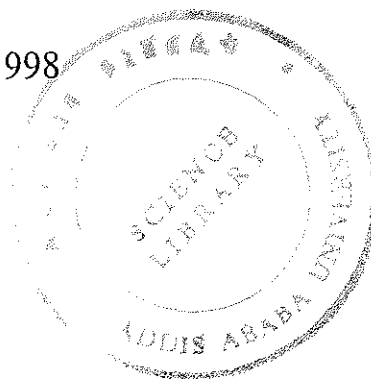


**Age and growth determination of
tilapia, *Oreochromis niloticus* L. (Pisces:
Cichlidae) in some lakes in Ethiopia**

A thesis presented to the School of Graduate Studies, Addis Ababa
University, in partial fulfilment for the degree of Doctor of Philosophy
in Biology

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December, 1998



Dedicated to the fishermen of Ethiopia

Abstract

Tilapia, *Oreochromis niloticus* L. is the most important fish in Ethiopia. Knowledge on age and growth of the fish is essential for fisheries management, and for further detailed studies. In this study, age and growth of *O. niloticus* in Lakes Zwai, Langeno and Chamo was studied from microzones and macrozones in otoliths. The usefulness of otoliths to determine age was established by examining the existence of regularly formed translucent and opaque macrozones. The effect of subtle changes in temperature on body growth and on otolith macrozone formation was also experimentally tested. The growth of the fish in various lakes was also compared.

Two translucent macrozones, each associated with *biannulus* (a type of annulus formed twice a year), were formed each year in otoliths of *O. niloticus* in Lake Zwai. Biannulus formation was connected to fluctuations in temperature, quality and quantity of food, and to intensive spawning activity.

Translucent macrozone was formed in otoliths, and somatic tissue growth was slow, in tilapia that were transferred from 24°C to slightly lower temperature treatments. Fish that were transferred from 24°C to higher temperatures grew rapidly, and more opaque material was deposited in their otoliths. At the high test temperatures, translucent macrozone was formed in otoliths of fish that had ripening or ripe gonads.

O. niloticus in Lake Zwai has two spawning peaks, hence two major annual recruitment cohorts. Fish from the two cohorts were discriminated and age was determined from the number of biannulus in otoliths by relating median hatch-dates with the dates of capture. Ages determined in this manner (macrozonal ages) were highly correlated ($r^2 = 0.85$) with microzonal ages.

Growth of juvenile *O. niloticus* in Lakes Chamo, Zwai and Langeno was described by Gompertz model fitted to length and microzonal age data. Growth was most rapid in Lake Chamo, intermediate in Lake Zwai and slowest in Lake Langeno. Rapid growth of juvenile *O. niloticus* in Lake Chamo was attributed mainly to warm temperature and better food quality in this lake.

The growth of adult *O. niloticus* in Lakes Zwai, Awassa and Haiq was described by von Bertalanffy model fitted to mean length and macrozonal age data. Growth rate was most rapid in Lake Haiq, intermediate in Awassa and least in Zwai. Rapid growth in Haiq was attributed to better quality food in this lake.

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Acknowledgements

I am very grateful to my supervisors Drs Ingemar Ahlgren and Seyoum Mengistou for their valuable advice, guidance and support. Drs I. Ahlgren and Gunnel Ahlgren were deeply involved in my study right from the inception up to the end. Above all, I am very grateful to the support and kind hospitality of Ingemar and Gunnel without whom this study would not have been materialised, let alone to be completed. Drs Getachew Teferra and Henrik Mosegaard are gratefully acknowledged for the valuable discussions we had when they were my supervisors at the beginning of the study. I came this far in part due to their constructive advice and guidance at the beginning of the study.

I am especially thankful to Dr. John Casselman, Ontario Ministry of Natural Resources (Canada), who introduced me well to the fascinating science of fish age and growth study. As a novice, I was not sure if I could age tilapia. However, I am inspired by his deep knowledge in the science which, over the years, was a source of stimulating comments, advice and encouragement.

I am grateful to my friends and colleagues Elizabeth Kebede, Zenebe Tadesse, Yosef T-Giorgis, Kebede Alemu and Elias Dadebo for their help and for the stimulating discussions we had both in the field and in the laboratory. I am especially indebted to Zenebe Tadesse and Elizabeth Kebede for being such nice companions and colleagues for so long a time.

Field work in Ethiopia was at times a real challenge, because this or that facility was not available as required. Therefore, support and co-operation from other persons and institutions was indispensable for my study. Space limits me to mention all of them, but I should thank especially the following: (1) the Ministry of Agriculture office and the staff at Zwai, particularly Yohannes Desta, Dawit, Meseret and Dirk Reyntjens, for participating in sampling, providing laboratory space and some equipment, (2) several fishermen, particularly Tashite,

Berisso, Asfaw and Banjaw who co-operated in sampling, and were also kind and so friendly, (3) my drivers, especially Fantaye Simeon, who also assisted me in my field work, and (4) several members of the Department of Biology, Addis Ababa University, were also very helpful.

I am thankful to the Institute of Agricultural Research (Awassa station), International Livestock Research Institute (Zwai station) and Northern Omo Agricultural Development Enterprise (Arbaminch) for providing me with some agrometeorological data.

My friends Tiruwork Kebede, Seyoum Halake and Ali Hussein deserve many thanks for their moral support, and for their interest in my work. I am thankful to my friends in Uppsala who made my stay there memorable and fulfilling by being part of my social life. They are too many to mention, but I should thank especially Zenebe, Elizabeth, Ferdu, Atalay, Tesfaye, Eden, Belai, Almaz, Getachew, Wubshet, Zebene, Yonas, Teebe and Terhas, and also all members of the Uppsala '*tena*' football club.

I would like to thank all members of the Department of Limnology, Uppsala University, for their friendliness and kind hospitality. Many of them were helpful in one way or another, but I should mention Dr. Peter Blomqvist, who spent many hours with me in discussing matters related to my study; Erik Höglund, for helping me in several ways, especially in scanning photographs of otoliths; Eva Lindström, for allowing me to use her video printer; Hans Olofsson, for his interest, and for providing me with various items for my experimental study; Karin Rengefors, for her concern and for being so friendly and kind. I am also grateful to Jan Johansson, Bo Swärd and Stefan Djurström for assisting me with various technical matters.

I am very grateful to the Swedish Agency for Research Co-operation with Developing Countries (SAREC) for financial support. The co-operation with SAREC was facilitated by the Ethiopian Science and Technology

Commission and Addis Ababa University, particularly the Research and Publications Office and the School of Graduate Studies. I am grateful to these offices.

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CHAPTER I

GENERAL INTRODUCTION

Food production in most parts of the world is not on a par with human population growth. Therefore, in addition to increasing agricultural production, it is necessary to search for alternative food sources. Exploitation of the aquatic ecosystem, particularly fishery, is a well developed activity in several parts of the world. However, in countries such as Ethiopia, where drought is one of the major factors reducing agricultural production, the aquatic ecosystem needs to be fully exploited so that the problem of food shortage can be ameliorated.

Ethiopia is endowed with several lakes which have a total area of about 7400 km², and numerous rivers, the main ones of which extend for a total of about 7000 km (Alem, 1993). These water bodies contain several edible fish species, and could provide a total sustainable annual yield of 30300 to 40300 t (Alem, 1993). Fishing is relatively a recent practice in Ethiopia however, and it is concentrated mainly on lakes most of which are located in the rift valley, the latter being part of the Great Rift of Africa. The Fishery resource is under-exploited as the total annual catch is seldom more than 20% of the potential (Alem, 1993; LFDP, 1996). Some water bodies, particularly rivers, are virtually unexploited. Nevertheless, the Ethiopian fishery is growing rapidly.

As is the case in the fisheries of most East African rift valley lakes (Fryer & Iles, 1972), the Nile tilapia (*Oreochromis niloticus* L., Family Cichlidae) is the most exploited fish species in Ethiopia. The species is found in almost all of the fresh waters of the country. Therefore, detailed study on the biology, such as on age and growth, of such species is an important development leading to a proper exploitation and management of fisheries. Accurate information on important parameters such as mortality, survival, recruitment, yield, etc. can be

obtained from knowledge on age and growth (Ricker, 1975). To study growth, a temporal measurement such as age is essential.

The age of fishes is determined in one or more of three basic methods: the empirical, the mathematical and the anatomical. Detailed account of these methods is given by several authors (De Bont, 1967; Bagenal & Tesch, 1978; Brothers, 1979; Casselman, 1987). A brief description of each method is given below.

The empirical method is based on direct observation of fishes held in confinement (ponds, cages, aquaria, etc.) or fishes marked and released, and then subsequently recaptured. Accurate 'known-age' data would be obtained if the fish are artificially fertilised, but if they are captured from the natural environment, marked and released, upon recapture 'partly known-age' data would be obtained to the time between marking and recapture (Casselman, 1987). The empirical approach is, therefore, based on artificial conditions and factors. However, it has been used by several workers who mostly used it to test the validity of age data obtained by other methods of age determination (e.g., Rinne, 1975; McCaughran, 1981; Smith, 1984; Admassu, 1989).

The mathematical method (also called length-frequency analysis or Petersen's method) involves indirect assessment of fish age from length-frequency distributions. It is based on length data from which frequency distributions are constructed to feature a series of modes corresponding to successive age groups. For this method to be applicable spawning activity of the fish should be restricted to a relatively short period of time during the year such that a regular influx of new recruits occurs. Thus, adequate and randomly taken length data would depict frequency distribution with a series of modes corresponding to age groups (Iles, 1971; Tesch, 1971; Pauly, 1983).

The anatomical method (also called osseochronometry) is used most commonly, and it involves interpreting age from checks and optical zonation in

the fish's calcified structures such as otoliths, scales, fin rays, vertebral centra, opercula and cleithra (Casselman, 1987). Depending on the environment in which the fish lives, these calcified structures frequently bear checks and optical zonations to which a regular time scale can be assigned. This makes osseochronometry the most commonly used method in the study of fish age and growth.

When calcified structures are microscopically examined at low magnifications (mostly < 40x) the method is referred to as *macrozone* or *macrostructure* analysis. This is in contrast to *microzone* or *microstructure* analysis which refers to examination of otoliths, usually thin sections, at higher magnifications to reveal the details of the microstructures. Macrostructure analysis provides an estimate of age on annual (Casselman, 1987) or sub-annual (Admassu, 1989; Yosef* & Casselman, 1995) time scale, whereas microstructure analysis provides age in days mainly for juvenile fish (Pannella, 1971; Campana & Neilson, 1985).

Macrozones in fish calcified structures are used to determine age if they conform to the definition of the *annulus*. As defined by Casselman (1983) "annulus is a mark on or in a calcified structure that is associated with the distal edge of a concentric ring in the form of a check in scales and a translucent [macro]zone in other calcified structures; and is considered to separate the check or [macro]zone associated with the principal annual cessation or reduction in growth from the tissue deposited [i.e., opaque macrozone] when growth resumes or increases." The term *biannulus* has been introduced relatively recently (Yosef & Casselman, 1995), and it is a similar demarcation to the annulus, but associated with translucent macrozone that forms biannually.

*Yosef T/Giorgis & also Getachew Teferra have indicated preference to be cited by first name, all other Ethiopian authors are cited by last name.

One of the basic criteria to use the annulus or biannulus to determine age is that a regular time scale can be assigned to the checks and macrozones (Beamish & McFarlane, 1983; Casselman, 1983). Their time of formation must be ascertained and they should be differentiated from 'pseudoannuli' or 'pseudobiannuli'. Old and slow growing fishes, especially, present considerable difficulty as it is almost impossible to decipher all annuli or biannuli in their calcified tissues.

A number of techniques are available to test the validity of age determination methods (Bagenal & Tesch, 1978; Casselman, 1987). A relatively simple technique to ascertain the time of annulus or biannulus formation involves studying the annual growth cycle of the calcified structure from a seasonal record on the type of the macrozone at the edge, and from calculations of relative marginal increment. Relative marginal increment is the width of the opaque macrozone at the edge divided by the mean width of that particular opaque macrozone in calcified structures taken from fish sampled later in the growing season (Casselman, 1987). Enumeration of microstructures has also been used to validate age assessment from macrostructure of otoliths (e.g., Victor & Brothers, 1982), but it is often difficult to obtain the expected number of daily increments if light microscopy is the only equipment available (Campana & Neilson, 1985).

Most of the methods of age and growth determination work reasonably well for fish living in seasonal habitats, such as in temperate region water bodies. However, the application of the methods has often been difficult for fish living in tropical lakes. The empirical method of age determination is virtually impractical in the tropics, because the resources involved in mark-recapture experiments are prohibitive. The length-frequency method is also less useful for tropical fish, because most fish in the tropics spawn throughout the year, and their life cycle is often short (Welcomme, 1967). Furthermore, due to the small

seasonal fluctuation in the tropical climate, regular checks and macrozones may not form in calcified structures of the fish.

However, seasonal variation exists in many tropical waters, associated primarily with rainfall and winds (Lowe-McConnell, 1987; Melack, 1996). Although tropical fish breed throughout the year, some have periods of peak breeding activity often associated with rainfall (Lowe-McConnell, 1982) or factors associated with it such as increased food quantity (Admassu, 1996). Age and growth of such fish may be studied by length-frequency analysis (Pauly, 1983; Admassu, 1989; Yosef, 1990). In addition, median hatch-dates can be estimated for the peak breeding period using daily age determined from otolith microstructure (e.g., Alemu, 1995; Yosef & Casselman, 1995). Median hatch-date can be considered as an average 'birth-date', and incorporated into the procedure of age and growth determination (Admassu, 1989; Alemu, 1995; Yosef & Casselman, 1995).

Several studies have shown the annual formation of one or more checks and macrozones in calcified structures of tropical fish in general (Willoughby, 1974; Blake & Blake, 1978; Lecomte *et al.*, 1989; Wudneh, 1998) and tilapia in particular (Fagade, 1974; Admassu, 1989; Alemu, 1995; Booth *et al.*, 1995; Yosef & Casselman, 1995). The physiological mechanisms involved in the formation of annulus or biannulus are still far from being fully understood. However, a number of factors resulting in cessation of somatic tissue growth of the fish, which in turn result in the formation of checks and macrozones in the fish's calcified structures, have been identified. In the temperate region, drastic changes in temperature and associated biotic and abiotic factors are believed to be responsible for this effect (De Bont, 1967; Balon, 1972; Casselman, 1987). The formation of macrozones in calcified structures of fish in the tropics has been variously associated with growth changes due to variations in temperature, total dissolved solids, food quality and quantity, the cycle of wet-

dry season, and due to spawning-associated loss in body condition (Admassu, 1989 and references therein). Therefore, factors associated with annulus or biannulus formation in tropical fish could be different from those in temperate fish, but the difference could also be in the magnitude or amplitude of the seasonal fluctuation in the factors in question. Balon (1972), for instance, noted that the timing and factors associated with the formation of annulus in fish calcified tissues in all regions are connected to the main spawning period and/or to the period of increase in available food. Furthermore, subtle changes in temperature could also be an important clue in the cyclic growth of tropical fishes, because the fish are normally adapted to high temperatures (Admassu, 1989; Yosef, 1990).

The same basic principles and methods of age and growth determination developed for temperate fish can be used for some tropical fish species. The practical problems of the methods are also generally similar in all fish regardless of the environment. The consistency of results from several age and growth studies on tropical fish (Fryer & Iles, 1972; Admassu, 1989; Yosef, 1990; Getabu, 1992; Sanyanga, 1996; Wudneh, 1998) also provides evidence to the validity of the methods in general. However, checks and macrozones in tropical fish calcified structures should be examined in detail and systematically in a much more detailed manner than before.

If a valid age could be estimated from a calcified structure, a relatively small sample is enough to obtain length-at-age data by back-calculation (Casselman, 1987). Back-calculation is a technique of reconstructing growth history of a fish from an empirical relationship between fish—size and the size of its calcified structure. Back-calculation formulae are based either on the scale proportional hypothesis (SPH) or on the body proportional hypothesis (BPH) (Francis, 1990). In SPH, fish length is considered as an independent variable whereas in BPH fish length is considered as a dependent variable (Francis,

1990). Since back-calculation refers to estimation of fish length, formulae based on BPH, i.e., fish length as dependent variable, appear to be more reasonable than those based on SPH.

Growth can be described in terms of length or weight, but conversion is possible by using length-weight relationship. If length-at-age data are available, fish growth can be expressed in one of several models. Models are important in comparing growth between populations, and also their parameters are vital in yield estimation (Ricker, 1975).

Growth of juveniles is usually described by the Gompertz model (Gompertz, 1825 in Ricker, 1979). One of the commonly used integral forms of this model in terms of length is as follows:

$$L_t = L_0 * e^{k(1-e^{-gt})},$$

where L_0 is length at age 0 days (d), g is specific growth rate at the inflection of the curve, k is a dimensionless parameter such that $k*g$ is specific growth rate when $t = 0$ d. Growth of older fish is usually expressed by the von Bertalanffy growth function (von Bertalanffy, 1938), which in terms of length has the form:

$$L_t = L_{\infty} \left[1 - e^{-K(t-t_0)} \right],$$

where L_t is average length at age t (yr); L_{∞} is theoretical asymptotic maximum length to which the fishes grow; K (which is different from k in Gompertz model) is growth coefficient, and it measures the rate at which L_{∞} is approached; t_0 is a theoretical age when length is assumed to be zero if the fish grows according to the model. Methods of fitting are described by Pennington (1979) for the Gompertz model, and by Ricker (1975) for the von Bertalanffy model.

Growth of fishes in general is extremely plastic, because the same species grow at different rates in different water bodies. Growth plasticity is particularly common in tilapia (Fryer & Iles, 1972). This suggests that environmental differences are more potent than genetic ones in determining growth rates of a

particular species of tilapia living in different water bodies (Lowe-McConnell, 1982). Growth differences have, for instance, been attributed to differences in temperature, food quality and quantity, size of the habitat, and fishing pressure (Garrod, 1961; Ssentongo & Welcomme, 1985). Metabolic activity, such as assimilation of food, in tilapia is positively correlated with temperature (Caulton, 1982), thus tilapia in warm waters grow rapidly. Poor growth of tilapia in lagoons and small water bodies has been attributed to poor diet quality and quantity (Lowe-McConnell, 1958). Diet quality and its digestibility have been found to determine growth patterns of *O. niloticus* in natural waters (Bowen, 1982; Getabu, 1992). Heavy fishing pressure, like intensive predation, may result in the reduction of the average size of fish in the stock and a faster growth rate (Guerrero, 1982; Healey, 1980).

Scope of the Study

Validated age and growth information is not available for most fish species in the tropics. The present study was conducted to provide such information for *O. niloticus* in Ethiopia, particularly from Lakes Zwai, Langeno and Chamo. Yosef & Casselman (1995) have proposed a procedure of age and growth determination based on a systematic examination of macrozones in otoliths from juvenile *O. niloticus* in Lake Awassa, Ethiopia. The method uses biannulus not only to interpret age and growth, but also to assign individual fish to a specific recruitment cohort within a year. Other studies (Admassu, 1989; Alemu, 1995) have observed biannual translucent macrozones in otoliths of *O. niloticus*. The age and growth of the fish in other lakes is not known. In addition, Yosef & Casselman's procedure needs to be tested on these and other fish if it can be applied widely. Knowledge is also required on the time of, and factors associated with, biannulus formation, and with variations in body growth. Furthermore, information on spawning periodicity is essential to determine the

number of recruitment cohorts within a year. Age could then be more accurately determined from calcified structures by discriminating different recruitment cohorts of fish.

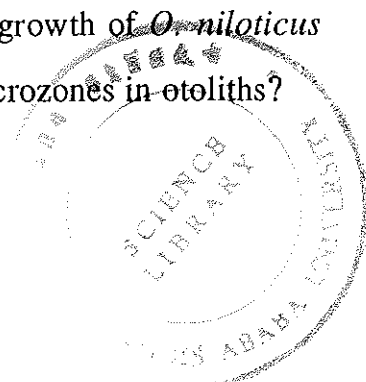
The effect of temperature on macrozone formation and body growth should be studied as temperature could be an important clue in the cyclic growth of tropical fishes. This important factor has been ignored due to the general assumption that tropical habitats are homothermous to the fishes. However, fishes could respond to very subtle changes in temperature (Casselman, 1990).

The growth of tilapia in natural waters is remarkably plastic (Lowe-McConnell, 1982). Therefore, research effort in comparing growth of the fish in various waters would provide insight into environmental factors affecting growth. Such information is also an important component of aquaculture development.

Objectives of the study

The general objectives of the study are to provide basic biological information which could be useful for proper exploitation and management of the Ethiopian fisheries, and for the promotion and usage of fishery resources for sustainable development. The specific objectives were to determine age for *O. niloticus* using otoliths, and compare the growth of the fish in various lakes. With in these specific objectives, the following issues were addressed:

- 1). is there a periodic growth cycle in otoliths of *O. niloticus* in Lake Zwai resulting in regular macrozones that could be useful to obtain valid age and growth information?
- 2). what factors are associated with fluctuations in the growth of *O. niloticus* and their otoliths under natural conditions to result in macrozones in otoliths?



- 3). is subtle experimental fluctuation in temperature sufficient to cause the formation of macrozones in otoliths of *O. niloticus*, and also, is this effect reflected on somatic tissue growth?
- 4). does the growth of juveniles and adults *O. niloticus* vary between lakes, if so, what are the possible factors for the variation? Comparison was made among juveniles in Lakes Zwai, Langeno and Chamo, and among adults in Lakes Zwai, Haiq and Awassa.

The thesis is divided into different chapters. Chapter I deals with a general introduction of age and growth studies, and with some of the associated problems. In Chapter II, a general description of the lakes considered in this thesis is presented. A more detailed description of each lake is also given in appropriate chapters. Chapter III deals with a comparison of growth of juvenile *O. niloticus* in Lakes Zwai, Langeno and Chamo based on age determined from microstructure analysis on otoliths, and also on growth that was back-calculated from measurements on the width of daily increments in otoliths. Chapter IV presents results from an experimental study on the effect of subtle fluctuations in temperature on formation of macrozones in otoliths, and on somatic tissue growth of *O. niloticus*. The fish were sequentially transferred from an acclimatisation temperature to a slightly lower and higher temperature treatments. Chapter V deals with age and growth determination of *O. niloticus* from Lake Zwai using macrostructure analysis on otoliths. Seasonal growth cycle of otoliths was determined from samples collected throughout the year to determine the time of translucent macrozone formation. This, together with period of recruitment inferred from otolith microstructure, was then used to determine age. In addition, Chapter V also presents a comparison of the growth of *O. niloticus* populations in Lakes Zwai, Awassa and Haiq. Furthermore, factors associated with macrozone formation in otoliths of the fish in Lake Zwai

are also discussed in this Chapter. Chapter VI presents summary and conclusions of the study.

CHAPTER II

GENERAL DESCRIPTION OF LAKES

The lakes that were sampled in this study are Zwai, Langeno and Chamo. Since previous data on age and growth of *O. niloticus* from Lakes Awassa and Haiq were also used for comparison in this study, a more general description of all these lakes will be presented in this chapter. Detailed description of the sampled lakes is given in appropriate chapters (Chapters III and V).

The lakes are located in the southern half of the Ethiopian rift valley except Lake Haiq which is located in northern Ethiopia and out of the valley (Fig. 1). The rift valley lakes are either tectonic or volcano tectonic in origin associated with the formation of the rift system. Lake Haiq is a highland crater lake (Kebede *et al.*, 1992). The lakes differ in several aspects of their physical, chemical and biological features (Table 1). In terms of area, Lake Chamo is the largest whereas Haiq is the smallest. However, the latter lake is the deepest with a maximum depth (Z_m) of 88 m. Lake Zwai is the shallowest ($Z_m = 7$) (Table 1).

Moist sub-humid to semi-arid climate is a characteristic feature of the region where the lakes are located (Gamachu, 1977). The main rainy season is mostly between July and September. However, a few weeks of more rainfall is common any time between January and May which could sometimes be a pronounced peak around Lake Chamo (Fig. 2). Water level of the lakes is dependent on the main rains. The dry season in the region is also mostly the coldest. This is the period between October and February when minimum air temperature can be as low as 6 °C particularly around Lakes Awassa, Haiq and Zwai (Fig. 3a). Surface water temperature of each lake varied by 3 to 6 °C between the yearly minimum and maximum (Fig. 3b). The temperature of Lake Chamo was almost always higher than that of the other lakes. Relatively cold

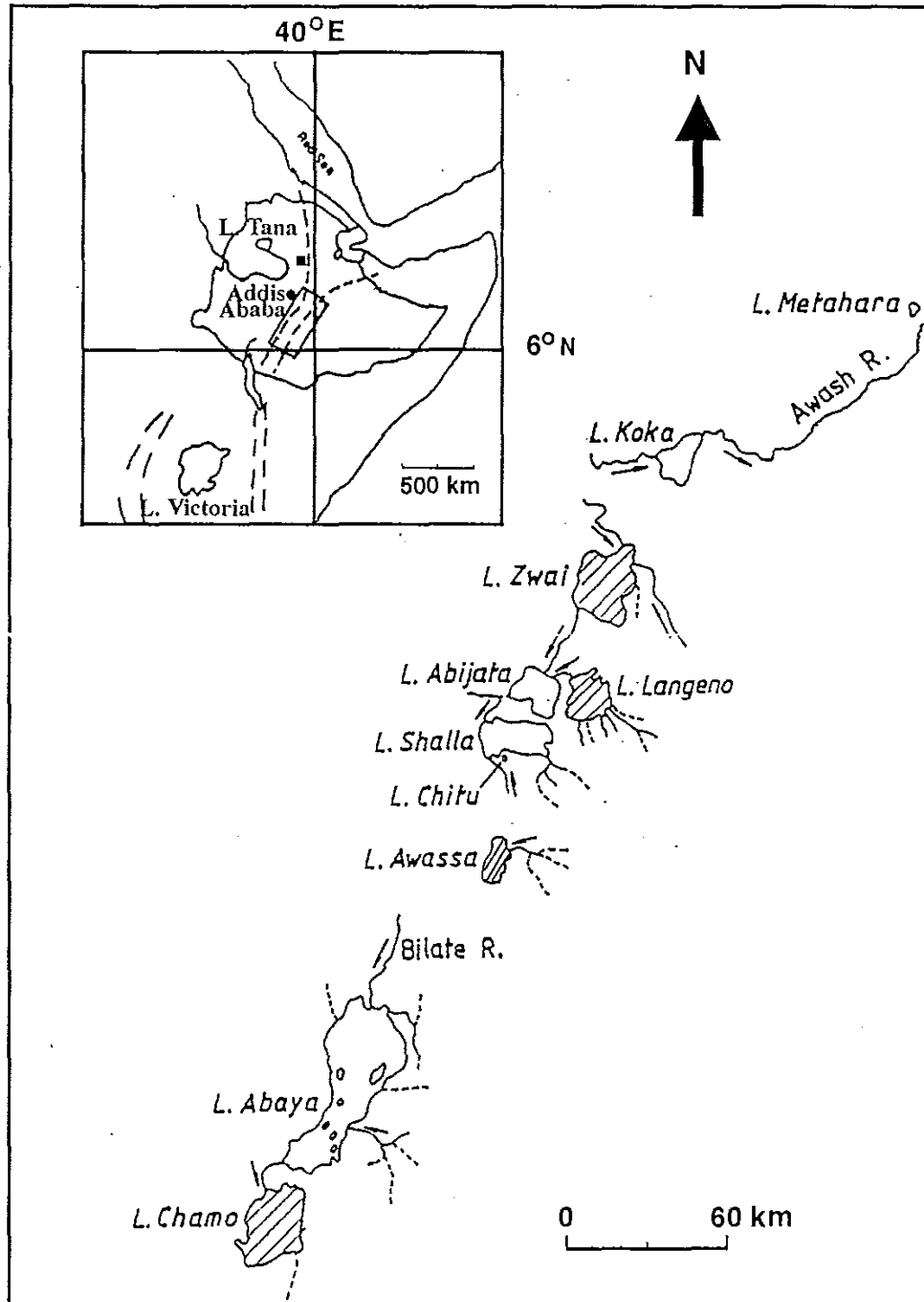


Figure 1. Map of eastern Africa showing Ethiopia and location of lakes in the rift valley, and relative location and drainage pattern of the rift valley lakes. Lakes in the study are highlighted. Lake Haiq lies out of this drainage; its location in the map is indicated by a dark square.

water temperatures were recorded in January, February, June, July and, in most cases, also in the last few months of the year. Highest temperatures were recorded mainly between March and May and also in late-August and September (Fig. 3b).

