Chapter 3: Growth patterns of some of the most important demersal fish species caught by trawling in the South West Arm of Lake Malawi

F. Duponchelle, A.J. Ribbink, A. Msukwa, J. Mafuka & D. Mandere

Introduction

Several methods exist to assess fish growth parameters, such as analysis of periodic marks on opercular bones, scales, vertebrae or otoliths, individual tagging or analysis of length frequency distributions (review by Casselman 1987, de Merona et al. 1988, Wootton 1990, King 1995). Among these methods, analysis of the modal progression of length frequency distributions (Ricker 1975) has been commonly used for African freshwater fishes despite its potential biases in tropical conditions, where lack of seasonality, long spawning periods, non-year events giving rise to variations in growth and survival rates (hence to age and size modes) may lead to erroneously interpret size modes as differing in age by units of year. Indeed, tropical species often have extended breeding seasons during which multiple broods are produced and several cohorts (a cohort is a group of fish born at the same time) are likely to be encountered. In these conditions following year classes is often difficult and hamper precise interpretation of length progression series (Fryer & Iles 1972, Casselman 1987, Lowe-McConnell 1987, de Merona et al. 1988, King 1995). As just seen in the previous chapter, most of the studied species have extended breeding seasons. However, when reasonably accurate information on the species biology is available, such as the breeding season and the maximum length, it is still possible to obtain correct estimates of growth using modal length progression analysis. For most of the species studied below, more than one cohort per year was identifiable and different sets of K and L_∞ provided reasonable fit of the length frequency distributions. In every case, we retained the set of parameters that best corresponded with the breeding patterns observed for the species (ie. which estimated date of birth best corresponded with breeding peaks) and that best described the distributions (ie. which went through the largest number of large modes). Also, as an extensive sampling was done monthly over a complete annual cycle, always on the same sites, it was assumed that for most species the maximum observed length was close to the asymptotic length (L_∞), which participated in selecting the best set of parameters. This was particularly true for the small abundant species, for which we fixed $L\infty$ within a few millimetres from the maximum observed length. This process also permitted to diminish the tendency of ELEFAN method to underestimate K and overestimate $L\infty$ (Moreau et al. 1995).

Despite the 35 mm cod end mesh size, the length frequency distributions were influenced either by the trawl selectivity or the absence of the juveniles from trawled areas. Indeed; juveniles of species were seldom caught before 50 mm and were usually accessible to the trawl gear between 60 and 90 mm depending on species and shapes. Consequently, adults were better represented in the catches than juveniles and length frequency distributions below the size of full selection were not adequate for mortality estimates. Whenever one or more suitable distributions were available, mortality estimates were based only on them. But in most of the cases, they were based on all the distributions. This must be kept in mind even

though mortality estimates often appeared reasonable. FiSAT allows correction of the bias due to fishing gear's selectivity, which often leads to a better estimation of the growth parameters (Moreau et al. 1995, Gayanilo et al. 1996). This correction was tried for every species and never lead to better estimations (according to the "goodness of fit" index of the ELEFAN routine, see Gayanilo & Pauly 1997). The weight given to small length systematically flattened out the rest of the distribution and the resulting fits were bad. All the estimations were therefore based on non corrected data. However, for every species except the small ones for which it was not necessary, the smoothing of the data by calculating the running averages over three length bins (5 mm for most of the species and 10 mm for large and not abundant species) helped to track the progression of modes.
All the lengths are standard lengths.

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 following equation was used to convert total lengths (TL) from literature into standard length (SL):

$$SL = 0.785\ TL + 3.477 \quad (1)$$

This equation was calculated from Table G1.

Table G1. Growth estimates (mm in TL) of Lake Malawi cichlids species given by Iles (1971) and Tweddle & Turner (1977) and the same growth estimates expressed in SL by de Merona et al. (1988).

Species	L∞ (TL)	K	References	L∞ (SL)	References
H. anaphyrmus	196	0,671	Tweddle & Turner (1977)	157	De Merona et al. (1988)
H. intermedius	229	0,571	Tweddle & Turner (1977)	184	De Merona et al. (1988)
H. virginalis	121	0,778	Iles (1971)	99	De Merona et al. (1988)
H. quadrimaculatus	190	0,65	Iles (1971)	153	De Merona et al. (1988)
H. pleurostigmoides	144	0,764	Iles (1971)	116	De Merona et al. (1988)
L. parvidens	208	0,487	Tweddle & Turner (1977)	166	De Merona et al. (1988)
L. longipinnis	202	0,571	Tweddle & Turner (1977)	162	De Merona et al. (1988)

Growth was estimated from the modal progressions of length frequency distributions of species at every sampled month. The growth parameters were calculated by the Von Bertalanffy Growth Curve (VBGC) equation (equation 2) fitted by the electronic length frequency analysis (ELEFAN) method (Pauly 1987) using the FAO-ICLARM Package FiSAT (Gayanilo et al. 1996, Gayanilo & Pauly 1997).

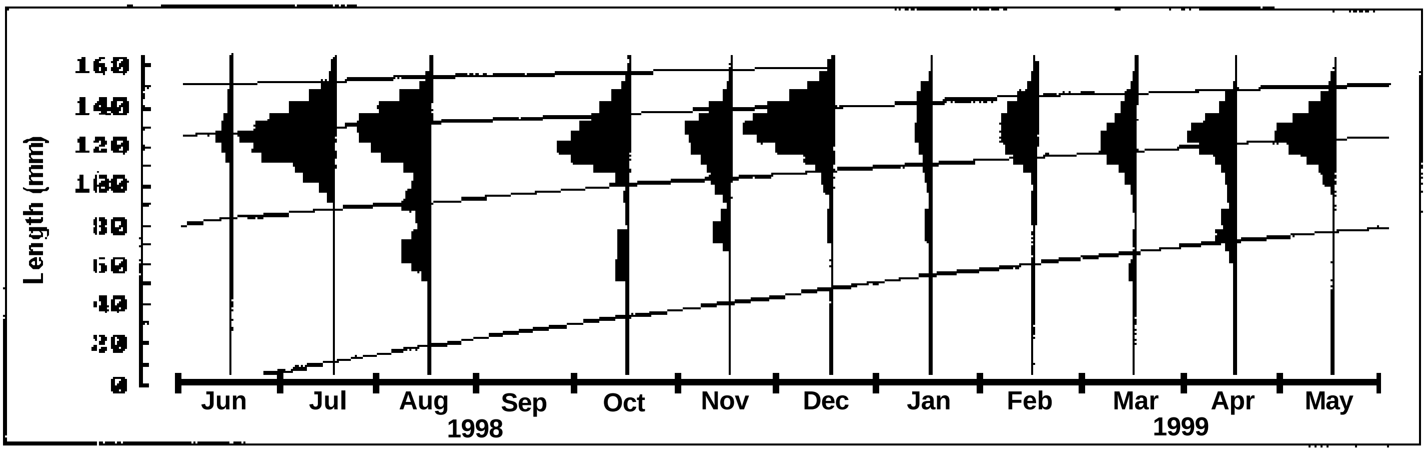
$$L_t = L_\infty (1-\exp(-K(t-t_0)) \quad (2)$$

Where L_t is the mean length at age t, L_∞ is the asymptotic length, K the growth coefficient and t_0 the size at age 0.

Among the several growth models available (VBGC, Richards, Gompertz, logistic, quadratic, exponential, ect. see Schnute 1981 for review), the VBGC model was retained for the following reasons: 1)- for African fish species the VBGC usually provides a good fit of the data (de Merona et al. 1988, Moreau et al. 1995). 2)- it proves useful for comparative purposes as it has been largely utilised for African freshwater species and cichlids particularly, for which synthesis are available (de Merona et al. 1983, 1988, Moreau et al. 1995). The ELEFAN method, used by Moreau et al. (1995) on 57 stocks of African freshwater species was also utilised in this study for comparative purposes.

Mortality estimates were obtained as described in Moreau et al. (1991) and Moreau & Nyakageni (1992) for Lake Tanganyika fishes. Total mortality (Z) was estimated by the method of the length-converted catch curves (LCC) (Pauly 1983). This method consists in pooling all the distributions while keeping their relative importance to obtain a single frequency distribution. This decreases part of the sampling biases. Total mortality is then calculated on the descending part of this single global distribution. But Z is determined in a given age/size range and the estimation makes sense only within this range. Natural mortality (M) was evaluated using Pauly's equation (Pauly 1980) based on $L\infty$, K and the mean annual environmental temperature of the species concerned. For each species, the mean annual temperature used for natural mortality estimates corresponds to the mean annual temperature at the depth to which the species was more abundant (see Chapter "Breeding and depth distribution"). Fishing mortality (F) was calculated as F = Z-M. All these methods were provided by the FiSAT package, including the estimation of the probability of capture.

The mean size at first capture by the trawl (Lc = length at which 50% of the fish entering the trawl are retained by the gear) was calculated for each species from the length-converted catch curves using FiSAT (Gayanilo & Pauly 1997).



FigureG1-1.Lengthfrequencyplotsfor *A.'geoffreyi'* intheSWAofLakeMalawi.

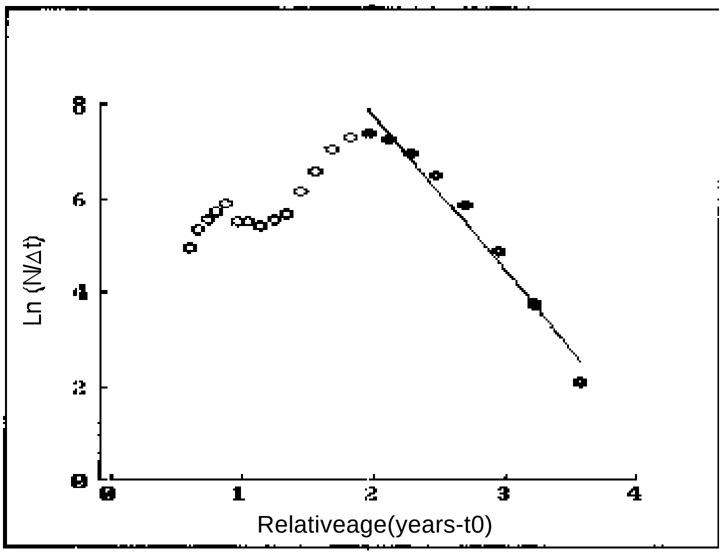
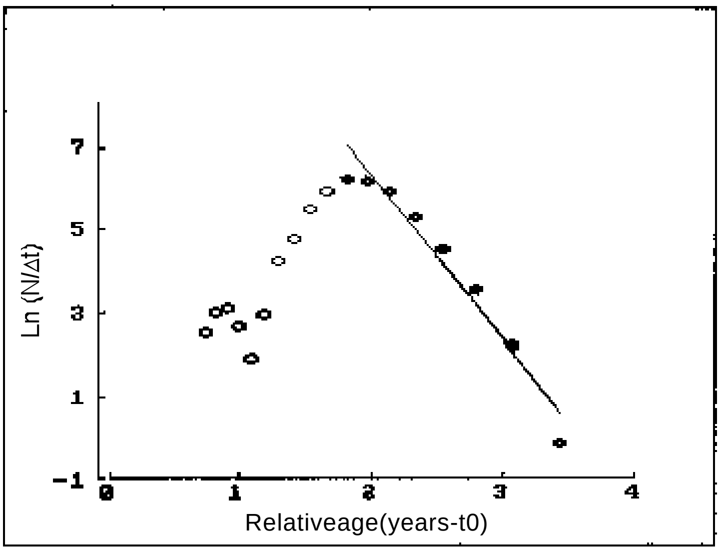
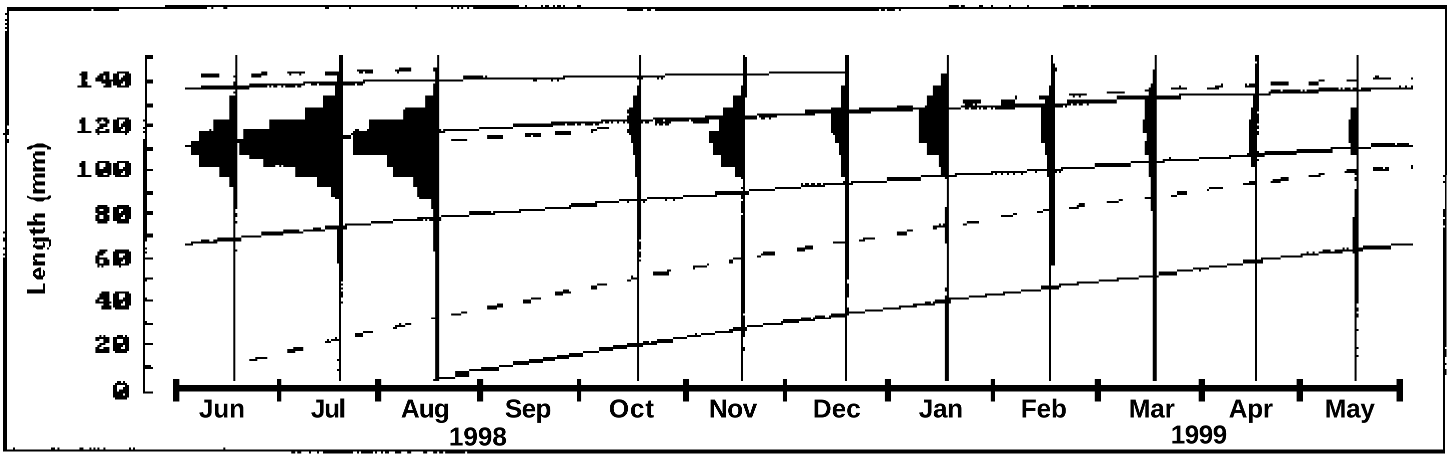


Figure G1-2. Length converted catch curve for *A. 'geoffreyi'*.



FigureG2-2.Lengthconvertedcatchcurvefor *A.macrocleithrum*.



FigureG2-1.Lengthfrequencyplotsfor *A.macrocleithrum* intheSWAofLakeMalawi.

Results

Alticorpus spp.

Alticorpus 'geoffreyi'

The length frequency distributions, based on 1721 fish are presented in Figure G1-1. Three year classes were identified by the model with L_∞=181 mm and K=0.6. The calculated date of birth (June) corresponded to the middle of the observed breeding peak.
Assuming a mean environmental temperature of 24°C and taking into account all the distributions, the mortality estimates were: Z=3.29, M=1.37 and F=1.92 for the age range showed in Figure G1-2. Given that the length frequency distributions were not adequate, it is likely that mortality was overestimated, particularly for a deep water species subjected to little if any exploitation in this part of the lake. The selectivity of the 35 mm cod end trawl net for this species was 120 mm.

Alticorpus macrocleithrum

A. macrocleithrum was not an abundant fish and only 437 specimens were measured over the sampling period. The length frequency distributions are presented in Figure G2-1. Two sets of growth estimates, correctly fitting the distributions and giving birth dates consistent with breeding observation were obtained: L_∞ = 166, K = 0.92 (dashed line) and L_∞ = 166, K = 0.6 (solid line). The calculated date of birth, May-June for the first set and July-August for the second corresponded to the middle of the observed breeding peak. Given the low number of individuals of the length frequency distributions, particularly in the small sizes (little peaks between 60 and 80 mm were all based on one or two fish only), it was difficult to decide for one or the other set of parameters.
Assuming a mean environmental temperature of 24°C corresponding to the depth distribution of *A. macrocleithrum* (75 to 125 m) and taking into account all the distributions, the mortality estimates were: Z=6.04, M=1.86 and F=4.18 with L_∞=166, K=0.92 and Z=3.94, M=1.40 and F=2.54 with L_∞=166, K=0.6. The mean size at first capture by the 35 mm cod end trawl net for this species was 106 mm with both sets of parameters. In both cases, mortality estimates were high partly because the shapes of distributions were not adapted to calculate mortality parameters. However, the second set of mortality estimates, though overestimated, appeared more realistic, particularly for a deep water species subjected to little if any exploitation. Furthermore, with K=0.92, fish would reach their maximum size and die at the end of their second year, which appears too fast for a fish of this size compared to others related species.

For these reasons, the set of parameters L_∞ = 166 and K = 0.6 was chosen for the calculation of age at maturity and mortality estimates (Z=3.94, M=1.40 and F=2.54 for the age range showed in Figure G2-2).

