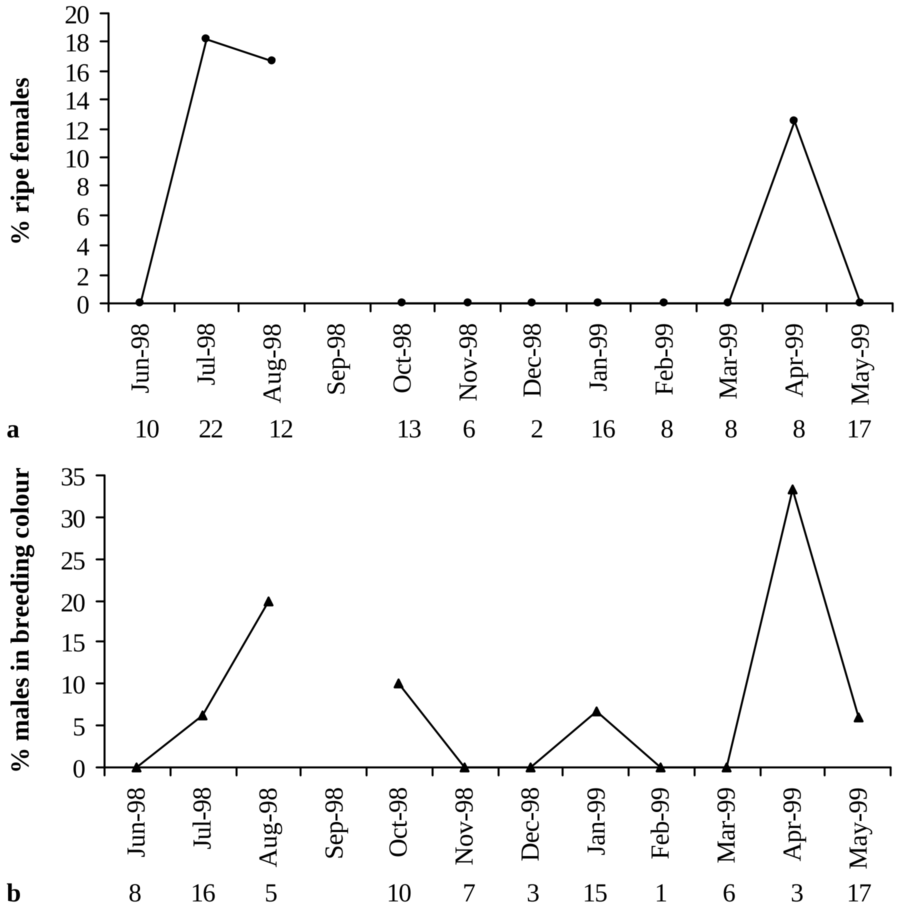

Figure 11-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Buccochromis nototaenia* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

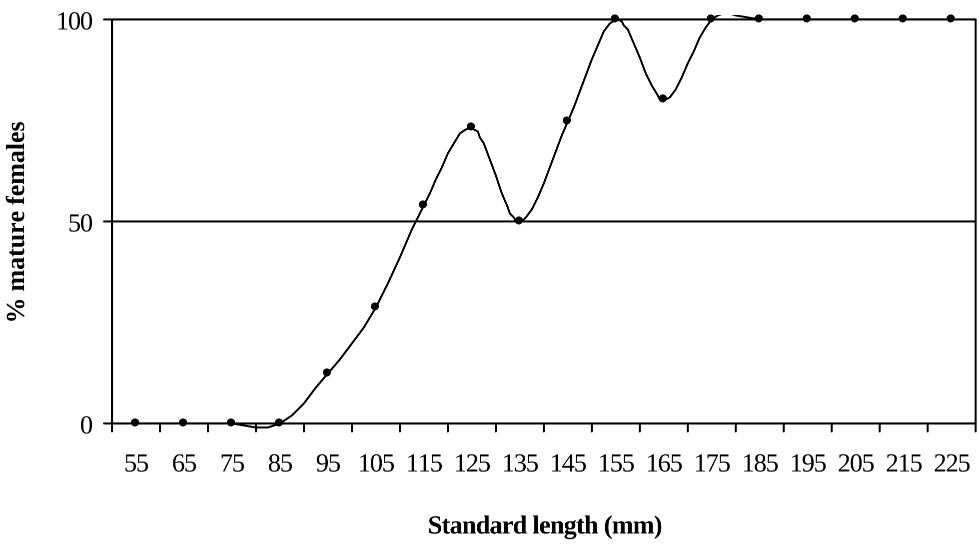

Figure 11-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Buccochromis nototaenia* in the SWA.

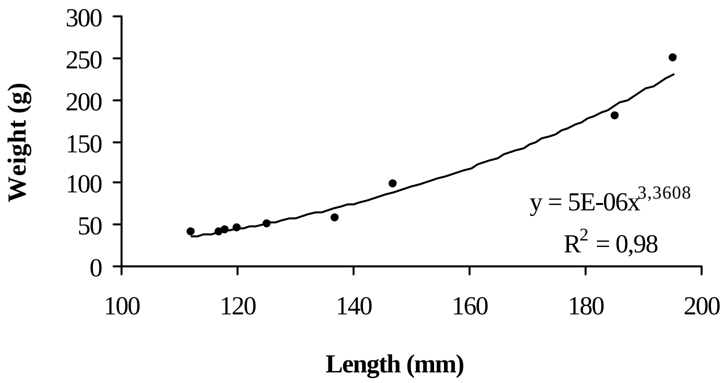

Figure 11-5. Length-weight relationship for *Buccochromis nototaenia* females in the SWA. (R^2 = determination coefficient).

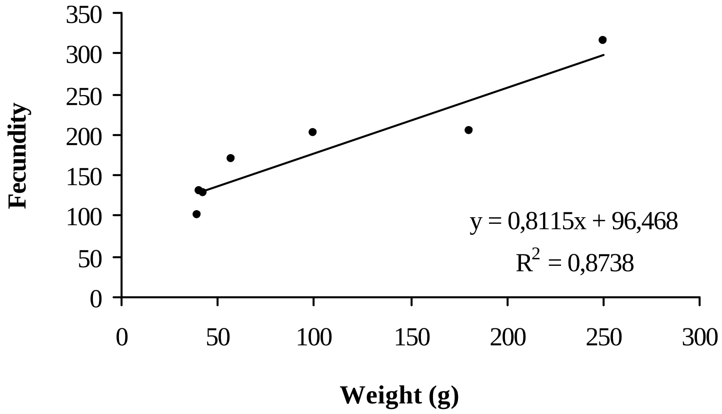

Figure 11-6. Fecundity-weight relationship for *Buccochromis nototaenia* females in the SWA. (R^2 = determination coefficient).

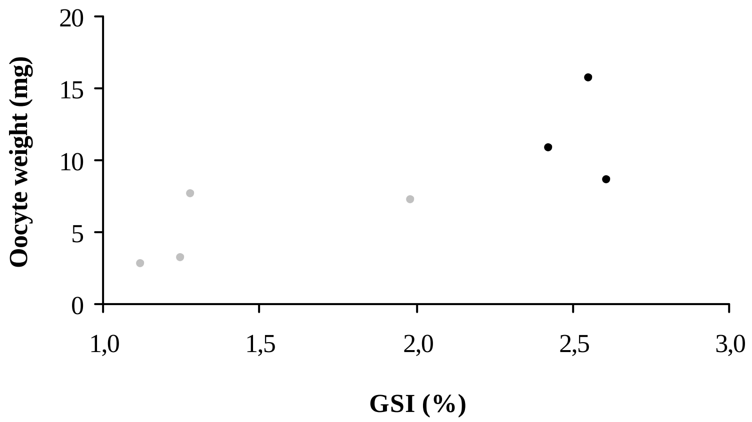

Figure 11-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Buccochromis nototaenia*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 2%. (R^2 = determination coefficient).

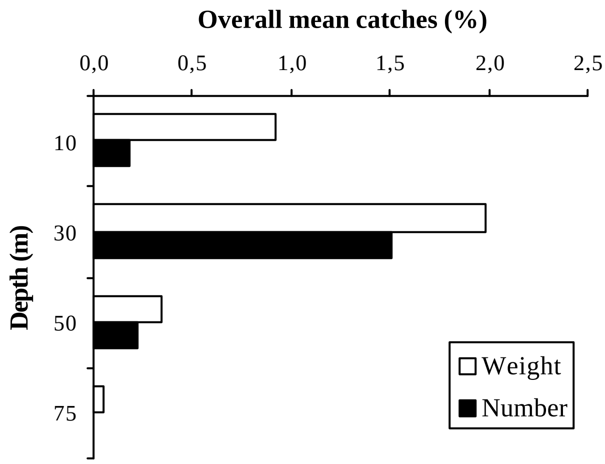

Figure 12-1. Mean occurrence and abundance in the catches per depth of *Copadichromis quadrimaculatus* in the SWA between July 1998 and May 1999.

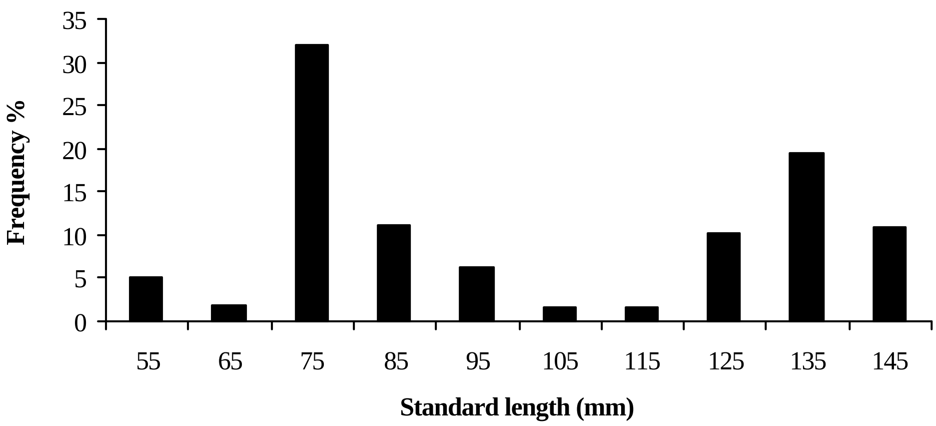

Figure 12-2. Size range and frequencies of *Copadichromis quadrimaculatus* caught in the SWA between July 1998 and May 1999.

Copadichromis spp.

***Copadichromis quadrimaculatus* (Regan)**

132 females and 214 males were analysed. *C. quadrimaculatus* was caught from 10 to 75 m but occurred more frequently at 30 m, where it constituted 2% and 1.5% of the catches, in weight and number, respectively (Figure 12-1). The mean CPUE per depth category was 6.9 kg in the shallow zone and 0.15 kg in the deep zone, which was about three times less than the value reported in Tómasson & Banda (1996) for the shallow zone (3.9 kg). The depth distribution observed in our study was much more restricted than that of Tómasson & Banda (1996), who reported *C. quadrimaculatus* from 8 to 135 m. Specimens caught ranged between 50 and 150 mm (Figure 12-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

The low sample size hampered the precise determination of breeding season and other life history traits. From data available about females (Figure 13-3a) and males (Figure 12-3b), it can be estimated that breeding season occurs from April to October. Taking into account the very low sample size of females in February-March and data from males, breeding season might actually start in February-March. This corresponds quite well with the % of active females observed in open waters during the SADC/ODA Project (Thompson et al. 1995, 1996). Most ripe females, males in breeding colour and immature individuals were found at 30 m, suggesting that spawning could occur at this depth (Table 12-1). The percentage of mature females (stage 3 and above) per size class is presented in Figure 12-4. No female was caught in the size range where maturity occurred. The 50% of mature females observed in the size range 80-90 mm was based on 2 females only and is probably overestimated. However, the second part of the curve from 120 mm upwards was based on consistent sample size and it can be reasonably estimated that maturity was reached around 100 mm, which was much less than the 15 cm TL (about 120 mm SL) reported for the same species in the open waters (Thompson et al. 1995, 1996). This corresponded to a mean age at maturity of 20 months.

Table 12-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Buccochromis nototaenia* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	29.3	20	2	37.6	1.4
30	52.4	50	75.5	57	76.8
50 m	14.6	25	22.4	5.5	21.7
75 m	3.7	5			

The length-weight and fecundity-weight relationships are given in Figure 12-5 and 12-6, respectively. Fecundity ranged from 15 to 62 for females weighing between 53 and 75 g. Using the length-weight and fecundity weight relationships, and assuming a 2 to 3 cm difference between standard and total length for a size range of 17 to 20 cm TL, the mean fecundity (50 eggs for females between 17 and 20cm TL) found by Thompson et al. (1996) corresponded with the fecundity we got for females of similar size. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight

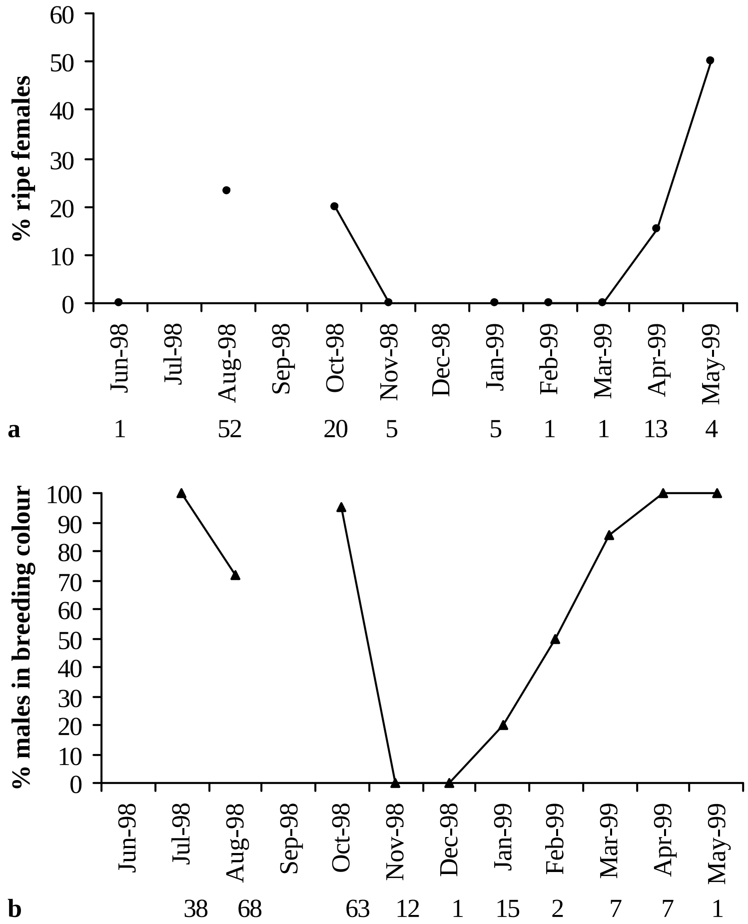

Figure 12-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Copadichromis quadrimaculatus* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

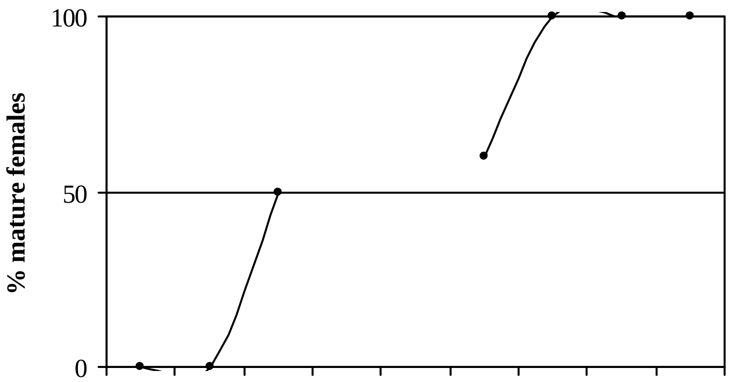

Figure 12-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Copadichromis quadrimaculatus* in the SWA.

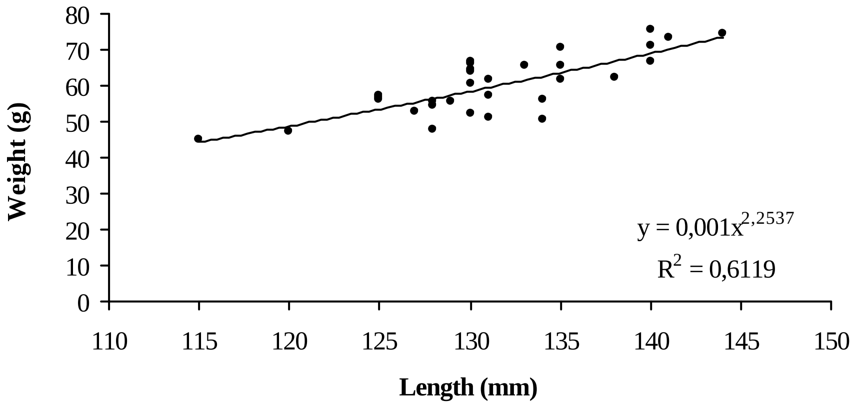

Figure 12-5. Length-weight relationship for *Copadichromis quadrimaculatus* females in the SWA. (R^2 = determination coefficient).

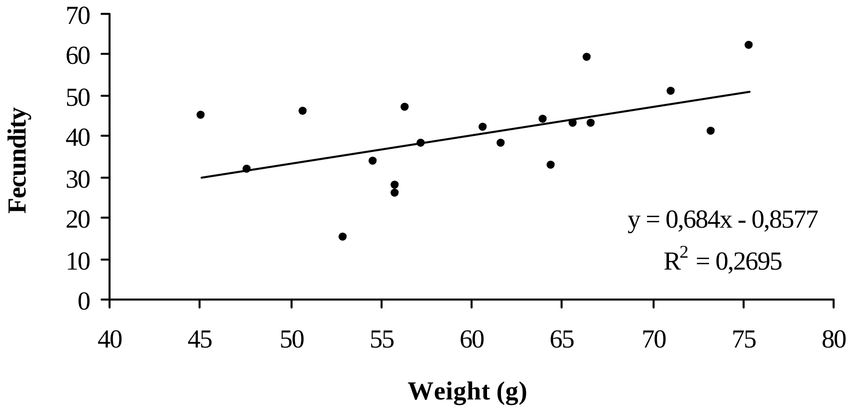

Figure 12-6. Fecundity-weight relationship for *Copadichromis quadrimaculatus* females in the SWA. (R^2 = determination coefficient).

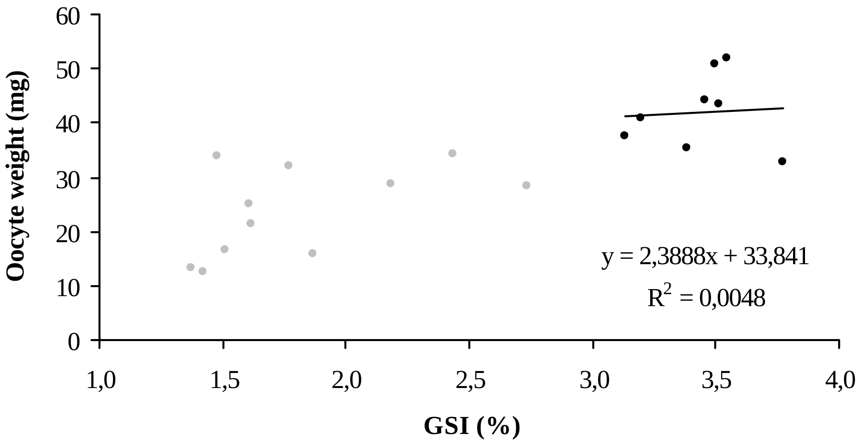

Figure 12-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Copadichromis quadrimaculatus*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

Plate 7. *Copadichromis virginalis* (by Dave Voorvelt).

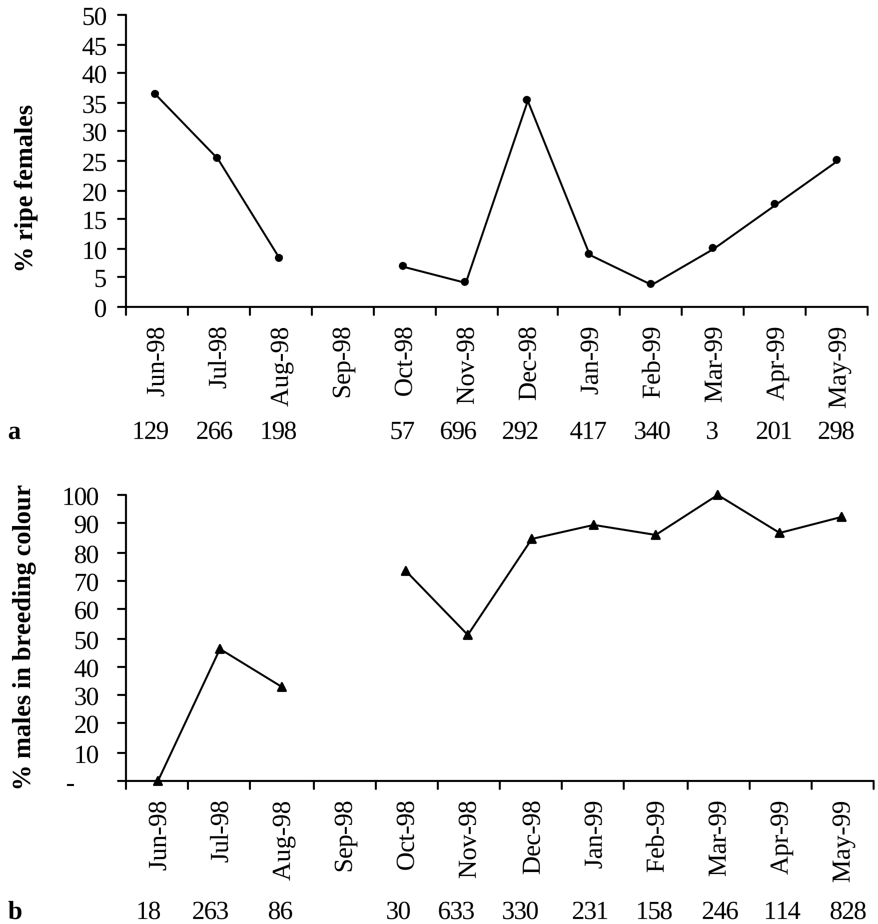

Figure 13-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Copadichromis virginalis* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

did no longer increase significantly was 3% (Figure 12-7). The mean oocyte weight was 42.05 mg (± 6.96 SD, N= 8).

Copadichromis virginalis (Iles) (Plate 7)

2886 females and 3052 males were analysed. *C. virginalis* was encountered from 10 m to 50 m and rarely at 100 m (Figure 13-1).

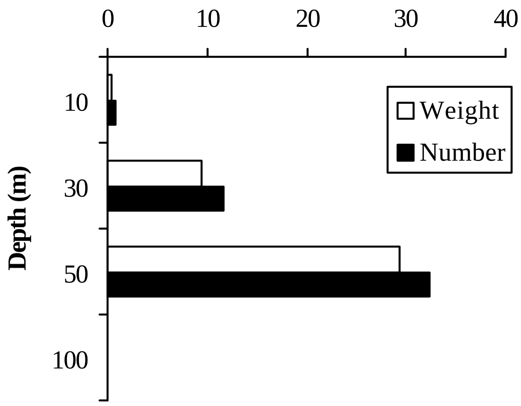

Figure 13-1. Mean occurrence and abundance in the catches per depth of *Copadichromis virginalis* in the SWA between July 1998 and May 1999.

It was one of the most abundant species in shallow water, where it constituted about 10% and 30% (both in weight and number) of the catches at 30 and 50 m, respectively. The mean CPUE per depth category was 97.7 kg in the shallow zone and 0.15 kg in the deep zone, which matched the value reported in Tómasson & Banda (1996) for the shallow zone (108.8 kg). As for *C. quadrimaculatus* the depth distribution observed in our study was a bit more restricted than that of Tómasson & Banda (1996), who reported *C. virginalis* from 8 to 120 m. Specimens caught ranged between 45 and 125 mm (Figure 13-2).

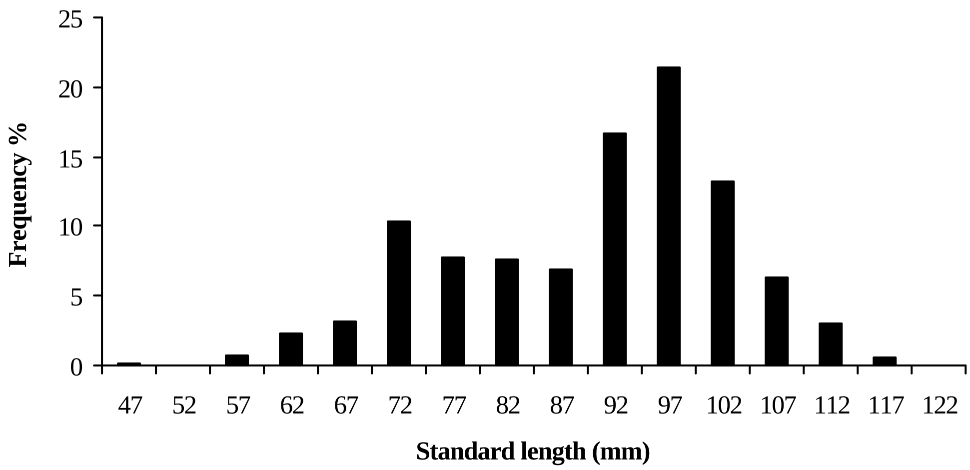

Figure 13-2. Size range and frequencies of *Copadichromis virginalis* caught in the SWA between July 1998 and May 1999.

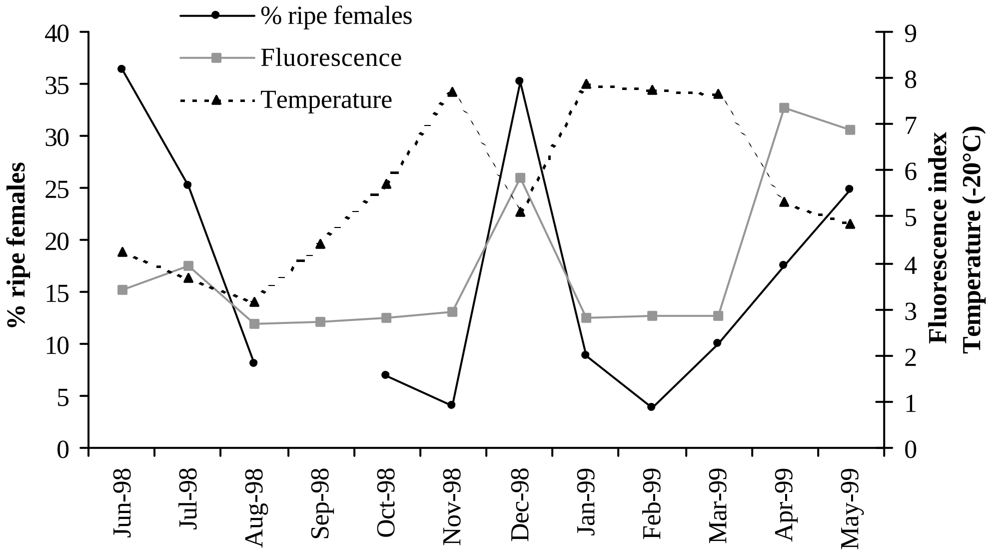

Figure 13-4. Monthly percentage of ripe females in relation with temperature (= temperature minus 20°C to fit the axis scale) and fluorescence, used as an index of chlorophyll a concentration.

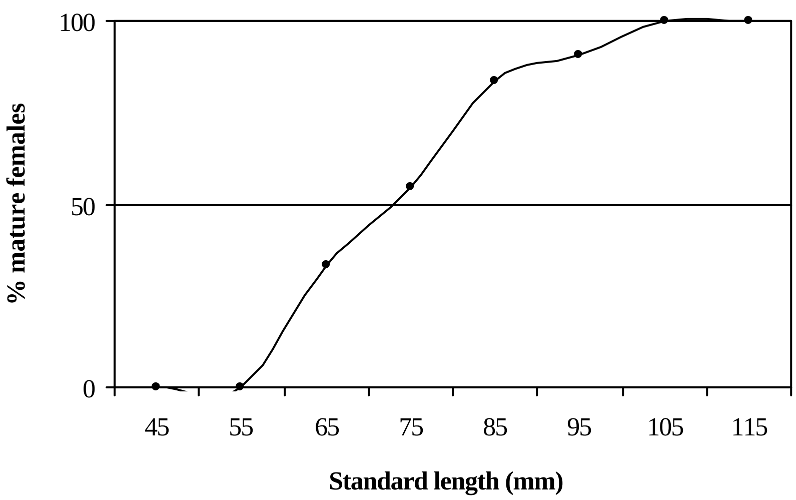

Figure 13-5. Percentage of mature females (stage 3 and above) per size class (standard length) for *Copadichromis virginalis* in the SWA.

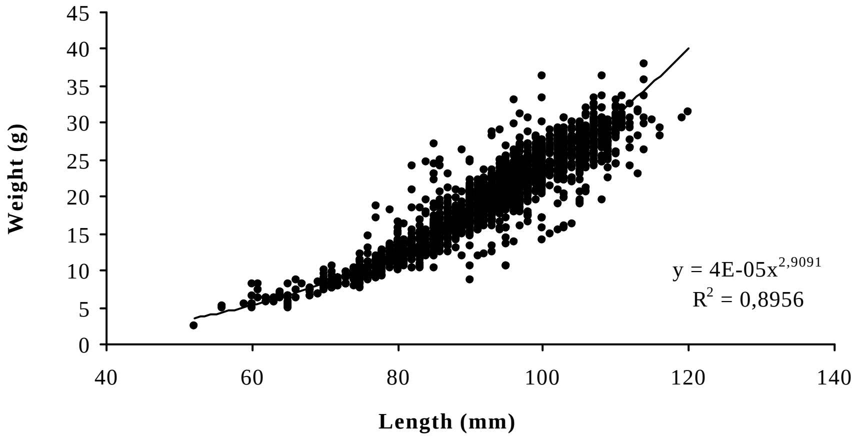

Figure 13-6. Length-weight relationship for *Copadichromis virginalis* females in the SWA. (R^2 = determination coefficient).

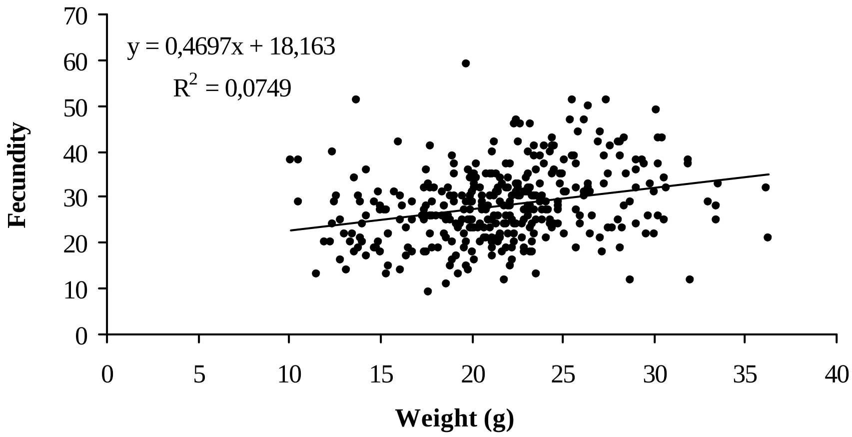

Figure 13-7. Fecundity-weight relationship for *Copadichromis virginalis* females in the SWA. (R^2 = determination coefficient).

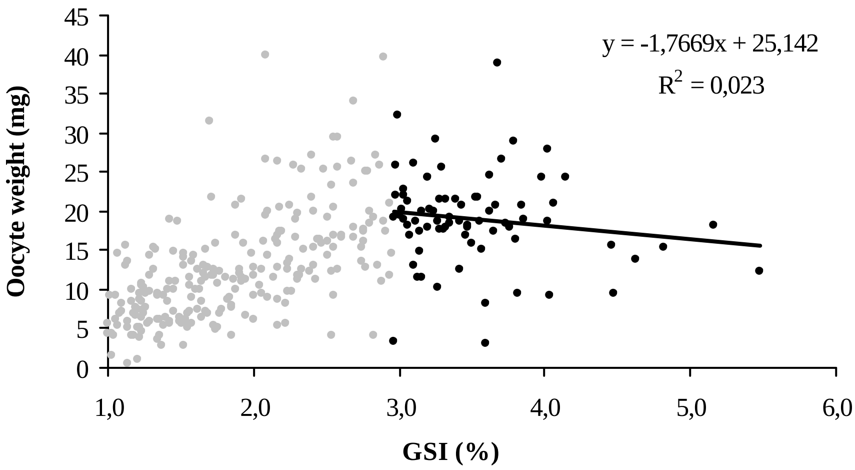

Figure 13-8. Relationship between oocyte weight and gonado-somatic index (GSI) for *Copadichromis virginalis*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

The sex ratio observed over the full sampling period was F/M 0.5/0.5.

C. virginalis was found to breed throughout the year (Figure 13-3a and b) with two peaks of activity, a punctual one in December and another one from May to July (Figure 13-3a). This figure markedly differed from Iles's (1971) observations who reported a very restricted breeding season (March to May) in the region of Nkata Bay. The percentage of ripe females seemed inversely related to water temperature (Figure 13-4), being higher during the cold water season (windy season) from April-May to August, and directly related to the chlorophyll a concentration. As *C. virginalis* is a zooplankton feeder (Iles 1960, 1971, Turner 1996, present study see chapter "Diet"), most of the sexual activity occurred during windy season when the water column was mixed up and the rich cold upwelling increased the phytoplankton production and consequently the zooplankton abundance. The punctual peak of sexual activity observed in December 1998 corresponded with a drop of temperature of about 3°C, an associated increased concentration in chlorophyll a and then an increased zooplankton availability. More than 70% of the ripe females and males in breeding colour were found at 50 m (Table 13-1) and the rest at 30 m, suggesting that spawning could occur mostly at 50 m and in a lesser extent at 30 m. Maturity was reached in their first year at 12 months old at a mean size of 75 mm for females (Figure 13-5).

Table 13-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Copadichromis virginalis* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	0.3	0.5	1.7	0.3	4.8
30	17.8	26.2	24.8	7.7	25.2
50 m	81.9	73.1	73.3	92	69.4
100 m	0	0.2	0.1	0	0.6

The length-weight and fecundity-weight relationships are given in Figure 13-6 and 13-7, respectively. Fecundity ranged from 9 to 59 for females weighing between 10 and 36 g and was not correlated to body weight. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 13-8). The mean oocyte weight was 18.93 mg (± 5.90 SD, N= 76).

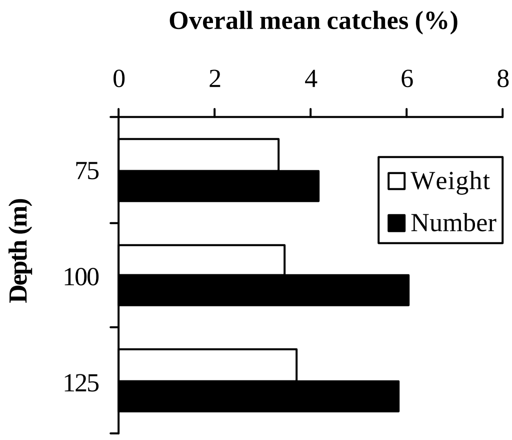

Figure 14-1. Mean occurrence and abundance in the catches per depth of *Diplotaxodon apogon* in the SWA between July 1998 and May 1999.

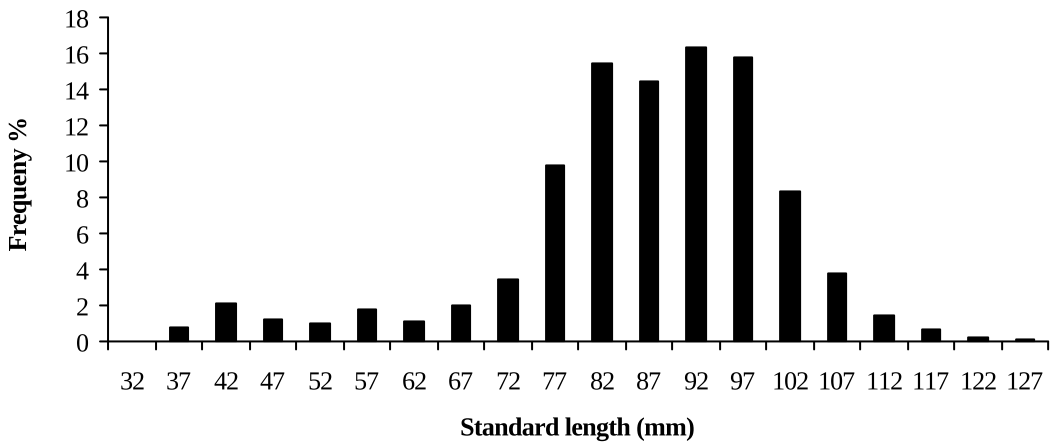

Figure 14-2. Size range and frequencies of *Diplotaxodon apogon* caught in the SWA between July 1998 and May 1999.

Diplotaxodon and Pallidochromis spp.

Pallidochromis tokolosh (Turner) is the only species of this genus. Despite its anatomical distinctness that separates it from Diplotaxodon, recent molecular evidence suggested that this species is a member of the *Diplotaxodon* clade (Turner et al. 1999). It will then be presented together with the *Diplotaxodon spp*..

Diplotaxodon apogon **(Turner & Stauffer)**

616 females and 729 males were analysed. *D. apogon* was found from 75 to 125 m, where it constituted between 3 and 4% of the catches in weight and 4 to 6% in number (Figure 14-1). The mean CPUE per depth category was 15.6 kg in the deep zone and 6 kg in the very deep zone. There was no record for this species in Tómasson & Banda (1996). Specimens caught ranged between 33 and 130 mm with a mode from 75 to 105 mm (Figure 14-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Breeding activity was detected in August 98 and from November 98 to April 99 for females (Figure 14-3a) whereas more than 60% of males in breeding colour were found at every sampled month (Figure 14-3b). Despite the very high percentage of males in breeding colour throughout the year, female data suggested a bimodal breeding season with a major peak from November to March and a smaller one around August. More than 60% of the ripe females were found at 100m (Table 14-1). More than 80 % of the males in breeding colour were evenly distributed at 75 and 125 m, but aggregations of such breeding males (50 to 90 individuals) were found at all three depths. No particular indication about spawning depth was drawn from these results. Maturity was reached in their second year at 21 months old at a mean size of 88 mm for females (Figure 14-4).

Table 14-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Diplotaxodon apogon* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	27.4	14.1	5.8	40.3	13.3
100 m	43.3	62.5	79.5	16.1	53.4
125 m	29.3	23.4	14.7	43.6	33.3

The length-weight and fecundity-weight relationships are given in Figure 14-5 and 14-6, respectively. Fecundity ranged from 9 to 34 for females weighing between 16 and 39 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 2.7% (Figure 14-7). The mean oocyte weight was 46.04 mg (± 5.99 SD, N= 22).

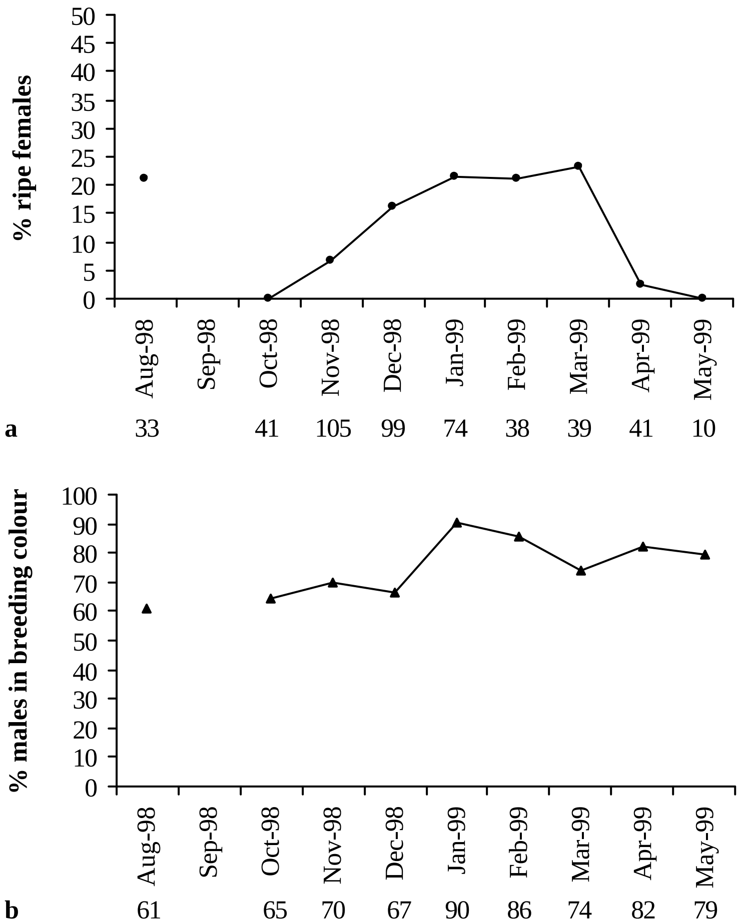

Figure 14-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Diplotaxodon apogon* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

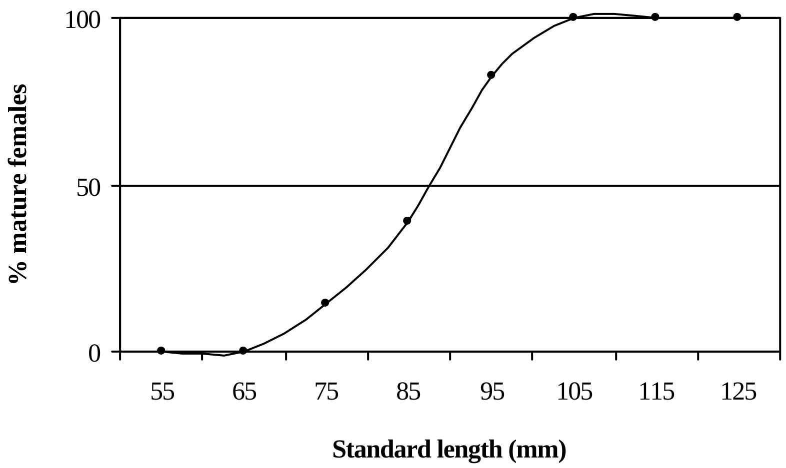

Figure 14-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Diplotaxodon apogon* in the SWA.

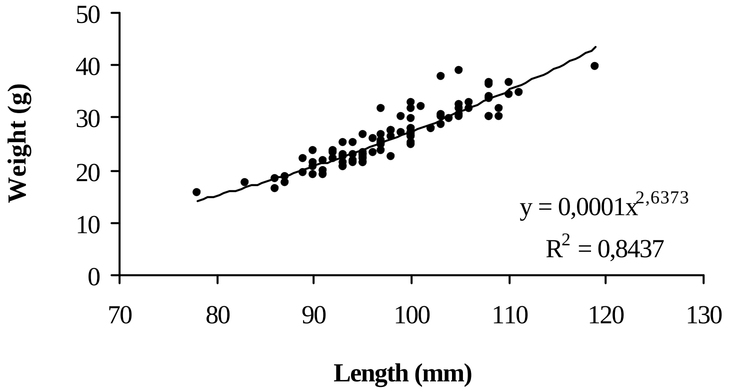

Figure 14-5. Length-weight relationship for *Diplotaxodon apogon* females in the SWA. (R^2 = determination coefficient).

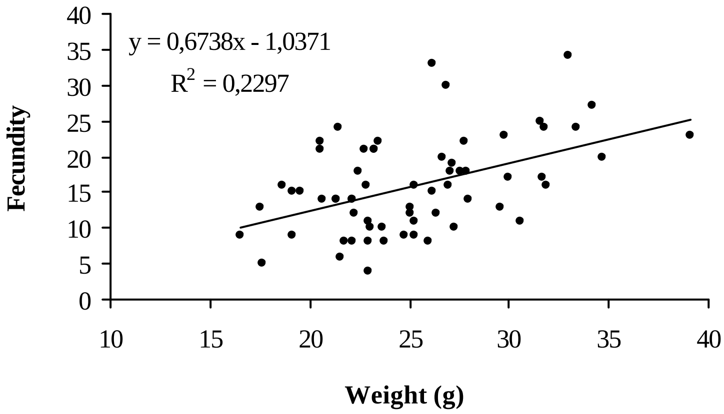

Figure 14-6. Fecundity-weight relationship for *Diplotaxodon apogon* females in the SWA. (R^2 = determination coefficient).