Phytoplankton community of the lakes is dominated by blue-greens, greens and diatoms (Kebede, 1996), and these are the main food source for *O. niloticus* (Z. Tadesse, unpublished). Algal biomass (Chlorophyll *a* concentration) is least in Lake Langeno, highest in Lakes Zwai and Chamo, and intermediate in Awassa and Haiq (Table 1). Dominant members of the zooplankton community include the genera *Mesocyclops*, *Thermocyclops* and *Diaphanosoma* (Defaye, 1988; Mengistou & Fernando, 1991). *Moina micrura* and *Daphnia barbata* are also dominant, particularly in Lakes Haiq and Langeno, respectively (S. Mengistou, personal communication). Zooplankton, together with other invertebrates such as chironomid larvae, are important food source for juvenile *O. niloticus* (Tudorancea *et al.*, 1988).

Piscifauna of the lakes is composed of between two (Lake Haiq) and twelve (Lake Chamo) species. All of them contain *O. niloticus*. Lake Chamo is also inhabited by other species such as Nile perch (*Lates niloticus*), catfishes and cyprinids. The other lakes contain six to seven species most of which are also shared with Lake Chamo. Sustainable fish yield from these lakes is not accurately estimated, but various survey suggest annual yield between 8000 and 10000 t (Alem, 1993; Herrmann, 1993). The total annual catch is between 50 and 60% of the potential (Alem, 1993; Herrmann, 1993; LFDP, 1996). However, the rapidly growing gillnet fishery is exploiting the maximum potential of some lakes, e.g., Lakes Awassa and Zwai (Herrmann, 1993). *O. niloticus* alone accounts for nearly 80% of the country's total value of landed catch, which is about 1.5 million USD (LFDP, 1996).

Table 1. Some physical, chemical and biological features of the study lakes. Data from Kebede (1996) unless indicated otherwise.

Feature	Haiq	Zwai	Langeno	Awassa	Chamo
Altitude (m)	2030	1636	1582	1680	1233
Surface area (km ²)	23	442	241	90 ^a	551
Depth (m) max. (mean)	88(37)	7(2.5)	46(17)	23(11)	13
Conductivity K ₂₅ (μS cm ⁻¹)	750 ^b	347-400 ^c	1500-1980 ^d	830	1400-1800 ^d
Salinity (g l ⁻¹)		0.4	2.4 (0.5-1.5 ^d)	0.8	1.0 (0.5-2.0 ^d)
NO ₃ +NO ₂ -N (μg l ⁻¹)	3	3.9	44.9	34.9	18.6
NH ₄ -N (μg l ⁻¹)	98 ^e	36.3	50	5.7	11.8
Tot-Phosphorus (μg l ⁻¹)	217 ^e	219	70	36.2	135
Chlorophyll <i>a</i> (μg l ⁻¹)	12.5-22.9 ^e	81-192 ^c	7 ^f	16.2	108 ^g

^aKebede *et al.*, 1994; ^bBaxter & Golobitsch, 1970; ^cTilahun, 1988; ^dminimum and maximum records during the study period (Z. Tadesse & D. Admassu, unpublished data); ^eKebede *et al.*, 1992; ^fBelay & Wood, 1984; ^gmeasured in March 1998 (G. Ahlgren & I. Ahlgren, unpublished data).

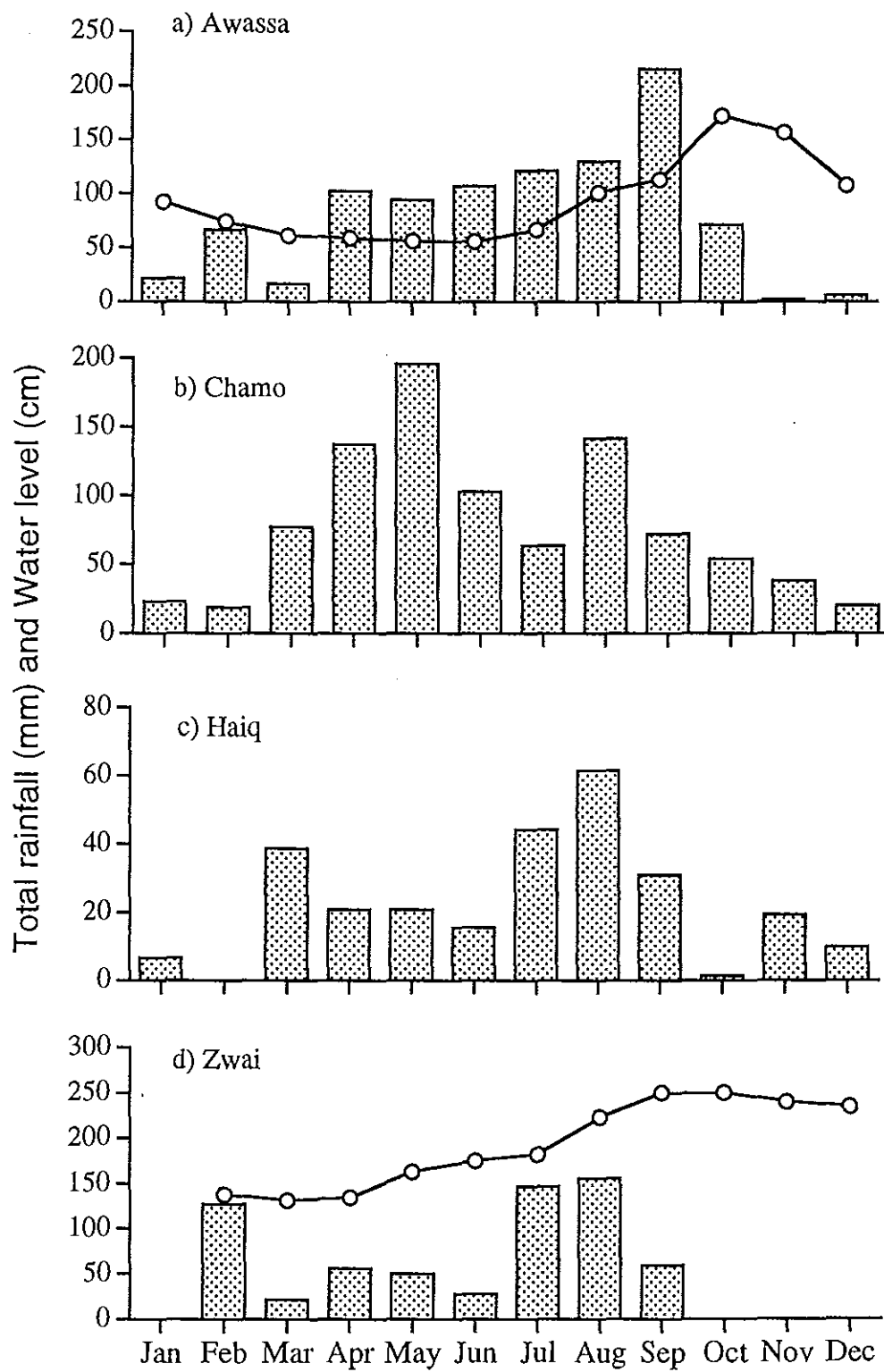


Figure 2. Monthly total rainfall around Lakes Awassa in 1988 (a), Chamo in 1996 (b), Haiq in 1994 (c) and Zwai in 1996 (d), and water level of Lakes Awassa and Zwai (curves).

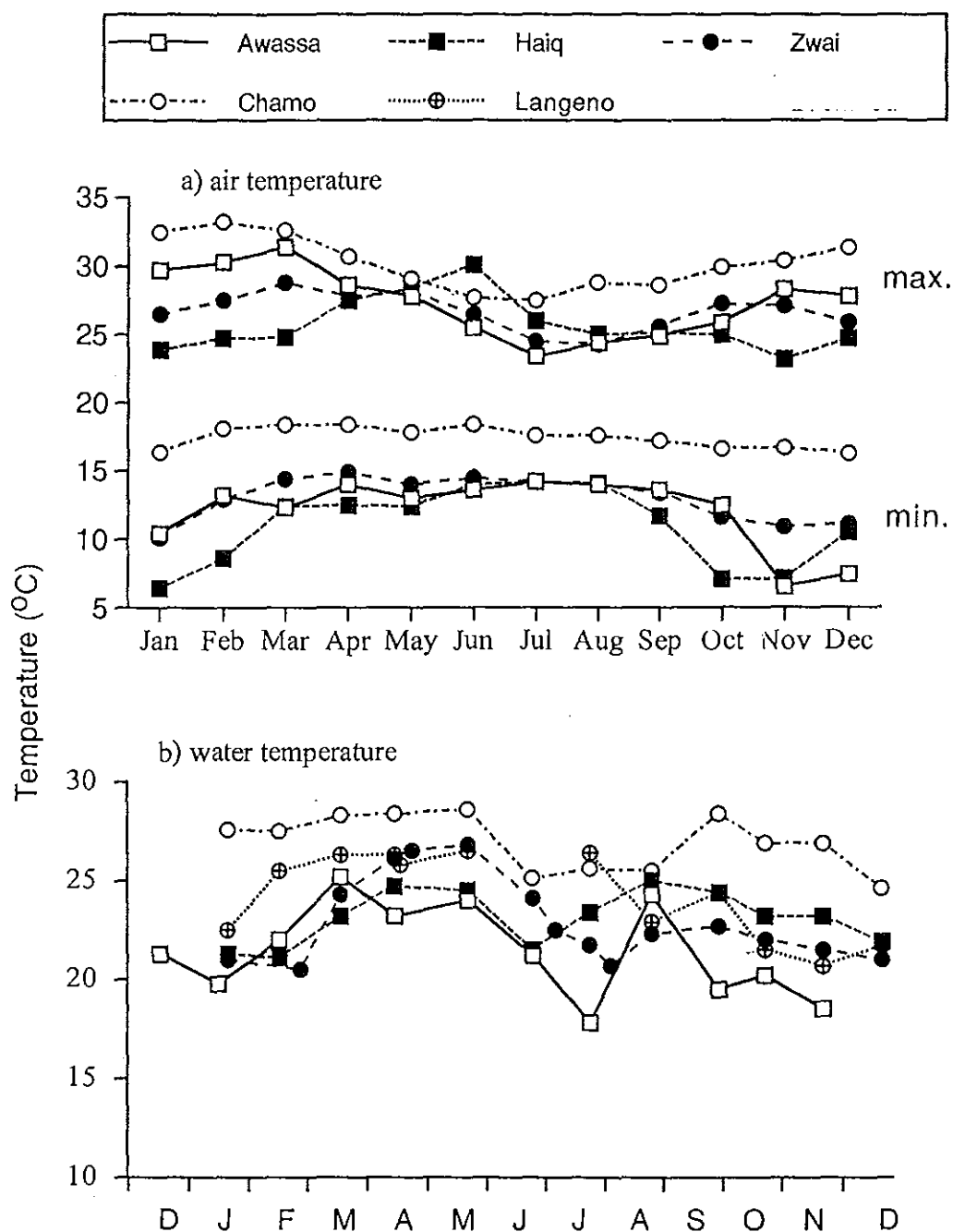


Figure 3. Monthly mean a) maximum and minimum air temperature of the lakes region, and b) surface water temperature of some lakes for the period Dec. 1987-Nov. 1988 (Awassa), in 1994 (Haiq) and in 1996 (the rest).

CHAPTER III

GROWTH OF JUVENILE TILAPIA, *Oreochromis niloticus* L. IN LAKES ZWAI, LANGENO AND CHAMO

Introduction

Fluctuation in year-class strength of fish stocks is believed to be determined by growth and mortality rates during the first year of life (Neilson & Geen, 1986; Houde, 1989; DeAngelis *et al.*, 1993). Therefore, knowledge on the growth of juvenile fish is essential for further detailed studies on the biology and management of fish stocks. Accurate estimate of growth and mortality rates are dependent upon accurate estimate of age. Daily increments in otoliths provide the best estimate of age for juvenile fish (Campana & Neilson, 1985). This provides length-at-age data needed to generate appropriate growth curves, and to estimate mortality (Essig & Cole, 1986; Jearld *et al.*, 1993). Daily formation of otolith microstructures has been validated for several species in the temperate region (Pannella, 1971; Campana & Neilson, 1985) and in the tropics (Taubert & Coble, 1977; Gjøsæter *et al.*, 1984; Yosef, 1990; Zhang & Runham, 1992a). Since there is a general synchrony between otolith and body growth (Casselman, 1990), the width of daily increments enable a reconstruction of individual growth histories (Campana, 1984; Penny & Evans, 1985). Recently, Paperno *et al.* (1997) showed that increment width is positively correlated with condition factor and growth rate.

Slowly growing fish may yield larger otoliths than similar sized but fast growing fish (Templeman & Squires, 1956; Reznick *et al.*, 1989). This may result in intraspecific variation in otolith size—fish size relationship affecting

back-calculation of individual growth (Secor & Dean, 1989). However, population-specific otolith size—fish size relationships are ubiquitous (Campana, 1990). In addition, back-calculation is believed to yield accurate information if it is done from the width of a group of daily increments to reconstruct growth of fish over a weekly or longer time scale (Campana & Neilson, 1985).

In this study microstructures in sagittal otoliths were used to determine age, and to fit growth curves for juvenile *O. niloticus* sampled from Lakes Zwai, Langeno and Chamo. Measurements of increment width were used to reconstruct bi-weekly and monthly growth histories. Condition factor and relationships between fish size and otolith size were determined. The growth of the fish in the three lakes was then compared, and the possible reasons for differences in growth between the three populations were discussed.

Study area

Lakes Zwai, Langeno and Chamo are located at altitudes between 1233 and 1636 m. Lakes Zwai and Langeno occupy the Zwai—Shala basin and are about 30 km apart. Lake Chamo is found at about 300 km further south in the Abaya—Chamo basin (Fig. 1).

In terms of surface area, Lake Chamo is the largest whereas Lake Langeno is the smallest. However, the latter lake is the deepest with a maximum depth of 46 m. Surface water temperature (mean±standard deviation), measured between 1130 and 1200 hr at the time of sampling, was largest for Lake Chamo ($28.2\pm0.5^{\circ}\text{C}$), smallest for Lake Zwai ($25.6\pm 1.7^{\circ}\text{C}$) and intermediate for Lake Langeno ($26.0\pm0.5^{\circ}\text{C}$). Lake Langeno is among the least productive of the Ethiopian rift valley lakes (Kebede, 1996) mainly due to a stable colloidal suspension of silt which has been found to be responsible for about 94 to 98%

of the total light attenuation (Wood *et al.*, 1978). In contrast, Lakes Zwai and Chamo are productive lakes (Table 1) (Tilahun, 1988; Kebede, 1996).

There is a remarkable difference in the composition of piscifauna among Lakes Zwai, Langeno and Chamo. Lake Chamo has a most diversified natural fish fauna containing 12 species. The main ones are *O. niloticus*, *Clarias gariepinus* Burchell, *Barbus* spp Rüppell, *Lates niloticus* L., *Bagrus docmac* Forsk., *Hydrocyon forskali* Cuv., *Labeo* spp Forsk. and *Synodontis schall* Peters. In addition to the first three species, Lakes Zwai and Langeno contain *Tilapia zillii* Gerv. and *Aplocheilichthys* sp. Furthermore, *Cyprinus carpio* and *Carassius carassius* are found in Lake Zwai; these two are introduced species as are *T. zillii* and *C. gariepinus*.

Approximate potential fish yield is 2000 t·yr⁻¹ in Lake Zwai, 1000 t·yr⁻¹ in Lake Langeno and 3000 t·yr⁻¹ in Lake Chamo (Welcomme, 1972; Schröder, 1984; Herrmann, 1993). Annual catches are about 200 tonnes from Langeno, 1100 to 2000 tonnes from Zwai and 1000 to 1200 tonnes from Chamo (Alem, 1993; Herrmann, 1993).

Materials and methods

Sampling

Samples of *O. niloticus* were caught approximately every three weeks between February and May 1996 from Lakes Zwai, Langeno and Chamo. We used an 18.3x2.7 m beach seine with a stretched mesh size of 6 mm. Immediately after capture, total length (TL, nearest 1 mm) and total weight (TW, nearest 0.1 g) of each fish were measured and fish were simultaneously sorted into 10 mm length groups. A random subsample of five to seven fish were then taken from each length group and preserved in 95% ethanol and transported to the laboratory.

In the laboratory, the TL of each individual was re-measured and its sagittal otoliths removed. Otoliths were thoroughly cleaned with water and

stored dry in labelled vials until examination. The effect of alcohol preservation on TL, which was tested using measurements on preliminary samples from Zwai, was found to be significant (paired t-test, $p = 0.0002$, $n = 73$). Thus, we fitted a regression equation (i.e., Fresh TL = $0.137 + 1.003$ Preserved TL, $r^2 = 0.99$, $n = 73$) to estimate fresh TL.

Otolith preparation and microstructure examination

Prior to microscopic examination, each otolith was weighed to the nearest 0.0001 g. Otoliths from each individual were then put in a dark dish containing 45% glycerol and maximum posterior radius measured under a stereoscope using a reflected light. Each otolith was then washed, air dried, and mounted (sulcus side down) on a microscope slide using thermoplastic resin. The grinding procedure followed was dependent on the size of the otolith. Otoliths from small fish (<30 mm, TL) were ground using a 12- μ m aluminium oxide lapping film, and polished by a well-used 12 μ m lapping film and followed by a 0.3- μ m aluminosilicate paste. Increments were readily visible in most otoliths after this stage of the procedure. If not, the slide was re-heated to soften the resin and the otolith was remounted with the polished surface down. Grinding and polishing were then resumed on the sulcus side as before.

Otoliths from larger fish were ground on the lateral (concave) side using a well used 600-grit sand paper and polished as described above. Grinding and polishing was performed until the increments in the outer one-third surface of the otoliths were readily visible. Otoliths were then remounted with the polished surface down, and grinding and polishing continued as before.

Increments were counted using a research microscope (250x or more) which was fitted with a video camera and a monitor. An initial count showed no significant difference (paired t-test, $p > 0.55$, $n = 46$) in the number of increments between the left-side and right-side otoliths from the same fish, thus

later counts were made only on the right-side otolith. Increments in each otolith were counted twice, and the average of the two was recorded. The distances from the centre of each otolith to the end of the 15th increment, and then to the end of every 30th increment (i.e., 30th, 60th, etc.) were measured. Measurements were conducted using a locally customised software (H. Mosegaard, unpublished).

Length and age relationship

Length and age relationship was described using the Gompertz growth model (Gompertz, 1825 in Ricker, 1979). Methods of fitting the model are described by Pennington (1979). In order to stabilise the variance, the natural logarithm form of the model was used, i.e., $\ln(TL) = \ln(TL_0) + k(1 - e^{-gt})$, where TL_0 is total length at age 0 days (d), g is specific growth rate at the inflection of the curve (rate of exponential decay), k is a dimensionless parameter such that $k \cdot g$ is growth rate when $t = 0$, and t is age in d. The parameters (i.e., TL_0 , k & g) were estimated by iterative non-linear regression technique. Using the fitted equations, growth curves were derived and age-specific growth rates were calculated and compared among fish from the three lakes.

An empirical regression equation relating fish length and maximum posterior radius of otoliths was fitted for back-calculation purposes. The relationship between otolith size (weight, radius) and fish length was investigated using regression analysis to determine if they vary between fish from the three lakes. In addition, Fulton condition factor of each fish was also calculated as $TW(g)$ in percent of $TL^3(cm)$ (Le Cren, 1951).

Results

Length and age relationship

Age in days was determined for fish ranging in TL from 10 mm to 60 mm. The smallest fish was 10, 12 and 14 mm in the sample from Lakes Langeno, Zwai and Chamo, respectively.

The hatching check, encircling the nucleus region of the otolith was prominently visible almost in all specimens. As also found by Zhang and Runham (1992a), a few and faint increments were present in the region between the otolith centre and the hatching check (Fig. 4). These were neither considered to be formed daily (Zhang & Runham, 1992a) nor included in subsequent increment counts. Increments after the hatching check were regular and prominent. Zhang and Runham (1992a) observed the hatching check at the edge of otoliths from larval tilapia which they sampled one day after hatch. Thus, the first daily increment was believed to be formed two days after hatch, and all counts were corrected accordingly.

The Gompertz growth model described the relationship between length and age quite well for fish from the three lakes (Figs 5a, 5b & 5c). The iterative technique used resulted in the following equations:

For tilapia from Lake Zwai:

$$\text{Ln}(\text{TL}) = 2.33 + 1.8939[(1 - e^{(-0.0106t)})], r^2 = 0.93, n = 210,$$

For tilapia from Lake Langeno:

$$\text{Ln}(\text{TL}) = 2.40 + 1.6806[(1 - e^{(-0.0112t)})], r^2 = 0.89, n = 198,$$

For tilapia from Lake Chamo:

$$\text{Ln}(\text{TL}) = 2.25 + 2.0650[(1 - e^{(-0.0167t)})], r^2 = 0.87, n = 129,$$

where TL is in mm and t is in d. The correlation coefficient of each equation suggest that each model explained more than 86% of the variation in length at age.

From the above growth models, length at hatch ($t = 0$ d) was predicted to be 10.3 mm for tilapia from Lake Zwai, 11.0 mm for those from Lake Langeno and 9.5 mm for those from Lake Chamo. These values are likely to be

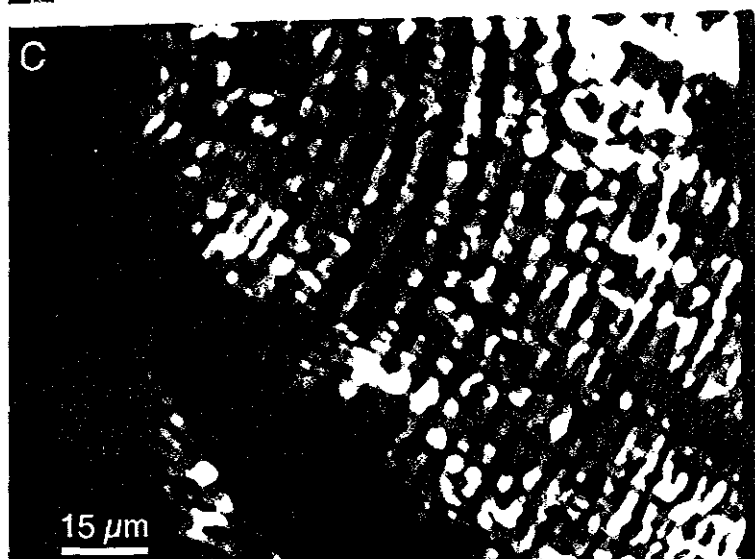
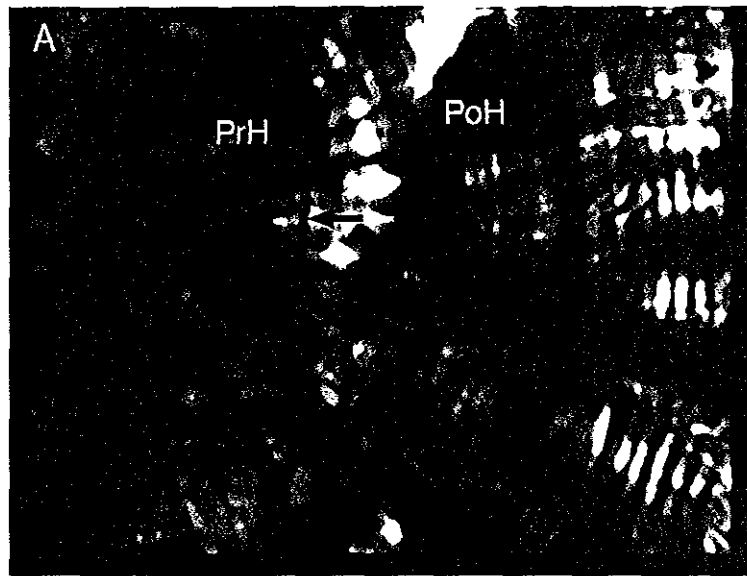


Figure 4. Photomicrographs of microstructures in sagittal otoliths of *Oreochromis niloticus* from Lakes Zwai (a), Langeno (b) and Chamo (c). Arrow head indicates the hatching check, PrH and PoH show pre-hatching and post-hatching increments, respectively.