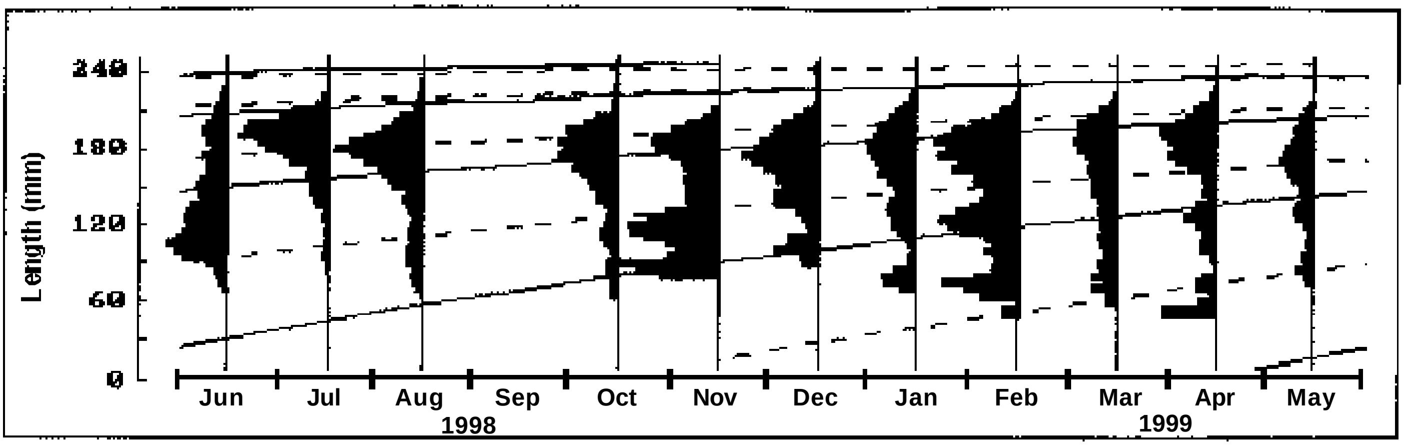


Figure G3-1. Length frequency plots for *A. mentale* in the SWA of Lake Malawi.

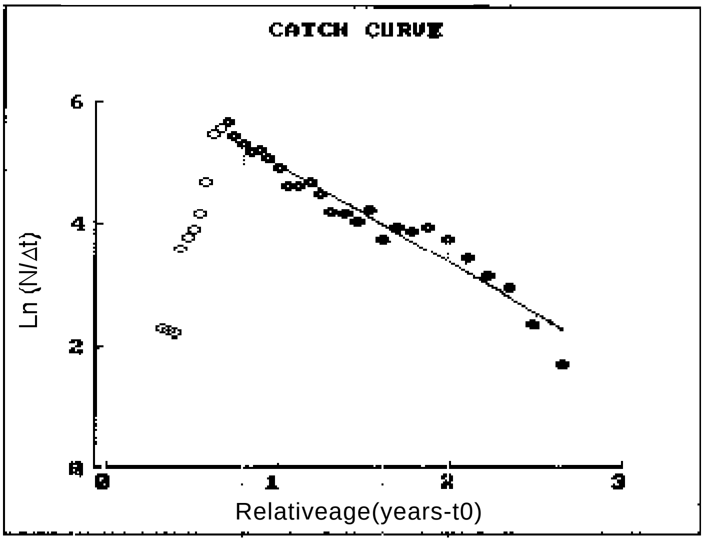


Figure G3-2. Length converted catch curve for *A. mentale*.

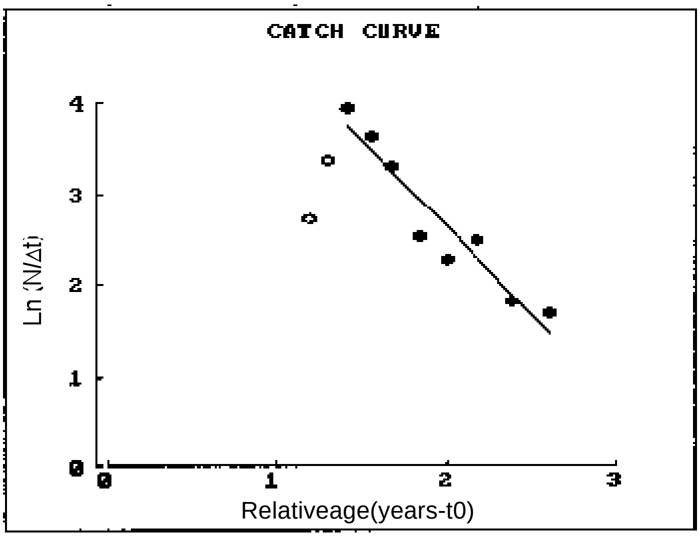


Figure G4-2. Length converted catch curve for *A. pectinatum*.

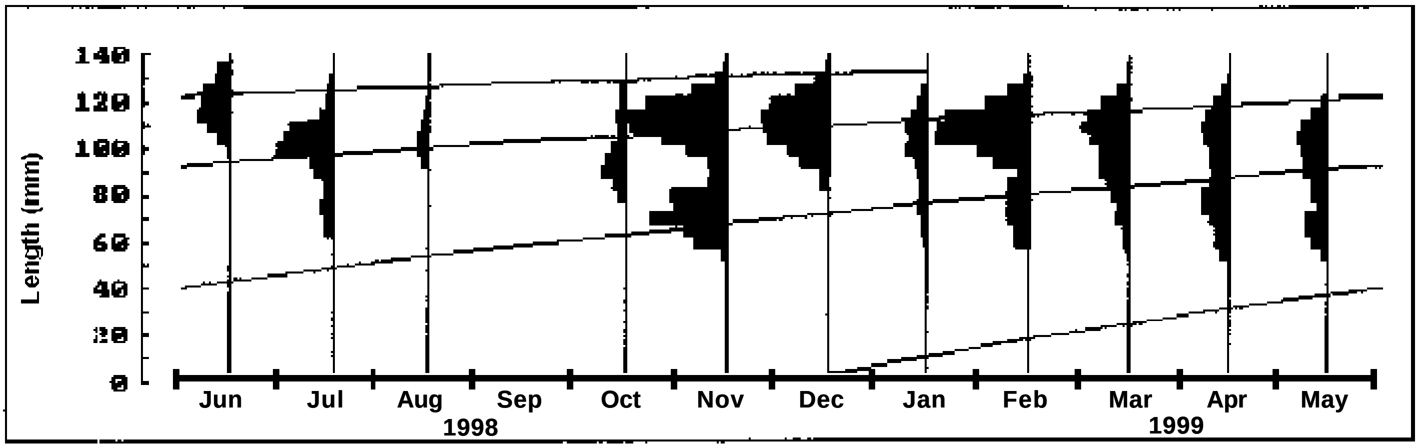


Figure G4-1. Length frequency plots for *A. pectinatum* in the SWA of Lake Malawi.

Alticorpus mentale

The length frequency distributions, based on 2150 fish are presented in Figure G3-1. Two year classes were identified by the software, with L_∞=266 mm and K=0.7 (solid line). The calculated date of birth, April corresponded with a period of intense breeding activity.

Assuming a mean environmental temperature of 24°C corresponding to the depth distribution of *A. mentale* (75 to 125 m) and considering only the June distribution, the mortality estimates were: Z=1.63, M=1.36 and F=0.27 for the age range showed in Figure G3-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 91 mm.

Another set of parameters provided a good fit of the distributions: $L\infty$=256 mm and K=0.68 (dashed line). The birth date, October-November also matched a period of intense breeding activity. However, the corresponding fit was going through a smaller number of large peaks than the first set of parameters, which was therefore considered better.

Alticorpus pectinatum

The length frequency distributions, based on 942 fish are presented in Figure G4-1. Three year classes were identified by the software with L_∞=160 mm and K=0.58. The calculated date of birth, December corresponded with a period of intense breeding activity.

Assuming a mean environmental temperature of 24°C corresponding to the depth distribution of *A. pectinatum* (75 to 125 m) and considering only the October distribution, the mortality estimates were: Z=1.90, M=1.39 and F=0.51 for the age range showed in Figure G4-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 84 mm.

Aulonocara spp.

Aulonocara 'blue orange'

The length frequency distributions, based on 7793 fish are presented in Figure G5-1. *Au. 'blue orange'* is a small species and juveniles were not caught by the net. Consequently a single year class was identified by the software with L_∞=80 mm and K=1.21. The calculated date of birth, December-January corresponded with a peak of breeding activity.

Assuming a mean environmental temperature of 26°C corresponding to the depth distribution of *Au. 'blue orange'* (10 to 30 m) and considering all the distributions, the mortality estimates were: Z=4.67, M=2.83 and F=1.84 for the age range showed in Figure G5-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 51 mm. Although *Au. 'blue orange'* is a short lived fast growing species with a high natural mortality (M), the estimated total mortality was probably overestimated owing to the shape of length distributions.

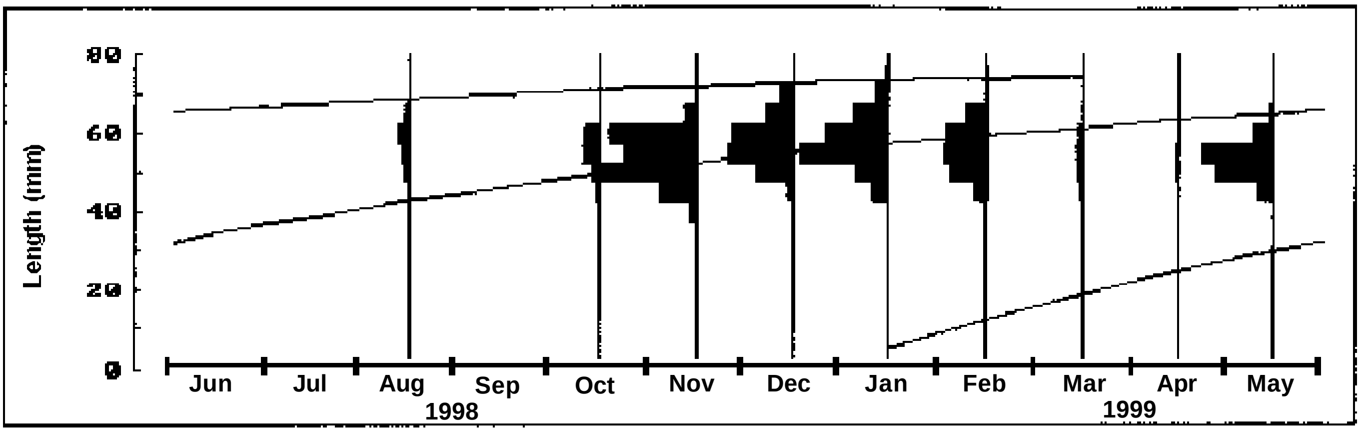
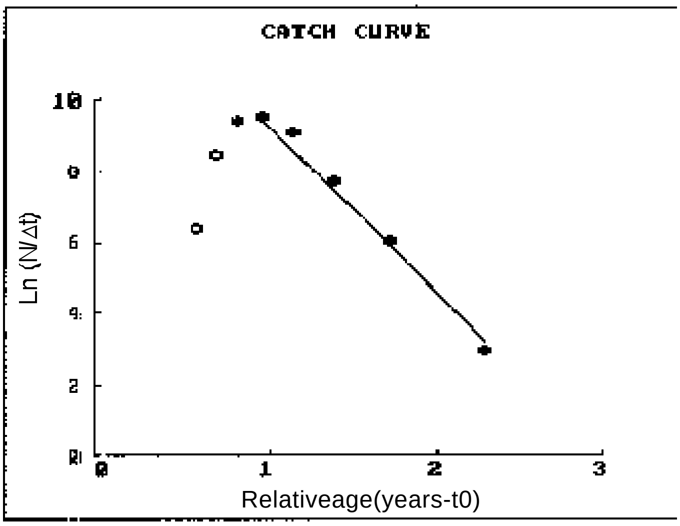


Figure G5-1.Lengthfrequencyplotsfor *Au.'blueorange'* intheSWAofLakeMalawi.



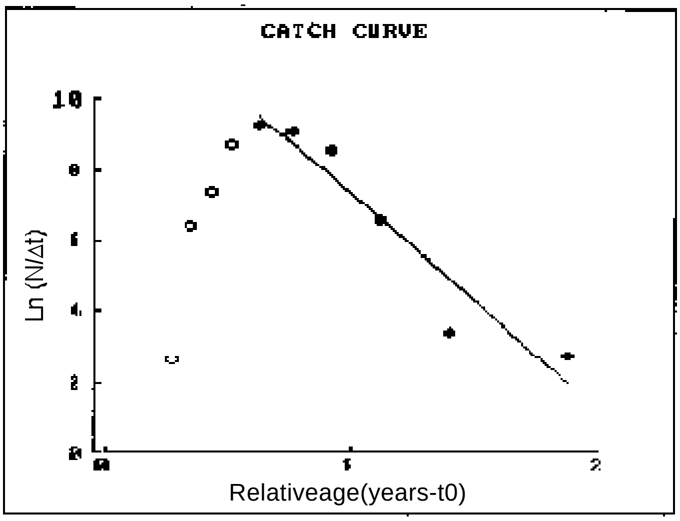


Figure G5-2. Length converted catch curve for *Au. 'blue orange'*. FigureG6-2.Lengthconvertedcatchcurvefor *Au.'minutus'*.

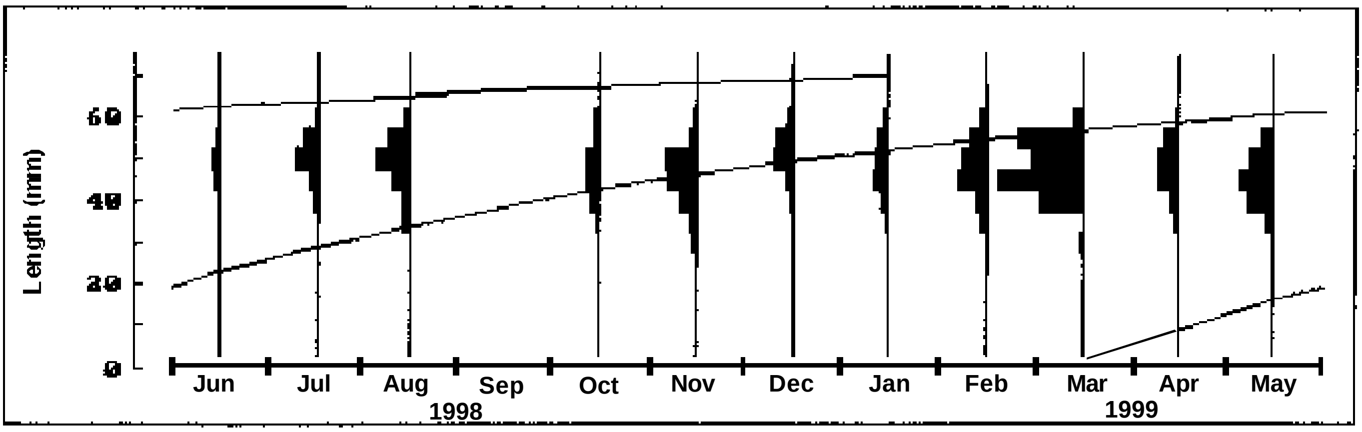


Figure G6-1.Lengthfrequencyplotsfor *Au.'minutus'* intheSWAofLakeMalawi.

Aulonocara 'minutus'

The length frequency distributions, based on 4539 fish are presented in Figure G6-1. *Au. 'minutus'* is also a small species and juveniles were not caught by the net. Consequently a single year class was identified by the software with L_∞=75 mm and K=1.44. The calculated date of birth, March corresponded with a period of intense breeding activity.
Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *Au. 'minutus'* (75 to 125 m) and considering all the distributions, the mortality estimates were: Z=6.07, M=3.08 and F=2.99 for the age range showed in Figure G6-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 41 mm. Although *Au. 'minutus'* is a short lived fast growing species with a high natural mortality rate (M), mortality estimates were probably overestimated owing to the shape of length distributions. Indeed, fishing mortality is likely to be close to zero in this deep part of the lake where almost no trawling activity takes place.

Copadichromis spp.

Copadichromis quadrimaculatus

C. quadrimaculatus was a relatively rare fish and only 631 specimens were measured over the sampling period. The length frequency distributions are presented in Figure G7-1. Despite the low sample size, a reasonably good growth estimation was obtained with L_∞=160 mm and K=0.58. The calculated date of birth, September corresponded with a period of breeding activity.
Assuming a mean environmental temperature of 25°C corresponding to the depth distribution of *C. quadrimaculatus* (10 to 75 m) and considering only the November and January distributions, the mortality estimates were: Z=1.95, M=1.41 and F=0.54 for the age range showed in Figure G7-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 59 mm.

Copadichromis virginalis

The length frequency distributions, based on 11982 fish are presented in Figure G8-1. Two year classes were identified by the software with L_∞=130 mm and K=0.84. The calculated date of birth, May corresponded to the middle of the main peak of breeding activity.
Assuming a mean environmental temperature of 25.5°C corresponding to the depth distribution of *C. virginalis* (10 to 50 m) and considering only the April distribution, the mortality estimates were: Z=3.55, M=1.93 and F=1.62 for the age range showed in Figure G8-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 72 mm.

