Trophic analysis of Lake Awassa using mass-balance Ecopath model

By

Tadesse Fetahi

A THESIS PRESENTED TO
THE SCHOOL OF GRADUATE STUDIES
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FOR THE DEGREE OF MASTER OF SCIENCE IN BIOLOGY

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“*Das Wahre ist das Ganze*”

The truth is the whole
(Hegel, 1807)

Dedicated to

Team work like football, unlike …

Table of Contents

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List of Tables

Pages

List of Figures

Abstract

Comparatively Lake Awassa is one of the most thoroughly studied lakes in Ethiopia. However no attempt was made to bring the available information together in order to see the foodweb relationship in the ecosystem. Perhaps one of the plausible reasons for not modeling lakes till now is lack of comprehensive and easy-to-use model. A friendly software model, Ecopath with Ecosim (EwE), was constructed for Lake Awassa using different published and unpublished data that were originally studied in the lake. Several parameters were also estimated from the present study such as primary productivity, phytoplankton biomass, Tilapia biomass and zoobenthos. The study was conducted between November 2003-August 2004. Thirteen functional groups including two ontogenic groups were used in the present analysis to see the trophic relationship and energy flow. The results of the model give an overview of the resources found in the lake simultaneously and reveal the degree of interactions. The consumers are heavily exploited in the system as shown by high ecotrophic efficiency while the producers including detritus are under exploited. Hence energy transfer from lower trophic level seems very low. Flows from detritus were as important as flows from phytoplankton, designating the importance of both detritus and grazing food chain in the system. Mixed Trophic Impact (MTI) analyses indicate that phytoplankton and detritus have positive impact on most other groups. On the other hand, herbivore zooplankton and tilapia had negative impact on phytoplankton, the former being stronger. Lake Awassa has a low ecological efficiency with a value of 0.001. System primary production/ respiration (P/R) ratio of Lake Awassa is 9.844 showing the lake is at developmental stage or a young ecosystem, warning that extra care should be given to human interventions. However, since production is high the lake can contribute in the food self-sufficiency program of the country. This trophic model analysis also enables us to confirm the previous works and pinpoint the critical research gaps. Production, biomass, mortality, feeding, reproduction etc for zoobenthos, *Garra* sp., *Labeobarbus amphigrama* and *Aplocheilichtyes* sp. are open to research. The biomass, mortality etc of *Labeobarbus intermidius* should also be studied.

Key words: Lake Awassa, Ecopath with Ecosim, modeling, trophic interaction, aquatic ecosystems

1. Background and Justification

Comparatively Lake Awassa is one of the most thoroughly studied lakes in Ethiopia. Many investigators have studied different aspects of the lake beginning long ago. Elizabeth Kebede and Amha Belay (1994) worked on phytoplankton and identified a total of 100 species where green algae (48%) and blue green (30%) were the dominant taxa. The dominant species were *Lyngbya nyassae, Botryococcus braunii* and *Microcystis* sp., but they are less nutritious food to herbivore animals. The former authors and Demeke Kifle and Amha Belay (1990) also studied the biomass and primary productivity of the phytoplankton. The hetrotrophic bacterioplankton of Lake Awassa was studied by Zinabu Gebre-Mariam (1988). The potential effect of Awassa Textile effluent on phytoplankton and fish was studied by Zinabu Gebre-Mariam and Zerihun Desta (2002).

Zooplankton of Lake Awassa was mainly studied by Seyoum Mengistou (1989) who identified Copepoda (*Mesocycolops, Thermocyclops*), Cladocera (*Diaphanosoma*) and Rotifera (*Brachionus and Keratella*) as the common zooplankters. Cyclopoid crustaceans were the dominant zooplankton as in many other tropical African lakes. The highest zooplankton biomass was recorded in September in 1986 (114 mg Dw m^{-3}) and November in 1987(103.3 mg Dw m^{-3}).

Herbivore zooplankton grazers (*Diaphanosoma, Thermocyclops and copepodites*) in Lake Awassa were inefficient in utilizing phytoplankton due to their large size and less nutritious value (Seyoum Mengistou, 1989). Taylor and Zinabu Gebre Mariam (1989), however, suggested that rotifers and ciliates were the important grazers of nano-plankton and were in turn eaten by the cyclopoid copepods. Copepods are intractable to predators. Hence Seyoum Mengistou (1989) hypothesized that carnivore zooplankton in Lake Awassa is a sink and not a link to higher trophic level.

Bentic organisms of Lake Awassa were studied by Tilahun Kibret and Harrison (1989). Accordingly Nematoda, Ostracoda and Chironomidae were some of the groups identified. However no fauna was observed beyond the eight meter isobath, leaving large portion of the bottom uncolonized and unutilized. The authors stated that macrophyte has a wider coverage in the littoral part of the lake and is more available in the rainy season.

The piscivore *Clarias gariepinus* in Lake Awassa mainly feeds on *Oreochromis niloticus* but it also consumes *Labeobarbus* species and *Garra* species (Elias Dadebo, 2000). The cyprinid large *Labeobarbus* (*Labeobarbus intermidius*) feeds on insects, macrophyte fruits, fish and mollusks. *O. niloticus* were the most common fish eaten by the *Labeobarbus intermidius* in Lake Awassa (Demeke Admassu and Elias Dadebo, 1997).

O. niloticus in Lake Awassa has a distinct biannual breeding activity being intensive during January to March and less intensive during July to September (Demeke Admassu, 1996). Phytoplankton was invariably almost the sole food item of *O. niloticus* above 25-30mm, whereas the fry is omnivorous feeding on benthic organisms, zooplankton and phytoplankton (Getachew Teferra and Fernando, 1989; Tudorancea *et al.*, 1988).

In Lake Awassa, fishing efforts have increased by fivefold and landings by nearly tenfold since the last two decades (LFDP, 1993, 1997). Among the three commercially exploited species in the lake (Tilapia, Catfish and *Labeobarbus*), Tilapia yield accounts for about 85% by weight of the total annual landings. As a result, the Tilapia stock has already shown signs of over-fishing (LFDP, 1998). However, the impact of increased fishing pressure on the ecosystem has not been adequately examined as the components of ecosystem are inextricably linked.

The foremost pattern of an ecosystem is the flow of energy upward through food chains (Odum, 1969; Lecren and Low-McConnell, 1981). Food-web structure also regulates the productivity of lakes other than nutrients and light. Fish yield, for example, strongly depends on primary production of phytoplankton (Melack, 1976; Ahlgren *et al.*, 2000).

Predation mortality is the factor that links the different functional groups (trophic level) in an ecosystem as mortality for a prey is consumption for a predator. Selective predation plays a major role in community composition (de Bernardi, 1981). Piscivores, for example, determine the size and species composition of the planktivorous fish (Tonn and Magnuson, 1982). The latter in turn have immense influence on the size structure and species composition of zooplankton (McQueen and Post, 1988). In a similar context, fishing (removing biomass) from a complex of species feeding on each other also affects the ecosystem (food web) (Pauly *et al.*, 2000).

Changes in species and size composition in one functional group consequently affect the other trophic levels directly or indirectly. Every organism, playing either major or minor roles in an ecosystem, contributes to the proper functioning and health of the ecosystem. Hence preserving the present biodiversity should be given much concern. This is much important in Ethiopia as the diversity of the freshwater biota is poorly known and the rate of degradation of the environment is very high (Abebe Getahun and Stiassny, 1998). Knowledge of the component of the ecosystem is very important in order to maximize resource utilization in a sustainable manner in addition to preserving biodiversity. This requires ecosystem study, which can be easily handled by computer models.

Identifying the major functional groups, estimating B, P/B and Q/B, and understanding their feeding interaction has profound implication in order to understand the complex ecosystem of the lake. Knowledge of trophic fluxes and the efficiency of energy assimilation, transfer and dissipation are also basic to understand ecosystem structure and functioning (Baird & Ulanowicz, 1993). A clear insight of ecosystem relationship in turn helps to devise a sound and correct lake management. However ecosystem work requires the quantification of the trophic relationships between the different groups in the system.

Even though relatively large literature data is available on various elements of Lake Awassa separately, it was not attempted to bring the information together in order to see the foodweb relationship in the lake. Seyoum Mengistou (1989) recommended switching from descriptive to analyses and data synthesis in order to understand the lake as an ecosystem. Perhaps one of the plausible reasons for not modeling lakes till now is lack of comprehensive and easy-to-use model. It also requires estimates of several functional groups of the ecosystem, which in turn require either working with different specialists or review the literature they documented that again needs time and energy.

However in recent years, a user friendly software model called Ecopath with Ecosim (EwE) has been widely used to describe the trophic relationships in aquatic ecosystems on quantitative bases. An Ecopath model is a system of linear equations describing the average flows of mass and energy between the species groups over a specified period of time. It has been applied to different ecosystems ranging from low latitude areas to the tropics and from ponds, rivers and lakes to estuaries, coral reefs, shelves, and the open sea. Ecopath software has more than 1500 registered users representing 120 countries (Pauly *et al.,* 2000).

Once an Ecopath model is constructed for an ecosystem, it is possible to have an overview of the resources simultaneously and the feeding interactions in the ecosystem. Ecopath, for example, can quickly identify an extinction prey group due to heavy consumption by a large number of predator groups (Pauly *et al.,* 2000). Ecopath was applied in Celestun Lagoon, Mexico and it was concluded that the model is a potential tool for use in the management of the lagoon (Vega-Cendejas, 2003).

Moreau *et al.* (1993) has confirmed both the accuracy of previous works (biomass and production estimate) and the underutilization of phytoplankton by fishes with the help of Ecopath model in Lake George, Uganda. Mavuti *et al.* (1996) also noted that by identifying mis-utilizations of food sources in the ecosystems (species groups), Ecopath can contribute to the development of fisheries in African inland waters.

There are good literature data concerning Lake Awassa to quantify most parameters of the model especially biomass, P/B and feeding matrix, and many others were generated during the present study. In addition to the data prerequisite for the model, some ecological change is anticipated in the future due to population growth in the nearby town that may have shoreline modification and augmented fishing pressure (over fishing of Tilapia has already been documented). The industrial effluent that drains to the lake could have also adverse effect on phytoplankton species and composition, which consequently affect the higher trophic level. Because of the above reasons, Lake Awassa was pioneered for this kind of ecosystem modeling work.

Therefore, a mass balance Ecopath with Ecosim Version 5 was constructed to Lake Awassa to understand the trophic interaction of the different functional groups and to figure out the flow of energy in the system.

General Objective

To characterize the food web structure of Lake Awassa ecosystem and to see the efficiency of energy transfer in the system.

Specific Objectives

- To identify the main components of the functional groups at different trophic levels in Lake Awassa;
- To estimate and/or organize literature information on Biomass(B), Primary Production (PP), Production /Biomass ratio (P/B), Consumption /Biomass ratio (Q/B) of the functional groups in Lake Awassa;
- To estimate and/or assemble available literature information on food consumption so as to produce the feeding matrix of each functional group; and
- To produce energy flow diagram and mixed trophic impact for the different functional groups using Ecopath.

2. The study site: Lake Awassa

Lake Awasa is located at an altitude of 1680 m in the central part of the Ethiopian Rift Valley (6^0 33' - 7^0 33' N and $38^0$22' - $38^0$29' E) (Figure 1), 275 km south of the capital, Addis Ababa. Daniel Gamachu (1977) documented that the Awassa area has a dry, subhumid climate and receives a mean annual rainfall of 1154 mm in the long eight rainy months (March to October). The annual potential evapotranspiration for the area is between 1100 and 1250 mm (Elizabeth Kebede and Amha Belay, 1994). The lake has a surface area of 90 km^2 (Makin *et al.,* 1975), a catchments area of 1250 km^2, a maximum depth of 22 m and a mean depth of 11 m (Welcome, 1972) although these values are subjected to seasonal variation. Some physical and chemical characteristics of Lake Awassa are presented in Table 1.

Lake Awassa is topographically a closed basin, where there is no known outflow. The lake is primarily fed by a small river named Tikur Weha that stems from Shallo swamp and also from the rivers (streams) on the north and west caldera walls, which are ephemeral.

Lake Awassa is an oligosaline sodium bicarbonate dominated lake (type II) under the classification system of Talling and Talling (1965). The salinity of the lake increased between the late 1930s and the mid 1950s (Wood and Talling, 1988) but since 1960s it became more dilute (decreased in salinity) (Zinabu Gebre-Mariam *et al.,* 2002). Despite being closed basin, it is striking that the lake water is relatively dilute. This may be due

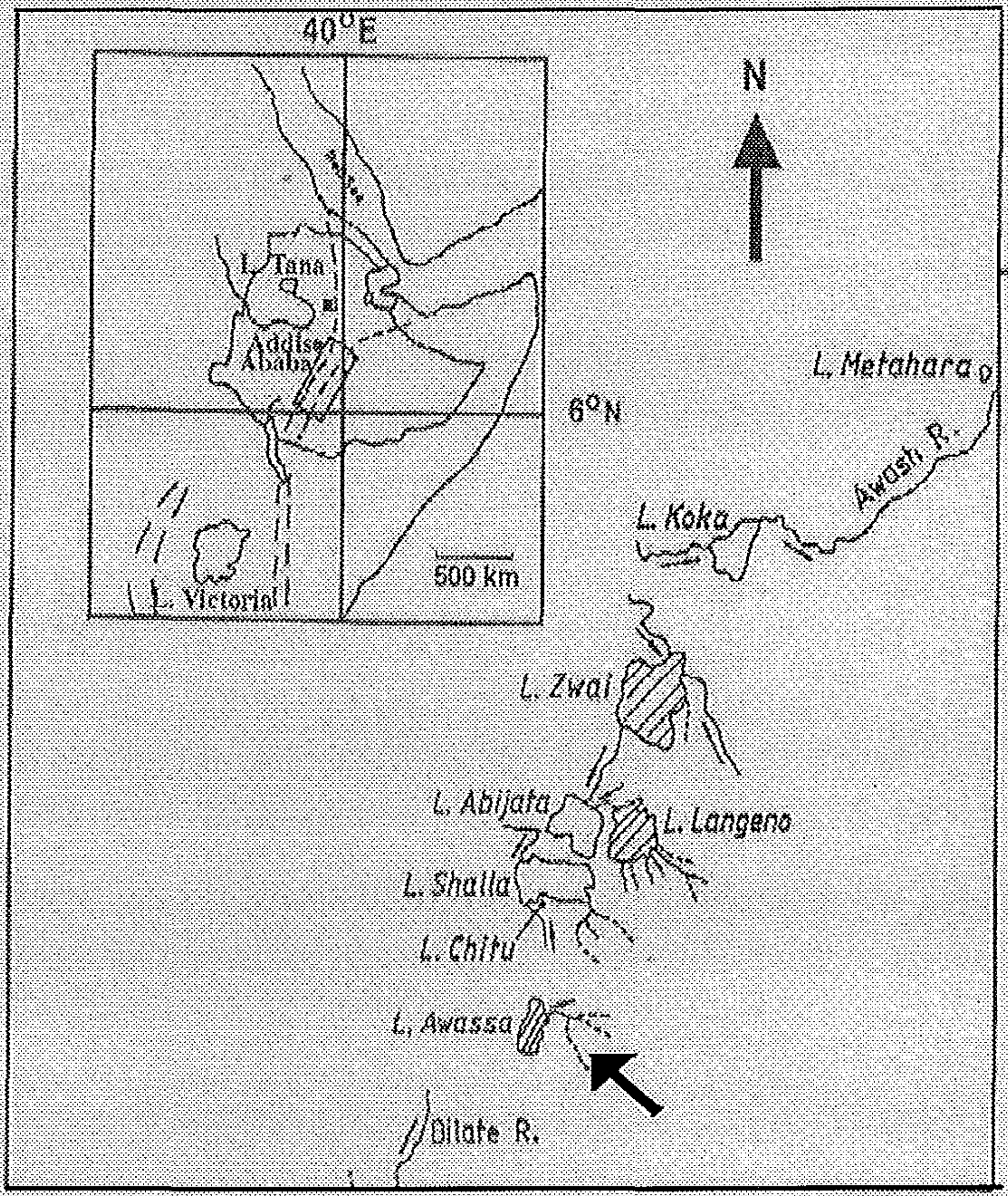


Fig. 1. Map of Ethiopia (inset) and the Rift Valley Lakes with their drainage basin pattern The arrow indicates Lake Awassa (Modified after Elizabeth Kebede *et al.*, 1994).

to the very low concentration of solutes in its inflows (Wood and Talling, 1988) and/or seepage out through the bed of the lake on the south-west and northern side as suggested by Makin *et al.* (1975). Recently Darling *et al.* (1996) presented isotopic evidence of ground water outflow to the north, which is the most plausible mechanism for maintaining low salinity in Lake Awassa.

