Age, Growth and Yield-per-recruit analysis of ndunduma, *Diplotaxodon limnothrissa* (Teleostei: Cichlidae), in the Southeast Arm of Lake Malawi

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AGE, GROWTH AND YIELD-PER-RECRUIT ANALYSIS OF NDUNDUMA, *DIPLOTAXODON LIMNOTHRISSA* (TELEOSTEI: CICHLIDAE), IN THE SOUTHEAST ARM OF LAKE MALAWI.

Abstract

Diplotaxodon limnothrissa Turner (1995) is a widely distributed species occurring throughout Lake Malawi, extending from the surface to a depth of at least 220m. It is probably the most abundant cichlid in the lake with biomass estimates of around 87 000 tonnes in the pelagic zone alone. The species is exploited commercially in the southern part of the lake but since its inception the fishery has never been assessed. As such this study investigates some aspects of age and growth of the species besides applying a yield-per-recruit analysis to assess the status of the fishery.

Analysis of sectioned sagittal otoliths revealed that *D. limnothrissa* is fast growing and relatively long-lived species, attaining ages in excess of 10 years. Growth in length was rapid in immature fish, with fish attaining almost half of their maximum size within their first year. Length-at-age was described by the von Bertalanffy growth model with combined-sex growth described as $L_t = 211.21(1-exp(-0.24(t+1.36)))$ mm *TL*. Total, natural and fishing mortalities were estimated at 0.76 yr^{-1}, 0.31 yr^{-1} and 0.45 yr^{-1} respectively.

Per-recruit analysis indicated that the *D. limnothrissa* stock in the southeast arm of the lake is fully exploited as indicated by the current spawner biomass-per-recruit ratios of 31-55% $(SB/R)_{F=0}$. Modelling indicated that the current age-at-capture (2.67 years) is lower than the age at which yield is optimised (> 5 years) based on the $F_{0.1}$ harvesting strategy. It is, therefore, recommended that the age-at-capture should be increased from 2.67 to 5 years to optimise yield.

CHAPTER 1

GENERAL INTRODUCTION

1.1 Fisheries Resources of Malawi

The fish stocks of Malawian waters are among the most important natural resources of the country as they provide food and income to a large proportion of the population. It is estimated that 60-70% of the nation's protein consumption is supplied by fish, and that more than 70% of this comes from the Lake Malawi system (Mkoko 1992). The lake supports a highly diverse capture fishery that can be categorised as large-scale commercial, small-scale commercial and subsistence (Banda *et al*. 2001). The large-scale commercial fishery is a mechanised fishery that operates trawls, purse seines or lift nets. The small-scale commercial fishery includes all fishers that use engines of less than 20 horsepower or no engine to catch fish intended primarily for sale. Gears used in this sector include beach seines, open water seines, gill nets, fish traps, long lines and hand lines. By contrast, most of the catch from subsistence fishing is consumed at the household level. If there is a surplus it is sold (Banda *et al*. 2001).

Total annual yield from all species in the lake is estimated at *ca.* 40 000 tonnes (Banda and Tomasson 1997). The small-scale commercial fishery accounts for about 80% of the catch, and provides employment to *ca.* 30 000 people. The large-scale commercial fishery, confined to the southern part of the lake, accounts for about 20%

of the annual catch and provides jobs to *ca.* 1000 people (Banda and Tomasson 1997) while the contribution from subsistence fishing is negligible.

Fisheries management in Malawi, as with most countries, is shifting towards an approach that emphasises biological sustainability as well as addressing social, economic and policy issues through co-management (GOM 1999; Welcomme 2001). In Malawi, most management guidelines are based on biological information and catch statistics. Catch and effort data is used to determine management related quantities generated from surplus production models, which include maximum sustainable yield (MSY) and optimum level of fishing effort (F_{MSY}). These data, together with some biological information such as spawning seasonality and gear selectivity, are used by the Department of Fisheries to develop management recommendations pertaining to technical restriction on fishing gears, restrictions of fishing areas or fishing times and minimum harvestable sizes (Bulirani *et al.* 1999). In agreement with current practices in fisheries management, the precautionary approach (FAO 1996) has also been employed in the management of the commercial fisheries (Bulirani *et al.* 1999).

Although a number of management measures have been developed for the fisheries in Lake Malawi, some fish stocks within the lake have declined in recent years (Bulirani *et al.* 1999). The most noticeable decline in catches has been in the commercially important inshore genera such as *Oreochromis* spp. (chambo), *Bathyclarias* spp. (bombe), *Bagrus meridionalis* (kampango), and *Copadichromis* spp. (utaka). The decline of the commercially important genera has been attributed to excessive effort resulting from the 'open-entry' nature of the small-scale commercial fishery and weak enforcement of regulations (Bulirani *et al.* 1999). It is evident that efficient management of Lake Malawi fisheries requires stringent control of effort and an improvement in the enforcement of regulations.

Following the decline of the inshore stocks (< 30 m depth), fishing pressure is now being directed towards the relatively unexploited offshore waters (> 30 m depth) that comprise about 80% of the lake's area (Menz 1995). Using acoustic methods, Menz *et al.* (1995) estimated the total fish biomass in the offshore and predominantly pelagic waters at 168 000 tonnes of which about 87 000 tonnes (52%) was composed of *Diplotaxodon limnothrissa*. Other important offshore species include *Diplotaxodon* 'bigeye' spp. (33 000 tonnes), *Copadichromis quadrimaculatus* (8 700 tonnes), *Engraulicypris sardella* (5 100 tonnes), *Synodontis njassae* (13 400 tonnes), *Rhamphochromis* spp. (16 800 tonnes), and two *Opsaridium* species, namely, *O. microcephalus* and *O. microlepis,* which together accounted for about 1 300 tonnes (Menz *et al.* 1995). These findings suggest that the genus *Diplotaxodon,* locally known as ndunduma, is probably the most important commercial group in the open waters of Lake Malawi and any future offshore fishery is likely to be based on them (Thompson 1995).

Ndunduma, endemic to Lake Malawi, are deep-water piscivorous and zooplanktivorous cichlids of the genus *Diplotaxodon* Trewavas (1935). They comprise over 13 species of which only four are formally described (Eccles and Trewavas 1989; Turner 1996). These include *Diplotaxodon argenteus* Trewavas (1935), *D. greenwoodi* Stauffer and McKaye (1986), *D. ecclesi* Burgess and Axelrod

(1973) and *D. limnothrissa* Turner (1994). Allison *et al.* (1995) and Turner (1996) provide detailed descriptions of the other unnamed species.

Ndunduma are widely distributed throughout the pelagic zone of the lake from the surface to a depth of at least 220m (Thompson *et al.* 1995). However, of all the species, only *D. limnothrissa* (Figure 1.1) is fairly well distributed and occurs in sufficient quantities to support viable fisheries throughout the lake (Menz *et al*. 1995). The species attains a maximum size of 190 mm total length (TL) and feeds mainly on plankton, dominated by the crustaceans *Tropodiaptomus*, *Mesocyclops* and *Diaphanosoma*. Filamentous diatoms such as *Aulacoseira*, *Engraulicypris sardella* fry and chaoborid larvae and pupae are also occasionally ingested (Allison *et al.* 1995).

Figure 1.1: Male *D. limnothrissa* sampled from southeast arm of Lake Malawi (source: Turner 1996).

1.2 The *Diplotaxodon limnothrissa* resource in southern Lake Malawi

Being a principally deep-water species (>50 m), the *D. limnothrissa* resource is mostly harvested by the trawl fisheries although occasional landings are also reported in small-scale commercial fishing gears such as chilimira (open water seine) nets and gill nets (Turner 1996). Exact quantities of the species harvested by the small-scale commercial sector are, however, unknown. The percentage composition of *D. limnothrissa* in the catches from the mid-water, demersal and pair-trawl fisheries within the southeast arm was estimated at *ca*. 53%, 18% and 5% respectively (Turner 1996). In 2001, the large-scale commercial sector landed about 1 222 tonnes of ndunduma out of a total catch of 4 927 tonnes. This represents about 25% of the annual total catch from the southeast arm of the lake (Figure 1.2). The increase in ndunduma catches in 2001 (Figure 1.2) can perhaps be attributed to the entry into the fishery of *M.V. Kampango*, a new midwater trawler owned by Maldeco Fisheries Ltd that fishes for both pelagic and semi-pelagic species.

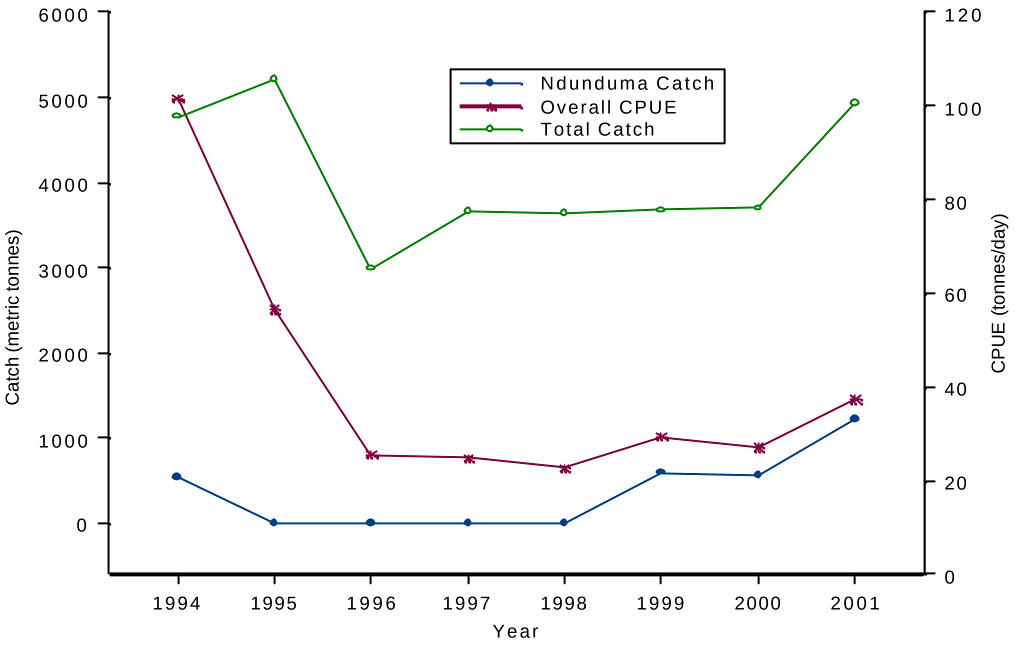


Figure 1.2: Trends in annual catches of all *Diplotaxodon* species in the large-scale commercial sector from 1994 to 2001 (source: Fisheries department).

The bi-annual monitoring surveys conducted in the southeast arm of the lake between 1996 and 1999 indicate that the composition of *D. limnothrissa* in the catches from the southeast arm of the lake has increased from 3% in 1996 to over 11% in 1999 (Figure 1.3). This change in species composition is probably linked to trawling (Turner 1976). It has been observed that the intensification of fishing activities in southern Lake Malawi has resulted in large changes in species composition with small species having replaced larger ones (Turner 1976).

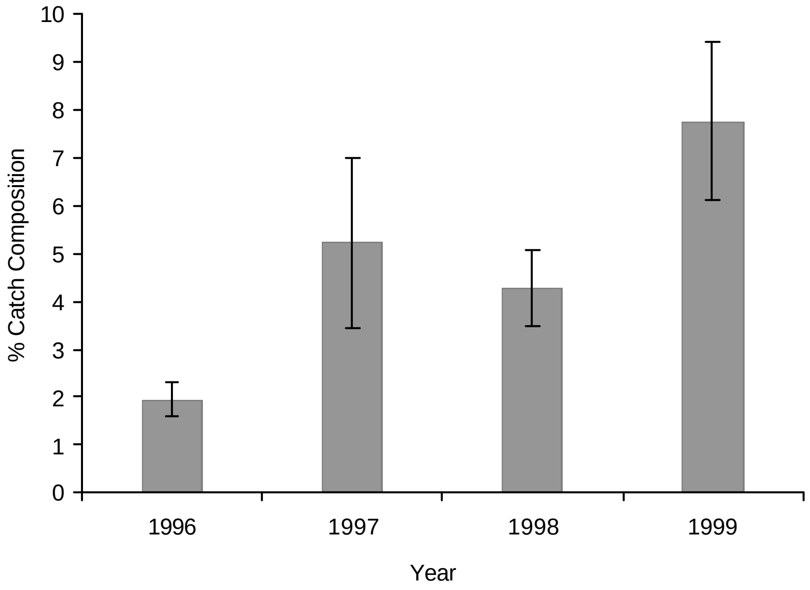


Figure 1.3: Percentage catch composition (±SD) of *Diplotaxodon limnothrissa* in the southeast arm of Lake Malawi based on bi-annual monitoring surveys conducted from 1996-1999 (source: Fisheries department).

1.3 Requirement for a management plan for ndunduma

The Malawi government is currently collaborating with the African Development Bank (ADB) to develop the deepwater/offshore fishery (M.C. Banda National Research Co-ordinator - personal communication). The rationale behind this project is to increase offshore fish yield thereby reducing fishing pressure on the inshore stocks, which has reached unsustainable levels. However, little is known about the offshore resources. The only information available is that from the work undertaken by the United Kingdom and the Southern African Development Community (UK/SADC) Pelagic Fish Resource Assessment Project in 1995, which assessed the fisheries potential of the pelagic zone of Lake Malawi (Menz 1995). Thompson (1995) undertook the assessment using a Beverton and Holt dynamic pool model and estimated yield and maximum exploitation levels for each of the pelagic species. The assessment was based on fish in the entire lake and it was assumed that natural mortality for ndunduma and other cichlids was 0.5 year^{-1}as direct estimates could not be made due to a lack of age data. It was noted that cichlids provide highest yields when harvested at a fairly large size and that spawning stock biomass was maintained at reasonable levels only when the size-at-capture was near or greater than the size-at-first maturity. They concluded that offshore cichlid fisheries might not be viable if the size-at-first capture was greater than the size-at-first maturity (Thompson 1995). These conclusions might not be entirely true for Lake Malawi cichlids, considering their low fecundity, high degree of parental care (Thompson 1995) and the fact that the size or age, which provides optimum yield is not known. Furthermore, they may not be applicable to specific stocks in various parts of the lake due to differences in exploitation levels and productivity - all of which have significant impacts on reproduction, growth rates and mortality. It is possible that most of these stocks have different population parameters and should therefore not be treated as a single stock. The sustainable exploitation of these stocks therefore depends on stock specific or area specific management plans.

1.4 Objectives of the study

The proposed development of the offshore fishery, which will likely target ndunduma, coupled with lack of management guidelines for sustainable exploitation of this resource imply an urgent need for a management plan. Unfortunately, the scientific information required for formulation of such regulations is not available. The central objective of this study is, therefore, to provide the scientific information required to undertake a per-recruit analysis of the *D. limnothrissa* component of the ndunduma stock, which will be the basis for providing management advice.

This thesis has been partitioned into six chapters, each addressing a specific aspect of the study. A description of the study area, the distribution of *D. limnothrissa*, available data and sampling methods are presented in Chapter 2. Chapters 3 and 4 present aspects pertaining to its age, growth, estimates of natural and fishing mortality and reproductive biology. These chapters provided the necessary input parameters for the per-recruit analyses presented in Chapter 5 where the *D. limnothrissa* resource was assessed using a Thompson and Bell yield-per-recruit model incorporating information on age-specific gear selectivity. A final discussion together with management recommendations is presented in Chapter 6.

CHAPTER 2

STUDY AREA, AVAILABLE DATA AND SAMPLING METHODS

2.1 The Study Area

The southern part of Lake Malawi (Figure 2.1) can be sub-divided into two regions- the southeast arm and southwest arm. This study was conducted in the southeast arm (Figure 2.1) because the area is generally more productive and has a higher concentration of fishing effort than the southwest arm (Banda and Tomasson 1997).