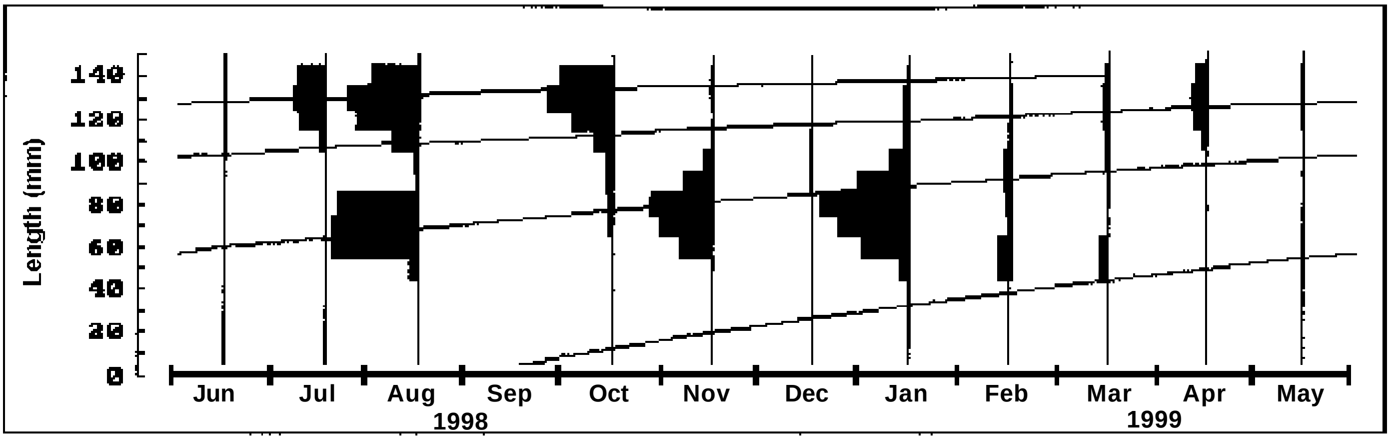
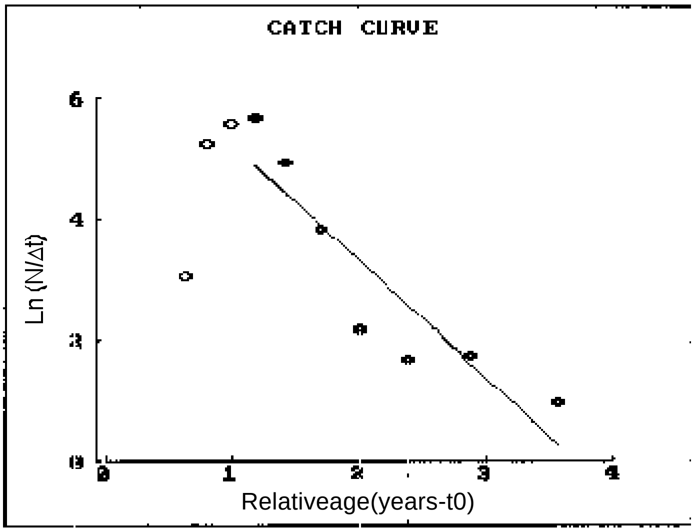


Figure G7-1. Length frequency plots for *C. quadrimaculatus* in the SWA of Lake Malawi.



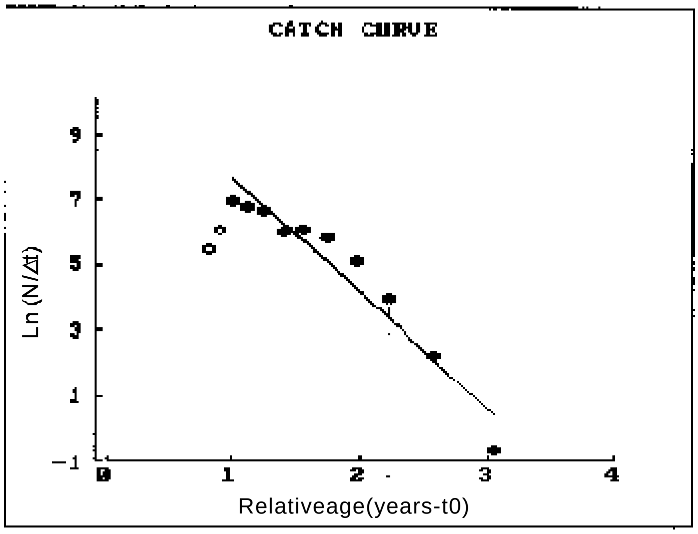


Figure G7-2. Length converted catch curve for *C. quadrimaculatus*.

Figure G8-2. Length converted catch curve for *C. virginalis*.

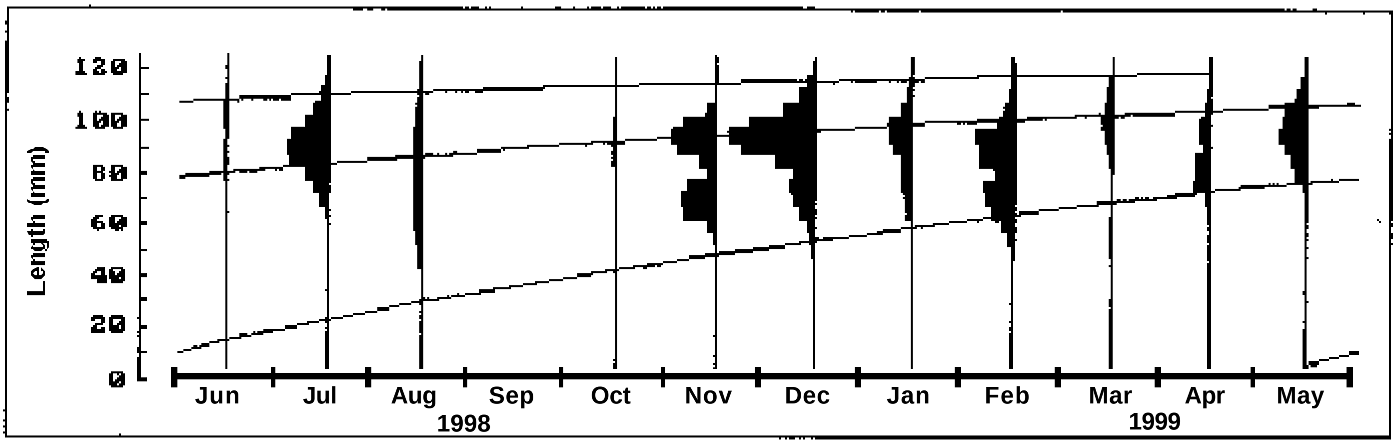


Figure G8-1. Length frequency plots for *C. virginalis* in the SWA of Lake Malawi.

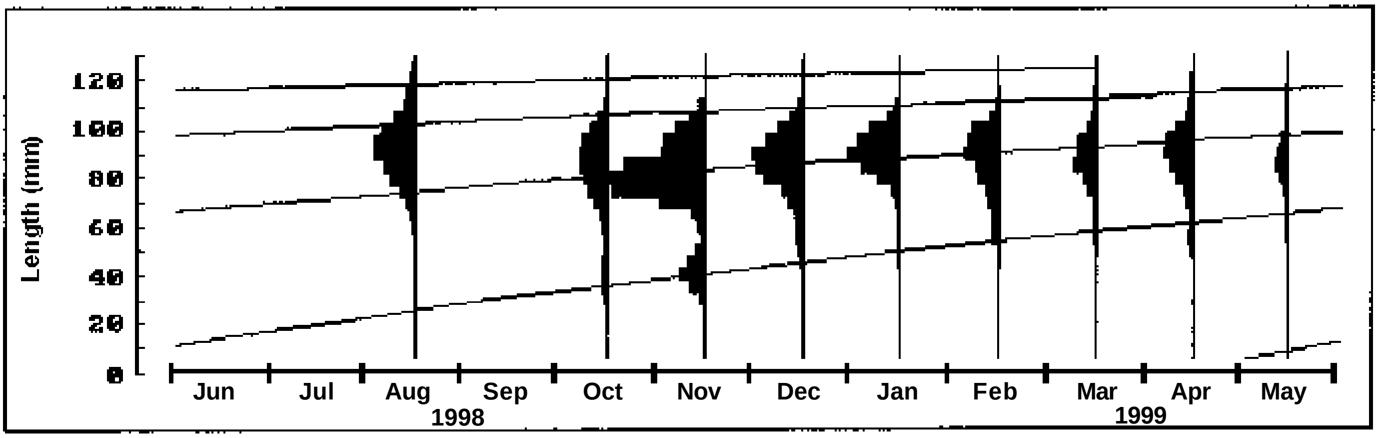
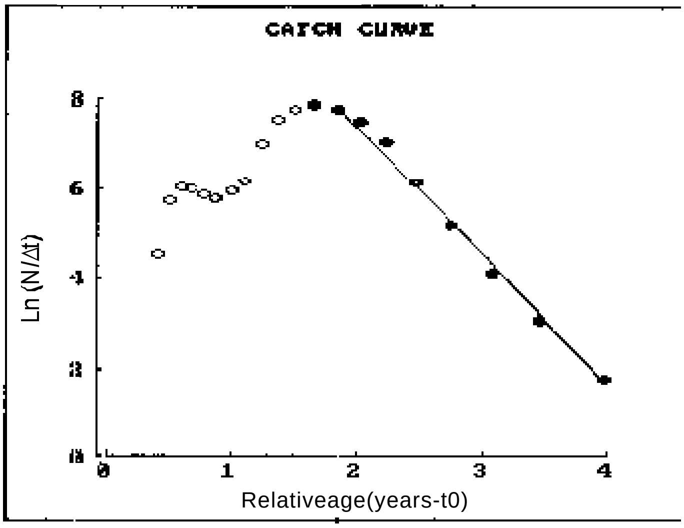


Figure G9-1. Length frequency plots for *D. apogon* in the SWA of Lake Malawi.



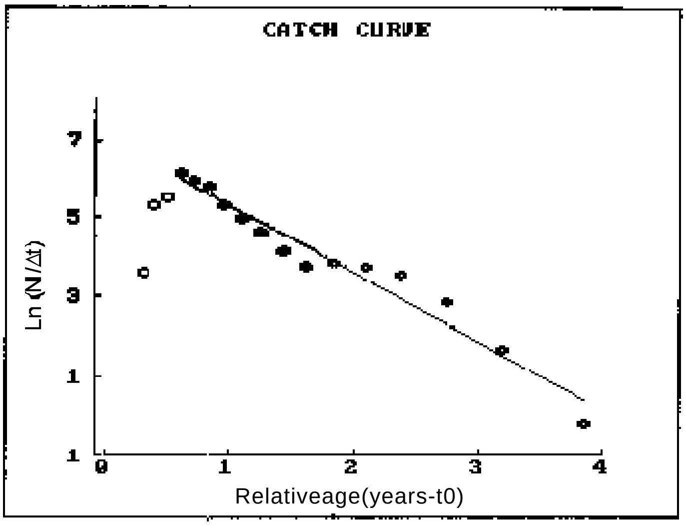


Figure G9-2. Length converted catch curve for *D. apogon*.

Figure G10-2. Length converted catch curve for *D. argenteus*.

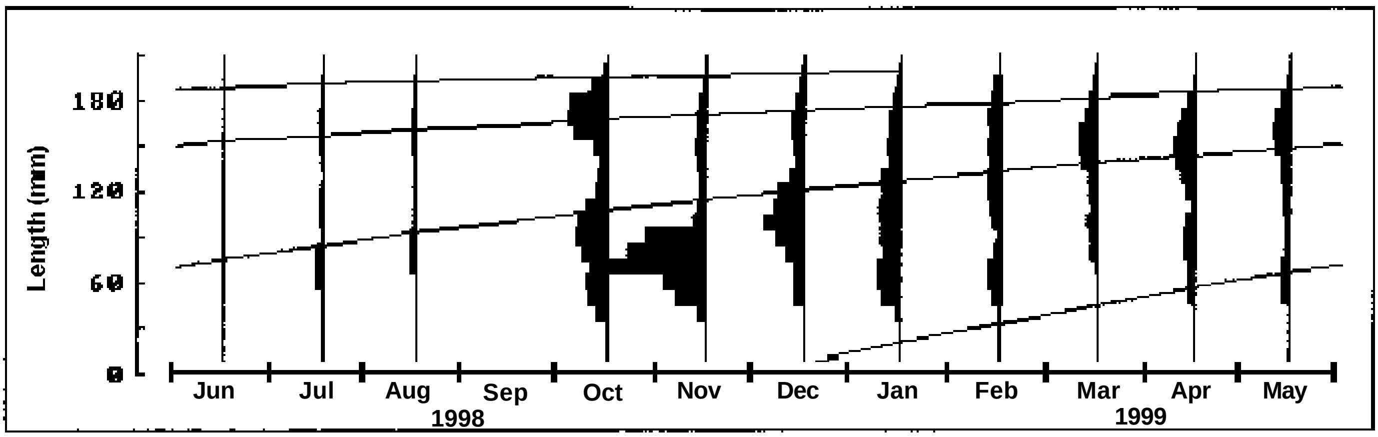
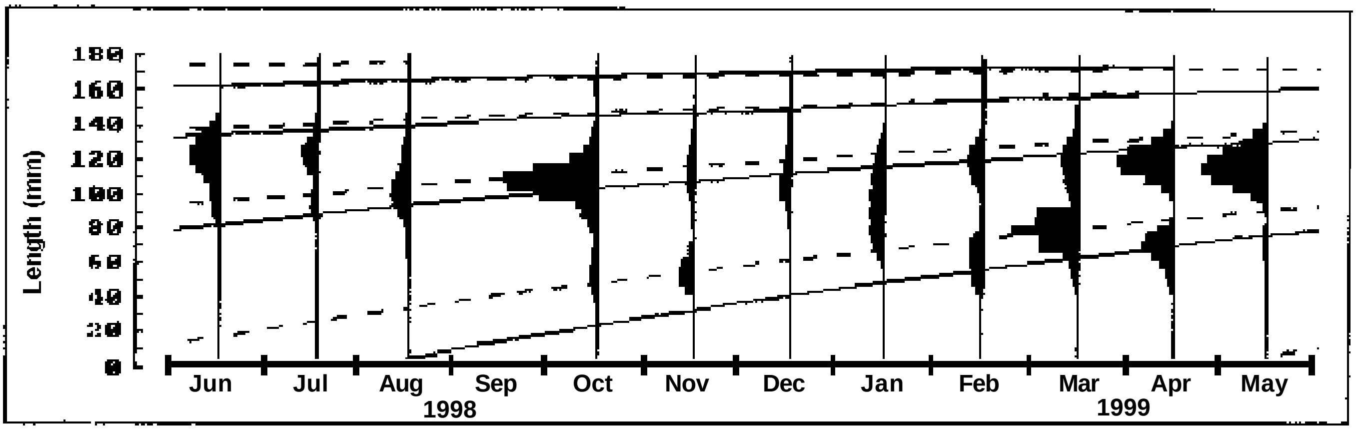
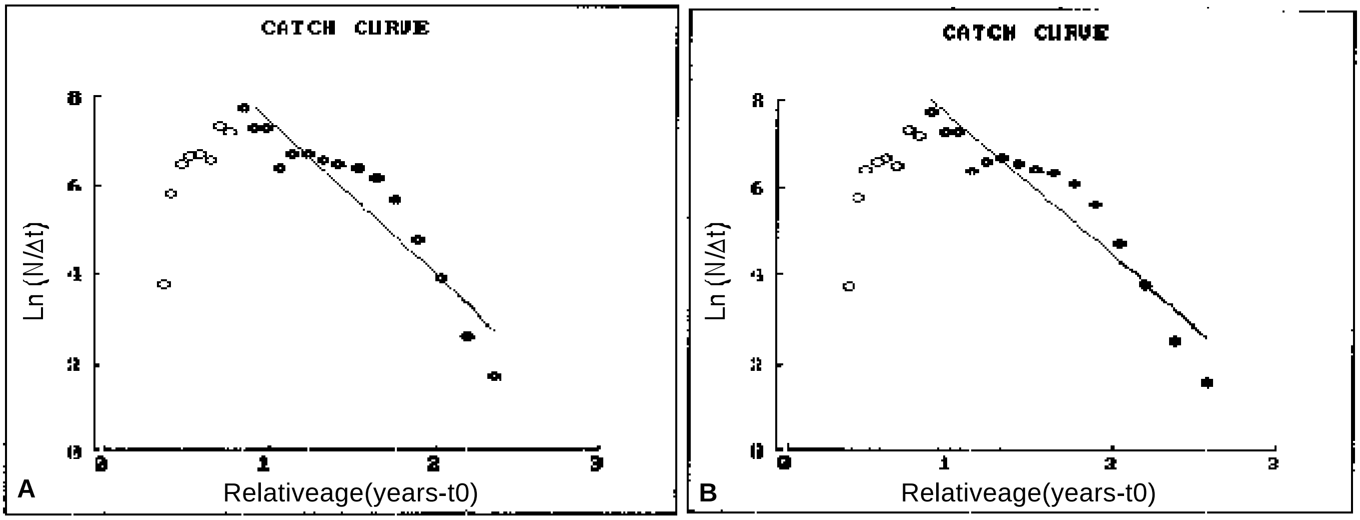


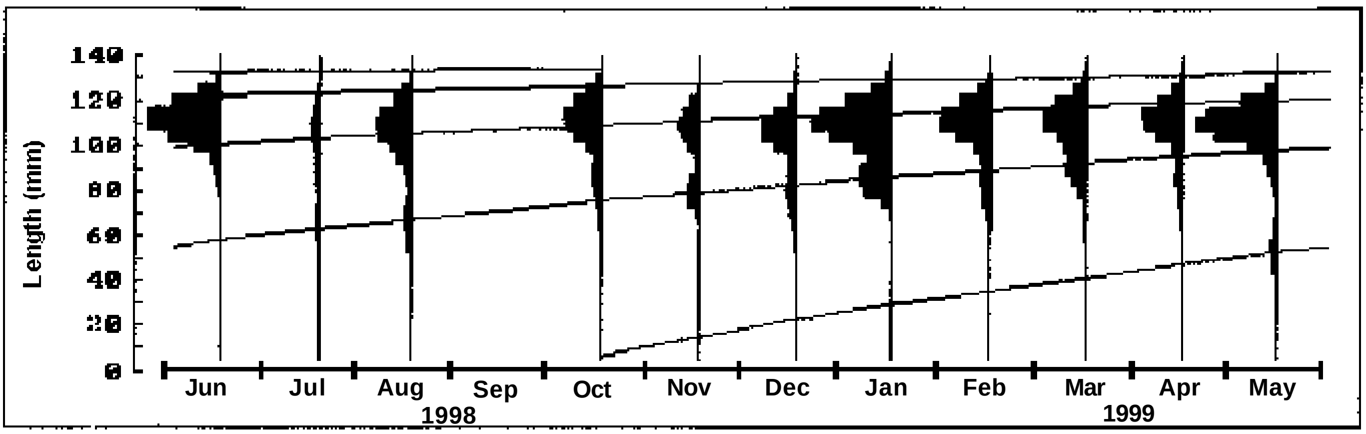
Figure G10-1. Length frequency plots for *D. argenteus* in the SWA of Lake Malawi.