The lake is classified as warm, discontinuous, polymictic under the scheme proposed by Lewis (1983). Stratification is strongest between February and May, followed by mixing in June and July. Short periods of stratification occur between August and January (Taylor and Zinabu Gebre-Mariam, 1989).

Mixing was associated with high rainfall and lower air temperature (Elizabeth Kebede and Amha Belay, 1994). With a mean phytoplankton biomass of 19 µg/L, Lake Awassa belongs to eutrophic category (Wetzel, 2001).

The phytoplankton in Lake Awassa is probably light limited. Nutrient limitation is most likely at the end of the dry season, when light penetration is greatest and stratification has been stable for an extended period (Taylor and Zinabu Gebre-Mariam, 1989). Since the ratio of nitrate to phosphate in the lake water is generally low, nitrogen is the nutrient most likely to be limiting (Elizabeth Kebede and Amha Belay, 1994).

The fish fauna of Lake Awassa consists of about six species. These are *Oreochromis niloticus, Labeobarbus intermidius, L. amphigrama, Aplochelichthys sp., Clarias gariepinus* and *Garra* species (Demeke Admassu, 1996). According to Seyoum

Mengistou and Fernando (1991) the dominant zooplankton species are *Mesocyclops aequatorialis, Thermocyclops consimilis, Diaphanosoma excisum, Brachionus and Keratella.* The dominant phytoplankton species include *Lyngbya nyassae, Botryococcus braunii and Microcystis* (Elizabeth Kebede and Amha Belay, 1994). The littoral is covered by an extensive belt of submergent and emergent rooted vegetation which extends about 150 m offshore (Tudorancea *et al.* 1988) and up to 4 m depth. The macrophytes vegetation includes *Cyperus* sp., *Nymphea caerulea. Potomogeton* species, *Typha angustifolia*, *Paspalidium geminatium* and *T. latifolia.* The benthic fauna include Ostracods (dominant), Chironomids, Cyclopoids and Cladocerans (Tilahun Kibret, 1985).

There is no study on the food web structure and energy flow of the lake, despite intensive and extensive works that have been done on bacterioplankton (Zinabu Gebre-Mariam, 1988), phytoplankton (Demeke Kifle, 1985; Elizabeth Kebede and Amha Belay, 1994), zooplankon (Seyoum Mengistou and Fernando,1991), and zoobenthos (Tilahun Kibret and Harrison, 1989) and fish (Yosef Tekle-Giyorgis and Casselman, 1995; Demeke Admasu, 1996; Demeke Admasu and Elias Dedebo, 1997; Getachew Teferra and Fernando, 1989).

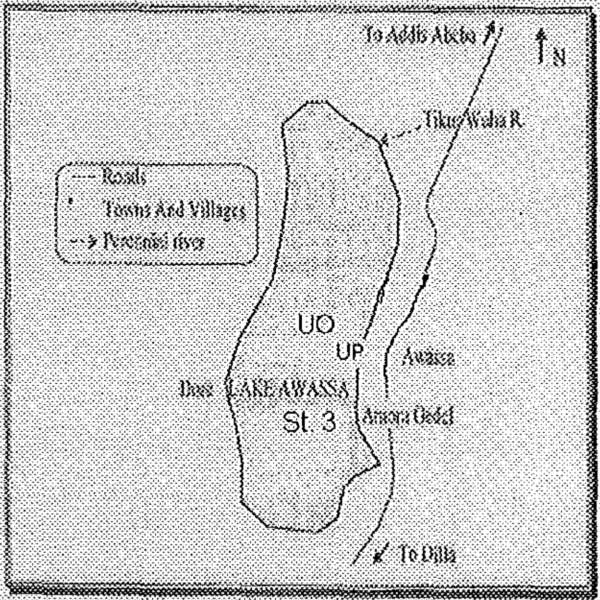


Fig. 2. Map of Lake Awassa showing sampling stations (Modified after LFDP, 1998).

Where: UO-Unique Open
UP-Unique Park
St. 3-Station 3

Table 1. Some physical and chemical characteristics of Lake Awassa

Characteristics	Values	Reference
Latitude	$6^{0}33'$ - $7^{0}33'$N	Welcome (1972)
Longitude	$38^{0}22'$ – $38^{0}29'$E	"
Altitude	1860m	"
Area	90 km^2	Makin *et al.* (1975)
Volume	$1.3*10^9 m^3$	Welcome (1972)
Depth - maximum	22m	"
- mean	11m	"
Maximum length	17km	"
Maximum width	11km	"
Shore-line length	52km	"
Catchments area	1250km^2	"
Na	7.1 meq/L	Zinabu Gebre-Mariam *et al.* (2002)
K	0.7 meq/L	"
Ca	0.5 meq/L	"
Mg	0.5 meq/L	"
Alkalinity	7.8 meq/L	"
Cl	0.8 meq/L	"
SO_4	0.2 meq/L	"
SiO_2	42.6 meq/L	Elizabeth Kebede *et al.* (1994)
PO_4-P	12.4 μg/L	"
Total P	36.2 μg/L	"
NO_3/NO_2-N	34.9 μg/L	"
NH_3-N	5.7 μg/L	"
pH	8.78	"
Conductivity	846 μS/cm	Demeke Kifle (1985)

3. Material and methods

3.1. Introduction to Ecopath Model

The Ecopath approach and software were first developed by Polovina (1984) to estimate biomass of various species or groups of an aquatic ecosystem. Christensen and Pauly later adapted Polovina's work and improved it to a user-friendly software package for personal computers through the inclusion of various routines implementing ecological theory (Christensen & Pauly, 1992, 1993; Pauly *et al.,* 2000). The software (version 5) allows for rapid construction and verification of mass-balance models of ecosystems. Detail description of Ecopath can be found in Christensen and Pauly (1992, 1993), Christensen *et al.* (2000) and Pauly *et al.* (2000).

Determining the main components and their feeding network in the ecosystem are the first steps in constructing Ecopath model. In Ecopath, a system is partitioned into boxes (functional groups) comprising species having a common physical habitat, similar diet and life history characteristics or ecological similarities (same prey, same predator), rather than taxonomic classification to be used to aggregate species to form the functional groups.

All trophic levels should be included and be represented at a similar level of detail. A maximum of 50 functional groups can be included and at least one must be a detritus group. Detritus is important since it is produced from all living groups of an ecosystem through excretion, egestion and decomposing carcasses. Detritus have to be placed after all living groups are entered. For each functional group, values of biomass (B), production /biomass ratio (P/B), consumption /biomass ratio (Q/B), diet composition (DC) and ecotrophic efficiency (EE) need to be determined. An Ecopath parameterization routine, however, estimates one parameter that was not entered (one of the unknown -- B, P/B, Q/B or EE) and informs the user whether the model is mass-balanced. EE is the most difficult to estimate and thus often left unknown for Ecopath, if the other parameters are entered. Otherwise EE can be guesstimated according to the exploitation of the given organism in order to estimate the other parameters such as biomass.

Ecopath no longer assumes steady state but instead bases the parameterization on an assumption of mass balance over an arbitrary period, usually a year (Christensen and Walters, 2000). The model assumes mass balance in that production of any given prey is equal to the biomass consumed by predators plus the biomass caught, (e.g. in fisheries) plus any exports from the system. That is Ecopath models obey the 1st law of thermodynamics that mass and energy are conserved within a closed system.

The flow of energy within and between the functional groups is best described by two master equations in the Ecopath model. The first equation is the energy balance for each functional group:

Consumption = Production + Respiration + Faeces + Urine ..... (eq. 1)

Hence, production is linked to consumption.

The second equation splits production as follows:

Production = catches + predation mortality + biomass accumulation + net migration + other mortalities ..... (eq. 2)

Predation mortality is the factor that links the different functional groups in an ecosystem. Thus the network of flows of biomass within an ecosystem links the plants with the herbivores, and the latter with the carnivores and predators. These linkages are commonly depicted as a foodweb and the position of each functional group within the foodweb is known as trophic level.

In its present form, Ecopath parameterizes eq. 2 as follows

$$P_i = Y_i + B_i + M_{2i} + E_i + BA_i + P_i*(1-EE_i) \; .... \qquad \text{(eq. 3)}$$

Where P_i = total production rate of i; Y_i = total catch rate of i; B_i = biomass of the group; M_{2i}= total predation rate of i; E_i= net migration rate (emigration minus immigration); BA_i= biomass accumulation rate for i; and EE_i= ecotrophic efficiency of i.

Equation 3 can be re-written as follows and becomes the basic equation of Ecopath

$$B_i*(P/B)_i * EE_i = Y_i + \Sigma\,(B_j)*(Q\,/B)_j * DC_{ij} \; \text{-----} \qquad \text{(eq.4)}$$

Where Bi = the biomass of prey group i; P/Bi =production /biomass ratio of group i; EEi = ecotrophic efficiency, Yi =its yield (= fishery catch); Bj =the biomass of predator group j;

Q/Bj= the food consumption per unit biomass of j, and DCji =the fraction of i in the diet of j.

Ecopath incorporates Ecosim which is a dynamic model with capability for exploring past and future impacts of fishing and environmental disturbances. Whether an analysis carried out with Ecosim is meaningful or not depends to a large extent on the quality of the model constructed in Ecopath as Ecosim uses files created by Ecopath.

Input data were standardized, biomass (B) as wet weight (t Km^{-2}) and production /biomass (P/B) and consumption /biomass (Q/B) rates per year for each component group. The ecotrophic efficiency (EE) is without unit.

3.2. Functional groups

Many of the functional groups in Lake Awassa are at species level, which is very much advantageous to use literature data directly without going to average different values of ecologically similar species to aggregate as one functional group. The different functional groups of Lake Awassa include:

African Hippo, Fish-eating birds, Tilapia, Juvenile Tilapia, Large *Labeobarbus,* Catfish, Juvenile catfish, Small *Labeobarbus, Aplocheilichthys* sp., *Garra* sp., Zoobenthos, Herbivore zooplankton, Carnivore zooplankton, Phytoplankton, and Macrophytes. Table 2 elaborates the functional groups of Lake Awassa.

3. 2.1. Fish eating birds and Hippo

There are many fish-eating birds around Lake Awassa and some of them are listed below.

White Pelicans, White-breasted cormorant, Long-tailed cormorant, Marabou Stork, African fish eagle, Pied king fisher, Malachite king fisher, Squacco heron and Hamerkop. Even though these and other bird species consume fish, they usually depend on the discarded fish rather than feeding through predation by themselves. Marabou Stork and White Pelicans, which have relatively a good number around the lake (pers. observation), are almost entirely scavengers in Lake Awassa, particularly in 'Amora Gedel' region. 'Amora Gedel' is the main landing site of the lake. The discarded fish has been already included in the calculated fish biomass. This probably leads to an intuitive conclusion that the impact of the fish eating birds on the live fish biomass may be insignificant. In addition to this, there is no documented work on the species, feeding habit, biomass, mortality etc of avifauna of the lake. Because of the above reasons, we decided to exclude fish eating birds' functional group from the present ecosystem model work until clear and full-fledged information is available.

The giant mammal African Hippo, which consumes macrophytes of the lake, has also been excluded from the present ecosystem modeling mainly due to lack of information. Both birds and Hippo, besides their ecological significance, are important in tourism industry.

Table 2. Ecological groupings used for Ecopath analysis for Lake Awassa trophic model

Ecogroups	**Species/ Groups**
Catfish	*Clarias gariepinus*
Juvenile catfish	Juvenile *C. gariepinus*
Large *Labeobarbus*	*Labeobarbus intermidius* Ruippell, 1836 (cyprinidae)
Tilapia	*Oreochromis niloticus* Tilapia (Linnaeus, 1758)
Juvenile Tilapia	Juvenile *O. niloticus*
Small *Labeobarbus*	*Labeobarbus amphigrama*
Aplocheilichthys	*Aplocheilichthys* sp.
Garra	*Garra* sp.
Zoobenthos	Ostracodes, chironomids, insects
Herbivore zooplankton	*Diaphanosoma excisum, Thermocyclops*
Carnivore zooplankton	*Mesocyclops sp.*
Phytoplankton	Blue green algae, diatoms and green algae
Macrophytes	*Potomogeton* species, Typha sp., *Paspalidum germinatium*

3.3. Sampling stations

In the present study three sampling stations were selected as a representative of both littoral and open zone of the lake (Fig. 2). Station 1 (Unique Park) with a mean depth of 2.78 m stand for littoral zone while Station 2 (Unique Open) and Station 3 are representatives of offshore with a mean depth of 15.29 and 18.25 meters respectively. Unique Park is located near Unique Park Hotel from where the station name is derived. Unique Open is very parallel to Unique Park and Church St. Gebriel from distant. Station 3 is found in the offshore parallel to Amora Gedel Recreaction Center. These studies were conducted from November 2003 – August 2004.

3.4. Phytoplankton

3.4.1. Phytoplankton biomass and primary productivity

The composite phytoplankton biomass was estimated from the determination of photosynthetic pigment concentration. Phytoplankton was sampled using one liter container from the surface of the lake and 0.2—0.3 liter was filtered with Whatman GF/C glass fiber filters of diameter 4.7cm and, ground and extracted using 90% acetone. After centrifuging, the extracted Chlorophyll 'a' pigment absorbance was measured at 665 nm spectrophotometrically and corrected for turbidity by subtracting the corresponding reading at 750 nm. The corrected value was used to calculate the concentration of

Chlorophyll 'a' using Talling and Driver (1963). Chlorophyll degradation products were not determined in this study.

