A Trophic Ecosystem Model of Lake George, Uganda

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Abstract

A trophic model of Lake George, Uganda, Central Africa, was constructed using published quantitative and qualitative information on the various biotic components of the lake and the ECOPATH II approach and software. It is shown that the available production and biomass estimates for the various groups in the system are consistent with each other, and that it is possible to make a balanced model of the major trophic interactions in Lake George.

Introduction

In this contribution, a trophic ecosystem model of Lake George in Uganda is presented, based on an approach already used to construct models of a number of other African lakes and ecosystems (see Degnbol this vol., Kolding this vol., Moreau et al., this vol.).

This paper aims:

1. to add Lake George, which has been well studied in terms of its ecology and constituent fauna and flora, to the series of lakes that have been described using the trophic modelling approach; and
2. to demonstrate further the utility and versatility of the ECOPATH II approach and software; and its use in integrating the work of different researchers.

Lake George is relatively small, 250 km², and has a mean depth of 2.4 m, with a maximum of 4 m. Although connected via the Kazinga Channel with Lake Edward (formerly Lake Idi Amin), Lake George can be considered a self-sufficient ecosystem, given the restricted nature of its connection with Lake Edward (Fig. 1).

Lake George has been studied rather extensively, both in terms of its fish fauna (Greenwood 1973) and in the context of the International Biological Program (IBP). Burgis and Dunn (1978), Beadle (1981) and Burgis and Symoens (1988) present reviews of the relevant works, which are considered below.

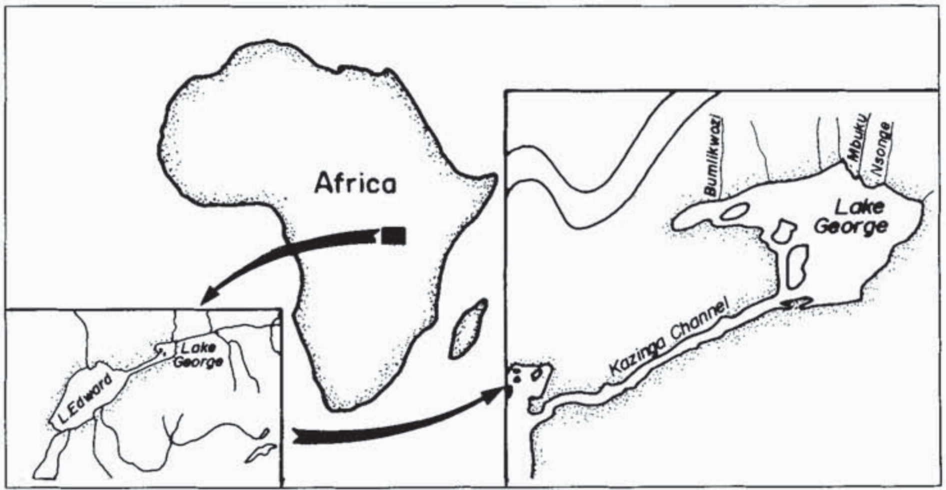

Fig. 1. Map of Lake George, showing its connection, via the Kazinga Channel, with Lake Edward, and their location in Africa.

Materials and Methods

The model of Lake George was constructed by applying the ECOPATH II approach and software of Christensen and Pauly (1992a, 1992b) to data collected by various authors in Lake George, and standardized by this paper's authors.

The basic equation of ECOPATH II expresses that for each group (i) in the model,

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

where B_i is the biomass of i, $(P/B)_i$ its production/biomass ratio, EE_i its ecotrophic efficiency, Y_i its yield (= fisheries catch), B_j the biomass of its k predators j, $(Q/B)_j$, the food consumption per unit biomass of j and DC_{ji} the fraction of i in the diet of predator j.

This equation implies equilibrium, i.e., input to a group is assumed to equal output from the group over the period considered. This assumption appears unavoidable in view of the scattered nature of the dataset considered here. It is justified, on the other hand, by the between-year consistency of phytoplankton biomass reported by Ganf and Viner (1973).

Table 1 presents the groups used to describe Lake George, along with some of their characteristics.

Except for the birds and the phytoplankton, all biomasses were estimated using ECOPATH II. Estimates of parameters were provided as follows.