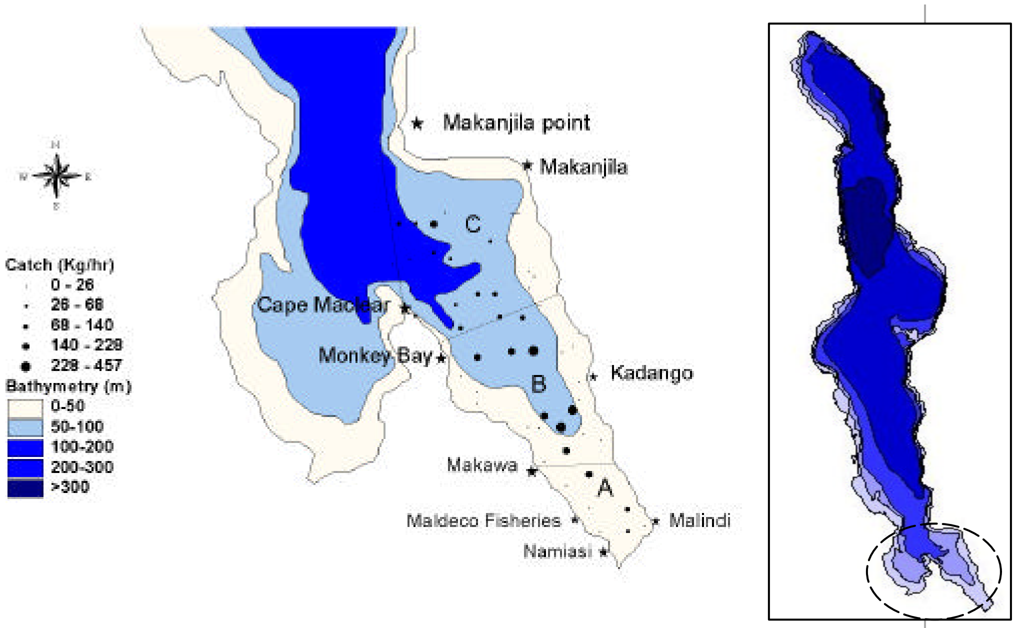


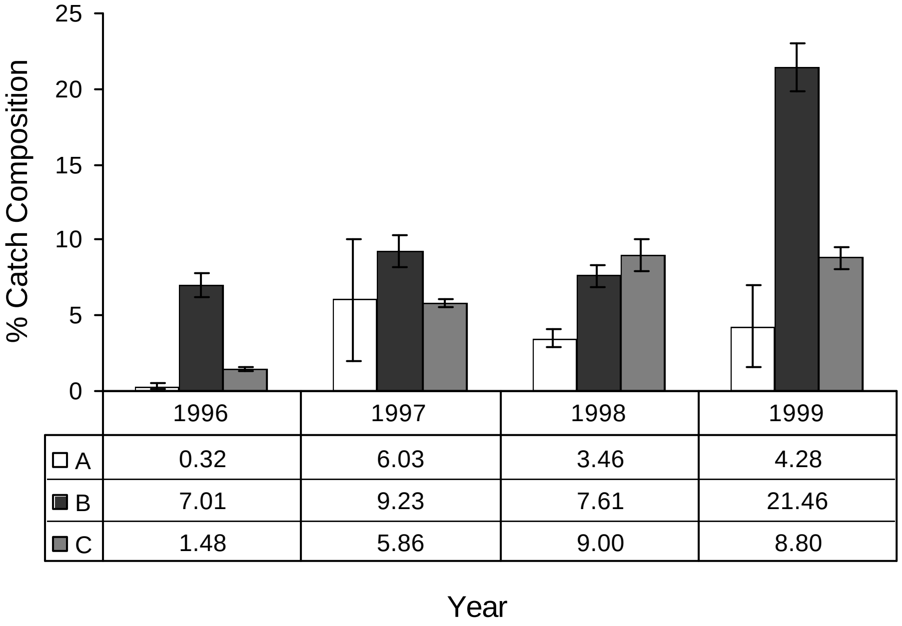
Figure 2.1: Map of the study area and Lake Malawi (insert). Also shown are average catch rates for *Diplotaxodon limnothrissa* in each of the management areas (areas A, B and C) based on the bi-annual demersal monitoring surveys of 1996-1999.

The southeast arm of Lake Malawi covers an area of 1 742 km^2 (Banda and Tomasson 1997) and is bounded in the south by the exit to the Shire River from the lake at

14°25'S, by the headlands of Makanjila point at 13°44'S on the east, and Cape Maclear at 13° 57'S on the west. The width at the southern end is approximately 10 km, while the broadest point between Monkey Bay and Makanjila is 35 km. Depth increases gently towards the north, attaining a maximum depth of 120m between Cape Maclear and Makanjila point. Of the several islands that are found in the southeast arm, Boadzulu Island, located in area A, is the largest (Eccles and Trewavas 1989).

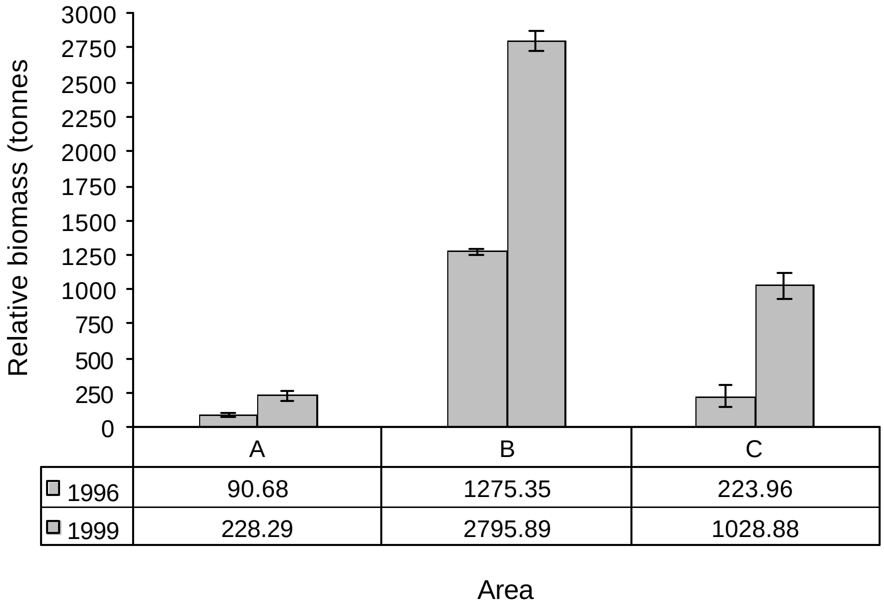
The southeast arm is sub-divided into areas A, B and C for purposes of research and licensing of fishing craft (Figure 2.1). Area A is designated as the southern part of the southeast arm south of Boadzulu Island, while Area B is described as that part of the southeast arm north of Boadzulu Island up to Monkey Bay. Area C includes the remaining portion of the southeast arm north of Monkey Bay. Area A is the shallowest of the three areas with maximum depth of approximately 50m. Area B embraces the highly productive shelf areas at 40-80 m depth - the main trawling grounds for both pelagic and demersal trawl fisheries. Area C is the deepest area with most of the area being between 90 and 120 m in depth (Turner 1996).

The distribution of *D. limnothrissa* within the southeast arm shows a distinct spatial pattern (Kanyerere 2000). As shown in Figure 2.1, the species is more abundant in deep waters of area B than in areas A and C. Estimated average catch rates obtained during the four demersal trawl surveys of 1996-1999 were 132 ± 3 kg hr^{-1} in deep waters of area B, 31 ± 2 kg hr^{-1} in area C and 45 ± 5 kg hr^{-1} in area A.



	1996	1997	1998	1999
□ A	0.32	6.03	3.46	4.28
■ B	7.01	9.23	7.61	21.46
▨ C	1.48	5.86	9.00	8.80

Figure 2.2: Percentage catch composition (± SD) of *Diplotaxodon limnothrissa* in areas A, B and C of the southeast arm based on bi-annual monitoring surveys conducted from 1996-1999 (source: Department of Fisheries).



	A	B	C
▨ 1996	90.68	1275.35	223.96
▨ 1999	228.29	2795.89	1028.88

Figure 2.3 Relative biomass estimates (tonnes ± SD) of *Diplotaxodon limnothrissa* in areas A, B and C of the southeast arm based on bi-annual monitoring surveys conducted in 1996 and 1999 (source: Department of Fisheries).

Data on catch composition by species, covering the period from 1996 to 1999 (Figure 2.2), illustrates the high abundance of ndunduma in areas B and C. The proportion of the species in the total catch also increased steadily over the same period from 0.32 to 4% in area A, 7 to 21% in area B and 1.5 to 9% in area C. The relative biomass of the species also increased over the same period from 90 to 228 tonnes in area A, 1 275 to 2 796 tonnes in area B and 224 to 1 029 tonnes in area C (Figure 2.3).

2.2 Sources of Data

The data used in this thesis was obtained from both fisheries dependent and independent sources and are summarised in Table 2.1.

Table 2.1: Sources of the data used in this thesis.

Data type	Fishery type	Source
Survey data		
R.V. Ndunduma, June-July 1999	Demersal (research)	Department of Fisheries
Length frequency data		
Pair trawl fishery, 2001	Demersal (commercial)	Department of Fisheries and National Aquatic Resource Management Project
Biological data		
R.V. Ndunduma, June-October, 2001	Demersal (research)	This study
Maldeco Fisheries Ltd, November-December, 2001; January-June, 2002	Demersal and midwater (commercial)	This study
Meteorological and limnological data		Patterson and Kachinjika (1995)

The survey data used in this thesis was obtained during routine bi-annual demersal monitoring surveys of the southeast and southwest arms of the lake which were undertaken in June-July 1999 using the Department of Fisheries research vessel - the

R.V. Ndunduma. A total of 83 predetermined stations were sampled in the southeast arm during the 1999 survey covering depths ranging from 10-150 m.

Length frequency data for the pair-trawl fishery was obtained from the pair trawl fishery operating in area A. The fishery employs a bottom trawl net with a codend mesh size of 25 mm.

Samples for biological studies were collected on board the research vessel *R.V. Ndunduma* and also from Maldeco Fisheries Limited. Due to technical problems, the *R.V. Ndunduma* was not operational for much of the year 2001 up to the end of the sampling program in June 2002. Therefore, from November 2001 to June 2002 all samples were collected from Maldeco Fisheries vessels operating in areas B and C.

2.3 Sampling Methods

The survey data, which comprise length frequency and catch, were collected on-board the *R.V. Ndunduma* between June and July 1999. Biological data was collected between June and October 2001 in areas B and C. The sampling procedure for these studies is described in Chapters 3 and 4 while the general procedure used during the research surveys is briefly described.

The trawl stations sampled during the surveys are fixed and their allocation takes into consideration the different depth gradients within the lake (Palsson *et al.* 1999). The *R.V. Ndunduma*, a 386 horsepower stern trawler, was used during the surveys. The fishing gear employed was the Gulltoper bottom trawl net which is also used in commercial demersal trawlers. The gear has a 38 mm codend and a 100 mm mesh in the wings. The headrope was 23 m long with a horizontal and vertical opening of 14.7 m and 4 m respectively. Each trawl had a duration of *ca.* 30 minutes at a trawling speed of 3.5 nautical miles hour^{-1}.

The sampling and recording of the catch closely followed guidelines outlined by Sparre *et al.* (1989). All catfishes of the genera *Bathyclarias, Clarias* and *Bagrus* as well as large cichlid and non-cichlid species were sorted out of the main catch. Thereafter the catch was divided on deck into four categories namely; small fish (mainly cichlids but also including *Synodontis njassae*), *Bagrus meridionalis,* clariid catfishes and all big cichlid and non-cichlid fishes. Each category was sorted into species, total length measured (mm) and whole weight recorded (g). The pair trawl fishery was also sampled using a similar procedure. Length frequencies and catch data for *D. limnothrissa* were raised to the total catch for each trawl as described by Weyl (2002).

CHAPTER 3

AGE, GROWTH, MORTALITY AND POPULATION STRUCTURE OF NDUNDUMA IN THE SOUTH EAST ARM OF LAKE MALAWI

3.1 Introduction

Accurate age determination is essential to both fisheries biology and management as it provides information pertaining to stock age structure, age-at-first maturity, spawning frequency, individual and stock responses to changes in the habitat, recruitment success and determination of population changes due to exploitation (Morales-Nin 1992; Francis *et al.* 1999). Age information also enables determination of growth and mortality, which form the basic input parameters for population dynamics models used in fishery analyses (Morales-Nin 1992; Sparre and Venema 1998; Campana and Thorrold 2001; Welcomme 2001). The ability to age *D. limnothrissa* is, therefore, essential.

Previous attempts to age *D. limnothrissa* using otoliths, scales and opercular bones proved unsuccessful (Thompson *et al*. 1995). No annuli were visible on either otoliths or opercular bones when viewed under direct, transmitted or polarised light and although growth zones were visible on the scales, there was little consistency in estimated ages for fish of the same size (Thompson *et al*. 1995). It was concluded that the growth zones noticed were not of an annual nature. The lack of visible annual growth zones was attributed to insufficient seasonal differences in the offshore environment, which probably failed to induce seasonally related growth rates (Thompson *et al*. 1995). In the absence of suitable hard structures, their study opted for length-based ageing models such as Shepherd's length composition analysis (SLCA; Shepherd 1987), and electronic length frequency analysis (ELEFAN; Pauly 1987). It was noted that both models could only age fish up to 3 years due to difficulties in separating length frequency modes from fish older than 1.5 years. Growth in *D. limnothrissa* is, therefore, largely unknown. This chapter aims to re-determine the age and growth pattern of *D. limnothrissa* in the southeast arm of Lake Malawi using burnt sagittal otoliths.

3.2 Materials and Methods

3.2.1 Age and Growth

D. limnothrissa were collected from Maldeco Fisheries Ltd between May 2002 and June 2002. A total of 508 fish, ranging in size from 25 mm to 195 mm TL were collected. Fish were measured for total length (TL) and standard length (SL) to the nearest millimetre and weighed whole to the nearest gram. Both saggital otoliths were removed, cleaned and stored dry in marked manila envelopes for later processing. Otolith maximum diameter (distance from anterior tip of rostrum to postrostrum) was measured to the nearest 0.01 mm using a Mitutoyo digitised calliper. For otoliths less than 2 mm maximum diameter, measurements were taken using a calibrated ocular eyepiece fitted to a Nikon compound light microscope.

3.2.2 Preparation of otoliths for examination

As no asymmetry in otolith shape was apparent, left or right saggital otoliths from each fish were arbitrarily selected for ageing. To enhance otolith growth zone visibility, a burning technique recommended by Brothers (1987) and Morales-Nin (1992), was employed. Each otolith was lightly burned to a light brown colour using a double coil electric hotplate with adjustable heat settings. To avoid charring, a specially designed tray was used to hold the otoliths about 5 centimetres (cm) above the heating element.

Preliminary examination indicated that growth zonation was most visible using transverse rather than longitudinal or diagonal sections. This observation was in agreement with Brothers (1987) recommendation that transverse sections were most appropriate for sagittae because of asymmetric sagittal growth. In readiness for sectioning, burnt otoliths were embedded in clear fibreglass casting resin, and sectioned to a thickness of about 0.5 mm through the nucleus using a double-bladed diamond saw. Sections were cleaned of excess water and residues prior to mounting on microscope slides with DPX mountant. The mounted sections were viewed with a Nikon stereo dissecting microscope under transmitted light using a magnification of 3.5 X.

3.2.3 **Interpretation of Growth zones**

Under transmitted light, the opaque zones appear as dark shadowy rings, while the translucent zones appear as bright light rings (Williams and Bedford 1973). A translucent and an opaque zone together constituted a complete growth zone. Opaque zones in *D. limnothrissa* are relatively thick and compound in nature. Interpretation was relatively difficult for otoliths having more than 8 rings and an index of readability (Table 3.1) was used to classify the otoliths according to appearance of the growth zones (Fossen *et al.* 2002).

Table 3.1: Criteria used for classifying otolith readability in *Diplotaxodon limnothrissa*.

Readability	**Growth Zone Appearance**
1	Believed to be reliable, good definition between translucent and opaque zones
2	Relatively clear zonation but not well defined, the error margin is expected to be ± 0.5 year (i.e. ± 1 ring).
3	The zones are vaguely marked, and the error margin maybe ±1 year or more (i.e. ± 2 rings).

Otoliths were read twice, at an interval of three weeks, without reference to the date of capture or length of the fish. A mean age was accepted if the number of opaque zones for each of the two readings was equal or their difference was less than or equal to two.

The precision of age determination was assessed using the average percent error method (Beamish and Fournier 1981). This method was chosen because it evaluates the degree of precision equally for all individuals unlike the percent agreement method, which is said to be insensitive to age distribution in a fishery (Beamish and Fournier 1981).

According to the percent error method, if N fish are aged and R is the number of times each is aged, then X_{ij} is the ith age determination of the jth fish and X_j, the average age for the jth fish is calculated as:

$$X_j = \frac{1}{R}\sum_{i=1}^{R} X_{ij} \tag{1}$$

The average error in ageing the jth fish as a fraction of the average of the age estimates, APE is:

$$APE = \frac{1}{R}\sum_{i=1}^{R} \left\{ \frac{\left| X_{ij} - X_j \right|}{X_j} \right\} \times 100 \tag{2}$$

The Index of Average Percent Error (IAPE) was modelled as:

$$IAPE = \frac{1}{N}\sum_{j=1}^{N} \left\{ \frac{1}{R}\sum_{i=1}^{R} \frac{\left| X_{ij} - X_j \right|}{X_j} \right\} \times 100 \tag{3}$$

The degree of precision is improved by minimisation of the percent error.

To evaluate the reproducibility of each age estimate, a coefficient of variation between readings was calculated (Chang 1982). Estimation involved replacing the average absolute deviation from the arithmetic mean with the standard deviation. An index of precision (D) was then used to estimate the percent error contributed by each observation to the average age class such that:

$$D = \frac{CV}{\sqrt{R}}$$

where CV is the coefficient of variation.

The percent error in each age was obtained by multiplying the index of precision (D_j), by the average age for the jth fish.