The average phytoplankton biomass (as chlorophyll a) of this study was 19 mg m^{-3} , but earlier reports give estimates of 34 mg m^{-3} (Demeke Kifle and Amha Belay, 1990) and 43 mg m^{-3} (Elizabeth Kebede and Amha Belay, 1994). This lead us to take a compromise mean value of 33 mg m^{-3} for this particular model. The value was converted into square meter unit (86.13 mg m^{-2}) by multiplying with the euphotic depth (2.61m). This value was also converted to wet weight using two successive conversion factors (Jones, 1979). The first was to change Chlorophyll a to Carbon as in

40:1 – carbon to Chlorophyll 'a' ratio

And the second conversion factor was used to convert carbon to wet weight as in

Carbon = 10% of wet weight

Hence average phytoplankton biomass (wet weight) of Lake Awassa was estimated to be 34452 mg m^{-2} (34.452 g m^{-2}).

Photosynthesis was measured using Winkler Oxygen Method and samples were taken from the surface and incubated between 4 AM and 8 PM at different depths of the euphotic zone. The collected lake water was siphoned into 300ml Pyrex light (clear) and dark glass bottles, which were attached at 0 m (surface), 0.25 m, 0.50 m, 1 m and 2 m depths on a metal-made hanger. This metal-made incubation material is well designed, where the glasses were suspended at 72 ^{0} apart with each other in order to avoid vertical shading. One of the shortcoming of this design is the bottles are suspended at fixed depth regardless of the light incidence of the day.

Winkler A and B were added to the incubated samples after about 2 hours of incubation and placed in a dark box. The fixed samples were digested with 50% H_2SO_4 and titrated using sodium thiosulphate ($Na_2S_2O_3.5H_2O$) in the laboratory. The sodium thiosulphate reading (titrant) was used to calculate dissolved oxygen using monochromatic method of Wetzel and Likens (2001) (see appendix 3). The dissolved oxygen (mg/L) was converted in to mg C/m^3/h using PQ (photosynthetic quotient) of 1.2 (Wetzel and Likens, 2000). The value in m^{-3} was changed in to m^{-2} using grid integrating method and was found to be 0.27 g C/m^2/h.

3.4.2. Phytoplankton / biomass ratio (P/B)

To determine P/B, primary production should be changed into appropriate form. Gross mean primary production was 0.2695 g C/m^2/h and assuming 10 hour production period per day the value was converted in to 2.695g C/m^2/ day. Multiplying by 365 the yearly primary production becomes 983.675 g C m^{-2}.

This value (983.675 g C/m^2/year) should be changed into wet weight in order to harmonize with the unit of phytoplankton biomass. To do this, a conversion factor of

10% wet weight to C was employed and the primary production of 9836.75 g WW m^{-2} $year^{-1}$ was obtained.

On average phytoplankton biomass of Lake Awassa is 34.452 gm^{-2}.
Therefore, production per biomass ratio (P/B) of phytoplankton was estimated to be 285 per year.

Phytoplankton identification was made using different guides including Whitford and Schumacher (1973); John *et al.* (2002); Rott and Lenzenweger (1994); A-Legnerova and Tavera (1996); Jeeji- Bai *et al.* (1997); Hindak (2000); and Komarek and Cronberg (2001) and the species/ genus name are shown in appendix 4.

3.5. Macrophytes

A quadrant of $0.25m^2$ area was thrown in three selected places – around Unique Park, Amora Gedel and Loke. The macrophytes in the quadrants were cut manually (until length of the reach of the hand) and weighed with spring balance. This fresh weight was taken as an estimate of macrophyte biomass. Though the estimate appears very high (2000 t/km^2), below ground biomass was not included in the biomass estimation.

3.6. Detritus biomass (D)

There were no available literature data regarding the biomass of detritus in Lake Awassa. Hence, the detrital biomass was calculated as a function of primary production and euphotic depth by employing the relationship suggested by Christensen and Pauly (1993):

$\log D = 0.954 \log PP + 0.863 \log E - 2.41$ ---- (eq. 5)

Where:

D= detrital biomass (g C/m^2); PP= primary production (in gCm^{-2} $year^{-1}$); E= euphotic depth in meter.

Euphotic depth was estimated from the Secchi depth transparency measurement. It was measured with black and white painted disc of 0.20 meter diameter and the readings ranged from 69 to 117 cm. Three times of the mean Secchi depth reading (0.87m) was used to calculate the euphotic depth (2.61 meters).

$$\log D = 0.954 \log PP + 0.863 \log E - 2.41$$

$$= 0.954 \log 983.675 + 0.863 \log 2.61 - 2.41$$

$$= 0.805 \text{ g C m}^{-2}$$

$D=6.379 \text{ g C m}^{-2}$

To change to wet weight, C to wet weight ratio of 10% was employed and hence wet weight detritus biomass of 63.79 g m^{-2} was obtained.

3.7. Zooplankton

3.7.1. Zooplankton abundance and biomass

Samples of zooplankton were taken from the water column with a No. 25 (64 μm mesh) townet having a mouth diameter of 0.31 meter. To determine abundance, the samples were hauled from 3m depth for both Station 3 and Unique Open, and half a meter for Unique Park. The concentrated sample was immediately preserved with formalin to yield the final concentration of 4-5 %.

The volume of water filtered through the sampling net was determined using the formula **$\Pi * r^2 * h$** (where r-radius, h- height (3 and 0.5m)) assuming 100% filtration efficiency. Accordingly the number of organisms per m^3 of the lake was calculated for each sample. Counting was done using Wild Microscope with 50 X magnification power. Twenty five milliliter was subsampled with a wide-mouth pipet from a well mixed 395ml sample and poured into grided petridish for counting. Three pre-selected grids were counted for each sample and the total organisms count was expressed in m^{-3} after using the correct multiplication factors. During counting the developmental stages (nauplii and copipodite) were lumped together except some separate count of nauplii and adult of cyclopoid groups in order to see the nauplii-adult ratio. The mean total number of zooplankton is given in 3 categories in Table 4.

Zooplankton was identified using different guides including Einsle (1971), Voigt and Koste (1978), de Velde (1984), Defaye (1988) and Dussart and Fernando (1988) and the list of the major zooplankton genera and sometimes species are given in appendix 1.

Seyoum Mengistou and Fernando (1991) estimated total biomass of most of the dominant zooplankton on dry weight basis. The biomass of herbivore and carnivore zooplankton was estimated as 17.54 and 26.31 mg DWm^{-3} , and converted into metric squared unit when multiplied by the mean depth of the lake (11m), which gives 192.94 and 289.41mg m^{-2}, respectively. Since the aforementioned values were in dry weight, relationship of Hall *et al.* (1976) and Burgis (1974) was used to determine the corresponding wet weights:

Dry weight = 20% of wet weight

Hence wet weight value of herbivore and carnivore zooplankton becomes 964.7mg m^{-2} (0.965 g m^{-2}) and 1447.05 mg m^{-2} (1.447g m^{-2}), respectively.

Production/ biomass ratio (P/B) for herbivore zooplankton (236.4) and carnivore zooplankton (18.7) were estimated by Seyoum Mengistou (1989) and were used in this work.

Consumption/ biomass ratio (Q/B)

Q/B for zooplankton was estimated based on assumed gross food conversion efficiency (P/Q) of 0.2 (Pauly *et al.*, 1993) and calculated as follows.

Herbivore zooplankton

Production (P) for *Thermocyclops* (149.4) and *Diaphanosoma* (1737.5) were estimated by Seyoum Mengistou and Fernando (1991) in mg DW m^{-3} y^{-1}. The summed value (1886.7 mg DW $m^{-3}y^{-1}$) was changed to fit the program unit in to 104 g $m^{-2}y^{-1}$(wet weight) after appropriate conversion factor and multiplication procedures used. Hence Q/B is equal to 538.86 per year.

Carnivore zooplankton

Production (P) for Mesocyclops was 494 mg DW $m^{-3}y^{-1}$ (Seyoum Mengistou and Fernando, 1991). Using a similar procedure as for Herbivore zooplankton (above), Q/B for carnivore zooplankton was estimated as 93.88 per year.

3.8. Zoobenthos

Weed bed samples were taken with a strong metal hand net having half a circle of 40 cm diameter. The length of the pole was about 1 m long. Samples were taken around

Unique Park in shallower parts having an average depth of 55 cm. Larger organisms were picked out and sorted by group/genus on the spot in a white enamel dish. Weight, length and volume measurement of each genus/group were taken in the laboratory of Faculty of Agriculture, Debub University.

The sample was taken three independent strokes at a sampling time with the hand net and sampled 7 times. The average zoobenthos biomass is presented in Table 5. The groups/genus names and other measurements data were tabulated and are presented in appendix 5. The samples were identified using keys of Pinder (1978), Macan and Joan (1973), Macan (1979) and Edington and Hildrew (1981).

The result obtained was

$$\textbf{Biomass} = \textbf{Weight} * \textbf{Number}$$
$$= 10.1\ \text{tkm}^{-2}$$

Production /biomass ratio (P/B)

Production /biomass ratio for benthic organisms were estimated using empirical formula of Brey (1999 cited in Christensen *et al.*, 2000):

$$\text{Log } P/B = 1.672 + 0.993*\log(1/A\text{max}) - 0.035*\log(M\text{max}) - 300.447*1/(T + 273) \text{ ---} \qquad \text{(eq.6)}$$

Where:

Amax -- maximum age (per year)

Mmax -- maximum individual body mass (g DM)

T -- Bottom water temperature (^{O}C)

Maximum individual body weight and maximum age for zoobenthos was determined as 0.2g wet weight and 1.5 year, respectively. To change the wet weight to dry weight, the following relationship was employed:

Dry weight = 20% of wet weight

Consumption/ biomass ratio (Q/B)

Q/B for zoobenthos was estimated based on assumed gross food conversion efficiency (P/Q) of 0.2 (Pauly *et al.*, 1993). Hence Q/B of 21.05 per year was found.

3.9. Fisheries

Commercially exploitable (Tilapia, Catfish and Large *Labeobarbus*) and un-exploited fish species (*Aplocheilichthys* sp., Small *Labeobarbus* and *Garra* sp.) of Lake Awassa were considered in this modeling analysis. All of the fish species share the following two (5 & 6) empirical relationship and their estimation were made separately.

6. Production /biomass ratio (P/B)

Production /biomass ratios are difficult to estimate directly and were taken as equivalent to total mortality (Z) (Pauly *et al.*, 2000) assuming steady-state ecosystem (Allen, 1971). It is because, under equilibrium condition, biological production has to compensate for losses due to mortality to perpetuate in the ecosystem.

Total mortality (Z) of the two exploited fish species (Tilapia and Catfish) was determined by summing the value of fishing mortality (F) and natural mortality (M) as Z=F+M. F will be determined subsequently. However M was estimated using the following Pauly's empirical equation (Pauly, 1984):

$$\mathbf{Ln\ (M) = -0.0152 - 0.279ln\ (L_{inf}) + 0.6543ln\ (K) + 0.463ln\ (T)\ ---\ (eq.7)}$$

Where L_{inf} and K are parameters of VBGF; and T= annual mean surface water temperature of the lake.

Natural mortality (M) for unexploited fish species including juveniles' of exploited fish species and Large *Labeobarbus* were estimated using Pauly's empirical formula in eq.7 and considered as equivalent to total mortality (Z) as they do not suffer from fishing mortality (F). This M value was directly taken as P/B.

Natural mortality and Q/B values of exploited and unexploited fish species were estimated using parameters compiled in Table 3.

6. Consumption /biomass ratio (Q/B)

This parameter expresses food consumption (Q) per unit biomass for a conventional period of one year, which means number of times a given population consumes its own weight per year. This quantity, for each consumer eco-group, was estimated using the following empirical relationship suggested by Palomares and Pauly (1998), and the parameters are tabulated in Table 3.

$$\mathrm{Log}\,(Q/B) = 7.964 - 0.204^{*}\log W_{inf} - 1.965^{*}T + 0.083^{*}A + 0.532^{*}h + 0.398^{*}d \text{ ----} \qquad \text{(eq.8)}$$

Where;

W_{inf} - is the asymptotic weight (g)

T - is an expression for the mean annual temperature of the water body expressed using T=1000/Kelvin (Kelvin=^{O}C + 273.15)

A- is aspect ratio (Ar=h^2/s- of the caudal fin of fish, given height (h) and surface area (s)

h - is a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores) and d - is a dummy variable also expressing food type (1 for detritivores and 0 for herbivores and carnivores)

Values of the above specified input parameters are summarized for each eco-group from different sources. Some of these parameters were estimated based on data collected during the present study while others were obtained from earlier studies, as indicated in Table 3.

3.9.1. Activity ratio (A)

Activity ratio is estimated by grid method for all fish species in Lake Awassa. Grid method is used for determining surface area of caudal fin of the fish. Then Surface area squared (S^2) divided by height (h) of the caudal fin give Activity ratio (A) as shown in Table 3.

Table 3. Growth and other parameters compiled for Q/B and M estimation.

	Tilapia	Juvenile Tilapia	Catfish	Juvenile catfish	Large *Labeobarbus*	*Aplocheilichthys*	Small *Labeobarbus*	*Garra* sp.
$L_{inf\,(cm)}$	40[a]	20.9[b]	121[c]	42.7[c]	75[d]	4.5[e]	17[e]	15[e]
$W_{inf\,(g)}$	1000[a]	185.59[b]	14475[c]	566.63[c]	5536[d]	0.6[e]	46.91[e]	24.85[e]
T (°C) [e] Surface Mean waterbody	 25 26	 25 26	 25 26	 25 26	 25 26	 25 26	 25 26	 25 26
K(y^{-1})	0.3[a]	0.5[b]	0.16[c]	1.6[c]	0.12[d]	1.5[f]	1.5[f]	1.5[f]
A[e]	1.8	1.8	1.5	1.5	3	1.4	2.5	1.4
H[g]	1	1	0	0	0	0	0	0
d[g]	0	0	0	0	1	0	0	0

[a] parameters estimated using von Bertalanffy growth equation fitted to length at age data of Demeke Admassu (1989).

[b] parameters estimated using von Bertalanffy growth equation fitted to length at age data of Yosef Tekle-Giorgis (1990).

[c] parameters estimates taken from age and growth work of Yosef Tekle-Giorgis (2002)

[d] $L_{inf\,(cm)}$,$W_{inf\,(g)}$ and K were taken from Senior Students' Project of Debub University

[e] Values estimated based on data collected during the present study

[f] An educated guess of K for *Aplocheilichtyes*, Small *Labeobarbus* and *Garra* was made in consultation with Dr. Yosef Tekle-Giorgis

[g] estimated based on information on feeding habit studies of Elias Dadebo (2000); Demeke Admassu and Elias Dadebo (1997); Getachew Teferra and Fernando (1989); Tudorancea *et al.* (1988); and Elias Dadebo (pers. com); Zerihun Desta pers. com.).

3.9.2. Tilapia

Catch statistics data were taken from the commercial fishery for about eight months intensively on a daily basis at the major landing site of the lake ('Amora Gedel'). Total length and the respective total weight of random samples of Tilapia were measured at regular interval during the study period. Total weight of each species landed by the gill net, total number of the gears used and total number of fishermen in operation were also recorded.

The catch data given in appendix 6 were summarized from the daily length measurements. These were obtained from the records of the sampled species that have been concurrently counted and weighed by determining appropriate raising factor to convert records of the daily total weight of the catch into total numbers. The length compositions of the total daily catch were estimated by multiplying the total numbers caught per day by the relative frequency of each length group in the daily sample. Then the total length frequency and total number of each fish species landed per week, month and year were determined by summing the frequencies of the respective length groups accordingly.