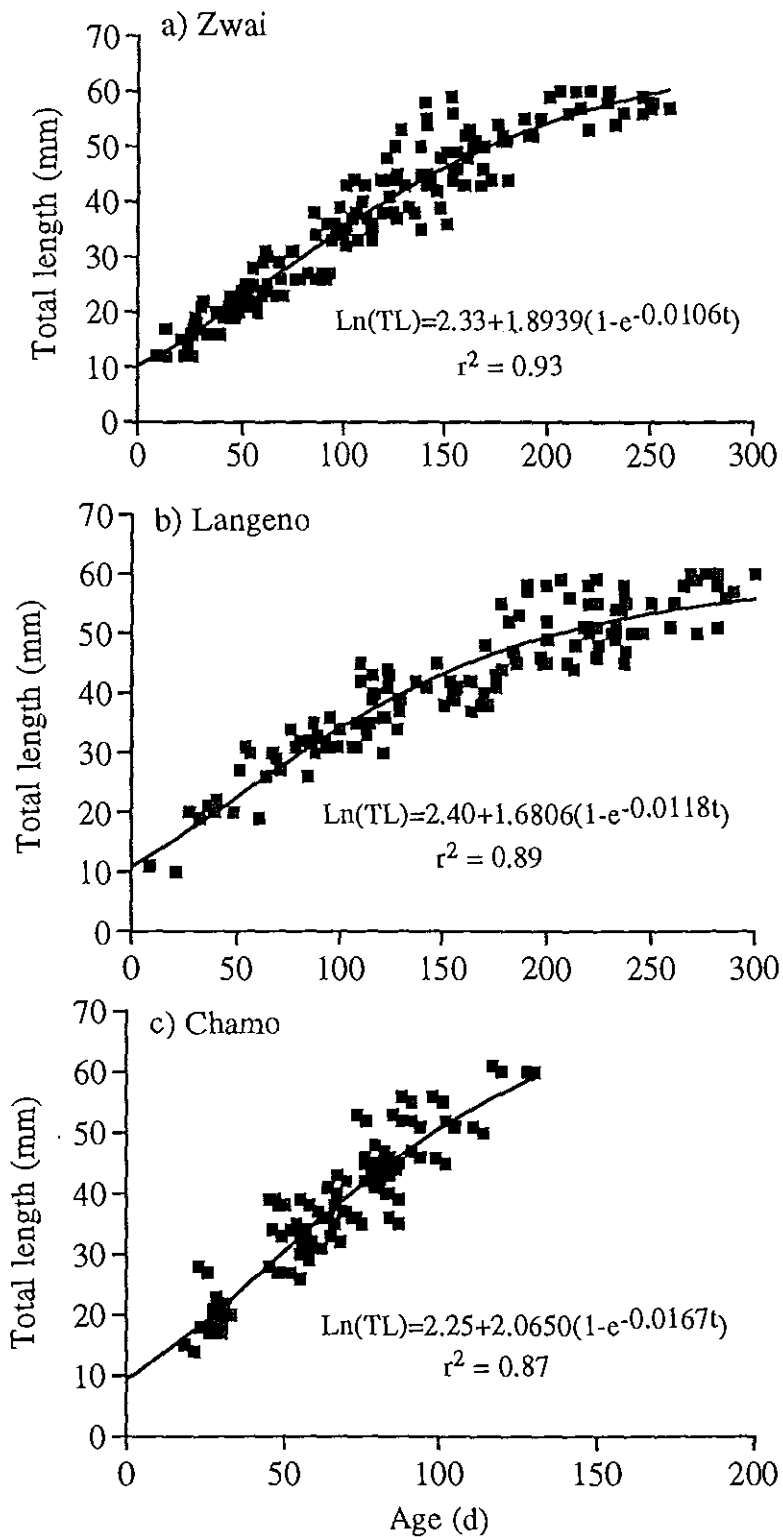


Figure 5. Gompertz growth curves for juvenile *Oreochromis niloticus* from Lakes Zwai (a), Langeno (b) and Chamo (c).

overestimates since we lack small-sized fish in the sample. Instantaneous growth rate at $t = 0$ d and $TL = TL_0$ was 0.0201, 0.0188 and 0.0345 for tilapia from Lake Zwai, Langeno and Chamo, respectively.

Average growth rate estimates from the Gompertz models indicated that *O. niloticus* juveniles from Lakes Zwai and Langeno grew at about similar rates for the first 50 d post-hatch, after which those from Zwai grew slightly more rapidly. In contrast, tilapia juveniles from Lake Chamo grew more rapidly than fish of comparable ages from the other two lakes (Table 2). Average growth rate (i.e., linear length increment per d) through the first 250 d after hatch predicted from the Gompertz equation was $0.20 \text{ mm}\cdot\text{d}^{-1}$ ($0.72 \text{ }\%\cdot\text{d}^{-1}$), 0.16 mm/d ($0.62 \text{ }\%\cdot\text{d}^{-1}$) and $0.39 \text{ mm}\cdot\text{d}^{-1}$ ($1.14 \text{ }\%\cdot\text{d}^{-1}$) for juveniles from Lake Zwai, Langeno and Chamo, respectively. Similar growth rates were estimated using simple linear regression equations between length and age: $0.20 \text{ mm}\cdot\text{d}^{-1}$, $0.15 \text{ mm}\cdot\text{d}^{-1}$ and $0.41 \text{ mm}\cdot\text{d}^{-1}$, respectively. Hence, among the sampled lakes average daily growth rate of *O. niloticus* juveniles was most rapid in Lake Chamo, intermediate in Lake Zwai and slowest in Lake Langeno.

Fish-size and otolith-size relationship

The relationship between fish length (between 10 and 175 mm) and otolith radius (R, mm) was best described by polynomial regression. The best fit equations for data from the three lakes were as follows:

For fish from Lake Zwai (Fig. 6a):

$$TL = 8.530 + 29.243R + 5.429R^2, r^2 = 0.99, n = 300,$$

For fish from Lake Langeno (Fig. 6b):

$$TL = 13.557 + 20.722R + 8.731R^2, r^2 = 0.99, n = 294,$$

For fish from Lake Chamo (Fig. 6c):

$$TL = 10.137 + 25.463R + 8.541R^2, r^2 = 0.99, n = 222.$$

Table 2. Growth rate at age (mm.d⁻¹ and %.d⁻¹) of *Oreochromis niloticus* juveniles from Lakes Zwai, Langeno and Chamo from hatch through 250 days estimated using Gompertz growth model fit.

Age (d)	Zwai (mm.d ⁻¹)	Langeno (mm.d ⁻¹)	Chamo (mm.d ⁻¹)	Zwai (%.d ⁻¹)	Langeno (%.d ⁻¹)	Chamo (%.d ⁻¹)
0	0.21	0.21	0.33	2.00	1.88	3.45
10	0.22	0.22	0.40	1.80	1.67	3.06
20	0.24	0.23	0.46	1.62	1.48	2.72
30	0.25	0.23	0.52	1.46	1.32	2.42
40	0.26	0.24	0.56	1.31	1.17	2.15
50	0.26	0.24	0.58	1.18	1.04	1.91
60	0.27	0.23	0.60	1.06	0.93	1.70
70	0.26	0.23	0.59	0.95	0.82	1.51
80	0.26	0.22	0.58	0.86	0.73	1.34
90	0.25	0.21	0.56	0.77	0.65	1.19
100	0.25	0.20	0.54	0.70	0.58	1.06
110	0.24	0.19	0.51	0.63	0.51	0.94
120	0.23	0.17	0.47	0.56	0.46	0.84
130	0.21	0.16	0.44	0.51	0.41	0.74
140	0.20	0.15	0.41	0.46	0.36	0.66
150	0.19	0.14	0.37	0.41	0.32	0.59
160	0.18	0.13	0.34	0.37	0.28	0.52
170	0.17	0.12	0.31	0.33	0.25	0.46
180	0.15	0.11	0.28	0.30	0.22	0.41
190	0.14	0.10	0.25	0.27	0.20	0.37
200	0.13	0.09	0.23	0.24	0.18	0.33
210	0.12	0.08	0.20	0.22	0.16	0.29
220	0.11	0.07	0.18	0.20	0.14	0.26
230	0.10	0.06	0.16	0.18	0.12	0.23
240	0.09	0.06	0.15	0.16	0.11	0.20
250	0.09	0.05	0.13	0.14	0.10	0.18

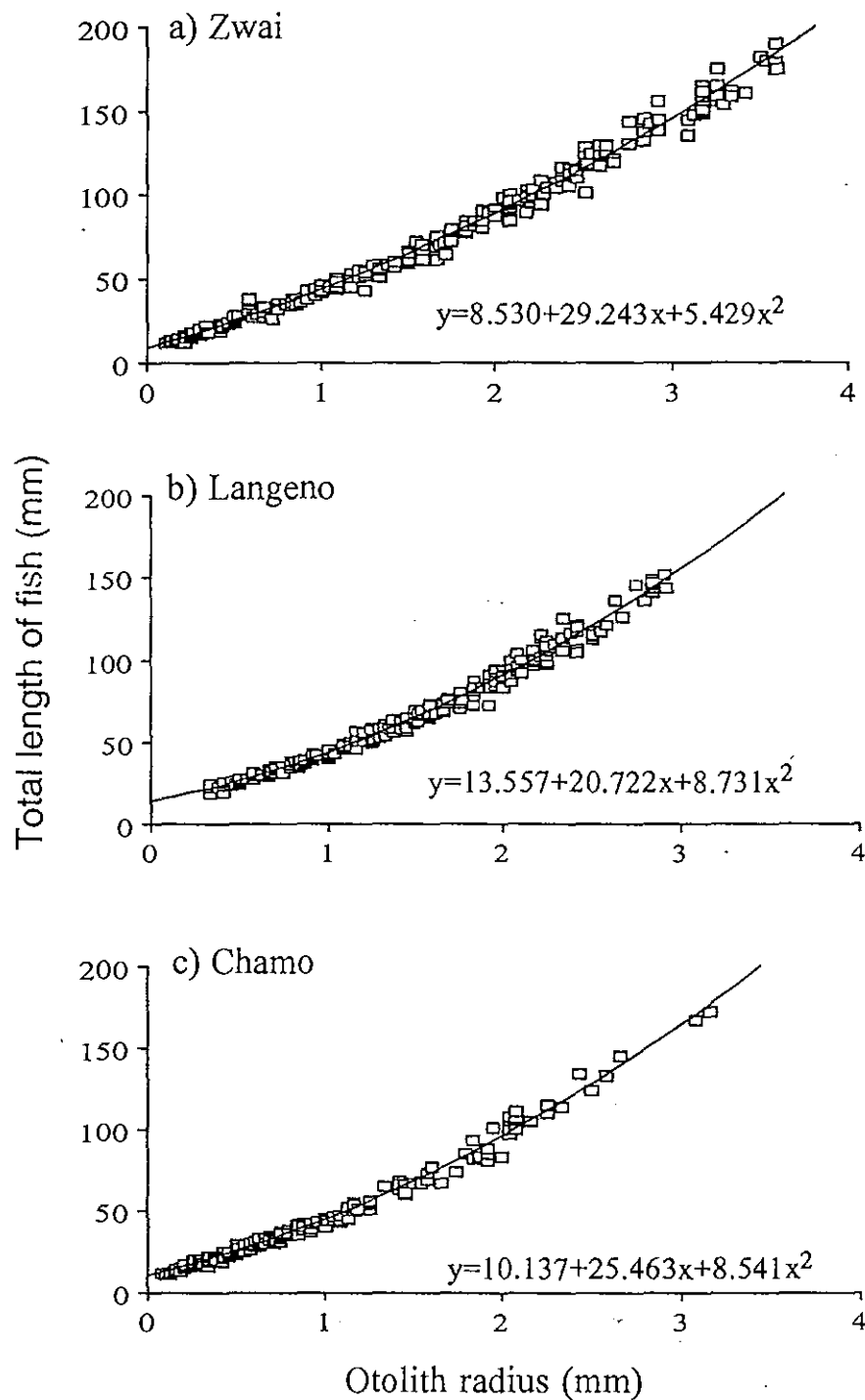


Figure 6. Relationship between otolith radius and fish total length in juvenile *Oreochromis niloticus* from Lakes Zwai (a), Langeno (b) and Chamo (c). $r^2 = 0.99$ for each equation.

The equations were highly significant (ANOVA, $p < 0.0001$), and the slopes and intercepts were significantly different from zero (t-test, $p < 0.0001$). Simple linear and log-linear regressions were also found to be significant, however, the residuals from both of these models were considerably non-random. Thus, the polynomial regression models were used for back-calculation purposes. The back-calculation formulae, according to the body proportional hypothesis (Francis, 1990), were as follows:

For tilapia from Lake Zwai:

$$TL_i = (TL_c(8.530 + 29.243R_i + 5.429R_i^2))/(8.53 + 29.243R_c + 5.429R_c^2),$$

For tilapia from Lake Langeno:

$$TL_i = (TL_c(13.557 + 20.722R_i + 8.731R_i^2))/(13.577 + 20.722R_c + 8.731R_c^2),$$

For tilapia from Lake Chamo:

$$TL_i = (TL_c(10.137 + 25.463R_i + 8.541R_i^2))/(10.137 + 25.463R_c + 8.541R_c^2),$$

where TL_i = fish total length (mm) at the i^{th} age in d,

TL_c = fish total length (mm) at capture

R_i = radius (mm) of otolith at the i^{th} age (distance from centre to the i^{th} increment),

R_c = total posterior radius (mm) of otolith at capture.

There was some variation in otolith radius among similar-sized fish of the three populations. At fish lengths of 20 to 30 mm, for instance, the radius of otoliths of fish from Zwai was 3 to 7% larger than those from Langeno, and 5% larger than those from Chamo. At fish length between 40 and 80 mm, the radius of otoliths of fish from Langeno was 1 to 2% larger than those from Zwai, and 3 to 4% larger than those from Chamo.

The relationship between total length and otolith weight was curvilinear and highly significant (ANOVA, $p < 0.0001$) for the fish from all the three lakes (Fig. 7). The fitted curves for fish from Lakes Zwai and Langeno overlapped considerably whereas the curve for fish from Chamo differed, the difference

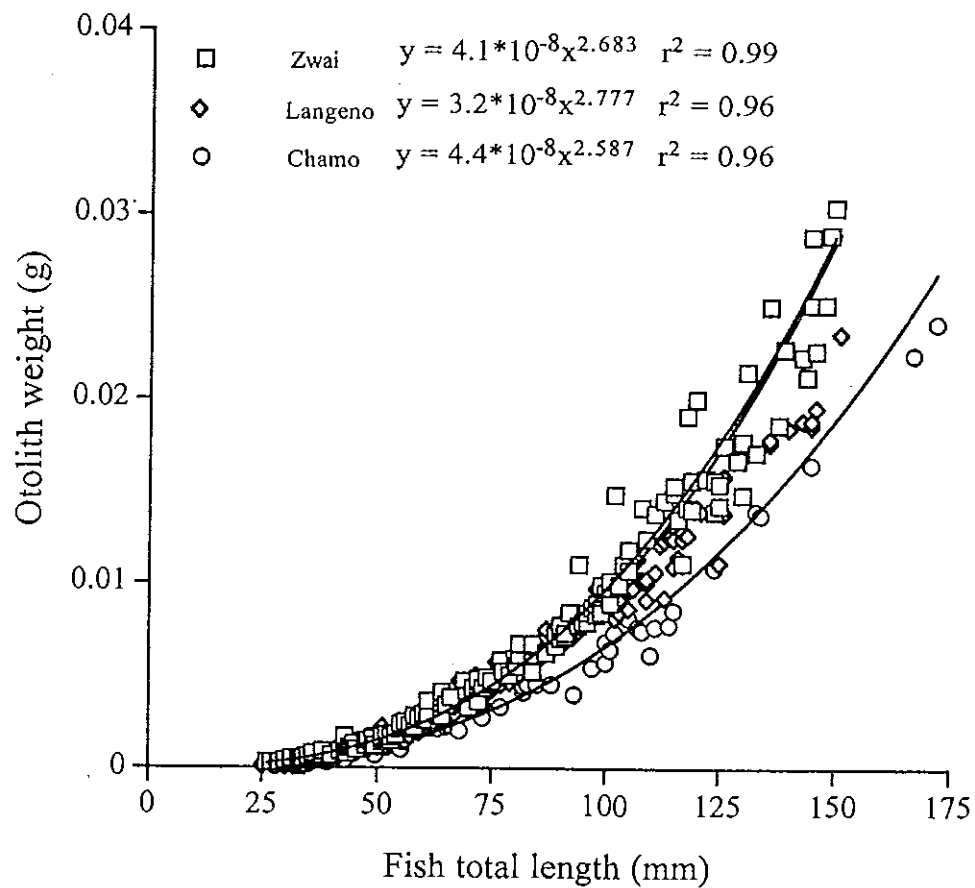


Figure 7. Relationship between otolith weight and fish total length in juvenile *Oreochromis niloticus* from Lakes Zwai, Langeno and Chamo.

being progressively larger with increase in fish length. Based on the fitted equations and at fish lengths of 25 to 60 mm, tilapia juveniles from Chamo would have otoliths about 27 to 30% lighter than tilapia from Zwai or Langeno. The difference in otolith weight between fish from Zwai and Langeno was generally very small except at 70 to 80 mm TL at which size fish from Zwai had slightly lighter otoliths.

Back-calculated growth history

Back-calculated growth data of fish from Lakes Zwai, Langeno and Chamo are presented in Tables 3, 4 and 5, respectively. Back-calculated data did not show a considerable Lee's phenomenon as there was no systematic change in back-calculated length-at-age with the age of fish used for back-calculation.

Tilapia from Lake Chamo were considerably larger at all ages than those from Lakes Zwai and Langeno except at age 15 d when the fish from Langeno were about 8% larger than those from Chamo, and 12% larger than those from Zwai. In addition, at age 30 d fish from Chamo and Langeno were of similar size, but those from Zwai were 7 to 8% smaller. However, there was an overlap in the 95% confidence limits of mean back-calculated length at ages 15 and 30 d (Fig. 8a). This suggests that tilapia growth during the first month after hatch may be similar in the three lakes. After the age of 30 d, fish from Lake Chamo attained significantly larger size-at-age than those from the other two lakes. Fish at similar ages (60 d and older) from Zwai and Langeno were of comparable sizes, but at age 60 and 90 d, the fish from Langeno were slightly larger than those from Zwai, whereas after an age of about 105 d fish from Zwai were slightly larger than those from Langeno (Fig. 8a). Fish from Chamo that were older than 60 d were remarkably larger than fish of similar ages from Lakes Zwai and Langeno. At 90 and 120 d of age, for instance, tilapia from Chamo were 28 to 30% larger than their counterparts from the other two lakes.

Table 3. Growth data for juvenile *Oreochromis niloticus* from Lake Zwai back-calculated from daily increments in otoliths.

Mean age at capture (d)	mean total length at capture (mm)	n	Back-calculated length (mm) at age (d)							
			15	30	60	90	120	150	180	210
26	17.1	17	15.5							
48	22.7	15	15.4	20.2						
74	29.9	17	14.4	18.9	23.3					
103	35.7	28	14.8	19.4	23.9	30.4				
135	46.1	14	15.1	19.9	24.5	31.2	39.6			
165	49.0	19	14.4	18.9	23.3	29.6	37.6	41.4		
205	57.0	5	14.3	18.0	34.5	43.9	49.8	52.0	54.3	
253	58.3	6	16.9	22.2	27.4	34.9	37.5	48.8	46.0	53.9
mean			14.3	19.1	24.7	31.7	39.5	45.1	48.8	53.9

Table 4. Growth data for juvenile *Oreochromis niloticus* from Lake Langeno back-calculated from daily increments in otoliths.

Mean age at capture (d)	Mean total length at capture (mm)	n	Back-calculated length (mm) at age (d)							
			15	30	60	90	120	150	180	210
47	24.0	19	18.4	20.4						
78	31.8	16	19.1	22.2	25.8					
108	37.4	29	17.1	20.1	25.3	31.4				
135	40.8	14	19.3	22.4	27.0	33.3	38.3			
165	46.4	13	20.8	24.1	30.1	33.9	38.9	44.0		
196	49.7	11	19.4	22.6	28.2	33.6	38.6	43.7	48.3	
241	53.4	18	16.2	20.4	27.2	31.0	37.9	42.8	45.5	50.9
mean			16.4	20.6	26.8	32.8	38.3	43.3	46.7	50.9

Table 5. Growth data for juvenile *Oreochromis niloticus* from Lake Chamo back-calculated from daily increments in otoliths.

Mean age at capture (d)	Mean total length at capture (mm)	n	Back-calculated length (mm) at age (d)				
			15	30	60	90	120
29	19.6	10	15.0				
50	30.6	23	16.6	21.9			
77	40.4	29	15.1	20.6	32.1		
100	50.4	1	15.4	20.3	31.6	45.8	
123	59.5	8	15.8	20.9	32.5	47.1	55.3
		mean	15.0	20.9	32.0	46.0	55.3

Mean back-calculated absolute growth rate ranged from 0.15 to 0.32 mm·d⁻¹ for tilapia from Zwai, from 0.11 to 0.28 mm·d⁻¹ for those from Langeno and from 0.28 to 0.43 mm·d⁻¹ for those from Lake Chamo. Since we lack back-calculated length at age prior to 15 d we used length at hatch that were estimated using the Gompertz growth models. Generally, daily growth rate decreased with age particularly for the fish from Zwai and Langeno (Fig. 8b). Growth rate up to 15 d post-hatch was similar for fish from the three lakes, after which fish from Chamo grew considerably more rapidly. Tilapia of 90 d and older from Lake Zwai grew slightly more rapidly than similar aged fish from Langeno. Prior to this age, however, growth rate of juveniles from the two lakes was approximately similar (Fig. 8b).

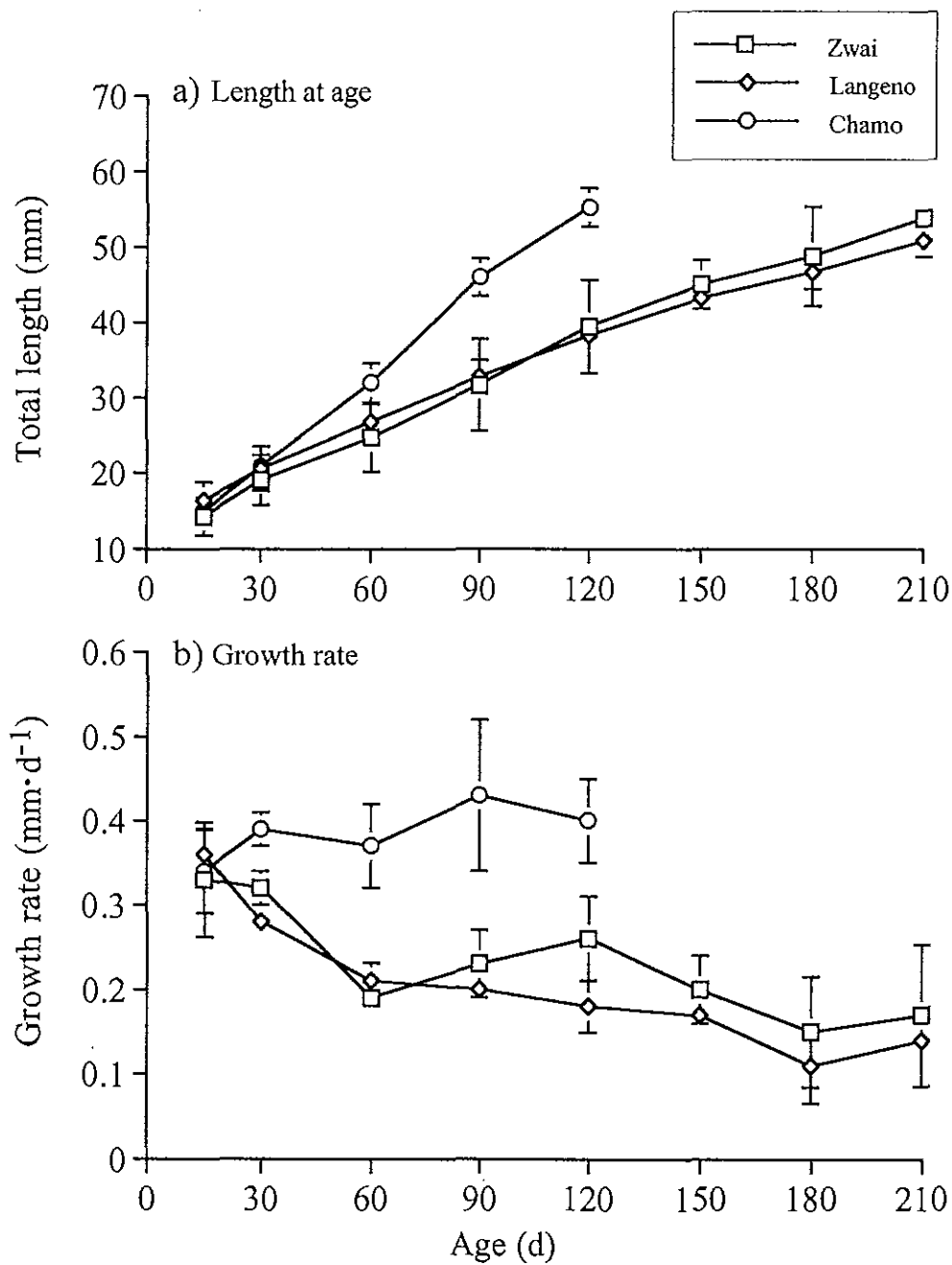


Figure 8. Back-calculated length at age (a) and growth rate (b) of juvenile *Oreochromis niloticus* from Lakes Zwai, Langeno and Chamo.

Fulton condition factor

Fulton condition factor ranged from 0.55 to 2.54 for *O. niloticus* from Zwai, 0.51 to 1.71 for those from Langeno and from 1.02 to 2.88 for those from Chamo. Mean condition factor values appeared similar among lakes for fish smaller than 30.0 mm, because the 95% confidence limits overlapped considerably (Table 6). Generally however, mean condition factor was largest for Lake Chamo fish, intermediate for Zwai fish and smallest for Langeno fish, the difference between fish in the latter two lakes being small.

Table 6. Fulton condition factor of juvenile *Oreochromis niloticus* from Lakes Zwai, Langeno and Chamo. n is sample size.