3.2.4 Validation

The use of calcareous structures for ageing depends on the assumption that periodic features are deposited at a constant frequency. Calcareous structures, however, frequently exhibit false zones that can be misinterpreted as being periodic. Validation is, therefore, essential (Wootton 1998; Beamish and McFarlane 1987). Growth zone formation periodicity for *D. limnothrissa* was indirectly validated by following the progression of zones formed on the margin of the otolith throughout the year using samples collected at monthly intervals. The marginal composition of otoliths was graded as opaque, narrow hyaline or wide hyaline upon comparison with the width of the preceding hyaline zone (Francis *et al*. 1999). Each otolith was examined twice to ensure correct identification of the status of the marginal zone such that the reading was only accepted if two readings were identical. Growth zone deposition periodicity was identified by plotting a graph of the monthly percentage of otoliths with opaque, narrow and wide hyaline zones (Morales-Nin 1992) as a function of time with a minimum of 30 otoliths per month. The presence of a periodic trend was then tested statistically using autocorrelation and autoregressive integrated moving average models (ARIMA) (Priestley 1981). These models describe the temporal dependence structure and length of the deposition period. According to Priestley (1981) if x_t is a stationary time series with mean m and variance σ_x^2, and assuming that t takes on the values $t = 0, \pm1, \pm2, \ldots$ The autocovariance function of x_t at lag k is defined as:

$$g(k) = E(x_t - m)(x_{t+k} - m)$$

Since x_t is stationary, the autocovariance function does not depend on t and the autocorrelation function at lag k is defined as:

$$r(k) = \frac{g(k)}{g(0)} = \frac{g(k)}{s_x^2}$$

Both the autocovariance and autocorrelation functions are even functions; that is, $\gamma(k) = \gamma(-k)$ and $\rho(k) = \rho(-k)$. The autocorrelation function also satisfies the inequality:

$$|r(k)| \leq 1 \qquad \forall \qquad k = 0,\ \pm1,\ \pm2 \ldots\ldots\ldots\ldots \pm n$$

The software *S-PLUS 2000* (S-PLUS 1999) was used for all statistical computations.

3.3 Estimation of Growth Parameters

Length-at-age was modelled using the three-parameter von Bertalanffy growth model (VGBF), which is described as:

$$L_t = L_\infty\left(1 - \exp^{-K(t-t_0)}\right)$$

where L_t is length at time t, L_∞ is the theoretical asymptotic length, K is the Brody growth coefficient that determines the rate at which L_∞ is attained, and t_0 the age of zero length fish.

Growth parameter estimates were obtained using generalised non-linear least squares procedures with parameter variance estimates calculated using parametric bootstrap resampling with 500 bootstrap replicates. Confidence intervals were obtained from the sorted bootstrap data using the first-order bias-corrected percentile method (Efron 1987; Efron and Tibshirani 1993). The starting values for K and t_0 were estimated from the von Bertalanffy plot while L_∞ was estimated from the average of ten largest sampled specimens (Sparre and Venema 1998).

The relationship between otolith length and fish total length was described by linear regression (Maceina and Betsill 1987), while a power function was used to model the relationship between weight and fish total length (Pitcher and Hart 1990).

3.4 Mortality

Total annual mortality for *D. limnothrissa* in the southeast arm was estimated using two methods. An age length key, constructed from length-at-age data was used to transform length frequency distributions to age frequency distributions (Butterworth *et al*. 1989) from which instantaneous total mortality (Z) was estimated by catch curve analysis (Ricker 1975). The length frequency data was obtained from the bi-annual monitoring survey of 1999. Total mortality was also estimated using the equation developed by Cooke and Beddington (1981) of the form:

$$Z = Ln\left(1 + \frac{1}{(a_m - a_f)}\right)$$

where a_f is the age at full recruitment and a_m is the mean age of fully recruited fish. a_f and a_m were estimated from the gear selection ogives (chapter 5) at 7 and 8 years, respectively.

Natural mortality was estimated using Pauly's empirical formula (Pauly 1980) of the form:

$$Ln(M) = -0.0152 - 0.279 \times Ln(L\infty) + 0.6543 \times Ln(K) + 0.463 \times Ln(T)$$

where L_∞ and K are the von Bertalanffy growth parameters and T is the mean lake temperature (^{o}C). The mean annual water temperature on Lake Malawi is approximately 25 ^{o}C (Patterson and Kachinjika 1995).

Pauly (1980) observed that the empirical equation he developed generally overestimated the value of natural mortality for shoaling species and he therefore recommended that a correction factor of 0.8 should be used to reduce the bias. Since *D. limnothrissa* is a shoaling species, the estimated natural mortality was corrected for bias by multiplying it by 0.8. Fishing mortality *(F)* was obtained via subtraction as $Z = F+M$ (Gulland 1985).

3.5 Results

3.5.1 Age and Growth

Morphometric relationships between otolith length (mm) and fish total length (mm), and that between fish total length (mm) and weight (g) of combined sex *D. limnothrissa* are summarised in Table 3.2

Table 3.2: Morphometric relationships between otolith length (OL mm), fish weight (Wt g) and fish total length (TL mm) of *Diplotaxodon limnothrissa* from the southeast arm of Lake Malawi.

Relationship		**r^2**	**p**	**n**
OL (mm)	= 0.4451 + 0.02615 x TL (mm)	0.95	<0.0001	268
Wt (g)	= 0.000019 x TL $(\text{mm})^{2.85}$	0.99	<0.0001	508

3.5.2 Interpretation and Validation of Otolith growth zones

Growth zones in sectioned sagittal otoliths were noted optically as a succession of wide and opaque zones separated at regular intervals by narrower translucent zones. This configuration is illustrated in Figure 3.1.

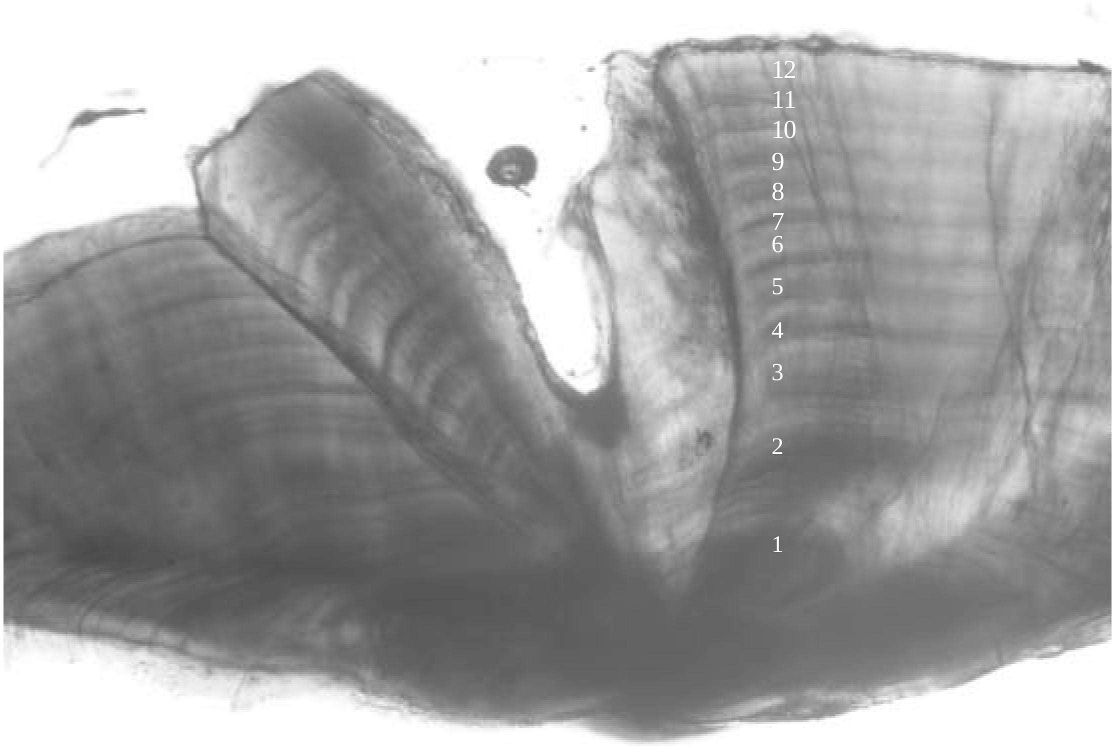


Figure 3.1: Photograph of a sectioned sagittal otolith from a six year-old *Diplotaxodon limnothrissa* with 12 opaque zones. The fish was 180 mm TL.

Of the 503 otoliths examined, 40 (8%) were rejected as unreadable (i.e. no growth zones visible), 117 (23%) could not be aged reliably (i.e. difference in growth zones > 2) and 346 (69%) were deemed to be reliable (i.e. difference in growth zones ≤ 2). The sample included 5 otoliths from juveniles of between 20 and 34 mm TL (collected from buccal cavities and therefore assumed to be zero years old) and were used in estimating growth parameters. Of the 346 otoliths, 73 (21%), 148 (43%) and 125 (36%) were classified as having readability 1, 2 and 3 respectively. Otolith readability was generally poor for fish aged between 3 and 4 years (Figure 3.2). In total, over 60% of the otoliths had relatively well-defined growth zonations.

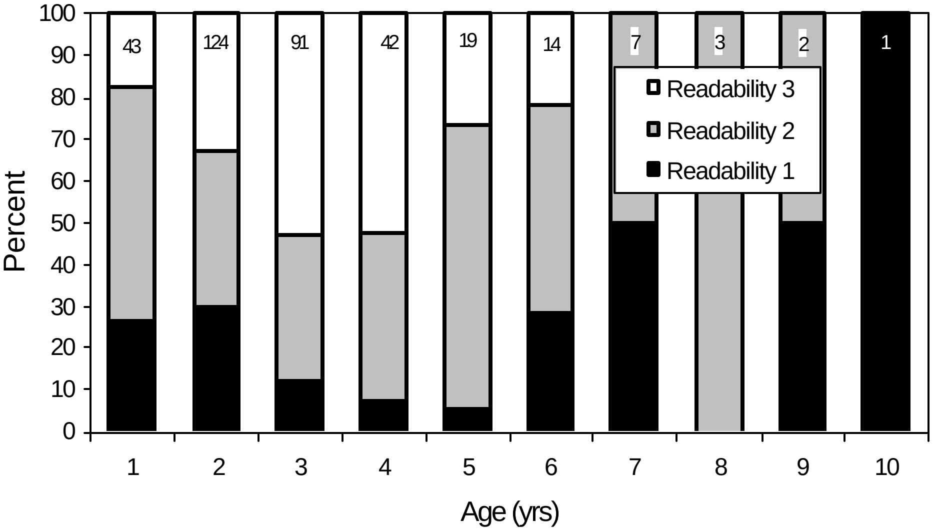


Figure 3.2: Readability of *Diplotaxodon limnothrissa* otoliths by age group. The number of otoliths per age group is indicated on top of each bar.

The monthly percentage of otoliths with opaque, narrow hyaline and wide hyaline margins collected between June 2001 and May 2002 is illustrated in Figure 3.3. The monthly examination of the otolith margins revealed that two opaque zones were deposited annually, one between April-May and the second during September-October (Figure 3.3).

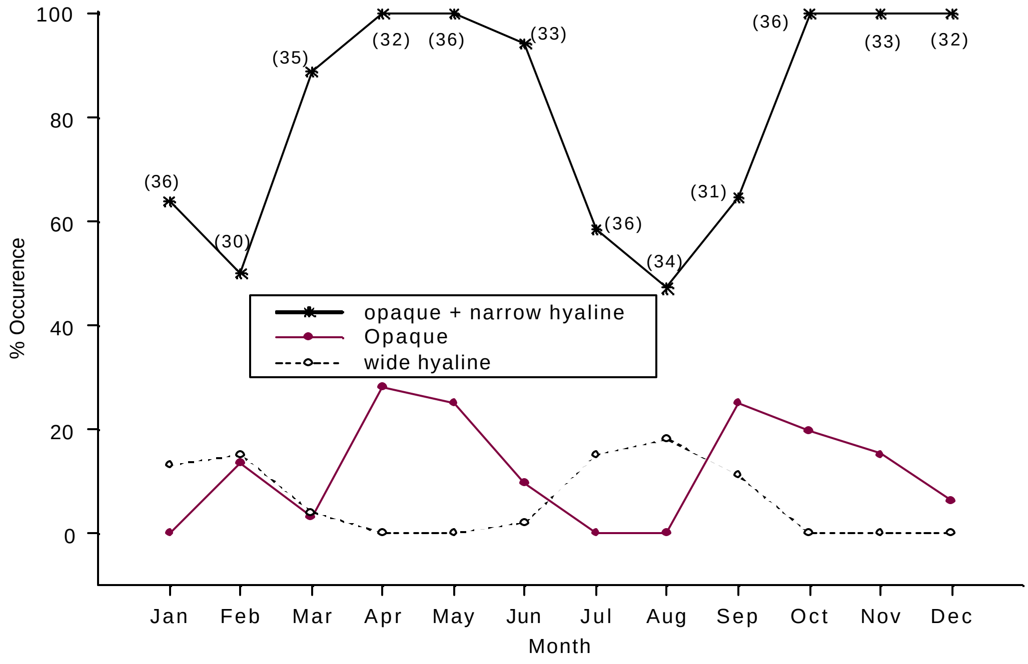


Figure 3.3: Monthly percent occurrence of otoliths with opaque, opaque + narrow hyaline and wide hyaline marginal zones showing periods of maximum and minimum deposition of opaque zones (n=404). The number of otoliths examined per month (enclosed in parentheses) is indicated alongside the opaque +narrow hyaline line.

The autocorrelation plot of otoliths with opaque and narrow hyaline margins is illustrated in Figure 3.4. The peaks at lags 0 and 6 in Figure 3.4 indicate that two opaque growth zones were deposited bi-annually. Modelling using a seasonal autoregressive model with a periodicity of 6 indicated that the deposition periodicity was significant $p < 0.05$, $r^2 = 0.95$. This analysis suggests that two opaque zones represent one year of growth. All counts of growth rings were, therefore, divided by two to obtain the approximate age in years.

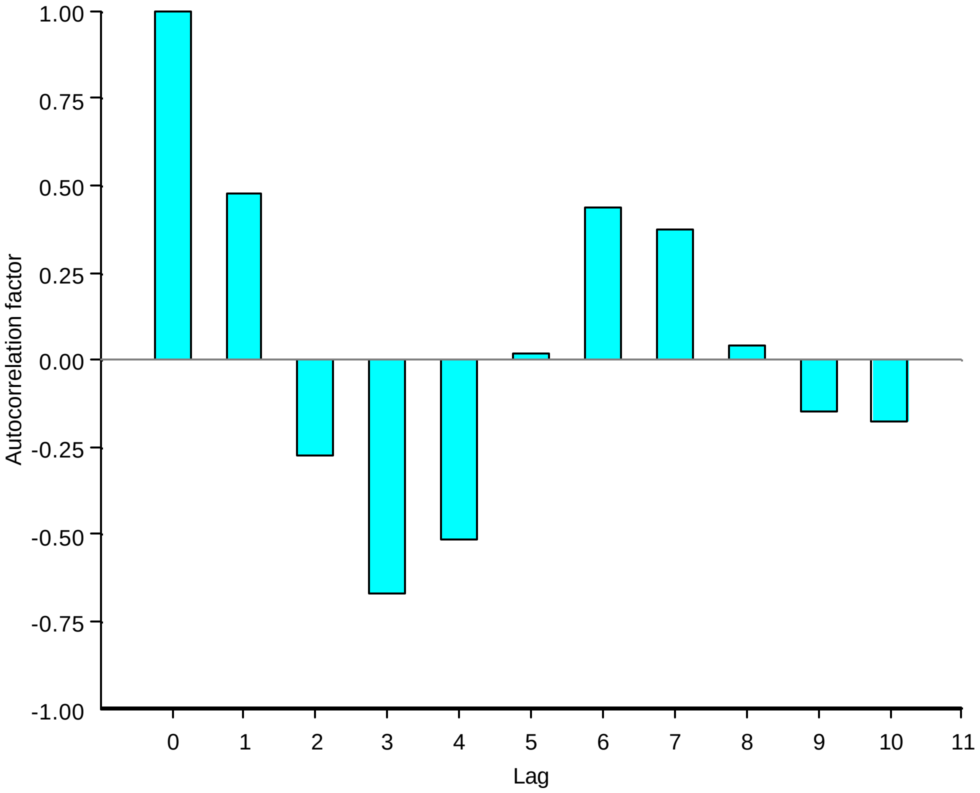


Figure 3.4: Autocorrelation plot of otoliths with opaque and narrow margins showing correlation between periods of maximum and minimum deposition of opaque growth zones.

3.5.3 Estimation of Precision

Age estimates were considered to be reasonably precise with an average percent error (APE%) of 10.5, a coefficient of variation (CV%) of 7.4 and an index of precision (*D*) of 5.3.

3.5.4 Estimation of growth parameters

The VBGF growth parameters are summarised in Table 3.3. The table indicates that *D. limnothrissa* attains a maximum length of 211 mm TL, with a curvature parameter (*K*) of 0.24 year^{-1} and an age at zero fish length (t_0) of -1.36 year.

Table 3.3: Point estimates, associated standard errors (SE) and 95% confidence intervals (CI) for combined sex length-at-age data fitted using the three parameter von Bertalanffy model for *Diplotaxodon limnothrissa* sampled from the southeast arm of Lake Malawi during May/June 2002.