Length- based cohort analysis were employed to estimate the fishing mortality coefficients (F) and the population number of fish in each length group (Jones, 1984). Then total mortality (Z) for exploited fish species is estimated as Z=F+M. Natural mortality coefficient was estimated using Pauly's empirical formula (eq. 7). Z value of 1.8

$year^{-1}$ was estimated for the exploited tilapia stock and this was considered as an estimate of P/B. Similarly, annual stock biomass and yield were estimated using length-based Thomson and Bell yield model (Thomson and Bell, 1934; Sparre and Venema, 1992). The annual yield and stock biomass of Tilapia in Lake Awassa were 6.972 t $km^{-2}year^{-1}$ and 8.6 t km^{-2}, respectively, as shown in Table 5.

The length weight relationship was taken from Yosef Tekle-Giorgis (1990)

$TW\ (gm) = 0.0171 * TL^{3.0831}$ $R^2=0.995$

3.9.3. Juvenile Tilapia

A biomass value of 8.6 t $km^{-2}$for Juvenile Tilapia was taken with the assumption that exploited and unexploited (juvenile) biomass of the species is equivalent (Yosef Tekle-Giorgis, pers. com.).

Q/B for Juvenile Tilapia was determined using equation 8 and parameters tabulated in Table 3. The following Length-Weight relationship was taken from Yosef Tekle-Giorgis (1990)

$$TW\ (gm) = 0.0182 * TL^{3.0364} \qquad R^2=0.9959$$

3.9.4. Catfish

Yosef Tekle-Giorgis (2002) has estimated catfish biomass of 919 gm/recruit. However, the model requires input in ton per square km currency. For calculating the required biomass, we assumed same number of catfish recruit as tilapia i.e. 0.5 million recruit per year (Yosef Tekle-Giorgis, 1990). Therefore, the above relative biomass estimate (biomass/recruit value) was multiplied by the stated value of recruit and was divided by 1,000,000 to obtain an absolute biomass estimate expressed in t km^{-2} as presented in Table 6. Likewise, an annual yield of catfish was estimated as 919 gm/recruit (Yosef Tekle-Giorgis, 2002) and this value was used after due conversion. The latter was obtained as an output of the Thomson and Bell yield estimation procedure mentioned earlier.

An estimate of total mortality for catfish (i.e. 1.3 y^{-1}) was obtained from Yosef Tekle-Giorgis (2002) and it was considered as P/B.

3.9.5. Juvenile catfish

A biomass value of 5.1 t km^{-2} for Juvenile catfish was taken with the assumption that exploited and unexploited (juvenile) biomass of the species is equivalent (Yosef Tekle-Giorgis, pers. com).

Q/B for Juvenile catfish was determined using empirical equation 8 and the parameters tabulated in Table 3. The following Length-weight relationship was taken from Yosef Tekle-Giorgis (2002).

$$TW = 0.005\ TL^{3.1}$$

3.9.6. Large *Labeobarbus*

LFDP (1998) reported that only about 2% of the total fish production of Lake Awassa was contributed by Large *Labeobarbus* and hence it is considered as a virgin stock for this particular case. This commercially important fish is mainly a bycatch in Lake Awassa.

Production/ biomass ratio (P/B)

Natural mortality (M) is taken as total mortality (Z) for this work since we have assumed the species as virgin stock. M was estimated using the empirical relationship shown by eq.7.

Animal Science students in Debube University have studied Large *Labeobarbus* for their senior research project in 2004. Thus the following length – weight relationship was taken for this modeling work.

$$W=0.003*L^{3.34} \quad R^2= 0.93$$

3.9.7. *Aplocheilichthys*

The biomass of *Aplocheilichthys* was estimated by hauling a known area along the shore line at different locations of the lake. Thirty-two meters by 1.5m beach seine net was used to enclose a semicircular area (r=10 m) along the shore line having an area of about 157 m^2. Hauling was done on three separate occasions during the whole year (i.e. every 4 months) at each of the three selected shore area of the lake.

During each hauling, a particular site was repeatedly hauled until the fish was exhaustively caught. In due regard, the average catch per net (in terms of weight) was calculated for each site and sampling occasion. Finally the data was combined for all sites and hauling occasion to give an average catch per net which was estimated as 388 gm per 157 m^2 area of the shore. Converting this into weights of catch per km^2 area, gave 2.47 tkm^{-2} and this was considered as an average biomass estimate of *Aplocheilichthys* (Table 5).

Similarly the length and weight of the fish were also recorded to establish the length-weight relationship for the species.

$$Tw(gm)=0.011*TL^{2.6564} \qquad R^2=0.7292$$

Production /biomass ratio

Natural mortality (M) of *Aplocheilichtys* was estimated using Pauly's empirical formula (Pauly, 1984) in eq.(7) and considered as total mortality (Z) as they do not suffer from fishing mortality (F). An educated guess of K (1.5 yr^{-1}) was made in consultation with Yosef Tekle-Giorgis. It was done as follows: A guess estimate of L_{inf} was done based on the largest length observed in the sample. According to the suggestion of Pauly (1984), L_{inf} can be estimated by dividing the largest length (L_{max}) observed by 0.95. Similarly, best estimate for W_{inf} can be made by dividing the largest observed weight (W_{max}) by 0.86 (Pauly, 1984). The largest 10% of lengths and weights recorded during the study were averaged to give estimates of L_{max} and W_{max}, respectively. The corresponding L_{inf} and W_{inf} were estimated (shown in Table 3) following the procedures suggested above. Then the value of K was estimated based on the suggestion of Pauly (1984) that the maximum age the fish live is 3/k; i.e. (t_{max}) =3/K.

Here t_{max} was estimated for *Aplocheilichthys* as 2 years. Hence replacing this in the above relationship gave a value of K=1.5 yr^{-1}.

3.9.8. Small *Labeobarbus*

Small *Labeobarbus* is one of the unexploited fish species in the lake. L_{max} and W_{max} (the length and weight of the largest fish) were estimated for this species by averaging the top 10% largest lengths and weights recorded during sampling (data from Zerihun

Desta). This gave estimates of L_{max} and W_{max} as 9.5cm and 8.5gm, respectively. Then using these values and following the procedure explained earlier for *Aplocheilichthys*, L_{inf} and W_{inf} values were estimated. Similarly, K was estimated from the VBG equation as explained for *Aplocheilichthys.* These values are shown in Table 3.

The length-weight relationship was fitted in the present study as

$TW\ (gm) = 0.0096 * TL^{3.0092}$ $R^2 = 0.995$

3.9.9. *Garra* species

Garra is a small fish which does not reach table size in its life time in Lake Awassa. Estimates of L_{max} and W_{max} as well as the corresponding values of L_{inf} and W_{inf} were made following the procedures explained above. Also an educated guess estimates of K was done as explained for the other two unexploited fish species. Values of these parameters are tabulated in Table 3.

The length-weight relationship was fitted in the present study as

$TW\ (gm) = 0.01 * TL^{2.9053}$ $R^2 = 0.9459$

3.10. Diet composition (DC)

The diet composition is the fraction of each prey species (group) which constitute the diet of consumer and is usually estimated from studies of stomach contents. Since the food web links the different functional groups in an ecosystem, information on diet composition is important for understanding the dynamics of the ecosystems. The average composition of the food of each consumer organisms was assembled from published information and personal communication. Diet composition of all consumers must be entered. Table 6 shows the diet matrix used for Lake Awassa ecosystem modeling.

3.11. Eco-trophic efficiency (EE)

It is the fraction of the production of any group that is consumed within the system (transferred through the trophic web), or caught by the fishery. This parameter is difficult to estimate and is usually assumed to range from low values (in apex predators) up to 0.95 (Ricker, 1969) or the software estimates it. An EE greater than 1 means that the input parameters are not physically possible, as EE by definition is a fraction between 0 and 1. EE are usually calculated from other parameters in the Ecopath model, since no field measurement or empirical relationship exists to estimate this parameter. Sometimes when other parameters such as biomass are unknown, then guesstimates for EE must be entered. Ecopath directs the fraction (1-EE) of the production toward the detritus, a feature that is of relevance when attempts are made to equilibrate the model. EE differs from gross efficiency that can be calculated as GE = (P/B)/ (Q/B), and is used to check the basic inputs. GE ranges from 0.1 to 0.3.

3.12. Balancing the model

Modify entries Q/B, P/B, biomass etc. including the diet matrix until input is equal to output for each box. If for example, the EE is greater than one, it is a red signal. Both gross efficiency and ecotrophic efficiency for all functional groups should be less than one.

A mass balance facility is incorporated in EwE version 5 to balance the system when EE>1. This routine enables the user to balance quickly than the manual adjustment.

In Ecopath, the trophic levels are the output or calculated results. If they are not in accordance with the expectation, one can check the diet compositions of the input data. If uncertain about trophic levels of fish, for example, the trophic levels given in FishBase could be checked for the same or similar species.

4. Results and Discussion

In the present study the average phytoplankton biomass was 19 µgL^{-1} with the range of 10.43 to 25.21 µgL^{-1} (appendix 2). This result is lower than Demeke Kifle and Amha Belay (1990) who reported average biomass of 34 µgL^{-1}. Elizabeth Kebede and Amha Belay (1994) also documented a higher value that ranged 20-50 µgL^{-1} in the upper 10 meter depth. Zinabu Gebre-Mariam *et al.*, (2002) indicated that the Chl. 'a' (an indicator of phytoplankton biomass) concentration consistently decreased in the lake during the 1990s (with less than 10 µgL^{-1} Chl 'a') compared to values recorded during 1980-1986 (>20 µgL^{-1} Chl 'a'). In the present study a rising trend is observed from 1990's (see appendix 2).

After converting per surface area, the average phytoplankton biomass (34.45 t km^{-2}) of Lake Awassa is lower than L. Kinneret, Israel (65 t km^{-2}, Walline *et al.*, 1993), L. Aydat, France (48 t km^{-2}, Reyes-Marchant *et al.*, 1993) but higher than most African lakes (L. Turkana, 18.5 t km^{-2}, Kolding, 1993; L. Tanganyika, 6.9 t km^{-2}, Moreau *et al.,* 1993; L. Malawi, 5.4 t km^{-2}, Degnbol, 1993; and L. Kariba, 3.7 t km^{-2}, Machena *et al.,* 1993) but is closer to L. George, Uganda (30 t km^{-2}, Moreau *et al.,* 1993).

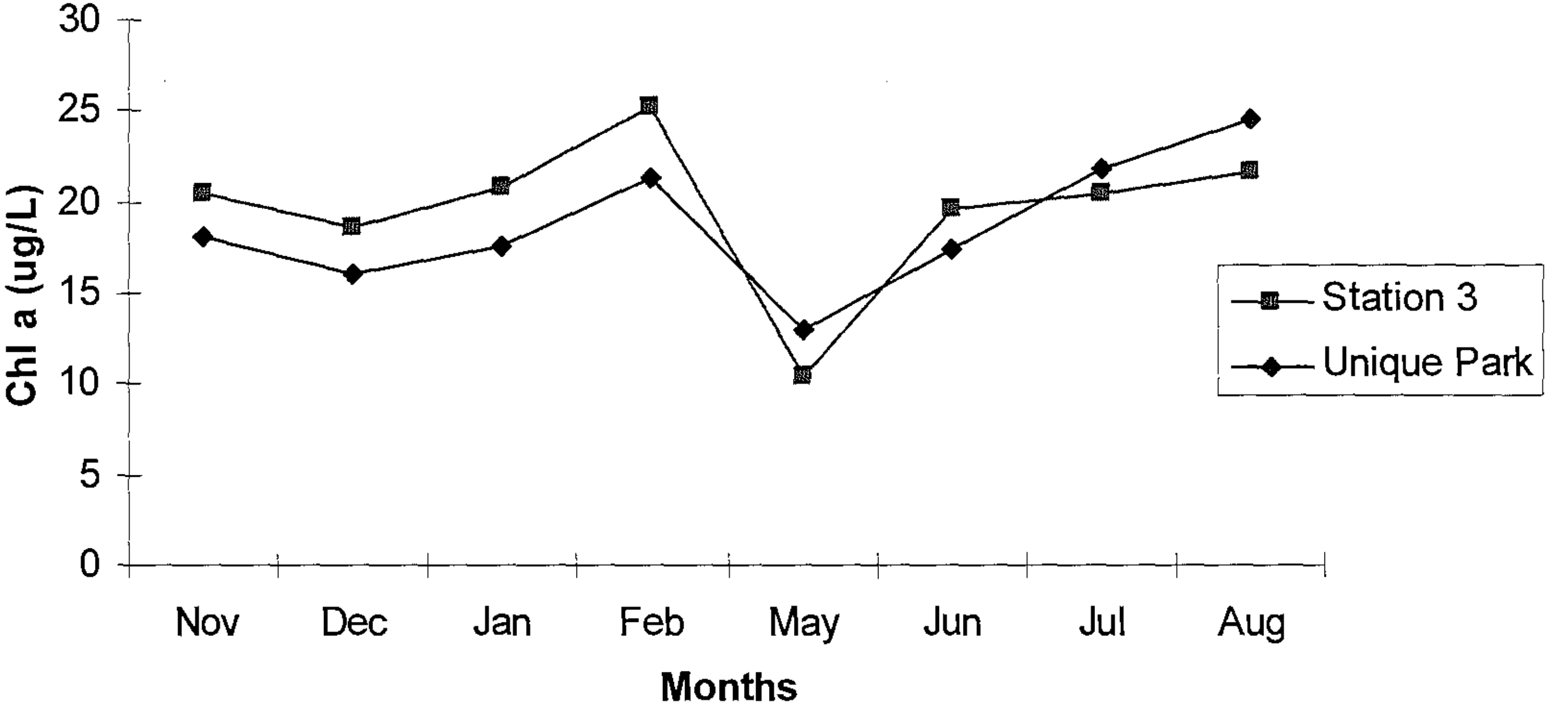


Figure 3. Temporal variation in phytoplankton biomass of Lake Awassa as indicated by Chl. a in two locations -- Station 3 and Unique Park

Station 3 has relatively higher biomass value than Unique Park location from November to June except the depression point in May (Fig. 3). However, the latter station exceeds the offshore beginning the month of July. This may be because of the rainfall in the period as the biomass in the lake is determined mainly by rainfall rather than by other parameters (such as light intensity) (Demeke Kifle, 1985), that coincided with the raise of biomass in the main rainy season in this study. Since the vegetation in the littoral has a buffering capacity, the effect of nutrient inflow may also be faster in the littoral region than the open water. Generally, the biomasses of the two stations are similar.

The lowest biomass for both littoral and open station occurred in May. This may be because of stratification which is strongest between February and May (Zinabu Gebre-Mariam and Taylor, 1989) that could lock nutrients in hypolminion even though there is enough sunshine. Or nutrients may be depleted since it is at the end of the dry season. On the other hand, the abundance of rotifera increased during this month that may play its part via grazing. Taylor and Zinabu Gebre-Mariam (1989) suggested that rotifers and ciliates were important grazers of nano-plankton. Girma Tilahun (pers. com.) found that smaller sized phytoplankton contribute much to the biomass of Lake Awassa that may be heavily eaten by high abundance of rotifera during this time and results in lower biomass value. The Chl. a concentration seems to have two peaks (February and August) in this study period. The numbers of rotifera in these months are either lower or declining (Fig. 4).

