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Analysis of trophic relationships in two shallow equatorial lakes Lake Naivasha (Kenya) and Lake Ihema (Rwanda) using a multispecifies trophic model

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Abstract

A multispecifies trophic model called ECOPATH II, which can be used to describe the trophic relationships in aquatic ecosystems on a quantitative basis, is briefly presented. When properly used, it can help to explain the trophic relationships in ecosystems and possible evolution of fishstocks after modifications of the environment (e.g. eutrophication, introduction of a new population and/or a significant increase of the fishing effort), and to compare the trophic structure of several ecosystems. Examples are provided on two shallow lakes: Lake Ihema and Lake Naivasha. They are compared with Lake George which was previously documented.

Introduction

Understanding of the functioning of a complex ecosystem and of the possible impacts of different kinds of ecological changes on the system as a whole, calls for quantification of the trophic relationships between the different groups in the system. This is one reason why Polovina (1984) developed the ECOPATH model which is a steady state model of trophic interactions in ecosystems. Using ECOPATH a system is partitioned into boxes comprising species having a common physical habitat, similar diet and life history characteristics (Polovina, 1984; Christensen & Pauly, 1992b). When necessary, the model produces estimates of mean (annual) biomass, (annual) biomass production and (annual) biomass consumption for each of the boxes in the ecosystem. The ECOPATH model assumes that the ecosystem considered is at equilibrium conditions, which means that input to a group should equal output from it for the period considered. This steady state condition makes possible to establish a system of biomass budget equations which, for each group, is:

$$\text{Production} - \text{all predation} - \text{non predatory mortality} - \text{all exports} = 0$$

ECOPATH expresses each term in this budget equation as a linear function of the mean biomass. The resulting equations become a system of simultaneous linear equations. The relative simplicity of the ECOPATH model compared to other multispecific models (e.g. simulation models such as Andersen & Ursin, 1977; Laevastu & Larkin, 1981) is apparent in its application to several marine and continental ecosystems (Christensen & Pauly, 1992a). The aims of this paper are:

(1) To introduce the reader to the ECOPATH II model and software, an improved version of the original ECOPATH model of Polovina (1984), as presented by Christensen & Pauly (1992b).

(2) To describe two different ecosystems: the shallow lakes Naivasha and Ihema (Figures 1 and 2) which

have been studied in the past by several specialists of different groups (see Beadle, 1981; Payne, 1986; Burgis & Symoens, 1987; Harper *et al.*, 1990; Mavuti, 1992; Plisnier, 1991; for review).

(3) To compare the results with the similar ones obtained in Lake George (Moreau *et al.*, 1993) which had been previously documented in detail (Burgis & Dunn, 1978).

This paper will also help to add two new ecosystems to the already numerous ones which have been analysed and compared by Christensen & Pauly (1993).

Two shallow lakes: Lake Naivasha and Lake Ihema

Lake Naivasha, Kenya (latitude 0° 45′ S, longitude 36° 20′ E, altitude 1890 m a.s.l. and area approximately 140 km^2) is a tropical freshwater lake in a closed basin in the eastern Rift valley of Kenya and approximately 100 km north west of the capital city, Nairobi. It has not surface outlet but the freshness of the water is maintained by dilute inflows, biochemical and geochemical sedimentation. The level of the lake has fluctuated tremendously in the recent past due to climatical and rainfall variations within the lake catchment. However, at all levels, the edge of the lake is fringed by emergent aquatic plants (Harper, 1992). The recent evolution of the lake is summarized in Fig. 1 and only the most recent phase refered to as the recovery phase (Harper, 1992) will be considered here. The level of the lake is rather low (mean depth: 5.5 m) the littoral aquatic vegetation has been reduced and the biomass of phytoplankton has increased significantly. Continuous increase of nutrient concentration shows the progressive eutrophication of the lake. The fisheries deal only with introduced populations (Welcomme, 1988): the largemouth black bass, *Micropterus salmoides, Oreochromis leucostictus, Tilapia zillii* and a crayfish, *Procambarus clarkii.* The crayfish population is expected to have reduced the abundance of macrophytes and has itself subsequently declined drastically to a low density of 0.2 to 0.3 individuals km^2 (Harper, 1992). Important populations of fish eating aquatic birds are permanently established around the lake.

Lake Ihema, Rwanda (latitude 1° 43′ S, longitude 31° 45′ E, altitude 1291 a.s.l. area approximately 90 km^2) is also a shallow lake (mean depth 4.5 m) situated in the Akagera basin. Its only tributary and outlet is the Akagera River and the level of the lake is closely related to the level of the river. The phytoplankton and primary production are quite abundant and the lake is considered as eutrophic (Kiss, 1976). At all the lake levels, the edges are fringed with littoral aquatic vegetation. The commercial fisheries species are composed of a catfish: *Clarias gariepinus* and several Tilapiine species: *O. niloticus, O. macrochir, O. leucostictus* and an hybrid of uncertain systematic position locally called "Tilapia intermediaire" (Plisnier *et al.*, 1988). An important unexploited stock of Haplochromines has also been described (Plisnier, 1991); other fish species are of very marginal importance. The lake is included in the Akagera National Park and displays an important aquatic avifauna (CECODEL, 1988).