FigureG11-1.Lengthfrequencyplotsfor *D.limnothrissa* intheSWAofLakeMalawi.



FiguresG11-2. Length converted catch curves for *D. limnothrissa*.



FigureG12-1.Lengthfrequencyplotsfor *D.macrops* intheSWAofLakeMalawi.

Diplotaxodon and Pallidochromis spp.

Diplotaxodon apogon

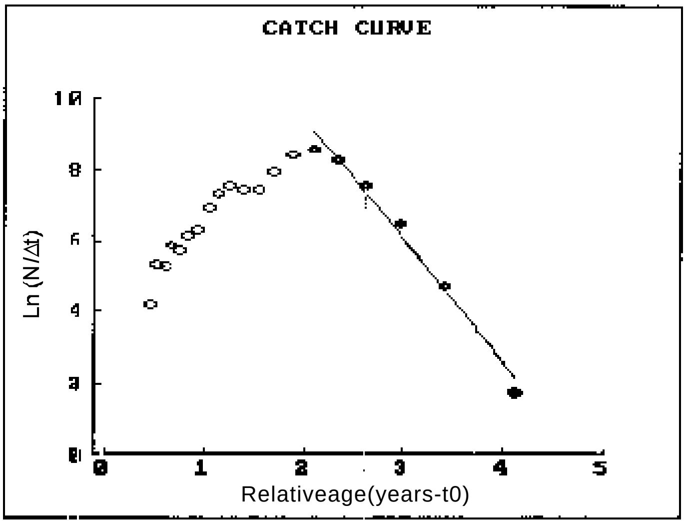
The length frequency distributions, based on 2754 fish are presented in Figure G9-1. Three year classes were identified by the software with L_∞=140 mm and K=0.56. The calculated date of birth, April corresponded to the end of the main peak of breeding activity.
Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *D. apogon* (75 to 125 m) and considering all the distributions, the mortality estimates were: Z=2.86, M=1.39 and F=1.47 for the age range showed in Figure G9-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 80 mm.

Diplotaxodon argenteus

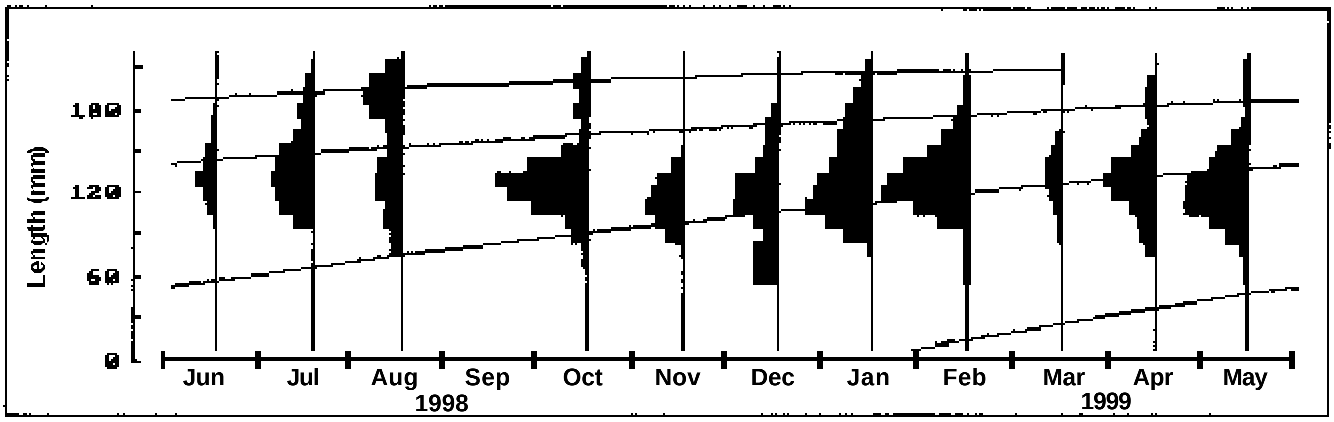
The length frequency distributions, based on 908 fish are presented in Figure G10-1. Two sets of parameters gave good fit of the distribution, each of them fitting three year classes. With the first set, L_∞=219 mm and K=0.78 (solid line), the date of birth was December. Assuming a mean environmental temperature of 24°C corresponding to the depth distribution of *D. argenteus* (50 to 125 m) and considering the November and December distributions only, the mortality estimates were: Z=2.19, M=1.54 and F=0.65 for the age range 0.8 to 3 years. With the second set of parameters, L_∞=220 mm and K=0.62 (dashed line), the date of birth was April and the mortality estimates were: Z=1.74, M=1.33 and F=0.41 for the age range 0.8 to 4 years.
The mean size at first capture by the 35 mm cod end trawl net for this species was 57 mm with both sets of parameters.
Both fits were good, however, the dashed line went better through the middle of the major peaks whereas the solid line went often through the end of the peaks (ex. October or December). Next, a birth in April, during the major breeding season appeared more reasonable than a birth in December after a little isolated breeding peak based on low sample size. Furthermore, mortality estimates and life span (Figure G10-2) obtained with the second set of parameters (L_∞=220 mm, K=0.62, dashed line), also appeared more reasonable for a deep water species subjected to little if any exploitation.
Consequently, the following parameters were considered to better represent the data and were used for the calculation of age at maturity: L_∞=220 mm, K=0.62, Z=1.74, M=1.33 and F=0.41.

Diplotaxodon limnothrissa

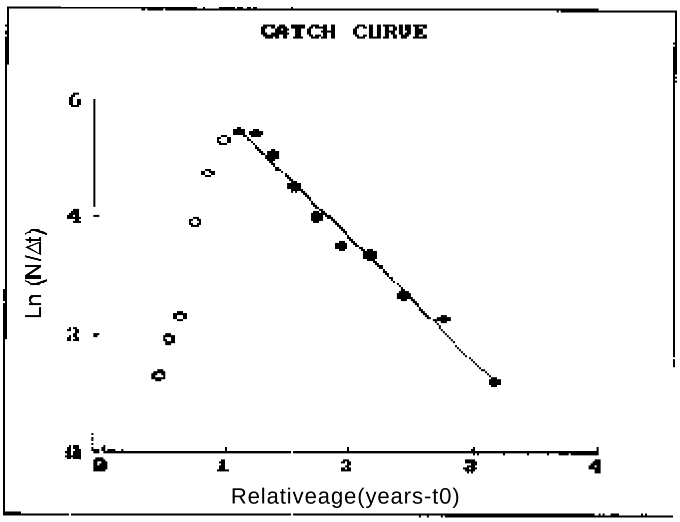
The length frequency distributions, based on 5823 fish are presented in Figure G11-1. Three year classes were identified by the software (solid line), with L_∞=192 mm, K=0.64. The calculated date of birth, July-August corresponded to the last two months of the breeding season.
Assuming a mean environmental temperature of 24°C corresponding to the depth distribution of *D. limnothrissa* (50 to 125 m) and considering only the August, November and March distributions, the mortality estimates were: Z=3.48, M=1.41 and F=2.07 for the age range showed in Figure G11-2A. Given that the length frequency distributions were not adequate, it is likely that mortality estimates were overestimated, particularly for a deep water species



FigureG12-2.Lengthconvertedcatchcurvefor *D.macrops.*



FigureG13-1.Lengthfrequencyplotsfor *P.tokolosh* intheSWAofLakeMalawi.



FigureG13-2.Lengthconvertedcatchcurvefor *P. tokolosh*.

subjected to little if any exploitation in this part of the lake. The mean size at first capture by the 35 mm cod end trawl net for this species was 77 mm.

More than one cohort per year class were present. The major peak in March appeared to be from the same year class that the lower peaks fitted by the solid lined model in February and April. The best estimation fitting that cohort (dashed line) was obtained with L_∞=188 mm, K=0.62. The calculated date of birth, May corresponded to the first two months of the breeding season. Mortality estimates were: Z=3.22, M=1.39 and F=1.83 for the age range showed in Figure G11-2B. The selectivity of the 10 mm cod end trawl net with this set of parameters was 74 mm.

These two estimations, one taking into account the cohort born in the beginning of the breeding season, the other considering the cohort born at the end of the breeding season were very similar and gave very close growth and mortality estimates. The cohort born at the beginning of the breeding season (dashed line) had a slightly slower growth leading to an age at maturity of 16 months old whereas the cohort born at the end of the breeding season (solid line) reached maturity at 15 months old.

Diplotaxodon macrops

The length frequency distributions, based on 5778 fish are presented in Figure G12-1. Three year classes were identified by the software with L_∞=143 mm, K=0.7. The calculated date of birth, September-October corresponded to the last months of the second peak of breeding activity. No correct fit gave a birth in the major breeding peak (January-May).

Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *D. macrops* (75 to 125 m) and considering all the distributions, the mortality estimates were: Z=3.12, M=1.6 and F=1.52 for the age range showed in Figure G12-2. Given that the length frequency distributions were not adequate, it is likely that mortality estimates were overestimated, particularly for a deep water species subjected to little if any exploitation in this part of the lake. The mean size at first capture by the 35 mm cod end trawl net for this species was 106 mm, which also appeared overestimated.

Pallidochromis tokolosh

P. tokolosh was not an abundant fish and only 375 specimens were measured over the sampling period. The length frequency distributions are presented in Figure G13-1. Despite the low sample size, a reasonably good growth estimation was obtained with L_∞=244 mm, K=0.62. The calculated date of birth, January corresponded to the middle of the observed breeding season.

Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *P. tokolosh* (75 to 125 m) and considering the June, July, October, January and February distributions, the mortality estimates were: Z=2.06, M=1.28 and F=0.78 for the age range showed in Figure G13-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 106 mm, which appeared overestimated though it translated the length distributions.

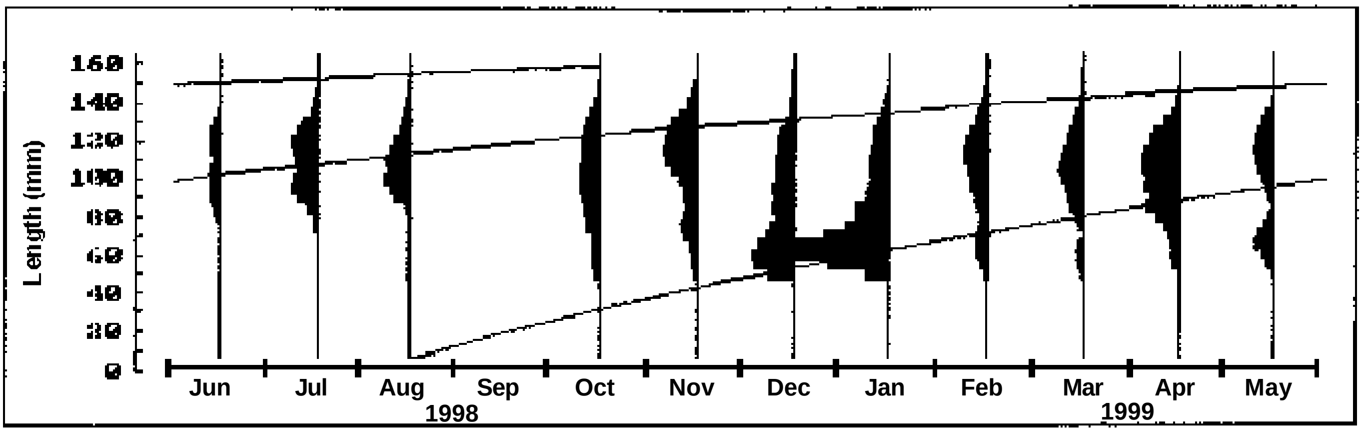
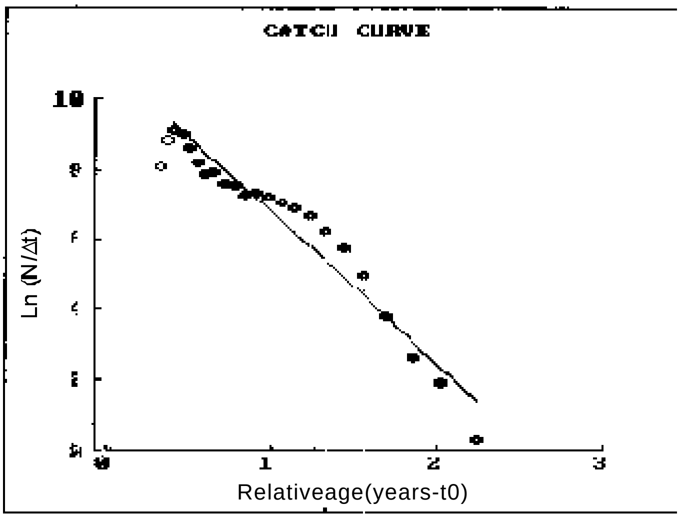


Figure G14-1. Length frequency plots for *L. argenteus* in the SWA of Lake Malawi.



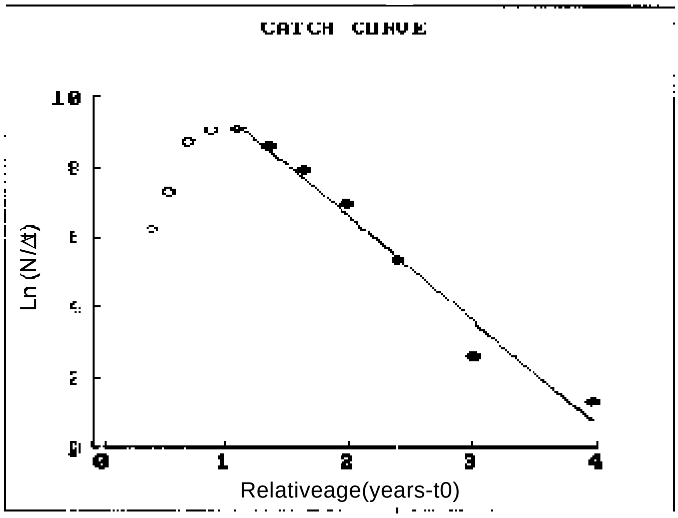


Figure G14-2. Length converted catch curve for *L. argenteus*. Figure G15-2. Length converted catch curve for *L. 'dwaltus'*.