Primary productivity of Lake Awassa, as measured by Oxygen Method, is given in the appendix. The gross photosynthesis ranges from 100 to 3400 mg O_2 m^{-3} h^{-1} exhibiting more than three fold variation. The integral photosynthesis ranges from 0.35 to 2.21g $O_2m^{-2}h^{-1}$ and is in agreement with Demke Kifle and Amha Belay (0.3-0.73, 1990) except the two outlier values (2.21 and 2.09 in December 2003 and August 2004, both of them in Station 3) of the present study. Zinabu Gebre-Mariam (1988) also reported a mean gross photosynthesis value of 0.957 g O_2 $m^{-2}h^{-1}$ that lies in the range of our result. The main difference may be due to incubation time; in our study the incubation time was about 2 hour contrary to 3-4 hours in previous work. Zinabu Gebre-Mariam (1988) found that long exposure time underestimates the productivity value by up to 30%.

The species composition of Lake Awassa was identified in the present study and the lists of species/genus are presented in appendix 4. Accordingly, about 39 species/genus were identified. The contribution of the taxa is 54% green alga, 26% blue green alga and 18% diatom, a proportion similar to Elizabeth Kebede and Amha Belay (1994). Generally the taxa are similar to the former author except some that are identified in the present, which were not reported in the previous list. *Pediastrum simplex* (two sub-species) and *Scenedesmus ecornis* are among them. However earlier Wood and Talling (1988) had reported *Pediastrum simplex.*

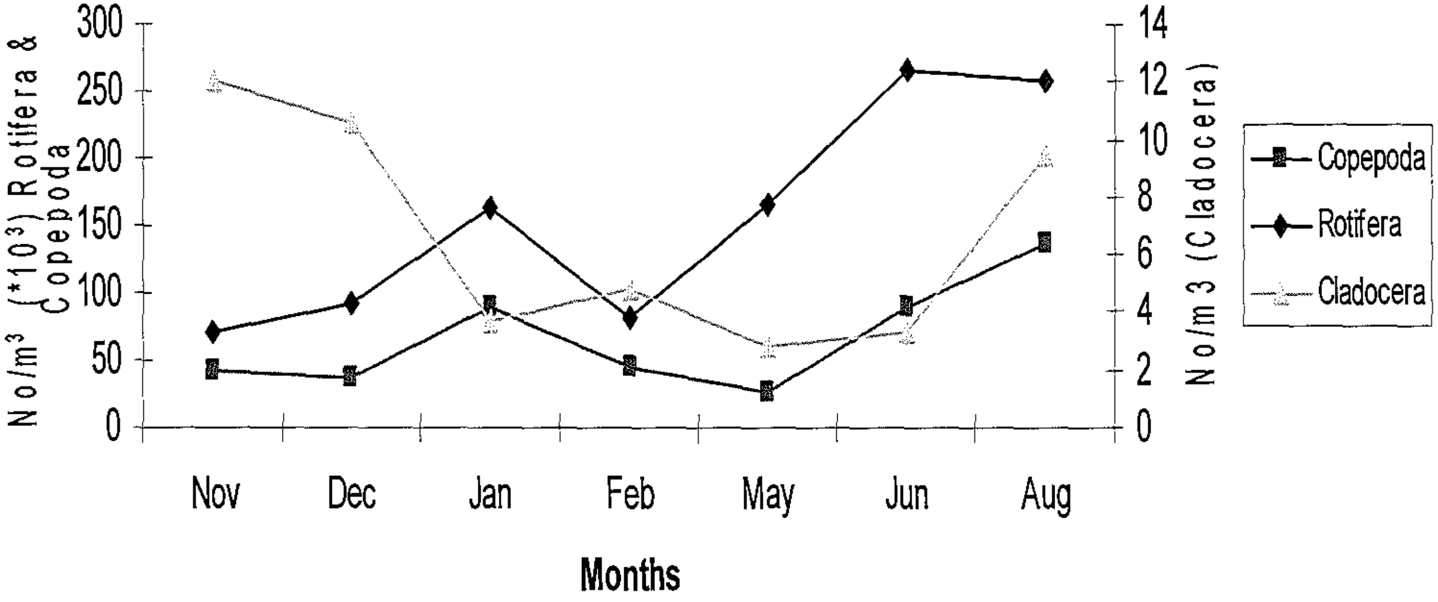


Figure 4. Mean monthly zooplankton abundance (Number m^{-3}) in Lake Awassa during 2003 to 2004

Generally the abundance of zooplankton is not much different from the previous reports. Seyoum Mengistou (1989) documented mean annual abundance of cyclopoid copepoda of about 68, 000 per m^3 and the present result gives 58, 000 m^{-3} (Table 4). Lower number may be due to the low value of Unique Park, a representative of littoral zone, where heavy predation is presumed. Cladoceran density is very low in the present study even lower than Seyoum Mengistou (1989) who reported a maximum of 18, 000 m^{-3}.

Table 4. Mean total number of zooplankton (No/m^3) in three stations of Lake Awassa

Site	Cladocera	Copepoda	Rotifera
Station 3	5366	93017	84821
Unique open	2273	58377	71415
Unique Park	210	22199	130181

Regarding rotifers, a maximum of 50, 000 m^{-3} was reported by Seyoum Mengistou (1989) that is about 3x lower than compared to the present result. However, Taylor and Zinabu Gebre-Mariam (1989) reported a maximum of 315, 000 m^{-3} - much higher values than ours. When the larger zooplankton decreased in number, rotifer usually flourishes. Taylor and Zinabu Gebre-Mariam (1989) suggested that rotifers are consumed by cyclopoid copepods in Lake Awassa. In the present study the number of adult cyclopoid is very low, which may give an opportunity for rotifers to reproduce very well. Brook Lemma (2003) also reported that cladoceran population is replaced by rotifers due to high predation pressure from the dominant juvenile *Labeobarbus* species in Lake Hora-Kilole. Seyoum Mengistou (1989) identified *Brachionus* and *Keratella* as the dominant rotifer species which however was replaced by the common *Filinia* and *Trichocerca* in most months of the present study.

A separate count of naupliii and adult cyclopoid was made in order to see the contribution of different age groups. Accordingly, 22% and 78% of adult and naupliii, respectively, contribute to the total count of cyclopoid copepoda in offshore and 14 and 86% in the littoral zone of Lake Awassa. In both locations, the major contribution for the abundance was from nauplii. However, Seyoum Mengistou (1989) reported that more than 90% of the total zooplankton was contributed by adult cyclopoids while nauplii and *Diaphanosoma* form 20 and 10%, respectively. An adult to nauplii ratio of 0.27 in the present study also indicate that the adult number is very much smaller than its developmental stage nauplii. In short, the larger contribution of adult cyclopoid in previous time is replaced by nauplii in the present study.

Based on the above result, we may speculate that cannibalism may be very minimal in the present condition, which was a hypothesis forwarded before two and a half decades (Seyoum Mengistou, 1989). This again may temporarily tell us that the feeding and ecology of the cyclopoid zooplankton has changed within the given time. But on the other hand, there seems heavy predation on adult cyclopoids. The abundance is particularly very low in the littoral, since this is the area of nursery and feeding ground of juvenile and unexploited fishes, which may consume zooplankton at some stages of their developmental time (Fernando, 1983).

Zooplankton biomass (2.8 t km^{-2}) per surface area of Lake Awassa is very low when compared with other African lakes (L. Tanganika- 14.6-31.7 t km^{-2}, Moreau *et al.*, 1993; L. Naivasha -18.5 t km^{-2}, Mavuti *et al.*, 1996; L. Victoria -10.4 t km^{-2} , Moreau *et al.*, 1993; L. Kariba - 8.7 t km^{-2}, Machena *et al.*, 1993) but closer to L. Chad (3.4 t km^{-2} , Palomares *et al.*, 1993) and L. Ihema (4 t km^{-2}, Mavuti *et al.*, 1996).

Ecopath analysis

The estimated basic parameters including the catches and the diet matrix were assembled from different published literature data that were originally studied in Lake Awassa. Most of them are very reliable and detailed estimates. Moreover most of the functional groups are represented at species level, which increases the precision of the estimates. In addition to these, different professionals were consulted while constructing the model. Therefore the model appears to represent Lake Awassa very well.

The process of constructing an Ecopath model provides a valuable end product in itself through explicit synthesis of work from many researchers (Christensen *et al.*, 2000). After gathering and estimating all relevant information about the functional groups identified in Lake Awassa, a mass balance Ecopath software model was applied to the lake. Estimates of basic parameters (B, P/B, and Q/B) that are used for Lake Awassa are summarized in Table 5 from various sources. Diet compositions of all consumers of the ecosystem component were also assembled from different literature and other sources as shown in Table 6.

While balancing the model, four of the EE's exceeded 1 and hence was not mass balanced in the first run, as was expected (Tilapia-1.09, Juvenile Tilapia-4.553, Zoobenthos – 6.672, and carnivore zooplankton – 3.639). With the help of automated mass balance facility that Ecopath provides, and some manual adjustment of biomass and P/B values, the EE was reduced to less than one and the Ecopath model was finally mass balanced. These mass-balanced values (Table 7) are used in the analysis of Lake Awassa ecosystem. Thereafter, different routine of Ecopath was used to produce several EwE outputs.

In general estimated basic input parameters (Table 5) and result of mass balance (Table 7) are in agreement with each other except for some differences. Biomass discrepancy of Juvenile catfish and zoobenthos is larger than expected. Zoobenthos biomass is very high in the result of mass balanced maybe because in our biomass determination, we did not include chironomidea, ostracoda etc, which are very abundant in the lake (Tilahun Kibret, 1985).

Table 5. Basic input parameters used for Ecopath modeling analysis of Lake Awassa ecosystem.

Species/ Group	**Yield** $t/km^2/y$	**B** t/km^2	**P/B** y^{-1}	**Q/B** [b] y^{-1}
Catfish	5.11[a]	5.1[a]	1.3[a]	4.75
Juvenile Catfish		5.1[d]	2.09[b]	9.2
Large *Labeobarbus*		2[d]	0.33[b]	20.38
Tilapia	6.972[b]	8.6[b]	1.8[b]	29.53
Juvenile Tilapia		8.6[d]	1.2[b]	41.64
Aplocheilichtyes		2.62[b]	3.5[b]	36.51
Small *Labeobarbus*		3[d]	2.59[b]	18.51
Garra sp.		1.2[d]	2.68[b]	17.08
Zoobenthos		10.1[b]	4.21[b]	21.05
Carnivore Zooplankton		1.447[c]	18.7[c]	93.88
Herbivore Zooplankton		0.965[c]	236.4[c]	538.86
Phytoplankton		34.452[b]	286[b]	
Macrophytes		2000[b]	1	
Detritus		63.79[b]		

[a] Yosef Tekle-Giorgis (2002); [b] present study; [c] Seyoum Mengistou (1989); [d] guesstimates

Table 6. Diet matrix showing proportional diet composition for Lake Awassa Ecosystem trophic level (in % weight of stomach content)

Prey															
No	Predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
1	Catfish		4.2	2.3	40.89	20		17.1	2.8	2.57		0.14		4	6
2	Juv Catfish[a]					71.6	10			9.2	0.51	1.09		5.4	2.2
3	L. *Labeobarbus* [b]					20	9			60	1.5	2	0.8	6.7	
4	Tilapia [c]											2	96		2
5	Juv Tilapia [d]									40	7	13	40		
6	*Aplocheilichtyes.*[c]									20	40	30	10		
7	S. *Labeobarbus*[f]									35	40	20	5		
8	*Garra* [e]									80	7	8			5
9	Zoobenthos[g]									20	5	10	3	3	59
10	Carni Zoopl.[h]									10		68	12		10
11	Herbi. Zoopl[h]									8			85		7

Groups 12,13 & 14 are phytoplankton, macrophytes and detritus respectively.

[a] Elias Dadebo (2000) with some recent modification with the author

[b] Demeke Admassu and Elias Dadebo (1997)

[c] Getachew Teferra and Fernando (1989)

[d] Tudorancea *et al.,* (1988)

[e] Elias Dadebo (pers. comm.)

[f] Zerihun Desta (pers. comm.)

[g] Taken from lake Naivasha (Kenya) Mavuti *et al.,* (1996)

[h] Seyoum Mengistou and Fernando (1991)

Table 7. Basic parameters (result of mass-balance) used for analysis of Lake Awassa ecosystem.

Species/ Group	Trophic level	Yield ($t/km^2/y$)	B (t/km^2)	P/B (y^{-1})	Q/B (y^{-1})	EE	*Food intake	**GE
Catfish	3.33	5.11	4.1	1.3	4.75	0.957	19.475	0.274
Juvenile Catfish	3.37		0.418	2.09	9.2	0.988	3.8456	0.227
Large *Labeobarbus*	3.19		1.367	0.33	20.38	0.996	27.859	0.016
Tilapia	2.02	6.972	8.955	1.8	29.53	0.954	264.44	0.061
Juvenile *Tilapia*	2.58		6.5	1.2	41.64	0.984	270.66	0.029
Aplocheilichtyes	3.02		1.2	3.5	36.51	0.835	43.812	0.096
Small *Labeobarbus*	3.20		1.354	2.59	18.51	0.991	25.063	0.140
Garra sp.	3.05		0.24	2.68	17.08	0.894	4.0992	0.157
Zoobenthos	2.16		27.5	4.3	21.05	0.988	578.88	0.204
Carnivore Zooplankton	2.72		2.055	20	93.88	0.958	192.92	0.213
Herbivore Zooplankton	2.00		1.337	236.4	538.86	0.922	720.46	0.443
Phytoplankton	1		34.452	238.5		0.097		
Macrophytes	1		2000	1		0.014		
Detritus	1		63.79			0.061		

* Food intake is calculated as Q/B * B; **Gross efficiency is computed as (P/B)/ (Q/B) and is usually between 0.1 and 0.3 (Christensen *et al.* 2000).

Usually in the food chain, if one consumes the other, the biomass in the upper trophic level should be larger than its lower level. However here we assumed the biomass of catfish and juvenile catfish to be equivalent. Hence the biomass of Juvenile catfish reduced in the present analysis significantly perhaps to induce density dependent relationship. Sissenwine (1986) found that pre-recruitment fish are only 10% of the biomass of the exploitable part of the population.

Trophic flows

One of the characteristics of mass balance ecosystem models is that all flows and biomasses can be shown in a single flow diagram (Christensen *et al.*, 2000). This flow diagram for Lake Awassa, as estimated by Ecopath, is given in Figure 5. Once energy is incorporated into carbon bonds via photosynthesis, it is passed from organism to organism through the food chain. At each trophic level, some of the energy is used in respiration and is lost from the ecosystem in the form of heat. This means that there will be less energy available at each successive level in the food chain and in most cases, so does biomass (Odum, 1975).