Material and methods

ECOPATH II, as used here is a modified version by Christensen & Pauly (1992) of the ECOPATH model proposed by Polovina (1984); Polovina & Ow (1985).

The first step in this modelling exercise is to determine the main components and the feeding network of these groups in the ecosystem. The data inputs required by ECOPATH II are assembled and standardized (e.g. to t km^{-2} fresh weight) for each component group.

It should be noted that the records available for use in this simulation effort describes only the recent years of Lake Naivasha (refered to as the third phase by Harper (1992) and to the conditions of maximum sustainable yield (as defined by Munyandorero, 1993), which seem to have occurred in 1985–1987 in Lake Ihema.

For each group, the main assumption of ECOPATH II is:

Ecological production = actual catch
+ what is consumed of it by all its predators
+ amount of production which goes to the detritus.

The basic equation of ECOPATH II is that for each group (i) explictely included in the model:

$$B_i(P/B)_i EE_i = Y_i + \Sigma_j(B_j Q/B_j DC_{ji}), \quad (1)$$

where B_i is the biomass of the group i, (P/B_i) its production/biomass ratio, EE_1 its ecotrophic efficiency, Y_i its yield (= fishery catch), B_j the biomass of its predator j, Q/B_j the food consumption per unit biomass of j, and DC_{ji} the fraction of i in the diet of j.

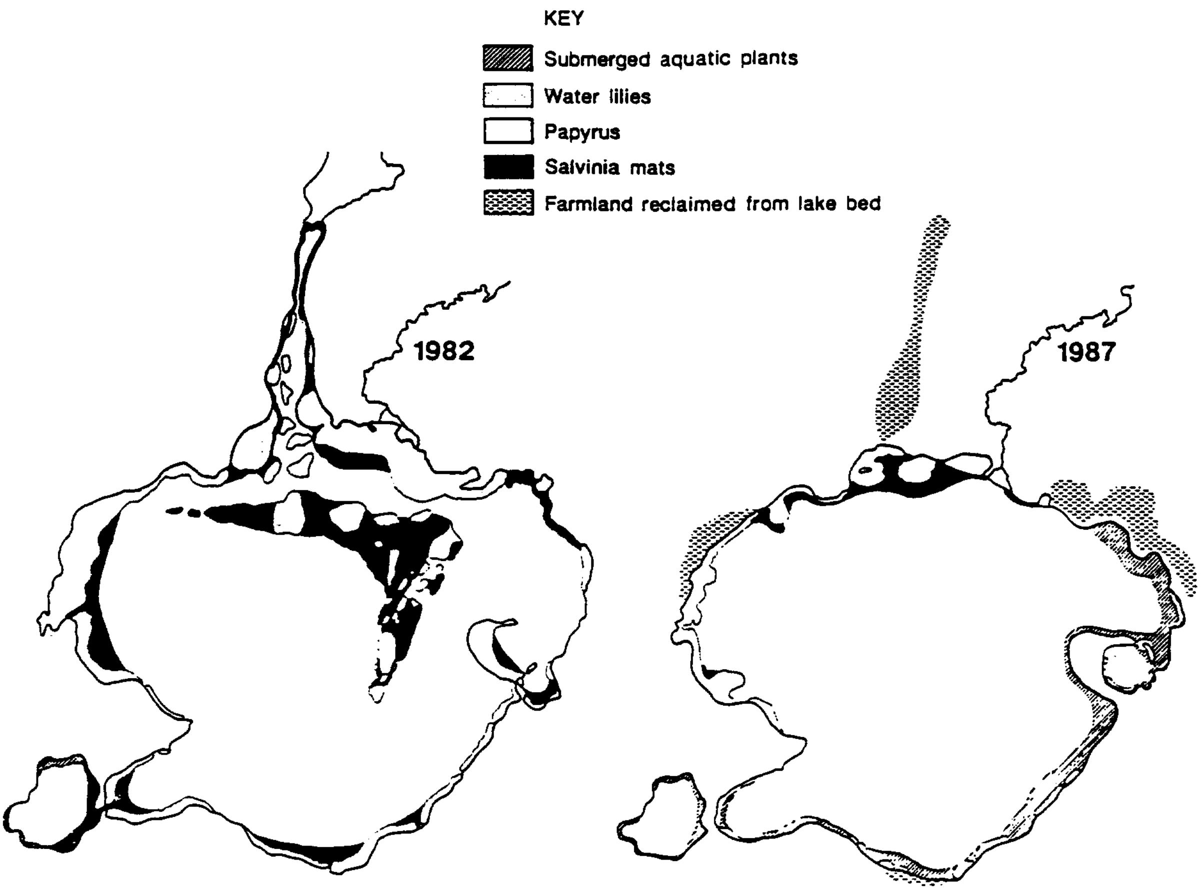

Fig. 1. General map of Lake Naivasha showing the recent evolution of the lake as described by Harper (1992).

This equation implies equilibrium (i.e. biomasses are at the end of the period considered equal to those at the beginning of that period).

Tables 1 and 2 present the groups used to describe the two different ecosystems.

When unavailable from the literature, biomasses were estimated via ECOPATH II, i.e. via a system of linear equations such as (1), for which estimates of most parameters were provided, as follows. Otherwise, one of the other parameters of the equation 1 was estimated.