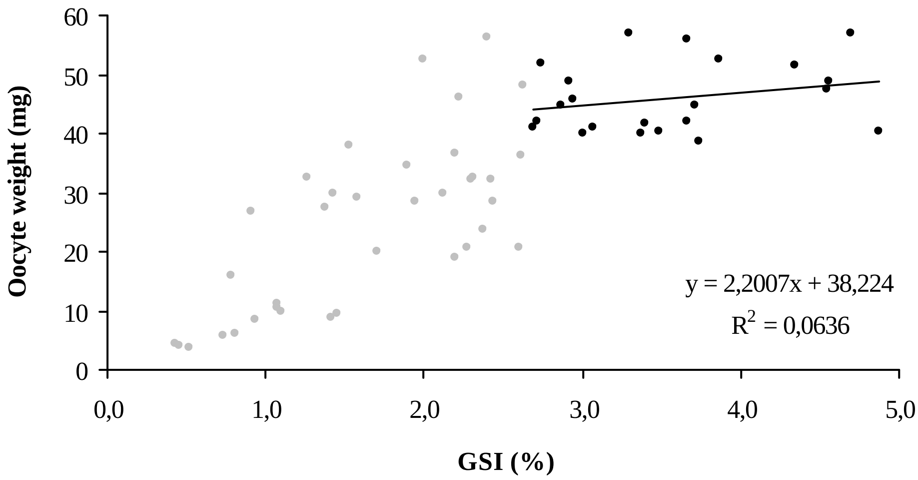

Figure 14-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Diplotaxodon apogon*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 2.7%. (R^2 = determination coefficient).

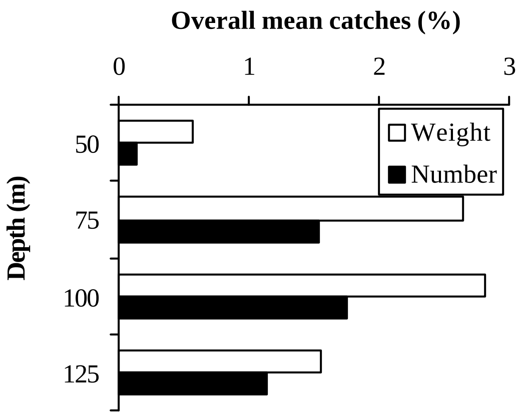

Figure 15-1. Mean occurrence and abundance in the catches per depth of *Diplotaxodon argenteus* in the SWA between July 1998 and May 1999.

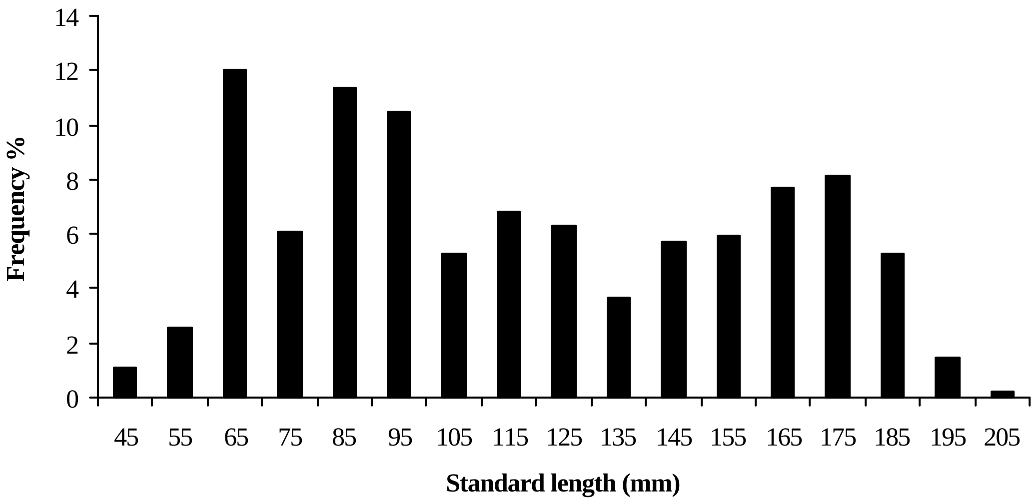

Figure 15-2. Size range and frequencies of *Diplotaxodon argenteus* caught in the SWA between July 1998 and May 1999.

Diplotaxodon argenteus (Trewavas)

278 females and 343 males were analysed. D. argenteus was found between 50 and 125 m but became more frequent from 75 m downwards, where it constituted between about 1 and 2% of the catches in number and 1.5 and 3% in weight (Figure 15-1). The mean CPUE per depth category was 1.5 kg in the shallow zone, 11 kg in the deep zone and 3.3 kg in the very deep zone, which matched the values reported in Tómasson & Banda (1996) for the shallows (1.2 kg) but was about three times more for the deep (3 kg) and very deep zones (1.3 kg). Specimens caught ranged between 48 and 206 mm (Figure 15-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

Owing to irregularity in the catches of this species and low sample size of individuals above the size at maturity, precise determination of breeding season was not possible. Breeding females were found in October-November 98 and from February to May 99 (Figure 15-3a). More than 30% of males in breeding colour were found all year long excluding June 98 were only one individual was caught (Figure 15-3b). Considering the high percentages of breeding males and the extremely low sample size for females from June to September, it is likely that *D. argenteus* breed most of the year with a possible cessation in December-January. Ripe females were relatively evenly distributed between 75 and 125 m, whereas more than 60% of males in breeding colour were caught at 75 m, suggesting that spawning could mainly occur at 75 m (Table 15-1). Maturity was reached in their second year at 20 months old at a mean size of 140 mm for females (Figure 15-4).

Table 15-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Diplotaxodon argenteus* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
50 m	35.3	11.1	2.1	0.6	1
75 m	11.2	22.2	35.4	61.7	29.5
100 m	38.8	33.3	29.6	16.2	33.4
125 m	14.7	33.3	32.8	21.4	36

The length-weight and fecundity-weight relationships are given in Figure 15-5 and 15-6, respectively. Fecundity ranged from 25 to 53 for females weighing between 55 and 139 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 15-7). The mean oocyte weight was 73.03 mg (± 7.98 SD, N= 3).

Diplotaxodon limnothrissa (Turner) (Plate 8)

1462 females and 2723 males were analysed. *D. limnothrissa* was common from 50 to 125 m and was occasionally encountered at 10 m depth (Figure 16-1), which corresponds to the depth distribution reported by Thompson et al. (1996) and Tómasson & Banda (1996). It was a dominant species in the catches at 50, 75 and 100 m, where it constituted (in number and weight, respectively) 6.2 and 3.8%, 8.3 and 7.7% and 11.7 and 9.7% of the catches, respectively. The mean CPUE per depth category was 14.7 kg in the shallow zone, 34.1 kg in

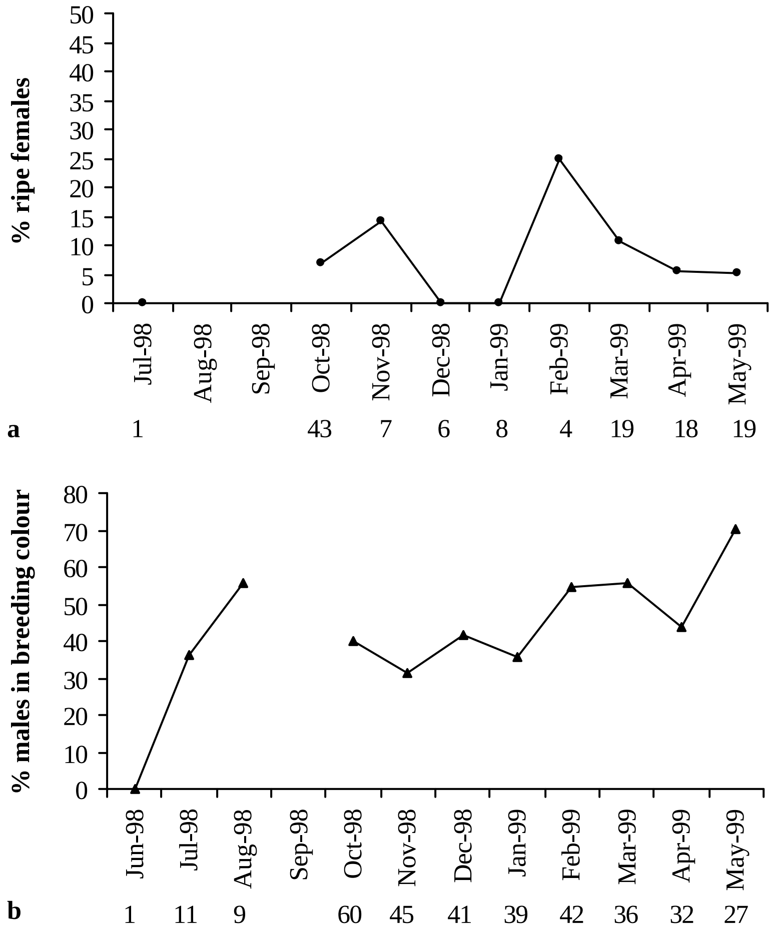

Figure 15-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Diplotaxodon argenteus* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

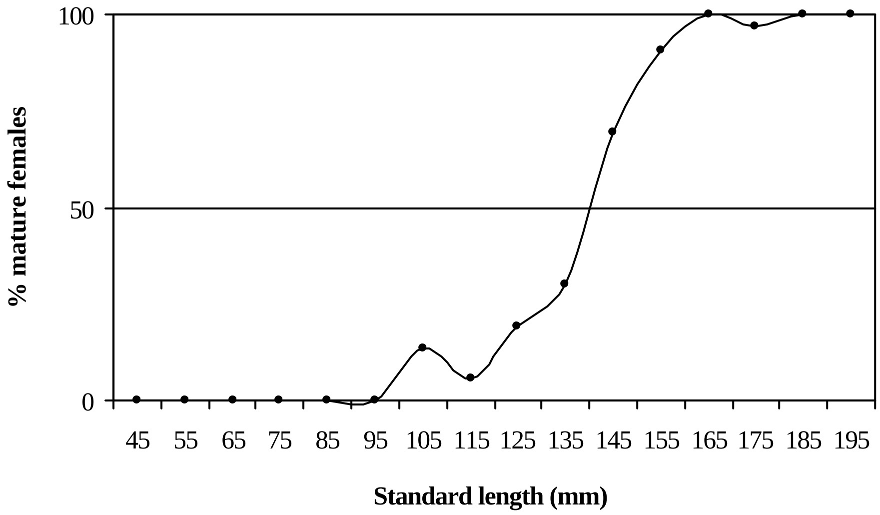

Figure 15-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Diplotaxodon argenteus* in the SWA.

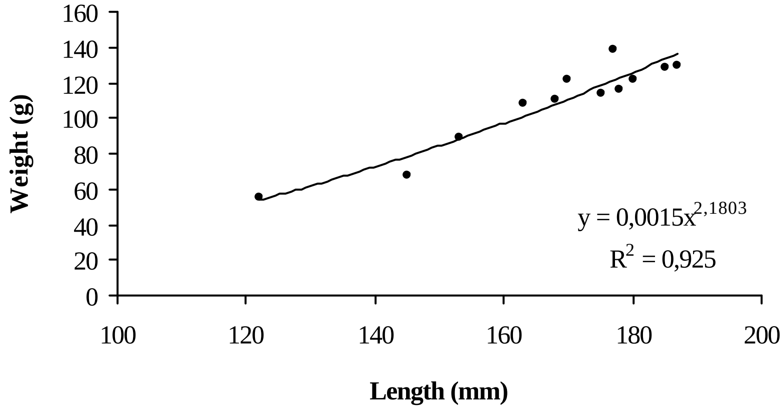

Figure 15-5. Length-weight relationship for *Diplotaxodon argenteus* females in the SWA. (R^2 = determination coefficient).

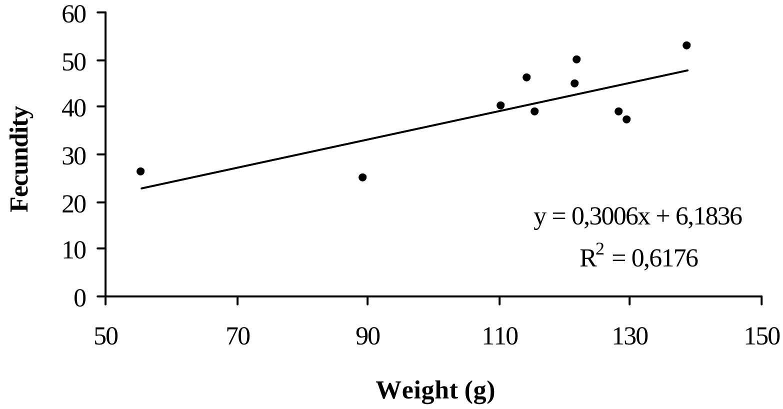

Figure 15-6. Fecundity-weight relationship for *Diplotaxodon argenteus* females in the SWA. (R^2 = determination coefficient).

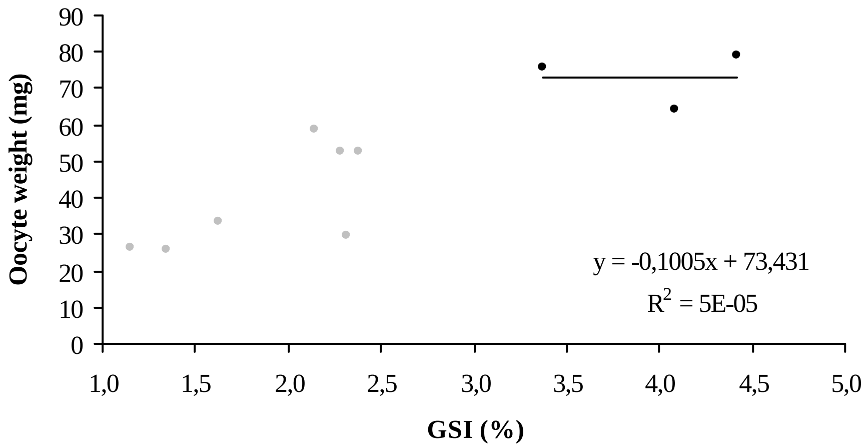

Figure 15-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Diplotaxodon argenteus*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 2.7%. (R^2 = determination coefficient).

Plate 8. *Diplotaxodon limnothrissa* (by Dave Voorvelt).

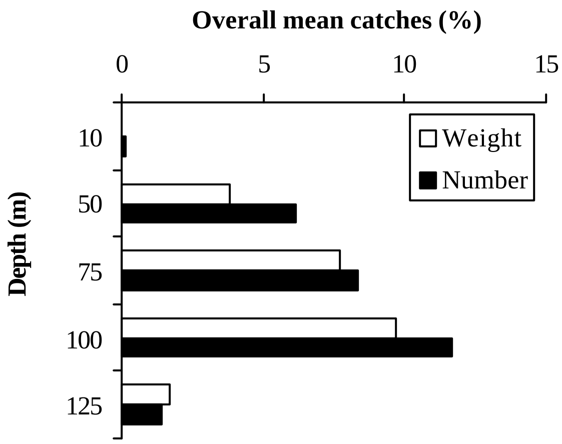

Figure 16-1. Mean occurrence and abundance in the catches per depth of *Diplotaxodon limnothrissa* in the SWA between July 1998 and May 1999.

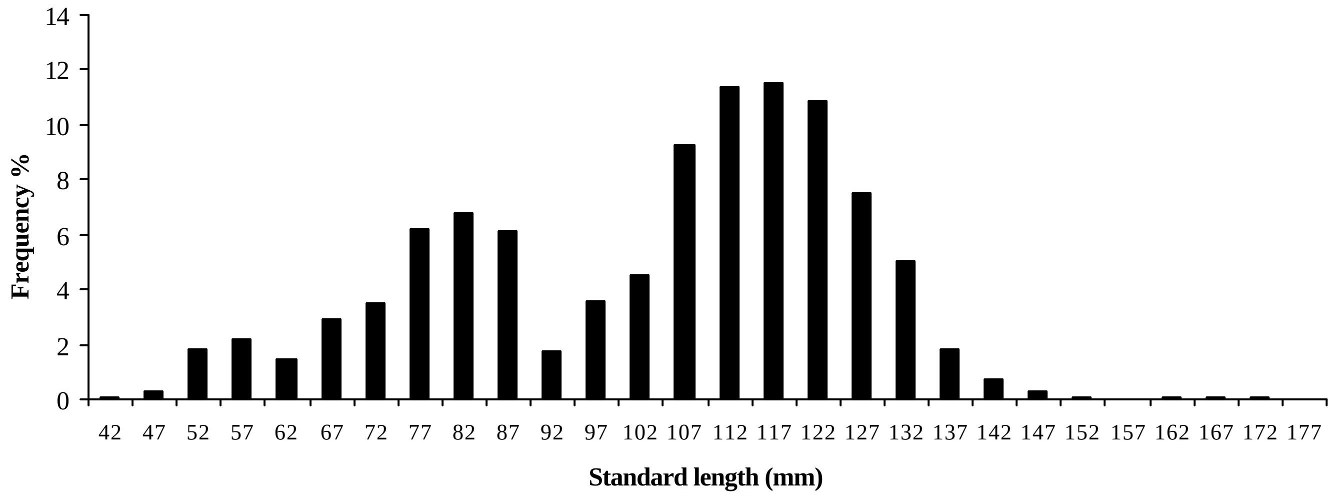

Figure 16-2. Size range and frequencies of *Diplotaxodon limnothrissa* caught in the SWA between July 1998 and May 1999.

the deep zone and 4.1 kg in the very deep zone, which approximately matched the values reported in Tómasson & Banda (1996) for the deep (36 kg) and very deep zones (7.1 kg) but was about twice as much for the shallows (6.7 kg). Specimen caught ranged between 40 and 175 mm (Figure 16-2). The sex ratio that was observed over the full sampling period was F/M 0.3/0.7.

Breeding season for females in the SWA occurred from March to August with a peak between April and June (Figure 16-3a) whereas males in breeding colour were caught throughout the year except in June (Figure 16-3b). These results being based upon pretty consistent sample size, the reason for the lack of fitting between females and males results is too be found elsewhere. Ripe females of the same species were found almost all year with a peak in March-April from offshore fishing locations and with a peak in May-June from inshore fishing location in the SEA (Thompson et al. 1996). Ripe females and males were also recorded from all over the Lake at any time of the year (Turner 1994a, Robinson R. L. pers. com.). Recent molecular analyses have shown that *D. limnothrissa* was constituted of a single wide spread population all over the Lake (Turner et al. 1999). This implies no breeding isolation from any part of the Lake and then large scale migrations of individuals. It is therefore likely that the breeding season we observed in the SWA between June 98 and May 99 was only a fixed and reductive picture of what happens at the Lake scale. Taking into account all the available information, it is probable that *D. limnothrissa* breeds all year long, but with seasonal geographical peak of activity, which would explain our observed pattern. Ripe females and males in breeding colour were found from 50 to 125 m with a higher frequency at 125 m for females and at 75 m for males (Table 16-1). It was previously thought that *D. limnothrissa* was not forming demersal spawning arenas because aggregation of breeding males had never been observed (Turner 1994a, Thompson et al. 1996). This was used to emphasised that some of the pelagic cichlid species might be able to spawn independently of the bottom of the lake (Thompson et al. 1996), as already observed for *Copadichromis* ("*Haplochromis*") *chrysonotus* (Eccles & Lewis 1981). However, large aggregations of males in breeding colours (more than 300 specimens) were found at 75 and 100 m in the SWA in April and May 99, suggesting that spawning probably occur close to the bottom at these depths. As already reported by Turner (1994a, 1996), *D. limnothrissa* females were observed to moothbrood young to large sizes, up to 23 mm SL. Maturity was reached early in their second year at 16 months old at a mean size of 105 mm for females (Figure 16-4), a size a bit smaller than the 14 cm TL (about 113 mm SL) reported by Thompson et al. (1996).

Table 16-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Diplotaxodon limnothrissa* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	0.2	0	0.4	0	0.7
50 m	14.4	25.7	18.5	4.1	34.7
75 m	39.6	11	31.5	53.4	34.4
100 m	35.4	17.8	41	31.2	27
125 m	10.4	45.5	8.5	11.3	3.3

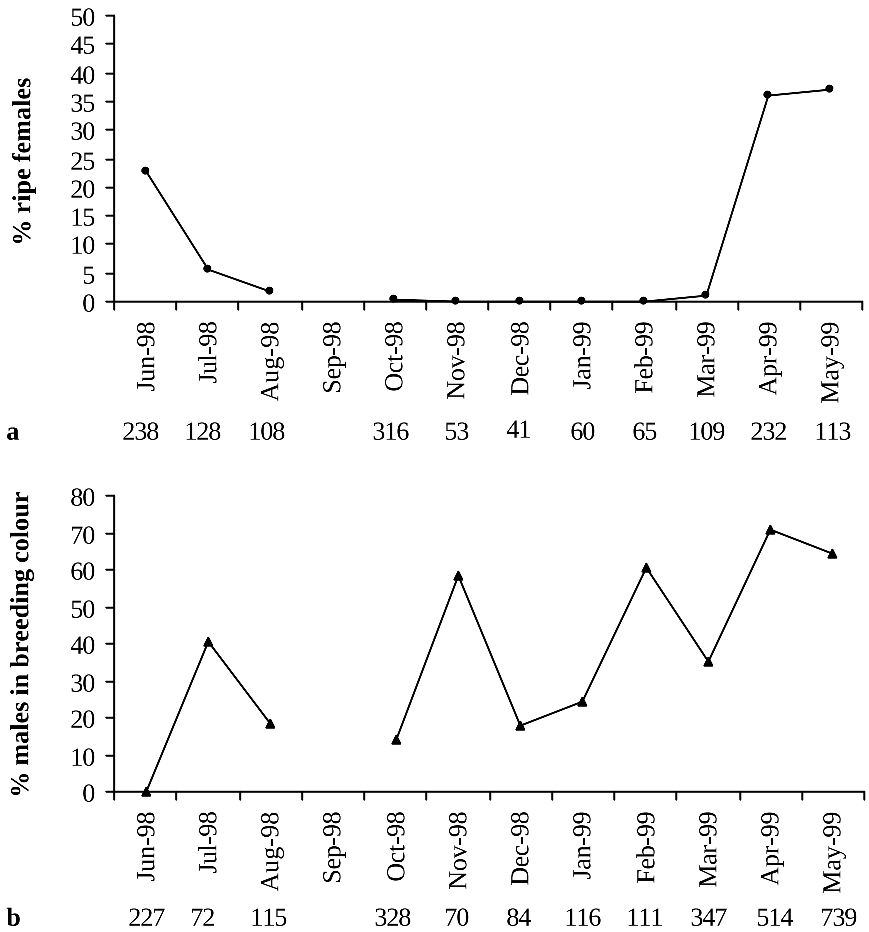

Figure 16-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Diplotaxodon limnothrissa* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

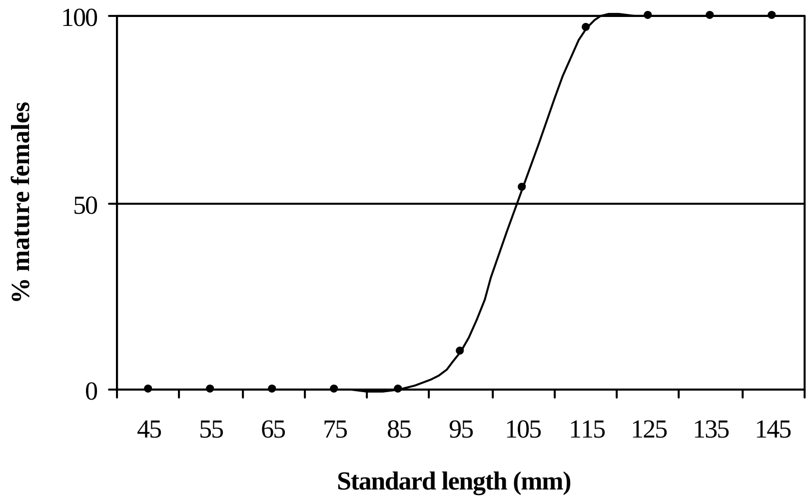

Figure 16-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Diplotaxodon limnothrissa* in the SWA.

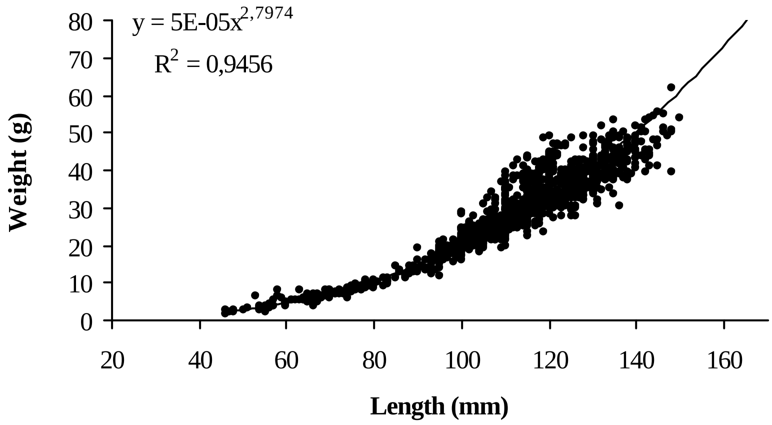

Figure 16-5. Length-weight relationship for *Diplotaxodon limnothrissa* females in the SWA. (R^2 = determination coefficient).

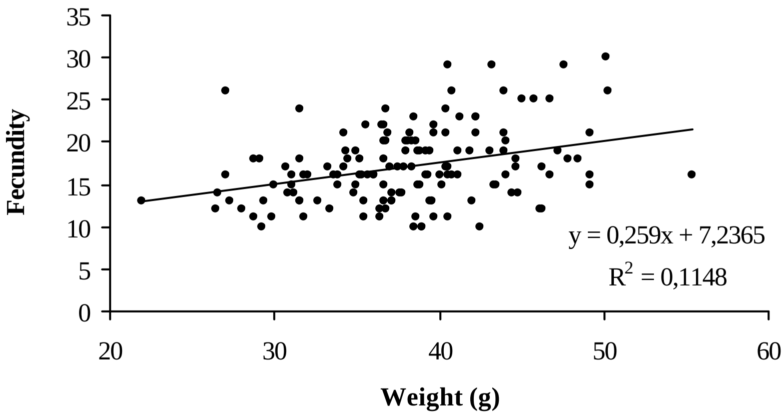

Figure 16-6. Fecundity-weight relationship for *Diplotaxodon limnothrissa* females in the SWA. (R^2 = determination coefficient).

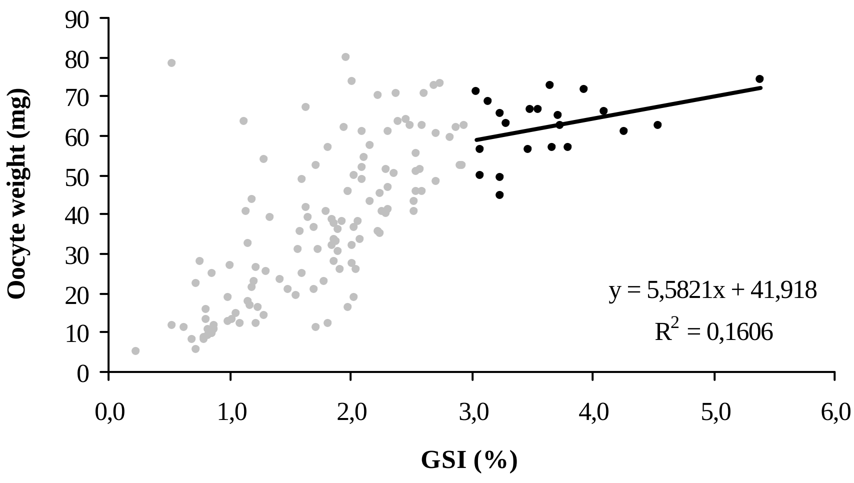

Figure 16-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Diplotaxodon limnothrissa*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

Plate 9. *Diplotaxodon macrops* (by Dave Voorvelt).

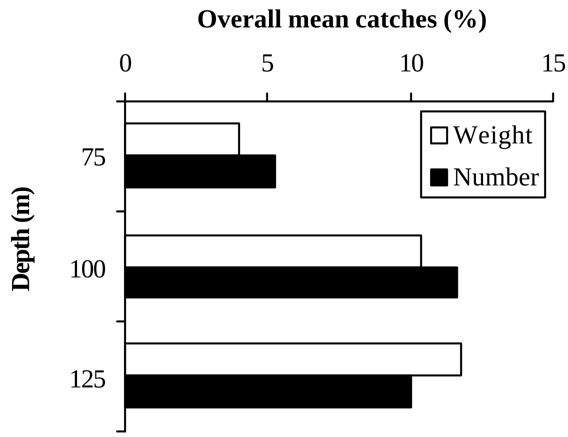

Figure 17-1. Mean occurrence and abundance in the catches per depth of *Diplotaxodon macrops* in the SWA between July 1998 and May 1999.

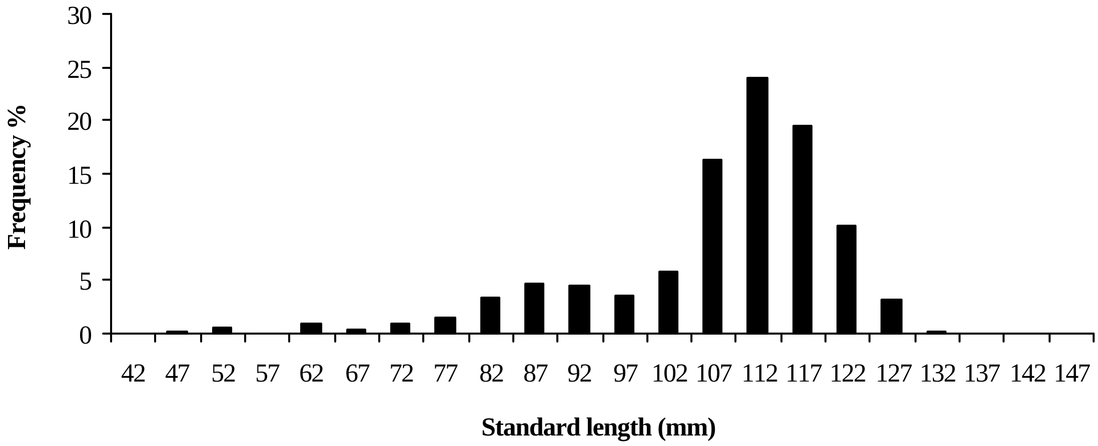

Figure 17-2. Size range and frequencies of *Diplotaxodon macrops* caught in the SWA between July 1998 and May 1999.

The length-weight and fecundity-weight relationships are given in Figure 16-5 and 16-6, respectively. Fecundity ranged from 10 to 30 for females weighing between 22 and 55 g and was not correlated to body weight. The fecundity range we found corresponded with the average fecundity of 15 eggs observed by Thompson et al. (1996) for females of 14-18 cm TL. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 16-7). The mean oocyte weight was 62.30 mg (± 7.93 SD, N= 21).

Diplotaxodon macrops (Turner & Stauffer) (Plate 9)

1664 females and 2919 males were analysed. *D. macrops* was caught from 75 to 125 m (Figure 17-1). It was a dominant species in the catches at 75 100 and 125 m, where it constituted (in number and weight, respectively) 5.3 and 4%, 11.6 and 10.4% and 10 and 11.8% of the catches, respectively. The mean CPUE per depth category was 39.3 kg in the deep zone and 24 kg in the very deep zone. There was no record for this species in Tómasson & Banda (1996). Specimens caught ranged between 40 and 135 mm (Figure 17-2). A single individual measuring 150 mm was caught, which was probably a specimen of the resembling *D. 'offshore'* that grows larger (Robinson R. L., pers. com.). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

Ripe females (Figure 17-3a) and males (Figure 17-3b) were found throughout the year with a decline between October and December and a peak of activity from February to April. Most ripe females and males in breeding colour were found at 100 and 125 m (Table 17-1). All the large aggregations of breeding males (between 100 and 400 specimens) observed in August 98, January, February, March , April and May 99, were caught at 100 and 125 m, suggesting that spawning probably occurs at these depths. The mean size at maturity for females was about 98 mm (Figure 17-4), which corresponded to a mean age at maturity of 20 months.

Table 17-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Diplotaxodon macrops* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	11.9	5.1	24.9	11.5	33.2
100 m	52.1	49.1	47.8	30.4	46.5
125 m	36.1	45.8	27.3	58	20.3

The length-weight and fecundity-weight relationships are given in Figure 17-5 and 17-6, respectively. Fecundity ranged from 10 to 37 for females weighing between 20.6 and 51 g and was not correlated to body weight. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 17-7). The mean oocyte weight was 56.04 mg (± 9.4 SD, N= 46).

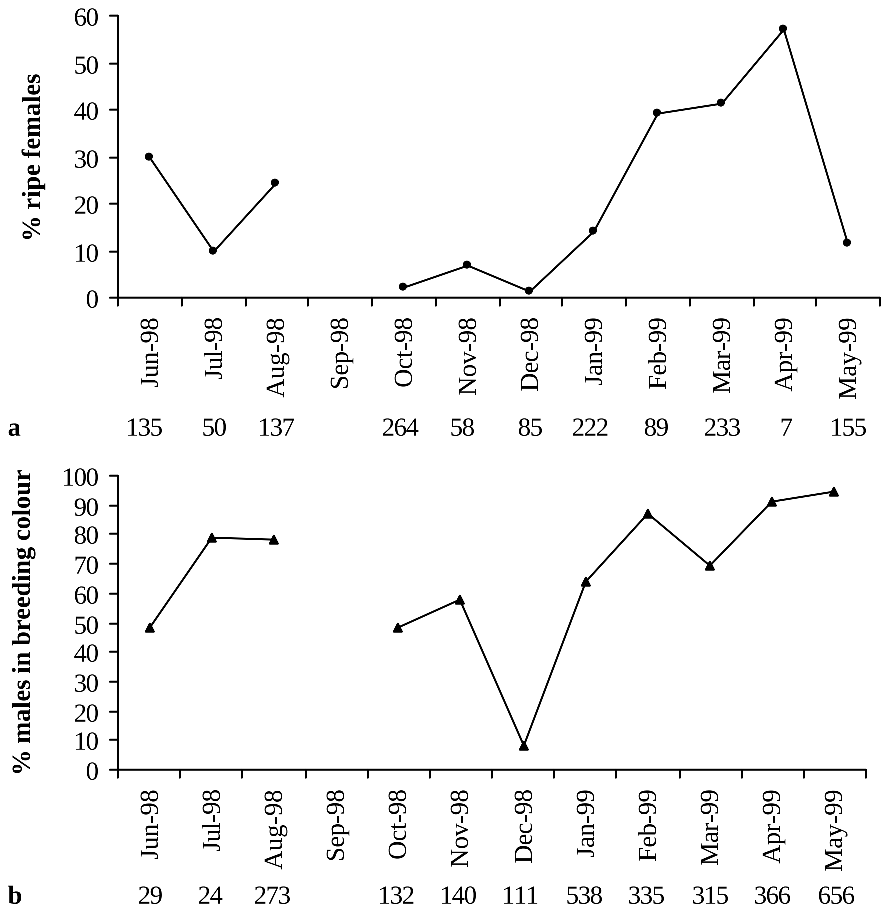

Figure 17-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Diplotaxodon macrops* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

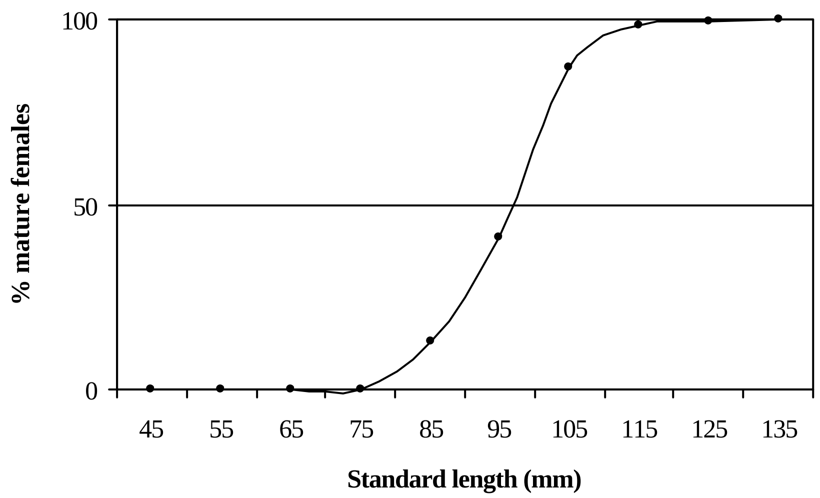

Figure 17-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Diplotaxodon macrops* in the SWA.

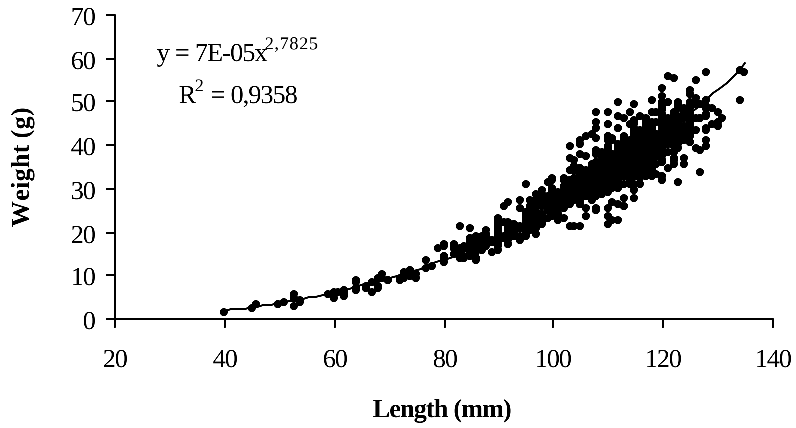

Figure 17-5. Length-weight relationship for *Diplotaxodon macrops* females in the SWA. (R^2 = determination coefficient).

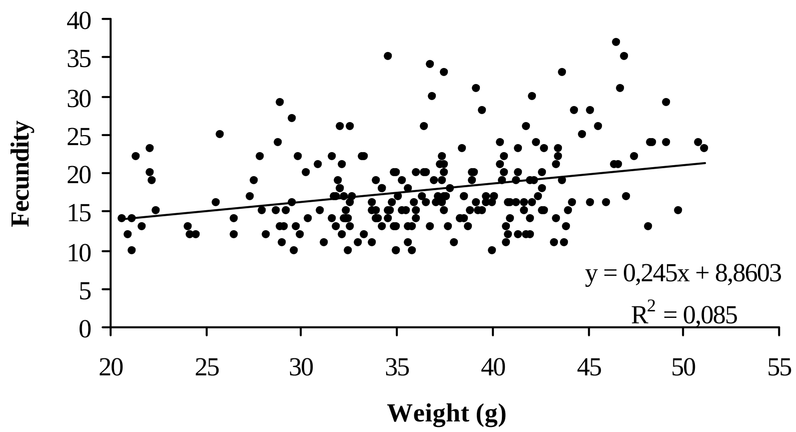

Figure 17-6. Fecundity-weight relationship for *Diplotaxodon macrops* females in the SWA. (R^2 = determination coefficient).

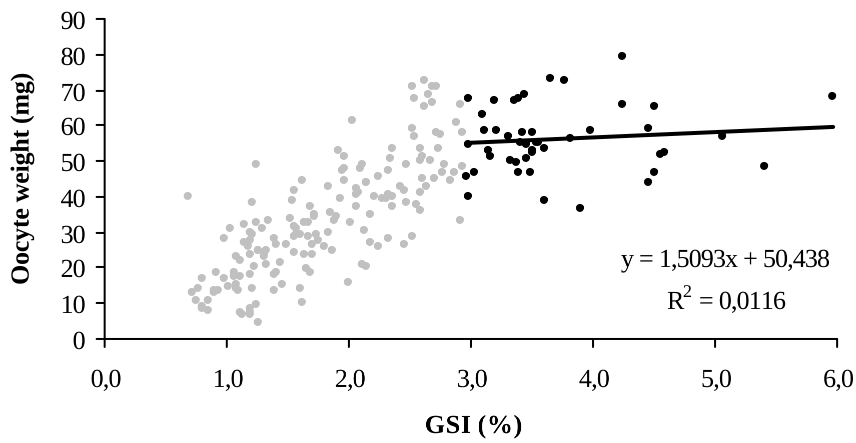

Figure 17-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Diplotaxodon macrops*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

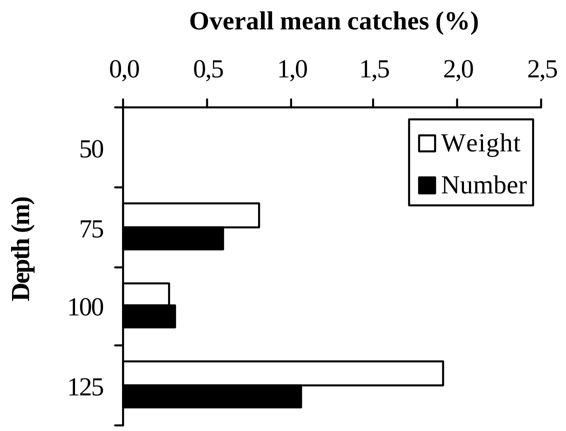

Figure 18-1. Mean occurrence and abundance in the catches per depth of *Pallidochromis tokolosh* in the SWA between July 1998 and May 1999.

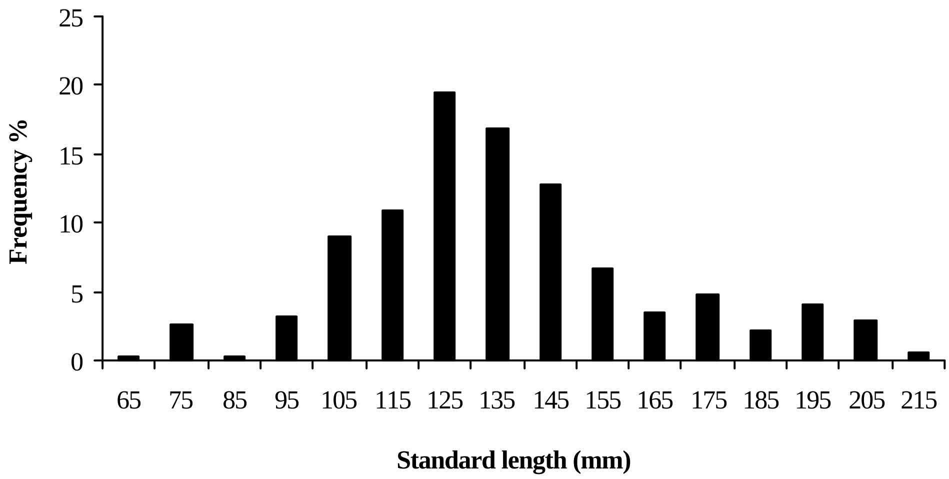

Figure 18-2. Size range and frequencies of *Pallidochromis tokolosh* caught in the SWA between July 1998 and May 1999.

Pallidochromis tokolosh **(Turner)**

210 females and 134 males were analysed. *P. tokolosh* was common from 75 to 125 m and was occasionally caught at 50 m (Figure 18-1). It was more frequent at 125 m, where it constituted 1.1 and 1.9% of the catches in number and weight, respectively. The mean CPUE per depth category was 0.15 kg in the shallows, 3.6 kg in the deep zone and 4.4 kg in the very deep zone, which matched the values reported by Tómasson & Banda (1996) for the shallow and deep zone but was more than twice as much for the very deep zone (1.8 kg). Specimens caught ranged between 62 and 213 mm with a mode from 100 to 160 mm (Figure 18-2). The sex ratio observed over the full sampling period was F/M 0.6/0.4.