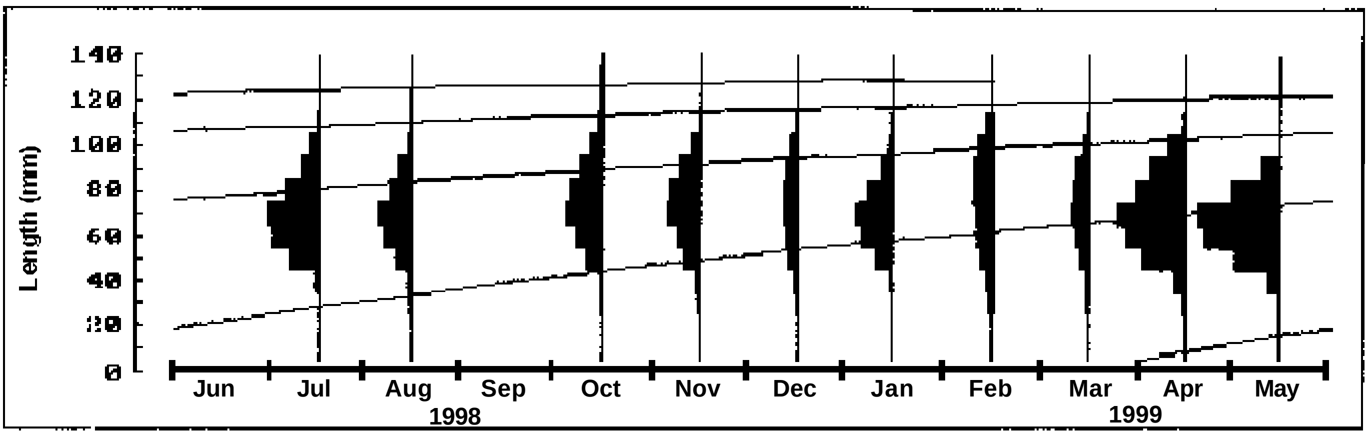


Figure G15-1. Length frequency plots for *L. 'dwaltus'* in the SWA of Lake Malawi.

Lethrinops spp.

Lethrinops argenteus

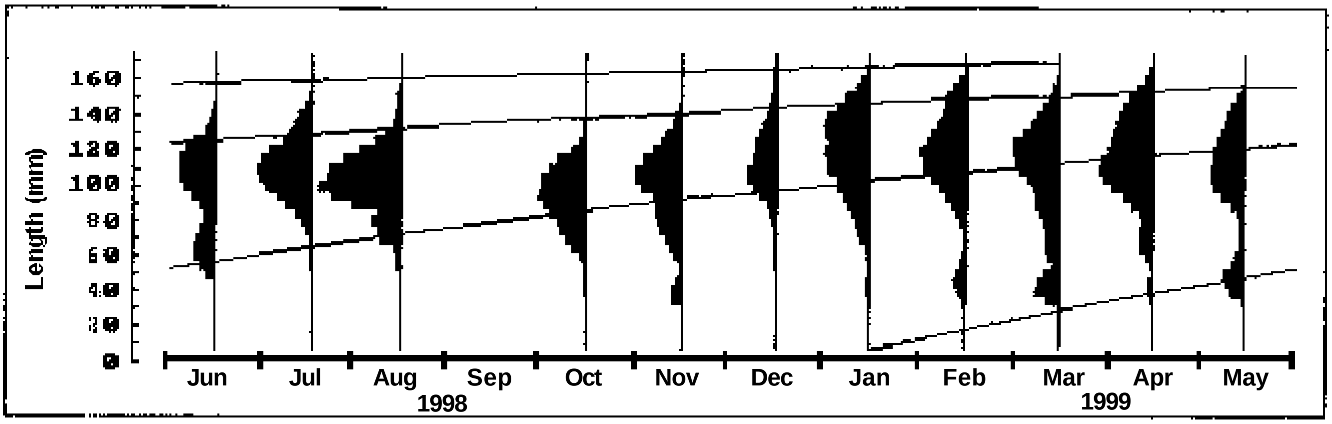
The length frequency distributions, based on 9225 fish are presented in Figure G14-1. Two year classes were identified by the software with L_∞=182 mm, K=0.94. The calculated date of birth, August corresponded to a major peak of breeding activity.
Assuming a mean environmental temperature of 25°C corresponding to the depth distribution of *L. argenteus* (10 to 50 m) and considering only the December and January distributions, the mortality estimates were: Z=4.38, M=1.87 and F=2.51 for the age range showed in Figure G14-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 55 mm.

Lethrinops 'deep water altus'

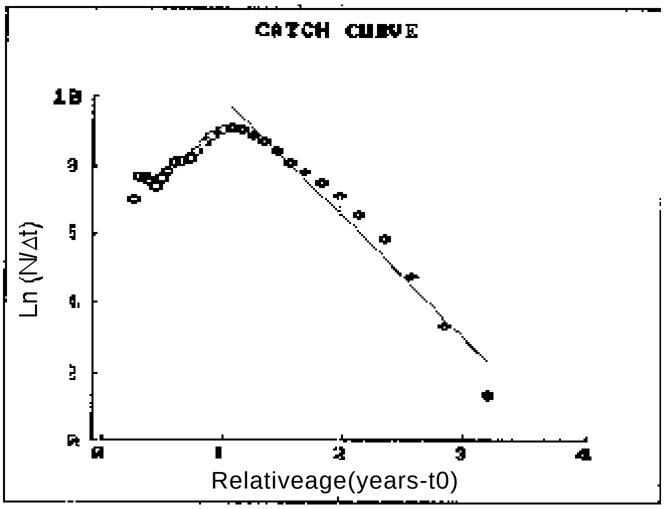
The length frequency distributions, based on 1510 fish are presented in Figure G15-1. Despite the relative homogeneity of length distribution among successive months, it was possible to fit a VBGC, which gave reasonable estimates with L_∞=142 mm, K=0.62. The calculated date of birth, March corresponded to the main peak of sexual activity.
Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *L. 'deep water altus'* (75 to 125 m) and considering only the December and January distributions, the mortality estimates were: Z=2.94, M=1.48 and F=1.46 for the age range showed in Figure G15-2. As the deep zone in this part of the lake is almost not exploited, it is very likely that mortality were overestimated owing to the under-representation of juveniles in the length distributions. The mean size at first capture by the 35 mm cod end trawl net for this species was 58 mm.

Lethrinops gossei

The length frequency distributions, based on 8072 fish are presented in Figure G16-1. The best combination was obtained with L_∞=185 mm, K=0.78. The calculated date of birth, March corresponded to the peak of breeding activity.
Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *L. gossei* (75 to 125 m) and considering all the distributions, the mortality estimates were: Z=3.48, M=1.60 and F=1.88 for the age range showed in Figure G16-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 99 mm. Again, as the deep zone in this part of the lake is hardly exploited, it is very likely that mortality was overestimated owing to the inadequate length distributions.



FigureG16-1.Lengthfrequencyplotsfor *L.gossei* intheSWAofLakeMalawi.



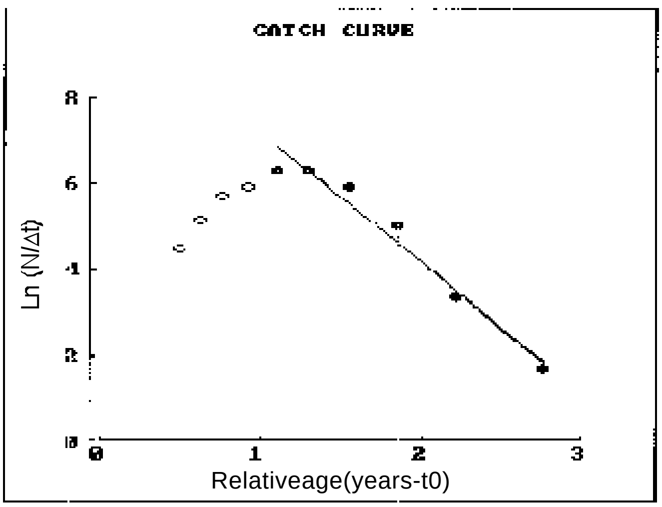
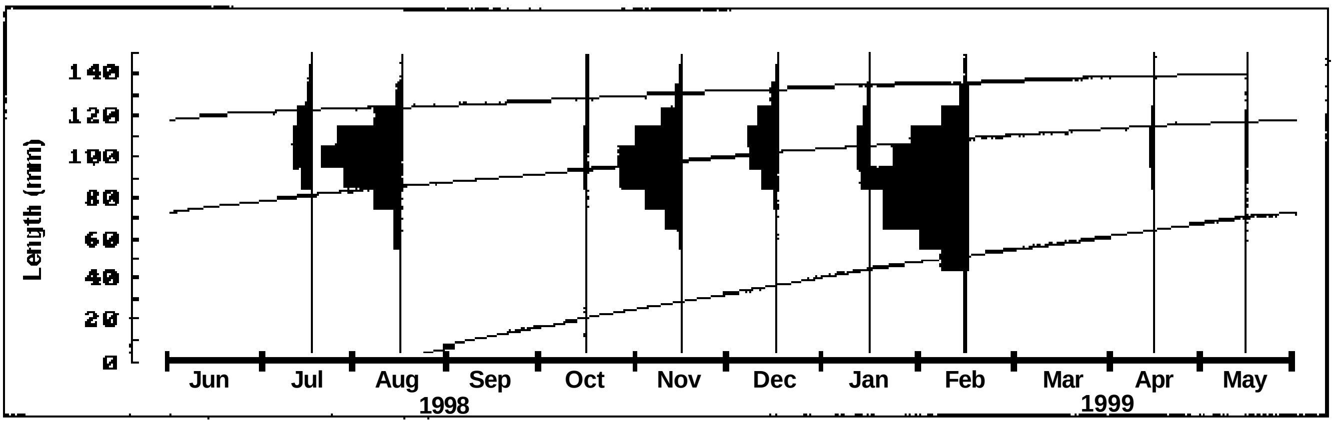


Figure G16-2. Length converted catch curve for *L. gossei*.

FigureG17-2.Lengthconvertedcatchcurvefor *L.longimanus*.



FigureG17-1.Lengthfrequencyplotsfor *L.longimanus* intheSWAofLakeMalawi.

Lethrinops longimanus

L. longimanus was not an abundant fish and only 553 specimens were measured over the sampling period. The length frequency distributions are presented in Figure G17-1. Despite the low sample size and the lack of clear progression in length modes, a reasonable growth estimation was obtained with L_∞=160 mm, K=0.75. As it was impossible to determine the precise breeding season for this species, it was difficult to assess the quality of the calculated date of birth, August. However, it occurred at the period when most breeding activity was observed.

Assuming a mean environmental temperature of 25°C corresponding to the depth distribution of *L. longimanus* (30 to 125 m) and considering all the distributions, the mortality estimates were: Z=3.00, M=1.67 and F=1.33 for the age range showed in Figure G17-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 82 mm.

Despite the poor appropriateness of the data set to this kind of study, the estimates were in agreement with the values obtained for other *Lethrinops* species of comparable size.

Lethrinops 'oliveri'

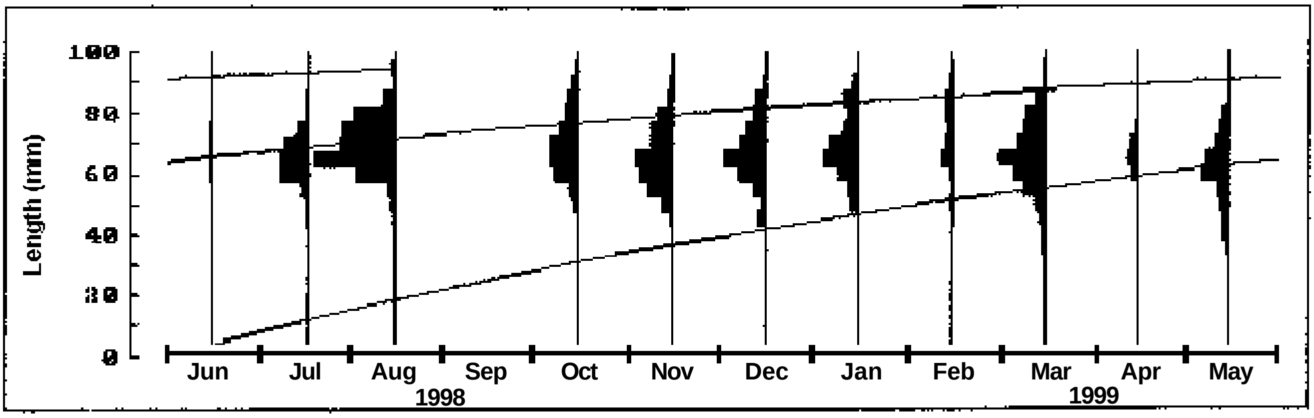
The length frequency distributions, based on 9020 fish are presented in Figure G18-1. As for the other small species a relative homogeneity of length distribution among successive months was observed. However, it was possible to fit a VBGC, which gave reasonable estimates with L_∞=110 mm, K=0.88. The calculated date of birth, June corresponded to the middle of the main breeding season.

Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *L. 'oliveri'* (75 to 125 m) and considering all the distributions, the mortality estimates were: Z=4.31, M=2.0 and F=2.31 for the age range showed in Figure G18-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 60 mm. Again, as the deep zone in this part of the lake is lightly exploited, it is very likely that mortality was overestimated owing to the non adequate length distributions.

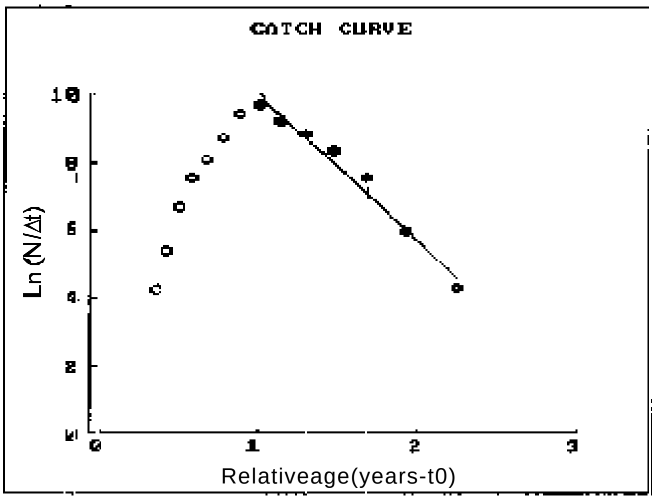
Lethrinops polli

The length frequency distributions, based on 1681 fish are presented in Figure G19-1. The best estimation was obtained with L_∞=134 mm, K=0.78. The calculated date of birth, August-September corresponded to the end of the main observed breeding season.

Assuming a mean environmental temperature of 24°C corresponding to the depth distribution of *L. polli* (75 to 125 m) and considering only the July, August and May distributions, the mortality estimates were: Z=3.43, M=1.77 and F=1.66 for the age range showed in Figure G19-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 71 mm. Again, as the deep zone in this part of the lake is almost not exploited, it is very likely that mortality was overestimated owing to the non adequate length distributions.



FigureG18-1.Lengthfrequencyplotsfor *L.'oliveri'* intheSWAofLakeMalawi.



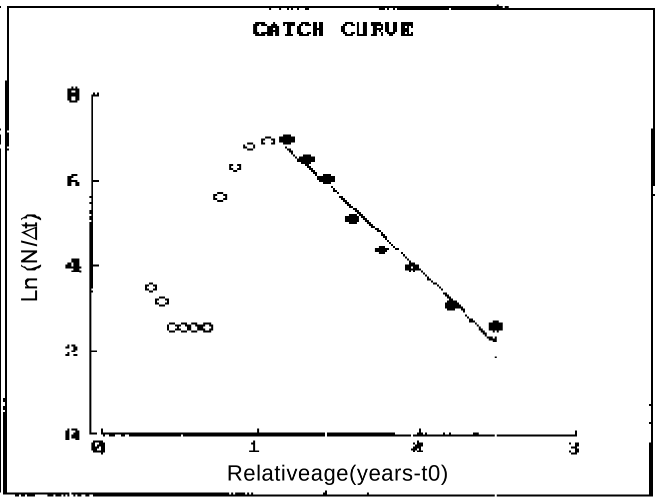
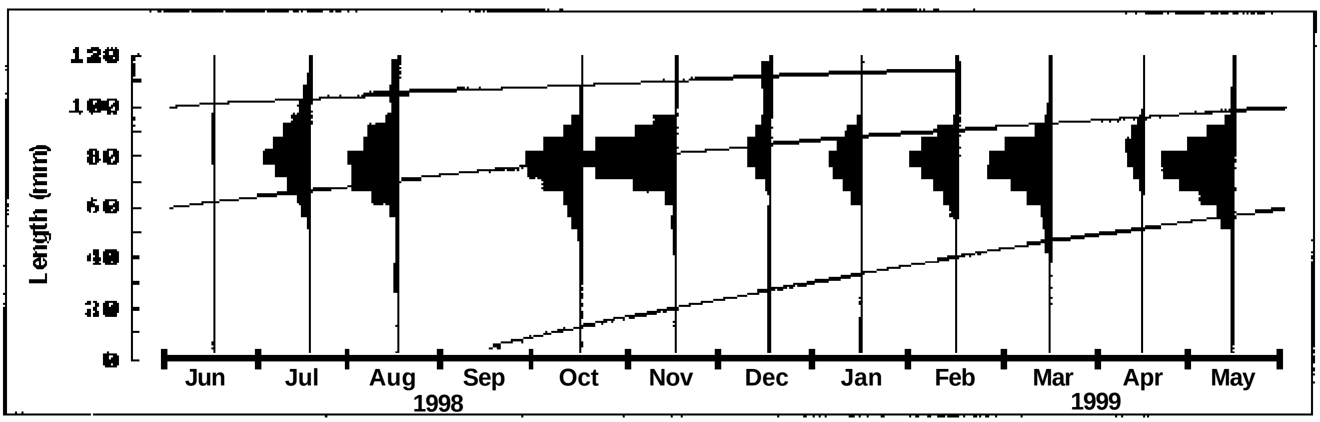
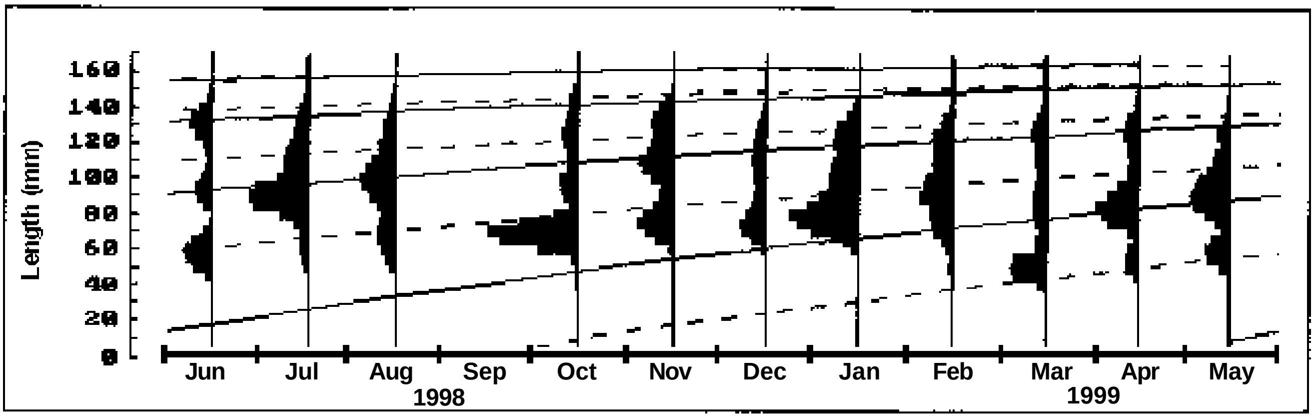


Figure G18-2. Length converted catch curve for *L. 'oliveri'*. Figure G19-2.Lengthconvertedcatchcurvefor *L.polli*.