Fisheries catches (Y)

Catch estimates were obtained from records of the Department of Fisheries of Kenya for Lake Naivasha and from Munyandorero (1993) for Lake Ihema. They are expressed here, like all other flows, in m t wet weight km^{-2} year^{-1} (Tables 1 and 2).

Production/biomass ratio (P/B)

As shown by Allen (1971), under an equilibrium assumption, and when the von Bertalanffy growth function (VBGF) can be assumed (as is here the case), P/B is equal to Z as defined in fisheries science and as available from the literature (Tables 1 and 2). Hence, when necessary, we have estimated this parameter for the fishes from length frequency data as outlined in Gayanilo *et al.* (1989). For the other groups, literature values were taken, some of them from Winberg (1971) and Payne (1986). All values of P/B presented here are annual.

Diet composition (DC)

The average composition of the food of each consumer organism in Tables 1 and 2, in terms of preys also included in those Tables, refers to weights, and was

Table 1. Key features for ECOPATH modelling of Lake Naivasha Ecosystem: (currency t km^{-2})

Group	Export (fisheries)	Biomass	P/B	Q/B	EE	Food intake	Gross efficiency	Flow to detritus
Fish eating birds		0.065 a	30.0 a	58.0 b	0.00	3.8	0.005	0.77
Black bass	0.4	3.6	0.7 c	6.5 d	0.95	23.5	0.108	4.83
O. leucostictus	1.0	7.7	1.3 c	19.0 d	0.95	146.4	0.068	29.78
T. zillii	0.05	1.1	1.3 c	19.0 d	0.95	21.7	0.068	4.42
Crayfishes	0.7	4.5	3.5 e	35.0 f	0.95	157.5	0.100	32.33
Zooplankton		18.5 g	28.0 g	150.0 f	0.61	2700.0	0.187	778.09
Zoobenthos		18.3	4.5 h	30.0 f	0.95	550.1	0.150	114.15
Phytoplankton		40.0 j	61.2		0.95			122.33
Benthic Producers		40.5	5.0 h		0.95			10.12
Macrophytes		170.4	1.0 k		0.50			85.22
Detritus		5.0			0.45			

(a) Brown & Hopcraft (1973). (b) Sumba (1983). (c) Dadzie & Aloo (1990); Merona (1983); Lévêque *et al.* (1977). (d) Palomares (1991). (e) Payne (1986); Winberg (1971). (f) Values adopted for a reasonable gross efficiency (Moreau *et al.*, 1993). (g) Mavuti (1983). (h) Symoens *et al.* (1980); Moreau *et al.* (1993). (j) Harper (1992). (k) Palomares *et al.* (1992).

Table 2. Key features for ECOPATH modelling of Lake Ihema ecosystem: (currency t km^{-2})

Group	Export (fisheries)	Biomass	P/B	Q/B	EE*	Food intake	Gross efficiency**	Flow to detritus
Fish eating birds	0.000	0.03 a	0.25 a	58.0 a	--	1.7	0.004	0.75
Catishes	0.800	3.20	0.85 b	5.0 c	0.85	15.8	0.170	7.57
Tilapiines	1.800	9.80	1.30 d	32.0 c	0.95	314.5	0.040	63.55
Arpagochromis	0.005	1.30	1.40 e	10.5 c	0.95	13.4	0.130	2.82
Insect. Haploch	0.010	2.80	2.10 e	13.5 c	0.92	37.8	0.156	8.05
Plank. Haploch.	0.010	2.40	4.10 e	40.5 c	0.93	96.0	0.100	20.50
Other fishes	0.030	1.50	1.00 e	11.0 c	0.95	16.7	0.090	3.41
Zooplankton		4.00	28.00 f	160.0 h	0.80	638.1	0.176	149.67
Zoobenthos		21.50	4.50 g	30.0 h	0.95	646.4	0.150	2417.33
Phytoplankton		19.00 j	180.00 k	--	0.29	--	--	10.68
Benthic prod.		43.00	5.00	--	0.95	--	--	

(a) CECODEM (1988); Sumba (1983). (b) Munyandorero (1993). (c) Palomares (1991). (d) Muganda (1989). (e) Maximum observed length from Fourniret *et al.* (1992) used with the methods of Merona (1983) and Lévêque *et al.* (1977). (f) Mavuti (1990); Moreau *et al.* (1993); Burgis (1974). (g) Winberg (1971); Payne (1986); Lévêque (1979). (h) Values adopted for a reasonable estimate of gross efficiency Polovina (1984); Polovina & Ow (1985); Moreau *et al.* (1993). (j) Kiss (1976). (k) Plisnier (1991).

*When necessary, values of EE are guessed values according to the known level of exploitation and/or predation of the group under consideration.

**Gross efficiency is computed as P/B / Q/B and is usually between 0.1 and 0.3.

assembled from published informations. Tables 3 and 4 present the diet matrixes used for the two ecosystems.