Length group (mm)	Condition factor (mean $\pm$ half 95% CI)					
	Zwai	n	Langeno	n	Chamo	n
10.0—19.9	1.46 $\pm$ 0.16	11	1.39 $\pm$ 0.25	10	1.86 $\pm$ 0.26	18
20.0—29.9	1.39 $\pm$ 0.11	43	1.23 $\pm$ 0.30	39	1.82 $\pm$ 0.33	35
30.0—39.9	1.53 $\pm$ 0.04	43	1.36 $\pm$ 0.02	45	1.88 $\pm$ 0.10	70
40.0—49.9	1.46 $\pm$ 0.18	37	1.26 $\pm$ 0.02	47	1.83 $\pm$ 0.09	29
50.0—59.9	1.55 $\pm$ 0.02	47	1.29 $\pm$ 0.05	52	1.74 $\pm$ 0.05	20
60.0—69.9	1.49 $\pm$ 0.02	15	1.34 $\pm$ 0.11	13	1.76 $\pm$ 0.12	13
all	1.46 $\pm$ 0.11	196	1.29 $\pm$ 0.19	206	1.77 $\pm$ 0.15	185

Discussion

It was assumed that increments are formed daily in otoliths of *O. niloticus* in this study, because this has been validated by several workers (Tanaka *et al.*, 1981; Zhang & Runham, 1992a; Yosef, 1990). Yosef (1990), for instance, validated daily formation of increments using tetracycline injected fish from Lake Awassa. In addition, Zhang and Runham (1992a) have found that in experimentally reared juvenile *O. niloticus*, after hatching increments are deposited daily. Furthermore, Tanaka *et al.* (1981) reported that the number of incremental zones is well correlated with chronological age in days after hatch in juvenile *O. niloticus*. Thus, we believe that the number of increments in otoliths of the fish in this study provide an estimate of age in days.

Back-calculation of growth from increments is based on two basic assumptions: that increments are formed daily and that otolith and somatic tissue growth rates are coupled. We strongly believe that the first assumption is met in *O. niloticus* in this study. However, it is not known if otolith and somatic tissue growth in this species are coupled resulting in a direct relationship between increment width and daily somatic growth rate. The results on otolith size—fish size relationship indicated that, relative to their counterparts in Lakes Zwai and Langeno, juvenile tilapia from Lake Chamo grow rapidly, and have smaller otoliths at a given length. Similar results have been found for experimentally reared *O. niloticus* (Zhang & Runham, 1992b), and other fish species under experimental conditions (Reznick *et al.*, 1989; Secor & Dean, 1989) and in the wild (Templeman & Squires, 1956; Neilson *et al.*, 1985; Penny & Evans, 1985). However, our back-calculation procedure may not be affected by 'uncoupling', because we used population-specific otolith size—fish size relationships each of which were highly significant. Secor and Dean (1989) stated that within a species, there are population-specific relationships which are related to growth rates. In addition, since we used the width of a group of increments to

reconstruct growth over a bi-weekly and monthly time scale, our back-calculated growth data may not be seriously biased (Campana & Neilson, 1985). Furthermore, the absence of considerable Lee's phenomenon in the data may suggest that growth effects (Campana, 1990) were not significant.

There was a close agreement between length-at-age data estimated using the Gompertz growth model and those estimated by back-calculation. However, relative to estimates from Gompertz models, back-calculated lengths at ages 15 and 30 d were slightly larger for the fish from Zwai (5 to 10%) and Langeno (12 to 14%). In addition, back-calculated length was 5% larger than that estimated using Gompertz model for Zwai fish of 180 d old, whereas length from Gompertz model was 9% larger for Chamo fish of 60 d old. Except these differences, back-calculated lengths and those estimated from Gompertz models were within 1 to 2% of each other. Thus, results from the two procedures of growth estimation corroborate each other.

Our study showed that juvenile *O. niloticus* in Lake Chamo grow at a much faster rate than those in Lakes Zwai and Langeno. The growth of the fish from Lakes Zwai and Langeno is comparable. The difference in growth rate was also reflected in the observed population-based differences in the condition factor of the fish (Table 6). However, growth rate of the fish through the first 15 d after hatch appeared similar in the three lakes.

The Chamo fish appears to grow more rapidly than the species in other Ethiopian lakes as well. Juvenile *O. niloticus* grows $0.21 \text{ mm}\cdot\text{d}^{-1}$ in Lake Awassa (Yosef & Casselman, 1995) and $0.25 \text{ mm}\cdot\text{d}^{-1}$ in Lake Haiq (K. Alemu & D. Admassu, unpublished data). Thus, the growth rate of the fish in the latter lakes is comparable to that in Lakes Zwai and Langeno, but considerably slower than the growth rate of the fish in Lake Chamo. Interpopulation variability in growth is common in tilapia. Fryer & Iles (1972: Table 14), who presented growth data for various species of tilapia, showed that first year growth of

tilapia could vary between 0.20 and 0.41 mm·d⁻¹, the value for Lake Chad *O. niloticus* (0.37 mm·d⁻¹) being comparable to that of Lake Chamo *O. niloticus*.

Several factors could have resulted in the observed difference in growth of juvenile tilapia between Lakes Zwai, Langeno and Chamo. Lowe-McConnell (1982) stated that in tilapia the same species grow at different rates in different waters and suggested that environmental differences are more potent than genetic ones in determining maturation and maximum sizes. Temperature appears to be important in the present study as there was a distinct difference among the sampled lakes. The temperature of Lake Chamo was high as compared with that of Zwai and Langeno. Strikingly, our measurements show that even the bottom water (7 m depth) temperature of Lake Chamo could be higher than the surface water temperature of Lake Zwai and Lake Langeno (data not shown). The temperature of Lake Chamo is also distinctly high as compared with the temperature of Lake Awassa and Lake Haiq (Admassu, 1989; Chapter II). Since tilapia are generally strongly thermophilic (Caulton, 1982), the high temperature of Lake Chamo may have resulted in elevated metabolic rates and favoured a much faster growth in *O. niloticus*. Caulton (1982) has shown that juvenile tilapia experimentally subjected to a thermal gradient (between 21 to 39°C) preferred high temperatures (30 to 36°C). In addition to its direct effect on metabolism and growth, high temperature also favours foraging and feeding activity (Caulton, 1982).

Differences in food quantity and quality result in growth variations in tilapia (Bowen, 1982). It is not known whether or not food quantity in any of these lakes is low enough to limit growth of juvenile tilapia. Primary productivity of Zwai can be estimated to be at least 10 times that of Langeno (Belay & Wood, 1984). Lake Chamo is as productive as Zwai. Since juvenile tilapia feed also on algae (Tadesse, 1988; Tudorancea *et al.* 1988), their growth could be a reflection of productivity of the lakes.

A concurrently conducted study (Z. Tadesse, personal communication) observed that the fish in Langeno feeds mainly on detritus, and the nutrient content in the food and assimilation efficiency are quite low. In contrast, in Lake Chamo and Zwai the fish feeds mainly on planktonic algae, and nutrient content and assimilation efficiency were higher in these lakes being much so in Chamo than in Zwai (Z. Tadesse, personal communication). The higher assimilation efficiency in Chamo tilapia could be a result of high temperature as assimilation efficiency in tilapia is positively correlated with temperature (Caulton, 1982).

We are uncertain about the influence of predation on population density, and hence growth of tilapia in Lake Chamo. In contrast to Lakes Zwai and Langeno, Lake Chamo contains voracious and specialised piscivores such as Nile perch (*L. niloticus*) and tiger fish (*H. forskali*) which are known to feed on juvenile tilapia (Lowe-McConnell, 1982; Ogari, 1985). In addition, based on our preliminary observation on otolith microstructure, we believe that tilapia grows rapidly in the nearby Lake Abaya (Fig. 1). Interestingly, Lake Abaya contains similar fish fauna to Lake Chamo, but it is equally light-limited and as unproductive as Lake Langeno (Kebede, 1996). Furthermore, because of their proximity we presume the temperature of Lakes Chamo and Abaya to be similar, and equally higher than that of the northern lakes in the series. Thus, we believe that differences in the growth rate of tilapia in these lakes may be attributed more to differences in temperature and associated factors. Nevertheless, further detailed study is required to address this interesting problem as predation is important at least in culture systems where species such as *L. niloticus* are used to improve growth in tilapia (Guerrero, 1982).

Intensity of fishing influences growth rate (Healey, 1980). Its effect on growth of juvenile tilapia could be indirect, through its effect on the adult fish. Adult tilapia in Lakes Zwai and Chamo are more heavily exploited than those in

Lake Langeno (Alem, 1993; personal observation). There is a considerable overlap of diet between juveniles, which also feed on algae, and adults (phytoplanktivores) *O. niloticus* (Tadesse, 1988; Tudorancea *et al.* 1988). Thus, juveniles in Lake Langeno may be under a more intense competition with the adults since the latter are not heavily exploited. Healey (1980) has shown that growth of lake whitefish (*Coregonus clupeaformis*) increased in experimentally exploited lakes, the degree of increase being proportional to the intensity of fishing. However, differences in fishing intensity can not explain the observed growth difference between tilapia of Zwai and Chamo, because the former is more heavily exploited than the latter (Alem, 1993).

In conclusion, our study showed that the growth of juvenile *O. niloticus* in Lakes Zwai, Langeno and Chamo is best described by the Gompertz growth model. Growth estimated using the Gompertz model agreed very closely with growth back-calculated from otolith microstructure. Thus, results from the two methods corroborated each other. We found that the growth rate of juvenile tilapia through the first 250 d post-hatch was fastest in Lake Chamo ($0.39 \text{ mm}\cdot\text{d}^{-1}$), intermediate in Lake Zwai ($0.20 \text{ mm}\cdot\text{d}^{-1}$) and slowest in Lake Langeno ($0.16 \text{ mm}\cdot\text{d}^{-1}$). Indirect supportive evidence is found in that the condition factor of the fish in Lake Chamo was largest followed by that from Zwai and from Langeno. In addition, juvenile *O. niloticus* from Chamo have smaller otoliths than similar-sized fish from Zwai and Langeno indicating that the fish from Chamo grow more rapidly. The rapid growth of the Chamo population could be attributed to high temperature and factors associated with it, and to a better quality food consumed by the fish in this lake. In addition, the influence of differences in predation and fishing intensities can not be ruled out.

CHAPTER IV

THE EFFECT OF EXPERIMENTAL TEMPERATURE FLUCTUATION ON OTOLITH MACROZONE FORMATION AND BODY GROWTH IN TILAPIA, *Oreochromis niloticus* L.

Introduction

The age and growth of adult fish is interpreted commonly from seasonally formed optical macrozones in calcified structures such as otoliths. Macrostructure of otoliths, when examined at low magnifications (<40x) using a reflected light source and against a dark background, appears as contrasting white and dark concentric growth zones. The white zone, which is referred to as opaque macrozone (Casselman, 1983), is relatively more dense. Its higher density hinders the passage of light rays as a result of which it appears white. In contrast, the dark zone, which is called translucent macrozone (Casselman, 1983), is less dense and allows the passage of light rays such that the background colour could be seen. Direct evidence from studying fluorescent tetracycline injected fish showed that translucent macrozones are formed during periods of slow somatic tissue growth whereas opaque macrozones are formed during periods of a more rapid growth (Casselman, 1990).

Temperature fluctuation is the most important factor associated with the formation of opaque and translucent macrozones in fish of the temperate region (Bagenal & Tesch, 1978). In the tropics, however, seasonality in the climate is generally assumed to be lacking or insufficient. Indeed, the temperature of tropical lakes may not fluctuate drastically, but still subtle changes in temperature may suffice to cause variation in fish somatic and calcified tissue growth (Casselman, 1990). The surface water temperature of some Ethiopian

lakes, for instance, varies by about 3 to 6°C in a year (Chapter II). Seasonally cold water temperature at these lakes is coincident with translucent macrozone formation in otoliths of *O. niloticus* L. (Admassu, 1989; Alemu, 1995; Yosef & Casselman, 1995). Those authors have also showed that warmer water temperature and opaque macrozone formation were coincident. Hence, it is proposed that a temperature fluctuation of the magnitude observed in these lakes is sufficient to cause variations in body growth of the fish resulting in the formation of macrozones in otoliths.

In this study an attempt was made to investigate the effect of subtle changes (3 to 5°C) in temperature in the formation of macrozones in otoliths and in the growth of *O. niloticus*. Fish were first acclimatised at a temperature of about 24°C and sequentially transferred to lower and higher temperatures. Specific objectives of the study were: (1) to investigate the number and type of macrozone formed in otoliths of fish transferred from a high temperature treatment to a relatively low temperature treatment, and vice versa, (2) to determine if the effect of temperature on otolith growth is similar to that on somatic tissue growth.

Materials and methods

O. niloticus fry were obtained from the Institute of Aquaculture, University of Stirling, Scotland. The fry were hatched within the second week of May 1997. They were transported by air to our laboratory on 5 June 1997. Mortality due to transport-related stress was about 1%. In the laboratory, fish were acclimatised in two 40 l aquaria (aquarium A and aquarium B) at a temperature of about 24°C for 120 d. Some individuals were sacrificed for otolith sampling before the start of the experiment. Then two sets of experiments were simultaneously begun by transferring the fish either to lower or higher temperature treatments. The desired levels of temperature were achieved by

putting aquaria in constant-temperature rooms. Temperatures above 24°C were achieved by using adjustable aquarium heaters. Mortality during the entire experiment was quite low (<5%) except at the beginning of acclimatisation during which time mass mortality occurred due to failure of an aeration device. Other than this, sign of illness due to high levels of ammonia or other factors was not noticed in the entire experiment. The experimental design and water temperature, which was a simulation of annual changes in temperature of some Ethiopian lakes, during each treatment are shown in Figure 9.

Low temperature treatments (Fig. 9a)

Fish in aquarium A were transferred to a slightly lower temperature (treatment 2A in Fig. 1a) and some fish were left as controls in a 10 l aquarium at the acclimatisation temperature (C2 in Fig. 9a). We kept fish under conditions of treatment 2A and C2 for a period of 31 days during which time average temperature of the water was 19.8°C and 24.0°C, respectively. Then, we sampled five individuals from the 19.8°C aquarium and all individuals from the control aquarium (C2). From those remaining at the end of treatment 2A, some individuals were transferred back to the acclimatisation temperature, some fish were kept as controls, and the remaining were transferred to a 16.6°C aquarium (3A, 3B and C3 in Fig. 9a). The fish were kept under conditions of treatments 3A, 3B and C3 for a period of 30 days. Then all fish in treatment 3B and in C3 were sampled. In addition, eight fish from treatment 3A were sampled, and from the remaining, five were kept as controls whereas the rest were transferred to a 19°C aquarium (C4 and 4A in Fig. 9a). After a period of 33 days, all the fish in the control aquarium (i.e., C4) and six fish from the 19°C treatment were sacrificed. After keeping some fish as controls at about 19°C, the remaining were then transferred to a temperature of about 24°C (treatment 5A and C5 in

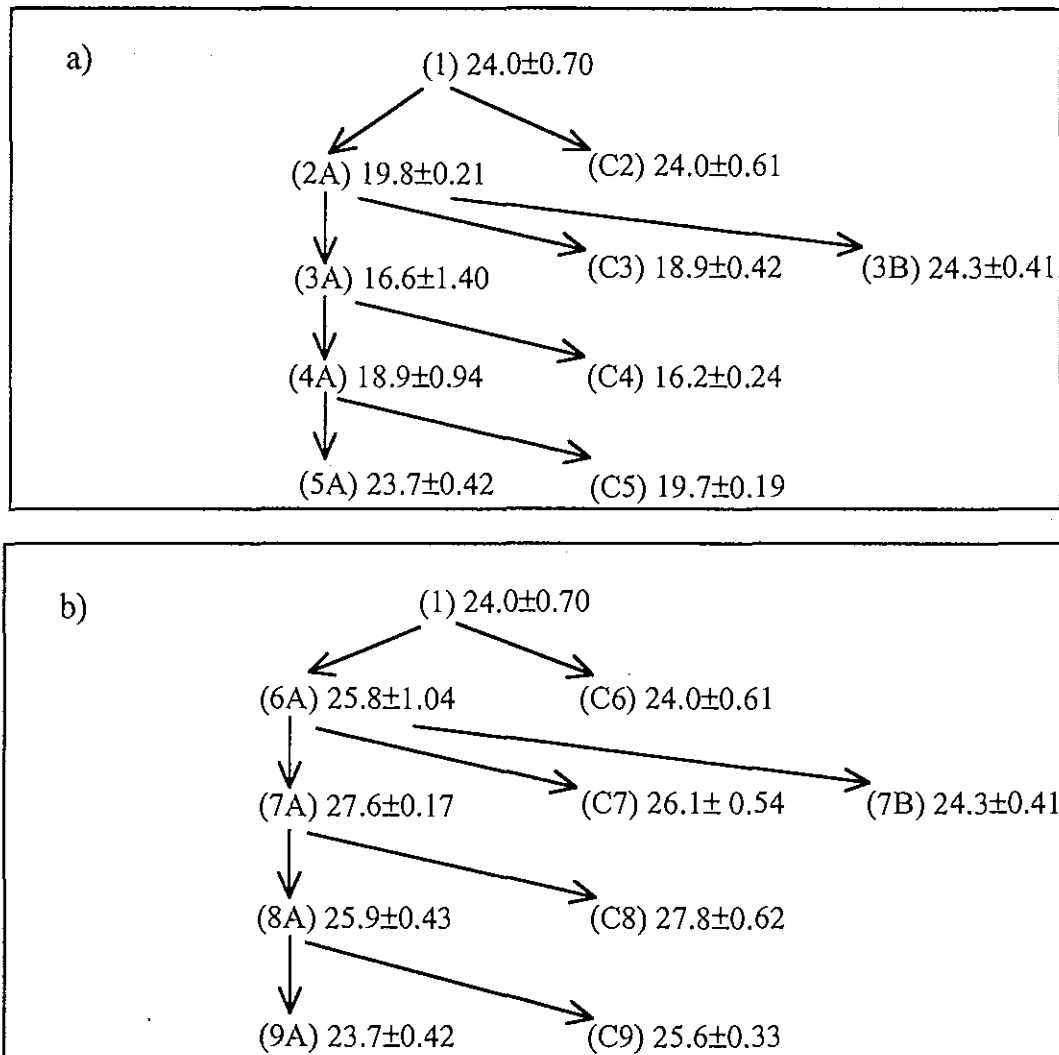


Figure 9. Experimental design to study the effect of a) low temperature, and b) high temperature treatments on otolith macrozone formation and body growth in tilapia. Temperature for each treatment is mean $\pm$ standard deviation of several measurements. Treatments are designated by alphanumerals. See Tables 7 & 8 for treatment durations.

Fig. 9a). The fish were maintained under the conditions of treatment 5A and C5 for a period of 52 days.

High temperature treatments (Fig. 9b)

Fish in aquarium B were transferred to higher temperature treatments before they were transferred back to the acclimatisation temperature (Fig. 9b). Water temperature in aquarium B was raised to about 26°C (treatment 6A in Fig. 9b) and some fish were left as controls in a 10 l aquarium at the acclimatisation temperature (C6 in Fig. 9b). Fish were grown under conditions of treatment 6A and C6 for a period of 31 days during which time the temperature of the water was 25.8°C and 24.0°C, respectively. All fish from the control aquarium, and five fish from the 25.8°C treatment (i.e., 6A) were then sampled. From the remaining fish, five were transferred back to the acclimatisation temperature (treatment 7B), five were kept as controls (C7), and the rest were grown at a temperature of about 28°C (treatment 7A, Fig. 9b). Fish were grown under the conditions of treatments 7A, 7B and C7 for a period of 30 days. Then, we sampled all fish in the 24.3°C and 26.1°C aquaria. In addition, seven fish were sampled from the 27.6°C treatment, and then after keeping some fish as controls, the rest were grown at a temperature of about 26°C (8A and C8 in Fig. 9b). After a period of 33 days, all individuals in the control aquarium (i.e., C8) and five fish from the 26°C treatment were sampled. The remaining were then transferred to a temperature of about 24°C (treatment 9A), but some individuals were kept as controls (C9). The fish were grown under conditions of treatment 9A and C9 for a period of 52 days.

Fish were fed with finely ground trout pellets for the first two months, but with micropellets afterwards. Food was provided until satiation each day. The aquaria used in the experiments were fitted either with a bottom-filter system or

with suction-pump filters. Additionally, water was changed every two or three days during which time excess food was siphoned out.

Otolith examination

Each fish was measured for total length (TL, nearest 1 mm) and total weight (TW, nearest 0.01 g) immediately after sampling. The developmental stage of gonads was recorded for each fish. Sagittal otoliths were then removed, thoroughly cleaned and kept dry in vials pending microscopic examination.

We examined the right-side otolith throughout the study. Prior to microscopic examination, each otolith was treated in 72% ethanol for 3 days followed by a one-week treatment in 45% glycerol to enhance the appearance of the macrozones (Sinha & Jones, 1967; Yosef & Casselman, 1995). Each otolith was then microscopically examined using a reflected light at magnifications between 6x and 12x. The presence of translucent and opaque macrozones was noted. The number of translucent macrozones and the type of macrozone at the otolith edge were recorded for each sample. Along with the number of translucent macrozones, we used symbols to describe the type of macrozone at the otolith edge (modified after Yosef & Casselman, 1995). Thus, the expression '2o', for instance, was used to describe a macrostructure pattern characterised by the presence of two translucent macrozones the last one being at the edge of the otolith. Similarly, the expression '2x' was used to indicate that the otolith had 2 translucent macrozones and an opaque macrozone at its edge.

Results

Acclimatisation temperature

Otoliths of all tilapia sampled from the acclimatisation temperature (e.g., Fig. 10a) had one translucent macrozone, and an opaque macrozone at the edge (treatment 1, Tables 7 & 8).

Low temperature treatments (Table 7)

Otoliths from fish that were transferred from the acclimatisation temperature to about 20°C (treatment 2A, Table 7) for a period of 31 d had two translucent macrozones, and their edge was similar (i.e., opaque) to those sampled from the acclimatisation temperature. Otoliths of most tilapia (80%) that were transferred back to the acclimatisation temperature (treatment 3B, Table 7) had the same number of translucent macrozones, and a similar marginal tissue type, as those

Table 7. Results of macrostructure analysis on otoliths of tilapia that were transferred from a 24°C treatment to lower temperature treatments (see Fig. 9a). Treatment duration, number of translucent macrozones (TMZ) in otoliths, condition at the otolith edge, and frequency (%) of fish with the corresponding macrostructure pattern are indicated. The symbols 'x' and 'o' indicate the presence at the otolith edge of opaque and translucent macrozone, respectively.

Treatment number	Temperature (mean±SD) (°C)	Treatment duration (d)	No. of TMZ & edge condition	Frequency (%)	Sample size
1	24.0±0.7	120	1x	100	7
2A	19.8±0.2	31	2x	100	5
C2	24.0±0.6	31	1x	100	4
3A	16.6±1.4	30	3o	100	8
C3	18.9±0.4	30	2x	100	5
3B	24.3±0.4	30	2x	80	5
			3o	20	
4A	18.9±0.9	33	3o	83	6
			4o	17	
C4	16.2±0.2	33	3o	100	4
5A	23.7±0.4	52	3x	80	5
			4o	20	
C5	19.7±0.2	52	3x	80	5
			4o	20	

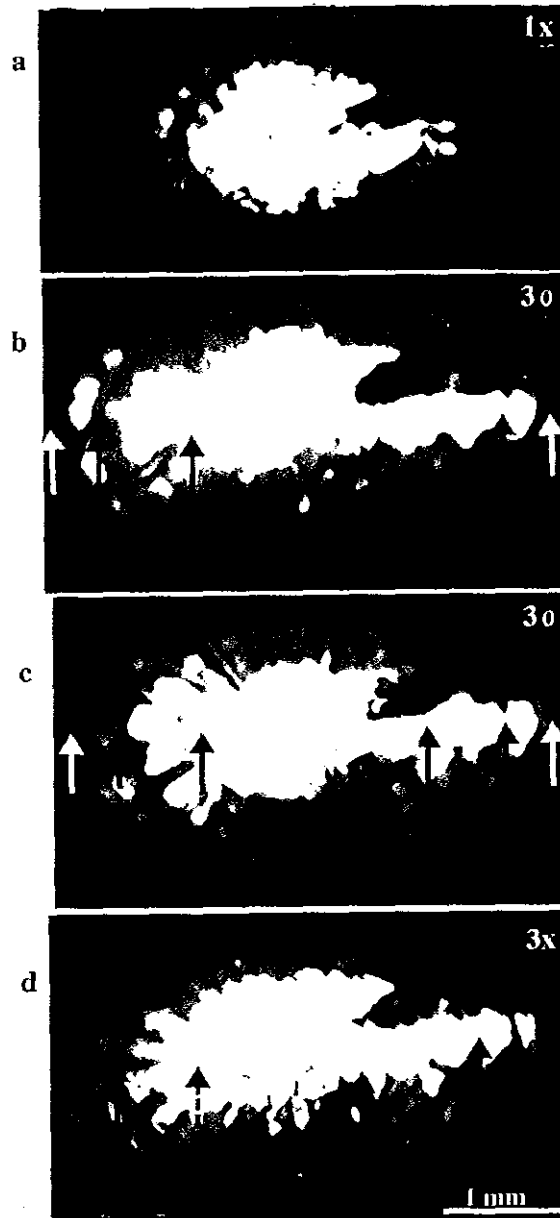


Figure 10. Photographs of otoliths from tilapia sampled at the end of some low temperature treatments. a) from 24°C aquarium (treatment 1) showing one translucent macrozone and a wide opaque margin. b) sampled from 16.6°C treatment, i.e., 3A in Fig. 9a, showing three translucent macrozones the last one being at the edge. c) sampled from 18.9°C treatment showing three translucent macrozones the last one of which is at the edge. d) from 23.7°C treatment showing three translucent macrozones and a wide opaque macrozone at the edge. See Fig. 9a for treatment history of each sample. The first translucent macrozone is not conspicuous in some photographs.

sampled from the 19.8°C aquarium (cf. treatments 2A & 3B, Table 7). However, one fish had a third translucent macrozone which was located at the otolith edge, i.e., macrostructure pattern of '3o'. Otoliths of all tilapia that were transferred from 19.8°C to the next lower temperature (i.e., 16.6°C, treatment 3A) had formed a third translucent macrozone which was located at the edge (e.g., Fig. 10b). There was no change in the otoliths of 83% of the tilapia transferred from the 16.6°C aquarium to a slightly higher temperature (treatment 4A, Table 7, Fig. 10c) except that one fish had one more translucent macrozone which was located at the otolith margin. No more translucent macrozone was formed in 80% of fish from the 23.7°C treatment (i.e., 5A), but an opaque macrozone was formed distal to, and delineating, a translucent macrozone (Fig. 10d), the later of which was presumably formed when the fish were in the 18.9°C aquarium (i.e., treatment 4A). One fish from treatment 5A had otoliths with four translucent macrozones the last one of which was located at the edge.