Parameter	Point estimate	SE	95% CI
L_{∞}	211.21 mm TL	10.56	[189.2, 242.2]
K	0.24 year^{-1}	0.03	[0.15, 0.32,]
t_o	-1.36 year	0.25	[-2.30, -0.89,]

The length-at-age von Bertalanffy growth curve for *D. limnothrissa* is illustrated in Figure 3.5, and the observed and expected mean lengths-at-age are summarised in Table 3.4. A length-at-age key is provided in Table 3.5.

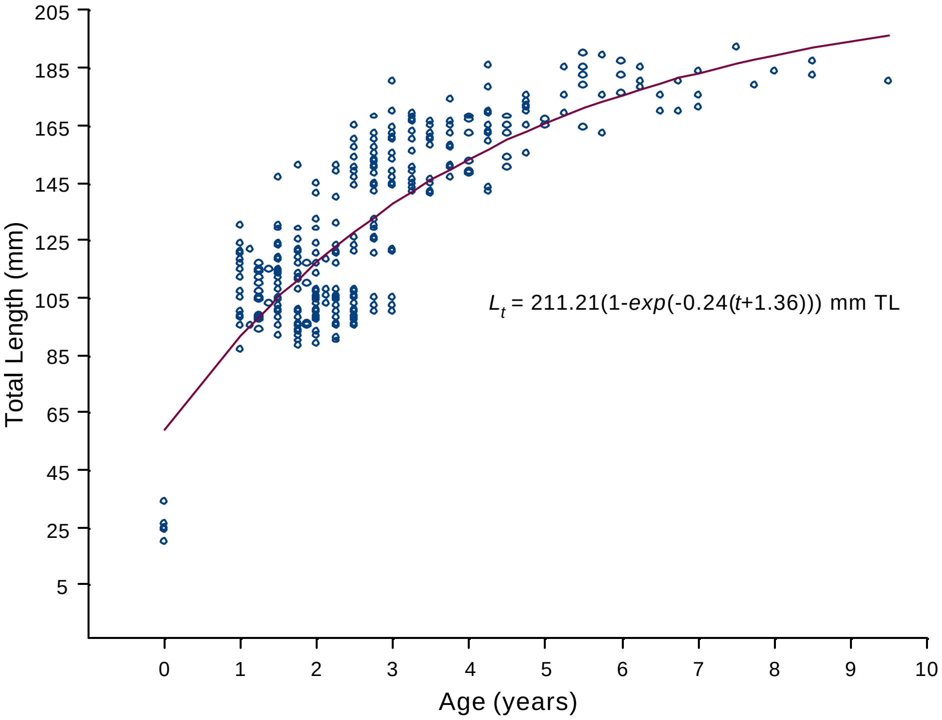


Figure 3.5: Observed individual lengths-at-age, and the expected von Bertalanffy growth curve for combined sex *Diplotaxodon limnothrissa* determined from sectioned sagittal otoliths sampled from the southeast arm of Lake Malawi between May and June 2002 (n = 351).

Table 3.4: Sample size, range (TL, mm), observed (TL ± standard deviation) and expected lengths-at-age determined from sectioned sagittal otoliths of *Diplotaxodon limnothrissa* sampled from the southeast arm of Lake Malawi.

Age (years)	n	Range (TL mm)	Mean observed length ± SD (TL mm)	Expected length (TL mm)
0	5	20-34	25.8 ± 5.1	59.1
1	43	87-130	106.7 ± 9.8	95.2
2	124	88-151	109.6 ± 14.8	114.7
3	91	95-180	136.4 ± 24.2	133.8
4	42	141-186	159.2 ± 10.5	151.6
5	19	150-185	167.2 ± 8.1	163.0
6	14	162-190	179.6 ± 8.4	173.8
7	7	170-184	175.0 ± 5.4	181.6
8	3	179-192	185.0 ± 6.6	187.8
9	2	182-187	184.5 ± 3.5	191.7
10	1	180-180	180.0	195.9

Table 3.5: Length-at-age key for *Diplotaxodon limnothrissa* from the southeast arm of Lake Malawi.

Length class (TL mm)	**Age (years)**											
	0	1	2	3	4	5	6	7	8	9	10	**Total**
0-19.9												
20-39.9	5											
40-59.9												
60-79.9												
80-99.9		13	35	7								
100-119.9		25	59	16								
120-139.9		5	22	14								
140-159.9			8	35	19	3						
160-179.9				18	22	15	6	5	1			
180-199.9				1	1	1	8	2	2	2	1	
n	5	43	124	91	42	19	14	7	3	2	1	**351**

3.5.5 Mortality

Natural mortality (M) was estimated at 0.31 year^{-1}. Age frequencies obtained from transformed length-frequency data provided first approximations of estimates of total annual mortality (Z). Total annual mortality was estimated at 0.76 year^{-1} using both the catch-curve analysis and the Cooke and Beddington (1981) method. The catch-curve is shown in Figure 3.6. Fishing mortality was obtained by subtraction (i.e. $F = Z - M$) at 0.45 year^{-1}.

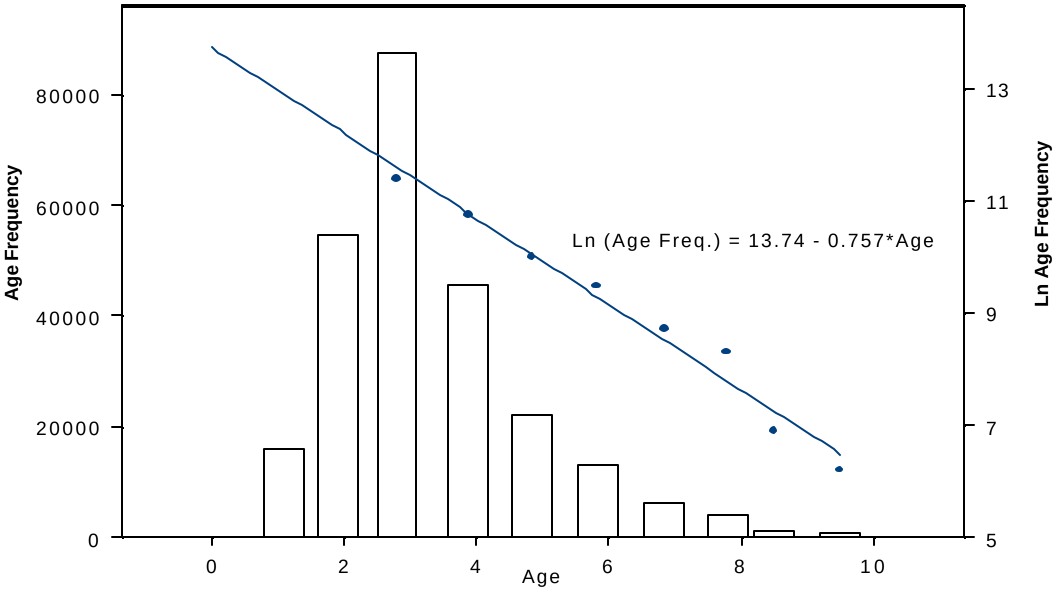


Figure 3.6: Age frequency distribution (bars) and catch curve (solid circles) for *Diplotaxodon limnothrissa* caught in the southeast arm of Lake Malawi. The slope of the descending limb of the catch curve provides an estimate of total mortality (Z).

3.6 Discussion

Growth zone formation in otoliths is at least partly caused by seasonal changes in food availability, temperature, spawning and light (Pannella 1980; Campana and Nelson 1985; Morales-Nin 1992). However, the presence of growth zones in immature fish suggests that growth zone formation probably also follows an internal rate of growth synchronised to seasonal environmental variations (Morales-Nin 1992). Unlike most tropical water bodies, Lake Malawi exhibits strong seasonal variations in both temperature and productivity (Patterson and Kachinjika 1995). These periodic variations are, therefore, expected to influence formation of growth zones.

The annual cycle of meteorological conditions on the lake can be conveniently divided into two periods; the hot, wet season and the cool, dry season. The hot and wet season is characterized by northerly monsoon winds known as *Mpoto* and extends from October to April. These winds are usually light although sometimes short-lived storms do occur. During this period, mean air temperature ranges between 24 and 27 ^{o}C (Figure 3.6). The northward movement of the Inter-Tropical Convergence Zone (ITCZ) establishes the cool dry season from May to September. Temperatures are lowest during this part of the year ranging between 20 and 24 ^{o}C (Figure 3.6). This period is characterized by the upwelling of deep nutrient rich waters caused by the strong south/southeasterly trade winds known as *Mwera* (Patterson and Kachinjika 1995).

Primary production in the open waters of Lake Malawi shows strong seasonal variation. The major algal divisions - Cyanophyta and Chlorophyta - dominate during the warm-wet season while the Bacillariophyta dominate during the cooler-mixing period (Degnbol and Mapila 1982; Patterson and Kachinjika 1995). Overall, phytoplankton biomass and primary production rates are higher during the cooler mixing period from May to September than during the warm-wet season. The open-water zooplankton community in Lake Malawi, which comprises four species of copepod, two cladocerans and the larvae of both the lake fly (*Chaoborus edulis*) and *Engraulicypris sardella,* also shows a similar seasonal pattern (Patterson and Kachinjika 1995). Zooplankton abundance is generally low during the warm-wet season (October - April) with lowest levels occurring towards the end of the season particularly between January and April and high during the cooler, dry period (May - September). However, highest abundance levels occur during the period extending from July to December (Patterson and Kachinjika 1995).

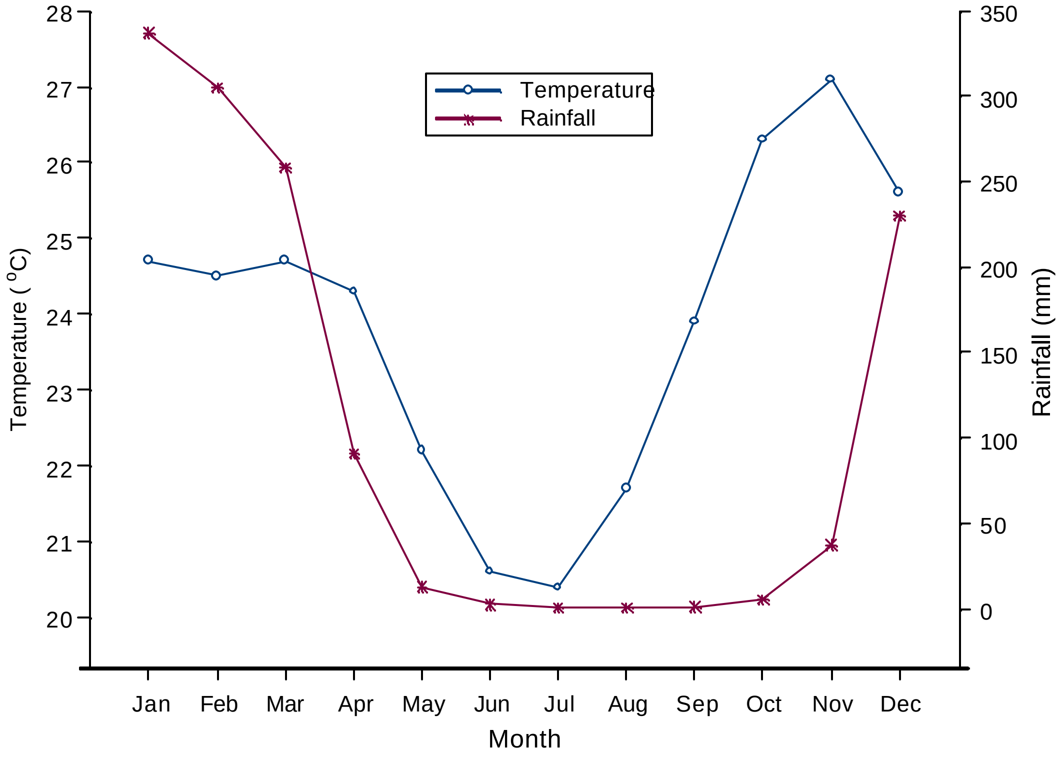


Figure 3.6: Monthly variation in air temperature (^oC) and rainfall (mm) on Lake Malawi (source: Patterson and Kachinjika 1995).

The use of otoliths for aging fish depends on understanding their growth pattern and the factors that may affect it. Growth in otoliths occurs by surface deposition of microcrystals through a cyclical process dependent on internal calcium metabolism rates and amino acid synthesis. Variations in calcium carbonate and protein deposition result in growth units or increments composed of an inner translucent (hyaline) band and an outer opaque band (Brothers *et al*. 1976; Mugiya *et al.* 1981). The opaque zone is usually deposited during a period of rapid growth and the translucent zone during a period of slow growth (Beckman and Wilson 1995). Periodic variations in growth, particularly where a season of fast growth is followed by a season of slow growth, are expected to influence deposition of these translucent and opaque growth zones, which can then be used to age the fish (Wootton 1998).

While earlier attempts to age *D. limnothrissa* using otoliths, scales and opercular bones were unsuccessful due to absence of 'annual' rings (Thompson *et al.* 1995), the results from this Chapter using burnt otoliths suggest otherwise. Ring deposition periodicity results indicate that in *D. limnothrissa* opaque rings are deposited twice a year, the first between April and May and the second between September and October with minimal deposition occurring during the coldest part of the year (June-July). Since the deposition of growth rings in the calcified tissues of bony fishes is partly caused by periodic changes in temperature cycles and food availability (Morales-Nin 1992), ring deposition in *D. limnothrissa* is probably also influenced by the strong seasonal variation in both temperature and zooplankton availability. The biannual deposition of opaque rings may also be as a result of strong intra-annual variation in temperature and zooplankton biomass. Low temperatures in June and July (mid-year) are likely to slow down the growth rate of the fish resulting in a corresponding reduction in otolith growth. Rising temperatures after August (Figure 3.6), stimulate the growth of the fish causing deposition of growth rings in September and October. However, the gradual reduction in zooplankton biomass towards the end of the warm-wet season particularly after

December probably causes a reduction in overall growth rates of these fishes resulting once again in little deposition in the sagittal otoliths. As zooplankton biomass begins to increase towards the beginning of the cool, dry season (beginning of upwelling) the growth rate increases again causing rapid growth which probably results in the deposition of growth rings in April and May.

Modelled length-at-age revealed that *D. limnothrissa* is a fast growing species that approaches its maximum size after 3-4 years. Growth in length reduces significantly after the fourth year of life probably due to diversion of resources to reproduction (see Chapter 4). The oldest fish sampled in this study measured 180 mm TL with an age estimate of 10 years. Rapid growth in the first few years prior to maturity is common in most fish including the cichlids (Fryer and Iles 1972; van der Waal 1985; Banda 1992; Weyl 1998). This growth pattern is advantageous in that it allows juvenile fish to quickly attain a size large enough to avoid predation, and to simultaneously cause the rapid attainment of sexual maturity (van der Waal 1985; Wootton 1998; Booth and Walmsley-Hart 2000).

Reliable age estimates are essential for all aspects of fishery research including studies of growth, production, population structure and dynamics (Brander 1973). Ageing precision estimates obtained in this study compare well with those of Kaunda (2001) and Maartens *et al*. (1999). Maartens *et al.* (1999) used sectioned illicia to age monkfish, *Lophius vomerinus* and achieved an average percent error (APE) of about 10.4%, coefficient of variation (CV) of about 6.3% and a precision estimate (D) of about 3.7. Kaunda (2001) using sectioned sagittal otoliths to age *Bathyclarias nyasensis*, obtained an APE of

14.2%, CV of 10% and a precision estimate (D) of 7.1. The estimates obtained in this study were an APE of 10.5%, CV of 7.4% and a precision estimate of about 5.3. In addition, over 60% of the otoliths had relatively well defined zonation implying that sectioned sagittal otoliths can be reliably used to age *D. limnothrissa*.

The failure of length frequency methods to age *D. limnothrissa* (Thompson *et al*. 1995) can be attributed to a number of factors. These methods age fish by monitoring the progression through time of identifiable modes in size classes (Morales-Nin 1992; Sparre and Venema 1998). Hence, they are of limited use in situations where there are no identifiable modes in size classes (Beamish and McFarlane 1987; Morales-Nin 1992). This seems to be the case with *D. limnothrissa* where growth was rapid for the first 3-4 years with no discernible modes of growth after about 1.5 years (Thompson *et al*. 1995). This suggests that length-based ageing methods are not suitable for ageing this species and are likely to provide unrealistically high estimates for growth (Beamish and McFarlane 1987).

The determination of age and growth rates in this study enabled the estimation of annual mortality rates for *D. limnothrissa*. Natural mortality was estimated at 0.31 year^{-1} using Pauly's empirical model. This estimate was accepted as being within the expected range for *D. limnothrissa* as cichlids are expected to have a low natural mortality due to the high degree of parental care and relatively long life span (Wootton 1998). Total mortality (Z) was estimated at 0.76 year^{-1} using both catch curve analysis and the Cooke and Beddington (1981) model. It was decided to use both methods because the catch curve analysis tends to produce substantially biased estimates of *Z* in situations where the numbers caught at any age included in the regression are low (Butterworth *et al*. 1989). In such instances the Cooke and Beddington (1981) method is recommended for estimation of Z. However, there was no substantial difference between the total mortality values estimated by the two methods. This suggests that no age group was under represented in the catch after fish were fully selected at 3 years of age.