Food consumption (Q/B)

This parameter expresses the food consumption (Q) of an age-structured population of fish relative to its biomass (B), for a conventional period of one year. The estimates of Q/B used here were obtained from

Table 3. Diet composition (in % of weight of the stomach content) of consumers in Lake Naivasha ECOPATH model

Group	1	2	3	4	5	6	7	8	9	10	11	
1 – Fish eating birds	–	22	70	5	3	–	–	–	–	–		a
2 – Black bass	–	5	25	5	60	–	5	–	–	–		b
3 – *O. leucostictus*	–	–	–	–	–	5	15	15	5	5	55	c
4 – *T. Zillii*	–	–	–	–	–	5	30	8	5	7	45	c
5 – Crayfishes	–	–	–	–	–	–	3	–	12	45	40	d
6 – Zooplankton	–	–	–	–	–	10	–	85	–	–	5	e
7 – Zoobenthos	–	–	–	–	–	5	8	1	30	1	55	f

Group 8, 9, 10 and 11 are respectively: phytoplankton, benthic producers, macrophytes and detritus.
(a) Brown & Hopcraft (1973). (b) P. Aloo (pers. com.); Harper (1990). (c) Muchiri *et al.* (1995). (d) Harper (1992). (e) Mavuti (1990). (f) Moreau *et al.* (1993).

the method of Pauly & Palomares (1987), using a software designed by Jarre *et al.* (1990) or via the predictive model of Palomares (1991). The latter is an extension of a similar model based on marine fishes (Palomares & Pauly, 1989). Estimates of Q/B are provided in Tables 1 and 2.

Table 4. Diet composition (in % of weight of the stomach content) of consumers in Lake Ihema ECOPATH model

Group	1	2	3	4	5	6	7	8	9	10	11	12	
Fish-eating birds	–	40	50	5	–	–	5	–	–	–	–		a
Catfishes	–	5	55	5	6	10	3	5	5	1	–	5	b
Tilapiines	–	–	–	–	–	–	–	4	1	92	2	1	c
Harpagochromis	–	–	–	–	5	30	50	5	5	1	–		d
Insectivorous Haploch.	–	–	–	–	–	–	–	–	3	90	5	2	d
Planctivorous Haploch.	–	–	–	–	–	–	–	5	20	70	2	3	d
Other fishes	–	1	1	2	2	1	30	15	5	35	5	3	e
Zooplankton	–	–	–	–	–	–	5	–	–	95	–		f
Zoobenthos	–	–	–	–	–	–	5	5	–	5	30	55	f

Groups 10, 11 and 12 are respectively: Phytoplankton, Benthic producers and Detritus.
(a) Sumba (1983); CECODEL (1988). (b) Muryanashyaka (1989). (c) Muchanda (1989); Trewavas (1983). (d) Fourniret *et al.* (1992). (e) Lauzanne (1977). (f) Payne (1986); Moreau *et al.* (1993).

Ecotrophic efficiency (EE)

This is the fraction of the production of any group that is consumed within the system, 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). Note that ECOPATH II directs the fraction $1EE$ of production toward the detritus, a feature that is of relevance when attempts are made to equilibrate an ECOPATH II model. Note also that EE values differ from gross efficiency $GE = (P/B)/(Q/B)$, used here to check the inputs in Tables 1 and 2.

Balancing of model

The equilibrium assumption implicit to equation (1) is very important here in that it strongly constraints the possible solution, i.e. the range of parameters that will satisfy a set of simultaneous equations such as (1). Thus, we accepted as realistic that solution which required the least modifications of our initial inputs (incl. the diet matrix), and yet generated biologically and thermodynamically possible outputs (i.e. all GE and $EE < 1$).

Additionally to the original routines of Polovina (1984), Christensen & Pauly (1992a) developed several new routines including one dealing with that is called below the 'mixed trophic impacts'. It allows to assess the effect that changes in biomass of a group will have on the biomass of the other groups in the system. The routine has been developed by following the method and approach of Hannon & Joiris (1989) and Ulanowicz & Puccia (1992).

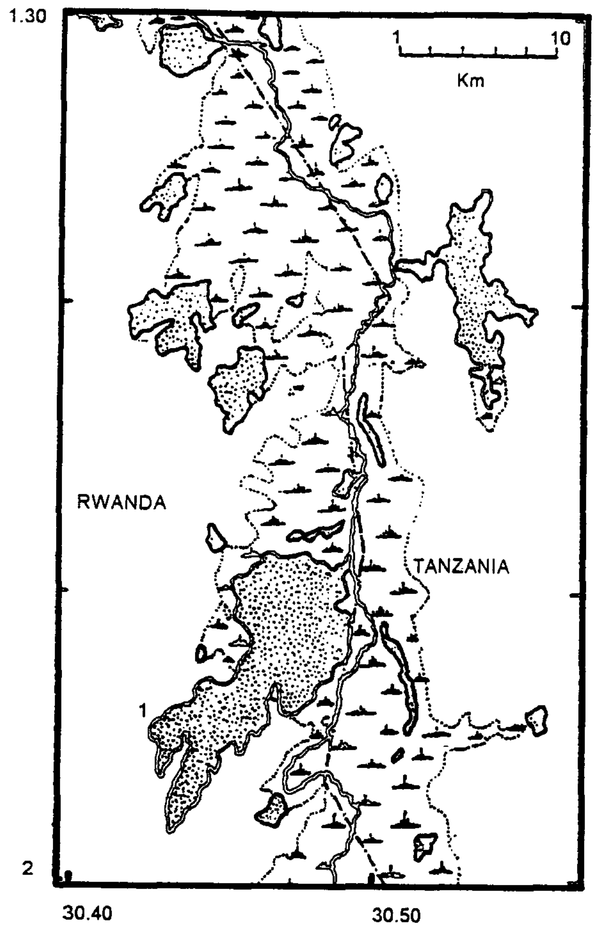

Fig. 2. General map of Lake Ihema (1), in the Akagera basin. Redrawn from Burgis & Symoens (1987).