FigureG19-1.Lengthfrequencyplotsfor *L.polli* intheSWAofLakeMalawi.



FigureG20-1.Lengthfrequencyplotsfor *M.anaphyrmus* intheSWAofLakeMalawi.

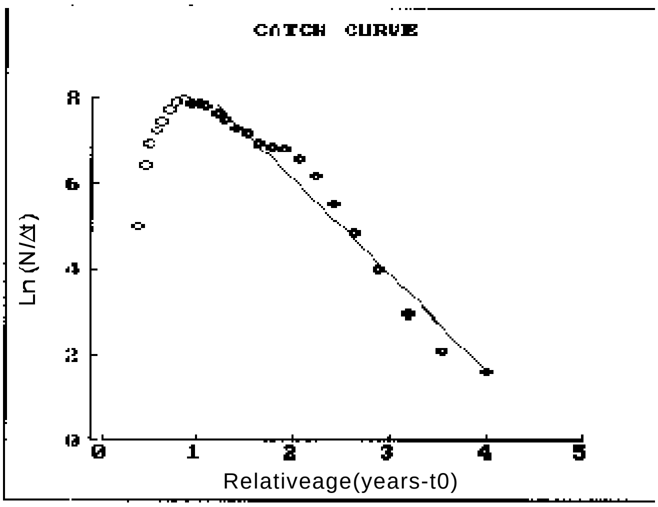
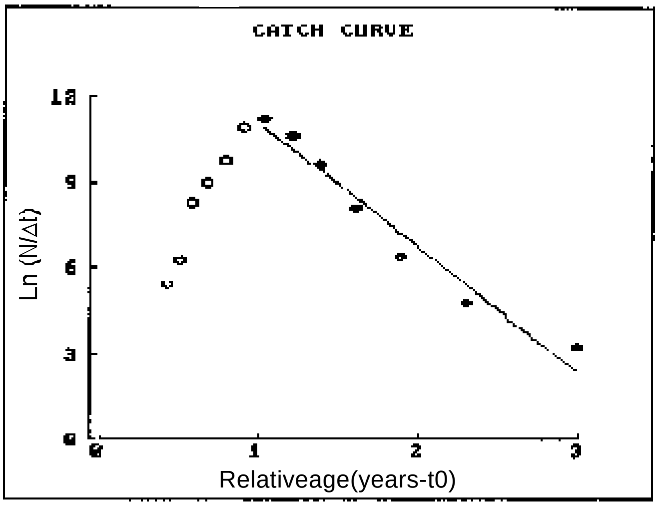
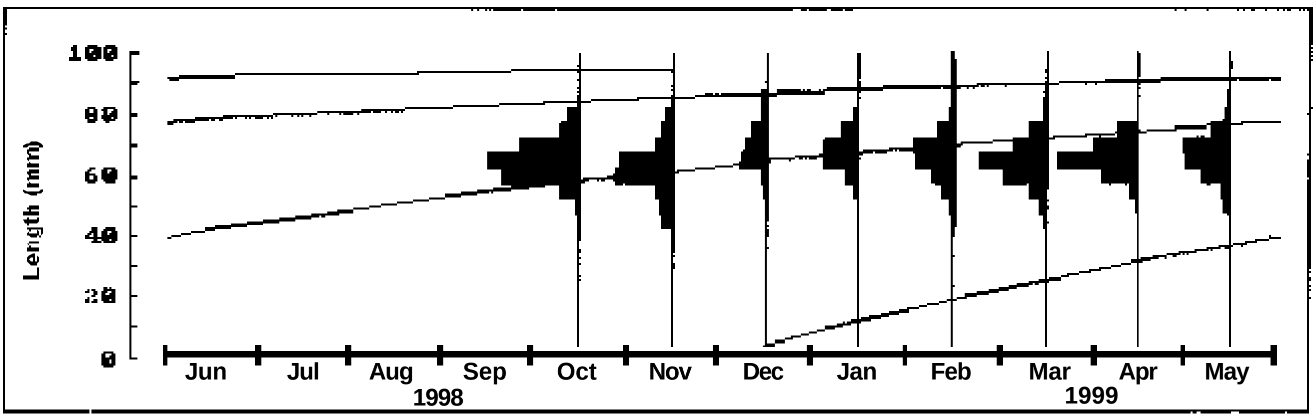


Figure G20-2. Length converted catch curve for *M. anaphyrmus*.



FigureG21-2.Lengthconvertedcatchcurvefor *N.'argyrosoma'*.



FigureG21-1.Lengthfrequencyplotsfor *N.'argyrosoma'* intheSWAofLakeMalawi.

Mylochromis spp.

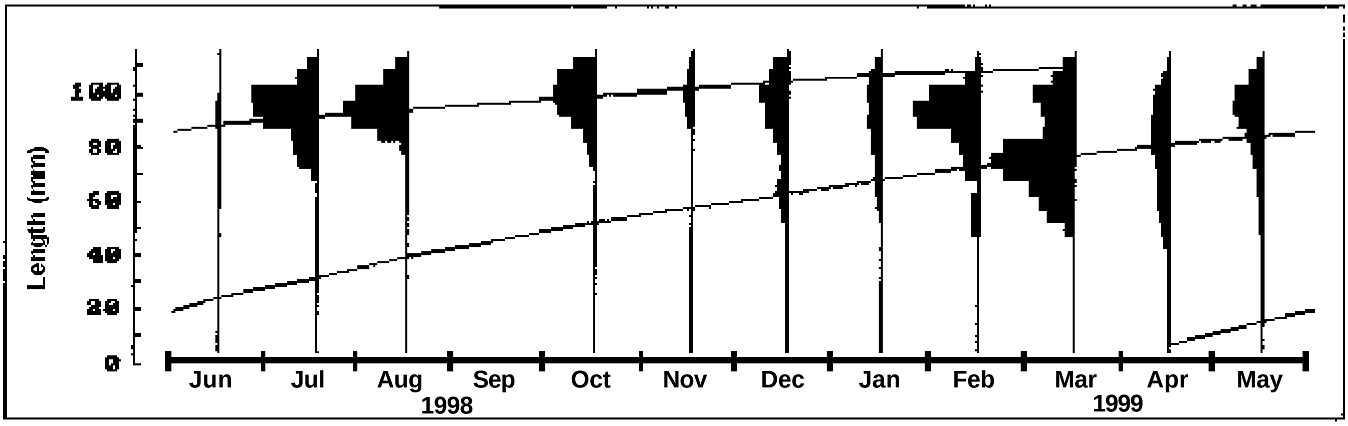
Mylochromis anaphyrmus

The length frequency distributions, based on 3007 fish are presented in Figure G20-1. Three year classes were identified by the software (solid line), with L_∞=180 mm, K=0.62. The calculated date of birth, May corresponded to the main peak of breeding activity.
More than one cohort per year class was present. The peaks of small sizes in March, April and May appeared to be from the same year class that the upper peaks fitted by the solid lined model in April and May. The best estimation fitting that cohort (dashed line) was obtained with L_∞=179 mm, K=0.52. The calculated date of birth, September corresponded to the last two months of the breeding season.
However, the estimation taking into account the cohort born in the middle of the breeding season (solid line) fitted the distributions best and was selected for the calculations of mortality. Assuming a mean environmental temperature of 26°C corresponding to the depth distribution of *M. anaphyrmus* (10 to 50 m) and considering all the distributions, the mortality estimates were: Z=2.22, M=1.46 and F=0.76 for the age range showed in Figure G20-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 72 mm.

Nyassachromis spp.

Nyassachromis 'argyrosoma'

The length frequency distributions, based on 34235 fish are presented in Figure G21-1. As for the other small species a relative homogeneity of length distribution among successive months was observed. However, it was possible to fit a VBGC, which gave reasonable estimates with L_∞=100 mm, K=1. The calculated date of birth, December corresponded to the major peak of breeding activity.
Assuming a mean environmental temperature of 26°C corresponding to the depth distribution of *N. 'argyrosoma'* (10 to 30 m) and considering all the distributions, the mortality estimates were: Z=4.38, M=2.34 and F=2.04 for the age range showed in Figure G21-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 59 mm. Again, it is very likely that mortality was overestimated owing to the inadequate length distributions.



FigureG22-1.Lengthfrequencyplotsfor *Pl.'platyrhynchos'* intheSWAofLakeMalawi.

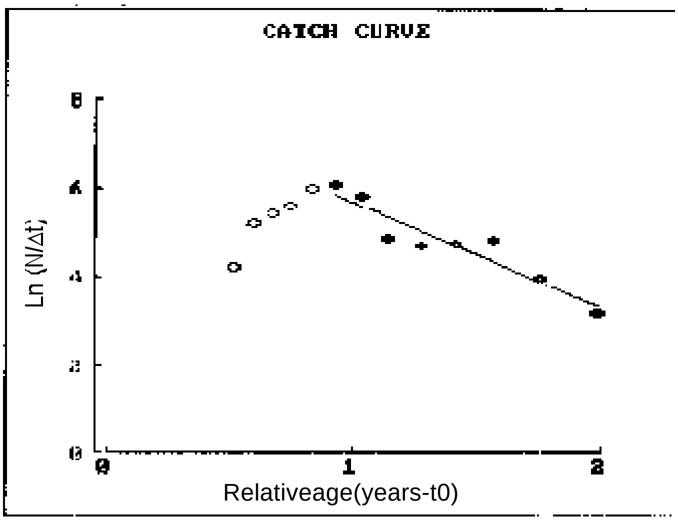
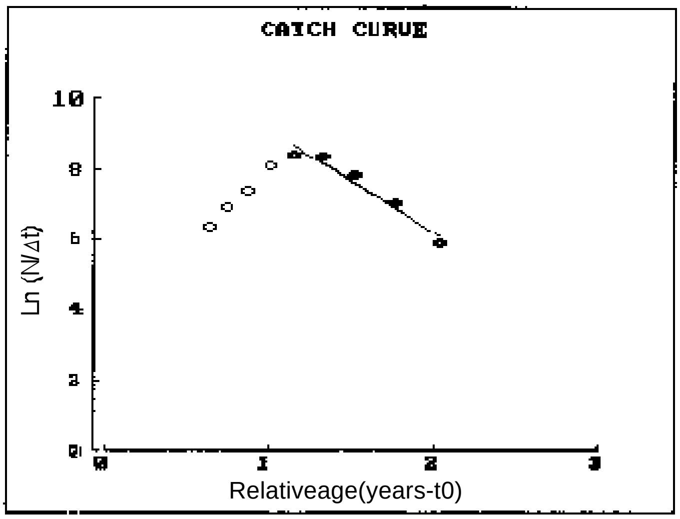
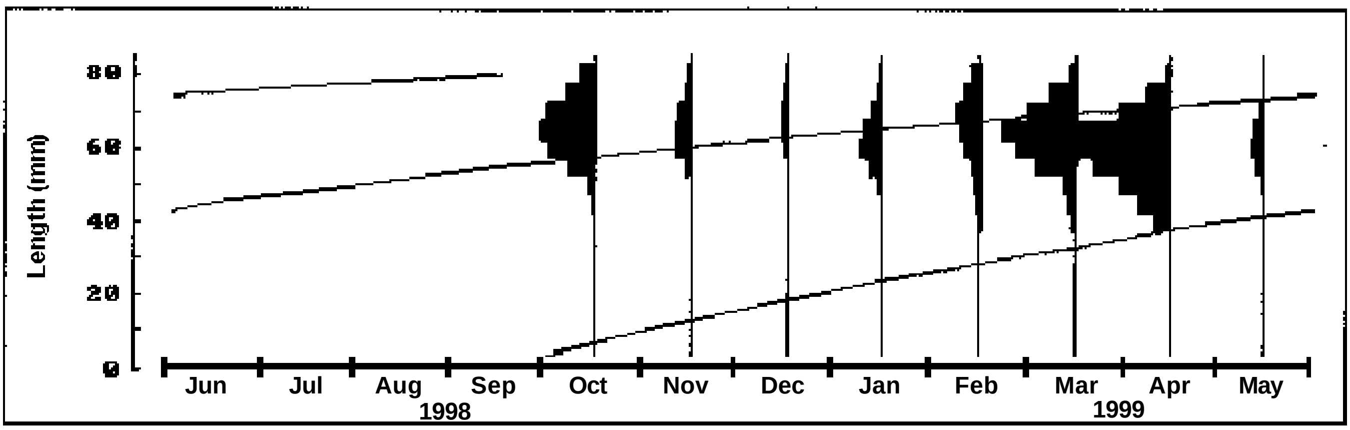


Figure G22-2. Length converted catch curve for *Pl. 'platyrhynchos'*.



FigureG23-2.Lengthconvertedcatchcurvefor *T.brevirostris*.



FigureG23-1.Lengthfrequencyplotsfor *T.brevirostris* intheSWAofLakeMalawi.

Placidochromis spp.

Placidochromis 'platyrhynchos'

The length frequency distributions, based on 1053 fish are presented in Figure G22-1. The best estimation, fitting two year classes, was obtained with L_∞=132 mm, K=0.9. The calculated date of birth, April corresponded to the middle of the main observed breeding season.

Assuming a mean environmental temperature of 23.5°C corresponding to the depth distribution of *P. 'platyrhynchos'* (75 to 125 m) and considering only the March distribution, the mortality estimates were: Z=2.43, M=1.93 and F=0.5 for the age range showed in Figure G22-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 64 mm.

Trematocranus spp.

Trematocranus brevirostris

The length frequency distributions, based on 3371 fish are presented in Figure G23-1. As for the other small species a relative homogeneity of length distribution among successive months was observed. However, it was possible to fit a VBGC, which gave reasonable estimates with L_∞=100 mm, K=0.79. The calculated date of birth, September seemed to correspond with a period of breeding activity.

Assuming a mean environmental temperature of 25°C corresponding to the depth distribution of *T. brevirostris* (around 50 m) and considering all the distributions, the mortality estimates were: Z=2.99, M=1.97 and F=1.02 for the age range showed in Figure G23-2. The mean size at first capture by the 35 mm cod end trawl net for this species was 55 mm.

Table G2. Growth parameters for 23 cichlid species from the SWA of Lake Malawi. L_∞ and K are the parameters of the Von Bertalanffy growth curve equation (VBGC). The TMM (mean maximum observed length) is the average length of the ten largest fish caught (de Merona 1983, Moreau & Nyakageni 1992). K' and L_∞' are rapid growth estimates calculated as follows: L_∞' = 1,248 TMM, K' = 153 / L_∞' (de Merona 1983). ΔG: growth difference at 2 years old obtained by fitting the VBCG with both sets of estimates (L_∞', K' and L_∞, K). Values indicate the magnitude of growth overestimation by the rapid growth estimation model.