Table 1. Basic information on elements ("boxes") of trophic model of Lake George.[a]

1.	Fish-eating birds	:	Fishing eagles, kingfishers, cormorants, pelicans
2.	*Bagrus docmac*	:	Catfish (85)
3.	*Clarias gariepinus*	:	Catfish (85)
4.	*Protopterus aethiopicus*	:	Lungfish (75)
5.	*Haplochromis squamipinnis*	:	Predatory dwarf bream (20)
6.	*H. angustifrons*	:	Benthophagous dwarf bream (12)
7.	*H. nigripinnis*	:	Phytoplanktophagous dwarf bream (10)
8.	*Oreochromis niloticus*	:	Nile tilapia (40)
9.	*O. leucostictus*	:	Tilapia (35)
10.	Zooplankton	:	*Thermocyclops hyalinus* + *Mesocyclops leuckarti*
11.	Zoobenthos	:	*Chaoborus* spp., Copepods, Oligochaetes, Ostracods (*Cyprinotus* spp.), *Chironomus* spp.
12.	Phytoplankton	:	Blue-green algae (*Anabaena*, *Microcystis*, *Lingbya*) (70% of biomass); Diatoms (*Melosira*, *Nitzschia*, *Synedra*); Chlorophytes (*Pediastrum* and *Scenedesmus*)
13.	Benthic producers	:	-
14.	Detritus	:	-

[a]Numbers in brackets refer to maximum length, in cm.

Fisheries Catches (Y)

Catch estimates pertaining to the 1970s were obtained for the fish groups in Table 1 from records of the Uganda Department of Fisheries (Gwahaba 1973; Dunn 1973, 1975, 1989). They are expressed here, like all other flows, in $t \cdot ww \cdot km^{-2} \cdot year^{-1}$.

Production/Biomass Ratio (P/B)

As shown by Allen (1971), under an equilibrium assumption, when von Bertalanffy growth can be assumed (as is here the case), P/B is equal to Z as defined in fisheries science. Hence 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 mainly 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 is presented in Table 3. The table is on a weight basis, and was assembled from published information.

Food Consumption (Q/B)

This parameter expresses the food consumption (Q) of an age-structured population in fishes relative to its biomass (B), on an annual basis. Except for *O. niloticus* and *H. nigripinnis*, the estimate of Q/B used here was obtained via the empirical model of Palomares (1991) who also showed that freshwater and marine fishes have similar Q/B values when their shapes, size, food type and environmental temperature are equal, thus justifying the use of a model based on both marine and freshwater fishes.

The Q/B estimated for *O. niloticus* and *H. nigripinnis* were taken from Palomares (1991), who based her computations on stomach contents data from Moriarty and Moriarty (1973).

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) to 0.95 (Ricker 1969). Note that ECOPATH II directs the fraction (1-EE) of production toward the detritus, a feature that is of relevance when attempts are made to equilibrate an ECOPATH II model. Note also that the EE values differ from gross efficiency, GE = (P/B)/(Q/B), used here to check the inputs in Table 2, but not further discussed.

Balancing of the Model

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

Results

Tables 2 and 3 present the key features of our model of Lake George, which is also illustrated in Fig. 2. The estimated biomasses are either within the ranges, or close to the biomasses so far published and, therefore, Fig. 2 represents a "possible" Lake George situation. The fish biomass is dominated by *O. niloticus*, an herbivore, whose central role in Lake George was previously emphasized by Gwahaba (1973), and by Moriarty and Moriarty (1973) and by *H. nigripinnis* and *H. angustifrons*, small phytoplanktivores (Moriarty and Moriarty 1973) and zoobenthivores, respectively (Gwahaba 1975). The major predators in the system are the lungfish *P. aethiopicus* and the catfish *C. gariepinus*, with consumptions of 7.3 and 6.2 t·km^{-2}·year^{-1}, respectively.

The predatory fishes are caught by fishers and by birds (Sumba 1983) and their EE (0.95) was assumed to be high. It is noted that the total consumption by birds (1.28 t·km^{-2}·year^{-1}) is far from negligible. It amounts to 8.5% of the actual catch (14.3 t·km^{-2}·year^{-1}). EE is also high for *Oreochromis* species which constitutes the bulk of the actual catch and of the food of the birds. In contrast, EE values are considerably lower for *H. angustifrons* and *H. nigripinnis*. These two groups are very poorly exploited and do not appear to suffer any severe predation (Moriarty et al. 1973; Dunn 1975).