Otoliths from tilapia that were kept as controls for the low temperature treatments (i.e., C2, C3, C4 & C5) had the same marginal tissue type, and the same number of translucent macrozones as otoliths of fish sampled before transfer (cf. treatments 1 & C2, 2A & C3, 3A & C4 in Table 7). However, the opaque macrozone at the edge was much more wider in the otoliths from C2 than from treatment 1, and in otoliths from C3 than those from 2A. Otoliths of fish from C5 had an opaque edge, but still they had the same number of translucent macrozones as those in treatment 4A. In addition, one fish had otoliths with four translucent macrozones, the last one being at the edge of the otolith (C5, Table 7).

All fish grown under the various conditions in the low temperature experiments had flesh-coloured and thread-like gonads indicating that they were not sexually mature. However, one fish each from treatment 5A and C5

had mature gonads, and otoliths from both of these fish had a macrostructure pattern of 4o (Table 7).

High temperature treatments (Table 8)

The effect of temperature on fish kept in high temperature treatments (Fig. 9b) appeared confounded by the effect of sexual maturation and gonadal development. Most fish sampled from each treatment were sexually mature; the males had cream-coloured or almost fully ripe testes, and the females had either ripening gonads or gonads containing almost fully ripe eggs. Otoliths from fish that were treated similarly showed different macrostructure pattern (Table 8). For instance, 60% of tilapia that were grown at 25.8°C had otoliths with one translucent macrozone and a wide opaque edge (Fig. 11a) whereas the remaining fish had otoliths with two translucent macrozones the last one being located at the otolith edge (treatment 6A, Table 8). These latter fish, all of which were females, had gonads containing several and small-sized eggs.

Otoliths from fish in the 24.3°C aquarium (treatment 7B) had two translucent macrozones and an opaque macrozone at the edge. Otoliths from all fish in the 27.6°C aquarium (treatment 7A), the next higher temperature, had two translucent macrozones the last one of which was located at the otolith edge (Table 8, Fig. 11b). Some fish from the 27.6°C treatment had ripening gonads whereas the majority were immature, but all had a similar otolith macrostructure, i.e., 2o.

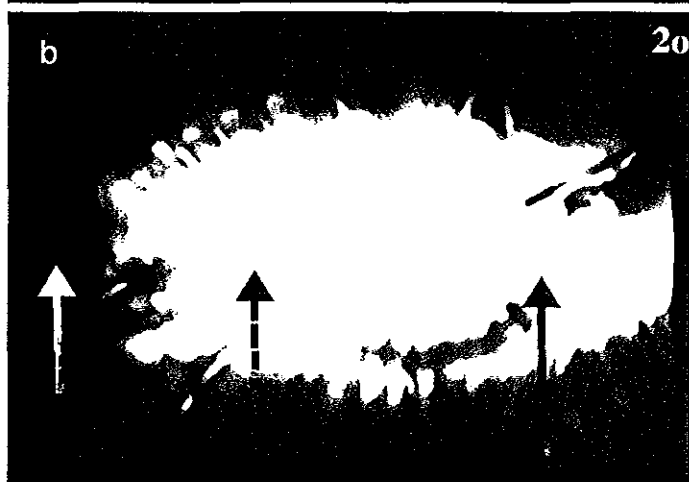
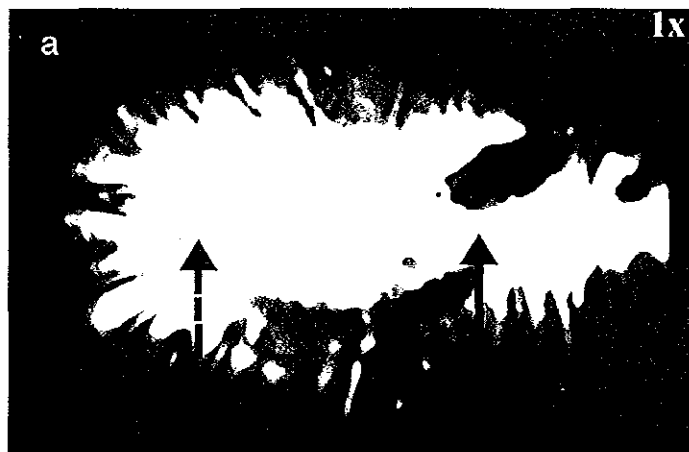
All fish sampled from the 25.9°C and 23.7°C treatments (i.e., 8A & 9A, respectively), and from the controls (C8 & C9) had ripening or ripe gonads. Among the fish in treatment 8A, 40% of them had two (e.g., Fig. 11c) whereas 20% had three translucent macrozones, the last one in both cases being located at the otolith edge. The remaining 40% had otoliths with three translucent macrozones and a wide opaque macrozone at the edge (Table 8). Fish kept in

treatment 9A had an opaque macrozone at the margin of their otoliths. However, 40% of them had two translucent macrozones (e.g., Fig. 11d) whereas the rest had 4 translucent macrozones (Table 8).

Table 8. Results of macrostructure analysis on otoliths of tilapia that were transferred from a 24°C treatment to higher temperature treatments (see Fig. 9b). Treatment duration, number of translucent macrozones (TMZ) in otoliths, condition at the otolith edge, and frequency (%) of fish with the corresponding macrostructure pattern are indicated. Symbols 'x' and 'o' are as in Table 7.

Treatment number	Temperature (mean±SD) (°C)	Treatment duration (d)	No. of TMZ & edge condition	Frequency (%)	Sample size
1	24.0±0.7	120	1x	100	7
6A	25.8±1.0	31	1x	60	5
			2o	40	
C6	24.0±0.6	31	1x	100	4
7A	27.6±0.2	30	2o	100	7
C7	26.1±0.5	30	2o	25	4
			2x	75	
7B	24.3±0.4	30	2x	100	4
8A	25.9±0.4	33	2o	40	5
			3o	20	
			3x	40	
C8	27.8±0.6	33	2x	20	5
			3o	20	
			3x	60	
9A	23.7±0.4	52	2x	40	5
			4x	60	
C9	25.6±0.3	52	2x	40	5
			3x	60	

Figure 11 (next page). Photographs of otoliths from tilapia sampled from some high temperature treatments. a) an otolith from 25.8°C treatment, i.e., 6A in Fig. 9b, showing a wide opaque edge and the first translucent macrozone. b) & c) from 27.6 and 25.9°C treatments, respectively, showing a wide translucent macrozone at the edge. d) from a fish with a ripe gonad sampled from 23.7°C treatment, showing a wide translucent macrozone and a wide opaque edge. The first translucent macrozone is not visible in this photograph. See Fig. 9b for treatment history of each sample.



Otoliths of tilapia from the control temperature of 24.0°C (C6) had the same otolith macrostructure as those from treatment 1 (Table 8). However, the otolith macrostructure of most tilapia from the other control temperatures differed from that of otoliths sampled from the respective treatment temperatures. Thus, otoliths of most of the tilapia from C7 were different from those in treatment 6A. In addition, otoliths from C8 were different from those in treatment 7A, and otoliths from C9 were different from those in treatment 8A (see Table 8).

Somatic tissue growth

Fish size, which was measured at the end of each treatment, appeared positively correlated with the treatment temperature. Generally, fish in the low temperature treatments (Fig. 12a) were smaller than those in the high temperature treatments (Fig. 12b). Fish sampled at the end of the acclimatisation period (treatment 1) were on average 69.0 mm TL and 6.27 g TW. Those sampled from the 19.8°C treatment (2A) were 92.0 mm in TL and 19.9 g in TW (Fig. 12a). Tilapia from the 16.6°C treatment (3A) were smallest which could be due to the extremely low temperature. Fish size progressively increased after the fish were transferred back to relatively higher temperatures, i.e., 18.9°C and 23.7°C (4A and 5A, Fig. 12a).

Total length and total weight of fish in the high temperature experiment increased after each transfer from a relatively lower to higher temperatures (Fig. 12b). There was no considerable difference in size between fish from the 25.9°C treatment (8A) and those from the 23.7°C (9A) which could be due to the relatively lower temperature of treatment 9A as compared with that of 8A.

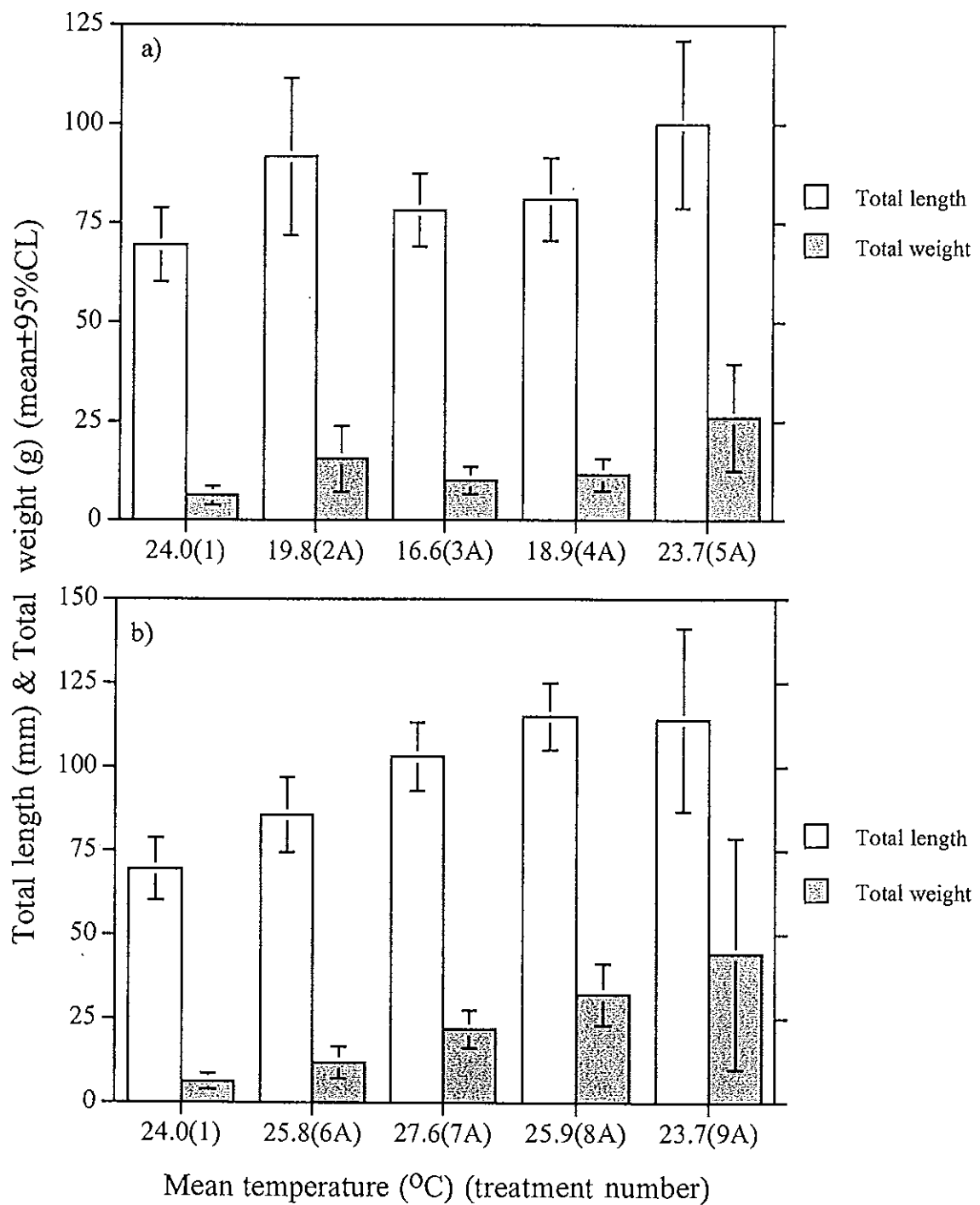


Figure 12. Mean ($\pm$ 95% confidence limit) length and weight of *Oreochromis niloticus* at the end of each low temperature (a) and high temperature (b) treatment.

Discussion

Otoliths taken from *O. niloticus* before the transfer experiment had one translucent macrozone (Fig. 11a). Increment counts on some of these otoliths suggested that the fish were about 2 months old at the formation of this translucent macrozone. The reason for its formation is unclear. However, it could be associated with the change in the type of feed from finely ground trout pellets to micropellets, which took place when fish were 60 d old. A narrow translucent macrozone has been observed in otoliths of juvenile *O. niloticus* from some Ethiopian lakes (Yosef & Casselman, 1995; Admassu, accepted; K. Alemu & D. Admassu, unpublished manuscript), and its formation is believed to be associated with the shift in diet which, according to the study of Tudorancea *et al.* (1988), is coincident with the formation of the translucent macrozone. Juvenile tilapia up to a size of 25–30 mm TL are omnivores, but at larger sizes they are mainly phytoplanktivores (Tudorancea *et al.*, 1988). However, it is not known if the difference in nutritive quality between ground trout pellets and micropellets in our study is as significant.

Our study showed that a temperature fluctuation of about 3–5°C, particularly within the range of 17 to 24°C, caused variation in the growth of somatic tissue and otoliths of *O. niloticus*. We found that tilapia transferred from an average temperature of 24°C to an average temperature of 19.8°C had a translucent macrozone in their otolith (i.e., in addition to that formed before the transfer). This translucent macrozone was presumably formed during the first few to several days after transfer, because the deposition of a wide opaque macrozone at the edge suggests that its formation has been completed some time before sampling. The presence of an opaque macrozone at the edge suggests that appositional growth had been rapid (Casselman, 1990). In addition, there was a considerable growth of somatic tissue, because by the end of each experimental period fish from the 24°C aquarium were on average 69.4

mm TL and 6.3 g TW, but those in the 19.8°C were 91.8 mm TL and 15.5 g TW. Fish kept at 24°C as controls (i.e. C2, Table 7) for a similar period as those kept at 19.8°C were 93.3 mm TL and 15.7 g TW suggesting comparable growth at 24°C and 19.8°C. Thus, fish transferred from 24 to 19.8°C seem to have adapted to the new temperature. The implication of this could be that in tropical lakes where temperature can be as low as 18—20°C, e.g., Lakes Awassa, Zwai and Haiq, translucent macrozone formation in otoliths of tilapia may take place during the first few to several days of exposure to the low temperature. However, samples of otoliths taken later in the season of low temperature (i.e., 19 to 20°C) may have opaque macrozone at their edge. Apparently, this may partly explain why in tilapia from Ethiopian lakes some had otoliths with opaque macrozone at the edge during periods when the majority had otoliths with a translucent macrozone at the edge.

A temperature fluctuation of a few degrees has been considered to be the most important factor associated with the formation of translucent macrozones and biannulus in otoliths of *O. niloticus* from Lakes Awassa (Admassu, 1989; Yosef & Casselman, 1995), Haiq (K. Alemu & D. Admassu, unpublished manuscript) and Zwai (Admassu, accepted; Chapter V). In these Ethiopian lakes, there is an amplitude of about 3—6°C between yearly maximum and minimum water temperature. In addition, Skornyakov (1964) and Nekrasov (1980) also believe that such temperature fluctuation may be sufficient to cause variations in the growth of tropical fish.

Otoliths of *O. niloticus* sampled, at the end of the treatment, from the 16.6°C aquarium (treatment 3A, Table 7) had three translucent macrozones: one associated with the diet change mentioned earlier, one formed due to the transfer from 24 to 19.8°C, and one due to the transfer from 19.8 to 16.6°C. The last one was located at the edge of the otolith indicating that its formation may have taken place throughout the treatment period in the 16.6°C aquarium. Fish

at the end of this treatment were 78.2 mm TL and 10.0 g TW, and they were smaller than those from the control aquarium (C3); the fish from the control aquarium (about 18.9°C) were 86.0 mm TL and 13.1 g TW. Thus, a temperature reduction of about 3 degrees (from 19.8 to 16.6°C) seem to have caused a significant decrease in the growth of the fish and its otoliths. Fish sampled from C4 (16.2°C) had otoliths with a macrostructure pattern of '3o', and did not grow well (TL = 81.6 mm, TW = 10.8 g). This also suggests that tilapia may not adapt well to temperatures around 16.0°C even when kept for an extended period. Although some species are more tolerant of low temperature than others, tilapia generally stop feeding completely at 16°C (Chervinsky, 1982), but the fish in our experiment were feeding, albeit rather slowly.

Otoliths of most *O. niloticus* transferred from 24°C to higher temperatures exhibited macrostructure pattern that could not clearly be attributed to temperature fluctuation. Sixty percent of tilapia transferred from 24°C to an average of 25.8°C had otoliths with a very wide opaque edge plus the translucent macrozone formed before the transfer (Table 8). This was similar to otoliths from fish kept as controls (i.e., C6). Thus, appositional growth of otoliths of these fish was more rapid and may be similar at 24 and 25.8°C. Average size of fish from the 25.8°C treatment was 85.6 mm TL and 12 g TW, but those in C6 had grown slightly larger (93.3 mm TL and 15.7 g TW), but this could as well be because of a relatively larger initial sizes of fish in C6.

The formation of translucent macrozones in otoliths from tilapia that were kept at high temperatures (Table 8) may be associated with sexual maturation and gonadal development in these fish. Sexual maturation and gonadal development represent a drain on metabolic resources for the production of reproductive products (Fryer & Iles, 1972; Balarin & Hatton, 1979; Jalabert & Zohar, 1982). This may also affect otolith growth, and hence, result in the formation of translucent macrozones. The same has been concluded for *O.*

niloticus from some Ethiopian lakes, for the related *O. andersonii* from the Okavango Delta, Botswana (Booth *et al.*, 1995), and for other fish in the tropics (Garrod, 1959; Balon, 1972; Nekrasov, 1980).

The results of this study confirmed previous suggestions that a reduction in temperature of about 3 to 5°C may reduce the growth of tilapia and their otoliths, with an associated formation of translucent macrozones. Fluctuation in water temperature has generally been assumed to be not sufficient in the tropics. Indeed, this important factor has just been ignored due to this general belief. However, as shown in this study, and earlier by Casselman (1990), fish generally respond to subtle changes in temperature. The response of tropical fish, particularly thermophilic species such as tilapia (Caulton, 1982), could be significant as they are normally adapted to high temperatures. This study has also provided supportive evidence to the general belief that sexual maturation and gonadal development may also be important in the formation of checks and translucent macrozones in otoliths and other calcified tissues of tropical fish. The experiment was not replicated mainly due to the lack of enough number of fish. Therefore, future study based on replicated experimental design may prove useful to confirm the results of the present study.

CHAPTER V

AGE AND GROWTH DETERMINATION OF TILAPIA, *Oreochromis niloticus* L. FROM LAKE ZWAI

Introduction

Yosef & Casselman (1995) have developed a procedure of age and growth determination for immature *O. niloticus* from Lake Awassa, Ethiopia. The method uses biannulus in otoliths not only to interpret age and growth, but also to assign individual fish to a specific recruitment cohort within a year. The procedure, which was validated by independently determined daily age from otolith microstructures (Yosef & Casselman, 1995), has been tested and found applicable to *O. niloticus* from Lake Haiq (K. Alemu & D. Admassu, unpublished manuscript) as well as mature fish from Lake Awassa (D. Admassu & J. Casselman, unpublished manuscript).

In the present work an attempt was made to test Yosef & Casselman's (1995) procedure on otoliths of *O. niloticus* from Lake Zwai. Biannulus formation in otoliths of the fish from Lake Zwai has been reported earlier (Admassu, accepted). However, that study was not conducted in detail and did not consider mature fish. Thus, in the present study an attempt was made to examine seasonal cycle of appositional growth of otoliths from fish of various sizes and age-groups in relation to water temperature. Other factors possibly associated with biannulus formation are also discussed. The age of the fish was then determined using biannuli in otoliths to discriminate cohorts. An attempt was also made to verify the procedure of age determination and cohort discrimination from macrostructures in otoliths using ages estimated from microstructure analysis. In addition, we have also attempted to refine Yosef &

Casselman's procedure by setting some general criteria to assign fish to a specific cohort within a year. Mean length-at-age data were then calculated and von Bertalanffy growth model was used to describe growth. Comparative growth of juvenile *O. niloticus* in Lakes Zwai, Langeno and Chamo has been presented in Chapter III. However, the same for adult fish has not been dealt with. In this chapter growth data for the fish in Lakes Awassa and Haiq from other studies (Admassu, 1989; Yosef & Casselman, 1995; K. Alemu & D. Admassu, unpublished manuscript; D. Admassu & Casselman, unpublished manuscript) were used, and growth of various tilapia populations was comparatively presented. Possible reasons for growth differences were also speculated.

Study area

Lake Zwai (Lat.: 7°52'—8°8' N; Long.: 38°40'—38°56' E) is located at an altitude of 1636 m in the central part of the Ethiopian rift valley, and it is the northern-most lake in the closed Zwai-Shalla basin (Fig. 13). The Bulbula River is the major outflow from Lake Zwai which connects this lake with the terminal lake, Lake Abijata. The major inlets to Lake Zwai are Rivers Katar and Meki in the North. Lake Zwai is a shallow lake (7 m maximum depth) (Kebede, 1996), however, 12 m deep rifts, some of which release hot springs, are present around the major islands (Schröder, 1984).

The Lake Zwai region is arid and semi-arid characterised by frequent winds throughout the year. Precipitation is usually greatest between July and August, with a less pronounced peak between February and May (Chapter II). Usually, the period between October and November is totally dry. Water level of Zwai, which is lowest between February and April and highest between August and December, is dependent on rainfall on distant highlands, because local precipitation rarely exceeds 600 mm per annum (Gamachu, 1977). The dry

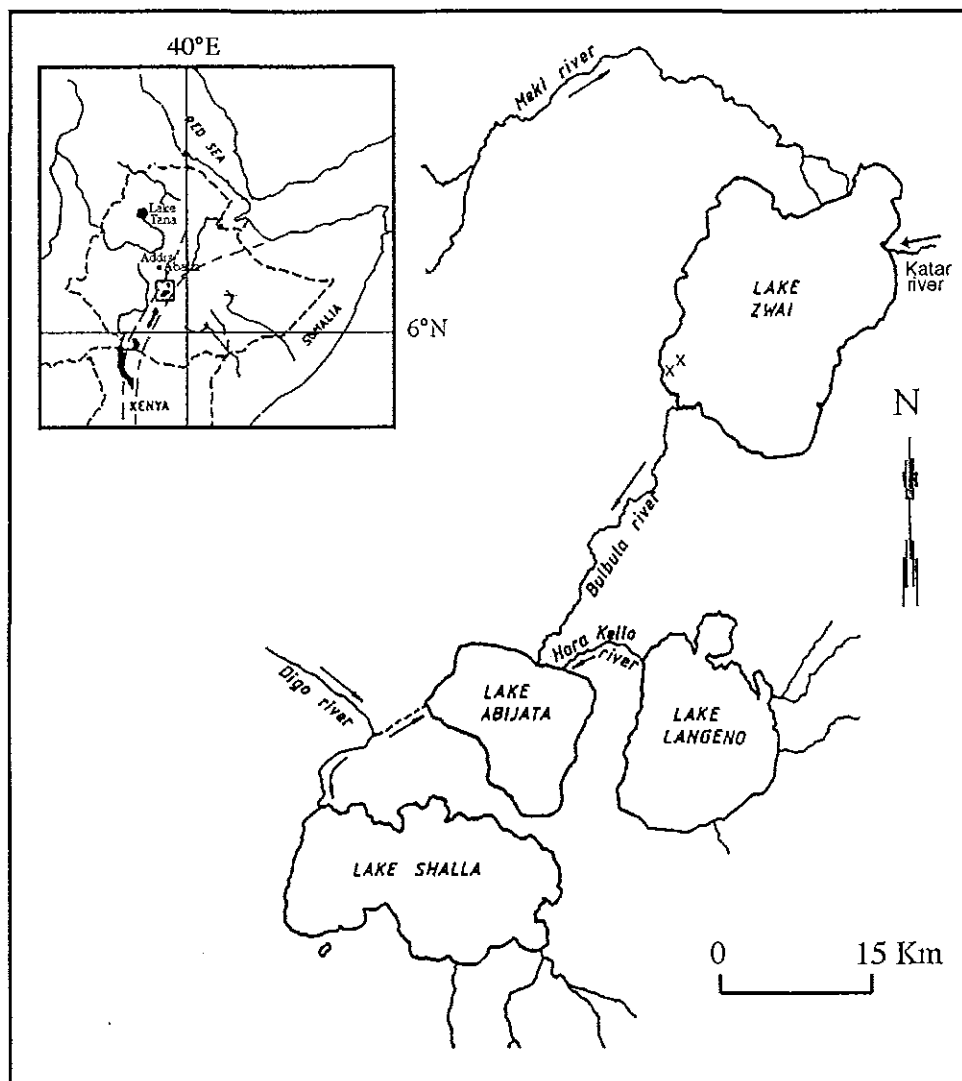


Figure 13. Lake Zwai and other lakes in the Zwai-Shala basin (sampling stations indicated by 'x'). Inset: East Africa showing Ethiopia and the Zwai-Shala basin in the rift valley.

season is also the coldest, because minimum daily air temperatures drop to 10°C during this period. Surface water temperature (mean of 3—5 measurements per sampling, between 1000 and 1100 hr) of the Lake ranged from 20.7 to 26.8°C, with relatively low measurements occurring in January, between June and early-August and also between November and December (Chapter II). Temperatures were highest between March and May, and also increased to 23°C in late-August and September from a yearly minimum of 20.7°C in early-August.

Nutrients such as SiO₂ (range of concentration: 18.6—49.7 mg l⁻¹), PO₄-P (5.5—16.2 µg l⁻¹) and NO₃-N (2.8—136.6 µg l⁻¹) occur in relatively high concentrations during or immediately after the heavy rains (Tilahun, 1988). Phytoplankton biomass (chlorophyll *a* concentration) begins to increase in February peaking in July and then falling to a lowest value between November and January (Tilahun, 1988).

The most important algal species in Lake Zwai are the cyanophytes *Cylindrospermopsis africana* and *Planktolyngbya limnetica* which account for 67% of the total algal biomass (Kebede, 1996). Other common genera include *Microcystis*, *Gymnodinium*, *Anabaena*, *Aulacoseira*, *Navicula*, *Botryococcus* and *Pediastrum* (Kebede, 1996). Zooplankton community of Lake Zwai is composed of *Mesocyclops* spp., *Microcyclops* sp., *Diaphanosoma* sp., *Brachionus angularis* and *Keratella tropica*.