Results

Estimates of biomass or EE and gross conversion efficiency, food consumption and flow to detritus obtained from the abovementioned input parameters are presented in Tables 1 and 2 and the trophic relationships are summarized in Figs 3 and 4.

In Lake Naivasha, the total biomass of fishes is 12.4 t km^{-2}; crayfishes are not included. The food sources are expected to be fully exploited except zooplankton (estimated EE is 0.61), macrophytes and detritus ($EE = 0.50$ and 0.45 respectively). The food consumption by fish eating birds is 3.77 t km^{-2} e.g. almost twice the catch by fishermen. The gross efficiency of the fisheries (actual catch/primary production) is 0.0009. The EE value of zooplankton ($EE = 0.61$) is in agreement with the findings of Mavuti (1990) who mentioned that "There is an absence of zooplanktophagous fishes in the limnetic area of the lake and the limnetic zooplankton is not utilised by higher trophic levels". It is possible that the diet of the native fish of Lake Naivasha *Aplocheilichthyes antenori* which as now disappeared did include zooplankton.

In Lake Ihema, the total biomass of fishes is 21 t km^{-2}. An important feature in Lake Ihema is the biomass of the Haplochromines groups. Total Haplochromine biomass was found to be about 6.5 t km^{-2} (Plisnier, 1990). Kudhonghania & Cordone (1974) give a similar estimate of 8.8 t km^{-2} of Haplochromines in the early 1970s in Lake Victoria before the invasion of the introduced Nile perch *Lates niloticus*. In Lake Ihema, this important biomass of Haplochromines is quite fully exploited by several predators but not by the fisheries. Among the food sources, zoobenthos and benthic producers are expected to be fully exploited ($EE = 0.95$ for both of them). However, phytoplankton and, most likely, zooplankton and underexploited ($EE = 0.29$ and 0.8 respectively). The food consumption by fish eating birds (1.74 t km^{-2}) is only 60% of the actual catch; the gross efficiency of the fisheries is 0.0007.

To try to understand the recent and future evolution of these two ecosystems, we used the mixed trophic impact routine of ECOPATH II which shows the effect that an increase in the biomass of a group would have on the biomass of the other groups in this ecosystem.

Figures 5 and 6 and Table 5 show the impacts an increase in the biomass of the group mentioned to the left (every primary producer for Lake Naivasha and Fisheries in Lake Ihema respectively) will have on the other groups mentioned above.

In Lake Naivasha, increasing the phytoplankton production has a positive impact on zooplankton, Tilapiine fishes and, indirectly, aquatic birds; the impact is greatest on zooplankton. The impact on other groups would be negligible. An increase in the abundance of benthic producers would contribute to increase the biomass of all groups except macrophytes, most likely because of possible competitions for nutrient, and on detritus production. The impact of a development of macrophytes would be very significant on crayfish (and indirectly on their main predators: birds and largemouth black bass and the fisheries). This is in agreement with Harper (1992) who mentions that the crayfish population collapsed consequently to the development of fishing effort toward it and to the recent decrease of aquatic macrophytes. For these three groups, an increase of biomass has a negative impact