	L_∞ (mm)	K (year^{-1})	TMM (mm)	L_∞' (mm)	K' (year^{-1})	DG (mm)
A. 'geoffreyi'	181	0,6	158,2	197	0,77	29
A. macrocleithrum	166	0,6	138,1	172	0,89	27
A. mentale	266	0,7	229	286	0,54	-13
A. pectinatum	160	0,58	134,5	168	0,91	31
Au. 'blue orange'	80	1,21	72,6	91	1,69	15
Au. 'minutus'	75	1,44	67,4	84	1,82	11
C. quadrimaculatus	160	0,58	147,5	184	0,83	39
C. virginalis	130	0,84	120,4	150	1,02	25
D. apogon	140	0,56	123,1	154	1,00	38
D. argenteus	220	0,62	197	246	0,62	19
D. limnothrissa	188	0,62	167,9	210	0,73	27
D. macrops	143	0,7	131,2	164	0,93	31
P. tokolosh	244	0,62	205,6	257	0,60	5
L. argenteus	182	0,94	156,5	195	0,78	0
L. 'deep water altus'	142	0,62	115	144	1,07	26
L. gossei	185	0,78	164,4	205	0,75	13
L. longimanus	160	0,75	136,5	170	0,90	18
L. 'oliveri'	110	0,88	96,3	120	1,27	20
L. polli	134	0,78	110,5	138	1,11	17
M. anaphyrmus	180	0,62	159	198	0,77	28
N. 'argyrosoma'	100	1	93,7	117	1,31	22
Pl. 'platyrhynchos'	132	0,9	114	142	1,08	16
Tr. Brevirostris	100	0,79	80,9	101	1,52	17

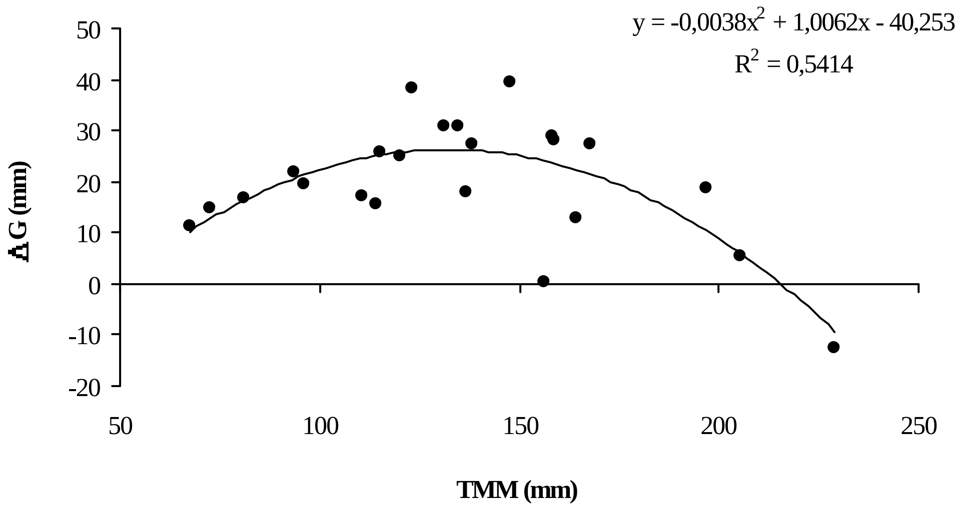


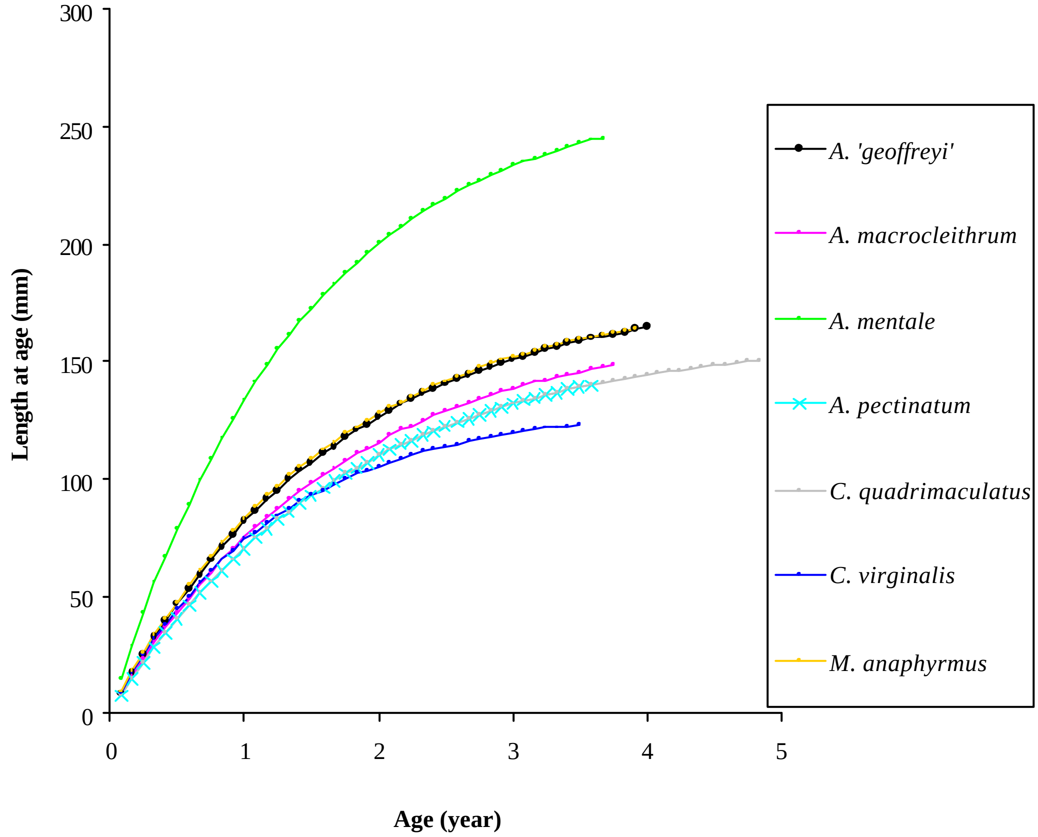
Figure G27. Distribution of G in relation with mean maximum observed length (TMM).

Discussion

As expected from the extended breeding seasons displayed by the studied species, more than one cohort per year class was usually present in the length frequency distributions. Knowledge about the species biology significantly helped us choosing among the various sets of growth parameters that correctly fitted the distributions. In particular, for a similar "quality of distribution's fitting", we always selected the set of parameters that gave a birth date consistent with the breeding season observed for the species (see previous Chapter). For this, we considered that the potential bias associated with the assumption that growth curve parameters applied right to zero, and not merely to the smallest sampled sizes (between 45 and 60 mm depending on species) was negligible. Although the breeding seasonality of species was studied over a single annual cycle, previous investigations over more than one annual cycle have suggested little or no inter annual variability of breeding patterns (Iles 1971, Tweddle & Turner 1977). Also, we decided to keep the asymptotic length (L∞) within a controlled ranged. The trawl, with its 35 mm cod end mesh size is a non species-selective gear, catching fish from about 50 mm (see the estimated length at first capture for the studied species) to more than 300 mm (ex. *Buccochromis spp.*). Large and fast predatory species such as *Rhamphochromis spp.* were also caught, sometimes to sizes up to 500 mm. As a consequence and given the large numbers of specimens caught for most of the species, we considered that the maximum observed lengths were likely to be close to the asymptotic lengths, for the sampled area. Therefore, L∞ was intentionally kept within a range of 1 to 2 cm above the maximum observed length for the medium and large species, and within a few millimetres above for the smallest species (*Au. 'bue orange'*, *Au. 'minutus'*, *N. 'argyrosoma'*, *T. brevirostris*).

Growth factor (K) values ranged from 0.56 to 1.44, averaging 0.77 (Table G2). As expected given the inverse relationship between L∞ and K (de Merona et al. 1988), the smallest species (L_∞ < 100 mm) had the highest K, ranging from 0.79 to 1.44 with an average value of 1.11. However, the largest species (*A. mentale*, *P. tokolosh* and *D. argenteus*) did not have the lowest K. Medium sized species did have them. For comparative purposes, growth estimates of individual species were fitted by the VBGC equation and grouped per genera or size classes (Figure G24). The VBGC have been fitted up to the maximum observed length (MOL) of species. Within a single genus, species with comparable lengths had slight growth differences, though usually not higher than 1 cm at 2 years old as illustrated by *A. macrocleithrum* and *A. pectinatum* (Figure G24a), *D. apogon* and *D. macrops* (Figure G24b), *L. argenteus* and *L. gossei* (Figure G24c) or *Au. 'blue orange'* and *Au. 'minutus'* (Figure G24d). Growth performances of species within genera, as expressed by length at age, were proportional to their maximum length for *Alticorpus*, *Diplotaxodon* and *Lethrinops spp.*, with the exception of *L. 'deep water altus'* having a slower growth than the smaller *L. polli.* Between genera comparison for species of similar lengths showed that *Lethrinops spp*. had better growth than *Alticorpus* and *Diplotaxodon spp*. (see *L. argenteus* and *gossei* versus *A. 'geoffreyi'* and *D. limnothrissa*). *Lethrinops* versus *Copadichromis spp.* comparisons were less clear as the similarly sized *C. virginalis* and *L. polli* had equivalent growths whereas *C. quadrimaculatus* had a slower growth than *L. longimanus*. *A. pectinatum* and *C. quadrimaculatus* had the same growth estimates and logically presented exactly the same growth curves, as did *A. 'geoffreyi'* and *M. anaphyrmus* (Figure G24a). Apart from *L. 'deep water altus'*, which growth was intermediate to those of *D. macrops* and *D. apogon*, *Lethrinops* species tended to have better growths than species of others genera with similar sizes.

a



b

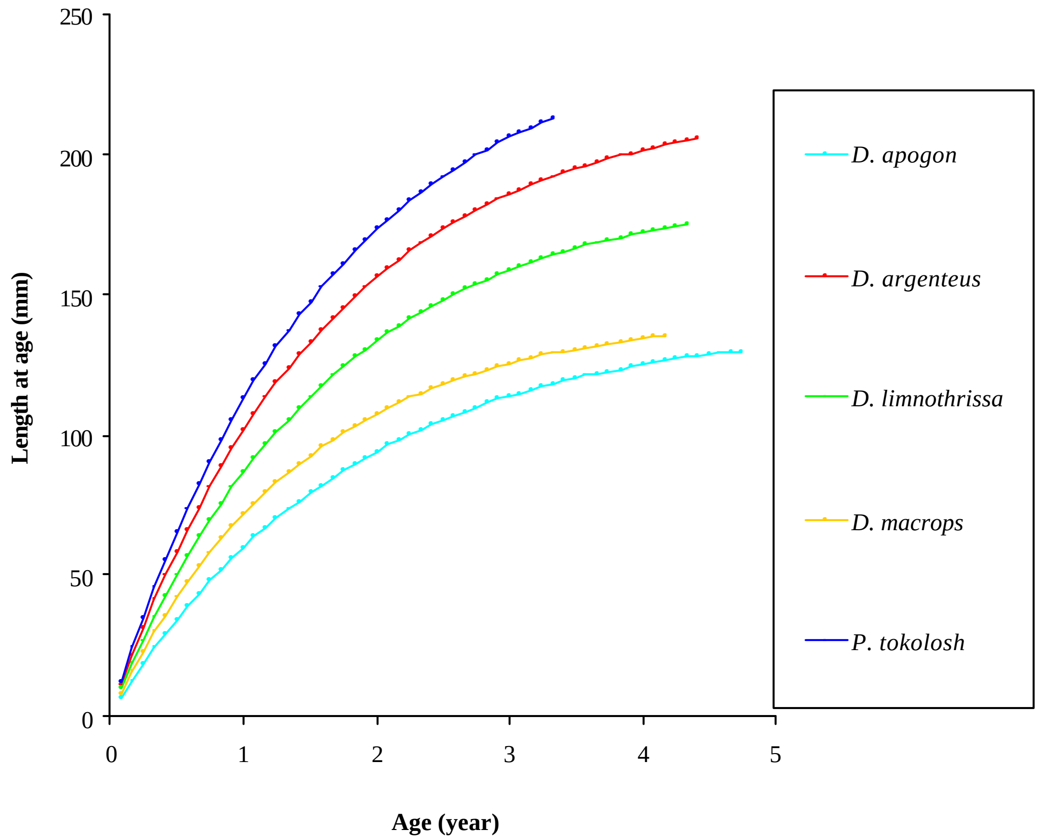
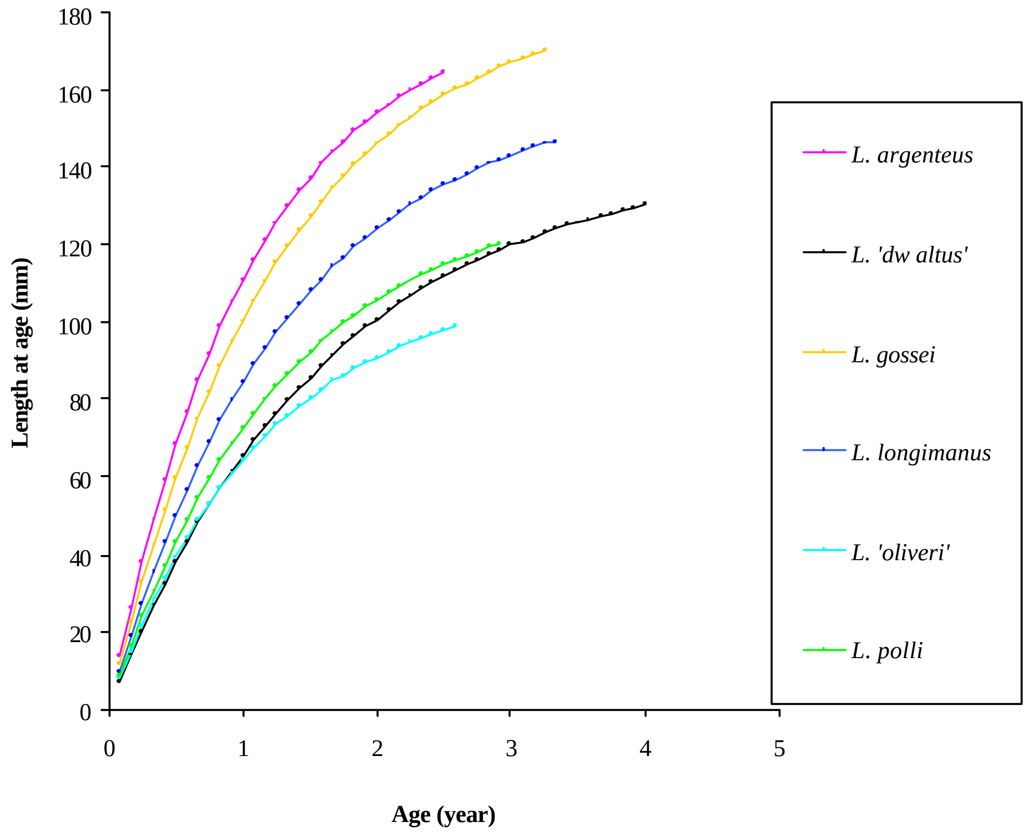


Figure G24. Von Bertalanffy growth curves for cichlid species caught by trawling in the SWA of Lake Malawi between June 1998 and May 1999. a: *Alticorpus*, *Copadichromis* & *Mylochromis spp.*, b: *Diplotaxodon* & *Pallidochromis spp.*.

c



d

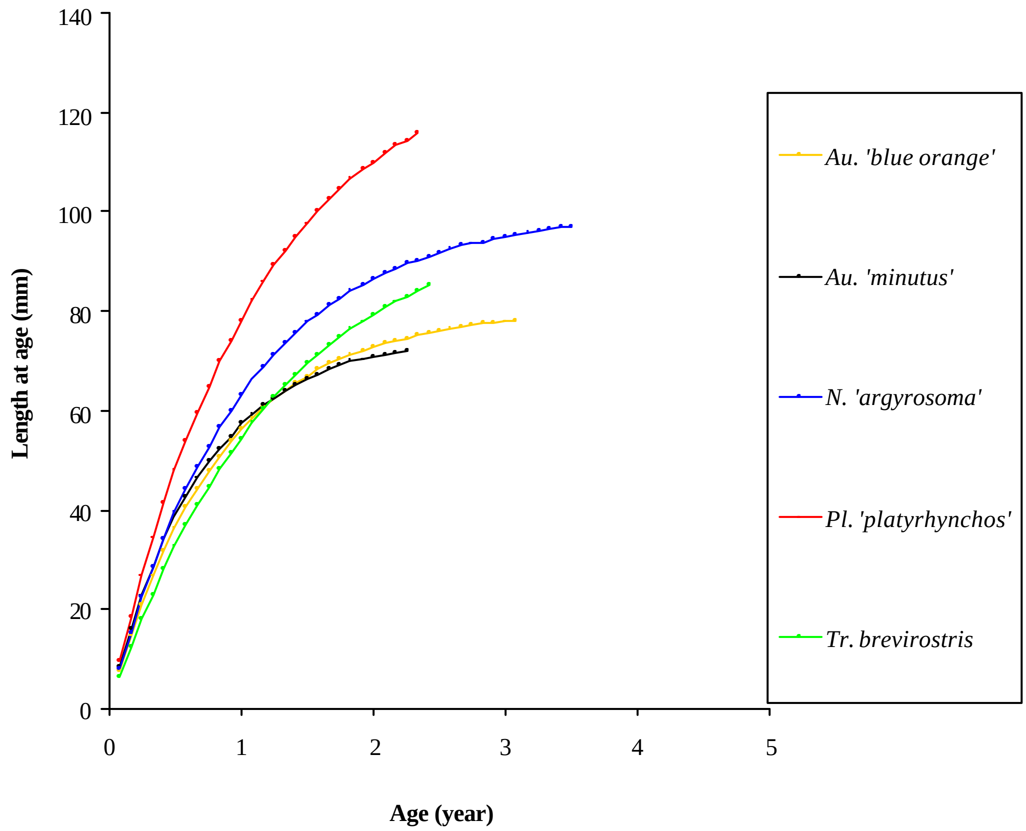


Figure G24. Von Bertalanffy growth curves for cichlid species caught by trawling in the SWA of Lake Malawi between June 1998 and May 1999. c: *Lethrinops spp.*, d: miscellaneous small species.