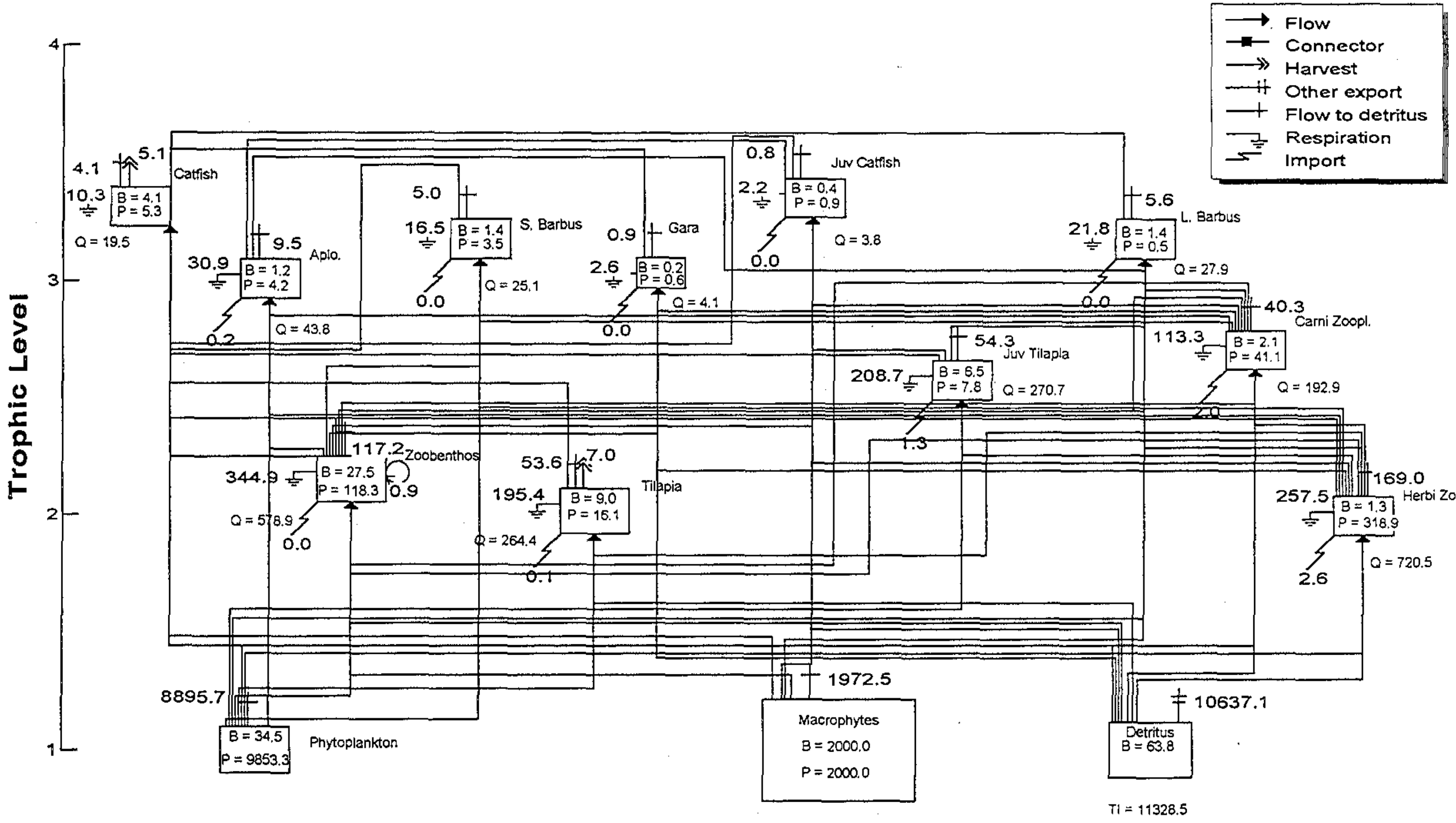


Fig.5. Flow diagram showing trophic flows in Lake Awassa. Flows are expressed in t/km2/year.

Flows from detritus were as important as flows from phytoplankton designating both detritus and grazing food chain in Lake Awassa (Table 8). The main sources for flow to detritus are phytoplankton and macrophytes, which contribute about 96% of the total flow (Figure 5). The larger trophic value is 3.37, which is an advantage as Odum (1963) indicated that the shorter the food chain the greater the available food energy.

In general, about 3 main food chain paths can be taken as example concerning the fishery of Lake Awassa.

➊ Phytoplankton– Herbivore/Carnivore Zooplankton–Unexploited fish–
Catfish

➋ Phytoplankton – Tilapia – Catfish

➌ Detritus – Zoobenthos – Large *Labeobarbus* – Catfish

Catfish may not gain the required amount of energy in the first food chain as most of the energy is lost in the long process. In addition, the energy transfer efficiency of carnivore zooplankton is much lower (mean 1.4%) than that of herbivores (mean 7.5%) (Brylinsky, 1980) and hence the link from carnivore zooplankton delivers little energy.

The second feeding path is very efficient for catfish for two reasons. One, the shorter the food chain, the greater the energy transfer. Two, since Tilapia is larger than the small sized unexploited fish species, catfish benefits by consuming larger food staff spending low energy and time to satiation.

The last food chain is a different one – it is detritus driven food chain. Catfish here may not benefit from this path as detritus has low energy value to transfer to the top predator. Besides catfish cannot easily catch *Labeobarbus* since the prey is fast swimmer than the predator (Table 3). But it is very important for Large *Labeobarbus*, which is a commercially important fish species in Lake Awassa. This fish species deserves due attention in food self-sufficiency program as detritus and zoobenthos are abundant to support the fish production. Exploiting this fish may give Tilapia break time from the current heavy exploitation to grow and reproduce in a sustainable way.

Table 8. Transfer efficiency of Lake Awassa by trophic level

Source\TL	**II**	**III**	**IV**	**V**	**VI**	**VII**
Producer	24.4	15.5	7.8	16.2	24.7	
Detritus	26.2	10.1	10.1	17.4	24.7	
All flows	25.2	13.1	8.6	16.6	24.7	26.2
Proportion of total flow originating from detritus: 0.48						
Transfer efficiencies (calc. as geometric mean for TL II-IV)						
From primary producers:14.3%						
From detritus: 13.9%						
Total: 14.2%						

TL- trophic level

Comparison of mixed trophic impact

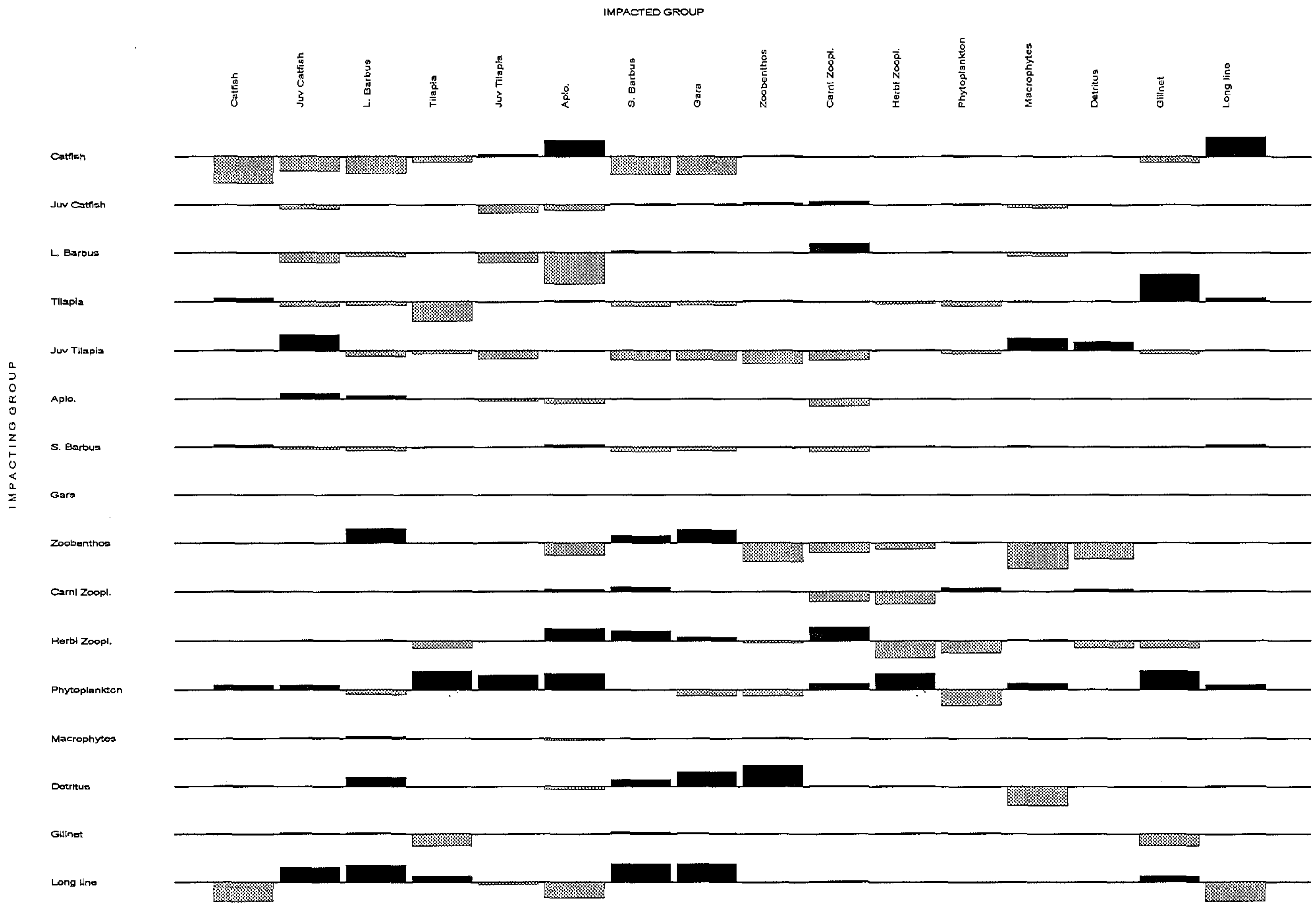
Ecopath gives the mixed trophic impacts within the ecosystem, which is shown in Fig. 6. Mixed Trophic Impact (MTI) allows assessing the impact that changes in biomass of a group will have on the biomass of the other groups in an ecosystem trophically (Christensen and Walters, 2000).

As a prey, a group causes a positive impact on its predators. As a direct predator, it has a negative impact on its prey. Phytoplankton and detritus have positive impact on most other groups. The impact was greatest on their direct predators. For instance, the impact of phytoplankton was greatest for herbivore zooplankton and Tilapia in Lake Awassa. On the other hand, herbivore zooplankton and Tilapia had negative impact on phytoplankton, the former being stronger (-0.283). Some examples of MTI and how to interpret the results are discussed below.

Catfish (an apex predator for this particular model) has a direct negative impact on its prey –Juvenile catfish, Large *Labeobarbus*, Tilapia, Small *Labeobarbus* and *Garra.* However, it has a cascading positive impact on *Aplocheilichthys*, which is the prey of Large *Labeobarbus* and Juvenile catfish. Large *Labeobarbus* in turn has a positive impact on carnivore zooplankton, as the former consume the predator of the latter (*Aplocheilichthys*, Small *Labeobarbus*, and *Garra*). Nevertheless due to the increase of carnivore zooplankton in biomass (predator of herbivore zooplankton), Large *Labeobarbus* seems to have a neutral effect on herbivore zooplankton, which otherwise should be positive.

The impact of catfish on Juvenile Tilapia is positive, even though the former feeds on Juvenile Tilapia directly. This may be because the catfish also feeds on the larger Tilapia, Larger *Labeobarbus* and Juvenile catfish and this overrules the direct impact of catfish on Juvenile Tilapia. Or it may be because catfish consume (and hence reduce) the abundance of Large *Labeobarbus* and Juvenile catfish, which are the main predators of Juvenile Tilapia, so that the latter prey species benefits from the interaction.

Figure 6. Mixed trophic impacts of the functional groups in Lake Awassa ecosystem showing the combined direct and indirect trophic impacts. Positive impacts are shown above each baseline in dark columns, while negative impacts are shown below the baseline.


IMPACTED GROUP
Catfish
Juv Catfish
L. Barbus
Tilapia
Juv Tilapia
Aplo.
S. Barbus
Gara
Zoobenthos
Carni Zoopl.
Herbi Zoopl.
Phytoplankton
Macrophytes
Detritus
Gillnet
Long line
IMPACTING GROUP
Catfish
Juv Catfish
L. Barbus
Tilapia
Juv Tilapia
Aplo.
S. Barbus
Gara
Zoobenthos
Carni Zoopl.
Herbi Zoopl.
Phytoplankton
Macrophytes
Detritus
Gillnet
Long line

Aplocheilichthys feeds on zoobenthos. Hence the increase of zoobenthos should be positive to *Aplocheilichthys.* However, zoobenthos have a negative effect to *Aplocheilichthys,* not in fact due to direct prey-predator relationship, but may be due to the interaction between zoobenthos and Large *Labeobarbus*. Zoobenthos is the main prey of Large *Labeobarbus* and its increase in biomass (abundance) benefits the predator. As a result, the increase of Large *Labeobarbus* negatively affects its prey *Aplocheilichthys*, which is an indirect effect.

Phytoplankton has a positive impact on catfish not because of being its direct prey but because it has a positive impact on the catfish prey (like Tilapia and Juvenile Tilapia) so that the prey food is available to catfish and results in a positive effect.

All the functional groups except detritus have a negative impact on themselves and this may show within group competition for resources (Christensen *et al.,* 2000). Detritus has neither positive nor negative impact to itself in many lakes including Lake Awassa; maybe because it is not a living organism.

Mixed trophic impact may help to explain short term changes (Mavuti *et al.,*1996) but it cannot be taken as an instrument for making medium or long term predictions (Christensen *et al.*, 2000).

Comparison of ecotrophic efficiencies (EE)

Ecotrophic efficiency, the proportion of the production that is consumed by predators or exported, varied considerably in this tropical African lake system (Table 7). All consumers have EE closer to 1 that shows full utilization of the animals. However the primary producers, macrophytes and phytoplankton including detritus, are far below under exploited.

Phytoplankton with EE= 0.097 indicates that a major part of the production dies off perhaps due to reduced predation pressure from the herbivore zooplankton, Juvenile Tilapia and Tilapia. That means supply exceeds demand, and with a fast turnover rate (238.5 y^{-1}), much of this excess production goes to detritus. This seems in agreement with Seyoum Mengistou (1989) who documented that herbivore grazers leave major portion of the phytoplankton uneaten based on the ratio of phytoplankton to zooplankton biomass. The observation of Tilahun Kibret and Harison (1989) also supported our result who stated that dead *Botryococcus* is the major organic matter in Lake Awassa. Microbial loop through bacteria and Protozoa is not included due to lack of data that may give some highlight on the flow, and this is a scope for future research in Lake Awassa.

The low EE of phytoplankton may be partially reasoned out by not including the bacteria in the model. Zinabu Gebre-Mariam (1988) reported that bacterial production (about 400 $mgCm^{-2}d^{-1}$) in Lake Awassa accounted for the removal of 8-30% of the gross primary production (about 359 mg $Cm^{-2}d^{-1}$), which seems a significant amount to contribute to higher ecosystem efficiency.

O. niloticus is a filter feeder, feeding mainly on phytoplankton in Lake Awassa. However, the low EE of phytoplankton triggers a question; does tilapia has an alternative source of food?

In Lake Awassa *Chroococcus, Oscillatoria and Botryococcus* were found to be an important diet of *O. niloticus* (Getachew Teferra and Fernando, 1989). These phytoplankton groups are less digestible. The author, for example, demonstrated that intact *Botryococcus* were found in the faeces of this herbivore fish indicating that hydrolysis of the food is dubious. Tudorancea *et al.* (1988) also reported a similar result for Juvenile Tilapia. On the other hand, the former author indicated that though not quantified, detritus was common in the stomach (sometimes full) of this fish in Lake Awassa. The energy source of suspended detritus for tilapia fish species was documented by Mann (1988).