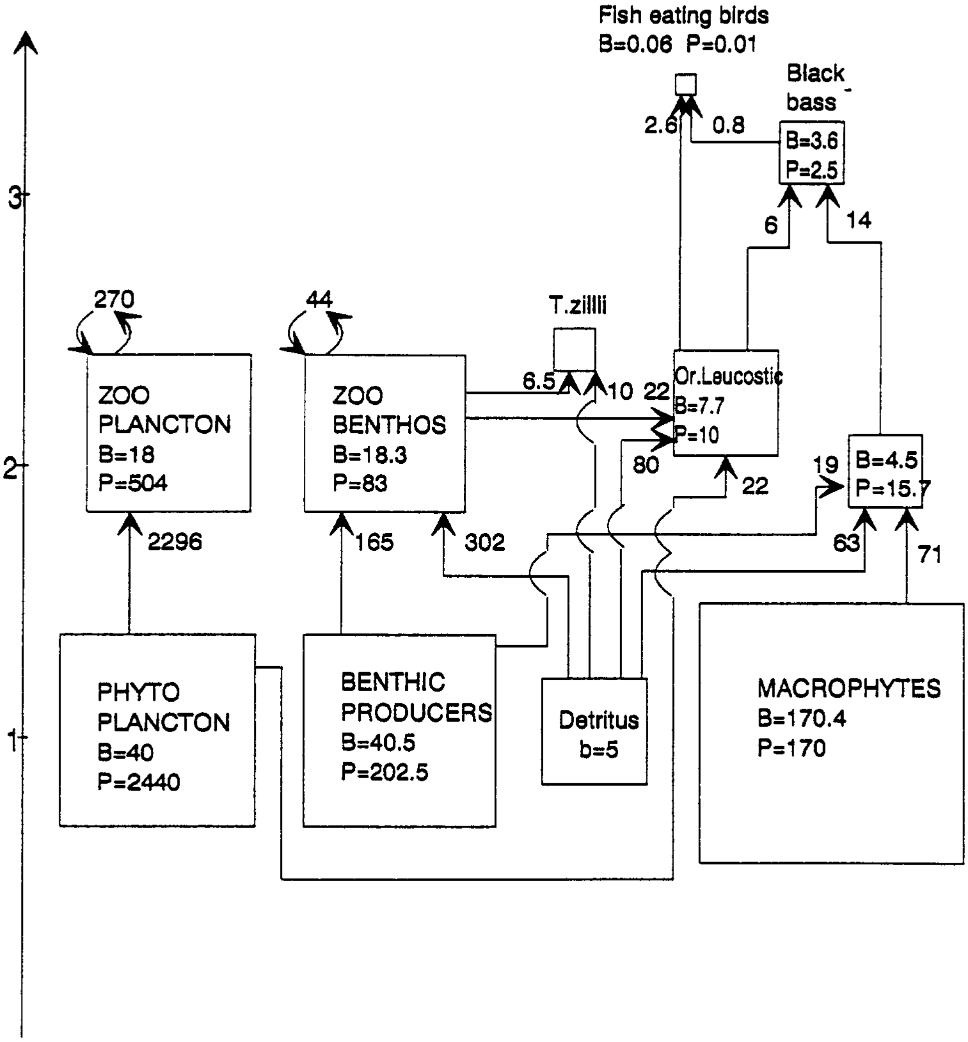

Fig. 3. ECOPATH II model of Lake Naivasha system for the period 1987–1990, indicating biomass of each group (area proportional to log B in km^{-2}) and the major flows connecting them. Less important flows are omited as are blackflows to the detritus box and fishery catches, for clarity sake. The horizontal axis of symetry of each box is aligned with the functional trophic level os this box (see Christensen & Pauly (1992) for detail on this concept).

on the group itself, reflecting increased within group competition for resources.

In Lake Ihema, the fishing effort, now directed toward the tilapiines and, incidentally, toward *Clarias gariepinus*, is still developing (Munyandorero, 1993) and this can be expected to decrease the biomass of these groups and to contribute to a slightly increase of biomass of other fishes mostly Haplochromines.

In the present context, the mixed trophic impact matrix helps to explain what happened recently in Lake Ihema and what is happening now and what we can expect in the very near future in Lake Ihema.

Discussion

The Ecopath model

Polovina (1984) and Polovina & Ow (1985) emphasized the sensitivity of ECOPATH, in its first verion, to variations of P/B values, mainly for groups on high trophic level (predators). In the present simulation efforts, the importance of the feeding matrix for accurate evaluations of biomass should be emphasized. One must quantify properly the qualitative information available on the diet composition of each group.