Among the food sources, e.g., zooplankton, benthos, phytoplankton and benthic producers, only the last one has been expected to be heavily predated upon. The huge primary production of Lake George is not fully exploited (EE=0.95) and, to some extent, this is also true for zooplankton (Burgis and Dunn 1978). EE (=0.8) is quite high for zoobenthos which is an important source of food for several fish species even if its biomass (10.8 t·km^{-2}) is low when compared to other

Table 2. Input values for the required parameters for ECOPATH modelling of Lake George ecosystem (see also Tables 1 and 3). Computed and observed biomasses are also shown. Values of EE are guesses based on the known level of exploitation and/or predation of the group under consideration. Catches come from several sources: Gwahaba (1973), Dunn (1973, 1989), Burgis (1978), G.W. Ssentongo (pers. comm.). They refer to the early 1970s. Gross efficiency is computed as (P/B)/(Q/B) and is usually between 0.1 and 0.3.

	Group	Catches (t·km^{-2} year^{-1})	Biomass (t·km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	Computed biomass (t·km^{-2})	Observed biomasses (t·km^{-2})
1.	Birds	0.0	0.022[a]	0.25[a]	58.00[a]	-	-	(0.022)[a]
2.	*B. docmac*	0.3	-	0.90[b]	5.45[b]	0.95	0.50	(0.4-0.5)[f]
3.	*C. gariepinus*	0.8	-	0.90[b]	5.33[b]	0.95	1.16	(0.7-1.2)[f]
4.	*P. aethiopicus*	0.6	-	0.50[b]	4.85[b]	0.95	1.50	(1.4-1.6)[f]
5.	*H. squamipinnis*	0.8	-	1.70[c]	8.80[c]	0.95	0.62	(0.4-0.7)[f]
6.	*H. angustifrons*	0.4	-	2.50[c]	16.00[c]	0.30	2.55	(2.1-2.9)[f]
7.	*H. nigripinnis*	0.5	-	3.10[d]	17.50[e]	0.25	6.61	(5.2-6.9)[f]
8.	*O. niloticus*	10.5	-	1.30[f]	12.80[e]	0.95	9.89	(8.5-12.1)[f]
9.	*O. leucostictus*	0.4	-	1.10[f]	12.50[e]	0.95	0.59	(0.4-0.6)[f]
10.	Zooplankton	0.0	-	26.00[g]	140.00[i]	0.60	4.47	(2.7-5.8)[g]
11.	Zoobenthos	0.0	-	4.50[h]	26.00[i]	0.80	10.80	(9.8-11.4)[k]
12.	Phytoplankton	0.0	30.0[j]	66.00[j]	0.00	-	-	(30)[j]
13.	Benthic producers	0.0	-	5.00[h]	0.00	0.95	19.81	-

[a] Sumba (1983).

[b] Moreau et al. (this vol.).

[c] Guessed values based on the maximum observed length for P/B (see Moreau et al., this vol.) and on the gross efficiency for Q/B.

[d] Computed from an estimate of natural mortality M = 2.9 year^{-1} by Palomares (1991), assuming F = 0.2 year^{-1} in a population which is lightly exploited.

[e] Moriarty and Moriarty (1973).

[f] Gwahaba (1973). The observed biomass for *O. niloticus* pertains only to the inshore waters.

[g] Burgis (1974).

[h] Payne (1986), Winberg (1971).

[i] Guessed values, based on the gross efficiency for these groups and estimates from Polovina (1984) and Polovina and Ow (1985).

[j] Ganf (1972, 1974, 1975), Burgis and Dunn (1978).

[k] Darlington (1977).

Table 3. Diet composition (in % of weight of stomach contents) of consumers in the Lake George ECOPATH II model. Groups 12, 13 and 14, respectively : phytoplankton, benthic producers and detritus. Estimates are from: Sumba (1983) for group 1; Moreau et al. (this vol.) for groups 2, 3, 4; Dunn (1975) for groups 5, 6, 7; Moriarty and Moriarty (1973) for groups 7, 8, 9; Trewavas (1983) for group 9; Burgis and Dunn (1978), Moriarty et al. (1973) for group 10; Payne (1986) and Palomares (1991) for group 11.