P. tokolosh is not an abundant fish and low sample size at some months hampered the correct determination of breeding season. Next, we never observed any particular breeding dress for males and therefore the percentage of males in breeding colour was impossible to assess. From the data available, it seemed that the breeding season would occur between October and February (Figure 18-3). The depth distribution of ripe females (Table 18-1) reflected the relative abundance per depth with 67% at 125 m and 30% at 75 m. No particular indication about spawning depth was drawn from these results. Maturity was reached early in their second year at 16 months old at a mean size of 135 mm for females (Figure 18-4).

Table 18-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Pallidochromis tokolosh* in the SWA. Sample size between bracket.

Depth	Non ripe females (70)	Ripe females (27)	Immature Specimens (185)
50 m	0	3.7	0
75 m	22.9	29.6	44.3
100 m	10	0	18.4
125 m	67.1	66.7	37.3

The length-weight and fecundity-weight relationships are presented in Figure 18-5 and 18-6, respectively. Fecundity ranged from 13 to 87 for females weighing between 36 and 143 g. No relation was found between oocyte weight and body weight. The largest and heaviest oocytes of all cichlid species studied were produced by *P. tokolosh*, the record being 85 mg. The GSI threshold above which the oocyte weight did no longer increase significantly was not determined owing to low sample size of high GSI (Figure 18-7). Nevertheless, assuming a 3% threshold as for the other species of the *Diplotaxodon* clade, the mean oocyte weight was 70.49 mg (± 12.53 SD, N= 3).

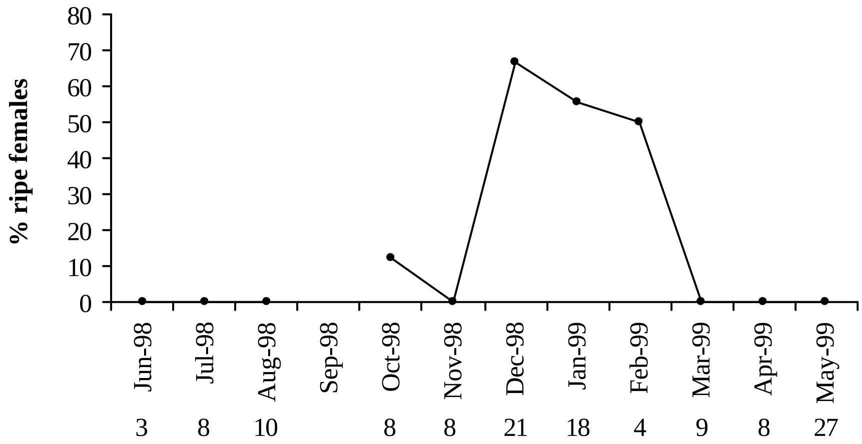

Figure 18-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females *Pallidochromis tokolosh* in the SWA The values below the x-axis are the effective (number of females which size was above the size at maturity) for each month.

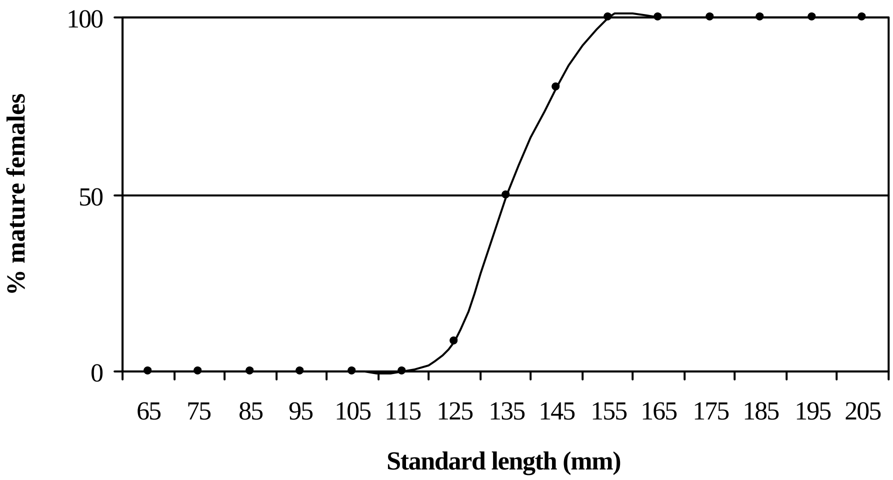

Figure 18-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Pallidochromis tokolosh* in the SWA.

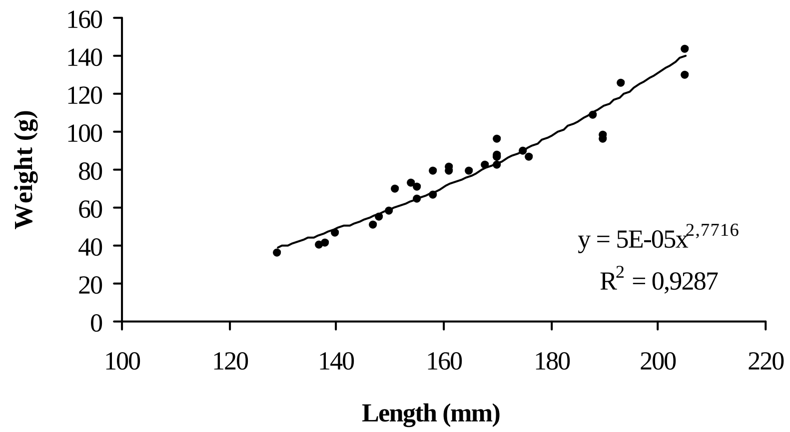

Figure 18-5. Length-weight relationship for *Pallidochromis tokolosh* females in the SWA. (R^2 = determination coefficient).

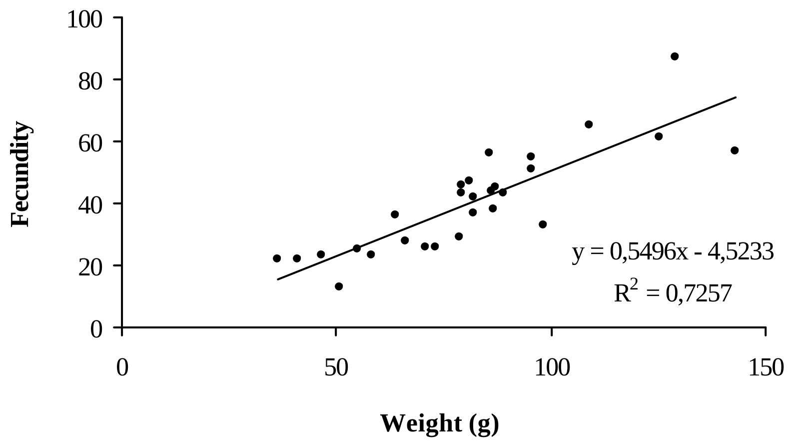

Figure 18-6. Fecundity-weight relationship for *Pallidochromis tokolosh* females in the SWA. (R^2 = determination coefficient).

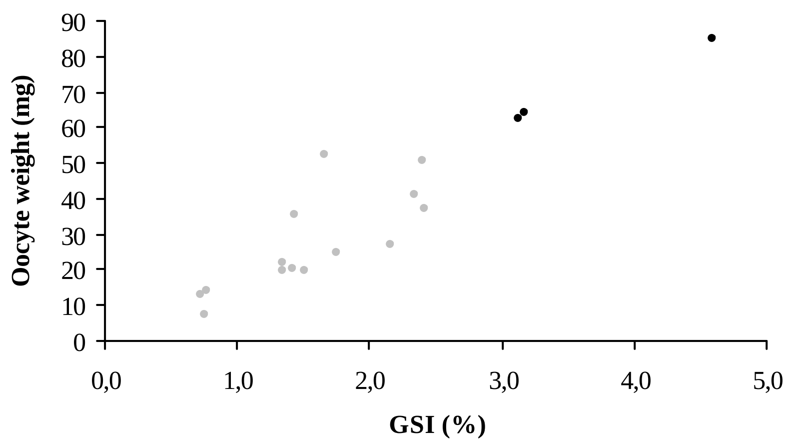

Figure 18-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Pallidochromis tokolosh*. Oocytes from females whose GSI was below (in grey) and above (in black) 3%.

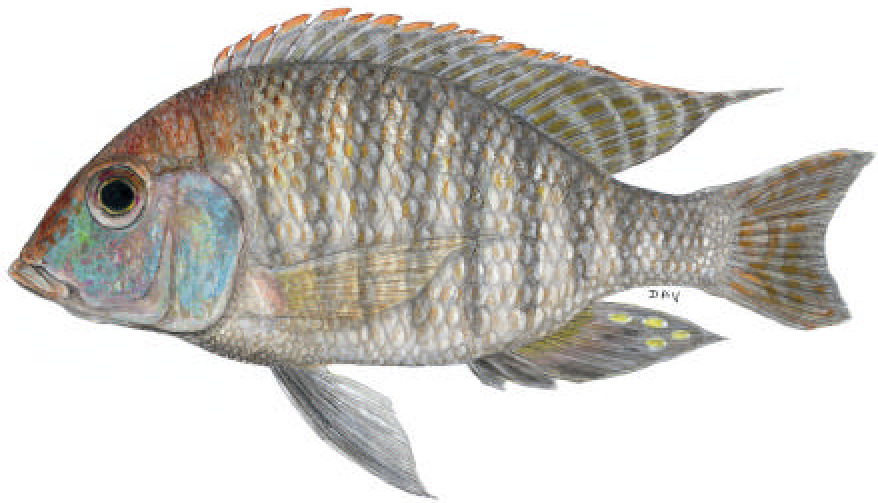

Plate 10. *Lethrinops argenteus* (by Dave Voorvelt).

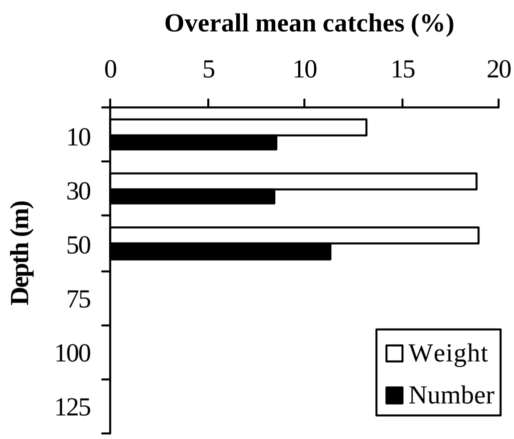

Figure 19-1. Mean occurrence and abundance in the catches per depth of *Lethrinops argenteus* in the SWA between July 1998 and May 1999.

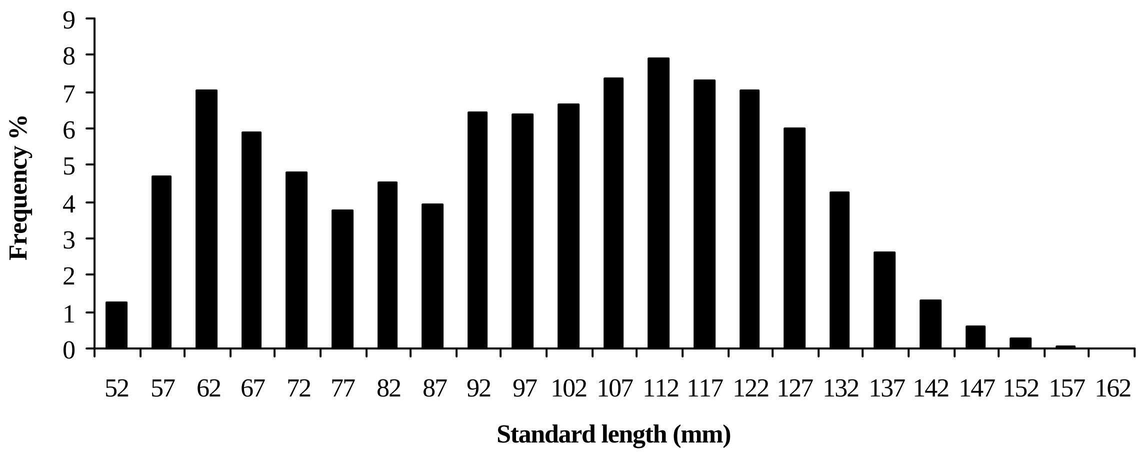

Figure 19-2. Size range and frequencies of *Lethrinops argenteus* caught in the SWA between July 1998 and May 1999.

Lethrinops spp.

Lethrinops argenteus **(Ahl) (Plate 10)**

3176 females and 2424 males were analysed. *L. argenteus* was caught from 10 to 125 m (Figure 19-1). It was abundant only between 10 and 50 m where it was a dominant species in the catches, constituting between 9 and 11% of the catches in number and between 13 and 19% in weight. The mean CPUE per depth category was 127.4 kg in the shallows, 0.15 and 0.3 kg in the deep and very deep zones, respectively. No reference was made to this species in Tómasson & Banda (1996), who probably included this species in the *L. longipinnis* group. Specimens caught ranged between 50 and 165 mm (Figure 19-2). The sex ratio observed over the full sampling period was F/M 0.6/0.4.

Ripe females (Figure 19-3a) and males (Figure 19-3b) of *L. argenteus* were found throughout the year with steady decline from March to June and in October and peaks of activity in August 98 and between December and February 99. 70% of males in breeding colour and 43% of ripe females were caught at 30 m (Table 19-1). Aggregations of breeding males, although small (between 30 and 80 individuals) compared to those observed for *Diplotaxodon spp.*, were always found at 30 m suggesting that spawning could occur at this depth. The mean size at maturity for females was about 108 mm (Figure 19-4), which corresponded to a mean age at maturity of 12 months.

Table 19-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Lethrinops argenteus* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	17.4	26.2	31.2	22.6	23.1
30 m	35.8	41.1	43.1	70.2	27.3
50 m	46.5	32.3	25.5	6.7	49.5
75 m	0.1	0	0.2	0.2	0.2
100 m	0	0.4	0	0	0
125 m	0.2	0	0.1	0.3	0

The length-weight and fecundity-weight relationships are presented in Figure 19-5 and 19-6, respectively. Fecundity ranged from 43 to 218 for females weighing between 12.5 and 103 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 4% (Figure 19-7). The mean oocyte weight was 20.09 mg (± 4.17 SD, N= 28).

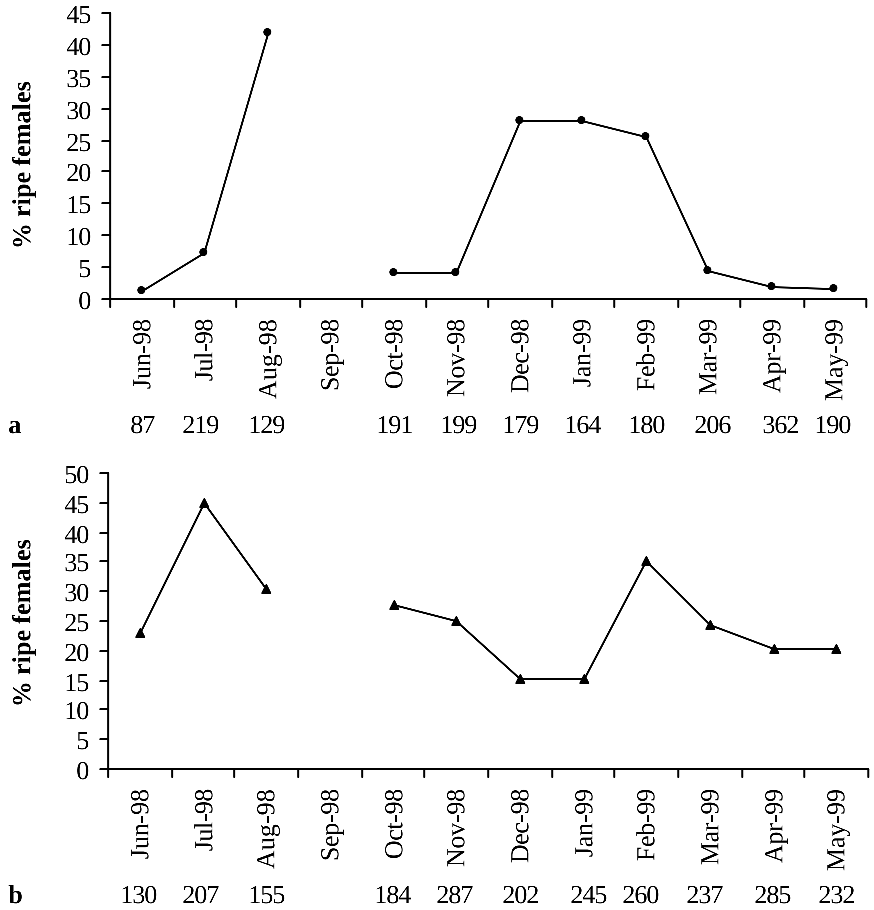

Figure 19-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Lethrinops argenteus* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

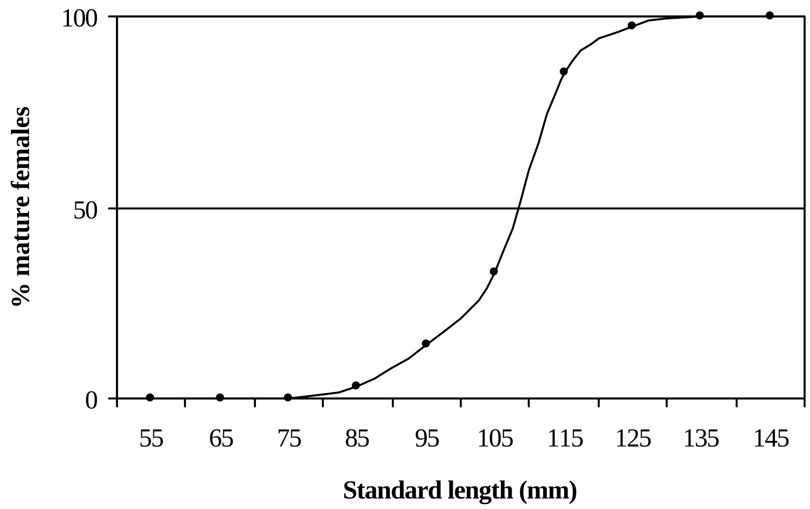

Figure 19-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Lethrinops argenteus* in the SWA.

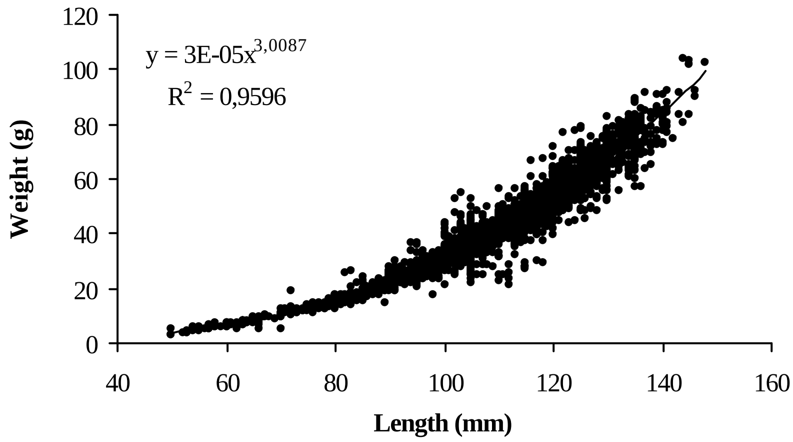

Figure 19-5. Length-weight relationship for *Lethrinops argenteus* females in the SWA. (R^2 = determination coefficient).

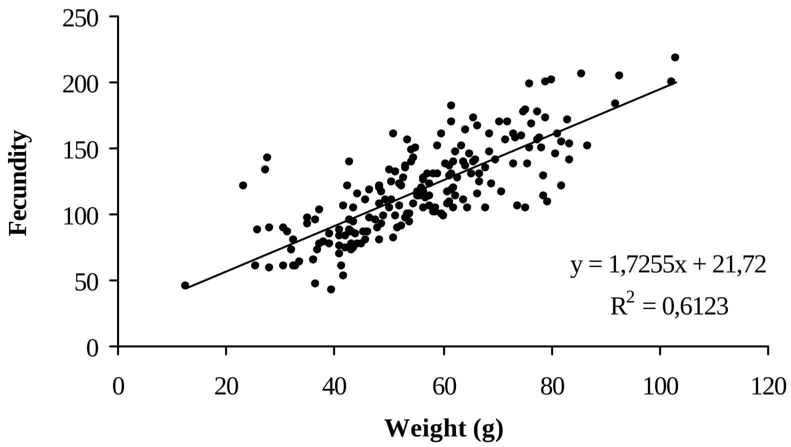

Figure 19-6. Fecundity-weight relationship for *Lethrinops argenteus* females in the SWA. (R^2 = determination coefficient).

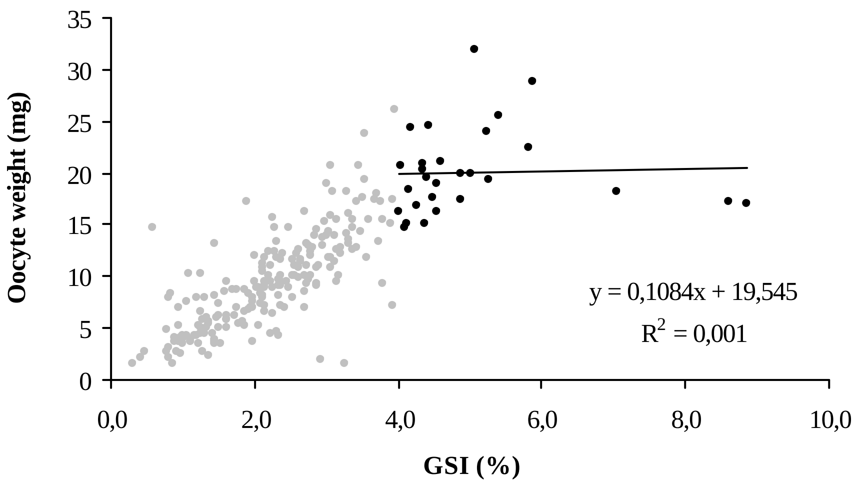

Figure 19-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Lethrinops argenteus* Oocytes from females whose GSI was below (in grey) and above (in black with regression) 4%. (R^2 = determination coefficient).

Plate 11. *Lethrinops 'deep water albus'* (by Dave Voorvelt).

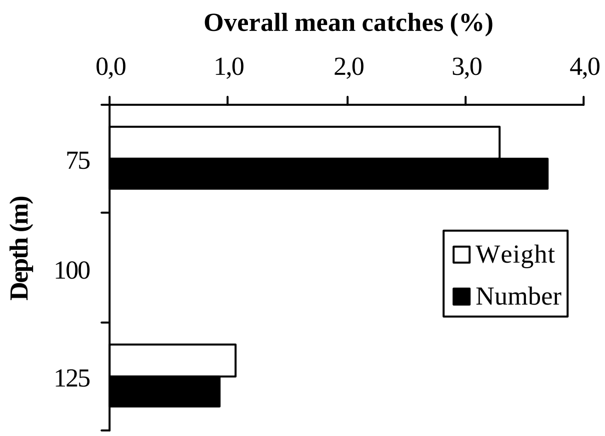

Figure 20-1. Mean occurrence and abundance in the catches per depth of *Lethrinops 'deep water albus'* in the SWA between July 1998 and May 1999.

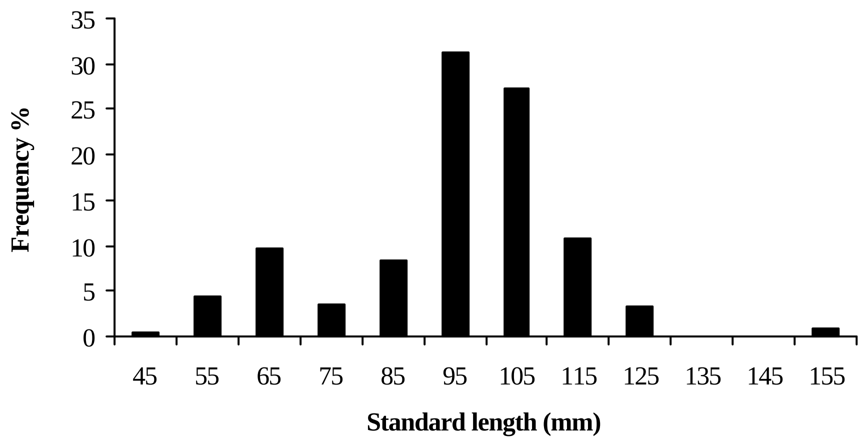

Figure 20-2. Size range and frequencies of *Lethrinops 'deep water albus'* caught in the SWA between July 1998 and May 1999.

Lethrinops 'deep water albus' (Plate 11)

303 females and 171 males were analysed. *L. 'deep water albus*' was caught from 75 to 125 m, though rarely at 100 m (Figure 20-1). It was not an abundant fish, always constituting less than 1% of the catches and often completely absent from the sampled part of the SWA. The 3.3 and 3.7% of the catches respectively in weight and number, observed at 75 m were due to an exceptional catch in November 98, during which *L. 'deep water albus*' made up to 31 and 33% of the catch in weight and number. However, *L. 'deep water albus*' was very abundant off Domira Bay and off Leopard Bay, being the dominant species in catches of 400 to 600 kg between 75 and 125 m. This species seemed to be dominant in the deep water catches when *Lethrinops gossei* was absent or rare. *L. 'deep water albus*' was often very abundant in the catches in these areas when we were targeting for *L. gossei*, and one or the other was dominant but never both of them at the same time. As a matter of fact, during the exceptional catch of *L. 'deep water albus*' at 75 m in the SWA in November 98, only 38 specimens of *L. gossei* were caught. As *L. gossei* was a consistently dominant species in the deep zone of the SWA (see further), it might explain why *L. 'deep water albus*' was rare. Specimens caught ranged between 40 and 160 mm (Figure 20-2). The sex ratio observed over the full sampling period was F/M 0.6/0.4.

Owing to irregularity in the catches of this species and low sample size for most of the months, precise determination of breeding season was not possible and. Ripe females were found from June to August 98 and in November and January 98 (Figure 20-3a) whereas males in breeding colour were found at each sampling date, including in May (Figure 20-3b). Size at maturity was estimated at about 82 mm for females and was probably slightly overestimated as this estimation was not done during the height of the breeding season but with all the data available for females (Figure 20-4).

The length-weight and fecundity-weight relationships are presented in Figure 20-5 and 20-6, respectively. Fecundity ranged from 65 to 151 for females weighing between 19 and 42 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was not determine precisely owing to low sample size, but was estimated at 4% (Figure 20-7). The mean oocyte weight was 10.27 mg (± 0.89 SD, N= 3).

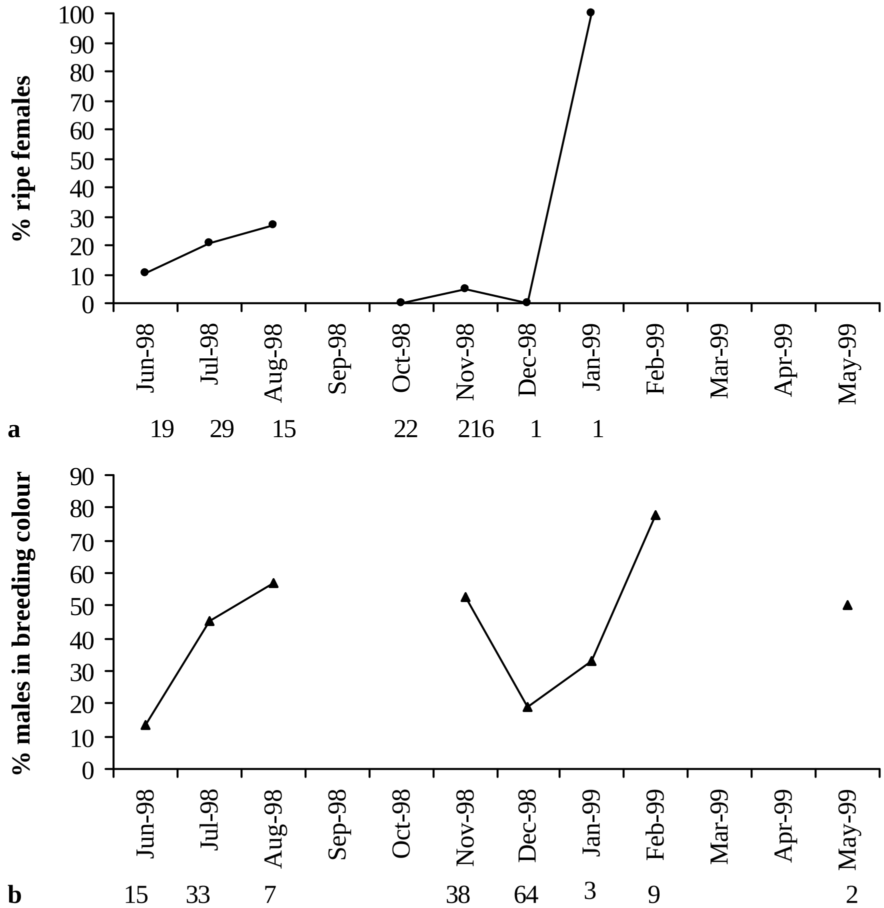

Figure 20-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Lethrinops 'deep water albus'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

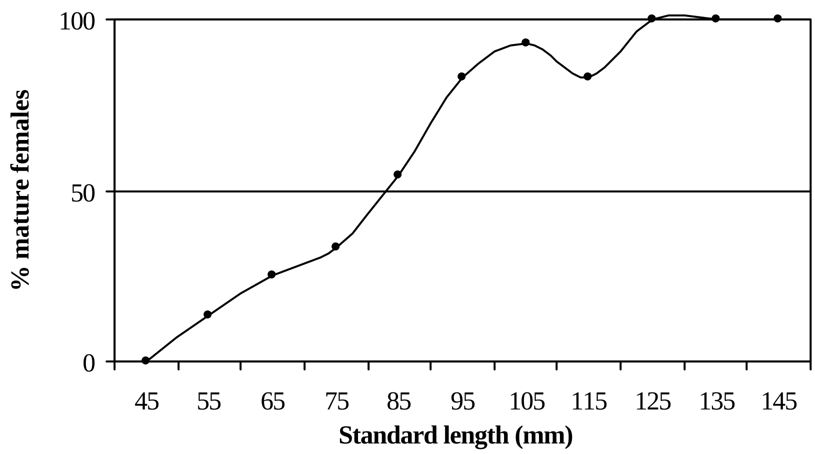

Figure 20-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Lethrinops 'deep water albus'* in the SWA.

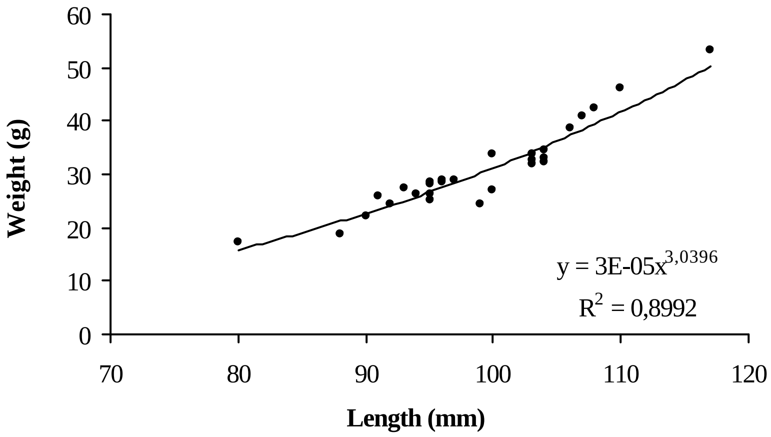

Figure 20-5. Length-weight relationship for *Lethrinops 'deep water albus'* females in the SWA. (R^2 = determination coefficient).

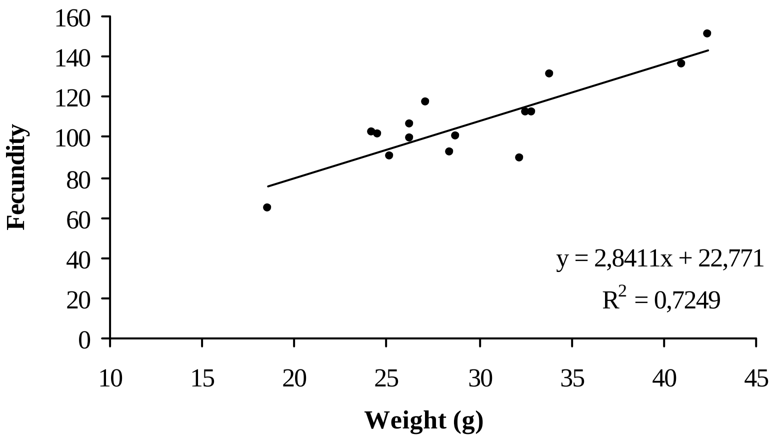

Figure 20-6. Fecundity-weight relationship for *Lethrinops 'deep water albus'* females in the SWA. (R^2 = determination coefficient).

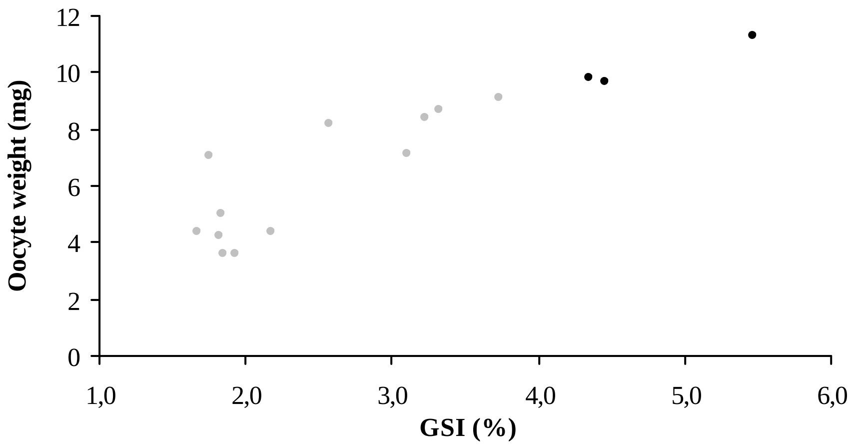

Figure 20-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Lethrinops 'deep water albus'* Oocytes from females whose GSI was below (in grey) and above (in black with regression) 4%. (R^2 = determination coefficient).

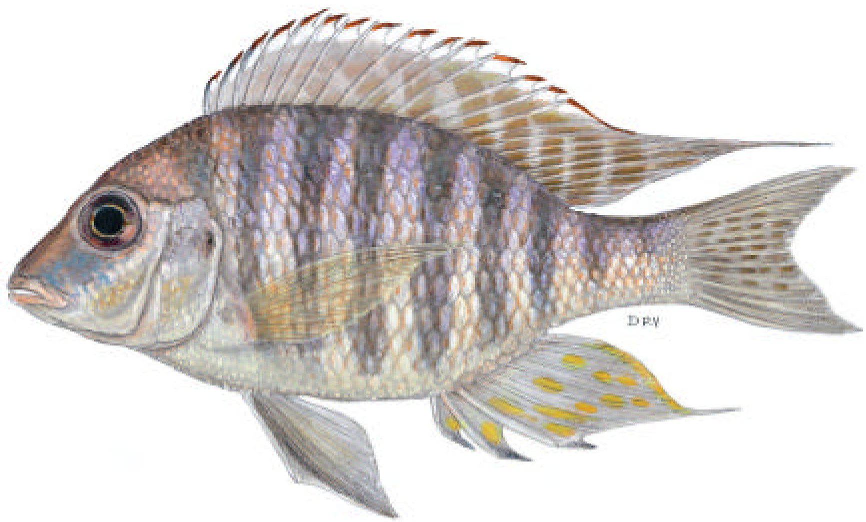

Plate 12. *Lethrinops 'deep water altus'* (by Dave Voorvelt).

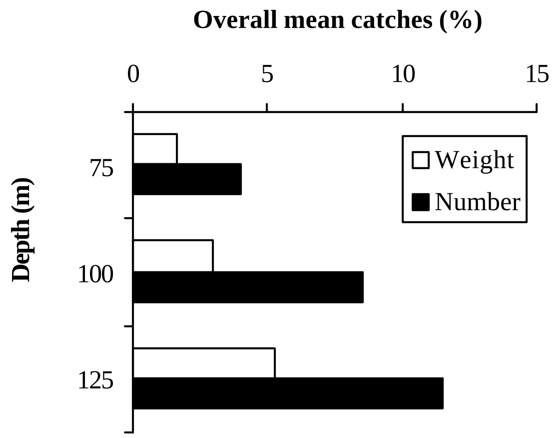

Figure 21-1. Mean occurrence and abundance in the catches per depth of *Lethrinops 'deep water altus'* in the SWA between July 1998 and May 1999.

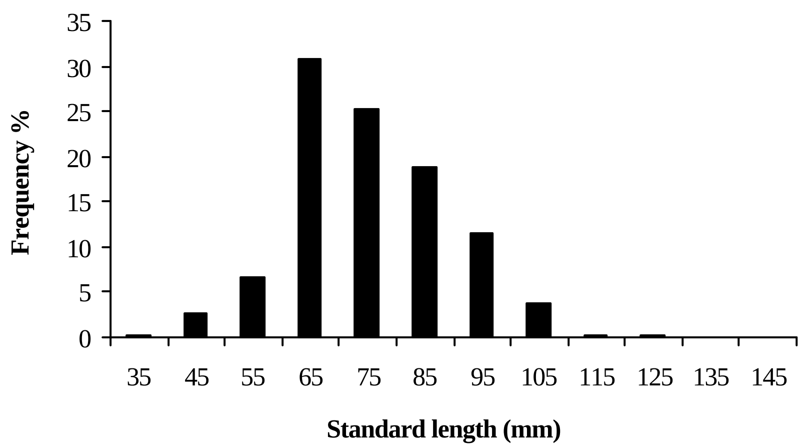

Figure 21-2. Size range and frequencies of *Lethrinops 'deep water altus'* caught in the SWA between July 1998 and May 1999.

Lethrinops 'deep water altus' (Plate 12)

625 females and 885 males were analysed. *L. 'deep water altus'* was an abundant species of the deep and very deep zones, increasing in occurrence and biomass with depth from 75 to 125 m to reach 5.3 and 11.5% of the catches in weight and number, respectively (Figure 21-1). The mean CPUE per depth category was 8.6 and 3.3 kg in the deep and very deep zones, respectively. No reference was made to this species in Tómasson & Banda (1996). Specimens caught ranged between 35 and 130 mm with a mode from 60 to 100 mm (Figure 21-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

Breeding season occurred between December and August-September with a peak of activity from February to June and a cessation in October-November confirmed by the lower percentage of active males during this period (Figure 21-3a and b). Ripe females and immature individuals were evenly distributed between 75 and 125 m, whereas about 60% of the males in breeding colour were caught at 125 m, suggesting that spawning could occur mostly at this depth (Table 21-1). The mean size at maturity for females was about 60 mm (Figure 21-4), which corresponded to a mean age at maturity of 11 months.

Table 21-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Lethrinops 'deep water altus'* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	14.2	29.5	12.6	11.5	23.5
100 m	46.2	34.7	37.1	31.3	37.3
125 m	39.7	35.8	50.3	57.2	39.2

The length-weight and fecundity-weight relationships are presented in Figure 21-5 and 21-6, respectively. Fecundity ranged from 10 to 84 for females weighing between 5 and 19 g and was not correlated with body weight. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 21-7). The mean oocyte weight was 8.08 mg (± 2.32 SD, N= 34).

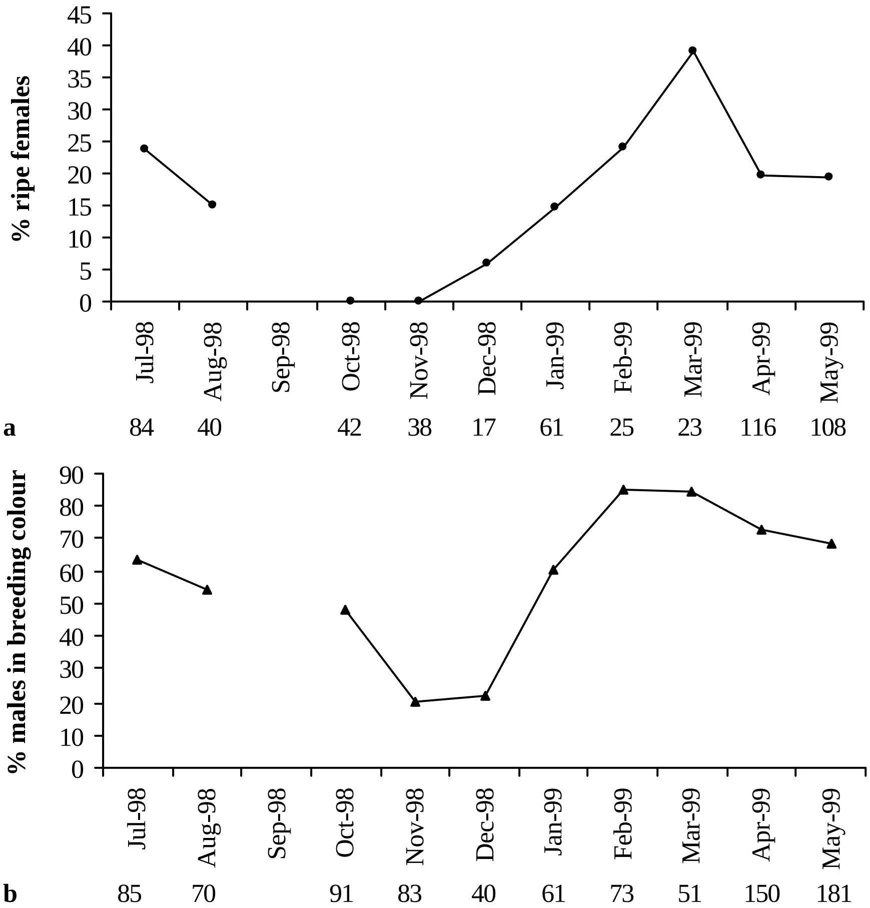

Figure 21-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Lethrinops 'deep water altus'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

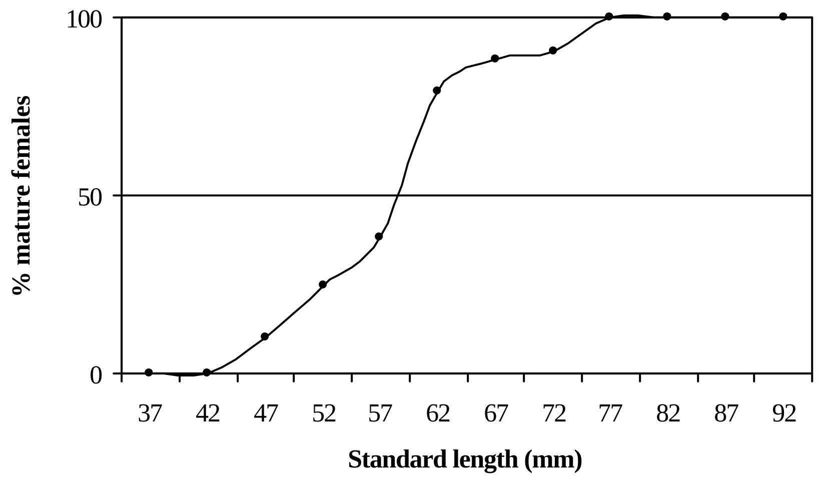

Figure 21-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Lethrinops 'deep water altus'* in the SWA.