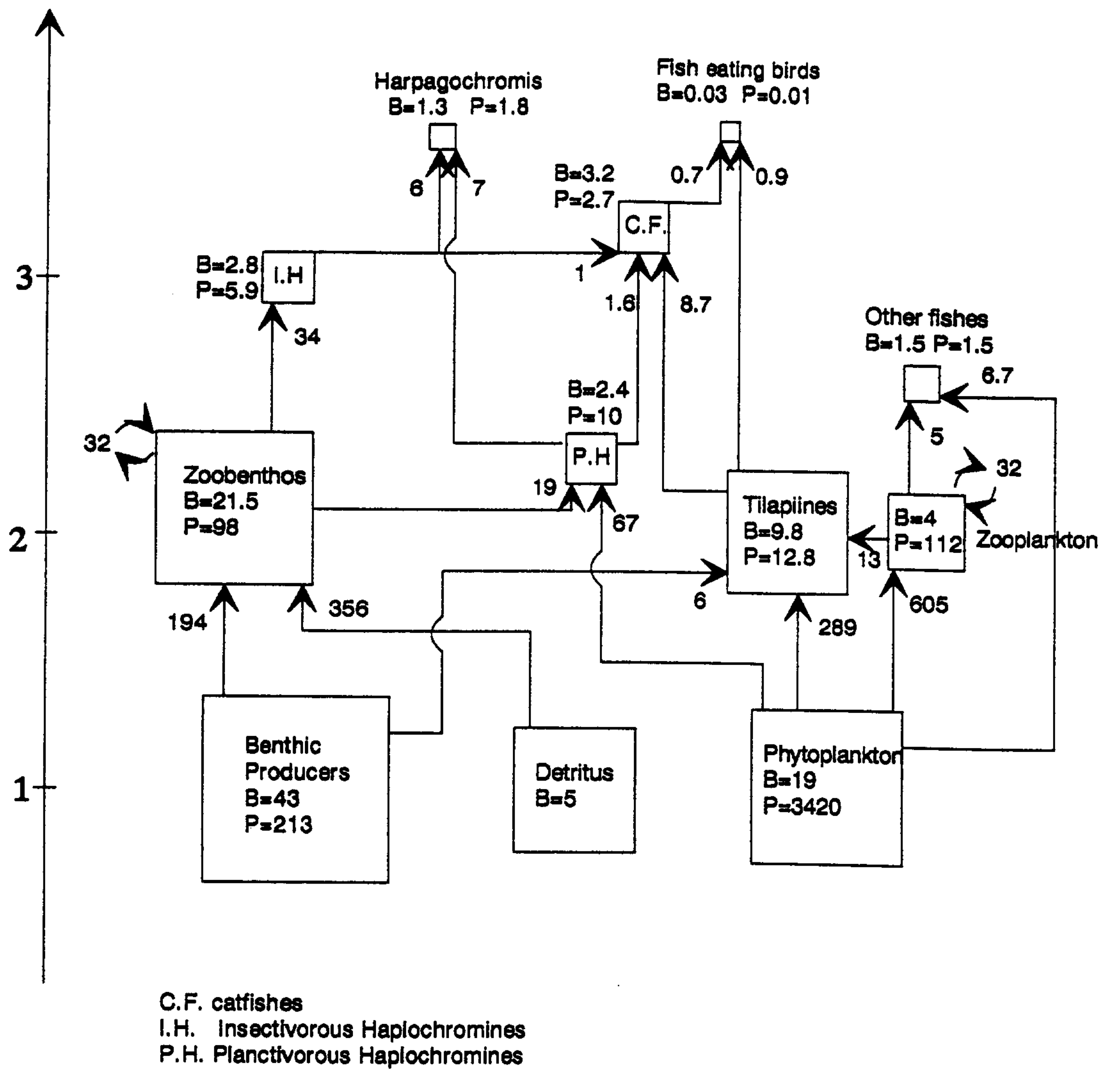

Fig. 4. ECOPATH II model obtained for Lake Ihema system. See Fig. 3 for explanation.

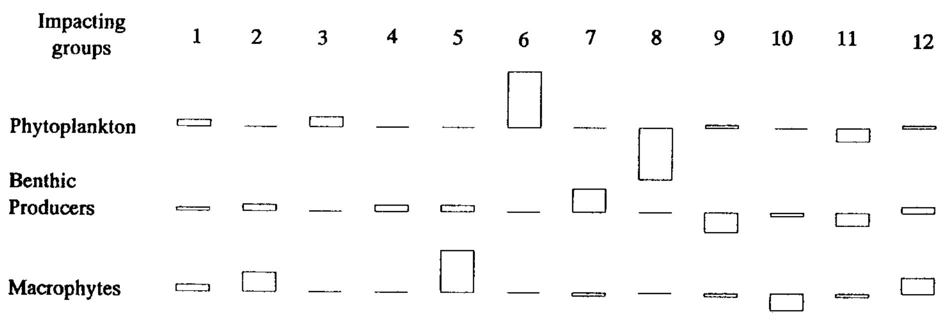

Fig. 5. Mixed trophic impacts in Lake Naivasha for the period 1987–1990. The figure shows direct and indirect impacts on living groups in the system that would result from an increase of biomass of the group given on the left. Positive impacts are shown above the base line, negative below. The impacts are relative but comparable between groups.

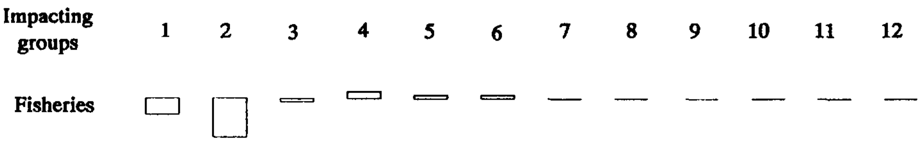

Fig. 6. Mixed trophic impacts in Lake Ihema. See Fig. 5 for explanation.

Table 5. (a) Matrix of mixed trophic impacts – Lake Naivasha

Impacted group	1	2	3	4	5	6	7	8	9	10	11	12
Impacting group:												
– Phytoplankton	0.04	−0.01	0.06	0.02	−0.03	−0.43	−0.02	−0.41	0.02	0.01	−0.09	0.02
– Benthic Prod	0.02	0.03	0.01	0.04	0.05	−0.01	0.17	0.00	−0.15	−0.3	−0.09	0.03
– Macrophytes	0.04	0.16	−0.00	0.01	0.33	−0.00	−0.02	0.00	−0.02	−0.13	−0.03	0.13

(1) Fish-eating birds; (2) Black bass; (3) *O. leucostictus*; (4) *T. zillii*; (5) Crayfish; (6) Zooplankton; (7) Zoobenthos; (8) Phytoplankton; (9) Benthic Producers; (10) Macrophytes; (11) Detritus; (12) Fisheries.

(b) Matrix of mixed trophic impacts – Lake Ihema

Impacted group	1	2	3	4	5	6	7	8	9	10	11	12
Impacting group: – fisheries	−0.06	−0.13	−0.01	0.02	0.0	0.01	0.00	0.00	0.00	0.00	0.00	0.00

(1) Fish-eating birds; (2) Catfishes; (3) Tilapiines; (4) *Arpagochromis*; (5) Insectivorous Haploch.; (6) Planktovorous Haploch.; (7) Other fishes; (8) Zooplankton; (9) Zoobenthos; (10) Phytoplankton; (11) Benthic Producers; (12) Detritus.