In conclusion, this chapter has shown that burnt sagittal otoliths can be reliably used to age *D. limnothrissa.* The age and growth information obtained in this study will enable a better understanding of growth, recruitment and mortality information required for the application of analytical fisheries models used to develop appropriate management strategies for the exploitation of this species.

CHAPTER 4

REPRODUCTIVE BIOLOGY OF NDUNDUMA IN THE SOUTHEAST ARM OF LAKE MALAWI.

4.1 Introduction

Investigating the reproductive biology of a fish species is an essential component in understanding its ecology, life history and population dynamics. Such studies also provide an understanding of the extent to which a species' reproductive strategies are controlled by abiotic factors, food availability, the presence of predators and the habitat of the parental fish (Lagler *et al.* 1977; Matthews 1998; Wootton 1998).

Reproductive strategies, such as size or age-at-maturity and spawning seasonality, are of particular interest to fisheries managers as they provide some of the information required for developing fisheries management regulations (Welcomme 2001). Size, or age at maturity, is often used for setting minimum mesh sizes, while spawning seasonality is used in defining closed seasons and closed areas (Welcomme 2001). Knowledge of a species’ reproductive biology also provides input parameters for the application stock assessment methods such as spawner biomass-per-recruit analyses (Gulland 1985; Thompson *et al.* 1995; Malcolm 2001). Understanding the reproductive biology of *D. limnothrissa* is, therefore, essential.

Several studies on the reproductive biology of *D. limnothrissa* (Thompson *et al.* 1995; Turner 1996 and Duponchelle *et al.* 2000) have been conducted in Lake Malawi.

These studies indicate that *D. limnothrissa* attains sexual maturity at about 14 cm TL and that breeding is seasonal. A main breeding peak occurs between February and April in offshore waters and between April and June in the southeast arm of Lake Malawi. Average fecundity is about 15 eggs.

However, due to difficulties in ageing *D. limnothrissa* (Thompson *et al*. 1995) these studies do not provide age-specific information about the reproductive biology of the species. This information is required in spawner biomass-per-recruit analyses (Gulland 1985; Thompson *et al*. 1995; Malcolm 2001) presented in Chapter 5. This chapter, therefore, seeks to provide such age-specific information with emphasis on reproductive seasonality and size/age-at-sexual maturity of *D. limnothrissa* in the southeast arm of Lake Malawi.

4.2 Materials and Methods

4.2.1 Breeding seasonality

To determine reproductive seasonality, a total of 725 assumed female fish, ranging in length between 125 mm and 197 mm were sampled between June 2001 and May 2002 with an average of 60 fish per month. These fish were sampled from both midwater and demersal trawlers operating within areas B and C of the southeast arm of Lake Malawi. Of the total sample (n = 725), 604 were females, 70 were males not in breeding colouration and 51 were immature fish with indiscernible sex. Only females above 14 cm TL (n = 604) were used for determination of reproductive seasonality. All fish were weighed to the nearest 0.01 gram, measured to the nearest millimetre total length and macroscopically sexed. Gonads were dissected from the fish, weighed (g) and staged visually according to the criteria outlined in Table 4.1 (source: Weyl and Hecht 1999).

Table 4.1: Macroscopic criteria used to stage *Diplotaxodon limnothrissa* ovaries.

Stage	Development	Macroscopic appearance
1	Immature	Not possible to distinguish sex. The gonad appears as thin translucent gelatinous strip.
2	Undeveloped to early developing	Possible to distinguish sex. Ovaries white or slightly yellowish or pinkish in appearance. Texture of ovary varies from granular to oocytes being readily distinguishable.
3	Developing	Oocytes enlarged and readily visible.
4	Ripe	Oocytes are of maximum size. Fully hydrated and are loose within ovary.
5	Mouth-brooding or spent	Ovary with few ripe eggs and/or evidence of mouthbrooding. Ovaries sac-like and flaccid.

Reproductive activity was assessed using monthly gonadosomatic index values (GSI) defined by Wootton (1998) as:

$$GSI = \left(\frac{gonad\ \ weight(g)}{somatic\ \ body\ \ weight(g)} \right) \times 100$$

where somatic weight is the weight of the body excluding the gonads.

The temporal dependence structure of reproductive activity and its periodicity were assessed statistically using autocorrelation and autoregressive integrated moving average (ARIMA) models (Priestley 1981). *S-PLUS 2000* (S-PLUS 1999) was used for the analysis.

4.2.2 Age-at-first Maturity

After the determination of breeding peak, a total of 461 female fish, ranging in length from 88 mm to 190 mm TL, and sampled between March and April 2002, were used to determine the age-at-sexual maturity. As *D. limnothrissa* exhibits no visible sexual dimorphism in either size or body proportions (Turner 1994) only female fish were used in this analysis. All the fish were weighed to the nearest 0.001 gram, measured to the nearest millimetre total length and macroscopically sexed. Gonads were dissected from the fish, weighed (g) and staged visually according to the criteria outlined in Table 4.1.

The age-at-sexual maturity in this study was determined by fitting a logistic ogive to the proportion of reproductively active female fish sampled during the spawning season in March and April (King 1995; Booth and Buxton 1997). An age-length key (Chapter 3) was used to transform the female length frequency distributions to age frequency distributions. The 2-parameter logistic ogive was fitted using a non-linear least squares procedure (Welcomme 2001) and is described by Booth and Buxton (1997) as:

$$P_a = \left(1 + \exp^{-\left(a - a_{50/d}\right)}\right)^{-1}$$

where P_a is the percentage of mature fish at age a, a_{50} is the age at 50% sexual maturity and d is the width of the ogive

4.3 Results

4.3.1 Breeding seasonality

The monthly percentage of females (> 14 cm TL) in developing, ripe, spent and resting maturity stages is presented in Figure 4.1 while Figure 4.2 illustrates the monthly gonado-somatic index (GSI) values for *D. limnothrissa* females.

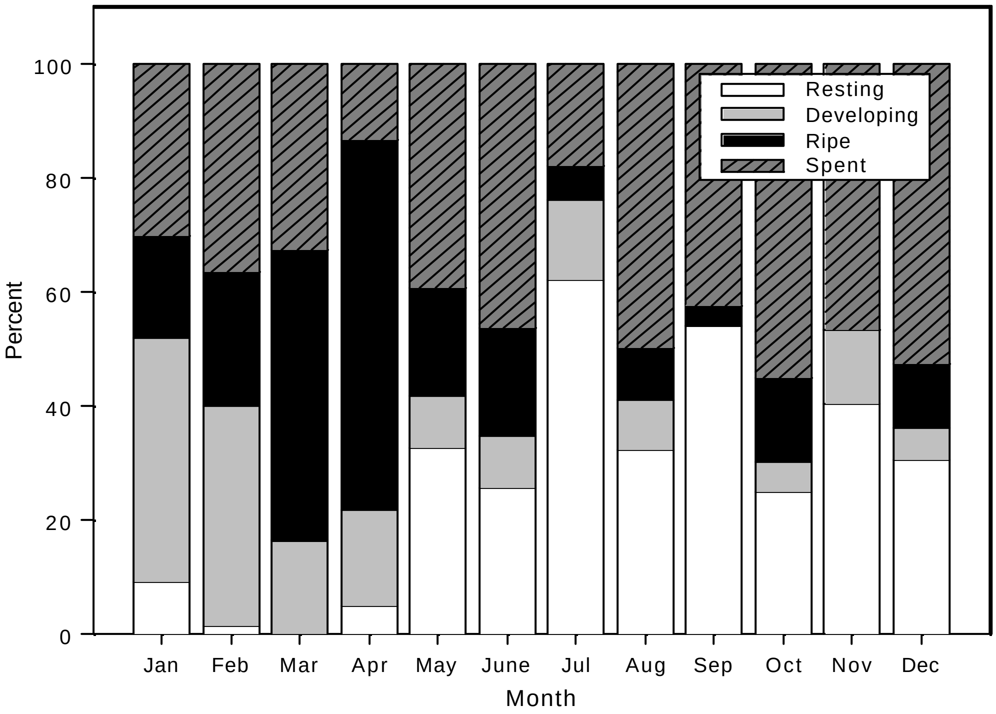


Figure 4.1: Female monthly maturity stages for *Diplotaxodon limnothrissa* sampled from the southeast arm of Lake Malawi (n = 604).

A progressive increase in the proportion of ripe females was observed between January and April (Figure 4.1). The proportion of ripe females increased sharply from 23% between January and February to over 65% between March and April. This was followed by a sharp decline in the proportion of ripe females to 19% between May and June with over 47% of the females being in the "spent" condition. The proportion of ripe females continued to decline reaching lowest levels in September (4%). No ripe females were recorded in November. A gradual increase in the proportion of ripe females was, however, noticed from November to April. A similar trend was observed in the mean monthly GSI, which ranged from a minimum of 0.23% in August to a maximum of 1.20% in April (Figure 4.2).

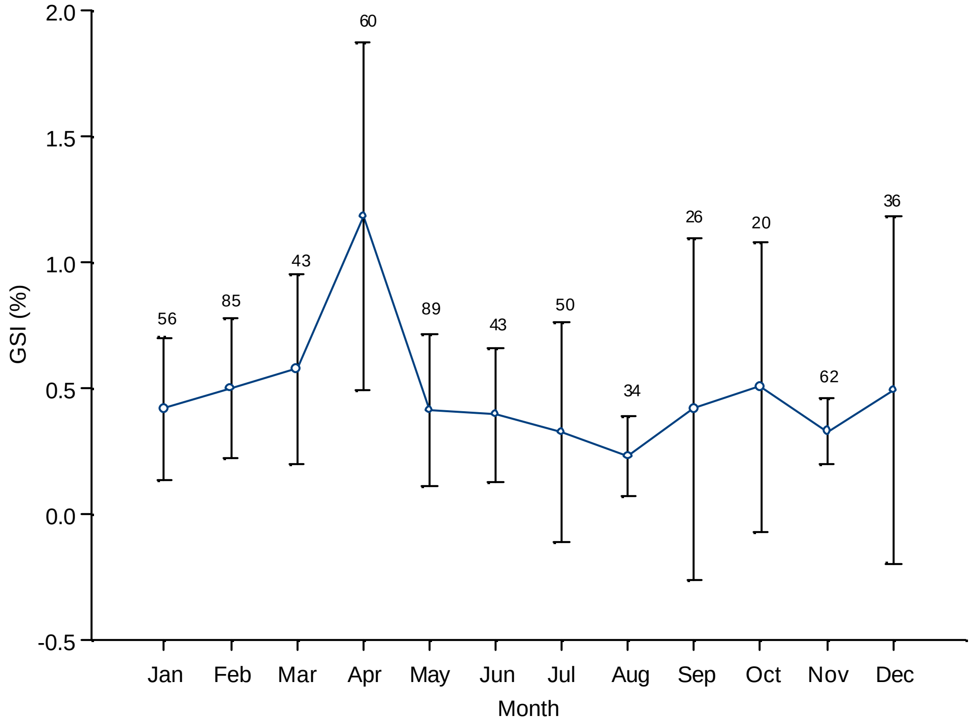


Figure 4.2: Mean monthly GSI values (± SD) for *Diplotaxodon limnothrissa* females sampled from the southeast arm of Lake Malawi. The number of samples per month is indicated above each error bar.

GSI increased from 0.42% in January to 1.2% in April where after a gradual decrease was observed to the lowest level in August (0.23%). An increasing trend was then observed from 0.23% in August to about 0.49% in December reaching a maximum in April. This trend suggests that *D. limnothrissa* have a protracted spawning season.

The reproductive peak for females seems to occur between March and May with the highest GSI values being observed in April (Figure 4.2). Breeding activity seems to be lowest between June and September, while a second but much smaller peak occurred in October (Figure 4.2).

The temporal dependence structure of breeding activity in *D. limnothrissa* is illustrated in Figure 4.3.

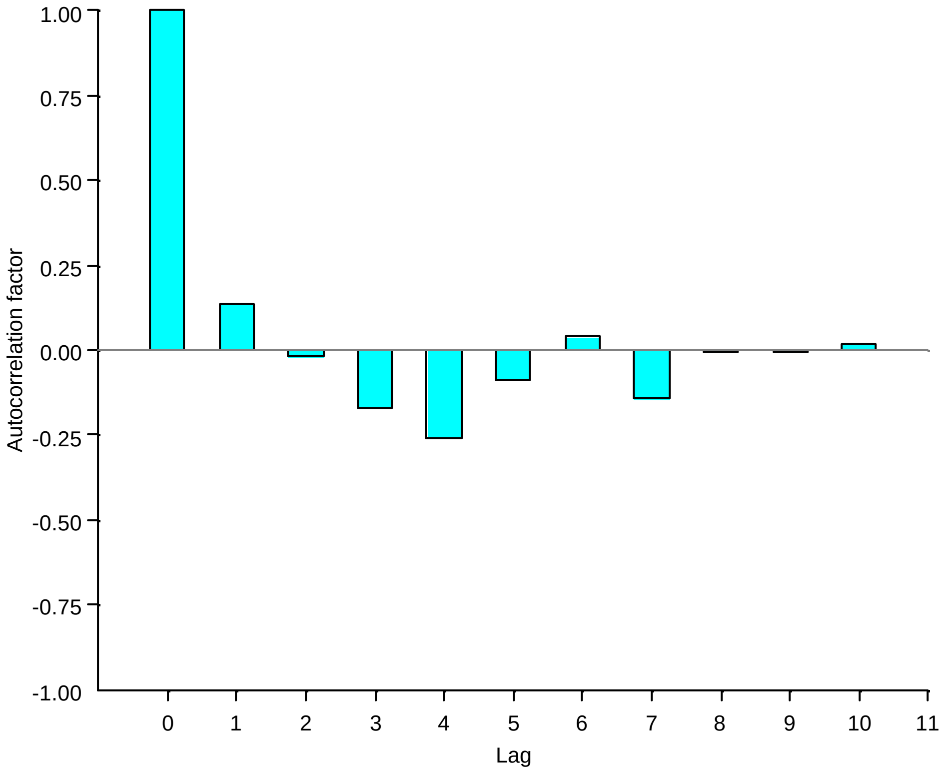


Figure 4.3: Autocorrelation plot of female GSI values showing periods of maximum and minimum breeding activity for *Diplotaxodon limnothrissa* sampled from the southeast arm of Lake Malawi (n = 604).

The figure shows that a main breeding peak occurred towards the beginning of the year (lag 0) while a less pronounced second peak occurred later in the year (lag 6).

Modelling using a seasonal autoregressive model with a periodicity of 6 indicated that the breeding periodicity was not twice a year $p > 0.05$, $r^2 = 0.57$. Breeding activity in *D. limnothrissa*, therefore, appeared to follow an annual cycle that occurred between March and May each year (Figures 4.2 & 4.3).

4.3.2 Age-at-first Maturity

The logistic ogive illustrating the relationship between sexual maturity and age for *D. limnothrissa* females is shown in Figure 4.4. The age-at-50% sexual maturity was estimated at 2.3 years and corresponded to a total length of 142 mm.

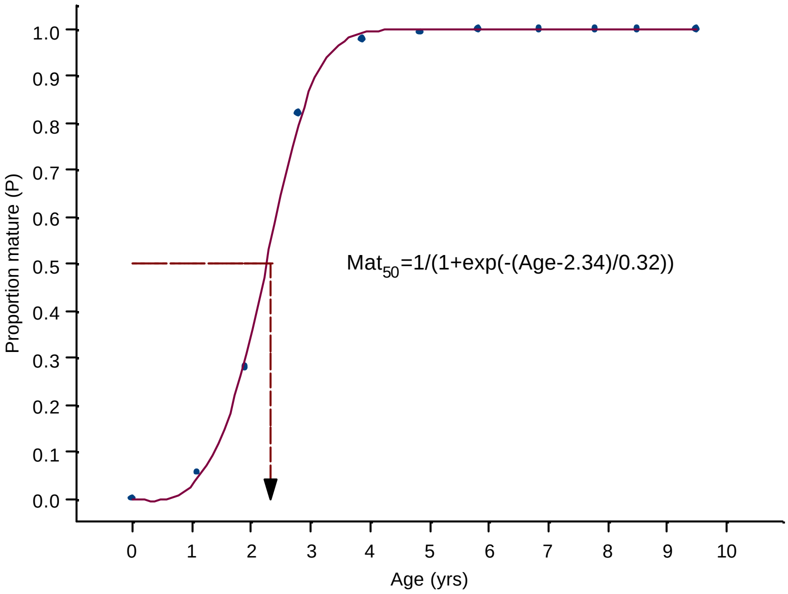


Figure 4.4: Proportion of sexually mature *Diplotaxodon limnothrissa* females-at-age sampled from the southeast arm of Lake Malawi (n = 461).