For a same population, values of L∞ and K can significantly vary from one cohort to another (Craig 1978). Examples of multiple cohorts within a same year class were given by *A. mentale*, *D. limnothrissa* and *M. anaphyrmus*, though they appeared for most of the medium and large species. For these three species, growth estimates of the two cohorts resulted in different growth performances (Figure G25).

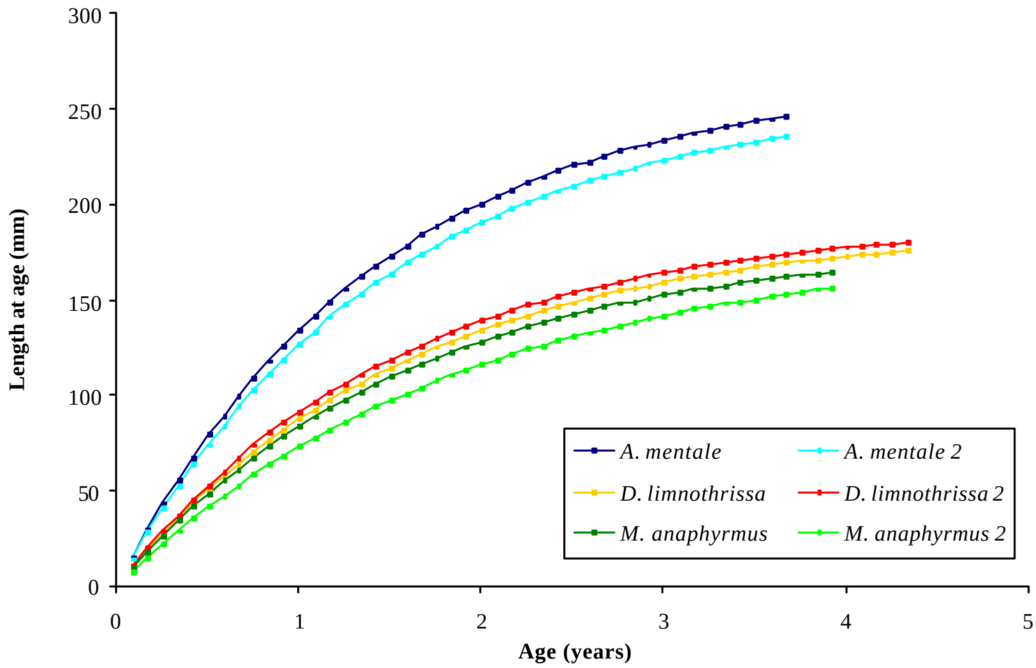


Figure G25. Von Bertalanffy growth curves illustrating differences among cohorts for three species caught by trawling in the SWA of Lake Malawi between June 1998 and May 1999. *Alticorpus mentale* = cohort born in April (L_∞ = 266, K = 0.7), *A. mentale* 2 = cohort born in October-November (L_∞ = 256, K = 0.68). *Diplotaxodon limnothrissa* = cohort born in May (L_∞ = 188, K = 0.62), *D. limnothrissa* 2 = cohort born in July-August (L_∞ = 192, K = 0.64). *Mylochromis anaphyrmus* = cohort born in May (L_∞ = 180, K = 0.62), *M. anaphyrmus* 2 = cohort born in September (L_∞ = 179, K = 0.52).

For *A. mentale*, the cohort born in April had a length of 200 mm at 2 years old against 190 mm for the cohort born in October-November (5.5 % difference). For *D. limnothrissa* the respective lengths at 2 years old were 134 mm for the cohort born in May and 139 mm for the cohort born in July-August (4% difference). The largest length difference at 2 years old (10.4%) was observed for *M. anaphyrmus*: 128 mm and 116 mm for the cohorts born in May and September, respectively. These growth differences appeared after only a few months and were already marked at one year old. This means that for fish of a same population, growth depends upon the period of birth, thus of the prevailing environmental conditions. The most important environmental parameters influencing growth are temperature, oxygen and food availability (Pauly 1980, Caulton 1982, Pitcher & Hart 1982, Wootton 1990). For the deep water species (*A. mentale*, *D. limnothrissa*) temperature variations over the year (less than two degrees, Figure G26a) were unlikely to influence growth. In the depth distribution of *M. anaphyrmus*, temperature variations were more important (between 4 and 5°C). However, during the period separating the two cohorts (May with best growth and September) temperature were at their minimum and increased from August until the next cold season (May to August). Temperature is therefore unlikely to account for the observed growth differences. The opposite pattern is observed for oxygen (Figure G26b) with higher seasonal fluctuations in the deep waters (about 5 $mg.l^{-1}$) than in the shallows (less than 2 $mg.l^{-1}$). In the deep zone, oxygen concentration increased from February to August and then decreased from September to January. For *A. mentale* (which presented the highest growth difference in the deep zone), the cohort with the slowest growth (born in October-November) faced a two fold decrease in oxygen concentration during its first three months. In December and January D.O. got down to 1.5 $mg.l^{-1}$, which represented about 17% saturation at 23°C and 100 m depth. It has been shown that growth of tilapia, which are well known to tolerate very low D.O., is reduced below 25% saturation (review by Chervinski 1982). Exposition to such low D.O. during at least two months might partly account for the observed growth difference between the cohorts. However both cohorts encountered periods of low oxygen concentration during their first six months and growth differences between cohorts were also observed for species which did not face low D.O. (*M. anaphyrmus*). Variations in food availability appears a more plausible explanation though little is known about seasonal variations of food availability for these three species with marked different feeding regimes: piscivorous, zooplanktivorous and malacophageous for *A. mentale*, *D. limnothrissa* and *M. anaphyrmus*, respectively (see chapter "Diet"). Nevertheless, whatever caused these growth differences among cohorts, it is striking that differences remained over time. Indeed, compensatory growth is well documented in fish and cichlids (review in Weatherley & Gill 1987, Melard et al. 1997). In Malawi cichlids for which fasting periods imposed by mouthbrooding are frequent, genuine capacities to buffer these periods are expected and probably exist (see Chapter 6).

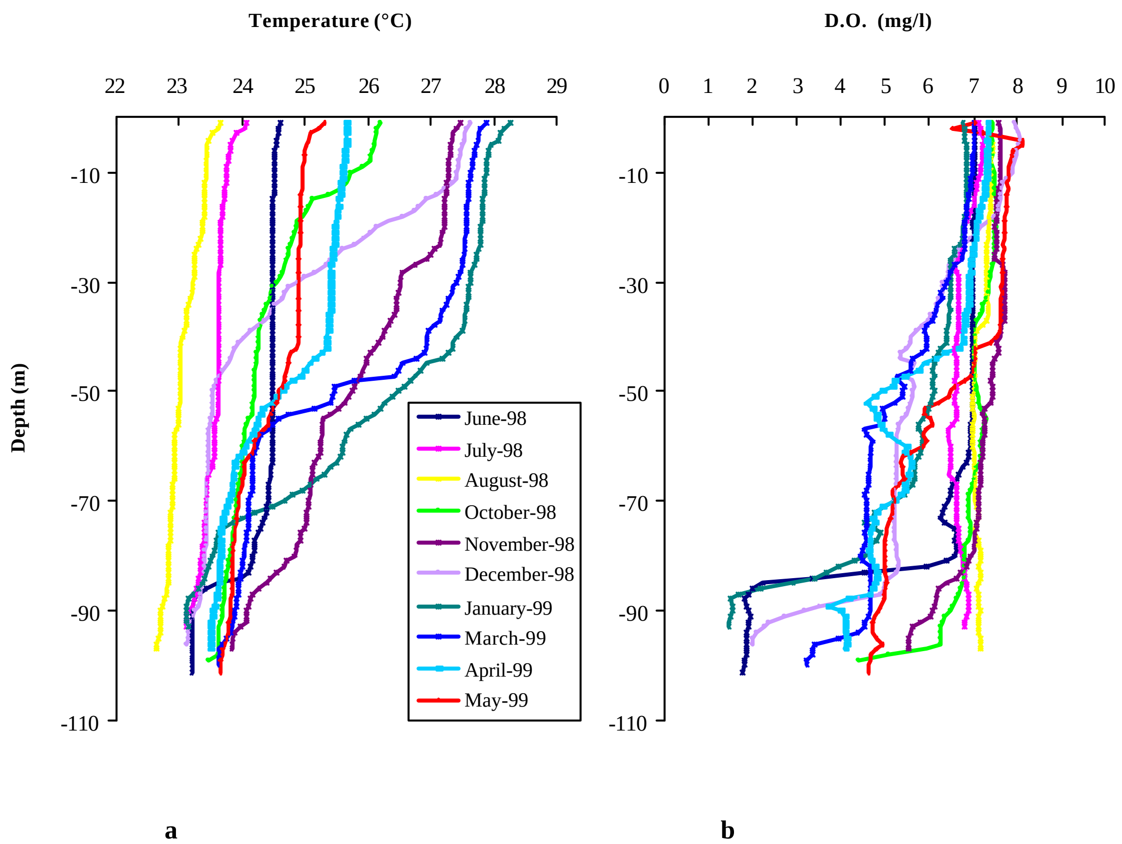


Figure G26. Seasonal variations of thermocline (a) and oxycline (b) at our 100 m transect in the SWA, Lake Malawi.

Equations allowing rapid estimation of Von Bertalanffy growth parameters were proposed for African freshwater fishes (de Merona 1983). These equations, based on 111 species, were:

$L_\infty' = 1.248$ TMM and $K' = 153 / L_\infty'$

TMM being the mean maximum length, usually calculated as the mean length of the ten largest specimen caught (Moreau & Nyakageni 1992). K' and L_∞' were calculated for our species and compared with K and L_∞ obtained from length progression analysis (Table G2). Rapid estimates of asymptotic length (L_∞') were always higher than the corresponding L_∞, except for *L. 'deep water altus'*, *L. polli* and *Tr. brevirostris* for which values were close. The same trend was observed with rapid estimates of the growth factor (K'), generally much higher than the K obtained from length frequencies. However, for the five largest and fastest growing species (*A. mentale*, *D. argenteus*, *P. tokolosh*, *L. argenteus* and *L. gossei*), rapid estimates were equal or lower than the observed K. The lack of fitting between the rapid growth estimates model and the estimates resulting from length progression analysis may lie in the fact that only half of the 111 species on which the model is based were cichlids, and most of them were tilapiine cichlids (de Merona 1983, de Merona et al. 1988). Only 9 species out of 111 were haplochromine cichlids. Next, the aim to this rapid growth estimates model was to provide a quick and reasonably reliable way to assess growth in absence of suitable data for other methods, not to replace them. The rapid growth estimation model does not seem well adapted to haplochromine cichlids, for which it tends to overestimate growth by an average value of 20 mm (ΔG) at 2 years old. However, the overestimation tended to be lower for small and large species than for medium sized ones (Figure G27).

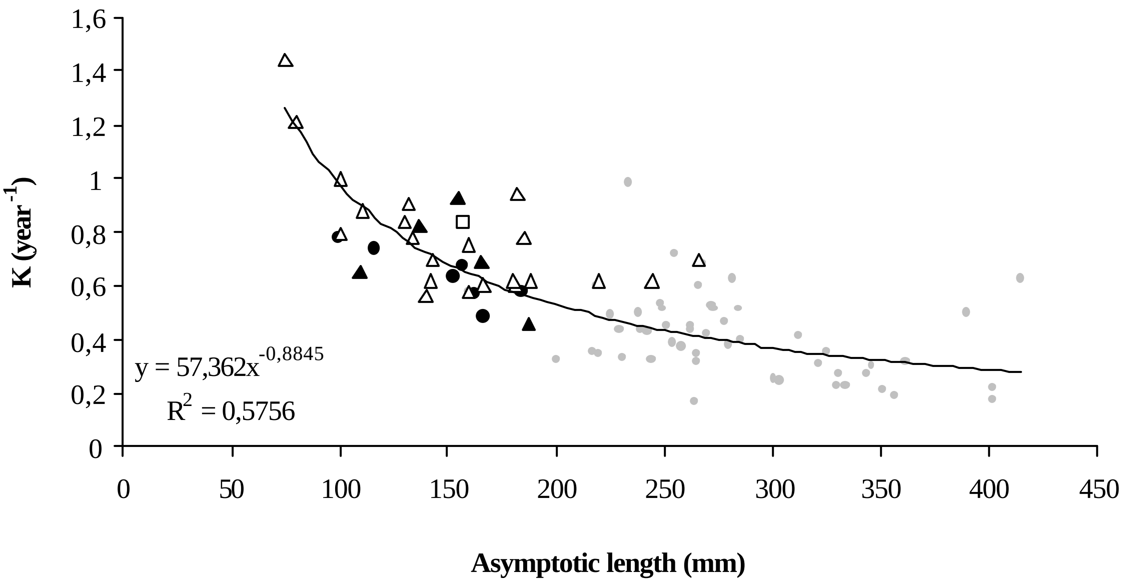


Figure G28. Relationship between K and L_∞ for 87 species of African cichlids. Grey spots = data from de Merona 1983, de Merona et al. (1988). Black spots = data from Iles (1971) and Tweddle & Turner (1977) for Malawi haplochromine cichlids, adjusted in SL by de Merona et al. (1988). Black triangles = data from Iles (1971) and Tweddle & Turner (1977) for Malawi haplochromine cichlids recalculated using ELEFAN by Moreau et al. (1995) and adjusted in SL using equation (1) (see Material and Methods). White square = *Diplotaxodon limnothrissa* from Thompson et al. (1995) adjusted in SL using equation (1). White triangles = data from this study.

Growth data available for 86 African cichlid species from Iles (1971), Tweddle & Turner (1977), de Merona (1983), de Merona et al. (1988), Moreau et al. (1995), and this study, were used to produce a general relationship between K and L∞ and to check how our estimates were fitting in it (Figure G28). Our estimates were within the range of reported values for other African cichlids and Malawian haplochromines and set new references for small species with asymptotic length below 100 mm. Out of the 23 species we studied, four had already been studied for growth parameters: *Copadichromis quadrimaculatus*, *C. virginalis* (Iles 1971, recalculated by Moreau et al. 1995), *Diplotaxodon limnothrissa* (Thompson et al. 1995) and *Mylochromis anaphyrmus* (Tweddle & Turner 1997, recalculated by Moreau et al. 1995). As growth estimates can vary from one cohort to another within a same population (Craig 1978, de Merona 1983 for review, this study), comparing our results with growth estimates obtained 20 to 30 years ago (Iles 1971, Tweddle & Turner 1977) in different geographic areas may appear useless. However, despite the time and distance separating the estimations, growth differences for a same species at 2 years old (calculated using equation 2) were within the range of the differences we found among cohorts of a same species, though growth performances were always better with our estimates. More striking were the differences of longevity we found compared to Iles's (1971) and Tweddle & Turner's (1977), who reported 5 to 6 years life span. As illustrated on Figure G24, the species were not growing older than 4.5 to 5 years, and most of them no older than 4 years. Similar life span were found by Moreau et al. (1995) from Iles's (1971) and Tweddle &Turner's (1977) data reanalysed using FiSAT package. Haplochromines and non tilapiine cichlids from other lakes also lived between 2 and 4.5 years (Moreau et al. 1995), which tends to confirm shorter life span than previously thought for non tilapiine cichlids. Attempts to determine accurately mortality rates were often not successful. Indeed, though within the range of mortality values reported for Malawi cichlids (Tweddle & Turner 1977, Moreau et al. 1995), mortality rates often appeared overestimated. Given the low fishing exploitation in the sampled area, reasonable estimates of instantaneous mortality rate (Z), particularly for the deep water species, should have been close to natural mortality estimates (M), which usually seemed reasonable. This was seldom the case. The reason mainly lie in the fact that length distributions were biased by lack or under-representation of smaller individuals. However, this is a common problem in Lake Malawi and even though juveniles were caught by fishing gears, it would be of little help considering the identification problems that would result. Consequently, though mortality rates were probably overestimated, they remain a useful basis for fisheries and trophic modelling.