The detritus that is found in the bottom of Lake Awassa which was constituted of dead phytoplankton – like *Botryococcus* –becomes suspended through frequent mixing of the lake. This tremendous amount of suspended detritus could be an important food source in Lake Awassa. But due to lack of distinguishing mechanism between ingested detritus and digested matter (Maitipe and Silva, 1985; Khoo and Tay, 1992) the proportion of digested matter and consequently live phytoplankton may be overestimated. Fange and Grove (1979) also reported that detritus may be considered as live phytoplankton as the herbivores have higher rate of digestion, hence overestimating the importance of phytoplankton.

In Lake Awassa detritus may be an important source of food, even comparable to live phytoplankton to Tilapia species (See Table 8). Getachew Tefera and Fernando (1989) suggested that detritus may be an important food source for Tilapia in Lake Awassa. Zenebe Tadesse (1999) reported that detritus was the major portion of tilapia diet in Lake Langeno. Studies in other lakes also showed that *Oreochromis* can sustain very well on detritus diet (Bowen, 1980; De Silva *et al.*, 1984) which suggests a critical re-investigation of Tilapia's food in Lake Awassa.

The EE values of macrophytes (EE=0.014) is very low adding considerable amounts of biomass to the detritus box in this model (Figure 3). Lower utilization of macrophytes may be due to excluding the African Hippo that consumes much of the macrophytes in the lake and/or may be the biomass was overestimated. The biomass of macrophytes is exactly equal to Lake Chad (2000 t km^{-2}, Machena *et al.,* 1993) but higher to many other African lakes (such as L. Kariba -187.8 t km^{-2}, Palomares *et al.*, 1993; Lake Naivasha - 170.4 t km^{-2}, Mavuti *et al.,* 1996).

Detrital biomass (63.79 t km^{-2}) was calculated taking only primary productivity of phytoplankton into consideration. A significant amount of macrophytes' (and periphyton) primary productivity was not included in the biomass calculation. Hence lower detritus biomass is reported in Lake Awassa than other tropical lakes (L. Turkana -415 t km^{-2}, Kolding, 1993; L. Kinneret -75 t km^{-2}, Walline *et al.,* 1993) though it is higher than L. George (10 t km^{-2}, Moreau *et al.,* 1993). Since Lake Awassa is a closed lake, detritus export is impossible and the value should be higher than we reported here.

Carnivores zooplankton consumes herbivore zooplankton and both of them are highly exploited by the unexploited fish species. The latter fish species (*Aplocheilichthys*, small *Labeobarbus* and *Garra*) are consumed by catfish, Juvenile catfish and Large *Labeobarbus* and here zooplankton is a link to the higher trophic level, contrary to the hypothesis of Seyoum Mengistou (1989) who stated that carnivore cyclopoid copepoda is a sink not a link, based on the previous condition and the nature of the species. This change is mainly due to change of zooplankton feeding trend. However, it is not a good and decisive link as observed in other lakes as a significant amount of phytoplankton biomass (primary production) is unutilized and goes to detritus. Detail study of zooplankton feeding behavior and its role in the food chain of Lake Awassa is undoubtedly very important.

Strong top-down effects on phytoplankton, including order-of-magnitude reductions of phytoplankton biomass, have been reported for cladoceran- dominated zooplankton in lakes (Sommer, 1986; Lampert, 1988). However herbivore zooplankton in Lake Awassa did not follow similar trends. First, the larger herbivore *Daphnia* that is largely responsible for grazing is absent (Seyoum Mengistou, 1989). Second, large colonial and filamentous phytoplankton species dominate the lake, which are unpalatable to herbivore species, particularly to the smaller sized *Diaphanosoma*. Third, herbivorous zooplankton is heavily predated by the planktivore species (carnivorous zooplankton and unexploited fish species) keeping the abundance very low and make them inefficient to utilize large phytoplankton biomass available. The abundance of cladocera in Lake Awassa is very low, even to the extent of being non-existent in some months of the present study. Lower cladocerans number was also reported by other researchers in the same lake (Seyoum Mengistou, 1989; Zinabu Gebre-Mariam, 1988). Duncan (1978) reported little or no cladocera and copepoda due to planktivorous fish in Sri Lankan reservoir. Due to these reasons, herbivore zooplankton does not control the phytoplankton biomass in Lake Awassa.

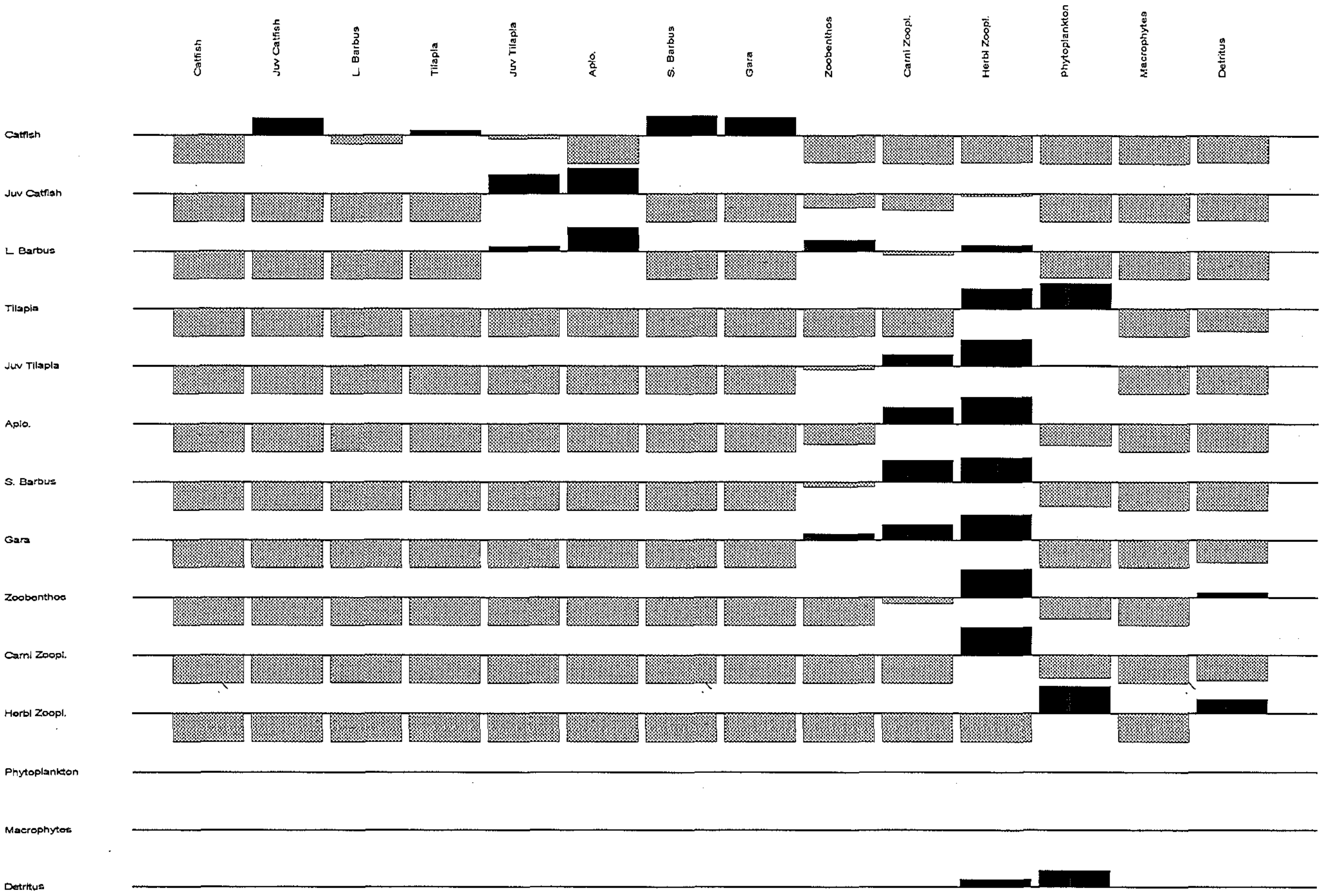
Electivity graph explains the preference diet of the consumers. Herbivore and carnivore zooplankton are preferred by many organisms; particularly the former is a favorite one (Figure 7). This shows that the species is predated heavily by several consumers and that is why they are very low in abundance, even to the extent of absence in some months of our samples.

On the other hand, zooplanktivory shapes the size and composition of zooplankton. Heavy predation on herbivore zooplankton reduces the size of the cladocera to small sized, which make them unable to utilize the low food quality available in Lake Awassa (Filamentous and colonial phytoplankton taxa). These reinforce the above explanation about the inefficiency of cladocera to consume large amount of phytoplankton. Since cladocera are slow and highly exposed to predators, their strategy to cope up with the heavy predation should be studied in future.

An interesting result of Ecopath is the EE of Large *Labeobarbus* (0.996) that is very much higher value than expected and seems paradoxical. The impact of the fishery in Lake Awassa consisted mainly of removing *O. niloticus* and catfish. Large *Labeobarbus* species is not exploited by the fishery, it is rather a by-catch by gillnets set for Tilapia. Higher EE may be due to lower estimate of biomass and P/B values. The biomass value was a guesstimate and the P/B represents only the natural mortality excluding the fishing mortality since it is considered as virgin stock. Large *Labeobarbus* deserves due consideration in future work as Demeke Admassu and Elias Dadebo (1997) believe that Large *Labeobarbus* is the second most abundant species following the commercially important *O. niloticus*.

Among the food sources, zooplankton, zoobenthos, phytoplankton, macrophytes and detritus, the former two groups are heavily consumed with EE 0.958 and 0.912, respectively. Therefore, energy flows to higher trophic levels are very low from phytoplankton, macrophytes and detritus (see Table 8). However, the EE value of zooplankton, Tilapia, Catfish, *Labeobarbus*, unexploited fish species and zoobenthos indicates that they are fully utilized in the ecosystem, which according to Dickie (1972) is unsustainable. He stated that ecotrophic efficiency in nature is unlikely to exceed a value of about 0.5.

Fig. 7. Electivity graph for Lake Awassa


Catfish
Juv Catfish
L. Barbus
Tilapia
Juv Tilapia
Aplo.
S. Barbus
Gara
Zoobenthos
Carni Zoopl.
Herbi Zoopl.
Phytoplankton
Macrophytes
Detritus
Catfish
Juv Catfish
L. Barbus
Tilapia
Juv Tilapia
Aplo.
S. Barbus
Gara
Zoobenthos
Carni Zoopl.
Herbi Zoopl.
Phytoplankton
Macrophytes
Detritus

Summary of *system statistics*

The result of Ecopath, system statistics, is shown in Table 9. The fishery has a low mean trophic level of 2.57 probably due to absence of specialized top predators and energy transfer efficiency seems better in the lake ecosystem as the food chain is short. However the ecological efficiency appears low. Ecological efficiency is a measure of the amount of energy transferred between trophic levels. It usually ranges from 0.05 to 0.2, i.e. 80-95% of the energy is lost at each transfer in the food chain (Lampert and Sommer, 1997).

Lake Awassa has low ecological efficiency as compared to other African lakes. The gross efficiency of the fisheries (actual catch/primary production) is 0.001 (Table 9), which indicates the inefficiency of the system. A very similar result was reported by Seyoum Mengistou (1989) that only a tiny fraction (0.0049 to 0.0067) of the carbon in phytoplankton ends in fish. Based on the present result, Lake Awassa is lower than L. George (0.0057, Moreau *et al.,* 1993) and L. Victoria (0.0082- after the introduction of Nile perch -- Moreau *et al.*, 1993) but closer to L. Victoria (0.0016- prior to the introduction of Nile perch- Moreau *et al.*, 1993) and slightly higher than Lake Ihema (0.0007) and Lake Naivasha (0.0009, Mavuti *et al.*, 1996).

The lower values of EE for food sources (phytoplankton, macrophytes and detritus) in Lake Awassa contribute to explain the low ecological efficiency of the system.

Table 9. Summary of system statistics obtained for Lake Awassa from Ecopath. (Flows are in kg/m^2/year; trophic level and gross efficiency are dimensionless)

Parameter	Value
Sum of all consumption	2151.517
Sum of all exports	10649.21
Sum of all respiratory flows	1204.062
Sum of all flows into detritus	11328.46
Total system throughput	25333
Sum of all production	12370
Mean trophic level of the catch	2.57
Gross efficiency (catch/net p.p)	0.001018
Total primary production/total respiration	9.844
Net system production	10649.21
Total primary production/total biomass	5.673
Total biomass/total throughput	0.082

System primary production /respiration (P/R): This is the ratio between total primary production (Pp) and total respiration (R) in a system. Odum (1969) demonstrated that P/R ratio describes the maturity of an ecosystem. The rate of primary production exceeds the rate of community respiration during early stages of ecosystem development, and hence P/R is greater than one. However in mature system the ratio approaches one in that energy fixed tends to be balanced by the energy cost of maintenance. Within this context, P/R ratio of Lake Awassa is 9.844, which is much larger than 1, leading to a conclusion that Lake Awassa is relatively at developmental stage or a young ecosystem.

A young ecosystem means it has not finished its ecological succession and the lake is naturally under changing conditions from time to time until a climax stage is reached. Since it is vulnerable for perturbation, extra care should be given to human intervention. Odum (1969) indicated that developmental stages are poor in resistance to external perturbations.

The other summary statistics (in Table 9) are meant to express the relative degree of maturity of an ecosystem. Some are explained below.

1. Net system production is the difference between total primary production and total respiration. The net system production will be large in immature systems and close to zero in mature ones.
2. Total primary production /total biomass ratio is also expected to be a function of its maturity. In immature systems, production exceeds respiration, and as a consequence, one can expect biomass to accumulate over time. This in turn will influence the system Pp/B ratio, which may decrease.
3. Total biomass/total throughput can be expected to increase to a maximum for the most mature stages of a system.

Yosef Tekle-Giorgis (1990) has hypothesized that higher density of immature *O. niloticus* may have stunted their growth. One reason for this was the presence of catfish as the only and slight predator of Tilapia.

However, in the present analysis Tilapia is heavily predated by catfish (adult and juvenile – see Table 6) and also by Large *Labeobarbus* (though slight). Large amount of

Tilapia biomass is also exported by human being. In addition to this a significant amount of Tilapia biomass is removed by fish-eating birds as indicated in other lakes (Mavuti *et al.*, 1996; Winkler, 1983; Schiemer and Duncan, 1987). The commercial size of the fish is also smaller than before (15cm in the present study than 18cm in Elias Dadebo, 2000) that may be the result of heavy exploitation. Accordingly it seems that density of the fish may not be a factor that limits the growth of Tilapia in Lake Awassa at present.

In Lake Awassa, catfish is the top predator excluding fish eating birds, even though unoccupied niche may be available in the open water. Hence only fishing contributes to its high EE value. This figure indicates that over-fishing is exercised. This result is in agreement with Yosef Tekle-Giorgis (2002) who stated that this species is getting exploited in the lake. Similarly, Tilapia (EE=0.954), which constitutes the bulk of the actual catch and of the major food of catfish, is over fished. This scenario was also documented by LFDP (1998).