4.4 Discussion

The onset of sexual maturity represents a critical transition in the life history of an organism. This is time that energetic resources that were previously allocated to growth and survival are now also required for reproduction (King 1995; Wootton 1998). Results from this study indicate that sexual maturity in *D. limnothrissa* was attained at an age of about 2.3 years, which corresponded to a mean length of 142 mm TL. This estimate was similar to that obtained by Thompson *et al*. (1995), Turner (1996) and Duponchelle *et al*. (2000). Thompson *et al*. (1995) and Turner (1996) (based on samples from the southeast arm of the lake) estimated the mean length-at-maturity to be around 140 mm TL, while Duponchelle *et al.* (2000) working in the southwest arm of the lake, obtained an estimate of about 105 mm SL (136 mm TL). Length-at-age data (Chapter 3) indicates that growth in *D. limnothrissa* is initially rapid but slows down after about 3-4 years of age. This period occurs shortly after *D. limnothrissa* has attained sexual maturity, and the observed decline in growth, is probably linked to the onset of reproduction.

Reproductive costs to an individual can be classified either as physiological or ecological (Wootton 1998). Physiological costs occur when the allocation of resources to reproduction detracts from allocation to physiological processes required for maintenance of the long-term condition of the individual. Ecological costs, on the other hand, occur when reproductive activities put the individual at risk from predation, infection by disease, or other deleterious consequences. Physiological costs of reproduction to an individual can be high as they entail meeting the costs of development of any secondary sexual characteristics, the energy required for reproductive behaviour, and the production of gametes (King 1995; Wootton 1998). In *D. limnothrissa*, secondary sexual characteristics take the form of breeding colouration in males, while females develop enlarged buccal cavities for mouth-brooding of eggs and juveniles (Thompson *et al.* 1995; Turner 1996). Additional energetic costs include courtship, gamete production (King 1995; Wootton 1998), and extended parental care of both eggs and juveniles by females (Thompson *et al*. 1995). As selection for either higher reproductive expenditure or faster somatic growth is at the expense of a decrease in either reproductive effort or somatic growth (Wootton 1998), the observed reduction in growth of *D. limnothrissa* after the age of 3-4 years can partly be attributed to the re-allocation of time and resources to reproduction.

Reproduction in most organisms is seasonal and tends to occur within a specific period (King 1995; Wootton 1998; Welcomme 2001). Changes in the gonado-somatic index (GSI) of a species can be considered a proxy to identify the seasonal timing of reproduction (King 1995; Wootton 1998). This is due to increases in the GSI during the reproductive cycle reflecting the growth of developing oocytes within the ovaries during vitellogenesis. In *D. limnothrissa,* the monthly GSI proportion of mature females suggests that the species has a protracted spawning season that occurred towards the end of the warm wet season particularly between March and May. Thompson *et al*. (1995) and Duponchelle *et al*. (2000) also reported similar findings. In their studies, Thompson *et al*. (1995) observed that peak spawning in the southeast arm occurred between April and June and off-shore between February and April. In the southwest arm of the lake, Duponchelle *et al.* (2000) also observed that peak spawning occurred between April and June. This suggests that within the southern part of the lake there is no temporal variation in spawning intensity of *D.*

limnothrissa. The main breeding season, therefore, occurred between March and May in southern Lake Malawi.

Seasonal reproduction in fish is largely governed by intra-annual variations in the suitability of environmental conditions for hatching, growth and survival of the young (Munro 1990; King 1995; Welcomme 2001). Through selective pressure it has also been generally timed to coincide with seasonal abundance of food resources, shelter from predators and benign abiotic conditions such as temperature, rainfall, salinity, light and moon phase (Balon 1975; King 1995). Seasonal availability of food has been correlated with breeding seasonality in many fish species (King 1995; Welcomme 2001) including some haplochromines from Lake Malawi (Marsh *et al.* 1986). Zooplankton, which comprise the main diet of *D. limnothrissa*, are most abundant during the cool, windy season reaching highest densities in June and July. It is during this period when hatching and mouth-brooding in *D. limnothrissa* is also the highest (Thompson *et al.* 1995). Synchronising spawning and hatching with the period when zooplankton is most abundant ensures that there is sufficient energy for reproduction for mature individuals, as well as for growth in larvae and juveniles. The weakening of stratification during this period results in uniform distribution of oxygen, plankton, nutrients and temperature in the surface as well as in the deeper layers of the water column (Patterson and Kachinjika 1995). This is advantageous in that it increases the range of suitable environment for the juveniles enabling them to maximise feeding and minimise risks of predation.

Besides governing reproduction, seasonal variation in the abiotic environment are also used as potential synchronising cues for spawning in most organisms including fish

(Munro 1990; King 1995; Wootton 1998; Welcomme 2001). For instance, periodic changes in temperature (either an increase or a decrease) are known to be an important triggering stimulus for spawning in temperate-water species (Morales-Nin 1992; King 1995). The larvae of these species are often produced in spring so that they can feed on phytoplankton blooms that occur during such periods. Examination of Figure 4.5 indicates that spawning in *D. limnothrissa* was generally synchronised with trends in temperature and rainfall with lowest GSI values coinciding with lowest temperature and rainfall.

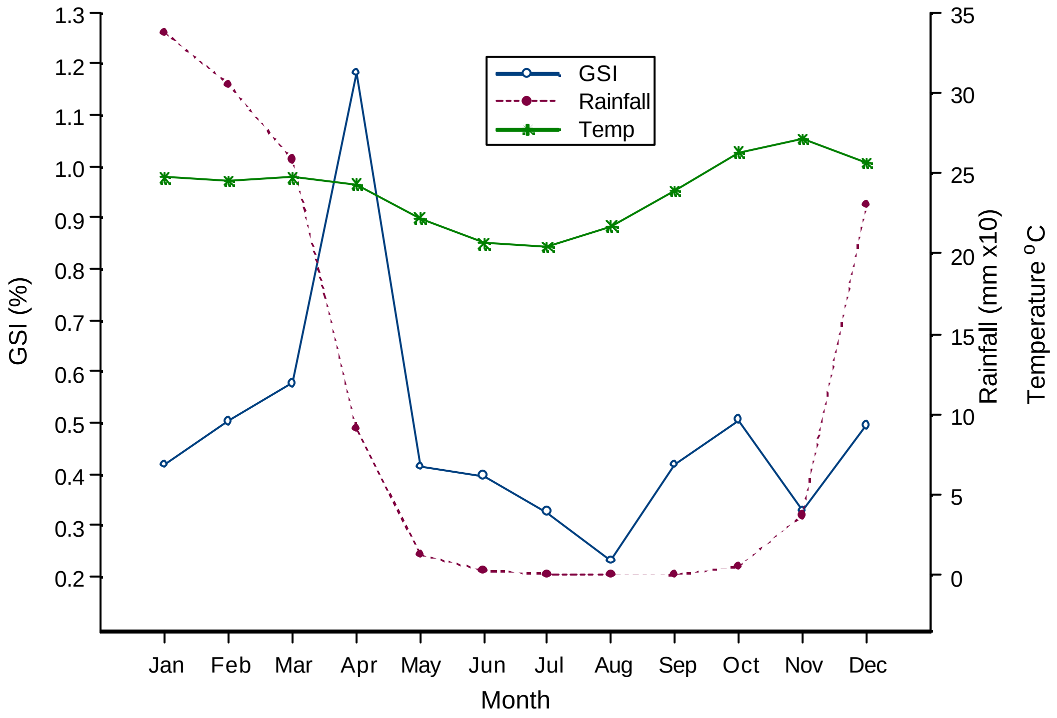


Figure 4.5: Temporal variation in gonado-somatic index (GSI) of *Diplotaxodon limnothrissa* in the southeast arm of Lake Malawi with respect to mean temperature and rainfall (From: Patterson and Kachinjika 1995).

This probably suggests that the seasonal cycles in water temperature and rainfall (i.e. temperature being highest at the end of the dry season and low during the rainy season - Figure 4.5) may have a predictive role or act as a potential synchronising cue for the increase in zooplankton biomass in June and July. However, there is little data to support this supposition.

It can, therefore, be concluded that restriction of breeding to between March and April enables *D. limnothrissa* to fully realise their reproductive potential. A protracted spawning season, low fecundity and precocial reproductive behaviour suggest that recruitment in *D. limnothrissa* might be dependent on spawner biomass (Thompson *et al*. 1995; Weyl 1998). Management initiatives should therefore aim at maintaining spawner biomass at relatively high levels (see Chapter 5).

CHAPTER 5

YIELD-PER-RECRUIT ANALYSIS OF NDUNDUMA IN THE SOUTHEAST ARM OF LAKE MALAWI

5.1 Introduction

Biomass dynamic models, also incorrectly referred to as surplus production models, are currently being used to provide advice on harvest policies in Lake Malawi. (Bulirani *et al*. 1999). These models describe the population dynamics of the exploitable portion of the resource without reference to age or length composition (Lleonart 1993; King 1995; Restrepo and Legault 1998). Their advantage lies in their simplicity - requiring only catch and effort data. The main disadvantage of these models lies in their inability to take account of other factors affecting the stock such as recruitment variability or fishing on associated species or to advise on changes in fishing pattern other than changes in the total amount of fishing. Most fisheries are, therefore, managed using age-structured models that explicitly take into account the age-structure of the resource (Deriso 1987; Lleonart 1993; Sparre and Venema 1998; Malcolm 2001). Age structured models can also incorporate information on the numbers of recruits entering the fishery each year, the rate at which they are caught (which is governed by total fishing effort), the range of sizes of fish that are caught (which depends on the selectivity of the gears), the rate at which fish die from natural causes, and the pattern of growth and the productivity of the population (Gulland 1983; Restrepo and Legault 1998).

Per-recruit analyses, the simplest form of age-structured population models, form a basis for the assessment of many fish stocks for which there is insufficient data (Gulland 1985; Griffiths 1997; Malcolm 2001). These models which currently include the formulations of Beverton and Holt (Beverton and Holt 1956), Ricker (Ricker 1975) and Thompson and Bell (Thompson and Bell 1934) incorporate the interplay between somatic growth and the probability of dying in order to predict the life-time yield of a cohort, and the spawner biomass remaining, under different combinations of fishing mortality and age-at-first capture (Butterworth *et al.* 1989; Punt 1993). Discrete per-recruit models analogous to the Thompson and Bell yield-per-recruit model are favoured for their numerical simplicity (Chen and Gordon 1997) and their ability to incorporate age-specific gear selectivity in the derivation of commonly used biological reference points (BRPs) - values that represent the state of a resource and provide information regarding stock status relative to an acceptable value or range (Caddy and Mahon 1995). Most BRPs are, therefore, used to propose levels of fishing mortality required to achieve some management objective.

From a per-recruit perspective, several BRPs have been suggested in an attempt to define fishing mortalities that will maximize long-term yield (Clark 1993; Punt 1993). The two commonly used BRPs are F_{MAX} and $F_{0.1}$. F_{MAX} is defined as the fishing mortality, which corresponds to the maximum on the yield-per-recruit curve while $F_{0.1}$ is the rate of fishing mortality that corresponds to a point on the yield-per-recruit curve where the slope is 10% of that at the origin (Gulland and Boerema 1973; Deriso 1987). The F_{MAX} strategy maximizes yield-per-recruit without regard to whether sufficient spawner biomass is conserved to ensure sufficient recruitment in the future (Deriso 1987; Clarke 1993). As a result it tends to be too high and usually leads to stock declines (Hilborn and Walters 1992). Although the $F_{0.1}$ strategy is more conservative than the F_{MAX} strategy, it does not take into account the effects of fishing on the spawning stock and subsequent recruitment (Punt 1993; Clarke 1993). Owing to the dependence of recruitment on spawner stock, it is now common practice in fisheries management to base BRP recommendations on the results of spawner biomass-per-recruit models (Butterworth *et al.* 1989; Griffiths 1997). Based on these models, a spawner biomass BRP ($F_{SB(x)}$) is defined as the fishing mortality at which spawner biomass-per-recruit is reduced to *x%* of its pristine level. Generally, spawner biomass-per-recruit recommendations lie between 25% and 50% of unexploited levels (Deriso 1987; Butterworth *et al.* 1989; Clarke 1991; Punt 1993; Mace 1994; Booth and Buxton 1997) and recruitment overfishing is said to occur when the relative SB/R is reduced to less than 20-30% of the unfished level (Clark 1991; Mace 1994). BRPs that have been proposed in the literature have been calculated for temperate demersal marine species with life-history characteristics that include high fecundity, pelagic spawning and little or no parental care (Booth 2001). In contrast, cichlids have low fecundities and exhibit varying levels of parental care ranging from guarding to mouthbrooding (Eccles and Trewavas 1989; Thompson *et al.* 1995; Booth 2001; Duponchelle *et al.* 2000). This suggests that these BRPs might not be appropriate for cichlid-dominated fisheries (Booth 2001). Booth (2001) therefore calculated cichlid specific BRPs with combinations of two spawner-recruit relationships within deterministic and stochastic frameworks. His findings suggest that a BRP of F_{SB40} should be recommended if the spawner-recruit relationship is unknown while a BRP of F_{SB50} is recommended if a Beverton-Holt spawner-recruit relationship is assumed. Owing to low fecundity and the general life-history characteristics of *D. limnothrissa* which include mouthbrooding (Thompson *et al.* 1995; Turner 1996) coupled with lack of information on the spawner-recruit relationship, a reduction of spawner biomass to 40% of pristine levels $(SB/R)_{F=0}$ was considered acceptable in ensuring the sustainability of the *D. limnothrissa* resource in the southeast arm of Lake Malawi.

The lack of long-term fisheries data, such as catch-at-age and catch rate data for *D. limnothrissa* precludes the use of more advanced age structured population models in the assessment of this fishery. Thus, the minimal data available can at most be used for spawner-biomass/yield-per-recruit modeling (Butterworth *et al.* 1989). In this chapter, the YPR model analogous to the Thompson and Bell YPR/SBR model that incorporates age specific gear selectivity and maturity was used to determine the optimal levels of fishing mortality and age-at-first capture for *D. limnothrissa* in the southeast arm of Lake Malawi.

5.2 Materials and Methods

5.2.1 Age-specific selectivity

Per-recruit analysis requires a model for the selectivity function, which provides an indication of how fishing mortality varies with age. Unlike other models, which assume selectivity to be "knife edged" (Butterworth *et al.* 1989), the per-recruit model used in this chapter incorporates age-specific selectivity based on the logistic model (Chen and Gordon 1997). Such an approach improves the precision of estimating fishing mortality (F) as all available age data are used in the analysis (Butterworth *et al.* 1989). In this chapter, the age-specific selectivity of stern and pair trawl fisheries was modelled using the logistic model (Butterworth *et al.* 1989; Booth and Punt 1998) described as:

$$S_a = \left(1+\exp^{-\left(a-a_{50/d}\right)}\right)^{-1}$$

where S_a is the selectivity of the gear on a fish of age a, a_{50} is the age-at-50%-selectivity, and d is a parameter related to the age range over which the selectivity changes from values near 0 to values near 1. As d tends to zero, this function approaches knife-edged selection (Butterworth *et al.* 1989).

Length-frequency data used for estimating the selectivity of the stern trawl fishery (demersal and midwater) was obtained from bi-annual monitoring surveys of 1999 while that of the pair-trawl was collected in 2001 from the pair trawl fishery in area A. An age-length key constructed in Chapter 3 was used to transform length frequency to age frequency. However, by virtue of its small contribution towards total landings of ndunduma (about 7%) in the southeast arm (Turner 1996), the pair trawl fishery was considered as having little impact on the stocks of ndunduma. The age-at-capture (t_c) for ndunduma in the pair trawl fishery was therefore held constant in all per-recruit simulations.

5.2.2 Per-Recruit Analyses

Per-recruit analysis is conducted by constructing a model of the development of a cohort through time that takes into account the growth and mortality of individuals (Butterworth *et al.* 1989; King 1995). This is based on the assumption that recruitment is constant and that the stock under consideration is at equilibrium

(Butterworth *et al*. 1989; Sparre and Venema, 1998). In this study, F_{SB25} was assumed as a BRP where the stock is at a high risk of collapse, while $F_{0.1}$ and F_{SB40} were calculated as BRPs that would maximize long-term yield.

Yield-per-recruit (YPR) was calculated using the YPR model analogous to that of Thompson and Bell (Chen and Gordon 1997) such that:

$$Y = \sum_{t=t_R}^{t_l} C_t W_t$$

where Y is the yield, C_t is the catch in numbers of the tth age class, W_t is the average weight of fish for the tth age class, t_R is the age of entry into the fishery, and t_l is the maximum age of fish that still contribute to the fishery. Incorporating the catch equation and exponential survival function (Ricker 1975), the YPR model becomes:

$$\frac{Y}{R} = \sum_{t=t_R}^{t_l} \left[W_t S_t F \frac{1 - \exp^{-S_t F - M_t}}{S_t F + M_t} e^{-\sum_{k=t_R}^{t-1} (S_k F + M_k)} \right]$$

where S_t is the selectivity coefficient for fish of age t, F is the fishing mortality for recruited fish. M_t is the natural mortality at age t, and the parameter M_t is commonly assumed to be constant equal to M for all groups in the YPR analysis.