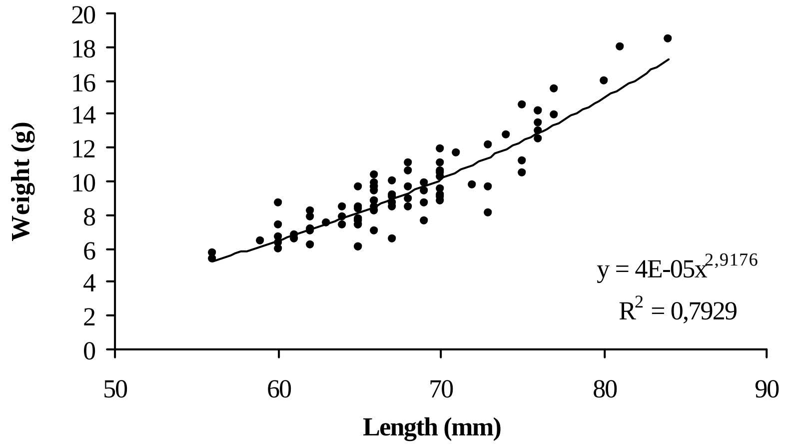

Figure 21-5. Length-weight relationship for *Lethrinops 'deep water altus'* females in the SWA. (R^2 = determination coefficient).

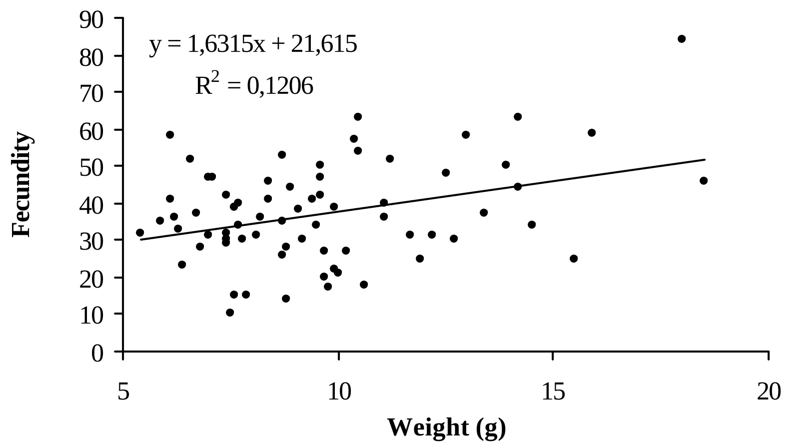

Figure 21-6. Fecundity-weight relationship for *Lethrinops 'deep water altus'* females in the SWA. (R^2 = determination coefficient).

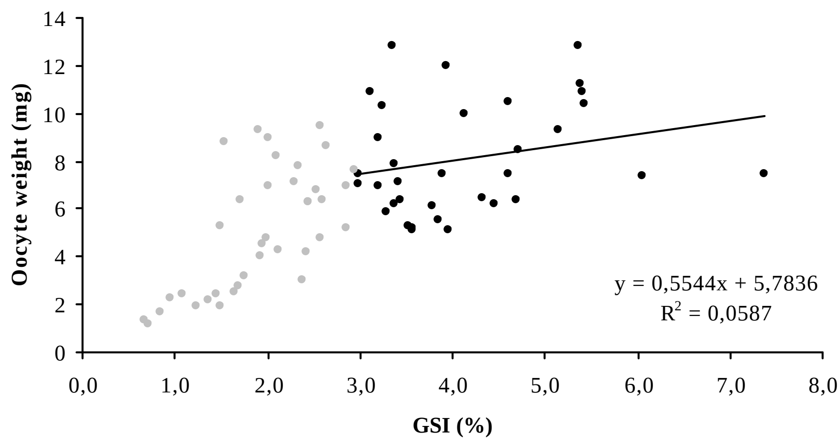

Figure 21-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Lethrinops 'deep water altus'* Oocytes from females whose GSI was below (in grey) and above (in black with regression) 4%. (R^2 = determination coefficient).

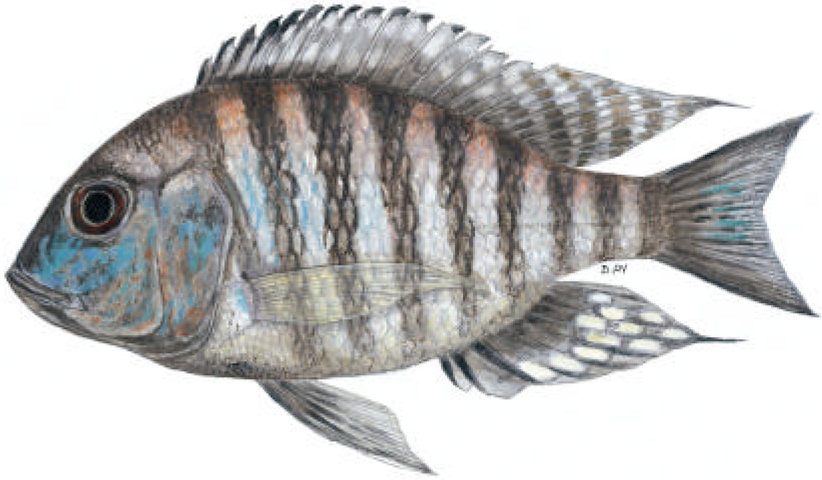

Plate 13. Lethrinops gossei (by Dave Voorvelt).

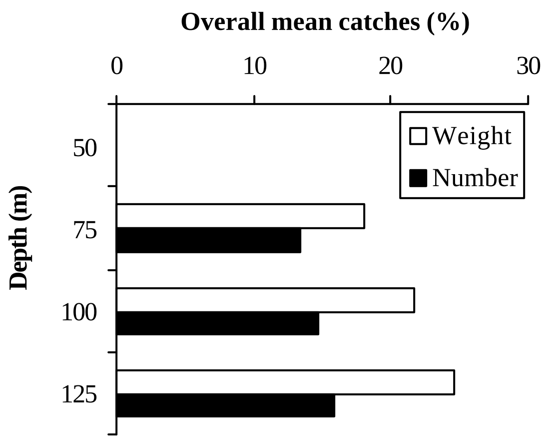

Figure 22-1. Mean occurrence and abundance in the catches per depth of *Lethrinops gossei* in the SWA between July 1998 and May 1999.

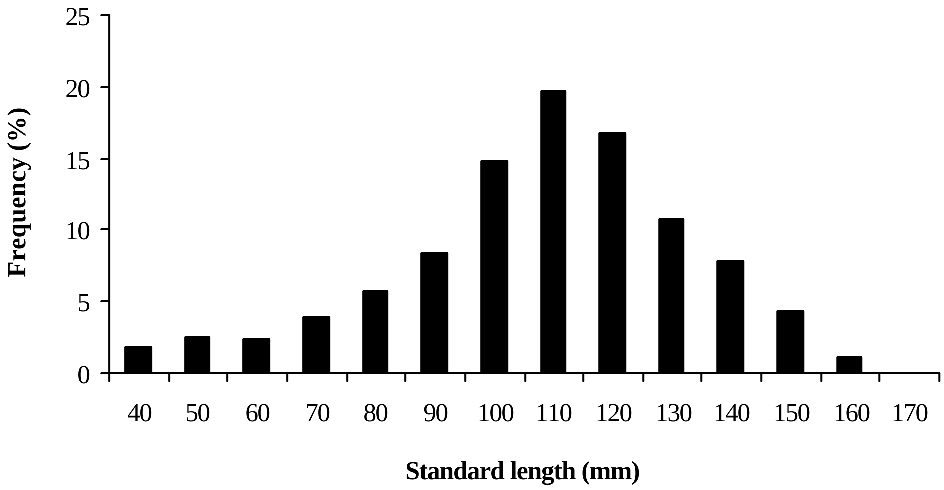

Figure 22-2. Size range and frequencies of *Lethrinops gossei* caught in the SWA between July 1998 and May 1999.

Lethrinops gossei (Burgess & Axelrod) (Plate 13)

3513 females and 3425 males were analysed. *L. gossei* was caught from 50 to 125 m, becoming very abundant form 75 m downwards (Figure 22-1). It was a dominant species of the deep and very deep zones, where it constituted between 13 and 16% of the catches in number and between 18 and 25% in weight. The mean CPUE per depth category was 0.3, 108 and 51.6 kg for the shallow, deep and very deep zones, respectively. Except for the very deep zone, this was very different from the values reported in Tómasson & Banda (1996), who caught much more *L. gossei* per time unit in the shallows (21.6 kg) and about two times less in the deep zone (61.9 kg). Specimens caught ranged between 35 and 170 mm with a mode from 95 to 135 mm (Figure 22-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Breeding season occurred between November and August with a peak of activity from January to March-April and a stop in September-October (Figure 22-3a). It was one of the rare species for which the profile of the percentage of ripe males followed exactly the female's one (Figure 22-3b). The breeding season we observed corresponded relatively well to that found by Lewis & Tweddle (1990), who reported a decline in October-November and a peak in March for the period 1983-85. Ripe females and males were evenly distributed between 75 and 125 m (Table 22-1), as were the aggregations of males in breeding colour (between 100 and 200 specimens), suggesting that spawning probably takes place at all three depths. The mean size at maturity for females was about 92 mm (Figure 22-4), which is much less than the 147 mm TL estimated by Lewis & Tweddle (1990). This corresponded to a mean age at maturity of 11 months.

Table 22-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Lethrinops gossei* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
50 m	0	0	0.1	0.1	0.2
75 m	33.5	42.1	28	27.8	44
100 m	26.9	36.8	39.3	37.8	36.4
125 m	39.6	21.1	32.6	34.3	19.4

The length-weight and fecundity-weight relationships are presented in Figure 22-5 and 22-6, respectively. Fecundity ranged from 23 to 234 for females weighing between 10 and 109 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 4% (Figure 22-7). The mean oocyte weight was 21.34 mg (± 4.34 SD, N= 190). A GSI of 12.4% was recorded for a *L. gossei* female (Figure 22-7), which was the highest GSI calculated on any cichlid species during the course of this study.

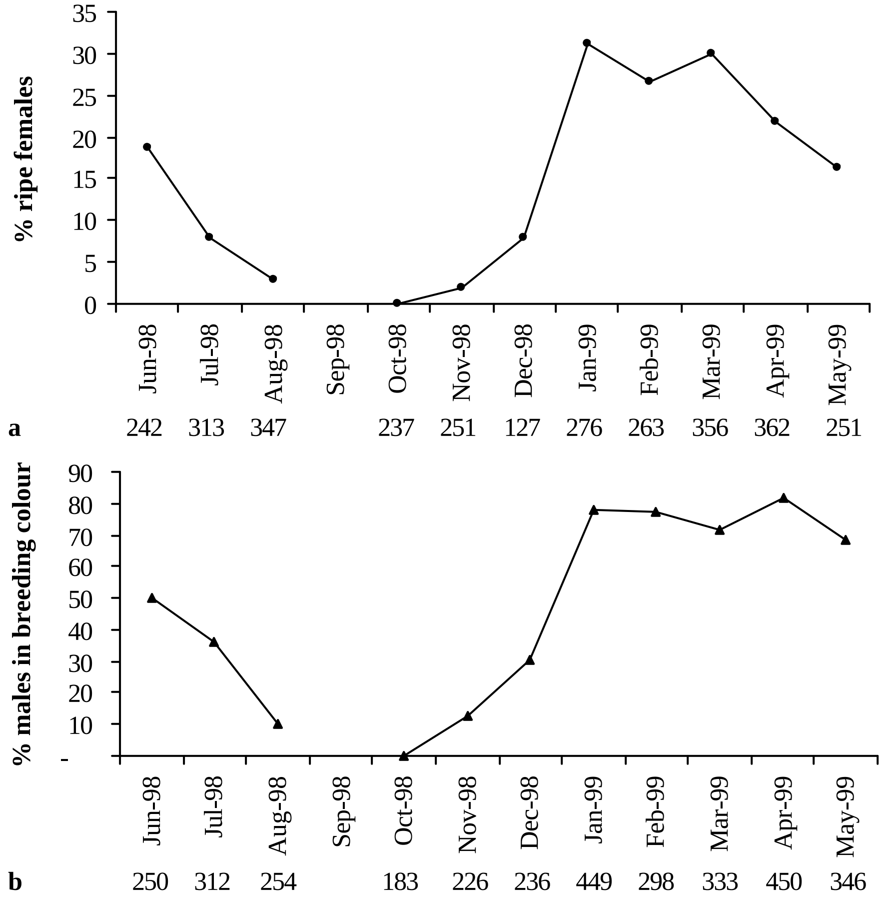

Figure 22-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Lethrinops gossei* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

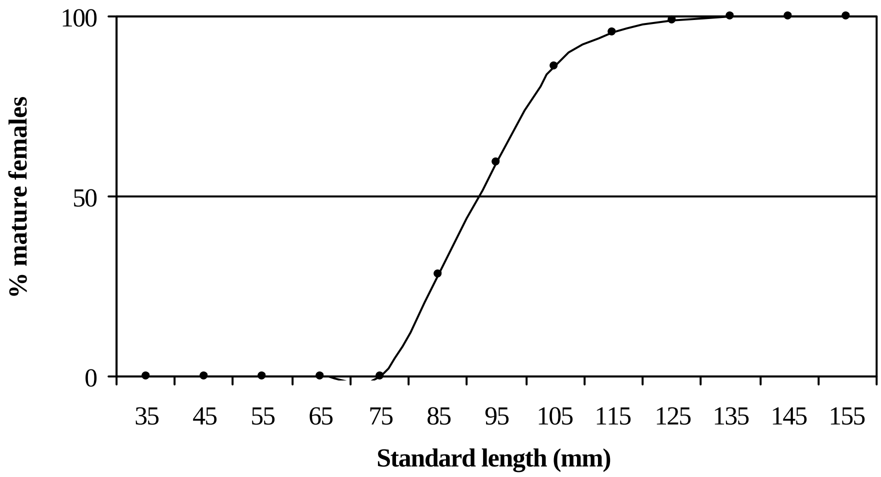

Figure 22-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Lethrinops gossei* in the SWA.

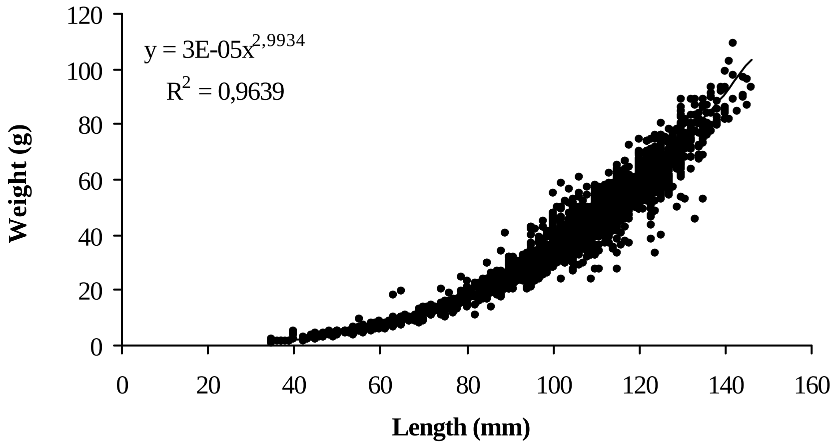

Figure 22-5. Length-weight relationship for *Lethrinops gossei* females in the SWA. (R^2 = determination coefficient).

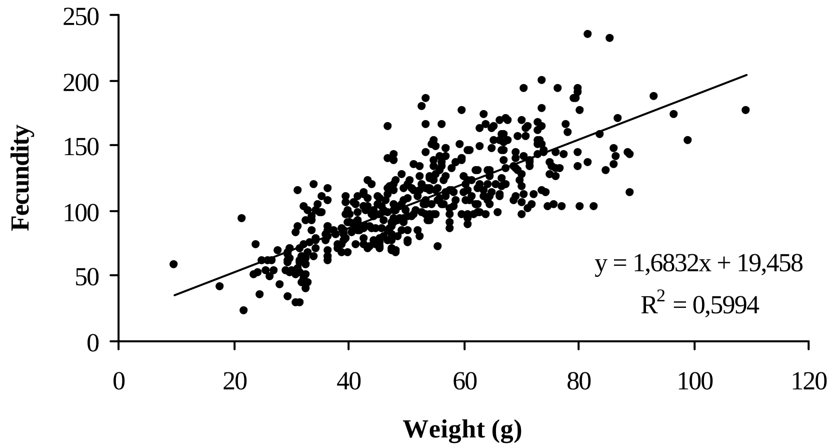

Figure 22-6. Fecundity-weight relationship for *Lethrinops gossei* females in the SWA. (R^2 = determination coefficient).

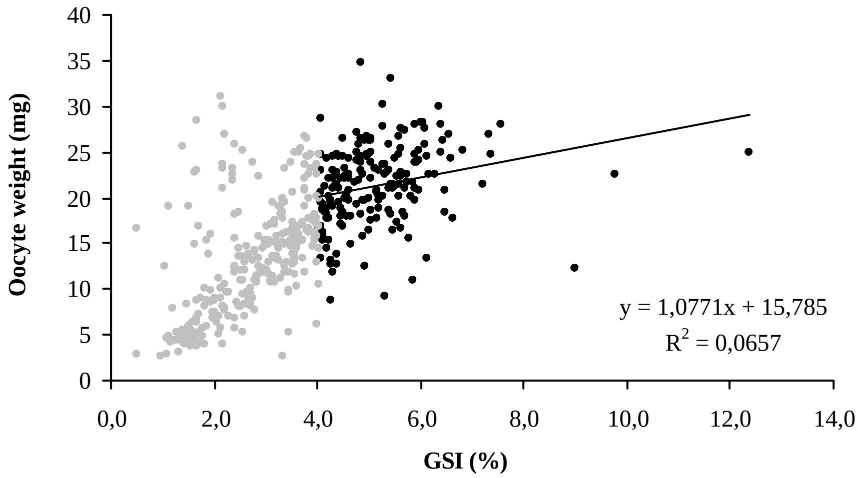

Figure 22-7. Relationship between oocyte weight and gonado-somatic index (GSI) for Lethrinops gossei. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 4%. (R^2 = determination coefficient).

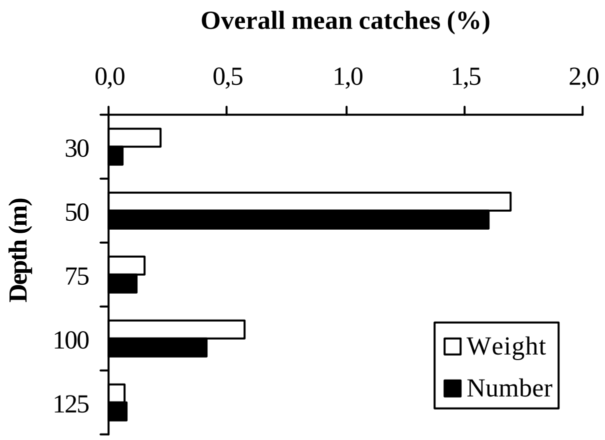

Figure 23-1. Mean occurrence and abundance in the catches per depth of *Lethrinops longimanus* in the SWA between July 1998 and May 1999.

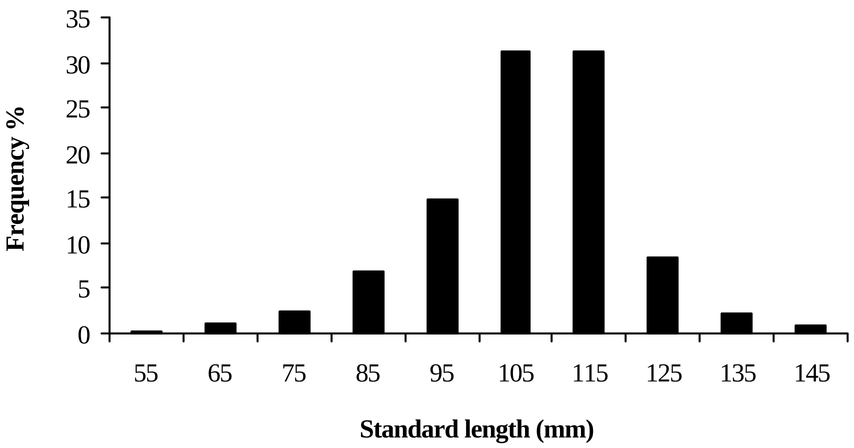

Figure 23-2. Size range and frequencies of *Lethrinops longimanus* caught in the SWA between July 1998 and May 1999.

Lethrinops longimanus (Trewavas)

210 females and 154 males were analysed. *L. longimanus* was caught from 30 to 125 m (Figure 23-1). It was a relatively rare fish averaging less than 1% of the catches at all depths except at 50 m where it made up to 1.6 and 1.7% in number and weight, respectively. The mean CPUE per depth category 11.7, 2 and 0.15 kg for the shallow, deep and very deep zones, respectively, were much lower than those reported by Tómasson & Banda (1996) (18.9, 23.1 and 3.7 kg, respectively). Specimens caught ranged between 56 and 147 mm with a mode from 100 to 120 mm (Figure 23-2). The sex ratio observed over the full sampling period was F/M 0.6/0.4.

Owing to low sample size at some months and bw number of ripe females caught, determination of precise breeding season was impossible. What can be said from the few data available is that breeding probably did not take place during the period from November to February when sample size were correct (Figure 23-3a). The only significant proportion of ripe females was found in August 98, and taking into account the data for males (Figure 23-3b), it might be hypothesised that breeding season occur from May-June to August-September. All the ripe females and 70% of the ripe males were found at 50m, suggesting that spawning might occur at this depth. However, most specimens of *L. longimanus* were caught at 50 m and this trend might reflect nothing more than the depth of occurrence. The mean size at maturity for females was about 107 mm, which was probably overestimated given that this estimation was done with all the data available for females, including females caught outside the breeding season (Figure 23-4). This corresponded to a mean age at maturity of 18 months, hence also probably overestimated.

Owing to the very narrow size range of females measured, it was impossible to assess the length-weight relationship. The fecundity-weight relationship is presented in Figure 23-5. Fecundity ranged from 57 to 99 for females weighing between 35 and 47 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was estimated at about 4% (Figure 23-6). The mean oocyte weight was 14.88 mg (± 1.97 SD, N= 4).

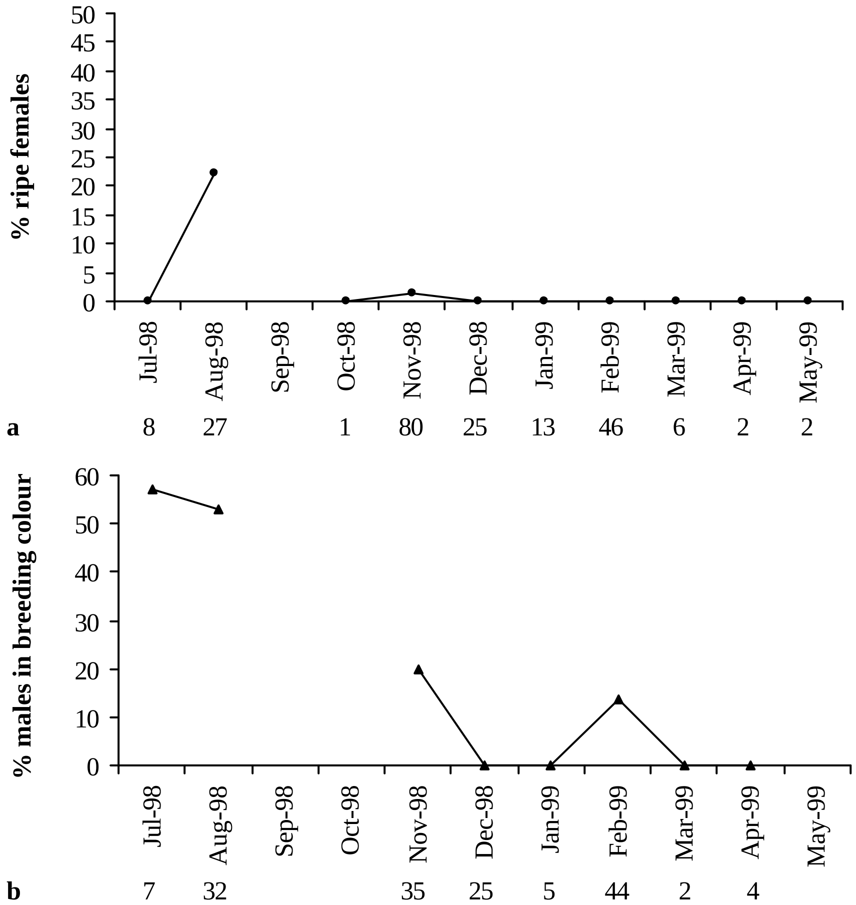

Figure 23-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Lethrinops longimanus* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

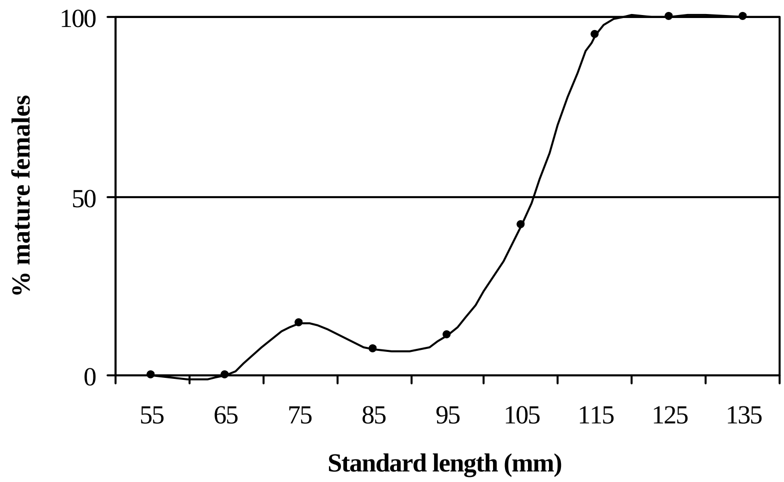

Figure 23-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Lethrinops longimanus* in the SWA.

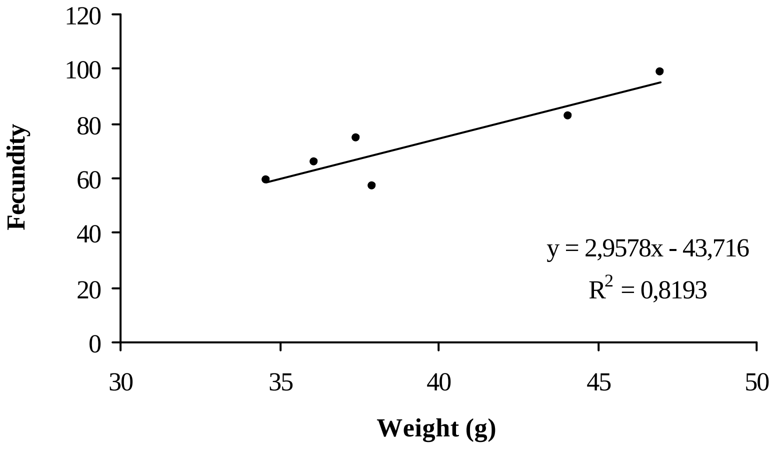

Figure 23-5. Fecundity-weight relationship for *Lethrinops longimanus* females in the SWA. (R^2 = determination coefficient).

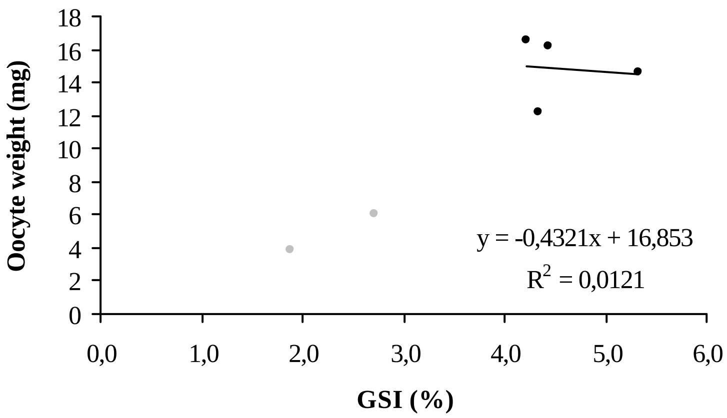

Figure 23-6. Relationship between oocyte weight and gonado-somatic index (GSI) for *Lethrinops longimanus*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 4%. (R^2 = determination coefficient).

Lethrinops macrochir (Regan)

L. macrochir is a rare species caught only at 10 m. It was usually absent from the catches, except for November to February and once in August. 42 females and 89 males were analysed, giving a sex ratio of F/M 0.3/0.7. Specimens caught ranged from 59 to 150 mm (**Figure 24-1**).

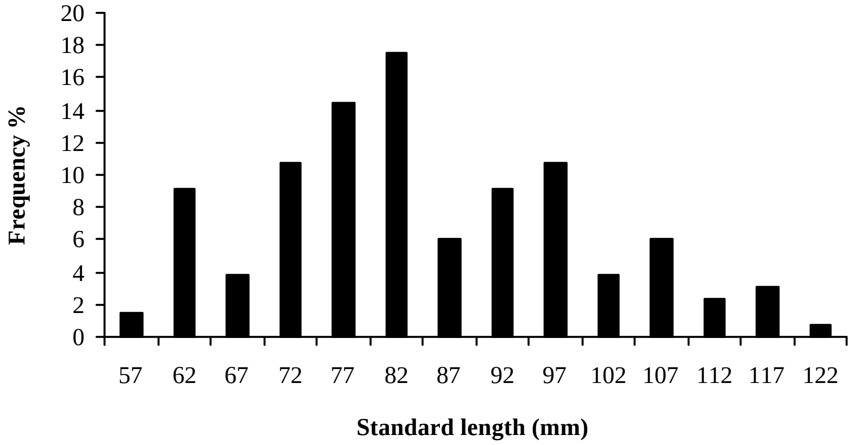

Figure 24-1. Size range and frequencies of *Lethrinops macrochir* caught in the SWA between July 1998 and May 1999.

Among the rare species, *L. macrochir* was one for which we caught some ripe females, allowing an estimation of the fecundity-weight relationship (**Figure 24-2**) and oocyte weight (for females whose GSI was above 4%, which is the maximum encountered for the genus): 11.87 mg (± 0.97 SD, N= 2).

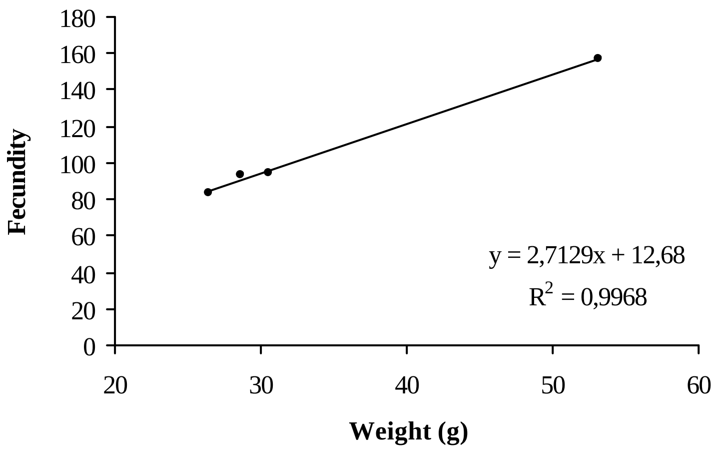

Figure 24-2. Fecundity-weight relationship for *Lethrinops macrochir* females in the SWA. (R^2 = determination coefficient).

Plate 14. *Lethrinops 'oliveri'* (by Dave Voorvelt).

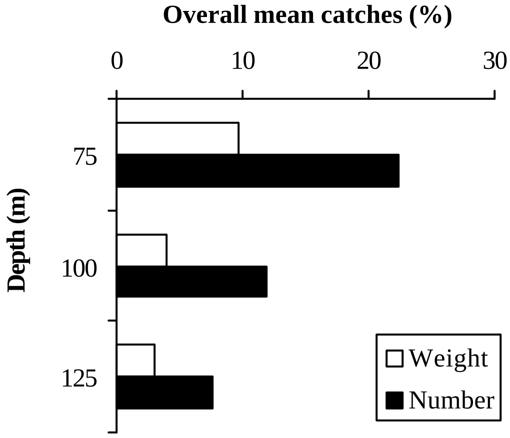

Figure 25-1. Mean occurrence and abundance in the catches per depth of *Lethrinops 'oliveri'* in the SWA between July 1998 and May 1999.

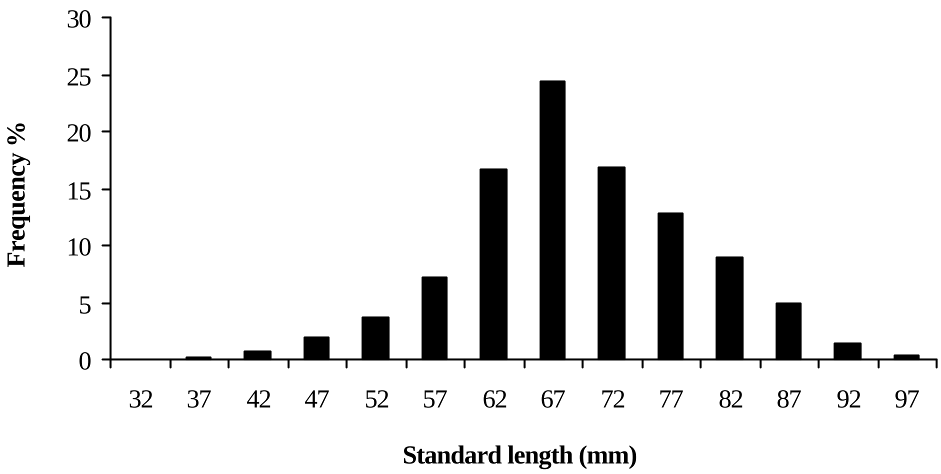

Figure 25-2. Size range and frequencies of *Lethrinops 'oliveri'* caught in the SWA between July 1998 and May 1999.

Lethrinops 'oliveri' (Plate 14)

875 females and 1017 males were analysed. *L. 'oliveri'* was caught between 75 and 125 m, with a decreasing occurrence and biomass with depth (Figure 25-1). It was a dominant species of the deep and very deep zones, constituting between 3 and 10% of the catches in number and between 8 and 22% in weight. The mean CPUE per depth category, 39.8 and 5.4 kg for the deep and very deep zones, respectively, matched the value reported by Tómasson & Banda (1996) for the deep zone (36.7 kg), but was about three times less for the very deep zone (16.7 kg). The depth distribution observed in our study was more restricted than that of Tómasson & Banda (1996), who reported *L. 'oliveri'* from 20 to 150 m. Specimens caught ranged between 33 and 98 mm (Figure 25-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Breeding occurred throughout the year with a trough from October to December and a peak of activity from February to April (Figure 25-3a). As for *L. gossei*, the profile of the percentage of ripe males followed exactly the female's one (Figure 25-3b). Ripe females and males were most abundant at 75 m, suggesting that spawning could occur mainly at this depth (Table 25-1). The mean size at maturity for females was about 60 mm (Figure 25-4), which corresponded to a mean age at maturity of 11 months.

Table 25-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Lethrinops 'oliveri'* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	45.3	46.5	37.2	67.7	43.5
100 m	38.3	31.6	38.1	27.3	36.6
125 m	16.3	21.9	24.7	5.1	19.9

The length-weight and fecundity-weight relationships are presented in Figure 25-5 and 25-6, respectively. Fecundity ranged from 19 to 81 for females weighing between 4 and 16 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 25-7). The mean oocyte weight was 7.21 mg (± 1.61 SD, N= 45).

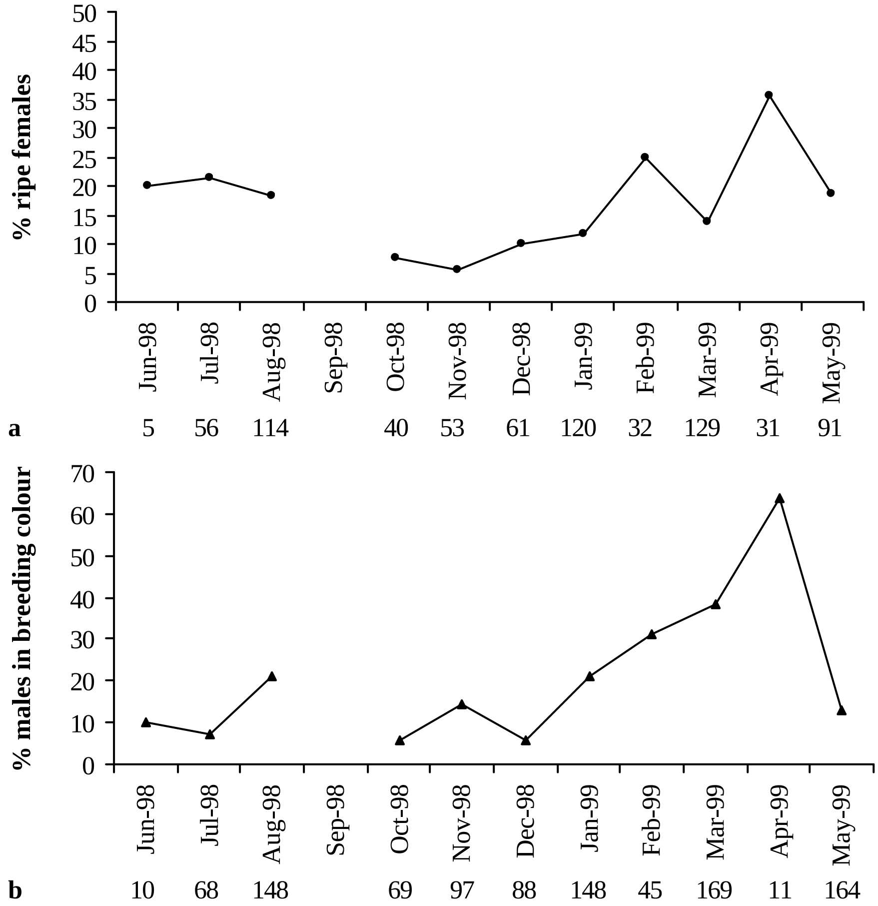

Figure 25-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Lethrinops 'oliveri'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

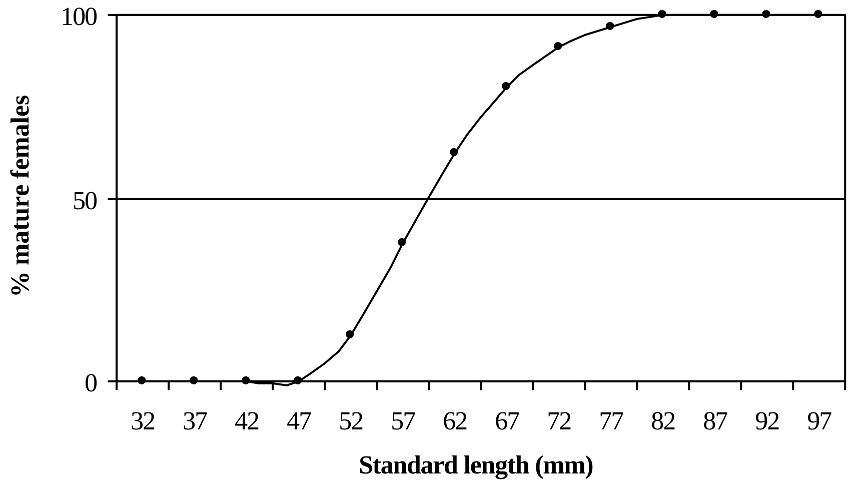

Figure 25-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Lethrinops 'oliveri'* in the SWA.

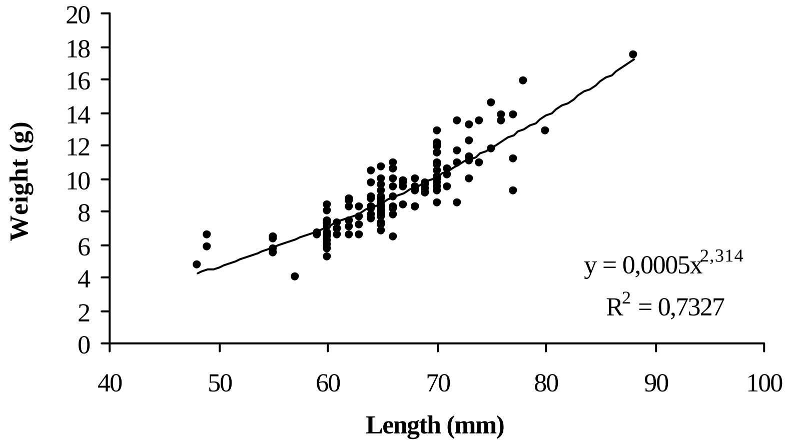

Figure 25-5. Length-weight relationship for *Lethrinops 'oliveri'* females in the SWA. (R^2 = determination coefficient).

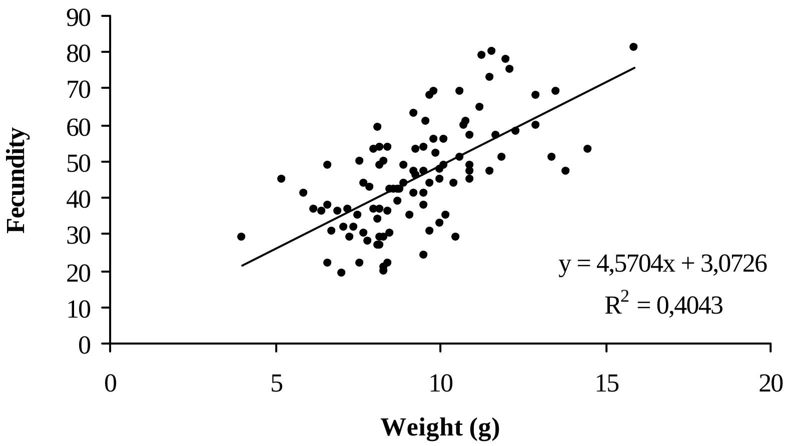

Figure 25-6. Fecundity-weight relationship for *Lethrinops 'oliveri'* females in the SWA. (R^2 = determination coefficient).

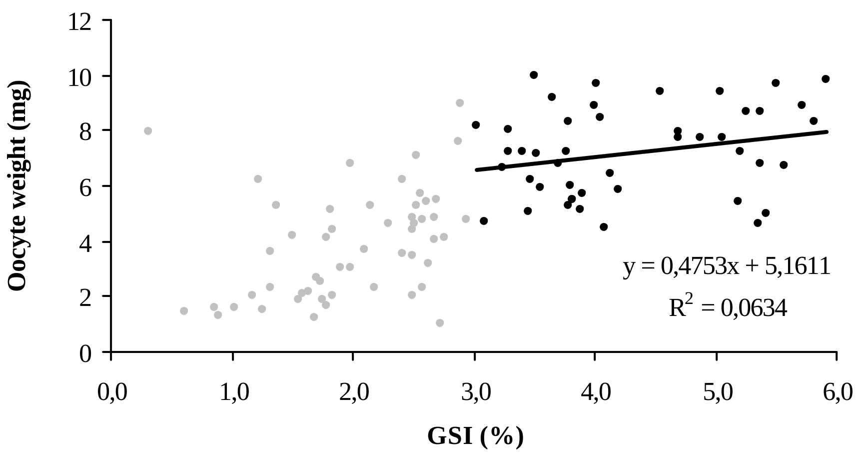

Figure 25-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Lethrinops 'oliveri'*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

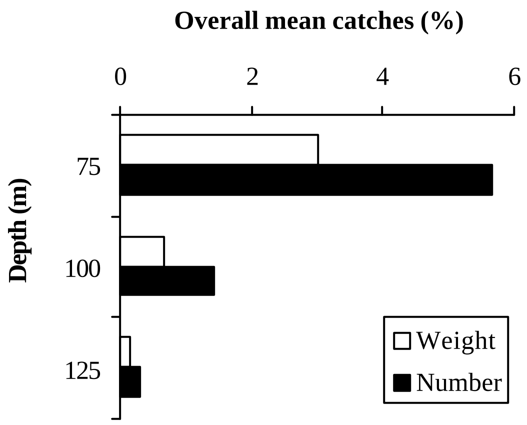

Figure 26-1. Mean occurrence and abundance in the catches per depth of *Lethrinops polli* in the SWA between July 1998 and May 1999.