5. Conclusion and recommendations

Whole lake ecosystem work using Ecopath with Ecosim model was exercised in Lake Awassa to introduce the principles and working of mass balance model. From the present analysis, we have been able to identify that the producers (Phytoplankton, macrophytes including detritus) are not well exploited by the organisms in the system and energy transfer to higher trophic levels are very low. This indicates that the primary production can support much more than the present herbivorous animals. In contrast the consumers are highly exploited by the system. Tilapia with EE=0.954, for example, is overexploited which is in agreement with LFDP (1998).

Practical and sound management is required for sustainable and efficient use of the lake. Critical investigation and interdisciplinary understanding is indispensable for a clear holistic picture of an ecosystem. Lakes should not be focused from the fisheries point of view only but the biology of the lake including diversity and conservation should also be given due consideration. Now-a-days, Lake Awassa is also becoming the site of tourism industry in addition to the fishery and any managerial decision must also take this into consideration. Another important management measure is to reduce the number of net set per day and to increase the mesh size of the net. This is particularly important for Tilapia during the breeding season.

The analysis also reveals that the lake is in developmental stage, which means it is very vulnerable for small perturbation, be it naturally or antropogenically-induced. Extra care should be given to maintain the natural and gradual development of the lake. On the other hand, young ecosystem means production is very high and we can exploit carefully in food self-sufficiency programs of the country. Ecopath enable us to evaluate the previous works and also to pinpoint critical gaps in the present knowledge.

The 13 ecotrophic groups that were used in this study are not the only important functional groups in Lake Awassa. Hence it should not be viewed as a complete analysis of the ecosystem. Fish eating birds and the African Hippo are also important groups, though they are not included in the present ecosystem work, mainly due to lack of information. Fish eating birds consume considerable amount of fish biomass. Cormorants alone, for example, consumed about 15 kg C $ha^{-1}y^{-1}$, which corresponded to the yield of the commercial fisheries in Sri Lanka reservoir (Winkler, 1983; Schiemer and Duncan, 1987). These cormorants, white-breasted and long tailed cormorants, are found in Lake Awassa in significant numbers. Mavuti *et al.* (1996) also reported that fish eating birds consumed 3.77 tkm^{-2}, almost twice the catch by fishermen in Lake Naivasha; indicating that the study of fish-eating birds in Lake Awasa is mandatory. Fish eating birds are important for the ecology of the lake primarily by removing fish biomass. Their feeding habit, abundance, biomass, mortality etc should be studied in the future in order to be included in such type of work.

The abundance, biomass, morality, feeding habit, reproduction etc of un-exploitable fish species; and the potential yield of Large *Labeobarbus* including the former parameters should also be studied.

No information is available for biomass, production and consumption of zoobenthos, which otherwise are very important in the food chain of tropical lakes (Fernando, 1994) including Lake Awassa.

Detritus driven food chain is very important but has not got due attention in our lakes. The main component of detritus, its chemical composition, biomass and clear-cut role in the food chain of Lake Awassa should also be examined.

The importance of rotifer in the food chain of Lake Awassa is not known (Seyoum Mengistou *et al.,* 1991). Ciliates may be important bacterial grazers in Lake Awassa (Zinabu Gebre-Mariam, 1988). The production, abundance, biomass, feeding habit, etc, of rotifers and ciliates should be studied as they are also members of the food chain in Lake Awassa. The microbial loop seems an important food chain in the lake.

The species composition of macrophytes was studied by Tilahun Kibret (1985). However its primary productivity, biomass etc are open to research.

There seems to be huge and unexploited phytoplankton production that needs due attention in future works in order to understand profoundly how and when to utilize this important primary resource.

After including the above important information and further refinement of the whole parameters, Ecopath should be run again for Lake Awassa. It should be noted that a balanced model does not imply accurate depiction of the existing condition. The predictions are only as reliable as the input parameters used. Better estimates used produce better representatives of the reality (Christensen *et al.,* 2000). Hence tuning-up all parameters including diet matrix is very important in order to have a clear picture of the lake. However the present analysis delivers essential baseline information from holistic point of view and identifies critical gaps in the present knowledge about Lake Awassa.

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Appendices

Appendix 1

Zooplankton species composition of Lake Awassa

Cladocera	Copepoda	Rotifera
Diaphanosoma sp.	*Mesocyclops sp.*	*Asplachna sp.*
Moina sp.	*Thermocyclops sp.*	*B. calyciflorus*
		Brachionus quadridentatus
		B. caudatus
		Filinia longiseta
		F. terminalis
		Keratella valga
		Lecane sp.
		Trichocerca elongata

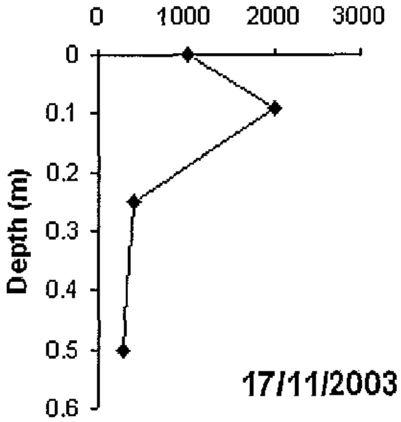
Appendix 2.

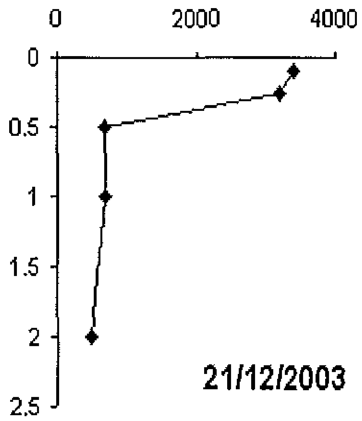
Phytoplankton biomass ((μgL^{-1} Chl 'a') values in two stations of Lake Awassa

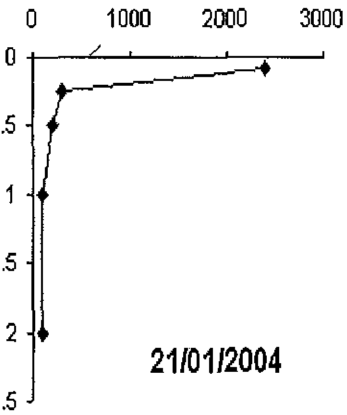
Months	Station 3	Unique Park
Nov	20.5	18
Dec	18.66	16.09
Jan	20.85	17.5
Feb	25.21	21.32
May	10.43	12.97
Jun	19.62	17.38
Jul	20.38	21.8
Aug	21.62	24.56

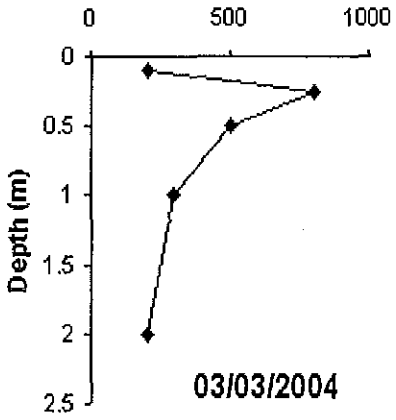
Appendix 3

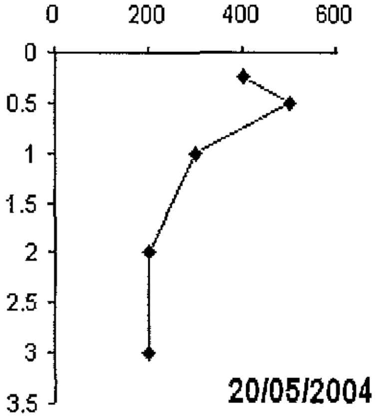
Primary Productivity of Lake Awassa in $mgO_2m^{-3}h^{-1}$ in Station 3 and Unique Park from December 2003 - August 2004.

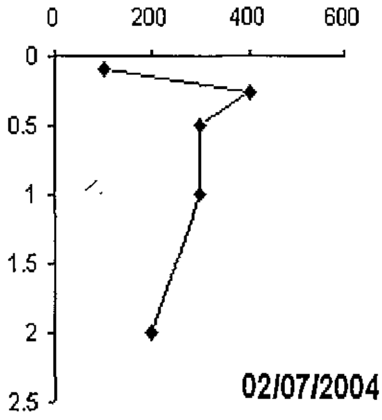


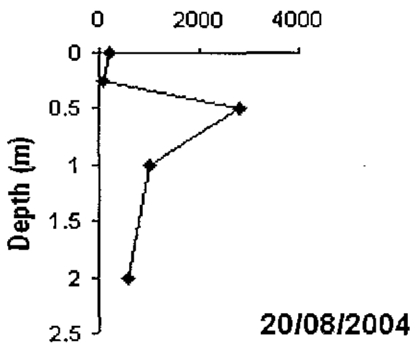




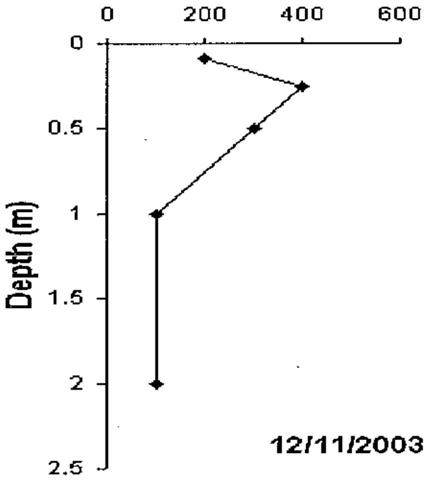








Unique Park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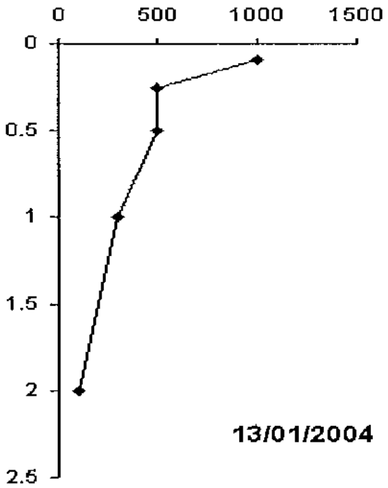
200
400
600
0
0.5
1
1.5
2
2.5
Depth (m)
12/11/2003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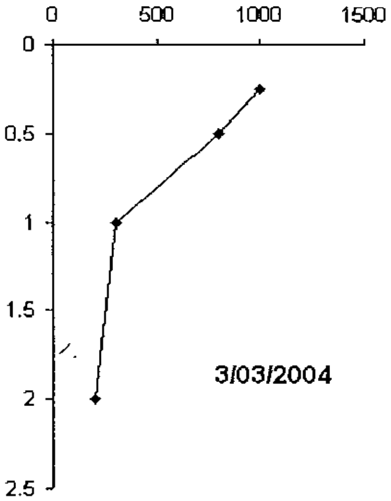
2.5
13/01/2004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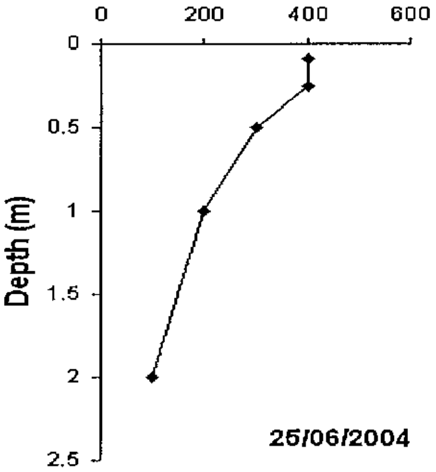
2.5
3/03/2004


0
200
400
600
0
0.5
1
1.5
2
2.5
Depth (m)
25/06/2004

Appendix 4

Phytoplankton taxa of Lake Awassa

Green algae	Blue green	Diatoms	Euglinoid
Ankistrodesmus			
Botryococcus sp.	*Anabena spp.*	*Cymbella*	*Phacus sp.*
Coelastrum spp.	*Limnothrix planctonics*	*Fragilaria*	
Cosmarium spp.	*Lyngya circumreta*	*Melosira spp.*	
Crucigenia quadrata	*Merismopedia glauca*	*Navicula spp.*	
Golenkinia sp.	*M. punctata*	*Surirella 1*	
Kirchneriella sp.	*Microcystis spp.*	*Surirella 2*	
Oocystis borgei	*Planktolyngyba regularis*	*Synedra*	
Pediastrum boryanum (Turp.) Meneghini	*Pseudoanabena limnetic*		
P.boryanum var. typicum	*Spirulina sp.*		
P.duplex			
P.duplex var. gracillium West & West			
Pediastrum simplex1			
Pediastrum simplex2			
Scenedesmus acuminatus			
S.acutus			
S.ecornis			
S.quadricauda			
Staurastrum spp.			
Straudesmus sellatus			
Tetrastrum sp.			

Appendix 5

Zoobenthos of Lake Awassa

Groups	Number (A)	Total volume(ml)	Total weight(g)	Single Weight(g)(B)	A*B	Length (cm)
Coleoptera	20	0.7	0.51	0.0255	0.51	0.8, 0.9
Bulinus	127	6.5	7.2	0.0567	7.2	0.8, 0.4
Melanoides	20	0.16	2.33	0.1165	2.33	3, 1.2, 0.8
Biomphilaria	10	0.8	0.83	0.083	0.83	1.3, 0.7, 0.3
Damselfly larvae	19	0.8	0.59	0.0311	0.5909	1.9, 1
Waterbugs (Diptera)	68	0.7	1.16	0.0171	1.1628	0.9, 0.6,0.5
Ephemeroptera	14	0.7	0.49	0.035	0.49	2.2, 1.5
Hydracarina	9		0.05	0.0056	0.0504	0.2
Dragonfly larvae	2	0.2	0.17	0.085	0.17	1.7, 1
Total	289		13.33		13.335	

Appendix 6

Out put from the length based Thompson and Bell yield prediction model for the *Oreochromis niloticus* caught off Lake Awassa

Length group (cm) (L1-L2)	Annual catch C(L1,L2)	Population Number N(L1)	Fishing mortality (yr^{-1}) F(L1,L2)	Mean weight (kg) W(L1,L2)	Annual yield (tons) Y(L1, L2)	Annual mean biomass (tons) B(L1,L2)
15-16	4470	5333439	0.006	0.072	0.32	50.76
16-17	23784	4978318	0.035	0.087	2.08	59.42
17-18	48030	4614471	0.073	0.104	5.01	68.36
18-19	150310	4238675	0.242	0.123	18.53	76.54
19-20	284501	3777859	0.501	0.144	41.08	81.93
20-21	470007	3209648	0.966	0.168	78.89	81.68
21-22	442611	2496320	1.131	0.194	85.73	75.78
22-23	452748	1858097	1.532	0.222	100.55	65.64
23-24	332644	1257569	1.592	0.253	84.2	52.89
24-25	234913	820455	1.646	0.287	67.4	40.96
25-26	129507	514172	1.332	0.324	41.91	31.47
26-27	88543	336050	1.312	0.363	32.17	24.52
27-28	55424	213764	1.199	0.406	22.51	18.78
28-29	35692	135220	1.133	0.452	16.14	14.25
29-30	21955	83770	1.033	0.502	11.01	10.66
30-31	15758	51188	1.139	0.555	8.74	7.67
31-32	7281	28511	0.827	0.611	4.45	5.38
32-33	5317	16829	0.950	0.671	3.57	3.76
33-34	4357	8714	0.500	0.735	3.2	6.41
Total	2807852	33973068			627.5	776.85