Similarly, spawner biomass-per-recruit as a function of F is described as:

$$\frac{S}{R} = \sum_{t=t_R}^{t_l} \left[W_t \Psi_t e^{-\sum_{k=t_R}^{t-1} (S_k F + M_k)} \right]$$

where Y_t is the proportion of fish at age t that are sexually mature, while W_t is the begin-year mass of a fish of age t such that:

$$W_t = q(L_t)^b \qquad and \qquad L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)$$

where $L_{¥}$, K and t_0 are the von Bertalanffy growth equation parameters, and q and b are the mass-length relationship parameters.

5.2.2.1 Input parameters

All the input parameters for the per-recruit analyses were obtained from Chapters 3 and 4 except for the proportions of the stern-trawl and pair-trawl fisheries, which were obtained from Turner (1996). Due to uncertainty associated with estimates of natural mortality (M), a range of M values were used in calculating the BRPs (Griffiths 1997; Weyl 1998; Malcolm 2001). Table 5.1 provides a summary of these parameters.

Table 5.1: Summary of parameters used in per-recruit analyses for *Diplotaxodon limnothrissa* in the southeast arm of Lake Malawi where $L_{¥}$ is asymptotic length (mm, TL), *q* and *b* are mass-length relationship parameters, *K* is a Brody growth coefficient, t_o is the age of zero length fish, *Z, M* and *F* are total, natural and fishing mortalities respectively.

Parameter	**Value**
$L_{¥}$	211.21 mm
K	0.24 yr^{-1}
t_o	-1.36 yr
Z	0.756 yr^{-1}
M	0.31 yr^{-1} (range 0.21 - 0.41)
F	0.45 yr^{-1}
q mass-length relationship	0.000019
b mass-length relationship	2.85
Age-at-maturity (M_{50}) logistic	2.34 yr
delta	0.32
Age-at-capture (t_c) -stern trawl logistic	2.67 yr
delta	0.72
Age-at-capture (t_c) - pair trawl fishery logistic	1.93 yr
delta	0.63
Maximum age (t_l)	10 yrs
Proportion of stern-trawl fishery	0.93
Proportion of pair-trawl fishery	0.07

5.2.2.2 Estimation of $F_{0.n}$ and $F_{SB(x)}$

The value of $F_{0.n}$ was obtained numerically by solving the equation (Punt 1997):

$$\left.\frac{dYPR}{dF}\right|_{F=F_{0.n}} = 0.n\left.\frac{dYPR}{dF}\right|_{F=0}$$

where a slope of 10% and 0% corresponds to $F_{0.1}$ and F_{MAX} respectively.

Fishing mortality corresponding to the quantity $F_{SB(x)}$ was obtained by solving the equation:

$$SBR_{CUR(x)} = (SBR_{F=0}) \times (x)$$

where $F_{SB(x)}$ is the fishing mortality that reduces spawner biomass-per-recruit to x% of the pristine $(SB/R)_{F=0}$.

Isopleth diagrams generated using yield and spawner biomass-per-recruit models were used to describe the response of yield and spawner biomass-per-recruit to different combinations of age-at-capture and fishing mortality at three levels of natural mortality. The data used to generate the YPR and SBR isopleths were a vector of fishing mortality values, a vector of age-at-capture values and a length of fishing mortality by length of age-at-capture matrix of YPR or SBR values which were calculated for each level of natural mortality. Yield-per-recruit was modeled in terms of slope on the YPR curve where slope isopleths of 10% and 0% corresponded to $F_{0.1}$ and F_{MAX} respectively. Current spawner biomass-per-recruit was modeled as a percentage of the pristine unfished spawner biomass $(SB/R)_{F=0}$ where SBR levels of 25, 35, 40 and 50 relate to levels where the current spawner biomass drops to 25%, 35%, 40% and 50% of the pristine $(SB/R)_{F=0}$, respectively. Fishing mortality corresponding to each of these levels was obtained graphically.

SPLUS 2000 (S-PLUS 1999) was used for all analysis. Isopleths were calculated using the bivariate interpolation method for irregular grids.

5.3 Results

5.3.1 Age Specific Selectivity

Selectivity of both the stern (demersal and midwater) and pair-trawl fisheries for *D. limnothrissa* in the southeast arm of Lake Malawi is illustrated in Figure 5.1. The age-at-(50%)-selectivity was estimated at 2.67 and 1.93 years for the stern trawl (demersal and midwater) and pair trawl fisheries, respectively. These ages corresponded to total lengths of 146 and 109 mm in the stern and pair-trawl fisheries, respectively.

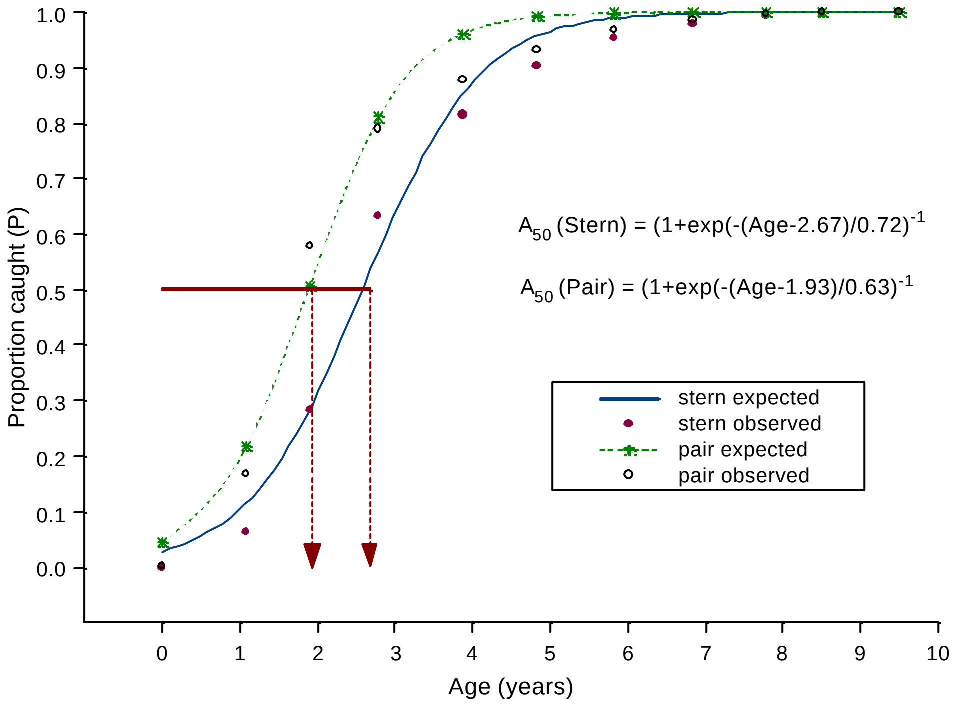
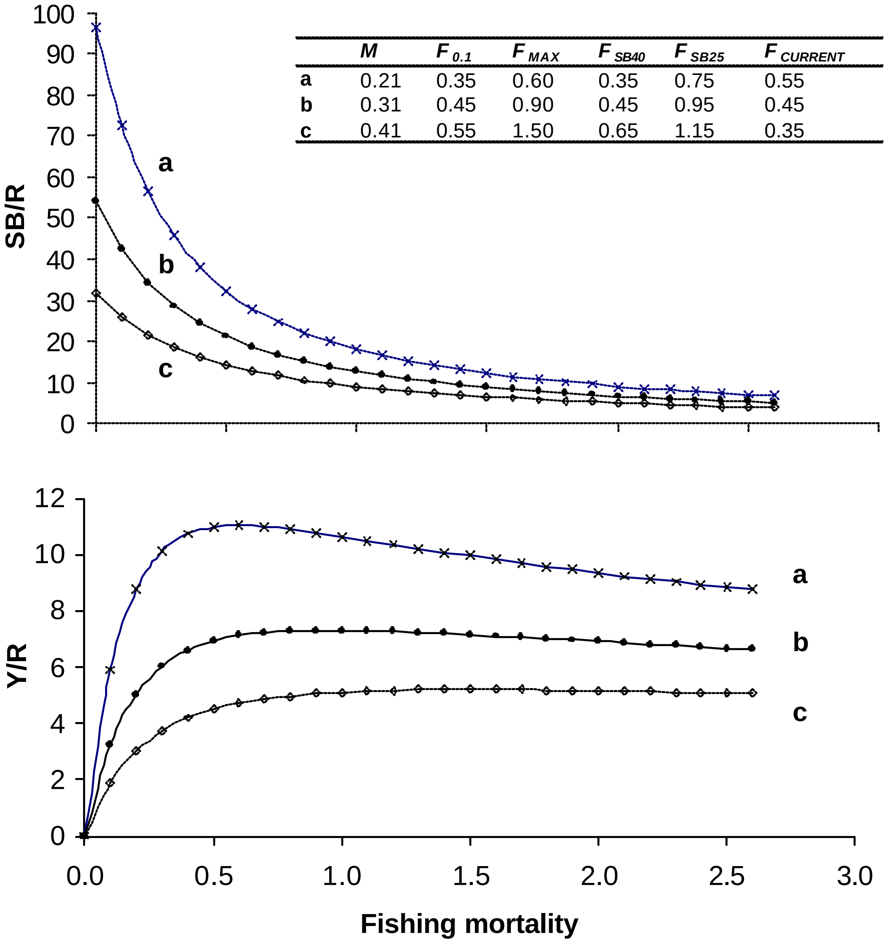


Figure 5.1: Selection ogives for *D. limnothrissa* in the Stern trawl (n = 249478) and pair trawl (n = 802) fisheries of the southeast arm of Lake Malawi.

5.3.2 Per-Recruit Analyses

Yield-per-recruit and spawner biomass-per-recruit curves for *D. limnothrissa* from the southeast arm of Lake Malawi at the current age-at-capture (t_c = 2.67 years) and at three levels of natural mortality (0.21, 0.31 and 0.41) are presented in Figure 5.2.



	M	$F_{0.1}$	F_{MAX}	F_{SB40}	F_{SB25}	$F_{CURRENT}$
a	0.21	0.35	0.60	0.35	0.75	0.55
b	0.31	0.45	0.90	0.45	0.95	0.45
c	0.41	0.55	1.50	0.65	1.15	0.35

Figure 5.2: Yield-per-recruit (Y/R) and spawner biomass-per-recruit (SB/R) as functions of fishing mortality (with biological reference points) for *Diplotaxodon limnothrissa* in the southeast arm of Lake Malawi at different levels of natural mortality (*M*), t_c = 2.67 years.

Maximum yield-per-recruit fluctuated widely with changes in natural mortality (Figure 5.2) with highest levels attained at the lowest natural mortality (0.21 yr^{-1}).

Exploitation levels corresponding to $F_{0.1}$ and F_{MAX} are observed to increase with increasing natural mortality. F_{MAX} and $F_{0.1}$ ranged between 0.60 - 1.50 yr^{-1} and 0.35 - 0.55 yr^{-1}, respectively (Figure 5.2), suggesting that productivity increases with increasing natural mortality. Fishing mortality was highest (0.55 yr^{-1}) at the lowest level of natural mortality (M = 0.21 yr^{-1}) and ranged between 0.35 - 0.55 yr^{-1}. At the current level of natural mortality (i.e. base case scenario M = 0.31 yr^{-1}) fishing mortality (F) approximated $F_{0.1}$.

SBR also declined rapidly with increased natural mortality (Figure 5.2) with the highest levels being attained at the lowest natural mortality (0.21 yr^{-1}). F_{SB40} and F_{SB25} ranged between 0.45 - 0.65 yr^{-1} and 0.75 - 1.15 yr^{-1}, respectively (Figure 5.2). The spawner biomass-per-recruit as a percentage of the pristine unfished condition ranged from 31% to 55% for natural mortality between 0.21 and to 0.41 yr^{-1}, while spawner biomass-per-recruit at the current level of natural mortality (M = 0.31 yr^{-1}) was estimated at 42% $(SB/R)_{F=0.}$ These results suggest that the fishery is fully exploited.

Isopleths describing the response of yield-per-recruit and spawner biomass-per-recruit, as functions of age-at-first capture and fishing mortality, at the three levels of natural mortality (M) are shown in Figures 5.3 and 5.4, respectively. It is observed from Figure 5.3 that the current fishing mortality (0.45 yr^{-1} - point **B** in the figure) is higher than $F_{0.1}$ (0.39 yr^{-1} -point **A** in the figure) confirming earlier observations (Figure 5.2) that the fishery is already being fished at levels above the optimum. The point marked **X** in Figure 5.3 indicates the age-at-capture that optimizes yield based on the $F_{0.1}$ harvesting strategy. It is noticeable from this figure that yield approaches maximum levels around 5 years (broken arrow in Figure 5.3) and is fully maximized between 7 and 8.5 years. The point marked **X** in Figure 5.3 also provides an estimate of the maximum exploitation level that a fishery can withstand based on the $F_{0.1}$ harvesting strategy.

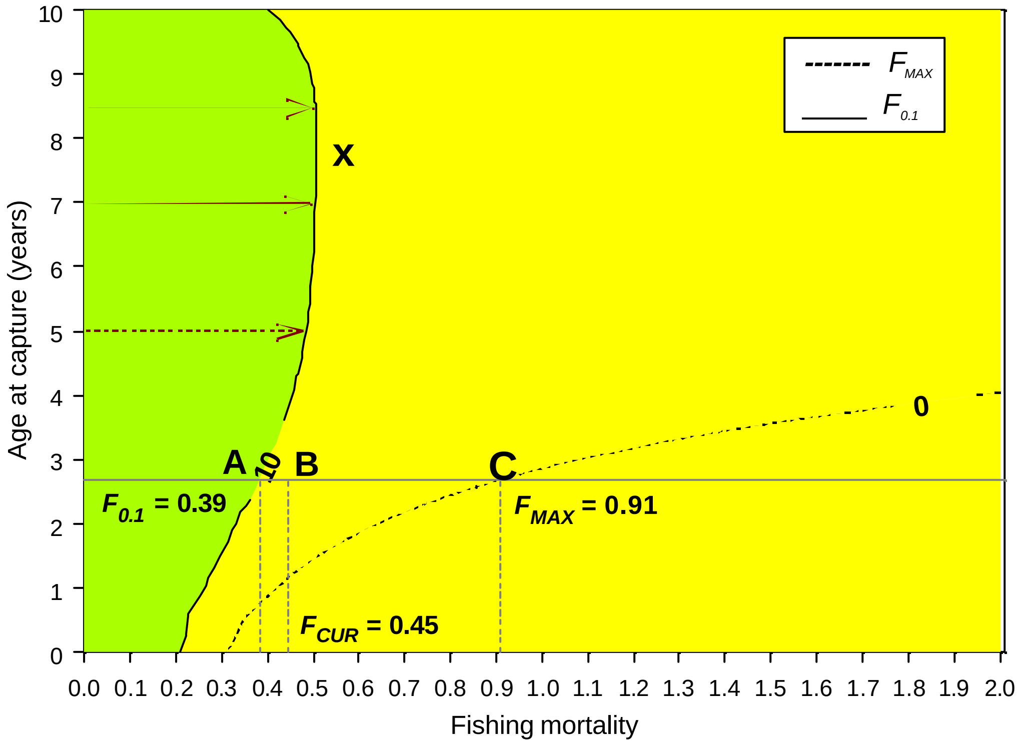


Figure 5.3: Isopleths of $F_{0.1}$ and F_{MAX} describing the response of yield-per-recruit to different combinations of age-at-first capture and fishing mortality at three levels of natural mortality (0.21, 0.31 and 0.41 yr^{-1}). The solid contour line (labeled 10) and dashed contour line (labeled 0) indicate the 10% and 0% slope isopleths representing $F_{0.1}$ and F_{MAX}, respectively. The solid horizontal line (line **ABC**) indicates the current age-at-capture (2.67 years). The intersection of this horizontal line with the $F_{0.1}$ and F_{MAX} isopleths (points **A** and **C**) provided estimates of $F_{0.1}$ and F_{MAX}. The current position of the fishery is indicated by the intersection of the horizontal line (line **ABC** - current age-at-capture) with the dashed vertical line at point **B** (current $F = 0.45$ yr^{-1}).