This has been possible by taking into account several sources of information available from the literature following previous quantifications (Moreau *et al.*, 1993; Palomares, 1991). Cannibalism, when it occurs, must be very low (most often less than 5% of the food) as suggested by Christensen & Pauly (1992); otherwise, the biomass estimates of the group under consideration and its preys become, in an unrealistic way, too high.

As already mentioned, the ECOPATH model was developed for static situations under general equilibrium conditions. We had to assume that this holds true for the two ecosystems analysed here. In reality, we know little about equilibrium states in fish communities and about the sensitivity of the model to perturbations caused by fishing or ecological modifications. It is one reason why Christensen & Pauly (1992) designed the mixed trophic impact routine of ECOPATH II. One of the inherent assumptions of this routine is that the diet composition matrix is not altered by changes in the biomass of any groups. This will hold true only for minor changes. One should therefore consider the impact routine as a tool for indicating the possible impact of direct and indirect interactions (including competition) in a steady state system. The present paper shows that it can also contribute to explaining short term variations. However, it cannot be an instrument for making medium or long term predictions (Christensen & Pauly, 1992).

Comparison with Lake George

Table 6 summarizes the main features of Lake Naivasha and Lake Ihema which are usefully compared with the same ones in Lake George. The biomasses and ecological productions of top predator and Tilapiine fishes are very similar even if both of them are introduced populations in Lake Naivasha. The Haplochromines fishes are significantly more abundant and productive in Lake George than in Lake Ihema. Another difference is that the production of the Haplochromines is almost entirely used by predators in Lake Ihema ($EE = 0.95$) and very poorly used in Lake George ($EE = 0.3$) as it was originally in Lake Victoria as well (Moreau *et al.*, 1993). Zooplankton is much more abundant in Lake Naivasha than in the two other lakes, most likely because of eutrophication (Mavuti, 1990). In the three ecosystems, this food

Table 6. Comparison of some key features of the ECOPATH models for Lake Naivasha and Lake Ihema with Lake George

Parameters	Lake Naivasha	Lake Ihema	Lake George
Top predators			
Biomass	3.6	3.2	3.2
Production	2.5	2.7	2.2
Tilapiine fishes			
Biomass	9.1	9.8	10.5
Production	11.8	12.8	13.5
Haplochromines			
Biomass	--	6.5	9.6
Production	--	17.3	27.5
EE	--	0.93	0.3
Zooplankton			
Biomass	18	4.0	4.6
Production	504	111.4	120.4
EE	0.61	0.8	0.6
Zoobenthos			
Biomass	18.6	21.5	10.7
Production	82.5	96.9	48.1
EE	0.95	0.95	0.8
Phytoplankton			
Biomass	40	19	20
Production	2448	3420	1980
EE	0.95	0.29	0.4
Consumption by aquatic birds	3.8	1.7	1.3
Actual catch	2.15	2.7	14.3
Gross efficiency of actual catch	0.0009	0.0007	0.0057

source is underutilised. The huge amount of zooplankton for Lake Naivasha is responsible of the heavy level of predation on phytoplankton which is observed in this lake and not in the two other ones. The biomass, production and utilisation of zoobenthos are similar in Lake Naivasha and Lake Ihema. They are significantly lower in Lake George which is also known for its poor zoobenthic fauna (Darlington, 1977). The primary limnetic production (phytoplankton) is poorly exploited in Lake George and Lake Ihema when compared to Lake Naivasha.

The predation on fishes by aquatic birds is considerable in Lake Naivasha (twice the actual catch by fishermen). It is also important in Lake Ihema (60% of the actual catch) and of minor importance in Lake George 8%). These figures can be assessed when considering the gross efficiency GE of the fisheries. GE is exceptionally low in Lake Naivasha and Lake Ihema when compared to Lake George and some other african lakes for instance Lake Victoria (Moreau *et al.*, 1993). This seems to come mainly from the underutilisation of most of the food sources as illustrated by their low ecotrophic efficiency (the EE values).

In fact this ECOPATH exercise on the two shallow Lake Naivasha and Lake Ihema has shown that one possibility of improving the potential production of inland waters could be to ensure all the food sources to be fully utilised; ECOPATH could be a useful tool for that purpose. This has been the aim of some introductions in open natural waters or in made man lakes (Moreau *et al.*, 1988). It has been demonstrated, when using ECOPATH, that the introduction of *Lates niloticus* did increase the ecotrophic efficiency of all the food producers (Moreau *et al.*, 1993).

Conclusion

Lake Ihema and Lake Naivasha, two shallow lakes of eastern Africa, have been successfully described by the ECOPATH software and model and have been usefully compared with Lake George. Differences in biomasses and productions for some groups have been pointed out, mostly for food sources and some of them appear to be underexploited. Therefore, the implementation of an optimal use of all the food sources in african inland waters appears to be a way of increasing the productivity of the fisheries. ECOPATH can contribute to the development of fisheries in african inland waters by identifying such misutilisations of food sources in the ecosystems.

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