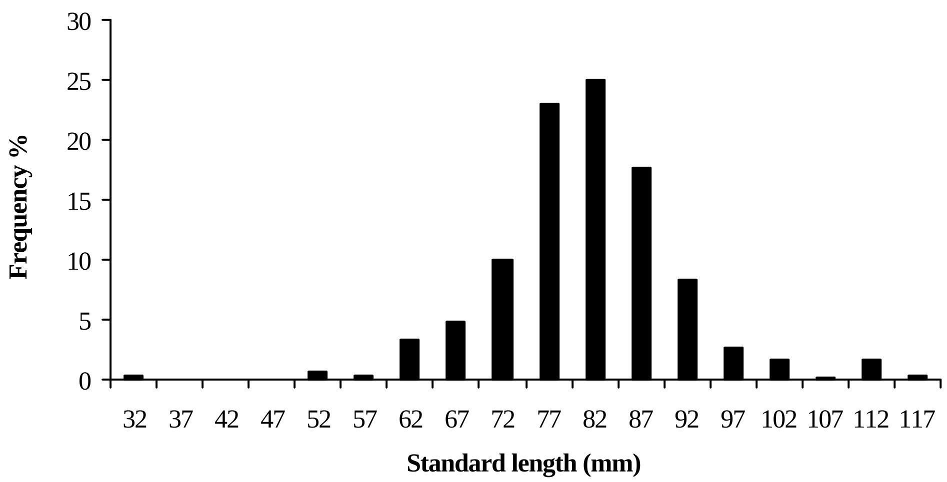

Figure 26-2. Size range and frequencies of *Lethrinops polli* caught in the SWA between July 1998 and May 1999.

Lethrinops polli (Burgess & Axelrod)

229 females and 198 males were analysed. *L. polli* was caught between 75 and 125 m, with a decreasing occurrence and biomass with depth (Figure 26-1). It was caught regularly in the deep and very deep zones, constituting between 0.1 and 3% of the catches in weight and between 0.3 and 5.6% in number. The mean CPUE per depth category, 12.3 and 0.3 kg for the deep and very deep zones, respectively, was about four times as much as the value reported by Tómasson & Banda (1996) for the deep zone (3 kg), and about seven times less for the very deep zone (2.2 kg). As for *L. 'oliveri'*, the depth distribution observed in our study was more restricted than that of Tómasson & Banda (1996), who reported *L. polli* from 10 to 140 m. Specimens caught ranged between 30 and 120 mm (Figure 26-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Breeding season occurred from May to August-September, with an isolated activity in December, in the middle of the resting period (Figure 26-3a). As for *L. gossei* and *L. 'oliveri'*, the profile of the percentage of ripe males followed exactly the female's one (Figure 26-3b). Ripe females and males were clearly most abundant at 75 m, suggesting that spawning could occur mainly at this depth (Table 26-1). The mean size at maturity for females was about 65 mm (Figure 26-4), which corresponded to a mean age at maturity of 10 months.

Table 26-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Lethrinops polli* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	68.9	76.3	50.4	85.5	83.3
100 m	28.9	21.1	41.1	10.1	5.6
125 m	2.1	2.6	8.5	4.3	11.1

The length-weight and fecundity-weight relationships are presented in Figure 26-5 and 26-6, respectively. Fecundity ranged from 11 to 89 for females weighing between 9 and 35 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 26-7). The mean oocyte weight was 12.26 mg (± 2.16 SD, N= 18).

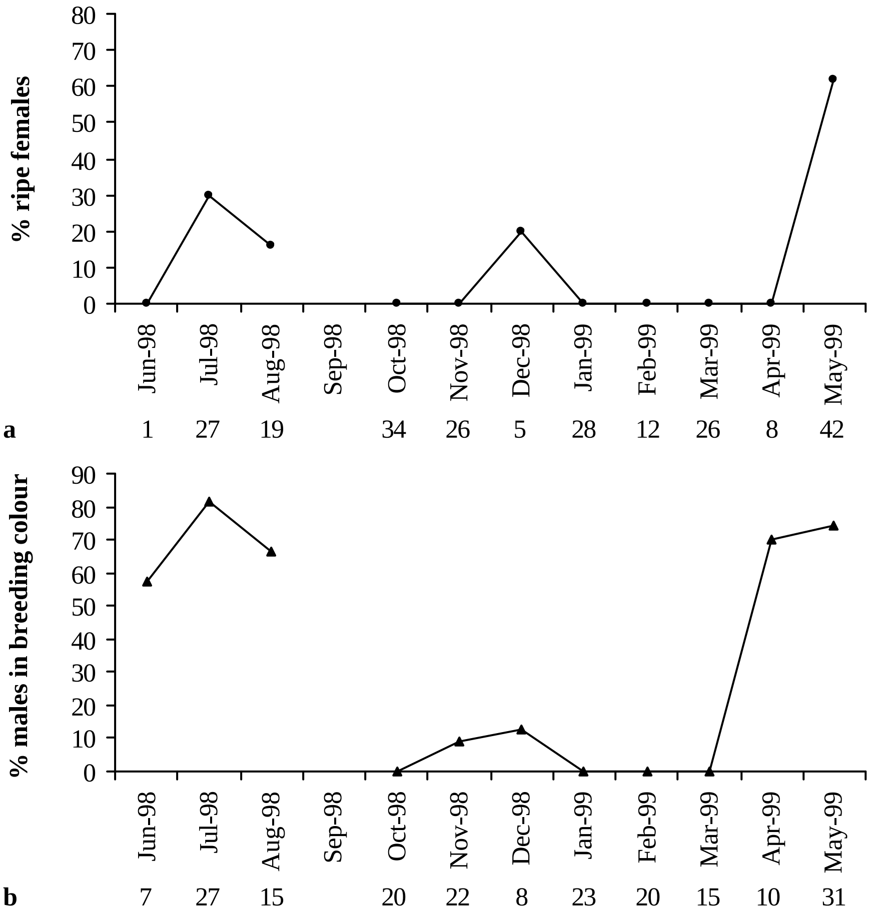

Figure 26-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Lethrinops polli* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

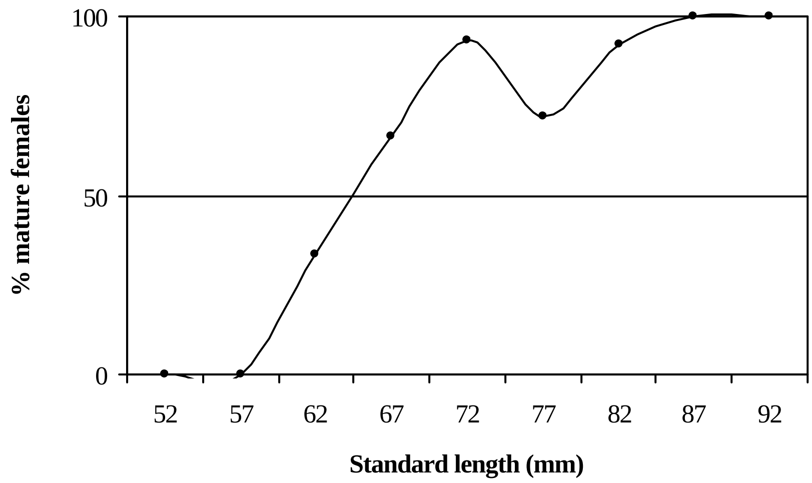

Figure 26-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Lethrinops polli* in the SWA.

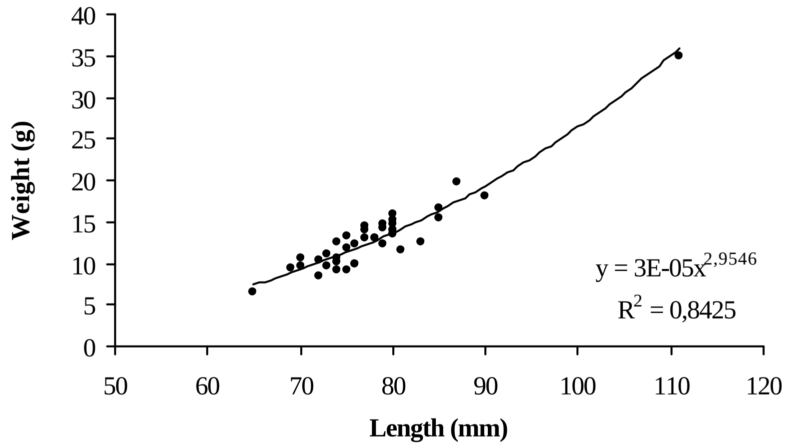

Figure 26-5. Length-weight relationship for *Lethrinops polli* females in the SWA. (R^2 = determination coefficient).

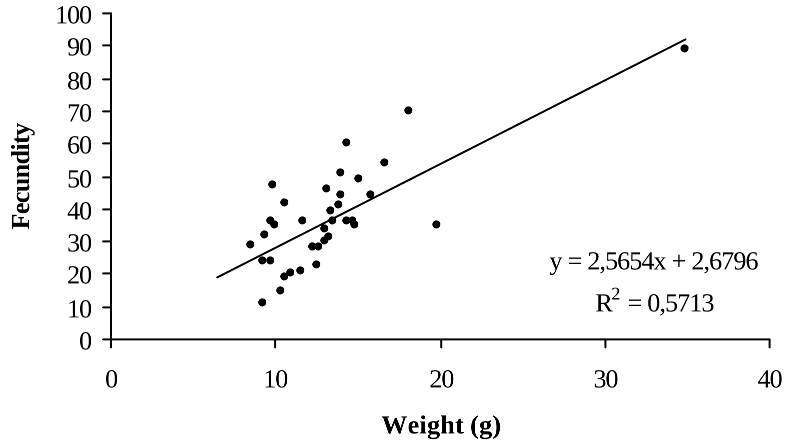

Figure 26-6. Fecundity-weight relationship for *Lethrinops polli* females in the SWA. (R^2 = determination coefficient).

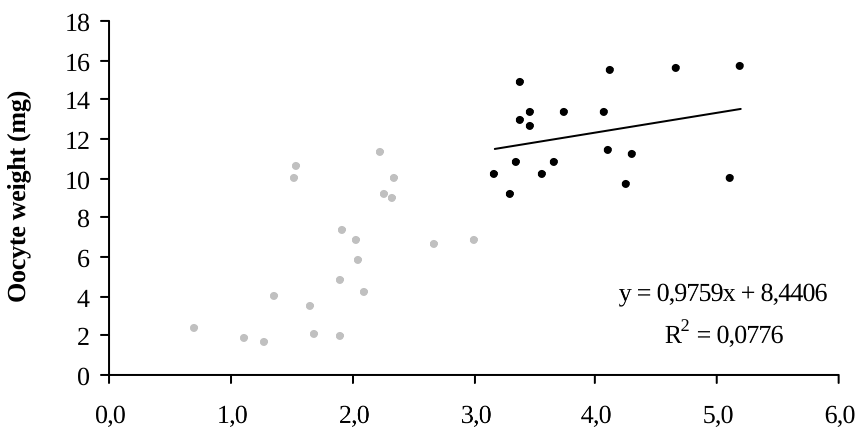

Figure 26-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Lethrinops polli.* Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

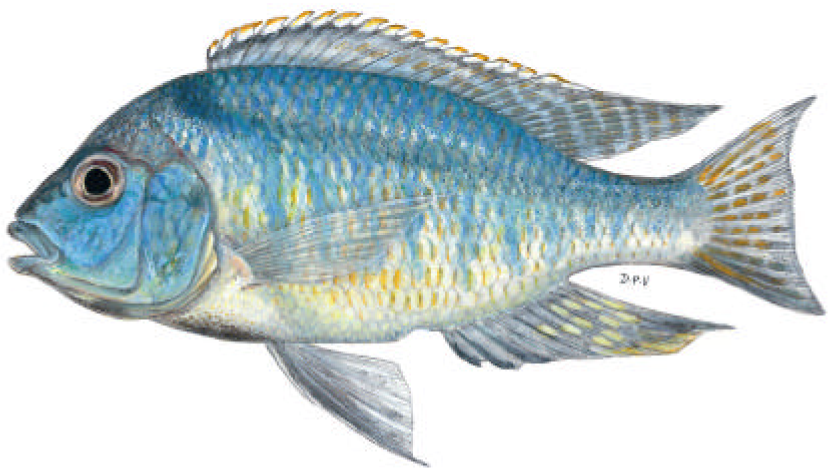

Plate 15. Mylochromis anaphyrmus (by Dave Voorvelt).

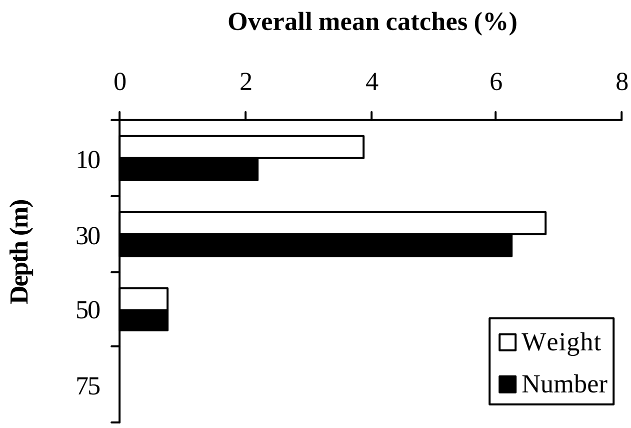

Figure 27-1. Mean occurrence and abundance in the catches per depth of *Mylochromis anaphyrmus* in the SWA between July 1998 and May 1999.

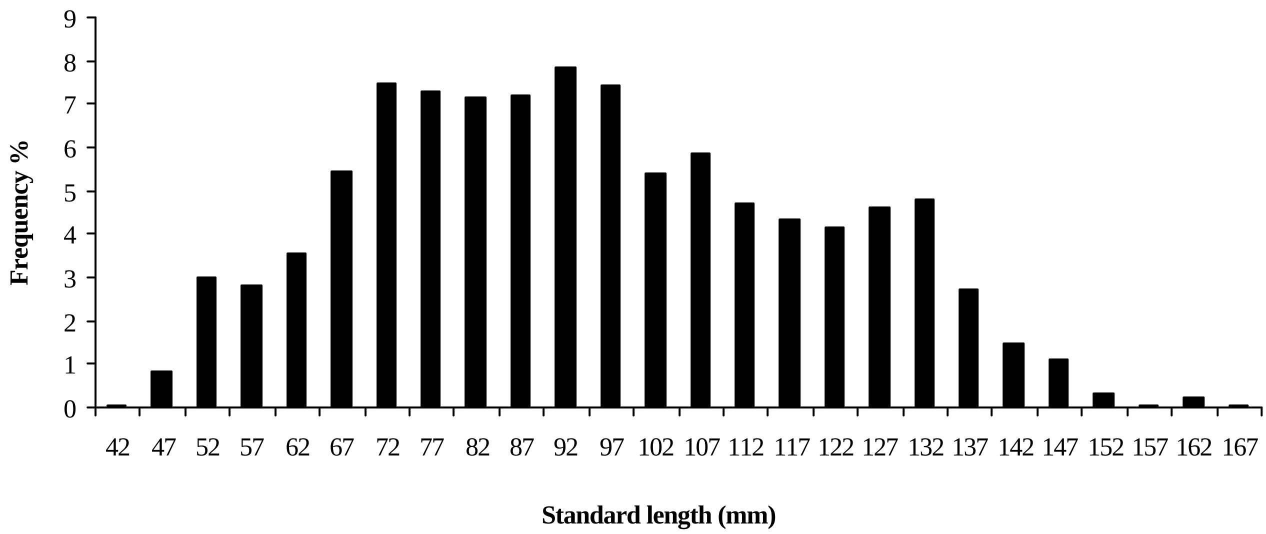

Figure 27-2. Size range and frequencies of *Mylochromis anaphyrmus* caught in the SWA between July 1998 and May 1999.

Mylochromis spp.

Mylochromis anaphyrmus (Burgess & Axelrod) (Plate 15)

1375 females and 1058 males were analysed. *M. anaphyrmus* was caught from 10 to 75 m, but mostly abundant at 10 and 30 m (Figure 27-1). Actually, a single specimen was caught at 75 m. It was a very common species in the shallow zone, constituting between 4 and 7% of the catches in weight and between 2 and 6% in number. The mean CPUE per depth category, 23.3 kg for the shallows, was more than twice as much as the value found by Tómasson & Banda (1996) (9.8 kg). The depth distribution they reported was very similar to the one we observed. Specimens caught ranged between 40 and 164 mm (Figure 27-2). The sex ratio observed over the full sampling period was F/M 0.6/0.4.

The breeding season was from January to October, with a peak between March and June, a steady decline in November, and ceasing in December (Figure 27-3a), even though occurrence of males in breeding colour was more erratic (Figure 27-3b). Ripe males and immature individuals were evenly distributed between 10 and 30 m (Table 27-1). However, as more than three quarters of the ripe females were found at 30 m, spawning probably occurs at 30 m. Maturity was reached early in their second year at 17 months old, at a mean size of 105 mm for females (Figure 27-4), which was less than the 160 mm TL (about 130 mm SL) and 3 years old reported by Tweddle & Turner (1977).

Table 27-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Mylochromis anaphyrmus* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	25.8	11.4	35.6	48.9	39.4
30 m	64.2	76.2	60.9	46.7	56.6
50 m	10	12.4	3.5	4.4	4.1

The length-weight and fecundity-weight relationships are presented in Figure 27-5 and 27-6, respectively. Fecundity ranged from 58 to 236 for females weighing between 21 and 98 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 27-7). The mean oocyte weight was 11.13 mg (± 1.93 SD, N= 21).

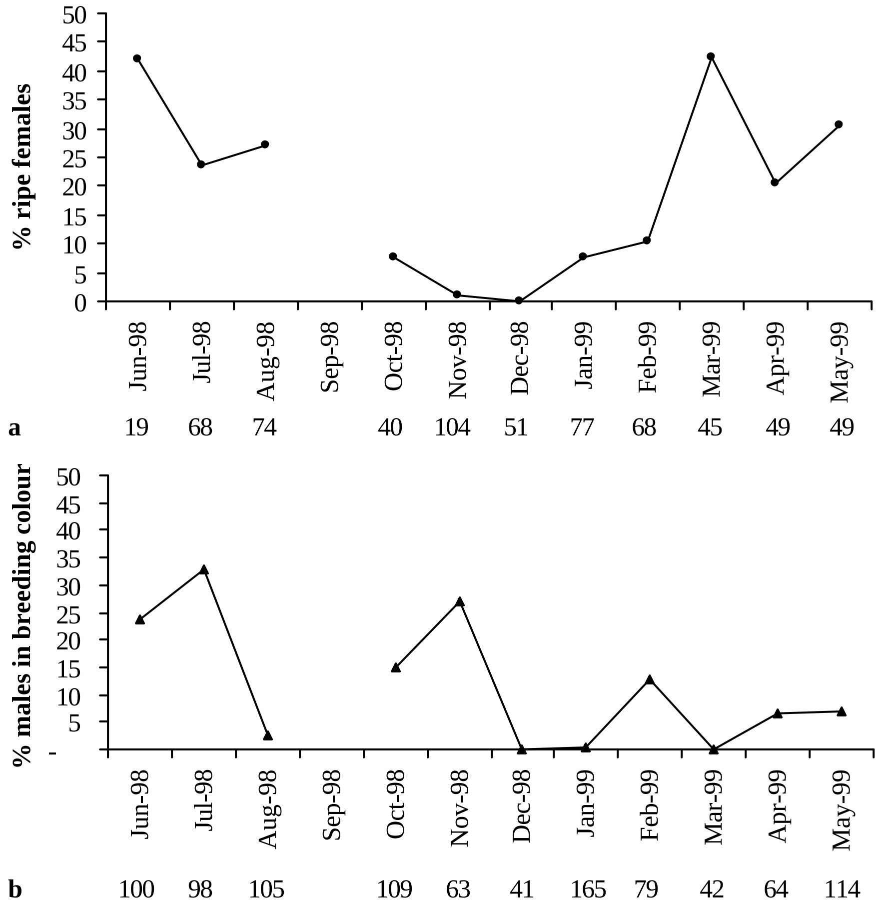

Figure 27-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Mylochromis anaphyrmus* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

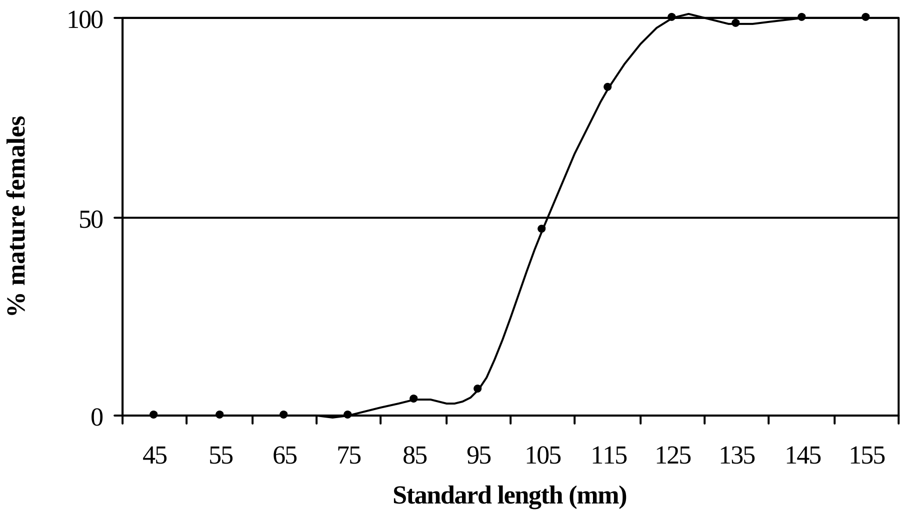

Figure 27-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Mylochromis anaphyrmus* in the SWA.

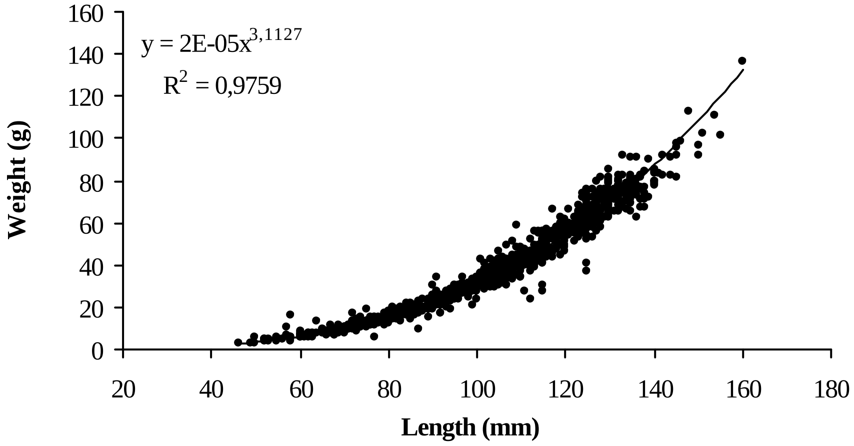

Figure 27-5. Length-weight relationship for *Mylochromis anaphyrmus* females in the SWA. (R^2 = determination coefficient).

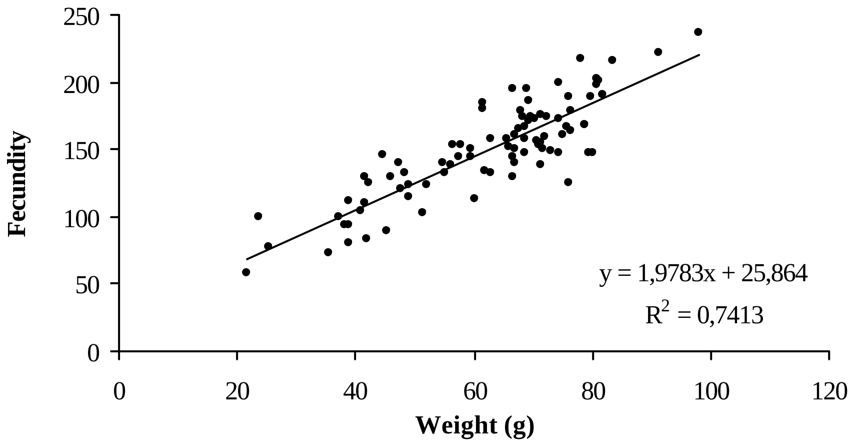

Figure 27-6. Fecundity-weight relationship for *Mylochromis anaphyrmus* females in the SWA. (R^2 = determination coefficient).

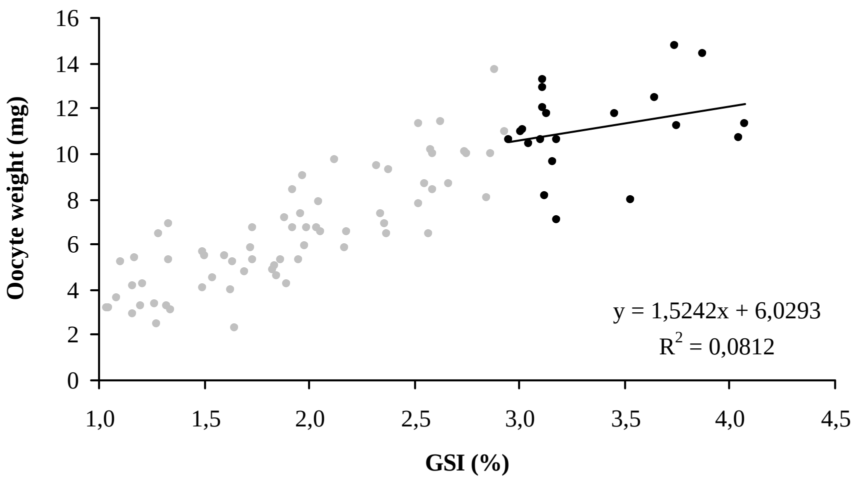

Figure 27-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Mylochromis anaphyrmus*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

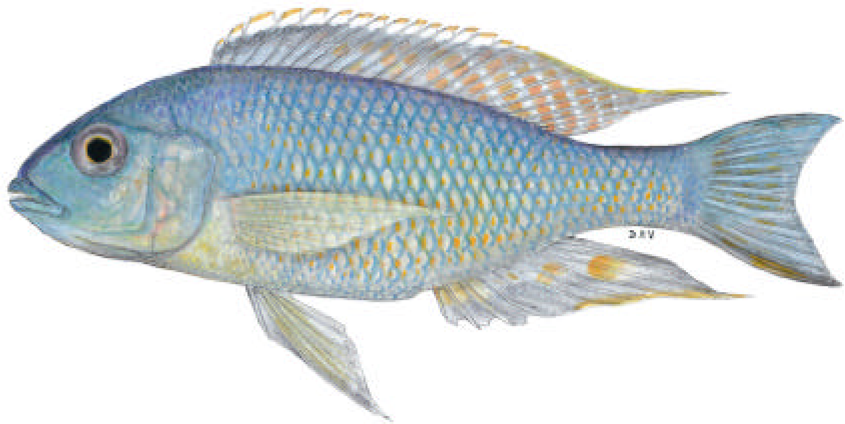

Plate 16. *Nyassachromis 'argyrosoma'* (by Dave Voorvelt).

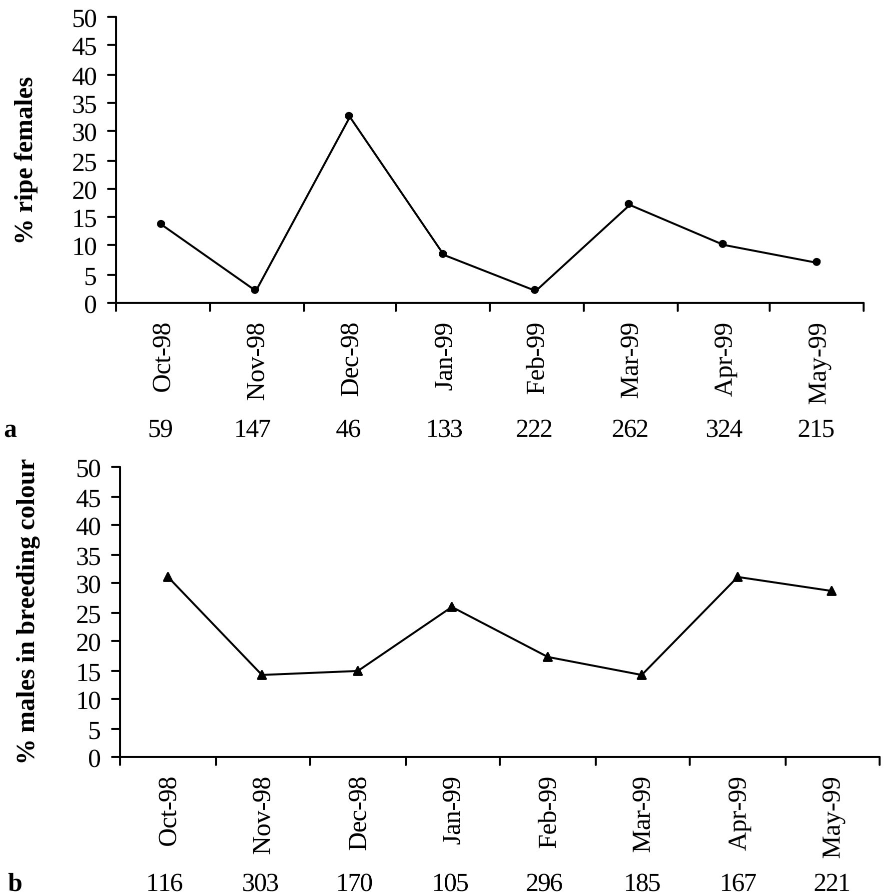

Figure 28-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Nyassachromis 'argyrosoma'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

Nyassachromis spp.

Nyassachromis 'argyrosoma' (Plate 16)

1440 females and 1563 males were analysed. *N. 'argyrosoma'* is a small species caught from 10 to 50 m, but was most abundant at 10 and 30 m (Figure 28-1).

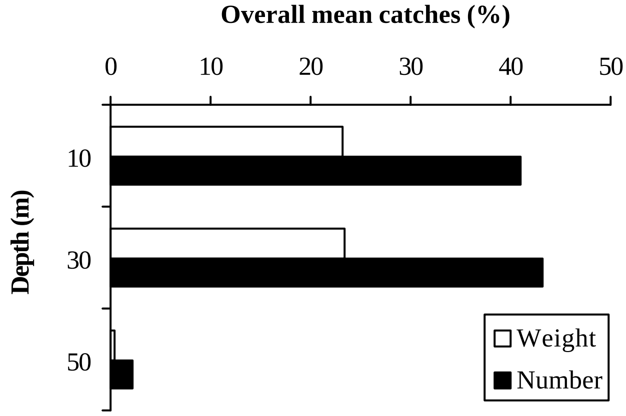

Figure 28-1. Mean occurrence and abundance in the catches per depth of *Nyassachromis 'argyrosoma'* in the SWA between July 1998 and May 1999.

With *Aulonocara 'blue orange'* and *Copadichromis virginalis, N. 'argyrosoma'* was a numerically dominant species in the shallow zone, constituting about 23% of the catches in weight, and 41 and 43% in number at 10 and 30 m, respectively. The mean CPUE per depth category was 91.8 kg for the shallows. No reference to this species (under this name at least) was made in Tómasson & Banda (1996). Specimens caught ranged between 38 and 97 mm (Figure 28-2).

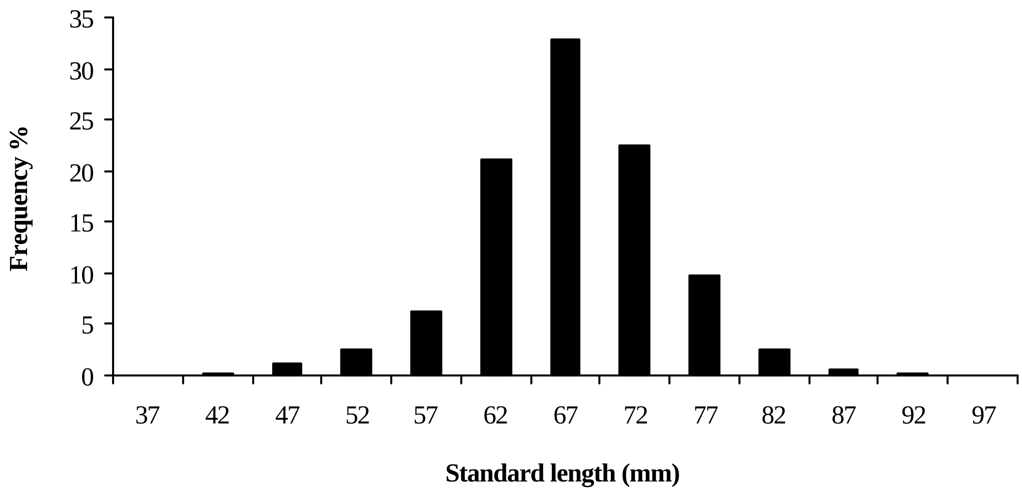

Figure 28-2. Size range and frequencies of *Nyassachromis 'argyrosoma'* caught in the SWA between July 1998 and May 1999.

The sex ratio observed over the full sampling period was F/M 0.5/0.5.

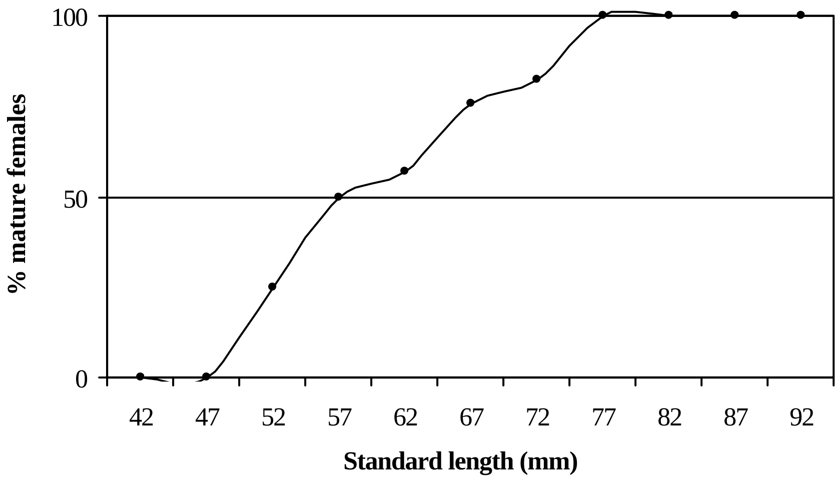

Figure 28-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Nyassachromis 'argyrosoma'* in the SWA.

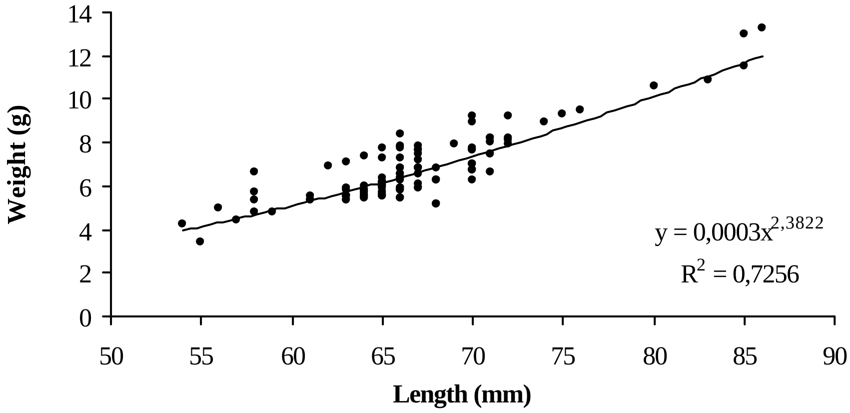

Figure 28-5. Length-weight relationship for *Nyassachromis 'argyrosoma'* females in the SWA. (R^2 = determination coefficient).

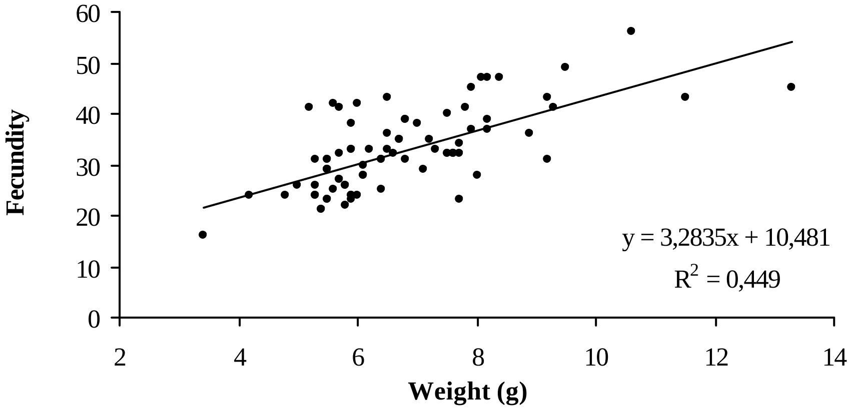

Figure 28-6. Fecundity-weight relationship for *Nyassachromis 'argyrosoma'* females in the SWA. (R^2 = determination coefficient).

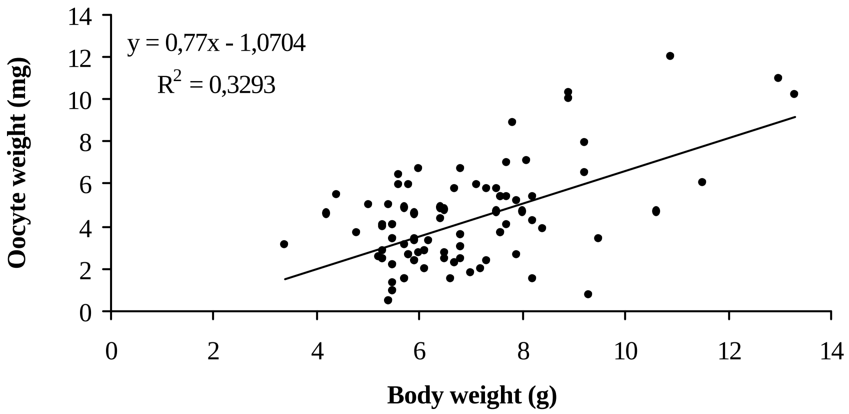

Figure 28-7. Relationship between oocyte weight and body weight for *Nyassachromis 'argyrosoma'* females in the SWA. (R^2 = determination coefficient).

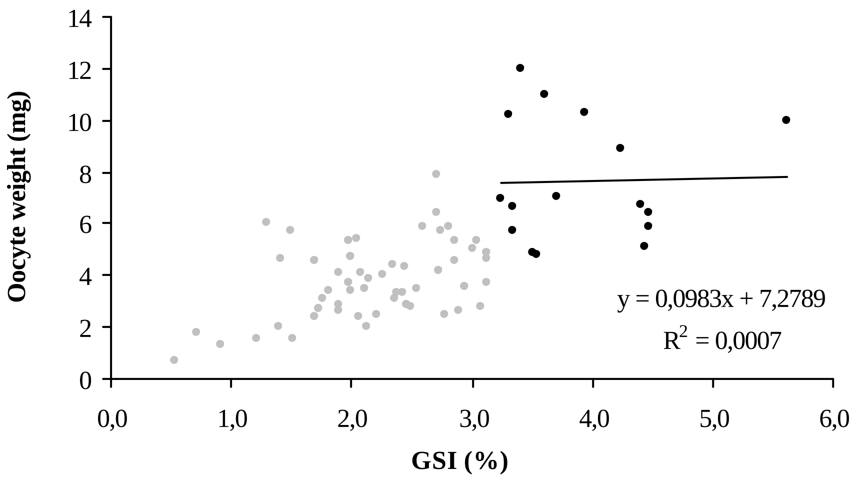

Figure 28-8. Relationship between oocyte weight and gonado-somatic index (GSI) for *Nyassachromis 'argyrosoma'*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3.2%. (R^2 = determination coefficient).

Ripe females (Figure 28-3a) and males (Figure 28-3b) were found at all the sampled months, with peaks in December and March and decreased activity in November and February. Owing to inconsistencies in species identification during the first three months of sampling, data were removed from analyses. However, it is likely that breading occurred all year long. Three quarters of the ripe females and more than half the ripe males were found at 10 m, the rest were at 30 m (Table 28-1), suggesting that spawning probably occurs between 10 and 30 m and mostly at 10 m. As most immature individuals were caught at 30 and 50 m, it appears that after being released, juveniles migrate into deeper waters. The mean size at maturity was about 57 mm for females (Figure 28-4), which corresponded to a mean age at maturity of 10 months. The upper part of the sigmoïd curve does reach 100% after various steps, which is unexpected for an abundant species. Even though we had to take into account data from months outside the peaks of breeding activity to increase the sample size in each size class, an alternative explanation can not be excluded for this species. The taxonomy of the *Nyassachromis spp.* complex is one of the most difficult and despite the particular attention given to this species on board, specimen of an other larger species might have been included, which would explain the significant occurrence of immature specimens above the mean size at maturity.

Table 28-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Nyassachromis 'argyrosoma'* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
10 m	48.9	74.1	47.3	57.6	16.5
30 m	51.1	25.9	45.8	30	31.7
50 m	0	0	6.9	12.4	51.8

The length-weight and fecundity-weight relationships are presented in Figure 28-5 and 28-6, respectively. Fecundity ranged from 16 to 56 for females weighing between 3 and 13 g. A positive correlation was found between oocyte weight and body weight (Figure 28-7). This is the only species for which a relationship between oocyte weight and body weight was found and it might be due to identification inaccuracies. The GSI threshold above which the oocyte weight did no longer increase significantly was 3.2% (Figure 28-8). The mean oocyte weight was 7.66 mg (± 2.36 SD, N= 16). The standard deviation was very high for such a low mean oocyte weight, which was probably due to the fact that oocyte weight was correlated with body weight.

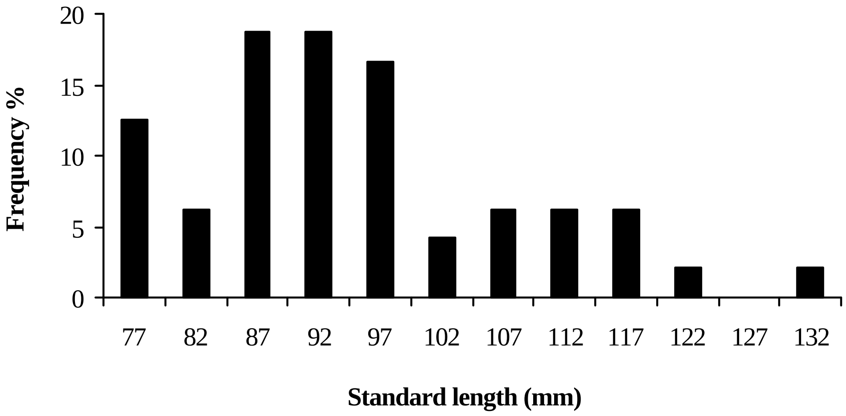

Figure 29-1. Size range and frequencies of *Otopharynx 'productus'* caught in the SWA between July 1998 and May 1999.

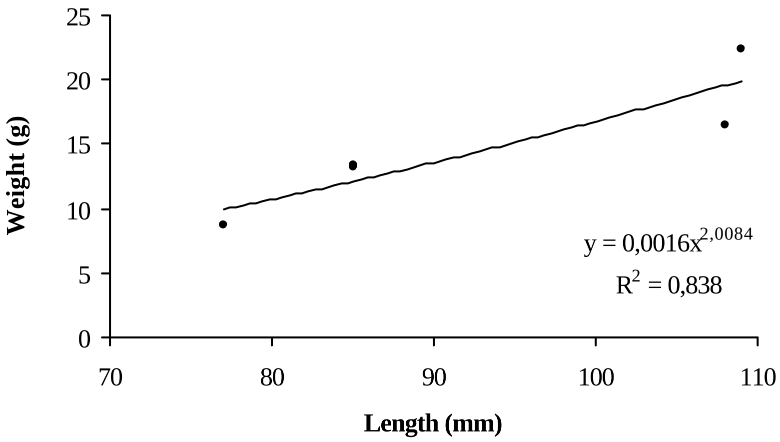

Figure 29-2. Length-weight relationship for *Otopharynx 'productus'* females in the SWA. (R^2 = determination coefficient).