The littoral zone of Lake Zwai is covered by various macrophytes the most common of which are *Scirpus* spp., *Cyperus* spp., *Typha angustifolia*, *Paspalidium geminatum* and *Nymphaea cerulea* (Tudorancea *et al.*, 1989). The macrophyte zone provides feeding, breeding and nursery ground for fish. *Hippopotamus amphibius* is also a common grazer in the littoral zone.

Lake Zwai supports an important fishery which is almost entirely dependent on *O. niloticus*. Gillnets and beach seines are the dominant gears

used. The proximity of the lake to Addis Ababa makes its fishery the most important in the country.

Materials and methods

Sampling

Samples of *O. niloticus* were gillnetted and seined approximately every two or four weeks throughout the year in 1996. We used 10 gillnets of various stretched mesh sizes (27, 32.5, 42, 50, 62, 75, 88, 100, 113 and 120 mm), which were connected end to end to make a 2.4x150 m panel of nets. The nets were set at the surface where the water depth was about 2.5 m (Fig. 13). Seining was conducted in shallower waters along the shore (Fig. 13) using a 2.7x30 m beach seine of 6 mm stretched mesh size.

Total length (TL, nearest 1 mm) of each individual was measured immediately after capture, and specimens were simultaneously sorted into length groups of 10 mm interval. A random subsample of seven to ten fish were then taken from each length group, and TL and total weight (TW, nearest 0.1 g) of each individual in the subsample were measured. Sagittal otoliths were then removed, cleaned and kept dry in vials until examination in the laboratory.

Macrozone analysis

From each sampling date, five to seven otoliths were randomly selected from each length interval. The right otolith was used throughout the study unless it was broken or lost. Prior to microscopic examination otoliths were treated as described in Yosef and Casselman (1995). Otoliths from large fish were held by the tip of the index finger and ground (lateral-medial grind) until the macrozones in the central region of the otolith were satisfactorily decipherable. Carborundum papers of 400 grit, and then 600 grit, were used for grinding.

Each otolith was then placed in a dark dish containing 45% glycerol, and examined under a stereo microscope (12x—40x) using a reflected light. The presence of optical macrozones (translucent and opaque) was then noted.

The number of translucent macrozones was recorded for each sample without knowledge on fish size and date of capture. In addition, the type and the relative width of the zone at the edge of each otolith was noted. Depending on the zone at the edge, each otolith was classified into one of the following categories (Yosef & Casselman, 1995):

- 'o' translucent zone associated with assigning age formed on the edge of the otolith.
- '*' translucent zone associated with the 'o' condition completely formed and delineated by a small amount of opaque material in the fastest growing region (longest radius) of the otolith.
- '+' opaque zone at the edge, 50% or less than the width of the preceding opaque zone, delineated by the translucent zone associated with the 'o' condition.
- '++' opaque zone at the edge, greater than 50% of the width of the preceding opaque zone, delineated by the translucent zone associated with the 'o' condition.

The maximum posterior radius, and the distance between the otolith centre and the distal and proximal edges of every macrozone was measured using an ocular micrometer fitted to the eye-piece of the stereo microscope.

Microzone analysis

After completion of macrozone analysis, otoliths were prepared for examination and analysis of the microzones. Microzones were not decipherable in otoliths from fish larger than 159 mm TL. Therefore, this part of the study was limited to

otoliths from smaller fish. The methods of otolith preparation and microzone counting followed in this chapter are as described in chapter III.

Translucent microzones (incremental zones) were counted at least twice (but not consecutively) from the centre to the posterior margin of the otolith, and averaged. In addition to the total count, also the number of increments up to the distal and proximal edges of each of the first few macrozones was recorded.

Determination of time of translucent macrozone & biannulus formation

The frequency of otoliths with the various edge conditions (i.e., 'o', '*', '+' and '++') was calculated for each sampling occasion. The data were then plotted by date of capture, and the time when the frequency of otoliths with translucent zone at the edge ('o' condition) was maximal was taken as the time of translucent macrozone formation. In addition, biannulus formation was considered completed at the time of peak in frequency of otoliths with '*' condition (Casselman, 1987; Yosef & Casselman, 1995). The time of peak in frequency of otoliths either with '+' or '++' condition was taken as the general time of rapid appositional growth of otoliths.

The seasonal growth cycle of otoliths was studied by calculating relative marginal increment which also served to verify results from the study on condition at the edge of otoliths (see above). Relative marginal increment is the width of the opaque macrozone on the edge divided by the mean width of that particular opaque macrozone in otoliths of tilapia that had completed their current seasonal growth (Casselman, 1987). The period of time when relative marginal increment was minimal was taken as the time of translucent macrozone formation. In addition, the time when relative marginal increment began to increase was considered to be the time when biannulus formation is completed.

Determination of recruitment cohorts, age and growth

The time of peak spawning was determined based on hatch-dates back-calculated from the date of capture and daily age determined from microzone counts (i.e., microzonal age). The proportion of fish hatched in each month was then calculated. Median hatch-date was also calculated for the peak spawning period.

As will be shown later, there were two major annual recruitment cohorts of *O. niloticus* in Lake Zwai. In addition, results from macrozone analysis suggested, and verified by microzone analysis, that a particular translucent macrozone in otoliths from the two cohorts was formed at different times of the year. Hence, samples from the two cohorts were discriminated from knowledge on the number of translucent macrozones, condition at the edge of the otolith, time of formation of macrozones and on date of capture.

After identifying the cohort of individuals, the age of each fish was estimated by relating the date of capture to the median hatch-dates. Mean total length-at-age was then calculated based on age interpreted from macrozone analysis (i.e., macrozonal age). It was found that tilapia with 'n+1' number of biannulus were older than those with 'n' number of biannulus by an average of 0.5 yr (range: 0.30 to 0.57). Thus, mean length-at-age data were grouped by the number of biannulus in otoliths (i.e., in half year intervals), and the parameters of the von Bertalanffy growth function (von Bertalanffy, 1938) were estimated following the procedure in Ricker (1975). The growth of the Lake Zwai *O. niloticus* population is then compared with that of other populations, particularly with those in Lakes Awassa and Haiq. Growth data for the latter two populations were obtained from D. Admassu & J. Casselman (unpublished manuscript) and K. Alemu & D. Admassu (unpublished manuscript). Growth performance index ($\phi' = \log K + 2 \log L_{\infty}$, Munro & Pauly, 1983) was also calculated for each population.

Results

Time of translucent macrozone and biannulus formation

Otoliths with a translucent macrozone at the edge (i.e., 'o' condition) were present throughout the study period. However, they were very common in January, February, July, early-August, November and in December (Figs 14a & 16a). Otoliths with a narrow opaque macrozone at the edge (i.e., '*' condition, e.g., Fig. 16b) were first observed at relatively high frequencies in mid-March and also in August peaking in early-April and in late-August (Fig. 14b). Otoliths with a wider opaque macrozone at the edge (i.e., '+' condition, e.g., Figs 16c & 17) were highly frequent between mid-March and May, and also between August and October (Fig. 14c). The frequency of otoliths with a '++' marginal condition progressively increased between March and June, and also between late-August and October, the peaks being in June and in October (Fig. 14d).

Seasonal cycle of relative marginal increment was similar for otoliths that had 1, 2, 3, 4 and 5 biannuli. Marginal increment was generally low in January and February, and also in July and early-August, but it was high between mid-March and late-June, and also between late-August and October (Fig. 15). Evidently, minimal marginal increment coincided in time with a high frequency of otoliths with translucent edge, whereas increased appositional growth was coincident with a high frequency of otoliths with opaque macrozone at the edge (cf. Figs 14 & 15).

The above results suggest that annually two translucent macrozones, each associated with biannulus, are formed in the otoliths of *O. niloticus* in lake Zwai: one in the period between November and February, and another between July and early-August. Annulus formation in calcified tissues from temperate fish (Casselman, 1987), and biannulus formation in tilapia from some Ethiopian lakes (Yosef & Casselman, 1995; K. Alemu & D. Admassu, unpublished manuscript), is considered completed when the translucent macrozone is

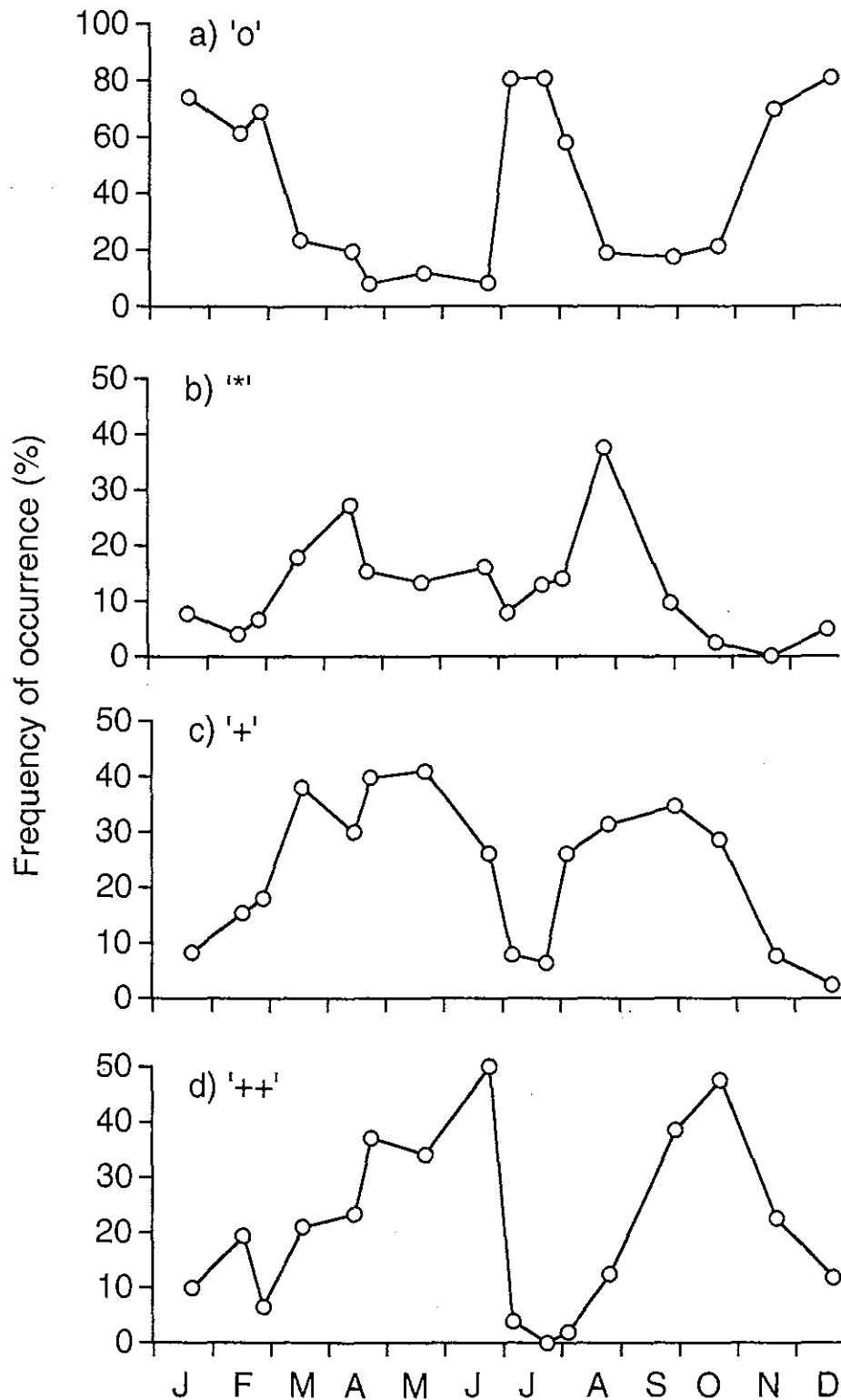


Figure 14. Annual cycle of the condition at the edge of otoliths of *Oreochromis niloticus* from Lake Zwai indicated by seasonal frequency of otoliths with a) 'o' condition; translucent macrozone at the edge, b) '*' condition; narrow opaque macrozone at the edge, c) '+' condition; opaque macrozone at the edge, that is 50% or less than the width of the previous biannual opaque macrozone, d) '++' condition; as in c, but > 50%.

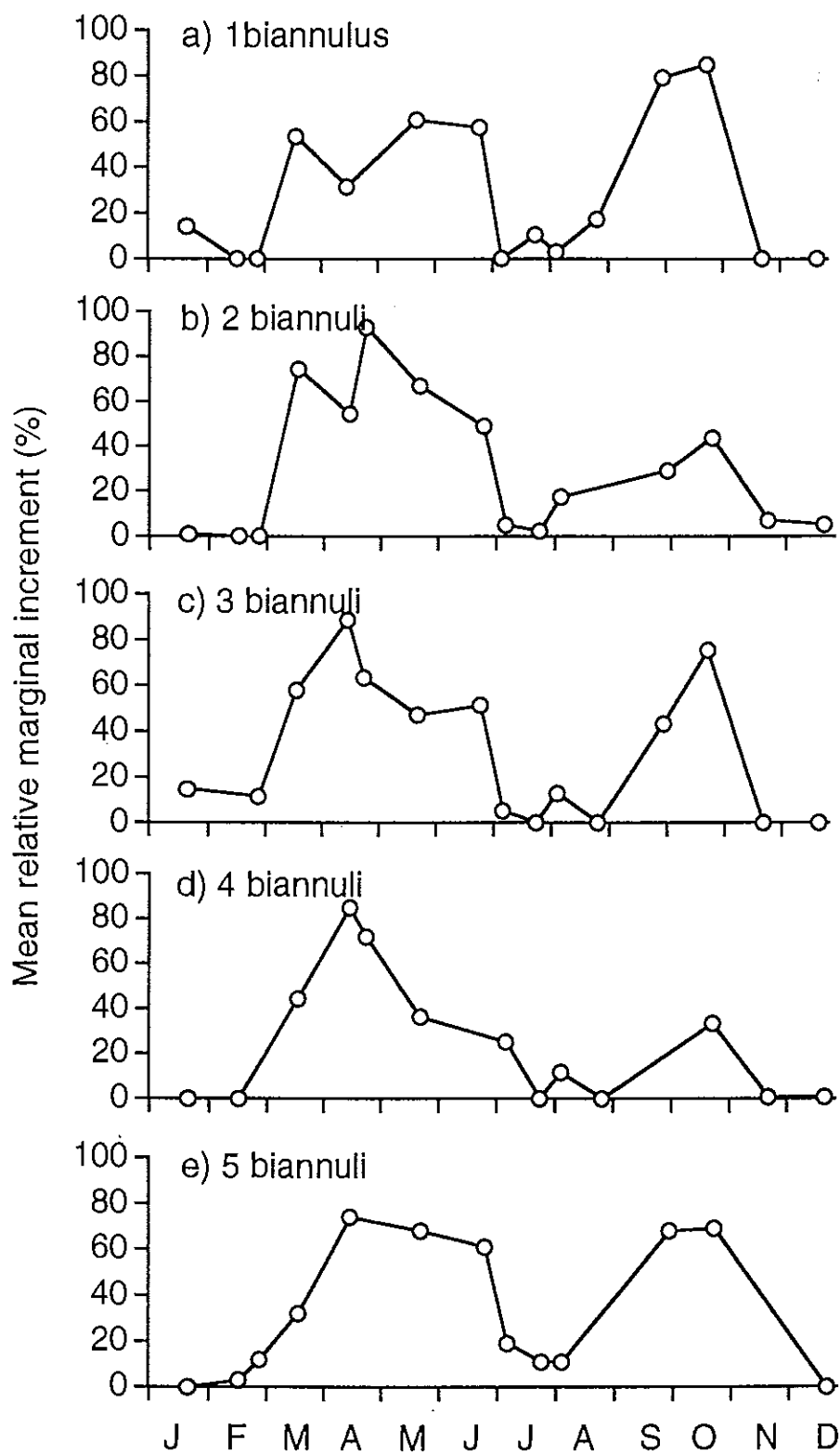


Figure 15 (a—e). Seasonal cycle in appositional growth of otoliths of *Oreochromis niloticus* from Lake Zwai indicated by fluctuation in mean relative marginal increment of otoliths that had 1, 2, 3, 4 and 5 biannuli, respectively.

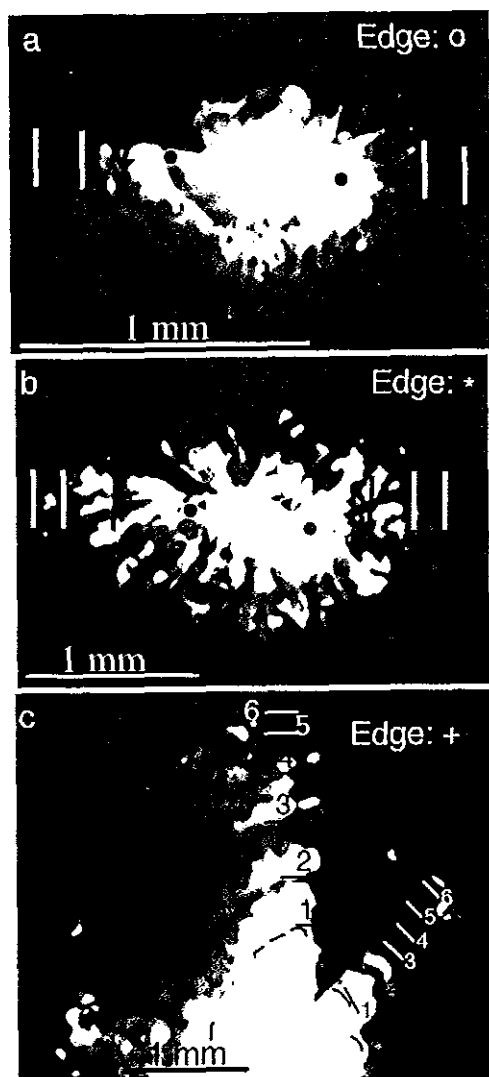


Figure 16. Photographs of otoliths of *Oreochromis niloticus* from Lake Zwai illustrating seasonal changes in the type of macrozone at the edge: a) an otolith from a 77 mm tilapia of the February 1995 cohort caught on 27 February 1996 showing a translucent macrozone at the edge and 2 biannuli & a pseudobiannulus (arrow); estimated age = 364 d, b) an otolith from a 90 mm tilapia of the February 1995 cohort caught on 28 August 1996 showing a narrow opaque macrozone at the edge and 3 biannuli; estimated age = 548 d, and c) an otolith from a 121 mm tilapia of the September 1993 cohort caught on 30 September 1996 showing a wide opaque macrozone at the edge and 6 biannuli, estimated age = 1124 d. Biannuli indicated by line segments. Juvenile marks indicated by dark dots in a and b. The first biannulus in c is highlighted.

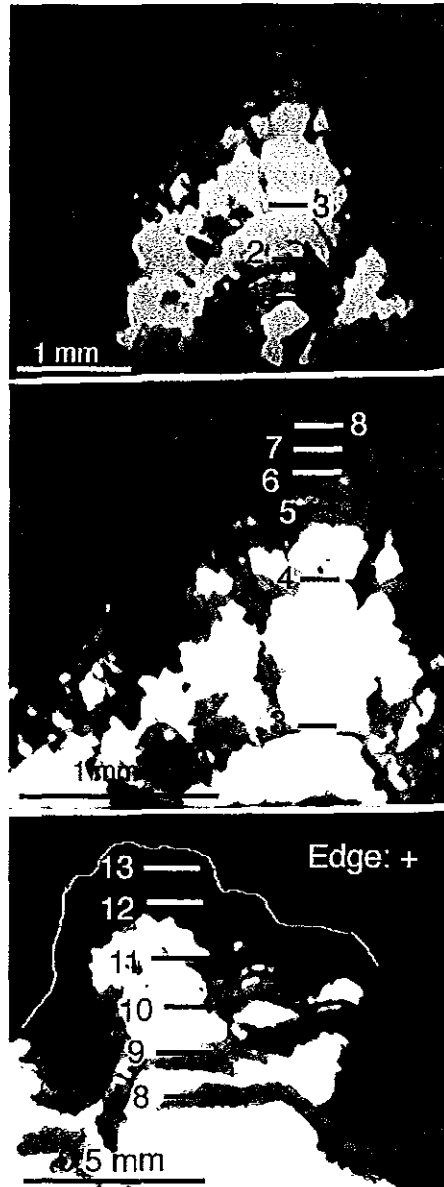


Figure 17. Anterior half of an otolith from a 325 mm *Oreochromis niloticus* showing closely spaced biannuli towards the otolith edge. Indicated are the first 3 biannuli in the upper panel, biannuli 3 to 8 in the middle panel and the rest in the bottom panel. The fish was from the September 1989 cohort caught on 27 February 1996. Indicated are 13 biannuli; estimated age = 2368 d. The anterior tip of the otolith is highlighted in the bottom panel.

delineated by a narrow opaque macrozone. Similarly, biannulus formation in otoliths of *O. niloticus* in Lake Zwai is believed to be completed in mid-March and in late-August during which time relative marginal increment commenced to increase from seasonally low values in the preceding months (Fig. 15). Time of biannulus formation determined from macrozone analysis was verified by independently interpreted microzonal ages (see below).

In addition to the biannual translucent macrozones, otoliths of *O. niloticus* have two juvenile marks. These were characterised by faint and relatively narrower translucent macrozones that were located close to the otolith centre. One or both of these juvenile marks were not clearly visible in otoliths from large fish due to calcareous overgrowth (Figs. 16 & 17). A study on otoliths from fry and juvenile fish (Admassu, accepted) showed that the first and second juvenile marks are formed at average ages of 17 d (fish mean TL = 13.8 mm) and 49 d (mean TL = 25 mm), respectively. Since their formation also did not follow any seasonal pattern (Admassu, accepted) they were not counted to determine age in this study. Juvenile marks were also observed in otoliths from tilapia in other lakes, and were not used to determine age (Alemu, 1995; Yosef & Casselman, 1995).

Spawning periodicity and cohort discrimination

Hatch-dates estimated from daily increments in otoliths suggested that *O. niloticus* in Lake Zwai spawns almost throughout the year. However, two spawning peaks were distinct: one between December and March and another between August and October (Fig. 18). Our results are similar to the breeding season of the fish determined from gonadal maturity data collected throughout the year (Tadesse, 1988). In addition, a large number of new recruits (between 9 and 12 mm TL) were caught in these two periods (D. Admassu, unpublished data). Back-calculation from daily increment counts in otoliths gave 28

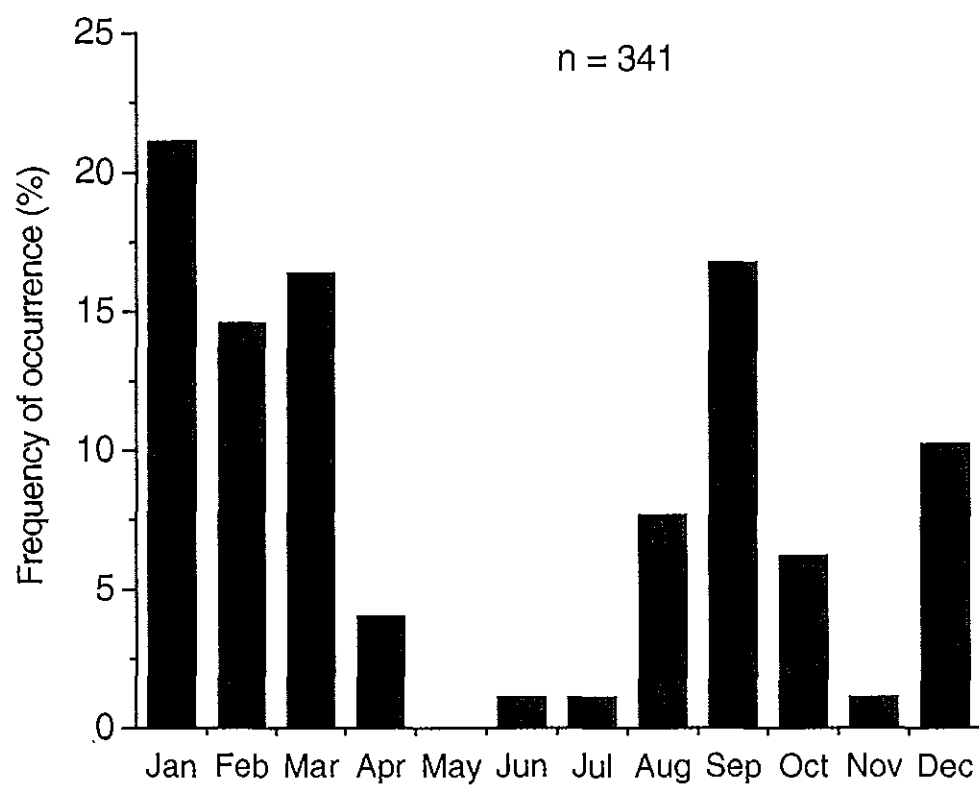


Figure 18. Hatch-date distribution of *Oreochromis niloticus* from Lake Zwai back-calculated from dates of capture and daily ages determined from otolith microzones. n = sample size.

February and 2 September to be the respective median-hatch dates for the two peak breeding seasons. Fish from the two recruitment periods were referred to as the February-cohort and the September-cohort, respectively.

A translucent macrozone associated with a particular biannulus (e.g., the first biannulus) was found to be formed at different times in otoliths from tilapia of the two cohorts. This allowed to discriminate between fish of the two cohorts. For instance, the translucent macrozone associated with the first biannulus in otoliths from tilapia that were caught in mid-March 1996 was formed presumably between November 1995 and February 1996. Thus, the fish may have been spawned between August and October 1995 (September-cohort). The mean microzonal age of fish with 1 biannulus that were caught in mid-March was 215 d (standard deviation = 96 d, $n = 8$). Thus, the mean hatch-date of these fish was estimated to be mid-August 1995 which agrees favourably with cohort discrimination from macrozone analysis. In addition, in otoliths from tilapia caught on 28 August 1996, and whose first biannulus had been completed, the translucent macrozone associated with the biannulus was formed presumably between July and early-August 1996. Thus, the fish seem to have been spawned between December 1995 and March 1996 (February-cohort). Fish with 1 biannulus and '*' edge condition which were sampled on 28 August had a mean microzonal age of 190 d (standard deviation = 87 d, $n = 7$). This gave an estimated mean hatch-date of mid-February 1996. Thus, results from microstructure analysis verified cohort discrimination and time of biannulus formation determined from macrozone analysis.