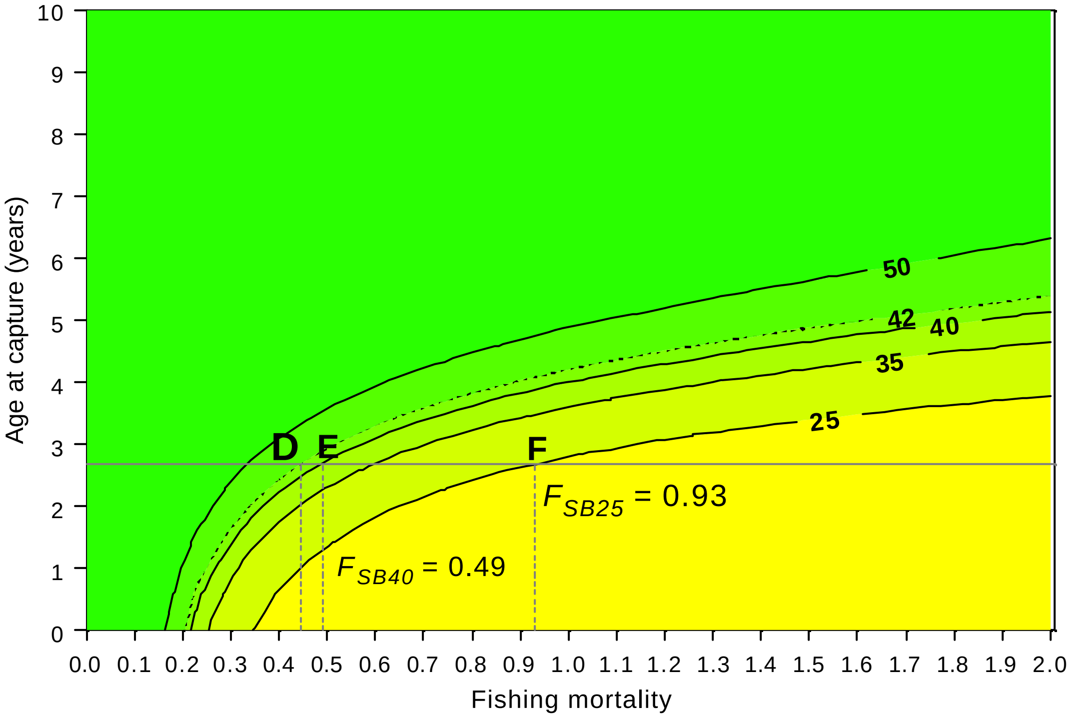


Figure 5.4: Isopleths of current spawner biomass-per-recruit as a percentage of pristine spawner biomass-per-recruit $(SB/R)_{F=0}$ describing the response of spawner biomass-per-recruit to different combinations of age-at-capture and fishing mortality at three levels of natural mortality (0.21, 0.31 and 0.41 yr^{-1}). The horizontal line (line **DEF**) indicates the current age-at-capture (2.67 years) while the contour lines marked 25, 35, 40 and 50 indicate the isopleths where the spawner biomass-per-recruit drops to 25%, 35%, 40% and 50% respectively of the pristine unfished spawner biomass-per-recruit $(SB/R)_{F=0}$. The intersection between the horizontal line (line **DEF** - current age-at-capture) and each of the isopleths (i.e. points **E** and **F**) provided an estimate of the corresponding fishing mortality at each level of spawner biomass-per-recruit $(SB/R)_{F=0}$. The current position of the fishery (point **D**) is indicated by the intersection of the current age-at-capture (line **DEF** - 2.67 years) with current fishing mortality (0.45 yr^{-1}).

For the ndunduma fishery in the southeast arm of Lake Malawi, this estimate is about 0.51yr^{-1}. It is also noted from Figure 5.3 that the current age-at-capture (2.67 years -

line **ABC**) is lower than the age at which yield is optimized (broken arrow in the figure) suggesting the possible occurrence of growth over-fishing in the fishery. In Figure 5.4 it is noted that spawner biomass-per-recruit generally increased with increase in age-at-capture. F_{SB40} (point **E**), and F_{SB25} (point **F**) were estimated at 0.49 and 0.93 yr^{-1} respectively.The spawner biomass-per-recruit as a percentage of the pristine $(SB/R)_{F=0}$ at the current position of the fishery was estimated at 42% (broken isopleth - Figure 5.4). The figure also indicates that the current exploitation level (point **D** - 0.45 yr^{-1}) is slightly below F_{SB40} (0.49 yr^{-1}).

5.4 Discussion.

Gear selectivity studies are essential for the determination of how fishing mortality varies with age (Butterworth *et al.* 1989). These studies also provide the information required for formulating management measures such as technical restrictions on mesh sizes or minimum harvestable limits.

An investigation of the pair and stern trawl fisheries operating in the southeast arm of Lake Malawi indicate that fish are recruited into the pair-trawl fishery at a younger age and smaller size than in the stern trawl fishery. Recruitment into the stern trawl fishery occurred after fish had attained sexual maturity while in the pair trawl fishery it occurred before the age and size-at-maturity (2.34 yrs/142 mm TL) was reached. This difference can be attributed to differences in gear sizes, cod-end mesh size and vessel power. Stern trawlers are equipped with more powerful engines (>90 horse power) to enable them cope with their heavier gears and greater fishing depths, while pair trawlers (< 30 horse power) fish in waters shallower than 50m (Bulirani *et al.* 1999). It is not surprising that pair trawlers are catching the fish at a younger age and smaller size than the stern trawlers because these vessels use a cod-end mesh size of 25 mm (which is sometimes illegally lined with mosquito netting) compared to 38 mm cod-end mesh size for stern trawlers. The smaller cod-end mesh size effectively retains most of the juveniles, while the lower pulling power means that older fish can possibly avoid the trawl net. The high incidence of juveniles in catches from the pair trawl fishery might also be due to the vessels fishing in a nursery area of *D. limnothrissa*.

Due to the absence of information on fisheries long-term catch-at-age data, per recruit analysis was used to assess the status of the ndunduma fishery in the southeast arm of Lake Malawi. However, these analyses have a number of limitations due to the assumptions on which they are based (Malcolm 2001). The assumption that the parameters for recruitment, growth and mortality are constant from one year to the next and, therefore, the stock is in a steady state is unrealistic. This is due to high variability in the abiotic and biotic environment that has a direct effect on recruitment, survival and growth (Beverton and Holt 1956; Malcolm 2001). As there is no real way of eliminating uncertainty in any fisheries assessment parameter (Sparre and Venema 1998; Malcolm 2001), results from any analyses might not fully reflect the true status of a stock. In light of these limitations, every effort was made to improve the accuracy of these analyses. The measures undertaken included using 3 levels of natural mortality and applying two analytical techniques, both of which arrived at a similar conclusion.

Research surveys conducted in the southeast arm of the lake between 1996 and 1999 indicate an increasing importance of ndunduma in the catches from the area. This can easily be misinterpreted as indicating that the fishery is healthy and that there is room for expansion. Findings from this study suggest otherwise. The per-recruit analyses suggest that the ndunduma stock in the southeast arm of Lake Malawi is probably fully exploited as indicated by the current spawner biomass of *ca.* 42% $(SB/R)_{F=0}$. Current fishing effort levels approximate $F_{0.1}$ and F_{SB40}, the exploitation levels that provide maximum long-term yield. This highlights the danger of basing management decisions on trends in catch rates or species composition only without due regard for exploitation levels.

The observed increase in importance of ndunduma in catches from the southeast arm suggests two things. Either current exploitation levels are not detrimental to recruitment or there is immigration and recruitment of individuals from other parts of the lake. As ndunduma are widely distributed, the possibility of the species immigrating into the southeast arm cannot be ruled out. However, assuming that there is no immigration, then the observed increase can only be due to growth of the population through recruitment. The three-dimensional modelling approach indicates that current exploitation levels are slightly below F_{SB40} suggesting that these levels are not detrimental to recruitment. The population is therefore expected to grow. This supposition is in agreement with the findings of Kanyerere (2000) who observed that since 1995, the distribution of ndunduma had remained relatively stable within the southeast arm of the lake. This stability can be attributed to a number of factors. Firstly, ndunduma are mainly caught in the mid-water/pelagic trawl fishery (Turner 1996) and currently there are only two mid-water trawlers that target ndunduma and other pelagic species. Secondly as offshore species, ndunduma are generally thought to be out of reach of small-scale fishing gears and their pelagic life style also renders them less susceptible to bottom trawlers. This results in effort on these stocks being relatively low. However, depletion to 40% of pristine SBR is quite high considering that only 5 trawlers target them and that the stock is widespread. Thirdly, the small difference between the current age-at-capture, 2.67 years, and that at maturity (2.34 years) coupled with their high abundance and wide distribution has probably enabled these fish to achieve high levels of spawning and recruitment success.

The three-dimensional modelling approach undertaken in this study has proved to be a very useful tool for describing the response of yield and spawner biomass-per-recruit to different combinations of age-at-capture, fishing and natural mortalities. Information obtained from such analyses includes the age-at-capture that optimises yield and the highest exploitation level that a fishery can sustain based on the $F_{0.1}$ harvesting strategy. These analyses indicate that yield in the ndunduma fishery in the southeast arm is optimised at an age-at-capture of 5 years or more. The current age-at-capture (2.67 years) is, therefore, lower than the age at which yield is optimised (i.e. 5 years). This suggests that the fishery is sub-optimally exploited and yield could be increased by raising the age-at-capture to 5 years or more. Considering that maximum size in *D. limnothrissa* is attained at an age as early as 4 years, raising the age-at-capture to more than 5 years would have a marginal difference in yield. It is therefore suggested that 5 years would be a suitable age-at-capture. At this age, the fish are expected to be between 160 and 180 mm TL instead of 145 mm TL (current size-at-capture). These analyses have also revealed that the ndunduma fishery in the southeast arm of Lake Malawi can probably withstand exploitation levels of close to

0.51 year^{-1} based on the $F_{0.1}$ harvesting strategy. As the $F_{0.1}$ strategy does not take into account the effects of fishing on the spawning stock and subsequent recruitment (Punt 1993; Clarke 1993), the exploitation level corresponding to F_{SB40} (i.e. 0.49 yr^{-1}) is instead recommended as the highest exploitation level that the fishery can withstand. Thompson (1995) also reported similar findings. In his analyses using the Beverton and Holt dynamic pool model, he observed that for *D. limnothrissa*, fishing levels in excess of 0.5 year^{-1} would result in recruitment over-fishing and stock collapse.

In conclusion, the ndunduma fishery in the southeast arm of Lake Malawi was fully exploited and exploitation levels approached F_{SB40}. To maximise yield, age-at-capture needs to be increased to about 5 years (160-180 mm TL) from 2.67 years (145 mm TL). This implies that selectivity studies may have to be conducted on the main gears exploiting *D. limnothrissa* in the southeast arm. Tentative management options for the fisheries in Lake Malawi including those of ndunduma are addressed further in Chapter 6.

CHAPTER 6

GENERAL DISCUSSION WITH MANAGEMENT CONSIDERATIONS FOR THE NDUNDUMA FISHERY IN SOUTHERN LAKE MALAWI

6.1 Introduction

The fisheries operating in Lake Malawi vary from subsistence fishing, where fishing is primarily conducted for household consumption, to commercial fishing where fish are sold for consumption or for ornamental purposes (Banda *et al*. 2001). The challenge to management is to ensure that the flow of benefits, however derived, is sustained at a level that is at or near its potential (Welcomme 2001). This specifically requires addressing issues like maintenance of adequate spawner biomass within acceptable biological limits (given underlying uncertainty), and creating a stable environment for economic and social development of the fishing sector and adjacent communities (Allison 1996).

The current scope of fisheries management in southern Lake Malawi attempts to address, both, biological sustainability, as well as, upliftment of the economic and social status of the fishing sector and its dependent communities (GOM 1999). The management framework of the large-scale commercial fishery which encompasses the demersal, pelagic and pair trawl fisheries is based on recommendations from monitoring programmes carried out by the Fisheries Department, which include the assessment of sustainable yields and allowable effort (Bulirani *et al.* 1999; Palsson *et al.* 1999). The sector is subject to a variety of regulations such as minimum mesh size, maximum gear size, closed hours, closed areas, minimum shore distance and minimum depth (Bulirani *et al*. 1999).

However, the effectiveness of these regulatory mechanisms appears to be limited. This is demonstrated by major declines in the catches of *Oreochromis* spp., *Bathyclarias* spp., *Bagrus meridionalis*, and *Copadichromis* spp. (Turner 1976; Bulirani *et al*. 1999). The ineffectiveness of these management measures has been attributed to weak regulation enforcement and the "open entry" nature of the small-scale commercial fisheries (Bulirani *et al*. 1999). Another important management issue pertains to the multi-species and multi-gear nature of the fisheries.

Inland fisheries, especially those within the subtropical and equatorial zones including those of Lake Malawi, are based on a large number of species and in many cases are carried out with a variety of fishing gears (Weyl 1998; Welcomme 2001; Booth 2001). These fisheries cannot be readily assessed by the more traditional methods of stock assessment, such as single species yield-per-recruit, due to the complexity of the interactions resulting from their multi-species and multi-gear nature (Allison 1996; Welcomme 2001). Difficulty in obtaining data on age structure, growth and mortality, all of which are required for commonly used stock assessment tools such as yield-per-recruit and virtual population analysis (VPA), is another major limitation (Allison 1996; Sparre and Venema 1998; Morales-Nin 1992). As a result, most regulations are based on length-at-maturity and gear selectivity information, both of which only aim at allowing escapement of part of the spawning stock without due consideration to the status of spawner biomass at various exploitation levels (Allison 1996). Management should, therefore, be based on suitable stock assessment tools that can provide information on the status of the resource and optimum exploitation levels besides taking into consideration the multi-gear and multi-species nature of the fisheries.

Multi-species/fishery-per-recruit models are particularly suitable for assessing data–poor fisheries due to minimal data requirements and their ability to handle multi–species and multi–gear problems (Pikitch 1987; Weyl 1998; Booth 2001). However, the information required for such analyses is not available for most of the species exploited in the large–scale commercial fisheries of Lake Malawi. Until such data is available, it is recommendable to priotise key species for management of the large–scale commercial fisheries operating in the southeast arm of Lake Malawi. Such key species should contribute significantly towards the fishery and show declining catch trends that indicate that management intervention is necessary (Weyl 1998). The ndunduma (*Diplotaxodon* spp.) stock in the southeast arm of Lake Malawi fulfils such a criteria.

6.2 Management Consideration for Ndunduma Fishery in the southeast arm of Lake Malawi

Low fecundity and the general life-history characteristics of cichlids were considered to be the most important factors in adopting the biological reference points (BRPs) for *D. limnothrissa* (Booth 2001). Since the spawner-recruit relationship for *D. limnothrissa* is unknown, a reduction of spawner biomass to 40% of pristine levels $(SB/R)_{F=0}$ was considered acceptable in ensuring the sustainability of the *D.*

limnothrissa resource in the southeast arm of Lake Malawi. Per–recruit analyses indicate that exploitation rates for *D. limnothrissa* in the southeast arm approached the $F_{0.1}$ and F_{SB40} BRP levels and corresponded to an SB/R reduction to 42% of pristine levels implying that the fishery was fully exploited.

Based on the results of this study, management strategies designed to enhance sustainable exploitation of pelagic resources particularly stocks of *D. limnothrissa* in southern Lake Malawi can be divided into three options:

Option 1

The first option takes into consideration the current status of the fishery and is based on the premise that since current exploitation levels are already at the optimum, the age-at-capture should be increased from the current 2.67 to about 5 years while maintaining current effort levels. Per-recruit simulations indicate that this option provides the highest optimum yield based on the $F_{0.1}$ harvesting strategy. This would allow the fish to be harvested at a higher individual weight of about 41 g instead of 24 g. Despite a decrease in YPR of about 17% this option would provide an increase in SBR of over 60%. As increasing the age-at-capture entails increasing codend mesh size for trawl gears as well, this option is also beneficial to species that are larger than *D. limnothrissa.*

Option 2

The second option is to increase both the age-at-capture and effort. The age-at-capture could be increased to 5 years while effort could be raised by 10% from 0.45 to levels corresponding to F_{SB40} (i.e. F=0.49 yr^{-1}). This option also provides the highest optimum yield possible under the $F_{0.1}$ harvesting strategy. However due to the multi-species nature of the southeast arm fisheries, the consequence of increased effort on the other species is not known and subsequently increased effort cannot be recommended.

Option 3

The last option would be to maintain both current exploitation levels and age-at-capture but impose a closed season during the peak- breeding season of *D. limnothrissa* that occurs around April-May. As there is currently no closed season for the trawl fisheries operating in southern Lake Malawi, the advent of a closed season would help in reducing fishing mortality of juveniles and mouth brooding females that are currently caught in large numbers by both midwater and demersal trawlers. This would also benefit other species whose breeding season coincides with that of *D. limnothrissa*. The imposition of a 2-month closed season would also have the effect of reducing overall fishing effort by at least 16%. As there are only 5 vessels in the commercial sector and considering that these vessels operate within a limited area (i.e. Areas B and C) implementation of such a strategy would not pose serious enforcement problems.

Based on the available information, the most suitable option for managing the *D. limnothrissa* resource in the southeast arm of Lake Malawi would be option 1. This option not only provides the highest optimum yield but would also safeguard the fishery against unprecedented increases in effort. Since Kanyerere (1999) showed that the 38 mm codend currently in use in southern Lake Malawi is inappropriate for most of the deep-water species (Table 6.1), increasing the codend mesh size would reduce growth overfishing for at least some of the other species in the fishery. Thus, although there might be a quantitative reduction in total yield, this option also ensures sustainable exploitation of the other deep-water species.

Table 6.1: Size at 50% selectivity in the 38 mm cod-end and size at 50% maturity for *Lethrinops gossei*, *L. alta* and *L. oliveri* (source: Kanyerere 1999).

Species	Size at 50% selectivity	Size at 50% maturity
Lethrinops gossei	89 mm TL	159 mm TL
Lethrinops alta	96 mm TL	120 mm TL
Lethrinops oliveri	83 mm TL	120 mm TL

Since it is impossible, in a multi-species fishery, to manage each species at its optimum level (Murawski 1984), this study recommends that population dynamics of other commercially important fish species in Lake Malawi be investigated. This would allow far more advanced age-structured population dynamics models such as multi-species YPR and multi-species virtual population analysis (VPA) to be used in obtaining management advice for the lake.

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