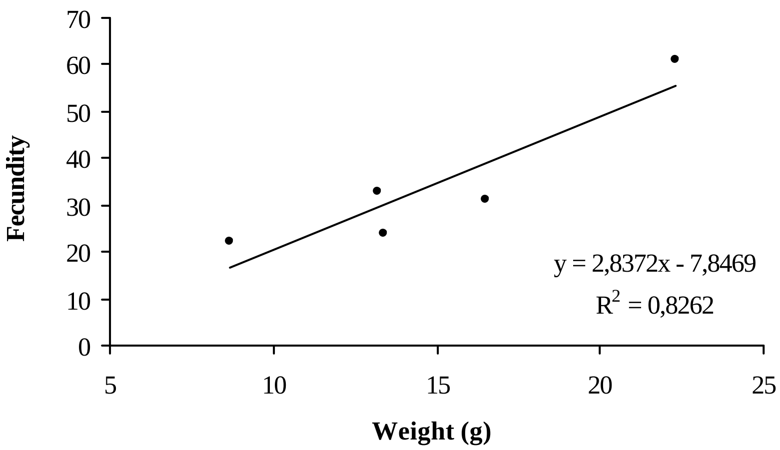

Figure 29-3. Fecundity-weight relationship for *Otopharynx 'productus'* females in the SWA. (R^2 = determination coefficient).

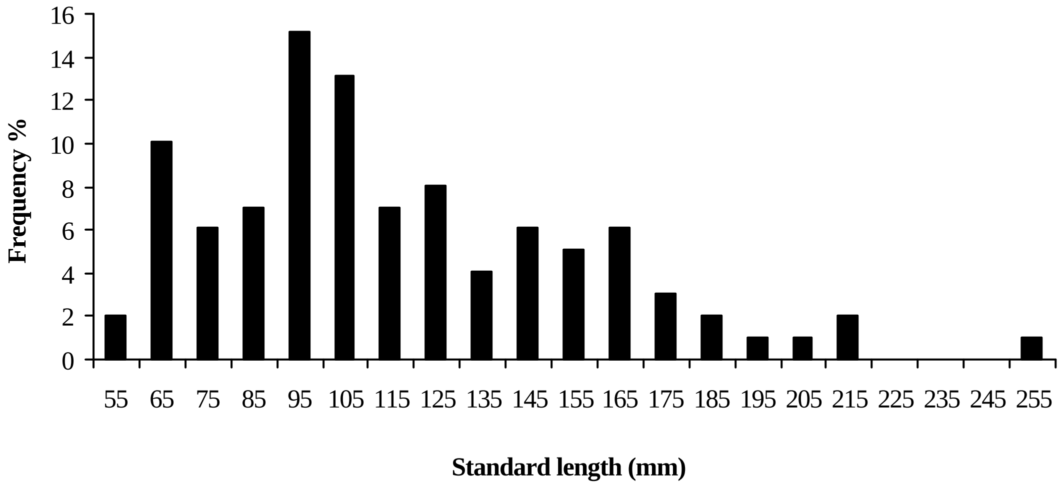

Figure 30-1. Size range and frequencies of *Otopharynx speciosus* caught in the SWA between July 1998 and May 1999.

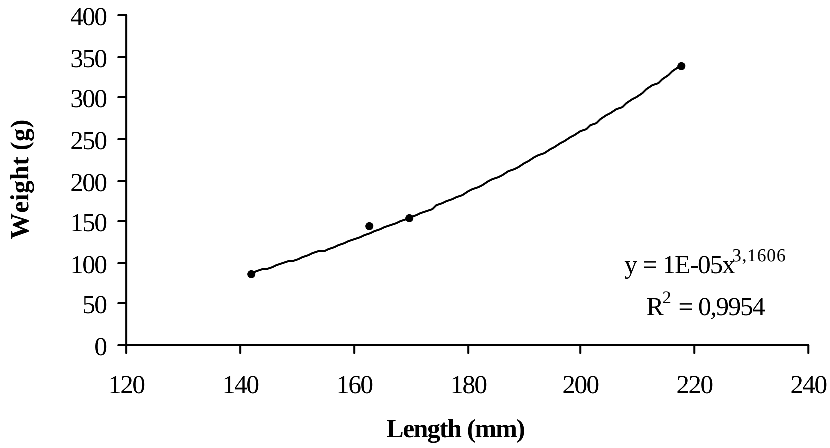

Figure 30-2. Length-weight relationship for *Otopharynx speciosus* females in the SWA. (R^2 = determination coefficient).

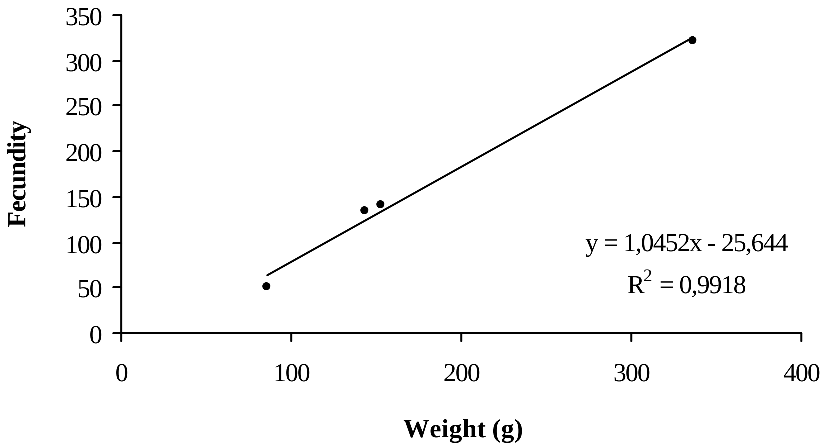

Figure 30-3. Fecundity-weight relationship for *Otopharynx speciosus* females in the SWA. (R^2 = determination coefficient).

Otopharynx spp.

Otopharynx 'productus'

O. 'productus' is a rare species encountered at 10 and 30 m. 27 females and 20 males were analysed, giving a sex ratio of F/M 0.6/0.4. Specimens caught ranged between 75 and 134 mm (Figure 29-1). Among the rare species, *O. 'productus*' was one for which we caught some ripe females, allowing an estimation of the length-weight (Figure 29-2) and fecundity-weight relationships (Figure 29-3). Fecundity ranged between 22 and 61 for females weighing between 9 and 22 g. The mean oocyte weight was impossible to assess from the few data available, but the largest oocytes weighed averaged 14.2 mg for a GSI of 2.8%.

***Otopharynx speciosus* (Trewavas)**

Like *O. 'productus*', *O. speciosus* is not an abundant species and was essentially caught between 30 and 75 m. 61 females and 38 males were analysed, giving a sex ratio of F/M 0.6/0.4. Specimens caught ranged between 55 and 260 mm (Figure 30-1). Among the rare species, *O. 'productus*' was also one for which we caught some ripe females, allowing an estimation of the length-weight (Figure 30-2) and fecundity-weight relationships (Figure 30-3). Fecundity ranged between 51 and 322 for females weighing between 85 and 337 g. The mean oocyte weight was impossible to assess from the few data available, but the largest oocytes weighed averaged 25 mg for a GSI of 2.9%.

Placidochromis spp.

Placidochromis 'long'

111 females and 180 males were analysed. *P. 'long'* is a small species caught from 10 to 50 m, with an increasing occurrence and biomass with depth (Figure 31-1).

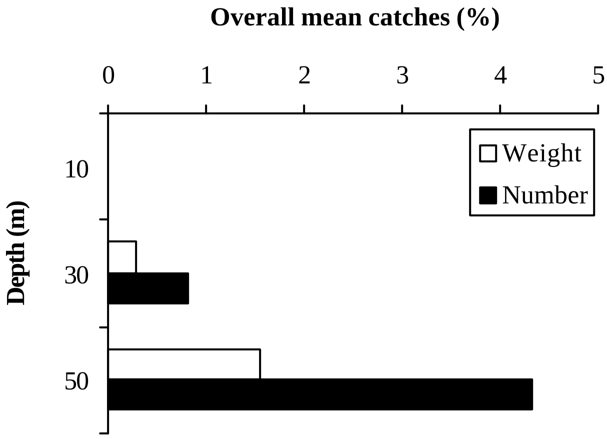

Figure 31-1. Mean occurrence and abundance in the catches per depth of *Placidochromis 'long'* in the SWA between July 1998 and May 1999.

It was most common at 50 m, where it constituted 1.6 and 4.3% of the catches in weight and number, respectively. The mean CPUE per depth category was 3.2 kg for the shallows. No reference to this species (under this name at least) was made in Tómasson & Banda (1996). Specimens caught ranged between 47 and 77 mm (Figure 31-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

Owing to low sample size or absence of data for some months, the precise determination of breeding season and size at maturity was not possible. Ripe females (Figure 31-3a) and males (Figure 31-3b) were found only in October and in April-May and breeding season might occur from April-May to October.

The length-weight and fecundity-weight relationships are presented in Figure 31-4 and 31-5, respectively. Fecundity ranged from 17 to 38 for females weighing between 4.7 and 6.7 g. No relationship was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight no longer increased significantly was estimated at 2% (Figure 31-6). The mean oocyte weight was 4.36 mg (± 1.30 SD, N= 10).

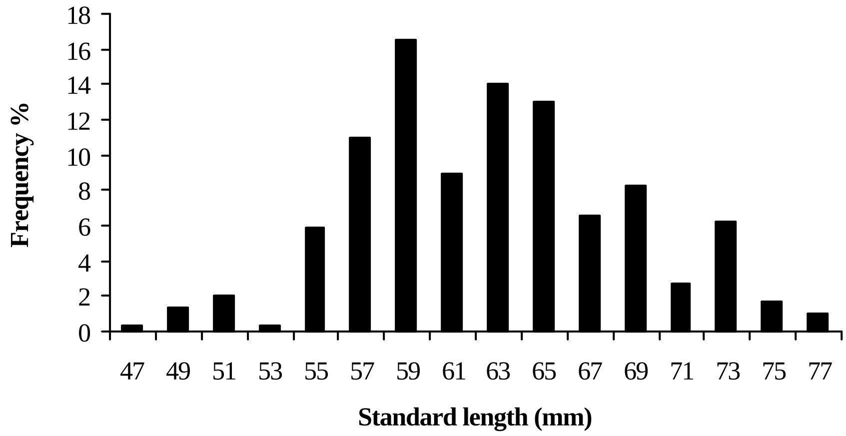

Figure 31-2. Size range and frequencies of *Placidochromis 'long'* caught in the SWA between July 1998 and May 1999.

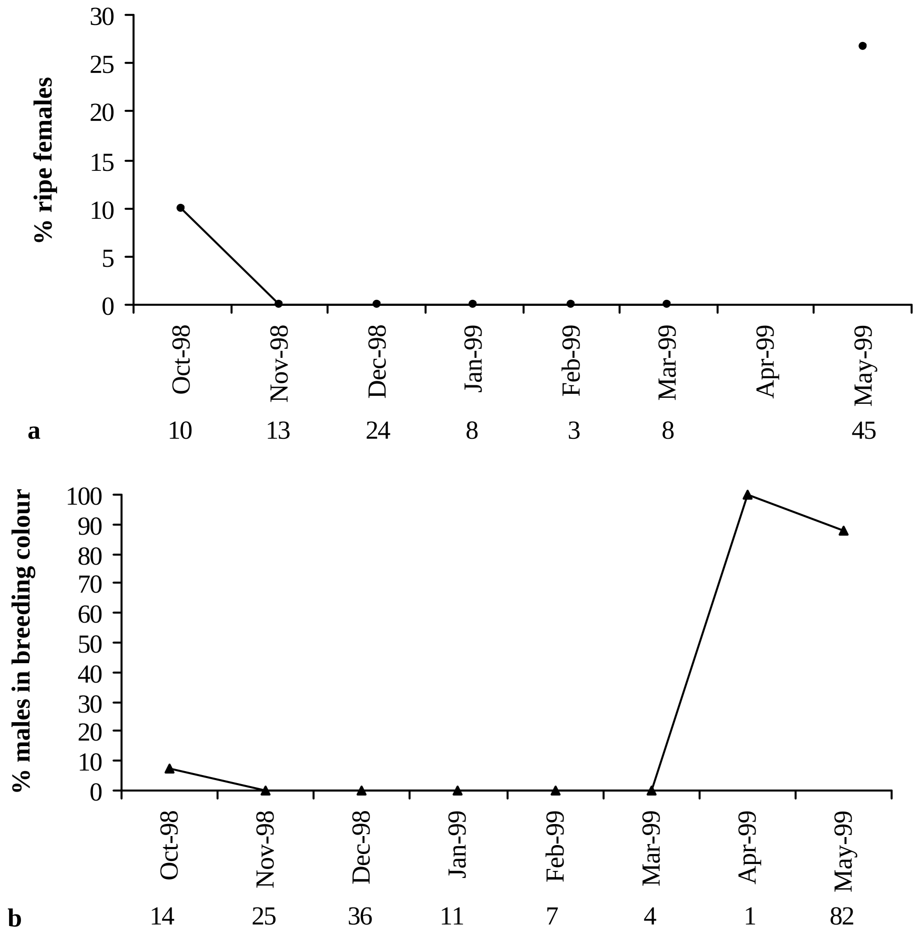

Figure 31-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Placidochromis 'long'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

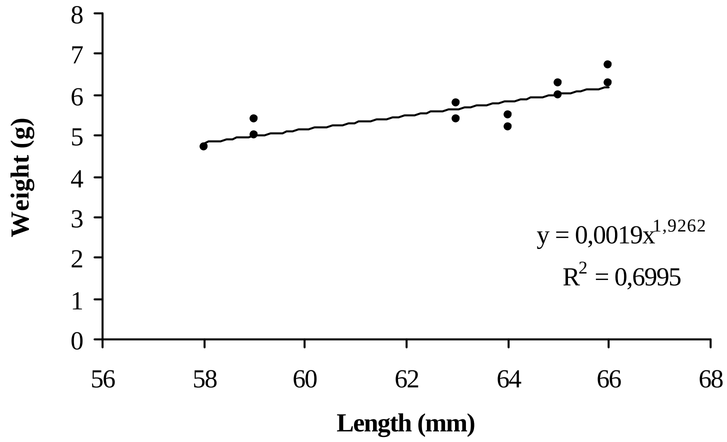

Figure 31-4. Length-weight relationship for *Placidochromis 'long'* females in the SWA. (R^2 = determination coefficient).

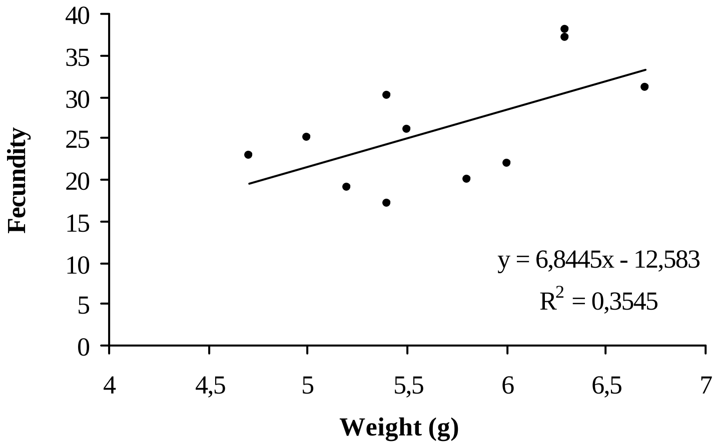

Figure 31-5. Fecundity-weight relationship for *Placidochromis 'long'* females in the SWA. (R^2 = determination coefficient).

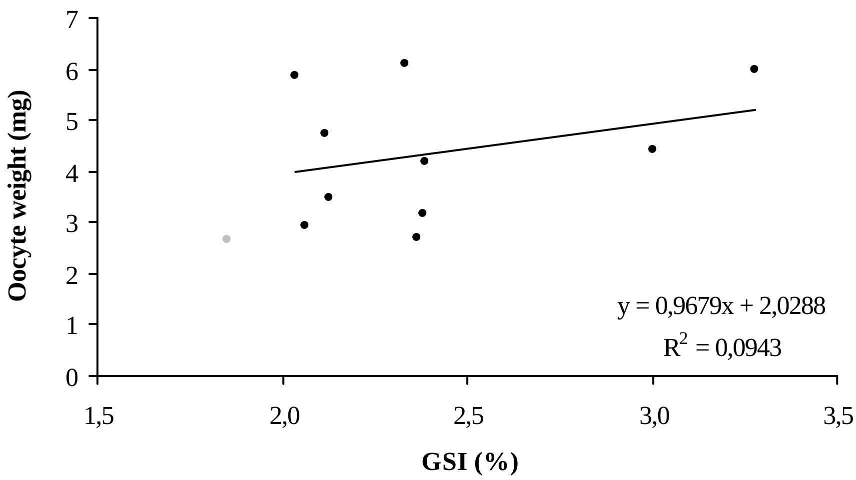

Figure 31-6. Relationship between oocyte weight and gonado-somatic index (GSI) for *Placidochromis 'long'*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3.2%. (R^2 = determination coefficient).

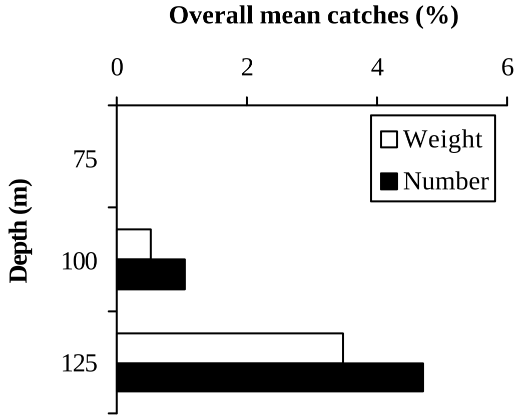

Figure 32-1. Mean occurrence and abundance in the catches per depth of *Placidochromis 'platyrhynchos'* in the SWA between July 1998 and May 1999.

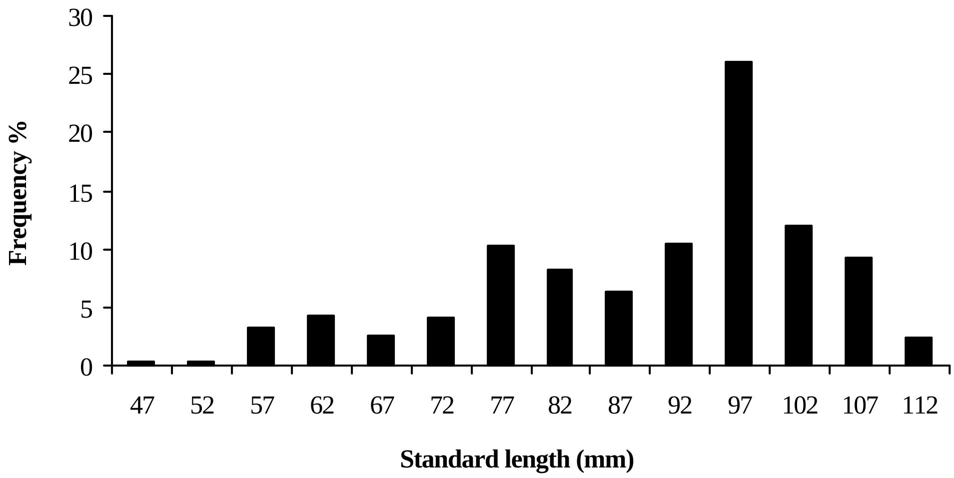

Figure 32-2. Size range and frequencies of *Placidochromis 'platyrhynchos'* caught in the SWA between July 1998 and May 1999.

Placidochromis 'platyrhynchos'

263 females and 225 males were analysed. *P. 'platyrhynchos'* is a relatively small species caught from 75 to 125 m, with an increasing occurrence and biomass with depth (Figure 32-1). It was a very common species at 125 m, where it constituted 3.5 and 4.7% of the catches in weight and number, respectively. The mean CPUE per depth category was 1.7 kg for the deep zone and 6.2 kg for the very deep zone, which matched with the value reported by Tómasson & Banda (1996) for the deep zone (1.4 kg) and was more than twice as much for the very deep zone (2.8 kg). Specimens caught ranged between 46 and 115 mm (Figure 32-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Ripe females were found from July to August and from December to May (Figure 32-3a). Considering the very low sample size for June, it can be estimated than breeding season occurred from December to October, with a peak from January to May and a cessation in November. This pattern was confirmed by males data, excluding the months with very low sample size such as August and November (Figure 32-3b). Nearly all the ripe females and males and the immature individuals were caught at 125 m, suggesting that spawning could take place at this depth (Table 32-1). The mean size at maturity was about 80 mm (Figure 32-4), which was probably overestimated given that this estimation was with all the data available to increase the sample size, including data outside the breeding season. This corresponded to a mean age at maturity of 12 months.

Table 32-1. Percentage of ripe females (stages 4 and 5), males in breeding colour and immature individuals (whose size is below the size at maturity) per depth for *Placidochromis 'platyrhynchos'* in the SWA.

Depth	Non ripe females	Ripe females	Males not in breeding colour	Males in breeding colour	Immature specimens
75 m	0	0	1.2	0	0
100 m	23.4	7.5	28.2	1.4	16.7
125 m	76.6	92.5	70.6	98.6	83.3

The length-weight and fecundity-weight relationships are presented in Figure 32-5 and 32-6, respectively. Fecundity ranged from 23 to 93 for females weighing between 9 and 31 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3.5% (Figure 32-7). The mean oocyte weight was 13.83 mg (± 1.88 SD, N= 24).

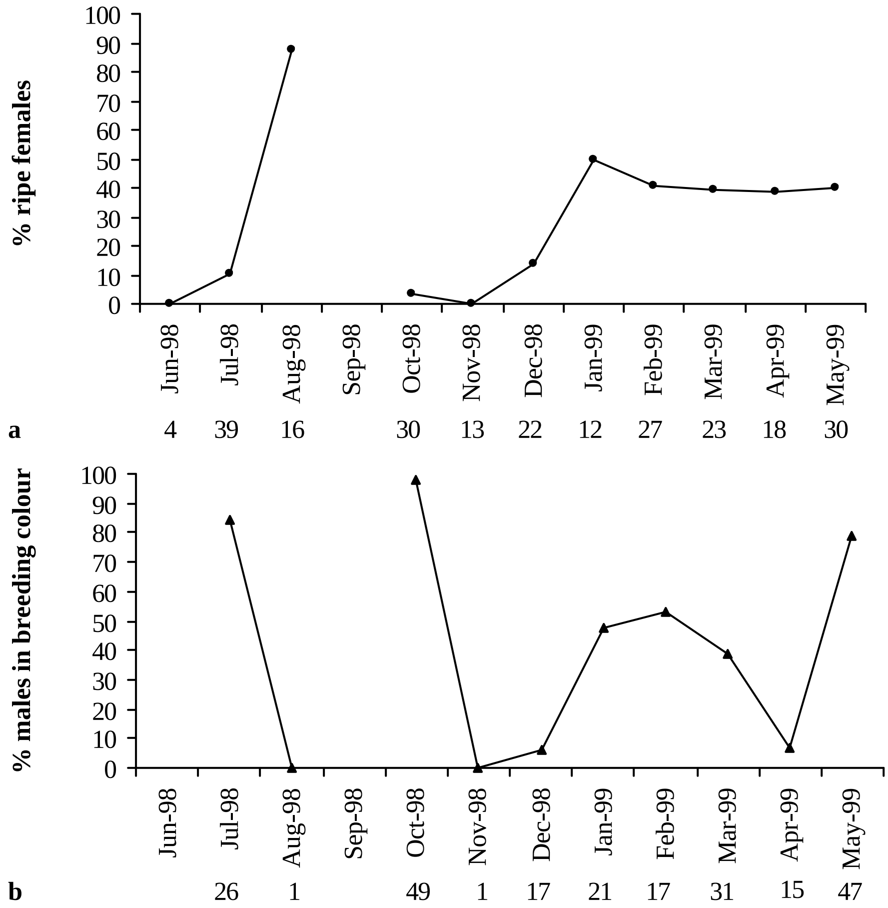

Figure 32-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Placidochromis 'platyrhynchos'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

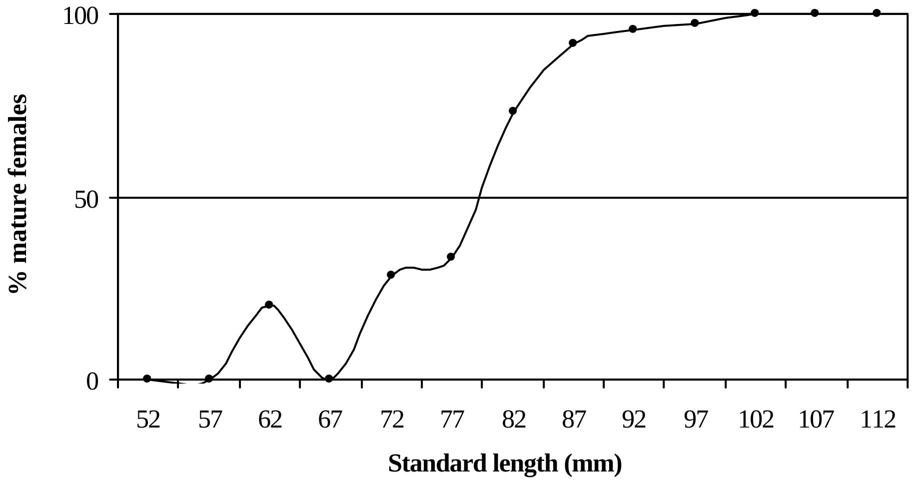

Figure 32-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Placidochromis 'platyrhynchos'* in the SWA.

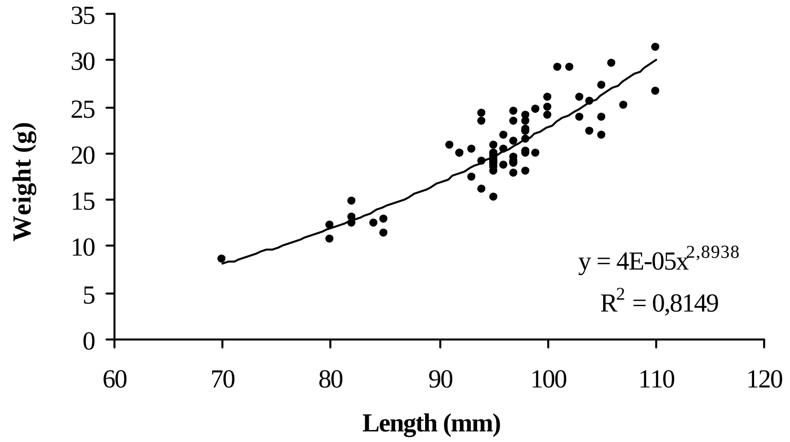

Figure 32-5. Length-weight relationship for *Placidochromis 'platyrhynchos'* females in the SWA. (R^2 = determination coefficient).

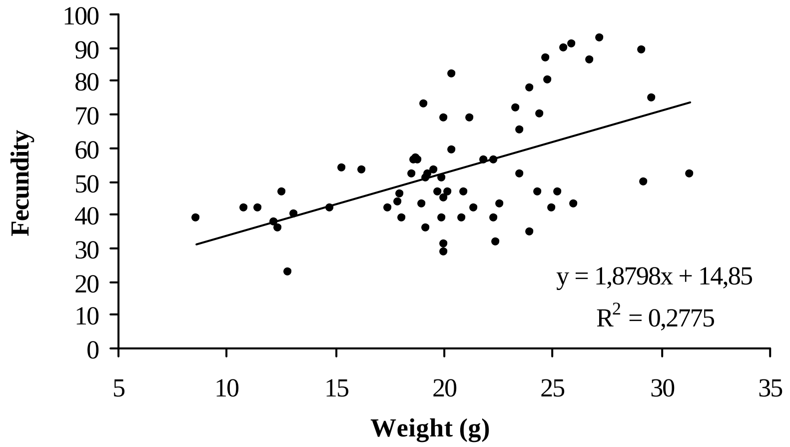

Figure 32-6. Fecundity-weight relationship for *Placidochromis 'platyrhynchos'* females in the SWA. (R^2 = determination coefficient).

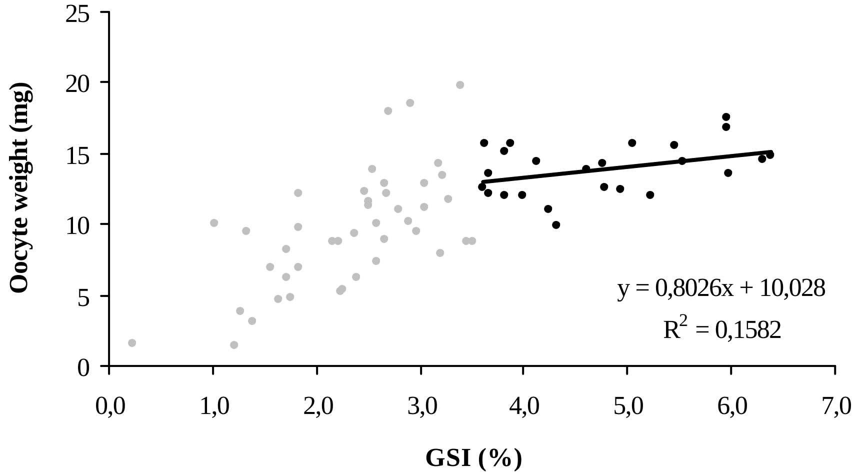

Figure 32-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Placidochromis 'platyrhynchos'*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3.5%. (R^2 = determination coefficient).

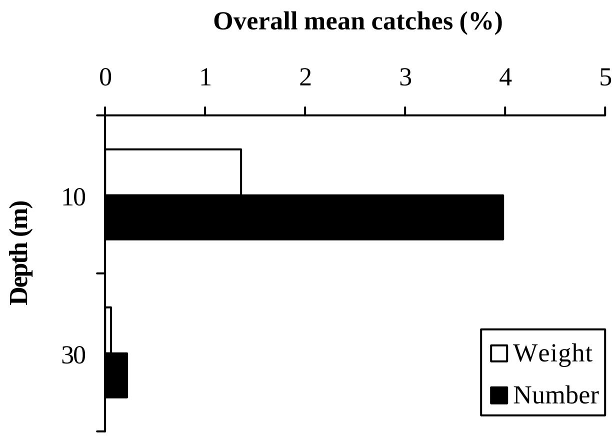

Figure 33-1. Mean occurrence and abundance in the catches per depth of *Pseudotropheus livingstonii* in the SWA between July 1998 and May 1999.

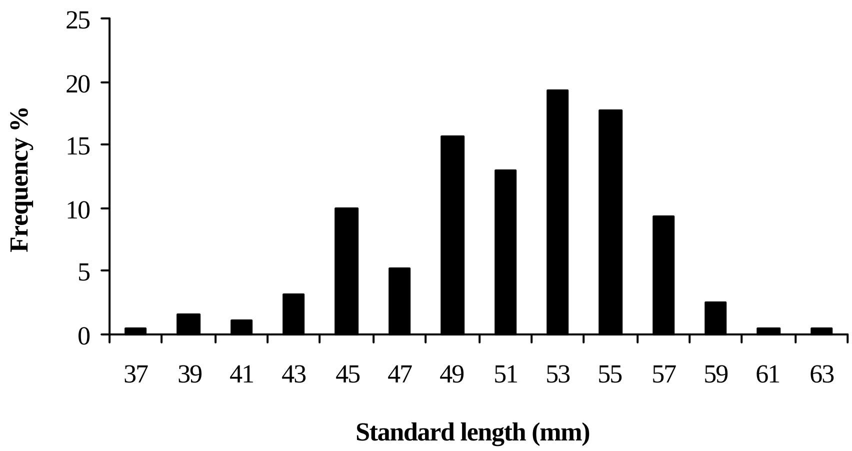

Figure 33-2. Size range and frequencies of *Pseudotropheus livingstonii* caught in the SWA between July 1998 and May 1999.

Pseudotropheus spp.

Pseudotropheus livingstonii (Boulenger)

68 females and 124 males were analysed. *Ps. livingstonii* is a small species principally caught at 10 and sometimes at 30 m (Figure 33-1). It constituted 1.4 and 4% of the catches in weight and number, respectively. The mean CPUE per depth category was 1.8 kg for the shallow zone, which was about five times less than the value reported by Tómasson & Banda (1996) (9.8 kg). Specimens caught ranged between 37 and 63 mm (Figure 33-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

As *Ps. Livingstonii* was sometimes relatively abundant and sometimes absent from the catches for a few months, precise determination of the breeding season was impossible. Each time it was present in the catches (October, November, March, April, May), ripe females were found (Figure 33-3a), which was not always the case for males in breeding colour (Figure 33-3b). Maturity was reached at about 37 mm for females (Figure 33-4).

The length-weight and fecundity-weight relationships are presented in Figure 33-5 and 33-6, respectively. Fecundity ranged from 15 to 33 for females weighing between 3 and 5 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was estimated at about 2% (Figure 33-7). The mean oocyte weight was 5.45 mg (± 0.59 SD, N= 7).

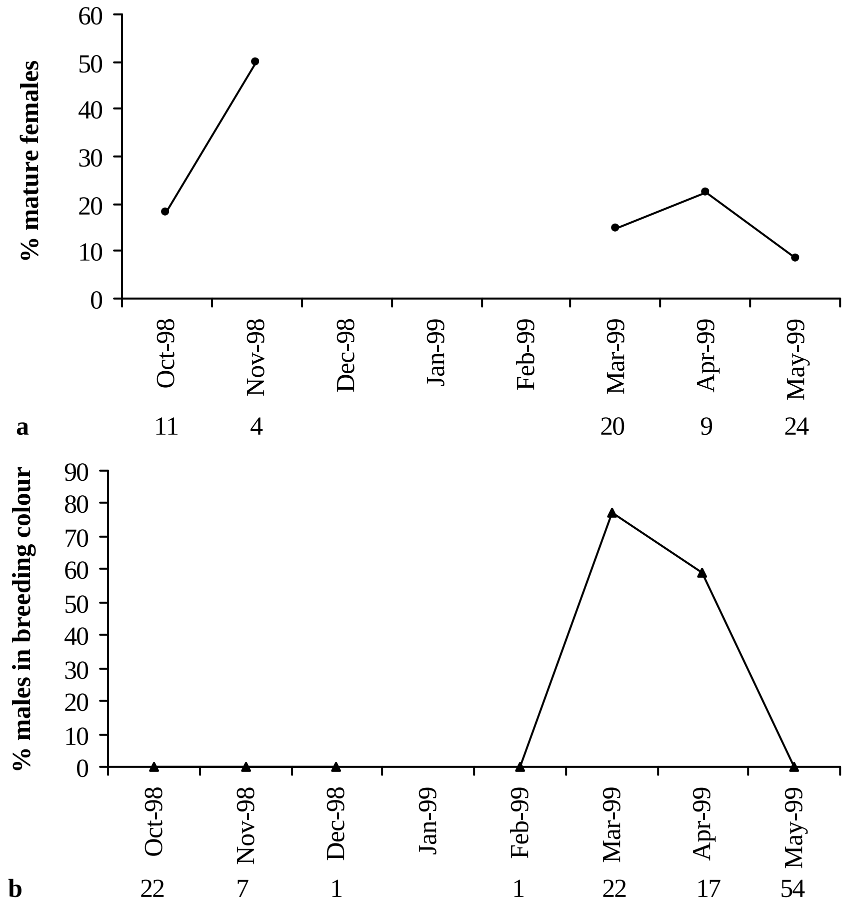

Figure 33-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Pseudotropheus livingstonii* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

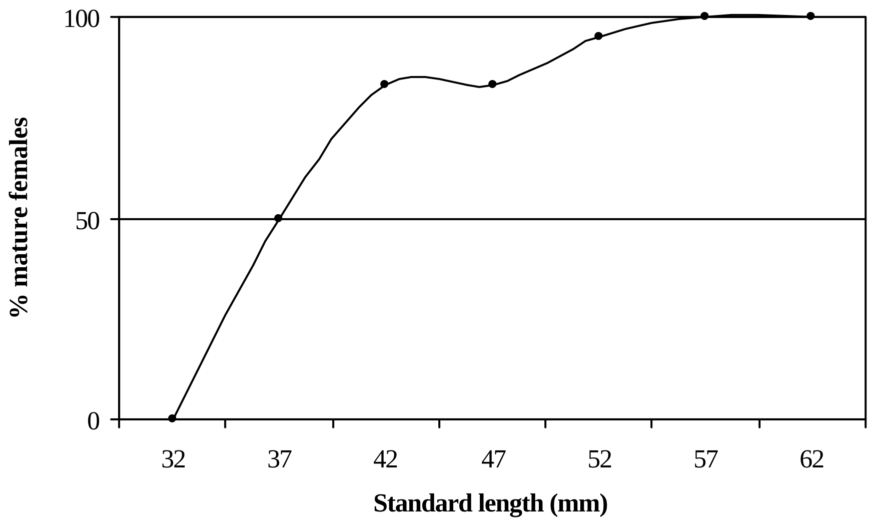

Figure 33-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Pseudotropheus livingstonii* in the SWA.

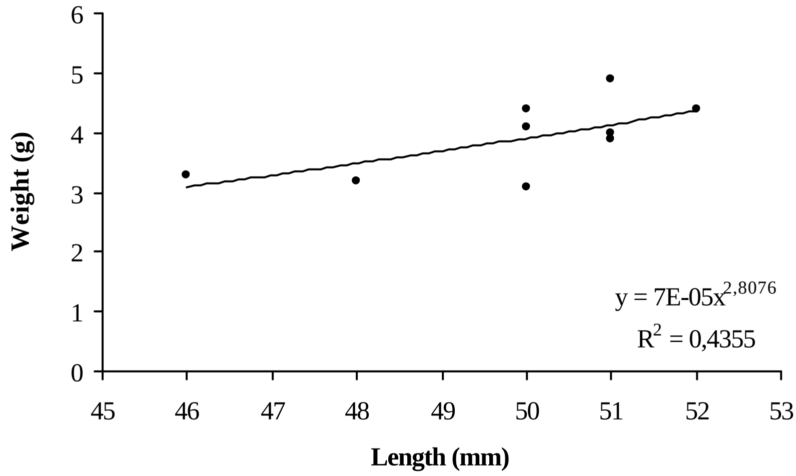

Figure 33-5. Length-weight relationship for *Pseudotropheus livingstonii* females in the SWA. (R^2 = determination coefficient).

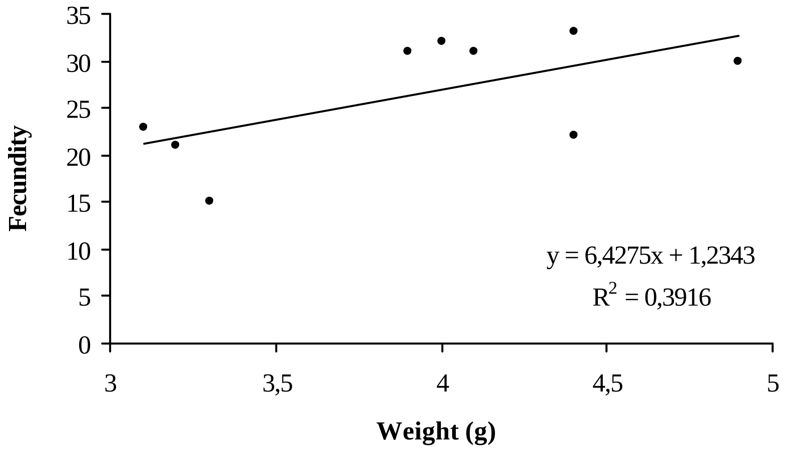

Figure 33-6. Fecundity-weight relationship for *Pseudotropheus livingstonii* females in the SWA. (R^2 = determination coefficient).

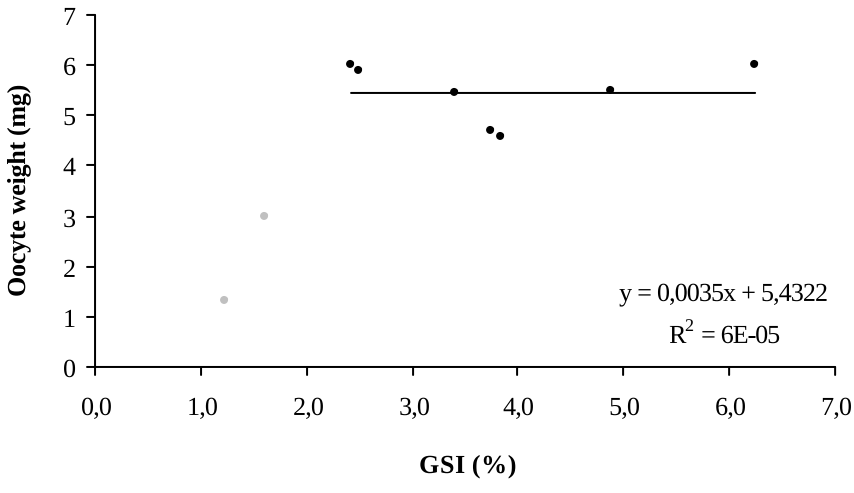

Figure 33-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Pseudotropheus livingstonii*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 2%. (R^2 = determination coefficient).

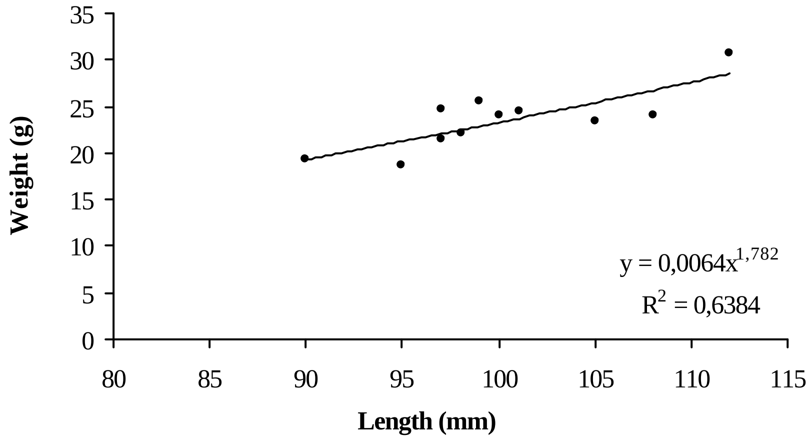

Figure 34-3. Length-weight relationship for *Sciaenochromis ahli* females in the SWA. (R^2 = determination coefficient).

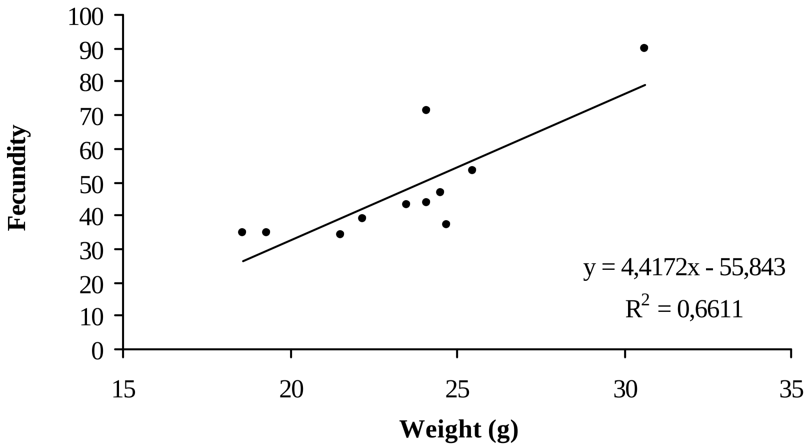

Figure 34-4. Fecundity-weight relationship for *Sciaenochromis ahli* females in the SWA. (R^2 = determination coefficient).

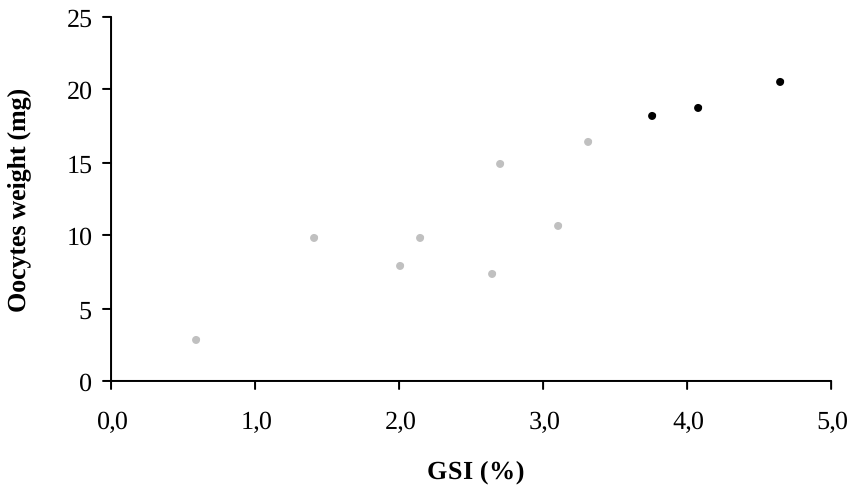

Figure 34-5. Relationship between oocyte weight and gonado-somatic index (GSI) for *Sciaenochromis ahli*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3.5%. (R^2 = determination coefficient).