In general, the presence of temporal differences in the formation of the first biannulus between fish of the two cohorts, and knowledge on time of capture and the number of biannulus in otoliths, allowed a means to discriminate between fish from the two cohorts. Thus, the procedure proposed by Yosef & Casselman (1995) is applicable to determine cohort and age of *O. niloticus* from

Lake Zwai. As was the case for adult *O. niloticus* from Lake Awassa (D. Admassu & J. Casselman, unpublished manuscript), the procedure could be simplified based on knowledge on number of biannulus and date of capture (Table 9). After cohort is identified using the criteria in Table 9, year class (YCS) could be estimated from number of translucent zones associated with biannulus (NTBA) and calendar year of capture (YCR) (D. Admassu & J. Casselman, unpublished manuscript):

$$YCS = YCR - [(0.5 \times NTBA) + \Omega],$$

where Ω was 0 for fish that had even NTBA (e.g., Figs 16a & 16c), but if NTBA was odd, then Ω was -0.5 and +0.5 for fish of the February-cohort (e.g., Fig. 16b) and September-cohort (e.g., Fig. 17), respectively. YCS estimated in this manner for fish that were caught in November and December was less by one year than that estimated by hindcasting from date of capture using knowledge on the number of biannulus. This is due to the fact that biannual translucent macrozone formation begins in November (see Figs 14 & 15). Thus, YCS was corrected accordingly.

Table 9. Criteria to distinguish between individuals of the February- and September-cohorts of *Oreochromis niloticus* from Lake Zwai. Criteria are based on time of capture and the number of translucent macrozones in otoliths.

Time of capture	Number of translucent macrozones	
	Even	Odd
November — June	February-cohort (e.g. Fig. 16a)	September-cohort (e.g. Fig. 17)
July — October	September-cohort (e.g. Fig. 16c)	February-cohort (e.g. Fig. 16b)

Age determination and growth estimation

The radius of otoliths and TL were significantly (ANOVA, $p = 0.001$) correlated in *O. niloticus* from Lake Zwai (Fig. 19a) indicating a close synchronisation between somatic tissue and otolith growth. There was a relatively larger variance in the fish length—otolith size relationship at fish lengths > 225 mm (Fig. 19a). This may be due to small sample size at this length range and/or related to the onset of sexual maturation. In addition, TL and the number of translucent macrozones in otoliths were also significantly (ANOVA, $p = 0.001$) correlated (Fig. 19b). Thus, seasonally formed macrozones in otoliths of *O. niloticus* from Lake Zwai could be used to determine the age and growth of the fish based on knowledge on time of capture, time of biannulus formation and time of recruitment cohort.

The first biannulus was considered to be formed in late-August in otoliths from the February-cohort and in the following March in otoliths from the September-cohort (Figs 14 & 15). Thus, at the time of the first biannulus formation fish from the February-cohort were on average 181 days old whereas those from the September-cohort were on average 194 days old. These estimates are comparable to age determined from daily increments in otoliths that had 1 biannulus (see above). In addition, the average number of daily increments between the first and the second biannulus was 176 (standard deviation = 88, $n = 30$) for fish from the February-cohort, whereas 139 (standard deviation = 69, $n = 30$) for those from the September-cohort. These estimates agree with the time lapse from late-August to mid-March (199 days) and from mid-March to late-August (166 days), respectively. The slight discrepancy could be due to underestimation of the number of daily increments because of the difficulty in resolving increments in large otoliths using light microscope.

The second translucent macrozone associated with biannulus may have been formed between November 1995 and February 1996 in otoliths from fish

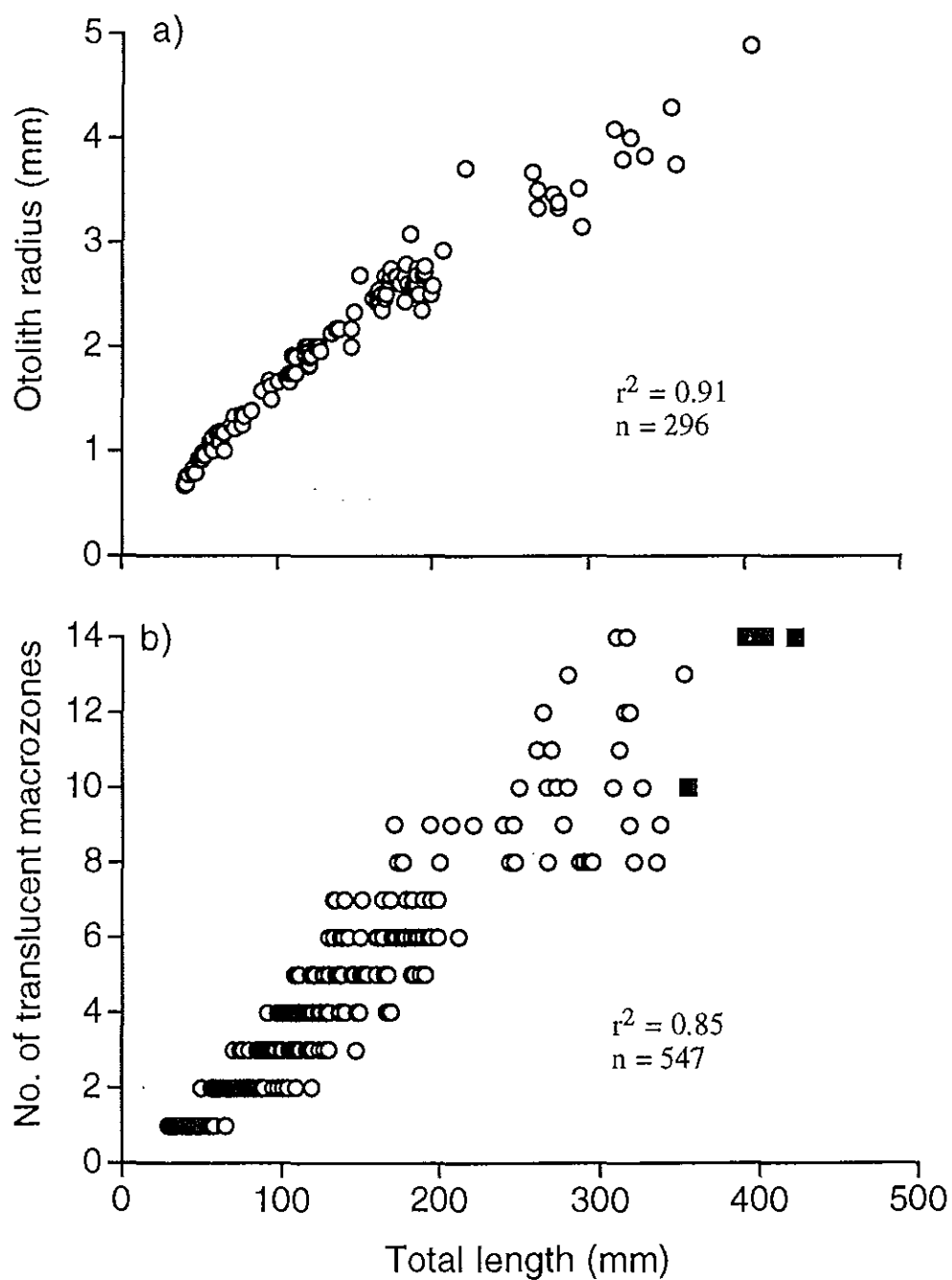


Figure 19. Relationship between total length and a) maximum posterior radius of otoliths, and b) the number of biannual translucent macrozones in otoliths in *Oreochromis niloticus* from Lake Zwai. The number of translucent macrozones in otoliths from large fish (dark squares) may have been under-estimated.

of the February 1995 cohort (e.g., Fig. 16a), but between July and early-August 1996 in otoliths from the September 1995 cohort. These fish were on average 391 d old (standard deviation = 25). In addition, the translucent macrozone associated with the third biannulus was just completed in late-August 1996 for fish from the February 1995 cohort (e.g., Fig. 16b) whereas in late-March 1996 in those from the September 1994 cohort. The average age of tilapia with 3 biannuli was estimated to be 558 d (standard deviation = 52). A similar procedure of age determination could be followed for older fish. Biannuli in otoliths from large/old fish however, usually those after the seventh or eighth biannulus, were closely packed and difficult to decipher (e.g., Fig. 17).

It was also found that in tilapia that were caught at the same time, otoliths from the February-cohort had one more biannulus than those from the September-cohort. The reason is the presence of temporal difference in formation of biannulus between fish of the two cohorts. However, fish from the two cohorts that had the same number of biannuli in their otoliths were approximately of the same age (Fig. 20a).

Macrozonal ages which were determined by calculating the time lapse between the median hatch-dates (i.e., 28 February & 2 September) and date of capture were highly correlated with the number of biannuli in otoliths (Fig. 20a). In addition, macrozonal age of a fish was also significantly (ANOVA, $p = 0.0001$) correlated with its microzonal age (Fig. 20b) verifying age determination using macrozone analysis.

The relationship between TL and macrozonal age showed that tilapia of the two cohorts grow at a similar rate (Fig. 21). Therefore, length-at-age estimates were combined for the two cohorts, and are presented in Table 10 for immature fish, in Table 11 for females and in Table 12 for males. These data grouped by number of biannulus are presented in Table 13. Similar data for the fish from Lake Haiq (K. Alemu & D. Admassu, unpublished manuscript) and

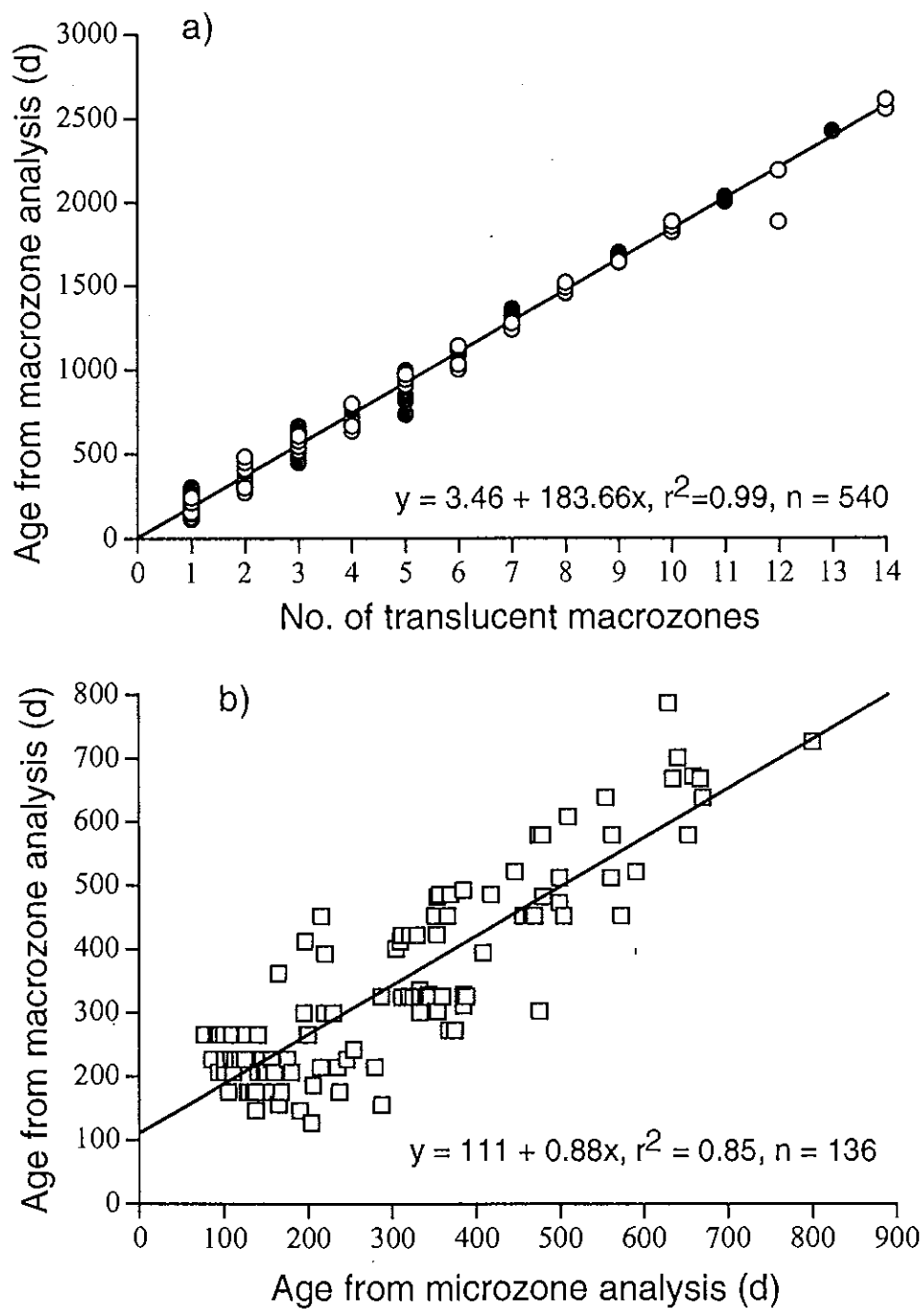


Figure 20. Relationship between macrozonal age and a) the number of biannulus in otoliths, and b) microzonal age in *Oreochromis niloticus* from Lake Zwai.

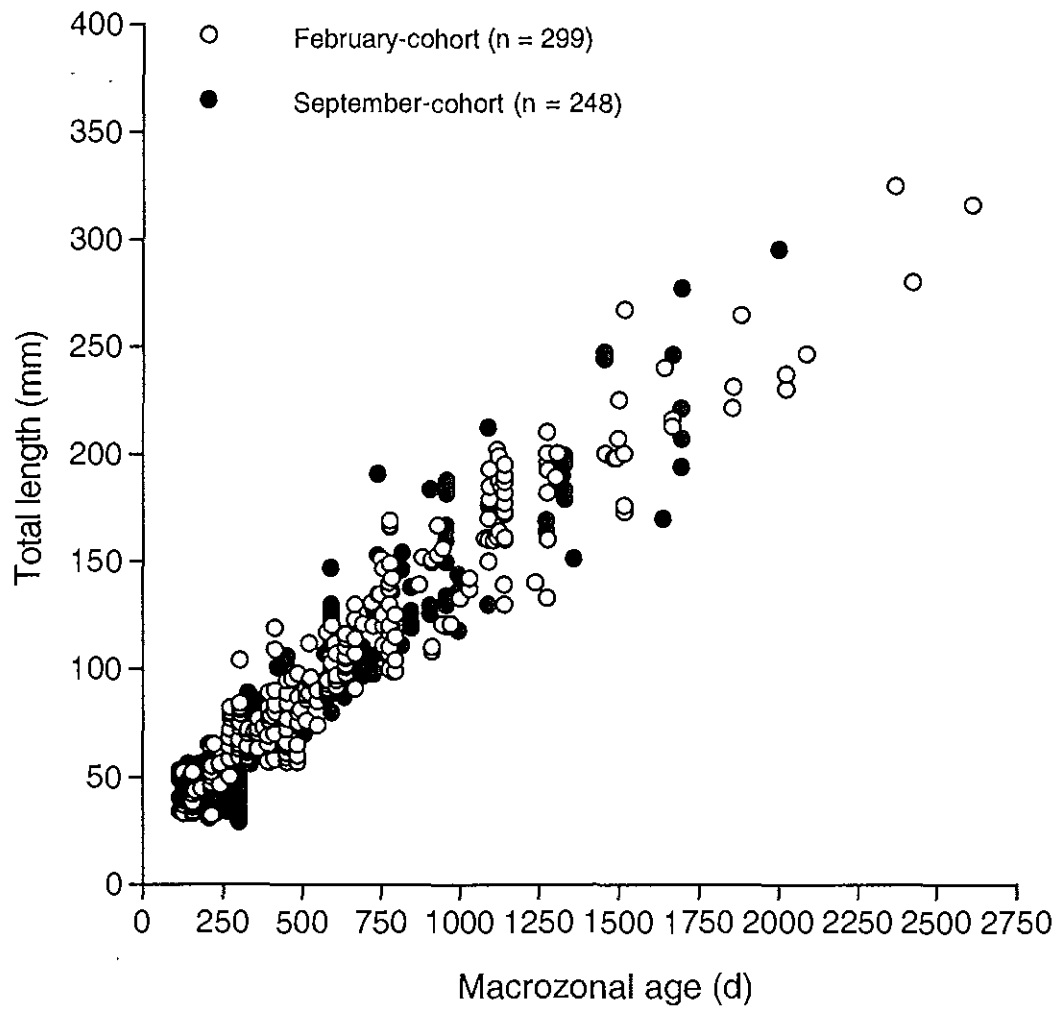


Figure 21. Scatter-plot to show relationship between total length and macrozonal age in February- and September-cohorts of *Oreochromis niloticus* from Lake Zwai.

Table 10. Length-at-age data for immature *Oreochromis niloticus* from Lake Zwai. Age determined from biannuli in sagittal otoliths. NBA = number of biannulus, Edge = relative width and type of macrozone at the edge of otoliths (see text).

NBA	Edge	Sample size	Total length (mm)		Mean age (d)
			Mean	95% CL	
1	o	69	43.5	1.43	163
	*	49	44.5	3.17	184
	+	25	54.8	3.15	215
	++	29	65.0	2.19	223
2	o	53	71.0	2.39	348
	*	10	73.0	8.04	377
	+	24	78.2	4.11	401
	++	14	81.5	6.68	493

Lake Awassa (D. Admassu & J. Casselman, unpublished manuscript) are also presented in Tables 14 and 15, respectively. Evidently, fish with otoliths that had one, two, three, etc. biannuli were each approximately half-year older. The data in Tables 13, 14 and 15 show that length attained at a given age by both females and males tilapia was larger in Lake Haiq than either in Awassa or in Zwai, and also larger in Awassa than in Zwai. The result suggests that the fish grows relatively faster in Lake Haiq and slowest in Lake Zwai.

von Bertalanffy growth equations that were fitted using mean length-at-mean age data (Tables 13, 14 and 15) were as follows:

Zwai tilapia:

$$\text{Females: } L_t = 301.9 [(1 - e^{-0.25(t + 0.27)})];$$

$$\text{Males: } L_t = 308.1 [(1 - e^{-0.27(t + 0.12)})],$$

Awassa tilapia:

$$L_t = 315.8 [(1 - e^{-0.35(t - 0.03)})]$$

Haiq tilapia:

Females: $L_t = 344.5 [(1 - e^{-0.45(t + 0.22)})]$;

Males: $L_t = 366.3 [(1 - e^{-0.40(t + 0.15)})]$

where L_t = mean total length, mm, at age t ; t = age in yr.

Table 11. Length-at-age data for females *Oreochromis niloticus* from Lake Zwai. Age determined from biannuli in sagittal otoliths. NBA = number of biannulus, Edge = relative width and type of macrozone at the edge of otoliths (see text).

NBA	Edge	Sample size	Total length (mm)		Mean age (d)
			Mean	95% CL	
2	++	2	83.5		412
3	o	9	95.4	4.07	467
	+	6	103.1	8.55	590
	++	11	112.0	8.11	603
4	o	14	120.9	5.98	694
	+	6	134.7	16.31	747
	++	8	137.0	15.55	777
5	o	8	139.0	15.9	872
	+	9	153.1	19.83	931
	++	5	167.0	15.71	931
6	o	6	159.7	11.43	1106
	+	9	161.4	15.46	1118
	++	5	202.0	10.06	1119
7	+	4	189.0	25.3	1303
8	o	4	198.0	49.2	1486
9	all	4	212.7	49.2	1668
10	o	2	221.5		1857
11	o	2	230.2		2023
13§	+	1	325.0		2368§

§ could be more

Table 12. Length-at-age data for males *Oreochromis niloticus* from Lake Zwai. Age determined from biannuli in sagittal otoliths. NBA = number of biannulus, Edge = relative width and type of macrozone at the edge of otoliths (see text).

NBA	Edge	Sample size	Total length (mm)		Mean age (d)
			Mean	95% CL	
2	+	9	90.0	19.3	412
3	o	15	96.1	5.7	524
	*	9	105.3	4.3	588
	+	7	117.1	17.4	577
	++	8	120.2	10.6	593
4	o	15	130.8	4.3	722
	*	6	134.8	13.4	742
	+	9	141.0	5.7	749
	++	5	142.2	23.6	785
5	o	10	152.3	10.9	884
	+	7	156.1	12.1	948
6	o	7	160.7	12.5	1078
	x (others)	6	184.3	5.4	1132
7	o	5	192.3	28.3	1279
	x	5	200.1	28.5	1308
8	o	5	198.1	46.1	1494
	x	5	206.9	42.9	1499
9	all	7	216.1	46.7	1667
10	all	7	231.1	27.5	1857
11	all	5	236.8	30.8	2023
12	o	4	246.2	34.3	2087
13 [§]	o	1	280.0		2426 [§]
14 [§]	o	5	366.0		2612 [§]
16 [§]	o	1	345.0		2902 [§]

[§] could be more

Table 13. Mean length-at-mean age data for females and males tilapia from Lake Zwai indicated by the number of biannulus. TL is total length and CL is confidence limit. Age for males is put in parenthesis if different from that of females. Fish with ≥ 13 biannuli were not used to estimate von Bertalanffy parameters.

Number of biannuli	Females				Males		
	Mean age (yr)	Mean TL (mm)	95% CL (mm)	sample size	Mean TL (mm)	95% CL (mm)	sample size
1 [§]	0.5	52.0	42.5-61.5	172	52.0	42.5-61.5	172
2	1.1	77.4	54.8-100.0	103	78.7	57.5-99.9	110
3	1.5	103.5	79.9-127.1	26	109.7	100.9-118.5	39
4	2.0	130.9	115.4-146.4	28	137.2	115.5-158.9	35
5	2.3(2.5)	153.0	136.6-169.4	22	154.2	127.4-181.0	17
6	3.0(3.1)	174.4	154.9-193.9	20	172.5	147.9-197.1	13
7	3.6	189.0	163.6-214.4	4	196.2	173.1-219.3	10
8	4.1	198.0	152.4-243.6	4	202.5	152.3-252.7	10
9	4.6	212.7	184.5-240.9	4	216.1	169.7-262.8	7
10	5.1	221.5		2	231.1	203.6-258.6	7
11	5.5	230.2		2	236.8	206.0-267.6	5
12	5.7				246.2	211.9-280.5	4
13	6.5(6.6)	325.0			280.0		1
14	7.1				366.0	319.0-396.0	5
16	7.9				345.0		1

[§] sex unidentified

Table 14. Mean length-at-mean age data for females and males tilapia from Lake Haiq indicated by the number of biannulus. TL is total length and CL is confidence limit. Age for males is put in parenthesis if different from that of females. Data from K. Alemu & D. Admassu (unpublished manuscript).

Number of biannuli	Mean age (yr)	Females			Males		
		Mean TL (mm)	95% CL (mm)	Sample size	Mean TL (mm)	95% CL (mm)	sample size
1§	0.4	60.2	56.2-64.2	187	60.2	56.2-64.2	187
2§	0.7	110.0	100.7-119.3	96	110.0	100.7-119.3	96
3	1.3	163.5	149.5-177.5	79	164.4	155.4-173.4	66
4	1.8	205.5	196.5-214.5	61	191.7	183.1-200.3	60
5	2.5(2.2)	239.2	230.4-248.0	55	221.1	214.2-228.0	30
6	2.8(2.7)	280.0	269.8-290.8	23	255.2	243.7-266.7	39
7	3.4(3.2)	283.0	271.7-294.3	12	283.0	266.8-299.2	19
8	4.3(4.0)	286.0	265.0-307.0	3	288.0	268.9-307.1	5

§ sex unidentifiable

Table 15. Mean length-at-mean age data for tilapia from Lake Awassa indicated by the number of biannulus in otoliths. CL is confidence limit. From D. Admassu & J. Casselman (unpublished manuscript) unless indicated otherwise.

Number of biannuli	Mean age (yr)	Total length (mm)		sample size
		Mean	95% CL	
1 [§]	0.6 [§]	60.1 [§]		
2 [§]	1.1 [§]	90.8 [§]		
3	1.6	127.8	118.0-144.0	26
4	2.2	161.5	147.0-199.0	98
5	2.7	203.5	190.1-218.0	60
6	3.2	217.0	216.0-225.0	37
7	3.7	221.1	209.0-235.0	26
8	4.2	239.2	231.0-251.3	19
9	4.5	251.9	248.1-253.0	5
10	5.0	258.7	251.1-262.0	5
11	5.5	268.0		2
12	6.0	276.2		2

[§] calculated from data in Yosef & Casselman (1995).

The von Bertalanffy growth curves that were fitted using the above equations showed that tilapia approach their maximum length at a faster rate in Haiq followed by in Awassa and then in Zwai (Fig. 22). The curves also show that females and males appeared to grow at approximately similar rate up to the age of 3.5 yr in Haiq and 2.5 yr in Zwai after which males grew slightly faster.

The above equations are based on growth data grouped on half-year interval, therefore, the estimated parameters K and t_0 are not on annual basis. The equations, however, can be converted to describe growth on yearly basis by multiplying K by 2, and by dividing the term $(t - t_0)$ by 2 (e.g., Robben &

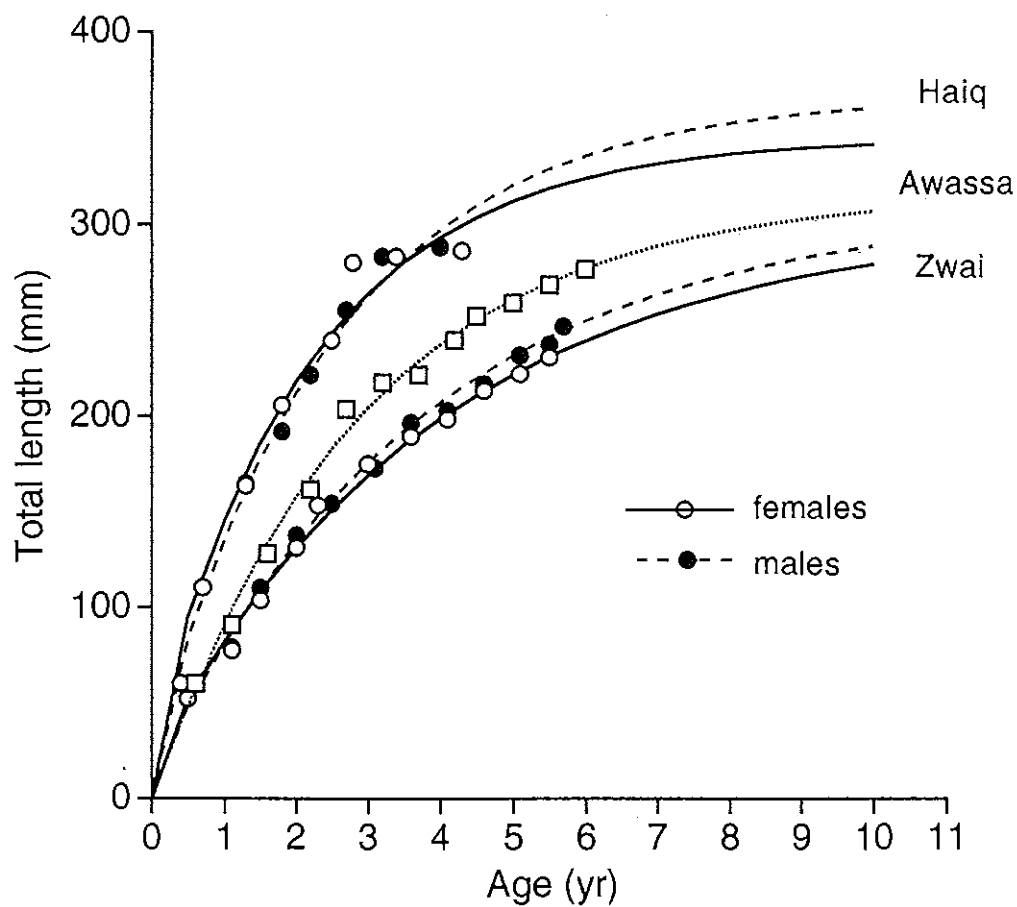


Figure 22. von Bertalanffy growth curves fitted to data on mean length (mm) at mean age (yr) of females and males *Oreochromis niloticus* from Lakes Awassa, Haiq and Zwai. Data were not separated by sex for Awassa fish.

Thys van den Audenaerde, 1984). Thus, for instance, the annual growth equation for Zwai females was:

$$L_t = 301.9 [(1 - e^{-0.50((t + 0.27)/2)}].$$

The same was done for the other equations, and the values of L_∞ and K of *O. niloticus* populations in this study, and also those of other *O. niloticus* populations, are presented in Table 16.

L_∞ and K of *O. niloticus* that were estimated in this study are within the range of values that were reported earlier for the same species in other water bodies (Table 16). The estimated L_∞ values were smaller than the size of the largest fish caught in this study (in Lake Zwai, for instance, largest female: 325 mm; largest male: 421 mm). In comparing the Ethiopian tilapia populations, L_∞ and growth coefficient of the Lake Zwai population were smaller than those of either Lake Haiq or Awassa population. The values were largest for the fish from Lake Haiq. Growth parameters of Awassa fish estimated earlier (Admassu, 1989) may have been biased, because large/old fish were lacking in that analysis (see Admassu, 1989). Based on a recent study (Wudneh, 1998), growth parameters of the fish in Lake Tana, Ethiopia (Fig. 1), are comparable to that in Lake Haiq, but K was larger for Lake Haiq population than for Lake Tana population (Table 16) indicating that the population in Lake Haiq approaches its maximum size at a more rapid rate.

Growth performance index (Φ' , Munro & Pauly, 1983), which was calculated based on K converted to per yr basis, showed that growth performance of the fish, among the populations listed in Table 16, is in the lower end of the range in Lake Zwai, and intermediate in Lakes Awassa and Tana. Growth performance index of *O. niloticus* in Lake Haiq was among the largest, but not as large as that of *O. niloticus* in Lakes Kainji and Nasser (Table 16).

Table 16. Estimates of von Bertalanffy growth parameters and growth performance index (Φ') of various populations of *Oreochromis niloticus*.

Lake/Locality	Sex	L_{∞} (mm)	K (yr ⁻¹)	Φ'	Reference & data source
Zwai	females	301.9	0.50	2.7	present study
	males	308.1	0.54	2.7	present study
Haiq	females	344.5	0.90	3.0	K. Alemu & D. Admassu, unpubl.
	males	366.3	0.80	3.0	K. Alemu & D. Admassu, unpubl.
Awassa	females	294.0	0.38	2.5	Admassu, 1989
	males	300.0	0.46	2.6	Admassu, 1989
	both	315.8	0.70	2.8	D. Admassu & J. Casselman, unpubl.
Tana	both	357.0	0.50	2.8	Wudneh, 1998
Itasy	both	715.0	0.14	2.8	Moreau, 1979 in Getabu, 1992
Kainji	both	704.0	0.41	3.3	Moreau, 1979 in Getabu, 1992
Nasser	both	578.0	0.55	3.3	Moreau, 1979 in Getabu, 1992
Mobutu	both	488.0	0.50	3.1	Moreau, 1979 in Getabu, 1992
Nyanza Gulf (Victoria)	both	646.0	0.25	3.0	Getabu, 1992
Egypt (pond)	both	314.3	0.69	2.8	Jensen, 1957
Syria	both	268.0	0.47	2.5	El Bolock & Koura, 1961
Chad	both	399.6	0.42	2.8	Placke <i>et al.</i> , 1964 in Fryer & Iles, 1972

Discussion

Translucent macrozone associated with biannulus in otoliths of *O. niloticus* from Lake Zwai was formed between July and early-August and between late-November and February. Biannulus formation was believed to be completed in mid-March and in late-August, because the translucent macrozone was delineated by a narrow opaque macrozone in these periods. The same was found for the immature fish in Lake Zwai (Admassu, accepted). Biannual otolith growth cycle has also been found in the same species from Lake Awassa (Admassu, 1989; Yosef and Casselman, 1995) and Lake Haiq (K. Alemu & D. Admassu, unpublished manuscript). Growth checks in scales of the species from Lake Awassa are found to be formed during December and January as well as during June and July (Admassu, 1989). Biannulus is formed between late-February and mid-March and in August in otoliths of the fish from Lake Awassa and Lake Haiq, respectively. Other studies (Holden, 1955; Garrod, 1959; Willoughby, 1974; Blake & Blake, 1978; Lecomte *et al.*, 1989) have also shown biannual growth cycle in calcified tissues from tropical fish. In Lake Kainji, Nigeria, for instance, checks are formed in January and during June to July each year in vertebrae of *Synodontis* spp. (Willoughby, 1974) and in operculum of *Labeo senegalensis* Peters (Blake & Blake, 1978). Biannual growth and reproductive cycles have also been observed in some temperate fish species (Moksness & Fossum, 1991). Differences in otolith microstructure in these temperate fish have been used to distinguish between individuals from the two spawning cohorts (Moksness & Fossum, 1991; May & Jenkins, 1992).

Seasonal fluctuations in water temperature and food quality and quantity, and spawning activity may be associated with biannulus formation in otoliths of *O. niloticus*. Generally, fluctuation in water temperature in the tropics is not drastic. The difference between the yearly maximum and minimum temperature of Lake Zwai was also only between 5 and 6°C. However, temperature

fluctuation of this magnitude may be sufficient to cause variations in the growth of *O. niloticus* and its otoliths. The same was confirmed by our experimental study (Chapter IV), because a temperature fluctuation of about 3 to 5°C, particularly within the range 16.6 to 24°C, had affected the growth of the fish and its otoliths. In addition, temperatures below 20°C had caused a reduction in body growth, and also in the formation of translucent macrozones in otoliths. It has previously been suggested that tilapia growth is reduced (Caulton, 1982), and activity and feeding are slowed (Chervinsky, 1982) at temperatures around 20°C. Thus, low water temperature may be one of the factors associated with the formation of biannulus in otoliths of *O. niloticus* in Lake Zwai. Temperature is also considered to be the most important factor associated with formation of translucent macrozones in otoliths, and of checks in scales, of the species from Lake Awassa (Admassu, 1989; Yosef and Casselman, 1995) and from Lake Haiq (K. Alemu & D. Admassu, unpublished manuscript). In Lake Kainji, Nigeria, Willoughby (1974) and Blake & Blake (1978) reported that one of the growth checks in the calcified tissues of the fishes they studied was formed during the period of minimum water temperature, whereas the other was formed during the period of limited food supply.

Other factors such as food quality and quantity, are considered important in formation of biannulus in otoliths of *O. niloticus* (e.g., Admassu, 1989; Yosef & Casselman, 1995). The same could be true in Lake Zwai, because Abebe & Getachew (1992) showed that the quality of the food (expressed in protein to energy ratio) consumed by tilapia in October, November, December, January and in May is not optimum to support growth. There is a time lag for the effect of low quality food to be reflected in reduced growth (Getachew, 1987). Thus, the periods of poor food quality approximately coincide with the two periods of translucent macrozone formation. Hence fluctuation in food quality may be important in biannulus formation in *O. niloticus* in Lake Zwai.

Formation of translucent macrozones in *O. niloticus* in Lakes Awassa, Haiq and Zwai was also coincident with the major spawning seasons of the fish. Thus, spawning could be important in biannulus formation in this fish. *O. niloticus* is a maternal mouth-brooder. Males, in addition to fertilising several females per spawning season, they are also occupied in building and guarding spawning grounds (Fryer & Iles, 1972). Thus, the quantity of the food consumed may be reduced when the fish are engaged in spawning activity. In addition, spawning can have a direct effect on growth, because it drains metabolic resources for the production of eggs and sperm (Fryer & Iles, 1972; Balarin & Hatton, 1979; Jalabert & Zohar, 1982). Our experimental study (Chapter IV) also showed that translucent macrozone was formed in otoliths of fish that had gonads containing well developed eggs or sperm, but not in otoliths of immature fish. Reproduction has been considered as one of the factors responsible for the formation of annuli in the closely related *O. andersonii* in the Okavango Delta, Botswana (Booth *et al.*, 1995). Several other workers have also suggested the importance of spawning in growth check formation in tropical (Garrod, 1959; Krishnaya, 1963; Balon, 1972; Payne, 1976; Nekrasov, 1980) and in some temperate (Balon, 1972) fishes. Nevertheless, spawning does not explain biannulus formation in immature fish (Admassu, accepted). The same was found for immature tilapia in other Ethiopian lakes (Yosef and Casselman, 1995; K. Alemu & D. Admassu, unpublished manuscript).

Hatch-date distribution determined from microzonal age suggest that *O. niloticus* in Lake Zwai spawns over an extended period. This could be the reason why macrozonal and microzonal ages differed by two to three months which is approximately half of the range of the major spawning season. Therefore, using a fixed median hatch-date could have resulted in a biased estimate of macrozonal age. A similar result has been observed for the species in

Lakes Awassa (Yosef & Casselman, 1995) and Haiq (K. Alemu & D. Admassu, unpublished manuscript). K. Alemu & D. Admassu (unpublished manuscript) minimised the difference between macrozonal and microzonal ages using actual hatch-dates of individual fish estimated using measurements on the radius of the first biannulus in a regression relating otolith radius and microzonal age. This could not be applied for Zwai fish, because the procedure did not give any better estimates of age (data not shown). The reason could be the relatively weaker correlation ($r^2 = 0.48$) between otolith radius and microzonal age in fish that had one biannulus.

The study showed that annually two major recruits are produced. Although fish from the two annual cohorts grow at approximately similar rate, it was possible to distinguish between them so that age and growth of each cohort can be determined separately. The first biannulus is formed in August in otoliths from the February-cohort whereas in March of the following calendar year in those from the September-cohort. This would result in a difference in the number of biannuli at capture between fish of the two cohorts. Thus, at a given capture date and considering the same year class, fish of the earlier cohort would have one more biannulus than those recruited later in the year. In addition, the fish of the first cohort are about 5 to 6 months older than those of the second cohort. However, regardless of cohort, the fish are of similar age if they have the same number of biannulus. The result is generally similar to that found for the species in Lake Awassa (Yosef & Casselman, 1995; D. Admassu & J. Casselman, unpublished manuscript) and in Lake Haiq (K. Alemu & D. Admassu, unpublished manuscript).

Some general criteria were developed to distinguish fish from the two cohorts based on the number of biannulus and knowledge on date of capture. As compared with Yosef & Casselman's procedure, the system proposed in this study is simple, and large number of individuals can be treated at the same time.

However, it could not be applied to otolith samples whose edge condition at capture was different from that of the majority. Since these are generally small in number, they can be excluded from the analysis as they do not seriously affect the procedure of age assessment for the population in general. However, detailed future study is required to explain why otolith edge condition differs in samples taken at the same time. Hatch-dates could then be determined more accurately for a more accurate age interpretation. In addition, accurate hatch-dates are essential to study differential survival among cohorts that recruit to the fishery at different times.

O. niloticus in Lake Zwai with one biannulus were about 196 days old and had an average length of 52 mm. Tilapia with one biannulus are on average 202 days old and 60.1 mm in length in Lake Awassa (Yosef & Casselman, 1995) whereas 60.2 mm and 116 days old in Lake Haiq (K. Alemu & D. Admassu, unpublished manuscript). In either of these three lakes, tilapia with two biannuli are approximately one year old by which time they grow to an average of 78.1, 90.8 and 110 mm, respectively, in Lake Zwai, Awassa and Haiq. The growth of juvenile *O. niloticus* in Lakes Zwai, Chamo and Langeno was found to be similar during the first month post-hatch, however, growth between 30 and 250 d of age was intermediate in Zwai and fastest in Chamo (Chapter III). At older ages, Lake Zwai fish attains relatively smaller length-at-age than the fish either in Lake Awassa or Lake Haiq. Thus, the fish grows relatively slowly in Lake Zwai than either in Awassa, Haiq, or Chamo, but relatively better in Zwai than in Langeno. The same was suggested by the von Bertalanffy growth parameters that were estimated in this study. Calculation of length-at-age using the von Bertalanffy parameters suggest that Zwai fish (average for the sexes) grow to 81.3, 132.5, 172.0, 202.3, and 225.9 mm at an age of 1, 2, 3, 4 and 5 yr, respectively. The corresponding length-at-age for Awassa fish are 90.9, 157.3,

204.1, 237.1 and 260.3 mm, and for Haiq fish are 140.3, 214.5, 263.0, 294.8 and 315.6 mm.

Genetic-based differences in growth rate between the Ethiopian *O. niloticus* populations can be ruled out because they are found to be genetically similar (Seyoum, 1989). However, differences in food quality, feeding rate and other factors could be important. Abebe & Getachew (1992) reported that the condition of Lake Zwai population is inferior to that of Lake Awassa population which they attributed to the inferior quality food consumed by Zwai fish. In addition, the feeding rate of Lake Zwai tilapia is much slower than that of Lake Awassa population (Tadesse, 1988; Getachew, 1987 & 1989). Furthermore, Tadesse *et al.* (in press), who found lower contents of lipids and fatty acids in muscle tissue of tilapia from Zwai and Awassa than from Haiq, pointed out that the quality of food consumed by Haiq fish is much superior to that consumed by either Awassa or Zwai fish. Rapid growth of juvenile tilapia in Lake Chamo than in any other lake was also attributed mainly to better quality food and to warm temperature and associated factors (Chapter III). However, temperature may not explain growth differences between tilapia in Zwai, Awassa and Haiq, because the temperature regime of these lakes is more or less similar (Fig. 3b).

The asymptotic length (L_{∞}) of Zwai tilapia was less than the maximum length actually caught during sampling. According to the von Bertalanffy growth model, L_{∞} is an average theoretical maximum size to which the fishes grow (von Bertalanffy, 1938). Therefore, as is the case in several other species of tilapia (Table 15: Admassu, 1989; Fryer & Iles, 1972), it is likely to find some individuals growing larger than L_{∞} . On the other hand, it is also possible that the L_{∞} values may have been underestimated due to underestimation of age for large fish because of the difficulty in deciphering all biannuli in their otoliths.

The von Bertalanffy curves as well as the observed mean length-at-mean age data show a relatively rapid growth in males than in females after the age of 3.5 yr in Haiq and 2.5 yr in Zwai. In Lake Awassa, males grow more rapidly than females after the second year of life (Admassu, 1989). Male growth superiority has been reported for several other species of tilapia as well (Fryer & Iles, 1972). It could be related to the maternal mouth-brooding habit of the fish forcing females to fast for a longer period, and also to the total egg weight produced during spawning (Fryer & Iles, 1972; Balarin & Hatton, 1979). In addition, genetic difference has also been suggested for growth differences between the sexes (van Someren & Whitehead, 1960). The phenomenon is probably related to the relative growth of the sexes, and also far more complex than it could be dealt with in this study.

Average linear length increments (combined for the sexes) between ages 1 and 4 yr, respectively, were 81.3, 51.2, 39.5 and 30.3 mm in Zwai. The corresponding length increments in Awassa were 90.9, 66.4, 46.8 and 33 mm, and those in Haiq were 140.3, 74.2, 48.5 and 31.8 mm. Length increment in subsequent years was generally small. This increment pattern is generally similar to that of other natural tilapia populations except the stunted ones (Fryer & Iles, 1972). First year's growth of *O. niloticus* in various water bodies, for instance, was found to be between 92 and 134 mm (Jensen, 1957; El Bolock & Koura, 1961; Placke *et al.*, 1964 in Fryer & Iles, 1972).

The oldest fish was about 4 yr in Haiq, 6 yr in Awassa and close to 8 yr in Zwai. However, these ages do not necessarily indicate life span of the fish in the respective lakes. Large, and probably old, fish in Haiq experience massive mortality due to anoxic conditions occurring mostly between November and January in this lake. Thus, large-sized fish were not well represented in the sample. In addition, it was difficult to determine age for large/old fish from Zwai and Awassa. However, except that of Haiq fish, the maximum ages found in this

study are within the range of maximum ages recorded for other tilapia populations (Table 14: Fryer & Iles, 1972).

In summary, the study showed that translucent macrozone associated with biannulus in otoliths of *O. niloticus* in Lake Zwai is formed during July and early-August, and also during late-November and February. This coincided with seasonally cold water temperature, spawning activity, and presumably with low food quality and quantity. Formation of biannulus was considered completed in mid-March and late-August each year. Hatch-date distribution obtained from microzonal ages suggested two annual spawning peaks, and also median hatch-dates of 28 February and 2 September. Biannulus interpretation provided not only a means to determine age, but also to discriminate between fish from the two major annual recruitment cohorts. In addition, results from biannulus interpretation were verified by microstructure analysis. Thus, biannulus interpretation to determine age by differentiating biannual recruitment, that was proposed by Yosef & Casselman (1995) for immature *O. niloticus* in Lake Awassa, is applicable to the fish in Lake Zwai. The estimated growth parameters of the fish in Zwai were within the range of values for other *O. niloticus* populations. Generally however, the growth of *O. niloticus* in Lake Zwai was found to be slower than that of fish either in Lake Awassa or Lake Haiq.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Summary

The growth of juvenile *O. niloticus* in Lakes Zwai, Langeno and Chamo was well described by the Gompertz growth model. The models that were fitted to length and microzonal age data were as follows:

for juvenile tilapia from Lake Zwai:

$$\text{Ln}(\text{TL}) = 2.33 + 1.8939[(1 - e^{(-0.0106t)})], r^2 = 0.93, n = 210,$$

for juvenile tilapia from Lake Langeno:

$$\text{Ln}(\text{TL}) = 2.40 + 1.6806[(1 - e^{(-0.0112t)})], r^2 = 0.89, n = 198,$$

for juvenile tilapia from Lake Chamo:

$$\text{Ln}(\text{TL}) = 2.25 + 2.0650[(1 - e^{(-0.0167t)})], r^2 = 0.87, n = 129,$$

where TL is in mm and t is in d.

Growth estimated using the Gompertz model agreed very closely with growth back-calculated from otolith microstructure. Thus, results from the two methods corroborated each other. Rate of linear increase through the first 250 d post-hatch was fastest in Lake Chamo (0.39 mm·d⁻¹), intermediate in Lake Zwai (0.20 mm·d⁻¹) and slowest in Lake Langeno (0.16 mm·d⁻¹). Indirect supportive evidence is found in that the condition factor of the fish in Lake Chamo (mean±95% CL = 1.77±0.15) was largest followed by that from Zwai (1.46±0.11) and from Langeno (1.29±0.19). In addition, juvenile *O. niloticus* from Chamo have smaller otoliths than similar-sized fish from Zwai and Langeno indicating that the fish from Chamo grow more rapidly. Rapid growth of juvenile *O. niloticus* in Lake Chamo could be attributed to high temperature and factors associated with it, and to a better quality food in this lake.

In addition, the influence of differences in predation and fishing intensities can not be ruled out.

The experimental study on the effect of temperature on otolith macrozonation and somatic tissue growth showed that a translucent macrozone was formed in otoliths and somatic tissue growth was reduced in tilapia that were transferred from 24°C to slightly lower temperature treatments. In contrast, opaque macrozone was formed in otoliths and somatic tissue growth increased when tilapia are transferred from 24°C to higher temperature treatments. The results suggest that a reduction in temperature of about 3 to 5°C may reduce the growth of tilapia and their otoliths, with an associated formation of translucent macrozones. The response of tropical fish, particularly thermophilic ones such as tilapia (Caulton, 1982), to subtle temperature fluctuations could be significant as they are normally adapted to high temperatures. Thus, this finding confirms our belief that the observed temperature fluctuation in Lake Zwai is sufficient to cause biannulus formation in otoliths of the fish. The same has been concluded for the fish in Lakes Awassa and Haiq. In addition, the results also showed that otolith and somatic tissue growth in *O. niloticus* are synchronised. Several fish in the high temperature transfer experiment had ripening or ripe gonads, and otoliths from these fish had deposited translucent macrozones. This was in contrast to otoliths from immature fish which had deposited more opaque material. The result confirms previous suggestions that sexual maturation and gonadal development may also be important in the formation of checks and translucent macrozones in otoliths and other calcified tissues of tropical fish.

This study demonstrated that two translucent macrozones are formed in otoliths of *O. niloticus* in Lake Zwai. Since these translucent macrozones were similar in appearance and could not be differentiated, each was considered to be associated with biannulus. Translucent macrozone was formed between July

and early-August and between late-November and February. Biannulus formation is believed to be completed in mid-March and also in late-August, because the translucent macrozone was delineated by a narrow opaque macrozone in these periods.

Seasonal growth cycle in the otoliths of *O. niloticus* in Lake Zwai was connected to fluctuations in temperature, food quantity and quality, and to intensive spawning activity. These factors appeared to overlap in time, thus, they might interact to cause biannulus formation in otoliths.

O. niloticus had two spawning peaks, thus two major annual cohorts, in Lake Zwai. The estimated median hatch-dates were 28 February and 2 September for the first and the second annual cohort, respectively. The first biannulus was found to be formed at different times of the year in otoliths from fish of the two cohorts. Hence, at a given date of capture, fish from the February-cohort had one more biannulus than those from the September-cohort of the same year-class. Therefore, knowledge on the number of biannulus and date of capture provided a means to discriminate between fish from the two cohorts. The difference in age between fish of the two cohorts of a given year was 5 to 6 months on average, but fish that had the same number of biannulus were approximately the same age. Ages determined in this manner were highly correlated with ages determined from counting the microstructure of otoliths. Thus, Yosef & Casselman's (1995) method of age determination using biannulus and differentiating biannual recruitment is applicable to the fish in this study.

Average linear length increments (combined for the sexes) between ages 1 and 4 yr, respectively, were 81.3, 51.2, 39.5 and 30.3 mm in Zwai. The corresponding length increments in Awassa were 90.9, 66.4, 46.8 and 33 mm, and those in Haiq were 140.3, 74.2, 48.5 and 31.8 mm. Length increment in subsequent years was generally small.

Mean total length (mm) of females *O. niloticus* in Lake Zwai that had one to ten biannuli, respectively, were as follows: 52, 77.4, 103.5, 130.9, 153, 174.4, 189, 198, 212.7, and 221.5. The same data for males were 52, 78.7, 109.7, 137.2, 154.2, 172.5, 196.2, 202.5, 216.1 and 231.1. The corresponding length data for the fish in Lake Awassa (combined for the sexes) were 60.1, 90.8, 127.8, 161.5, 203.5, 217, 221.1, 239.2, 251.9 and 258.7, respectively. Mean length of females *O. niloticus* in Lake Haiq that had one to eight biannuli, respectively, were 60.2, 110, 163.5, 205.5, 239.2, 280, 283 and 286. Those of males were 60.2, 110, 164.4, 191.7, 221.1, 255.2, 283 and 288. In each lake fish with one biannulus were about 0.5 yr old, and those with one, two, three, etc. biannuli were each half year older. Thus, the fish grows faster in Lake Haiq than either in Awassa or Zwai. The growth of adult *O. niloticus* in these Lakes was described by von Bertalanffy model. The parameter L_{∞} ranged from 301.9 to 366.3 mm, and K ranged from 0.50 to 0.90 yr⁻¹, both parameters being largest for fish in Lake Haiq and smallest for fish in Lake Zwai (Table 16). Thus, the rate at which *O. niloticus* approaches L_{∞} was most rapid in Lake Haiq, intermediate in Lake Awassa and least in Lake Zwai.

Conclusions

The following were concluded based on the results from the study:

- 1). Regular seasonal growth cycle exists in otoliths of *O. niloticus* in Lake Zwai. Translucent macrozone is formed during July to early-August and also during late-November to February. Opaque macrozone is formed during the rest of the year. Each biannual translucent macrozone is considered to contain biannulus.
- 2). Biannulus formation appears associated with seasonally cold water temperature, poor food quality and quantity, and also with intensive spawning

activity. These factors are believed to reduce the growth of the fish with a consequent formation of biannulus in otoliths.

3). Subtle changes in temperature (3 to 5°C) can affect the growth of *O. niloticus* and its otoliths. A reduction in temperature from 24°C to 20°C can result in the formation of translucent macrozones in otoliths. Thus, the observed fluctuation in temperature at Lake Zwai may be sufficient to cause biannulus formation.

4). The number of biannulus in otoliths of *O. niloticus* in Lake Zwai, together with knowledge on date of capture, can be used not only to determine the age of the fish, but also to identify individuals from a specific recruitment cohort within a year.

5). Two biannuli represent one year of growth, and the first biannulus is formed at an average age of 0.5 yr. Thus, *O. niloticus* in Lake Zwai with otoliths having 1, 2, 3, etc. biannuli are about 0.5, 1, 1.5 etc. years old, respectively.

6). The growth of juvenile *O. niloticus* is most rapid in Lake Chamo, intermediate in Lake Zwai and slowest in Lake Langeno. Superior growth of juveniles in Lake Chamo is attributed to high temperature and factors associated with it, and also to a better quality food consumed in this lake than either in Lake Zwai or Lake Langeno.

7). Mean length at age data determined based on biannulus interpretation showed that growth rate of *O. niloticus* population is fastest in Lake Haiq, intermediate in Lake Awassa and least in Lake Zwai. The difference in growth of *O. niloticus* among these lakes is attributable to differences in food quality, this being superior in Lake Haiq and most inferior in Lake Zwai.

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