<u>*Sciaenochromis spp.*</u>

***Sciaenochromis ahli* (Trewavas)**

38 females and 37 males were analysed. *S. ahli* is a relatively small species encountered at every depth from 10 to 125 m but never numerous in any of them. The mean CPUE per depth category was 0.9, 0.8 and 0.3 kg for the shallow, deep and very deep zones, respectively. No reference to this species (under this name at least) was made in Tómasson & Banda (1996). Specimens caught ranged between 62 and 124 mm (Figure 34-1).

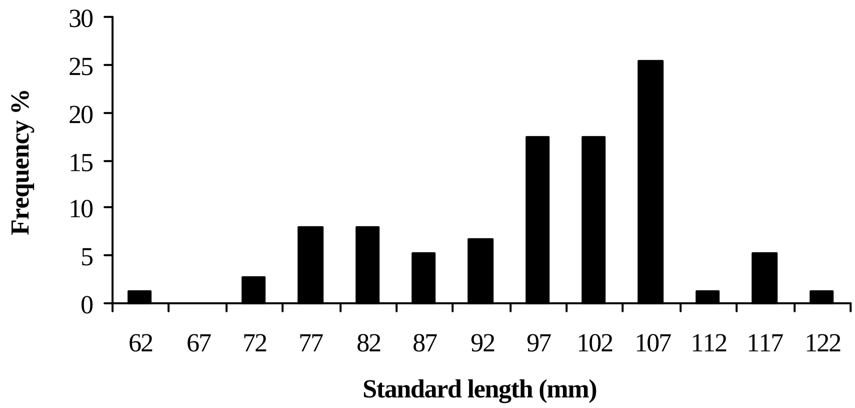

Figure 34-1. Size range and frequencies of *Sciaenochromis ahli* caught in the SWA between July 1998 and May 1999.

The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Owing to low sample size or absence of data for some months, the precise determination of breeding season and size at maturity was not possible. Ripe females were found at each sampling date except when sample size were almost null (March and April) (Figure 34-2). Only three males in breeding colour were found, in November and May, all at 75 m. Breeding season could then occur at least from October to May.

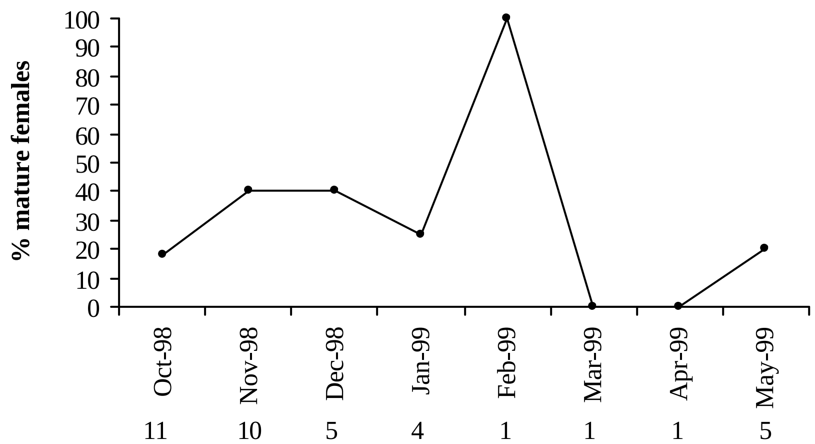

Figure 34-2. Seasonal progression of the percentage of ripe (stages 4 and 5) females *Sciaenochromis ahli* in the SWA The values below the x-axis are the sample size for each month.

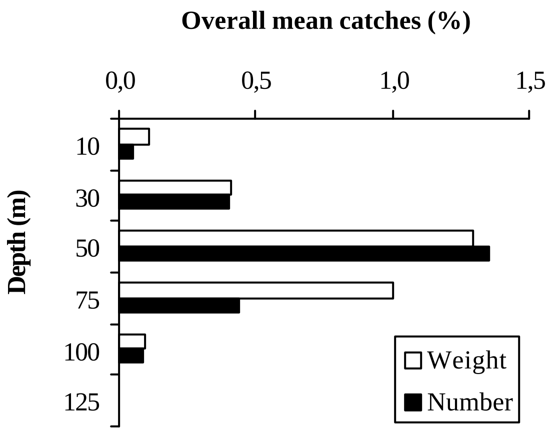

Figure 35-1. Mean occurrence and abundance in the catches per depth of *Sciaenochromis benthicola* in the SWA between July 1998 and May 1999.

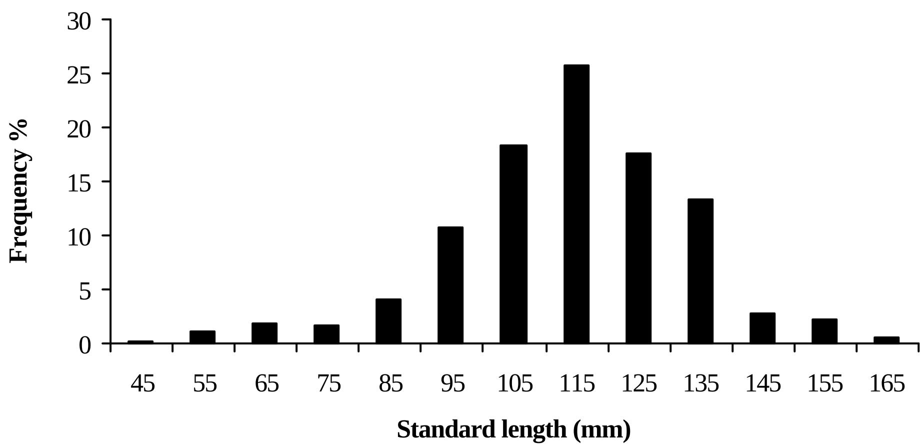

Figure 35-2. Size range and frequencies of *Sciaenochromis benthicola* caught in the SWA between July 1998 and May 1999.

The length-weight and fecundity-weight relationships are presented in Figure 34-3 and 34-4, respectively. Fecundity ranged from 35 to 90 for females weighing between 19 and 31 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was impossible to assess because of low sample size. However, despite the fact that oocyte weight apparently still increased with GSI above 3.5% (Figure 34-5), the mean oocyte weight was estimated from the three females whose GSI was above 3.5%, and was 19.11 mg (± 1.25 SD, N= 3).

Sciaenochromis benthicola (Konings)

188 females and 182 males were analysed. *S. benthicola* was encountered at every depth from 10 to 125 m but was more frequent at 50 and 75 m, where it constituted 1 to 1.3% of the catches in weight and 0.4 to 1.4% in number, respectively (Figure 35-1). The mean CPUE per depth category was 5.6, 2.4 kg and almost nothing for the shallow, deep and very deep zones, respectively. No reference to this species (under this name at least) was made in Tómasson & Banda (1996). Specimens caught ranged between 48 and 168 mm (Figure 35-2). The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Owing to low sample size or absence of data for some months, the precise determination of breeding season was not possible. Ripe females were found in June, August and from November to February, with peaks in August and December (Figure 35-3a). Data for males gave approximately the same pattern except for the period from June to August, when no ripe males were found (Figure 35-3b). 100% of the ripe females and 91% of the males in breeding colour were found at 50 and 75 m, suggesting that spawning could occur at these depths. The mean size at maturity was about 100 mm for females (Figure 35-4). Size at maturity has to be determined at the height of the breeding season to be accurate, but owing to the low sample size we had to consider every data available. As a consequence, females caught outside the peak of breeding season were included in the analyses, even large resting females, which explains the shape of the upper part of the curve.

The length-weight and fecundity-weight relationships are presented in Figure 35-5 and 35-6, respectively. Fecundity ranged from 32 to 99 for females weighing between 26 and 69 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight no longer increased significantly was 3% (Figure 35-7). The mean oocyte weight was 27.31 mg (± 4.12 SD, N= 13).

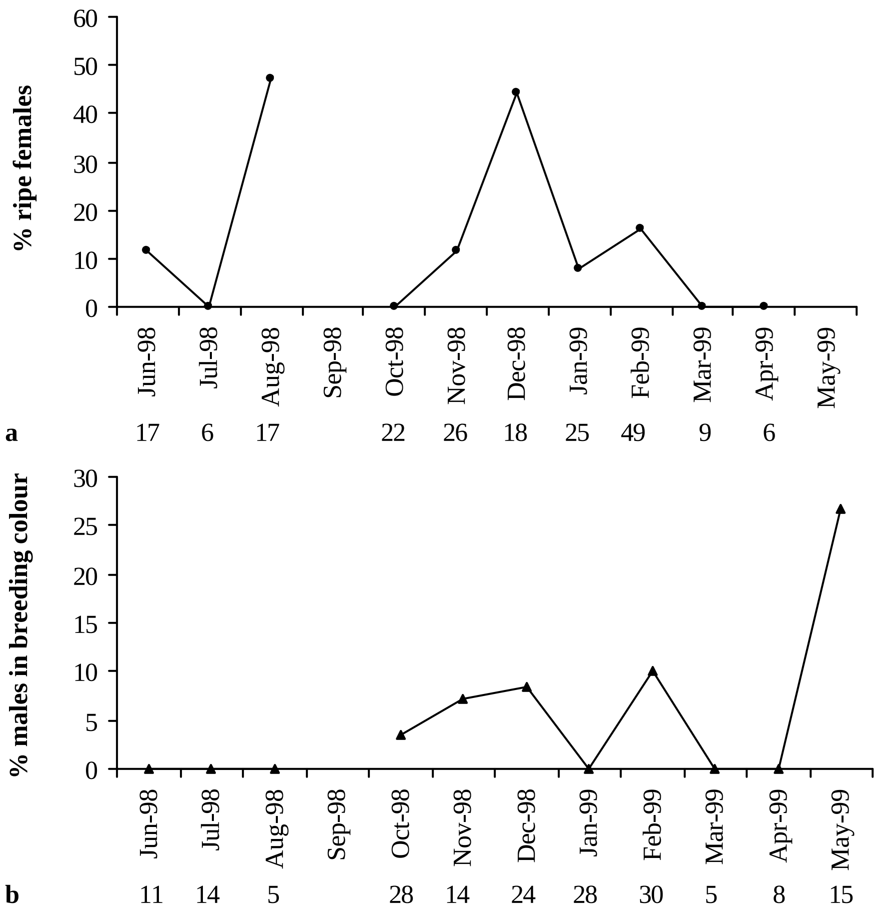

Figure 35-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Sciaenochromis benthicola* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

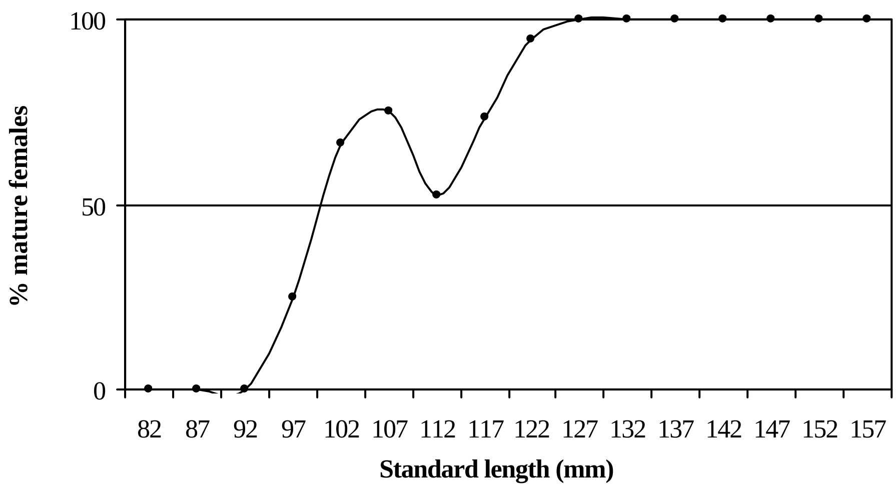

Figure 35-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Sciaenochromis benthicola* in the SWA.

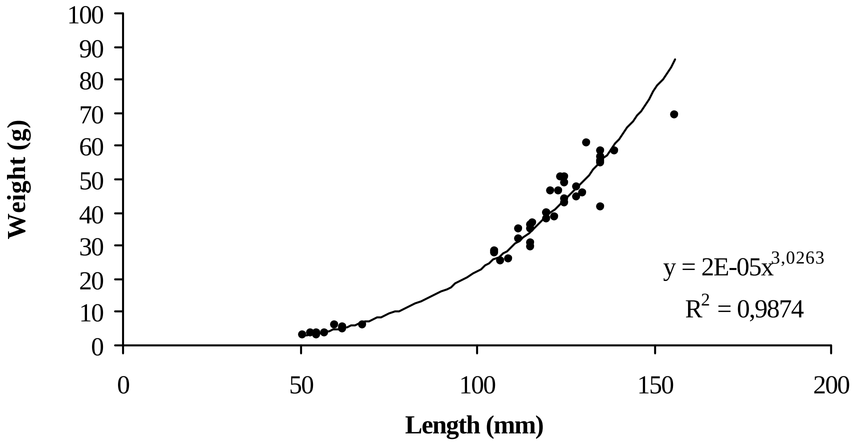

Figure 35-5. Length-weight relationship for *Sciaenochromis benthicola* females in the SWA. (R^2 = determination coefficient).

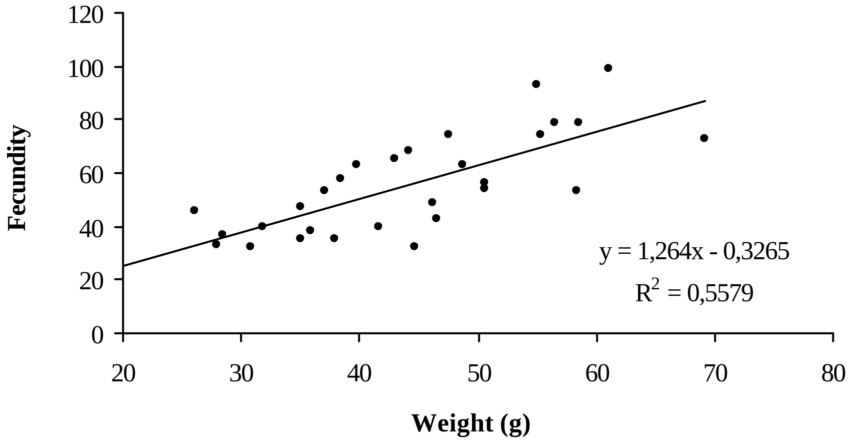

Figure 35-6. Fecundity-weight relationship for *Sciaenochromis benthicola* females in the SWA. (R^2 = determination coefficient).

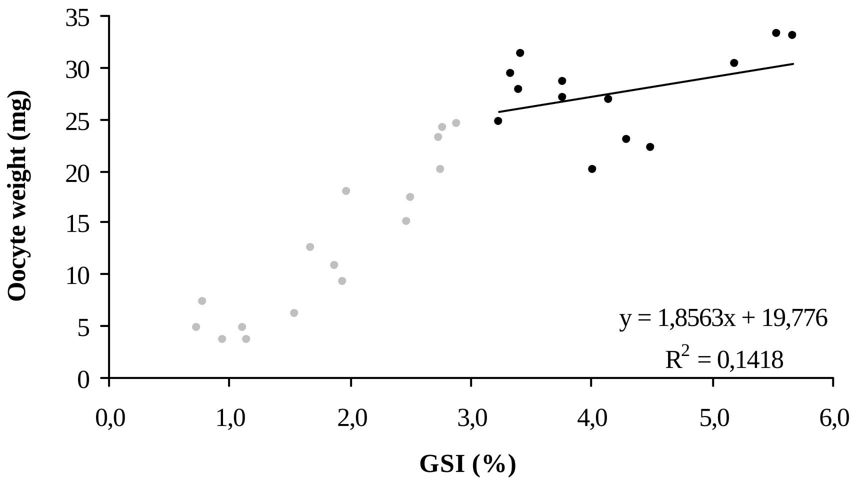

Figure 35-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Sciaenochromis benthicola*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

Stigmatochromis spp.

Stigmatochromis 'guttatus'

62 females and 22 males were analysed. *S. 'guttatus'* was encountered at every depth from 10 to 125 m but was never abundant in any of them although it occurred more frequently at 50 and 75 m. Specimens caught ranged between 64 and 147 mm (Figure 36-1). The sex ratio observed over the full sampling period was F/M 0.7/0.3.

Owing to low sample size or absence of data for some months, the precise determination of breeding season was not possible. Ripe females were found from October to December, in February and in April-May (Figure 36-2). The six males in breeding colour we found were caught at 50 m in March. The mean size at maturity was about 100 mm for females (Figure 36-3), which was probably overestimated as this estimation was not done during the height of the breeding season but with all the data available for females, to increase the sample size.

The length-weight and fecundity-weight relationships are presented in Figure 36-4 and 36-5, respectively. Fecundity ranged from 21 to 64 for females weighing between 20 and 46 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was 3% (Figure 36-6). The mean oocyte weight was 29.09 mg (± 2.97 SD, N= 4).

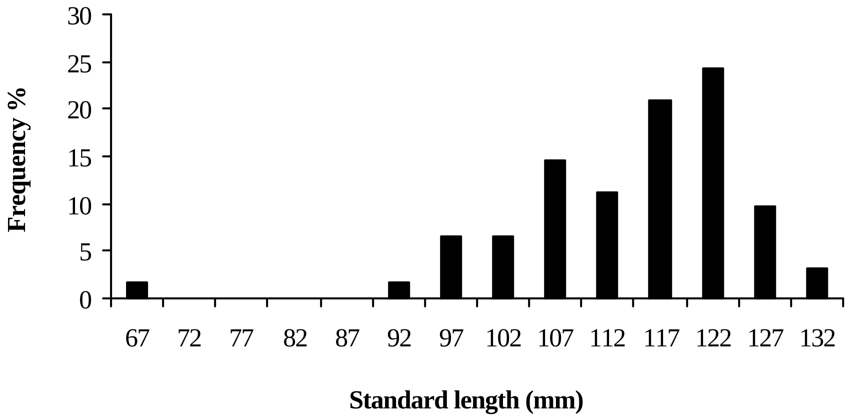

Figure 36-1. Size range and frequencies of *Stigmatochromis 'guttatus'* caught in the SWA between July 1998 and May 1999.

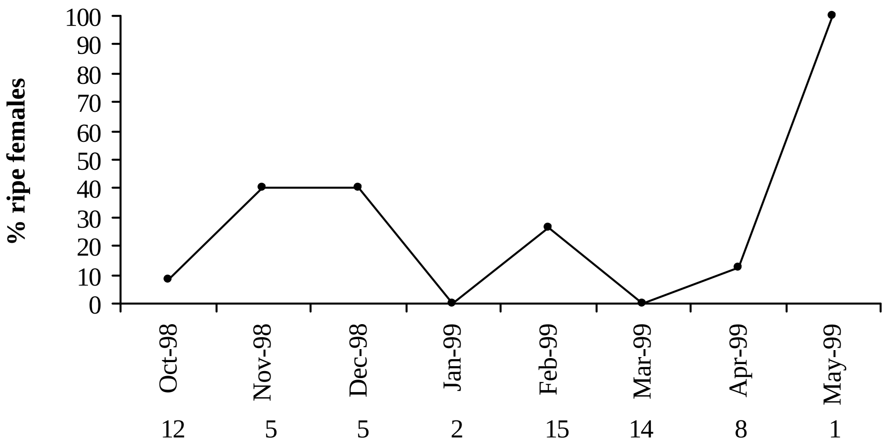

Figure 36-2. Seasonal progression of the percentage of ripe (stages 4 and 5) females *Stigmatochromis 'guttatus'* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

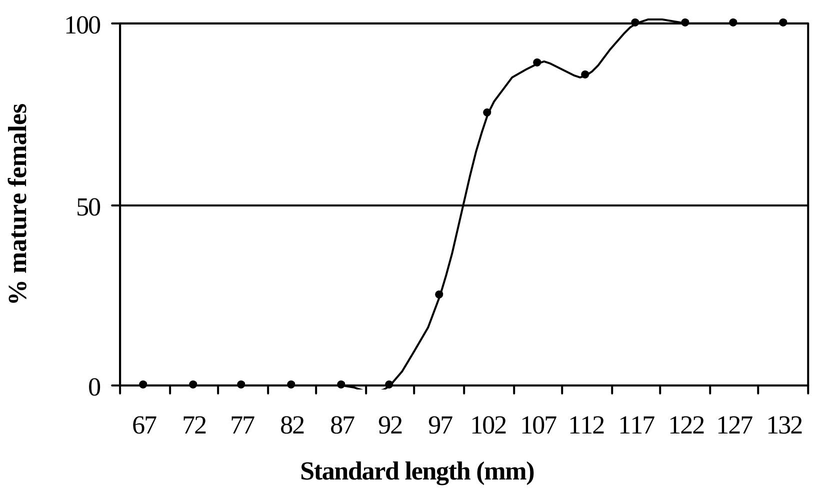

Figure 36-3. Percentage of mature females (stage 3 and above) per size class (standard length) for *Stigmatochromis 'guttatus'* in the SWA.

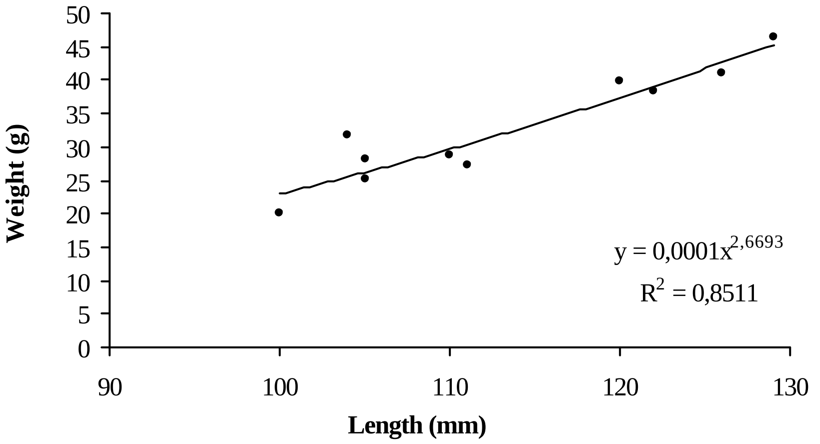

Figure 36-4. Length-weight relationship for *Stigmatochromis 'guttatus'* females in the SWA. (R^2 = determination coefficient).

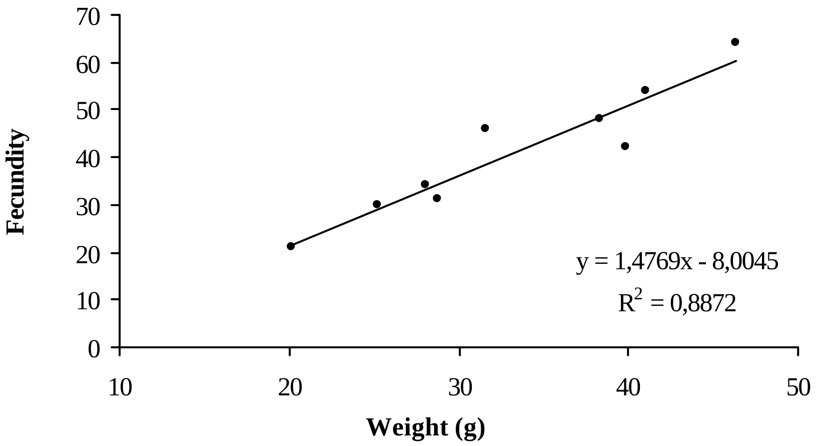

Figure 36-5. Fecundity-weight relationship for *Stigmatochromis 'guttatus'* females in the SWA. (R^2 = determination coefficient).

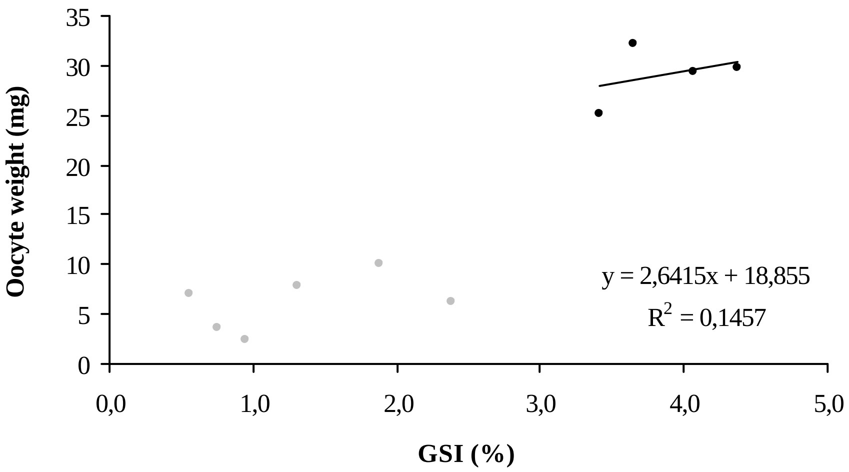

Figure 36-6. Relationship between oocyte weight and gonado-somatic index (GSI) for *Stigmatochromis 'guttatus'*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

Taeniolethrinops spp.

Taeniolethrinops furcicauda **(Trewavas) (Plate 17)**

135 females and 88 males were analysed. *T. furcicauda* was mostly encountered at 10 m where it made up to 1.2 and 1.6% of the catches in number and weight, respectively. It was also found sometimes at 30 m. Specimens caught ranged between 65 and 178 mm (Figure 37-1).

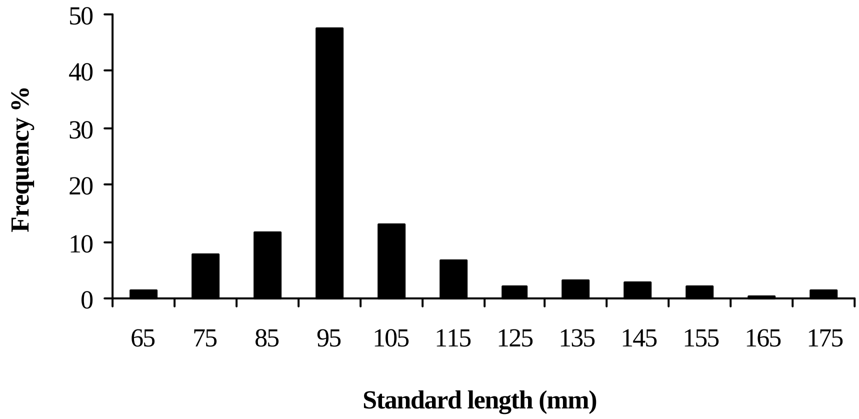

Figure 37-1. Size range and frequencies of *Taeniolethrinops furcicauda* caught in the SWA between July 1998 and May 1999.

The sex ratio observed over the full sampling period was F/M 0.6/0.4.

Owing to low sample size or absence of data for some months, the precise determination of breeding season was not possible. Ripe females were only found in July (Figure 37-2), as was the single male in breeding colour caught. The mean size at maturity was about 130 mm for females (Figure 37-3), which was probably overestimated as this estimation was not done during the height of the breeding season but with all the data available for females, to increase the sample size.

The length-weight relationship is not given because of the too narrow size range of females measured. The fecundity-weight relationship is presented in Figure 37-4. Fecundity ranged from 138 to 219 for females weighing between 88 and 109 g and was not correlated to body weight. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was difficult to assess owing to low sample size. However, as the oocyte weight did no longer increase above a GSI of 1.5% (Figure 37-5), the mean oocyte weight was estimated (probably underestimated) at 10.13 mg (± 0.83 SD, N= 3).

Plate 17. *Taeniolethrinops furcicauda* (by Dave Voorvelt).

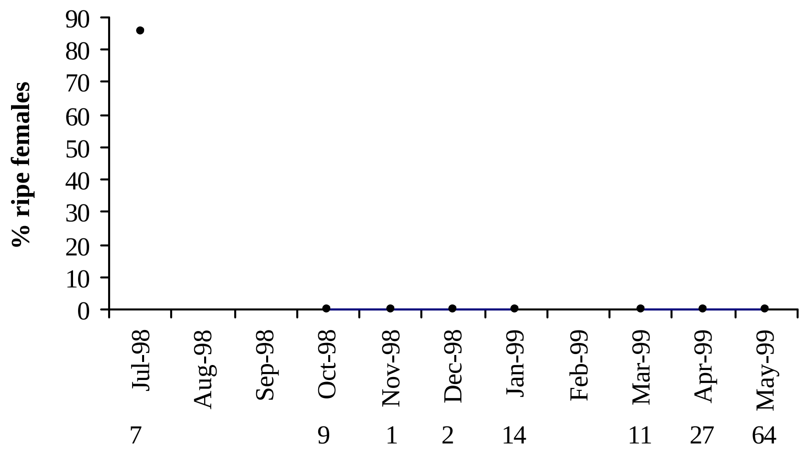

Figure 37-2. Seasonal progression of the percentage of ripe (stages 4 and 5) females *Taeniolethrinops furcicauda* in the SWA The values below the x-axis are the effective for each month.

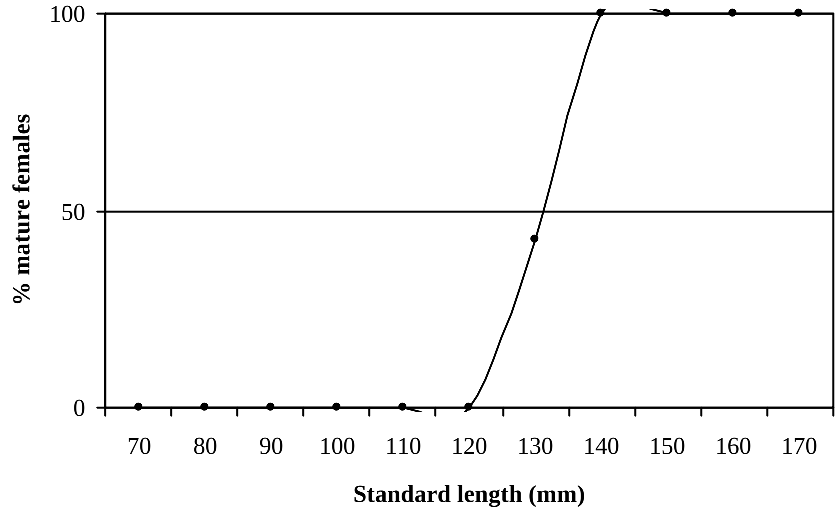

Figure 37-3. Percentage of mature females (stage 3 and above) per size class (standard length) for *Taeniolethrinops furcicauda* in the SWA.

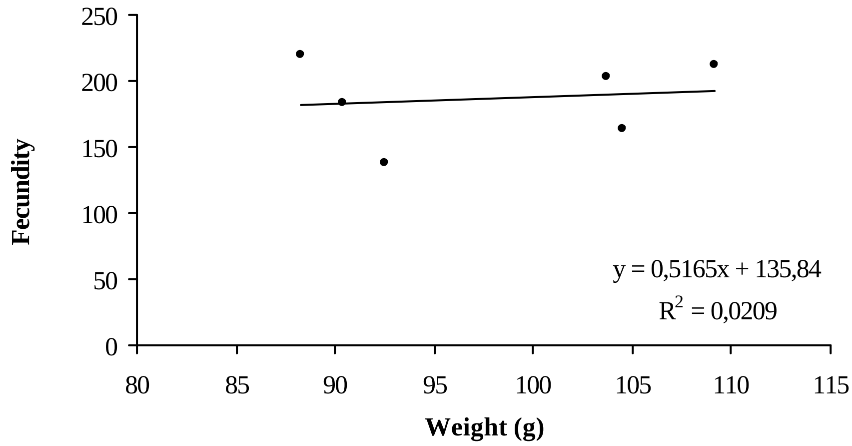

Figure 37-4. Fecundity-weight relationship for *Taeniolethrinops furcicauda* females in the SWA. (R^2 = determination coefficient).

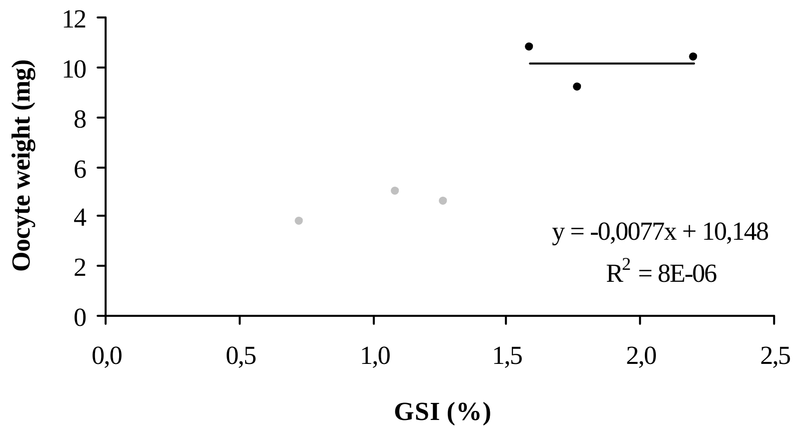

Figure 37-5. Relationship between oocyte weight and gonado-somatic index (GSI) for *Taeniolethrinops furcicauda*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 1.5%. (R^2 = determination coefficient).

Taeniolethrinops praeorbitalis (Regan) (Plate 18)

85 females and 78 males were analysed. *T. praeorbitalis* was encountered at 10 m and 30 m, but was never frequent at any depth. Specimens caught ranged between 71 and 199 mm (Figure 38-1).

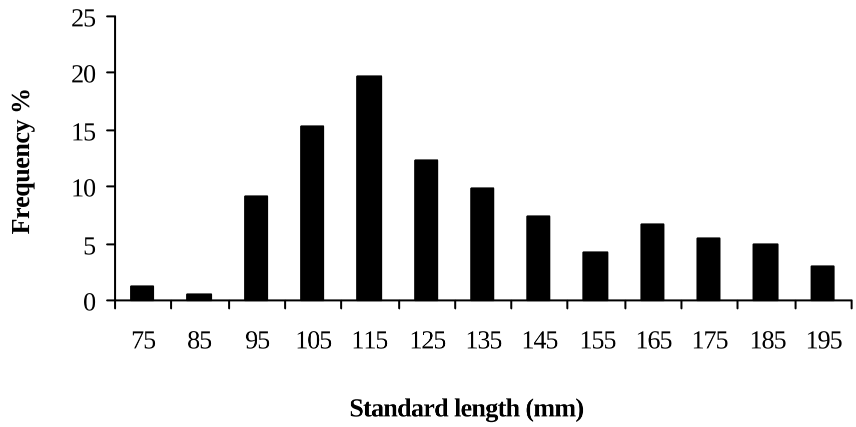

Figure 38-1. Size range and frequencies of *Taeniolethrinops praeorbitalis* caught in the SWA between July 1998 and May 1999.

The sex ratio observed over the full sampling period was F/M 0.5/0.5.

Owing to low sample size or absence of data for some months, the precise determination of breeding season was not possible. Ripe females were only found in August, and no male in breeding colour was ever caught. The mean size at maturity was about 155 mm for females (Figure 38-2), which was probably overestimated as this estimation was not done during the height of the breeding season but with all the data available for females, to increase the sample size. The first inflexion of the lower part of the curve came from the August data and it is likely that the mean size at maturity would rather be around 130 mm.

The length-weight and fecundity-weight relationships are presented in Figure 38-3 and 38-4, respectively. Fecundity ranged from 193 to 250 for females weighing between 135 and 184 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was estimated from the few data available at about 3% (Figure 38-5) and the mean oocyte weight was 25.73 mg (± 2.02 SD, N= 3).

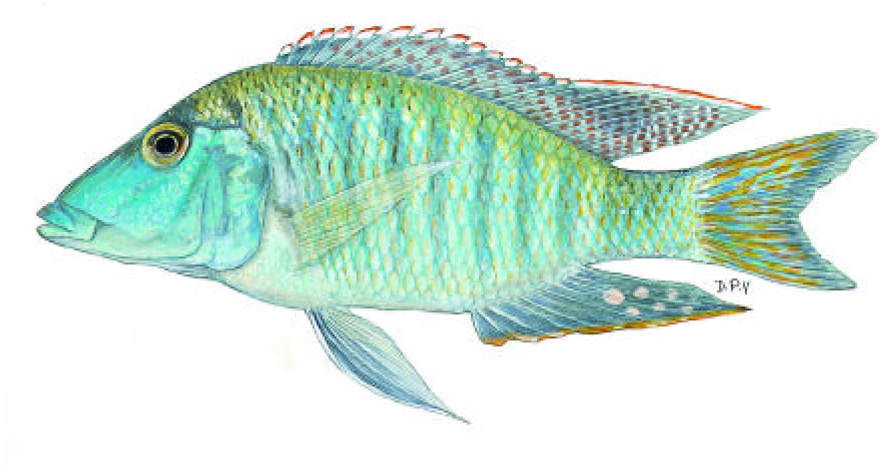

Plate 18. *Taeniolethrinops praeorbitalis* (by Dave Voorvelt).

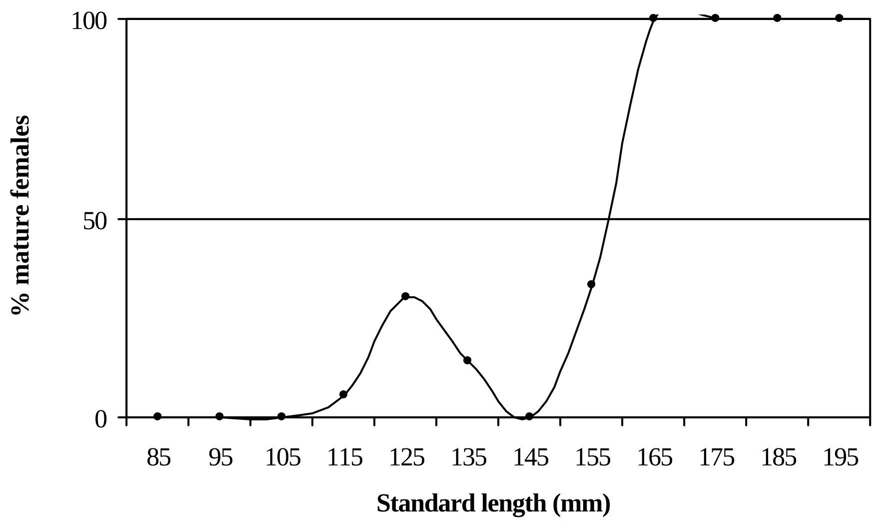

Figure 38-2. Percentage of mature females (stage 3 and above) per size class (standard length) for *Taeniolethrinops praeorbitalis* in the SWA.

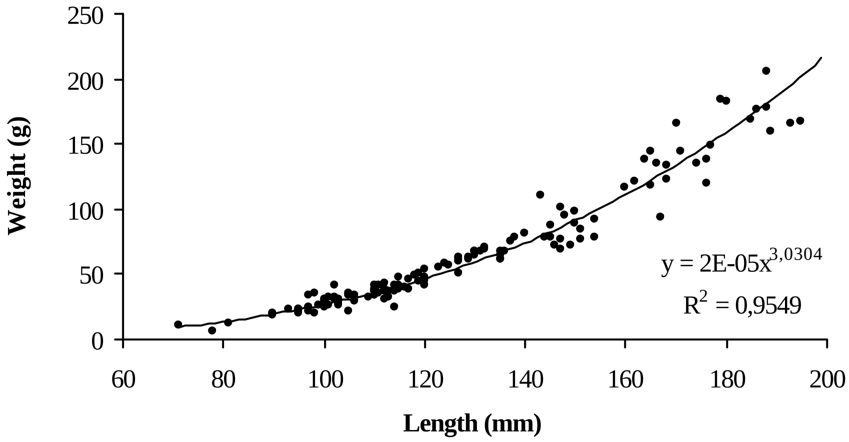

Figure 38-3. Length-weight relationship for *Taeniolethrinops praeorbitalis* females in the SWA. (R^2 = determination coefficient).

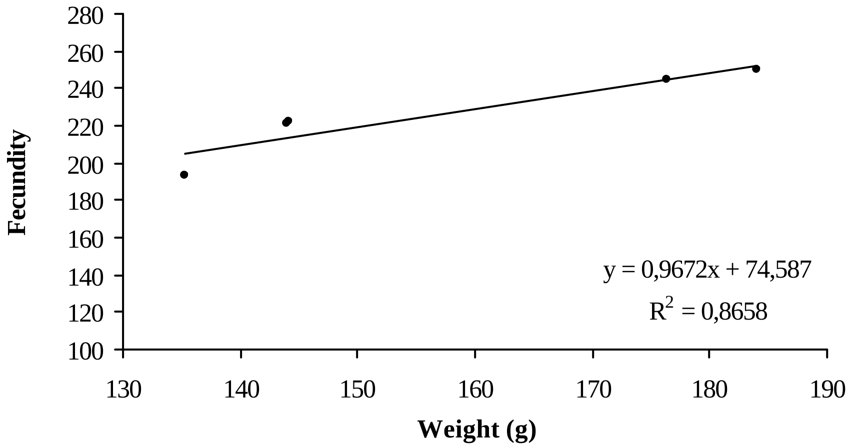

Figure 38-4. Fecundity-weight relationship for *Taeniolethrinops praeorbitalis* females in the SWA. (R^2 = determination coefficient).

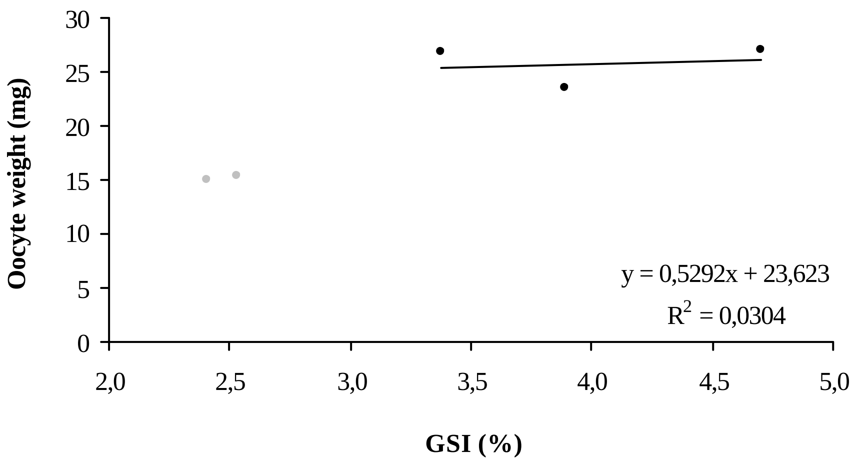

Figure 38-5. Relationship between oocyte weight and gonado-somatic index (GSI) for *Taeniolethrinops praeorbitalis*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

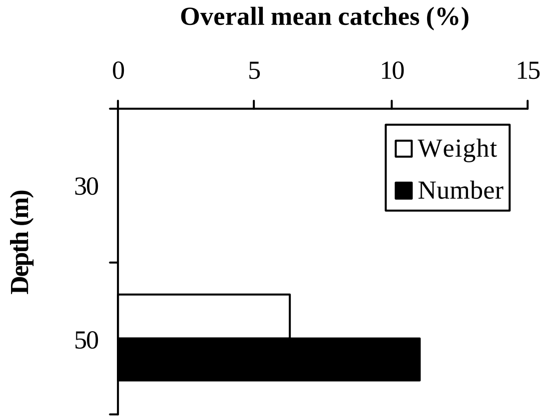

Figure 39-1. Mean occurrence and abundance in the catches per depth of *Trematocranus brevirostris* in the SWA between July 1998 and May 1999.

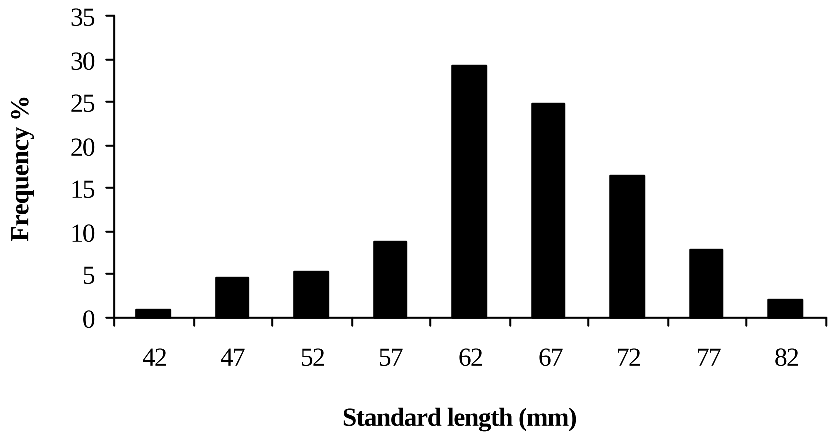

Figure 39-2. Size range and frequencies of *Trematocranus brevirostris* caught in the SWA between July 1998 and May 1999.

Trematocranus spp.

Trematocranus brevirostris **(Trewavas)**

162 females and 249 males were analysed. *T. brevirostris* is a small species encountered at 30 and 50 m but mostly present at 50 m where it made up to 6.3 and 11.1% of the catches in weight and number, respectively (Figure 39-1). The mean CPUE per depth category was 9.9 kg for the shallows. No reference to this species (under this name at least) was made in Tómasson & Banda (1996). Specimens caught ranged between 40 and 85 mm (Figure 39-2). The sex ratio observed over the full sampling period was F/M 0.4/0.6.

Owing to low sample size or absence of data for some months, the precise determination of breeding season was not possible. The monthly progression of ripe females (Figure 39-3a) and males (Figure 39-3b) were very similar, indicating a breeding activity from January to May, and in October, with a peak in March-April. According to the percentages of ripe females and males in May and October, it is likely that some breeding also activity occur between May and October. As almost all the specimens of *T. brevirostris* were caught at 50 m, spawning probably takes place at this depth. Maturity was reached in their first year at 11 months old at a mean size of 50 mm for females (Figure 39-4). Size at maturity has to be determined at the height of the breeding season to be accurate, but owing to the low sample size we had to consider every data available. As a consequence, females caught outside the peak of breeding season were included in the analyse, even large resting females, which explain the shape of the upper part of the curve.

The length-weight and fecundity-weight relationships are presented in Figure 39-5 and 39-6, respectively. Fecundity ranged from 13 to 47 for females weighing between 4 and 13 g and was not correlated to body weight. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was estimated from the few data available at about 3% (Figure 39-7) and the mean oocyte weight was 6.70 mg (± 1.12 SD, N= 12).

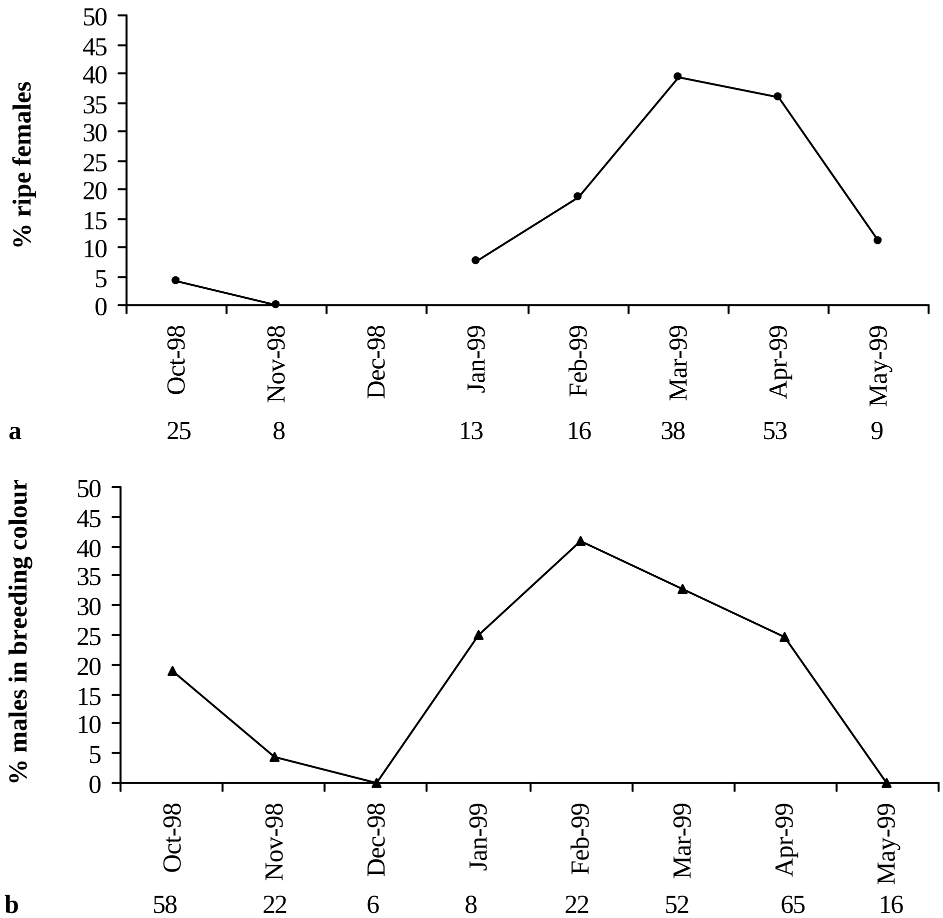

Figure 39-3. Seasonal progression of the percentage of ripe (stages 4 and 5) females (a) and males (b) *Trematocranus brevirostris* in the SWA The values below the x-axis are the effective (number of male or females which size was above the size at maturity) for each month.

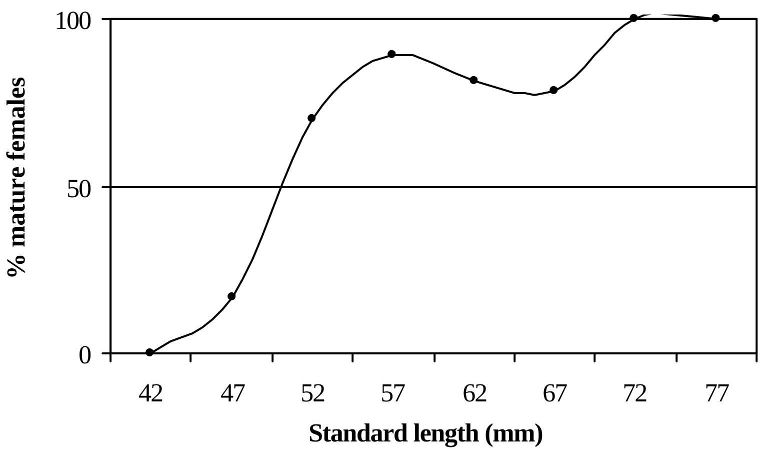

Figure 39-4. Percentage of mature females (stage 3 and above) per size class (standard length) for *Trematocranus brevirostris* in the SWA.

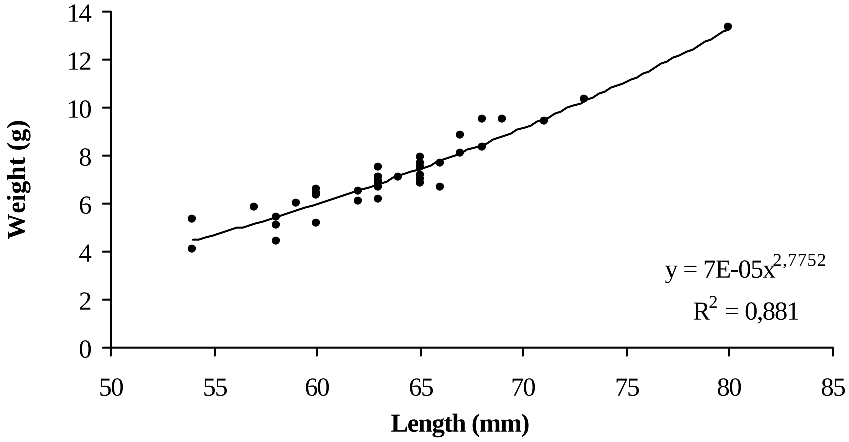

Figure 39-5. Length-weight relationship for *Trematocranus brevirostris* females in the SWA. (R^2 = determination coefficient).

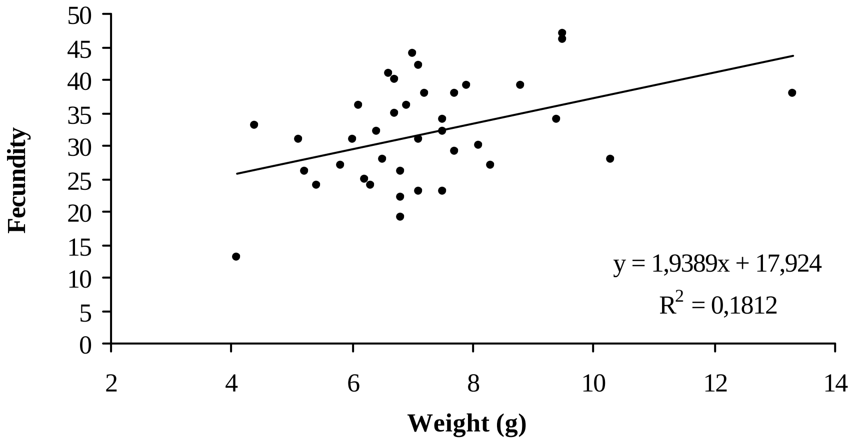

Figure 39-6. Fecundity-weight relationship for *Trematocranus brevirostris* females in the SWA. (R^2 = determination coefficient).

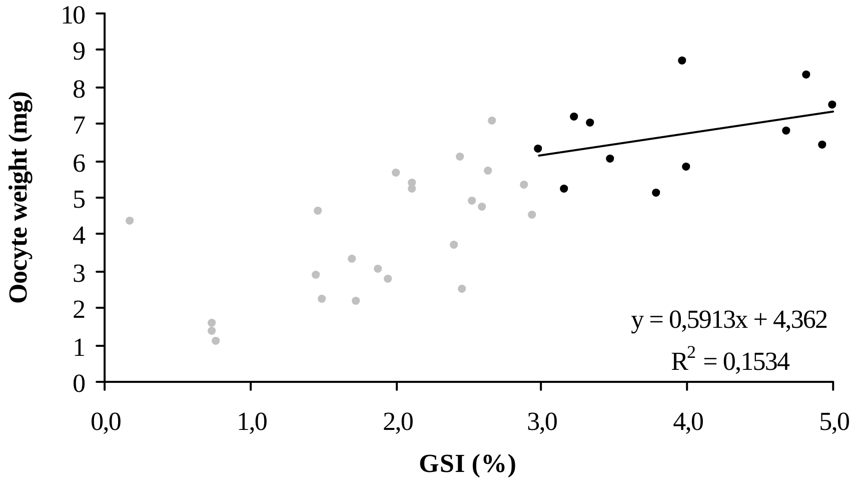

Figure 39-7. Relationship between oocyte weight and gonado-somatic index (GSI) for *Trematocranus brevirostris*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

Trematocranus placodon **(Regan) (Plate 19)**

34 females and 17 males were analysed. *T. placodon* is a common but not abundant species only encountered at 10 m. The mean CPUE per depth category was about 2 kg for the shallows, which was about three times less than the value reported (5.8 kg) by Tómasson & Banda (1996). Specimens caught ranged between 90 and 160 mm (Figure 40-1).

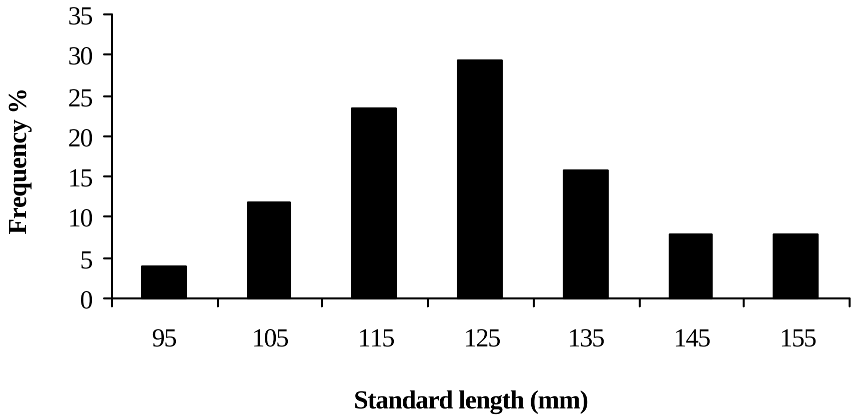

Figure 40-1. Size range and frequencies of *Trematocranus placodon* caught in the SWA between July 1998 and May 1999.

The sex ratio observed over the full sampling period was F/M 0.7/0.3.

Owing to low sample size or absence of data for some months, the precise determination of breeding season was not possible. Ripe females were found from June too August and in January-February (Figure 40-2). Only three males in breeding colour were caught, in July 98. The mean size at maturity was about 105 mm for females (Figure 40-3), which was probably overestimated as this estimation was not done during the height of the breeding season but with all the data available for females, to increase the sample size.

The length-weight and fecundity-weight relationships are presented in Figure 40-4 and 40-5, respectively. Fecundity ranged from 76 to 178 for females weighing between 41 and 91 g. No relation was found between oocyte weight and body weight. The GSI threshold above which the oocyte weight did no longer increase significantly was estimated from the few data available at about 2.5% (Figure 40-6) and the mean oocyte weight was 12.83 mg (± 1.15 SD, N= 5).

Plate 19. *Trematocranus placodon* (by Dave Voorvelt).

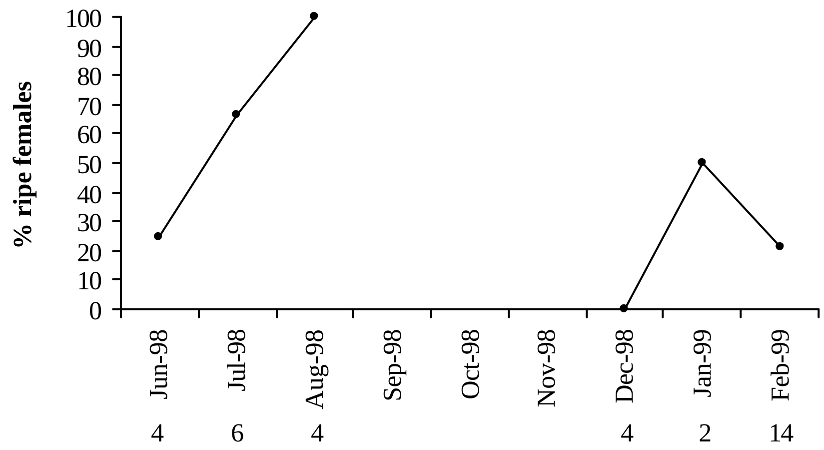

Figure 40-2. Seasonal progression of the percentage of ripe (stages 4 and 5) females *Trematocranus placodon* in the SWA The values below the x-axis are the effective for each month.

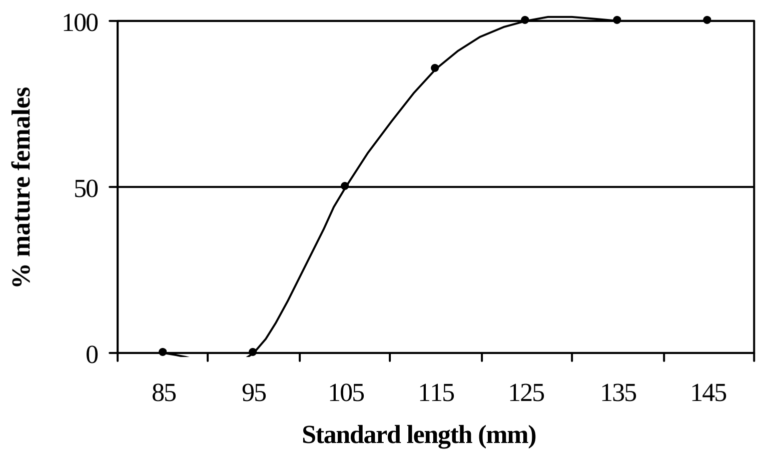

Figure 40-3. Percentage of mature females (stage 3 and above) per size class (standard length) for *Trematocranus placodon* in the SWA.

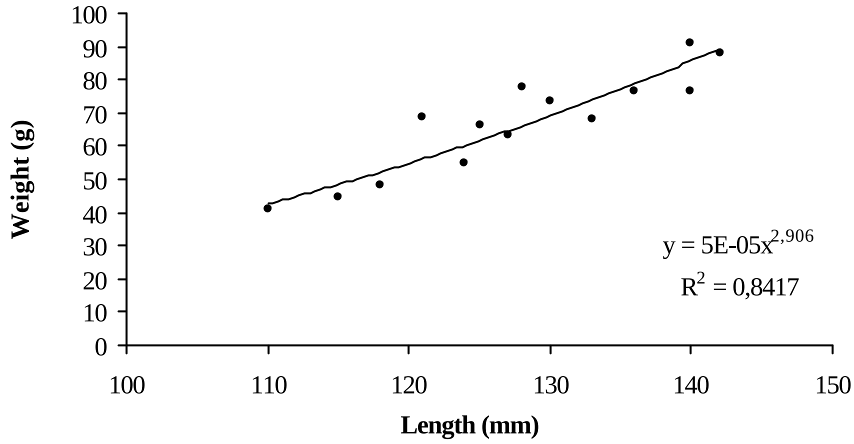

Figure 40-4. Length-weight relationship for *Trematocranus placodon* females in the SWA. (R^2 = determination coefficient).

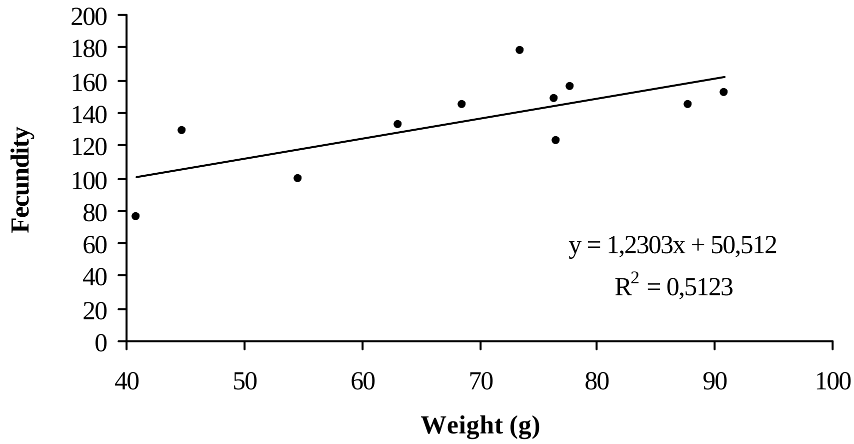

Figure 40-5. Fecundity-weight relationship for *Trematocranus placodon* females in the SWA. (R^2 = determination coefficient).

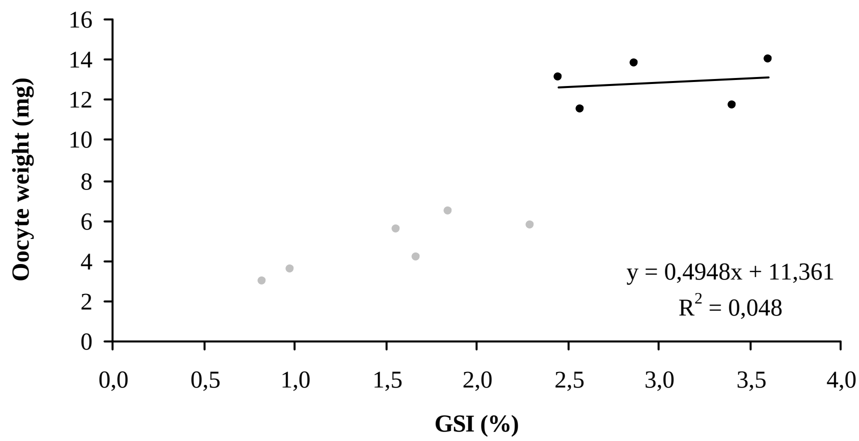

Figure 40-6. Relationship between oocyte weight and gonado-somatic index (GSI) for *Trematocranus placodon*. Oocytes from females whose GSI was below (in grey) and above (in black with regression) 3%. (R^2 = determination coefficient).

Table 41. Peak of breeding activity of species per depth category. X = data supported by good sample size, x = data supported by low sample size. "Intermediate" means common in both deep and shallow zone.

Depth category	Species	1998 Jun	1998 Jul	1998 Aug	1998 Oct	1998 Nov	1998 Dec	1999 Jan	1999 Feb	1999 Mar	1999 Apr	1999 May
Deep water (75-125m)	*A. 'geoffreyi'*	X	X	X								X
	A. macrocleithrum	***x***	X	X								x
	A. mentale					X		X	X			
	A. pectinatum							X	X			
	Au. minutus	X							X			
	D. apogon			X				X	X	X		
	D. macrops								X	X	X	
	P. tokolosh						X	X	X			
	L. 'deep water altus'	X							X	X	X	X
	L. gossei							X	X	X	X	
	L. 'oliveri'								X	X	X	
	L. polli											X
	Pl. 'platyrhynchos'			x				X	X	X	X	X
Intermed-iate	*D. limnothrissa*	X									X	X
	C. quadrimaculatus			x								
	C. virginalis	X	X									X
	L. longimanus			x								
	Sc. ahli				X	X						
	Sc. Benthicola			X			X					
Shallow water (10-50m)	*Au. 'blue orange'*			X	X		X					
	L. argenteus			X			X	X	X			
	M. anaphyrmus	X								X	X	X
	N. 'argyrosoma'						X			X		
	Pl. 'long'											x
	T. furcicauda		x									
	T. praeorbitalis			x								
	Tr. brevirostris									X	X	

Discussion

Depth distribution and mean CPUE for the major species were compared with those found by Tómasson & Banda (1996) in the SWA. Several of the species we regularly caught were absent of Tómasson & Banda (1996) survey of the SWA, and the other way round. This is likely due to identification differences between the two studies, some species being either lumped together under their generic names or accurately identified. Also, the smaller area covered might explain the absence of some species in our survey. However, global trends in CPUE were similar for both studies and the observed differences may lies in the fact that Tómasson & Banda covered the entire SWA whereas our work focused on the northern part of it.

Breeding species were found throughout the year at any depth. Some species were capable of breeding throughout the year (as already reported by Marsh et al. 1986, Lewis & Tweddle 1990, Thompson et al. 1996) with marked seasonal variations in the proportions of ripe individuals, whereas others appeared to have distinct breeding season (as the *Oreochromis spp*., Lowe-McConnell 1987 or members of the *Utaka* group, Iles 1960, 1971, Jackson et al. 1963), generally over 6 months long. Again, these patterns were independent from the depth distribution of the species. An interesting hypothesis linking the length of the breeding season to the fecundity of the species was proposed by Marsh et al. (1986): the lower the fecundity the longer the breeding season. If this hypothesis seemed to fit for the *mbuna*, it does however not hold for the demersal cichlids. Indeed, species such as *Lethrinops argenteus*, or *L. oliveri*, which had continuous breeding season also presented amongst the highest relative fecundity (2162 eggs.kg^{-1}, 4931 eggs.kg^{-1}, respectively) whereas species such as *Diplotaxodon apogon* with definite breeding season had amongst the lowest relative fecundity (632 eggs.kg^{-1}). Apart from a single species, *Copadichromis virginalis*, whose peaks of breeding activity were clearly related to plankton abundance, the breeding cycle of the other species was not directly related to any of the monitored environmental factors (temperature, oxygen concentration, photoperiod, algal abundance, conductivity). No particular breeding distribution pattern was found among the several species studied, when they were grouped per trophic category, per genera or per depth category. Even when focusing on the peaks of breeding activity per depth category (Table 41), no marked structure appeared. The peaks of breeding activity were evenly distributed over the year for the shallow water species. The only slight remarkable trend was that the highest concentration of breeding peaks occurred from January to May for the deep water species whereas no peak was recorded from January to March for the species with "intermediate" depth distribution. The period from December to April is the time of the year when the lake is most strongly stratified, the thermocline being around 40-50 m (Eccles 1974, see Figure 11 previous chapter). It also corresponds to the period of lowest phytoplankton and zooplankton abundance (Irvine 1995). However, most of the studied species are supposed to be benthic invertebrates feeders and the observed breeding patterns might be related to the relative abundance of their main food sources, as seems to be the rule for *mbuna* (Marsh et al. 1986). The seasonal progression of benthic invertebrate abundance and biomass, which is currently under study in the European Union Project: "The trophic ecology of the demersal fish community of Lake Malawi/Niasa", might shed a new light on the determinism of the observed breeding patterns. On the other hand, the reason for this apparent time sharing could lie in Fryer & Iles (1972) hypothesis of self-controlled population densities (population homeostasis) achieved through sharing of spawning territories. Lowe-McConnell (1979) also suggested that for tropical fishes asynchronous breeding could be a good way of maximising resource use for species with similar requirements. However, given the good correspondence between food availability and

Table 42. Ratio of length at maturity (L_{50}) to maximum observed length (MOL) for several cichlids species caught by trawling in the South West Arm of Lake Malawi between June 1998 and May 1999. The lengths are standard lengths. In italic are values for which determination of L_{50} was uncertain owing to low effective.

Species	MOL (mm)	L_{50} (mm)	Ratio
A. 'geoffreyi'	165	90	0.55
A. macrocleithrum	*148*	*100*	*0.68*
A. mentale	245	160	0.65
A. pectinatum	140	70	0.5
Au. 'blue orange'	78	48	0.62
Au. 'cf macrochir'	*134*	*100*	*0.75*
Au. 'minutus'	72	42	0.58
Au. 'rostratum deep'	140	75	0.54
B. lepturus	326	160	0.49
B. nototaenia	*300*	*115*	*0.38*
C. quadrimaculatus	*150*	*100*	*0.67*
C. virginalis	123	75	0.61
D. apogon	130	88	0.68
D. argenteus	206	140	0.68
D. limnothrissa	175	105	0.6
D. macrops	135	98	0.73
P. tokolosh	213	135	0.63
L. argenteus	165	108	0.65
L. 'deep water albus'	160	82	0.51
L. 'deep water altus'	130	60	0.46
L. gossei	170	92	0.54
L. longimanus	*147*	*107*	*0.73*
L. 'oliveri'	98	60	0.61
L. polli	120	65	0.54
M. anaphyrmus	164	105	0.64
N. 'argyrosoma'	97	57	0.59
Pl. 'platyrhynchos'	*115*	*80*	*0.69*
Ps. livingstonii	63	37	0.59
Sc. benthicola	168	100	0.60
St. 'guttatus'	147	100	0.68
T. furcicauda	178	130	0.73
T. praeorbitalis	199	130	0.65
Tr. brevirostris	85	50	0.59
Tr. placodon	160	105	0.66

breeding patterns for rock-dwelling species and *C. virginalis*, this is likely to be also the case for demersal species. For every species, more males than females in breeding condition were caught at any time of the year. This was also observed by Lewis & Tweddle (1990) on the three studied *Lethrinops spp*. Although not demonstrated for every species, the general trend of Malawi cichlids males to form breeding aggregations is likely to account for this difference, breeding males being more vulnerable to trawling when they form leks (Fryer 1972, 1984).

Among the species for which we determined the size at maturity, a few had already been studied: *Diplotaxodon limnothrissa* (Thompson et al. 1996), *Lethrinops gossei* (Lewis & Tweddle (1990), *Mylochromis anaphyrmus* (Tweddle & Turner 1977). The size at maturity we got for *L. gossei* and *M. anaphyrmus* were much smaller than those reported by Lewis & Tweddle and Tweddle & Turner. Size at maturity may vary among successive years for a same population under environmental variation (Duponchelle & Panfili 1998), or over longer time periods under fishing pressure (Stewart 1988, Lowe-McConnell 1982, Trewavas 1983). The observed differences in size at maturity could thus lie in the distant time period and geographical area between the studies. However, the method they both used overestimated the L_{50}. The average size at first maturation (L_{50}) is defined as the length at which 50% of the females are mature during the breeding season. Tweddle & Turner and Lewis & Tweddle considered the "length at the percentage point which is one-half of the maximum percentage of mature fish found in any length group", that is the highest point on the sigmoid curve. But as they considered in fact ripe fish as being mature, and that there is always only a fraction of the population in a "ripe" state, they consistently overestimated the L_{50}. That's the reason why their sigmoid never reached 100%. Iles (1971) stated that the ratio of length at maturity to asymptotic length for cichlids was characteristically a little above 0.7. The ratios found by Tweddle & Turner (1977) tended to confirm that mean value. However, as they overestimated the L_{50}, the ratios they found were also overestimated. In our study, the asymptotic length was not calculated for all the species (see Chapter "Growth"), thus the maximum observed length, considered to be close to the asymptotic length, was used to calculate the ratio (Table 42). Ratios ranged between 0.38 and 0.75 with an averaged value of 0.61. As the L_{50} for some species were probably overestimated due to low sample size (in italic in Table 42) and considering that the maximum observed length is usually smaller than the theoretic asymptotic length, the average ratio is likely to be a little below 0.6. In the case of *Lethrinops 'deep water altus'*, the ratio value of 0.46 might have been underestimated. Indeed, this low value might lie in misidentification of the largest specimens (up to 130 mm), as Turner (1996) reported a maximum size of 10 cm TL for this species. It is interesting to note that some genera present ratio values that tend to be close to 0.7 (e.g. *Diplotaxodon spp*., *Copadichromis spp*.) whereas others show values closer to 0.5 such as the *Buccochromis* and *Lethrinops spp*..

Despite the importance of this population parameter in fisheries management, age at maturity had only been estimated on a few species so far: *Lethrinops longipinnis*, *L. parvidens*, *Mylochromis* ("*Haplochromis*") *anaphyrmus*, *Copadichromis* ("*Haplochromis*") *mloto* (Tweddle & Turner 1977). These species were believed to reach maturity at the end of their third year except *C. mloto*, which matured at the end of its second year. *M. anaphyrmus* was the only common species between Tweddle & Turner study and ours. We found *M. anaphyrmus* was reaching maturity early in its second year at 18 months old. The growth parameters determined by Tweddle & Turner (1977), K=0.671 and $L\infty$=196 mm TL, being very similar to ours: K=0.62 and $L\infty$=180 mm SL (see Chapter "Growth"), the two fold difference in age at maturity observed between the two studies (which took place in the same area) lies mainly in the overestimation of size at maturity by the method used in Tweddle & Turner (1977). Assuming the same mean size at maturity of 160 mm TL (about 130 mm SL in our case), they would mature early in their third year (25 months) as well. It is very likely that this overestimation of age and size at maturity hold as well for the others species they studied. Growth and age at maturity were also estimated for *C.* ("*Haplochromis*") *virginalis* and *C.* ("*Haplochromis*") *quadrimaculatus* by Iles (1971). They were both reaching maturity at three years old whereas we found they matured in their first and second year at 12 and 20 months for *C. virginalis* and *C. quadrimaculatus*, respectively. Despite slight differences in growth parameters, the differences between the two sets of estimations lies in the fact that determination of the size at maturity was based on ripe females in Iles's study (Iles 1971, Jackson et al. 1963), which leads to an overestimation of L_{50}. Indeed, the size at maturity they determined represented 88 and 84 % of the maximum theoretical length (asymptotic length) for *C. virginalis* and *C. quadrimaculatus*, respectively. It is assumed that in unexploited stocks, which is certainly not the case for members of the Utaka group, the oldest fish reach only about 95% of their asymptotic length (review in Pauly 1980). This means that in Iles's case, they would breed for the first time close to their maximum size, which only few fish reach. Also, assuming the mean maturity length ratio Iles (1971) considered as the rule for cichlids (0.7), age at maturity would have been 1.6 and 2.0 years old for its populations of *C. virginalis* and *C. quadrimaculatus*, respectively, which would place them in the range of age at maturity we observed. The 22 species for which we determined A_{50} reached maturity before the end of their second year or during their first year for the smallest species (*Au. 'Blue orange'*, *Au. 'minutus'*, *N. 'argyrosoma'*…). It is more conceivable that highly exploited species with such low fecundity as the Lake Malawi cichlids, mature early in their life (around one year old) rather than in the last part of their lives (more than three years old). Indeed, very few species grew older than four years (see Chapter "Growth", see also the abacus of longevity versus mean maximum length drawn out of 111 species of African freshwater fishes by de Merona 1983). Next, as only a very small fraction of a fish population reach the asymptotic length, which is usually slightly higher than the maximum observed length, this means that very few fish indeed would reach maturity and would therefore reproduce to ensure the replenishment of populations or the species survival. This clearly appears when looking at the proportion of fish reaching the size at maturity on the length frequency distributions presented in Iles (1971). Species with such a life history strategy would have unlikely survive about thirty years of intense exploitation by fisheries, which systematically remove the large specimens of fish populations (Turner 1977b, Turner 1995, Turner et al. 1995).

It is a well known characteristic of Lake Malawi cichlids, they usually produce few but large eggs (see for review Fryer & Iles 1972, Konings 1995, Turner 1996). The forty species studied perfectly fitted into this trend. However, as already mentioned above, distinct reproductive strategies are distinguished among species and genera: species of the *Diplotaxodon* clade (sensu Turner et al. 1999) and *Rhamphochromis spp*. (pers. obs.) clearly presented the lowest relative fecundities and the largest eggs of all species. Although in a lesser extent, *C. quadrimaculatus* also presented low fecundity and large eggs. On the other hand, for a same body weight *Lethrinops*, *Alticorpus* or *Mylochromis* species produced much smaller but more numerous eggs. It appears that the species having a more pelagic life style such as the *Diplotaxodon spp.*, *Rhamphochromis spp*. (Allison et al. 1996, Thompson et al. 1995, 1996, Turner et al. 1999), or *C. quadrimaculatus* (Allison et al. 1996, Thompson et al. 1995, 1996) are characterised by reduced fecundity, very large eggs and delayed maturity (*Diplotaxodon* and *Copadichromis spp*. had the highest Lmax to L_{50} ratios). This reproductive strategy, which enable females to moothbrood young to very large sizes (observed for *D. limnothrissa* Turner 1994a, 1996, this study), is likely to be an adaptation to the pelagic environment. Egg size is an essential parameter of fish reproductive strategy for it conditions the ability to use a large array of food sources, to avoid predators and to survive unfavourable

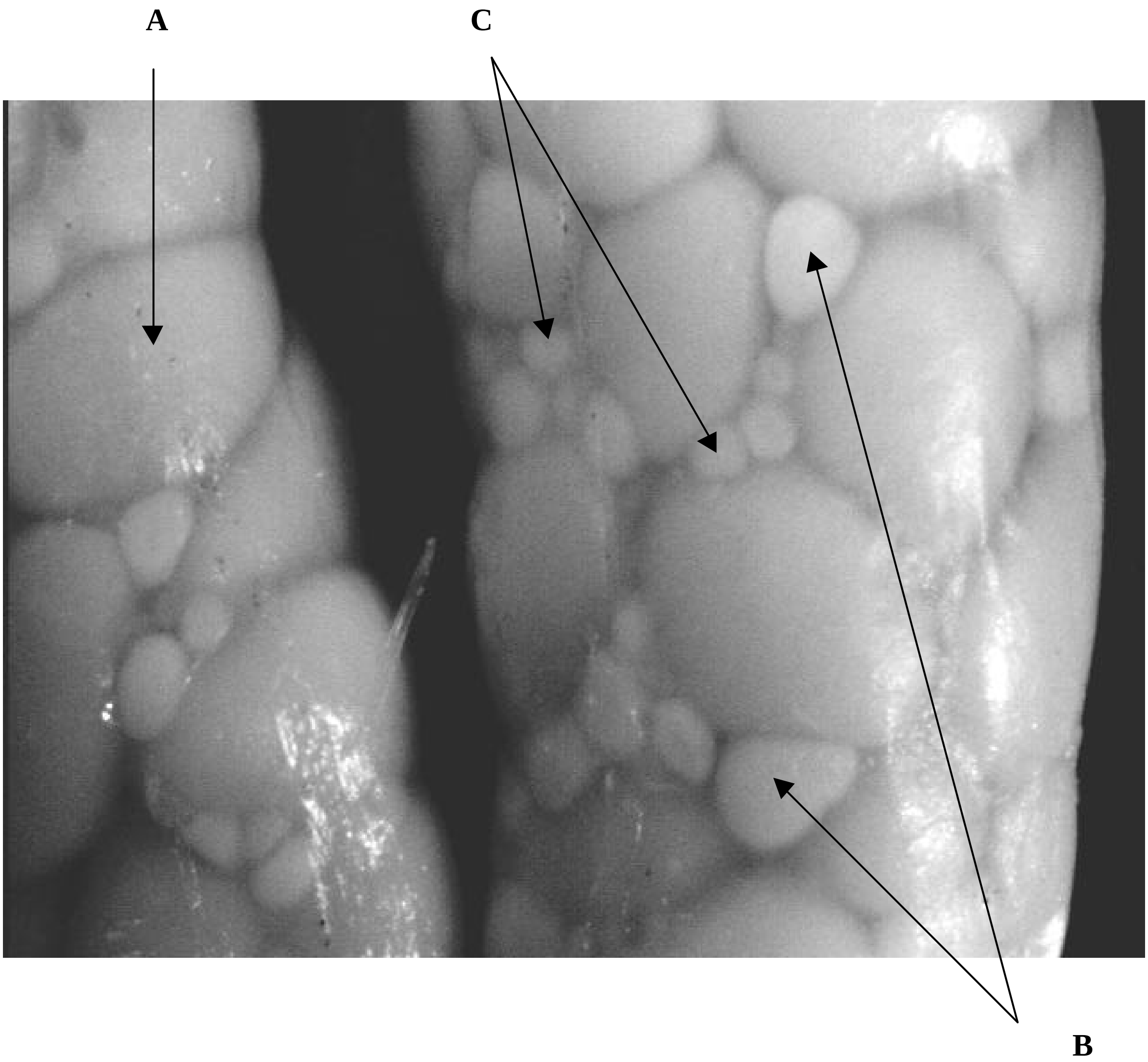

Plate 20. Gonad of a ripe Lethrinops longimanus female with at least three batches of oocytes. A = oocytes in late vitellogenesis that will be laid at the next spawn. B = second batch of developing vitellogenic oocytes (characteristic of a stage 3). C = third batch of oocytes in early development (characteristic of a stage 2).

environmental conditions (Bagenal 1969, 1978, Ware 1977, Mann & Mills 1979, Reznick, 1982, Marsh 1986, Sargent et al. 1987, Wootton 1990, Cambray & Bruton 1994, Wootton 1994). An inverse relationship links the egg size and the fecundity in most fish species (Mann & Mills 1979, Albaret 1982, Stearns 1983, Duarte & Alcaraz 1989, Elgar 1990) and in cichlids particularly (Peters 1963, De Silva 1986, Legendre & Ecoutin 1989, 1996, Duponchelle et al. 2000, this study). According to the energetic cost of gamete production, food is probably one of the most important environmental factors involved in the regulation of fecundity (Wooton & Evans 1976, Wooton 1979). Therefore, food availability being relatively poor in the pelagic zone, a logical strategy to improve both parents and offspring's fitness is to produce fewer eggs but of larger size and to moothbrood young to large size to enhance their survival. Indeed, the larger the fry when released by the female the more effective they will be in utilising the scarce food resources of the open waters. If this hypothesis is true, the cichlid reproductive strategy to adapt to pelagic environment would differ markedly from the strategy of most other pelagic fish families, which generally produce large numbers of small eggs (reviews by Duarte & Alcaraz 1989, Elgar 1990), including the freshwater pelagic cyprinids *Engraulicypris sardella* in Lake Malawi (Jackson et al. 1963) and *Rastrineobola argentea* in Lake Victoria (review in Witte & van Densen 1995), or the clupeids *Stolothrissa tanganicae* and *Limnothrissa miodon* in Lake Tanganyika (reviews by Coulter 1991, Marshall 1993, and Patterson & Makin 1998).

As pointed out by Fryer & Iles (1972), to know how many eggs each female produces at each brood is important but how many times a year that number is produced is even more essential for fisheries management. Determining the number of times a female can spawn during a breeding season is a difficult task in natural environments, particularly for the demersal Malawi cichlids. Cichlids are known world-wide for their capacity to have multiple spawning events during the same breeding season when environmental conditions are favourable (Lowe 1955, Trewavas 1983 for review, James & Bruton 1992). However, based on the observation of only one batch of eggs at a time in ovaries of ripe female cichlids in Lake Malawi, it was assumed that a same female was able to spawn only once per breeding season (Lowe 1955, Iles 1971, Tweddle and Turner 1977). Having analysed tens of thousands demersal cichlids pertaining to at least 170 species (Appendix 1) during the course of this study, three sets of evidence have emerged to suggest that annual multiple spawning is likely. The evidence is presented below:

(1) - For most of the studied species it was observed but not recorded that more than one batch of eggs were in the ovaries of ripe females. An example is given on Plate 20, which presents the ovaries of a ripe *Lethrinops longimanus* female. A minimum of three batches of developing oocytes are clearly visible: the batch that will be released soon (A), a second batch that already undertook vitellogenesis (B), and a third one of smaller oocytes in early development (C). To verify the observation, and taking the opportunity of a fishing cruise with the RV Ndunduma in the SWA in July 1999, a special survey was organised in order to check the existence of more than one batch of oocyte in cichlids ripe gonads. All the females found with ripe gonads had two and sometimes three batches of oocytes. The sample included the following species: *Alticorpus 'geoffreyi'*, *A. macrocleithrum*, *A. mentale*, *A. pectinatum*, *Aulonocara 'blue orange'*, *Copadichromis virginalis*, *Diplotaxodon greenwoodi*, *Hemitaeniochromis insignis*, *Lethrinops longimanus*, *L. gossei*, *L. 'oliveri'*, *L. polli*, *Mylochromis anaphyrmus*, *Otopharynx speciosus*, *O. brooksi* and *Sciaenochromis 'guttatus'*.

(2) - The gonad maturity stage 6-3 (see Material and methods) was frequently observed for all the studied species. This stage is characteristic of post-spawning females initiating another cycle of vitellogenesis.

(3) - Moothbrooding females of many species were often found with developing ovaries (stages 6-3 or 3).

These three sets of evidence strongly suggest that each female probably spawns more than once during the breeding season, for haplochromine cichlids at least. Indeed, it would be very poor energetic strategy for a female to initiate another vitellogenesis cycle if the developed oocytes were not to be laid. In such a stable environment as Lake Malawi, it is very unlikely that environmental conditions become so unfavourable that a female would resorb her eggs during the few weeks needed to complete a vetillogenesis cycle (four to five weeks in cichlids, Fishelson 1966, Gauthier et al. 1996, Tacon et al. 1996). Furthermore, although extensive breeding season does not mean that individual fish breed continuously, most of the studied species have breeding seasons lasting more than six months, and several showed continuous breeding seasons. It appears very reasonable in these conditions that individual fish, known to breed repeatedly in aquarium, may then reproduce more than once, as do cichlids everywhere else (reviews by Fryer & Iles 1972, Trewavas 1983, Lowe-McConnell 1987).

Although this study presents the most comprehensive work on Lake Malawi cichlids life histories, it is based on a one year survey only. As inter annual variability of reproductive characteristics can be important in African cichlids (Duponchelle & Panfili 1998, Duponchelle et al. 1999, 2000), the described breeding patterns might not represent a permanent situation but rather a situation representative of the prevalent environmental conditions. However, Lake Malawi is a stable environment where important environmental perturbations are unlikely. The likeliest unexpected fluctuations are in resource availability, which might modify the intensity of breeding activity rather than its periodicity (Duponchelle et al. 1999). Furthermore, the breeding season observed for *C.* ("*Haplochromis*") *virginalis* and *C.* ("*Haplochromis*") *quadrimaculatus* were the same over a period of five years (Iles 1971) and Lewis & Tweddle (1990) reported very similar trends in breeding seasonality among the three years of their study, which suggested little or no inter annual variability of breeding patterns.