	Prey													
Consumer	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Fish-eating birds	-	6	9	-	1	-	-	76	8	-	-	-	-	-
2. *B. docmac*	-	0.5	0.5	0.5	0.5	4	20	3	1	5	50	-	2	13
3. *C. gariepinus*	-	-	0.5	1	0.5	5	10	3	0.5	5	48.5	1	5	20
4. *P. aethiopicus*	-	0.5	0.5	0.5	0.5	3	10	2	-	5	60	2	5	11
5. *H. squamipinnis*	-	-	-	-	2	16	50	6	1	10	10	-	-	5
6. *H. angustifrons*	-	-	-	-	-	-	-	-	-	10	50	10	10	20
7. *H. nigripinnis*	-	-	-	-	-	-	-	-	-	2	-	90	3	5
8. *O. niloticus*	-	-	-	-	-	-	-	-	-	2	-	90	4	4
9. *O. leucostictus*	-	-	-	-	-	-	-	-	-	1	-	80	5	14
10. Zooplankton	-	-	-	-	-	-	-	-	-	5	-	95	-	-
11. Zoobenthos	-	-	-	-	-	-	-	-	-	10	5	5	30	50

African lakes (Beadle 1981; Payne 1986; Burgis and Symoens 1988).

To some extent, this ECOPATH II model of Lake George confirms the frequently mentioned assumption (Burgis 1978; Burgis and Dunn 1978; Beadle 1981) that this ecosystem has a low ecological efficiency as compared to other African lakes such as Lake Victoria (Moreau et al., this vol.). The gross efficiency of the fisheries (actual catch/primary production) is 0.0057 in Lake George, between that of Lake Victoria prior to (0.0016) and after the introduction of Nile perch (0.0082).

Discussion

Interactions between Organisms

The Lake George ecosystem is quite well studied, and it is comforting to see that ECOPATH II could describe it properly in terms of biomasses and ecological production.

For instance, the observed catch (14.3 $t \cdot km^{-2} \cdot year^{-1}$) is realistic if extracted from an average total fish biomass of 23.4 $t \cdot km^{-2}$. The latter figure is in agreement with the evaluations of Gwahaba (1975): 16.4 and 29 $t \cdot km^{-2}$, depending on how one raises to the whole lake area figures initially estimated only for some biotas and/or stations. The difference between the two figures given by Gwahaba seems to stem mainly from the method of taking into account the important inshore biomass of exploited *O. niloticus*. Furthermore, the low values of EE for food sources, and also for the haplochromine cichlids, contribute to explain the low ecological efficiency of the system (Burgis and Dunn 1978; Payne 1986). A significant amount of the primary production is sedimented and exported through the Kazinga Channel, the main outflow to Lake Edward (Fig. 1).

The assumed low ecotrophic efficiencies for the two haplochromines (No. 6 and 7) indicate that these species are incompletely utilized. It is estimated that a production of around 20 $t \cdot km^{-2} \cdot year^{-1}$, or more than the total present catches is unutilized. It is however not clear if this is an artefact caused by erroneous assumptions in the model or if the fishery on these groups could in fact be increased considerably.

As already mentioned, the ECOPATH model was developed for static situations under general equilibrium conditions. However, we know little on the states of tropical fish communities. Also, little is known of the sensitivity of the model to perturbations caused by fishing or ecological stresses.

The mixed trophic impacts (Fig. 3; see Christensen and Pauly 1992a and 1992b for description) suggest that the fishing pressure that is operating now has a negative impact on all fish groups except *Haplochromis angustifrons* and *H. nigripinnis*, which show slightly positive impacts. This indicates that the fisheries presently has, relative to predation and competition, limited impact on those two species.

Interaction among Scientists

During the IBP study of Lake George, specialists of different groups were associated with a team supported by IBP which provided opportunities to interact and to exchange informations on a qualitative basis. This has made possible the publication of several synthesis papers (see Burgis and Symoens 1988 for review). ECOPATH II shows how the quantitative data on each group can be used to describe the ecosystem as a whole. Thus, we could verify that the estimates of biomasses and production of each main group provided by the IBP team were largely consistent with each other. We could also show the gaps in knowledge of this lake, at the end of the IBP project. To some extent, these gaps have forced the authors of

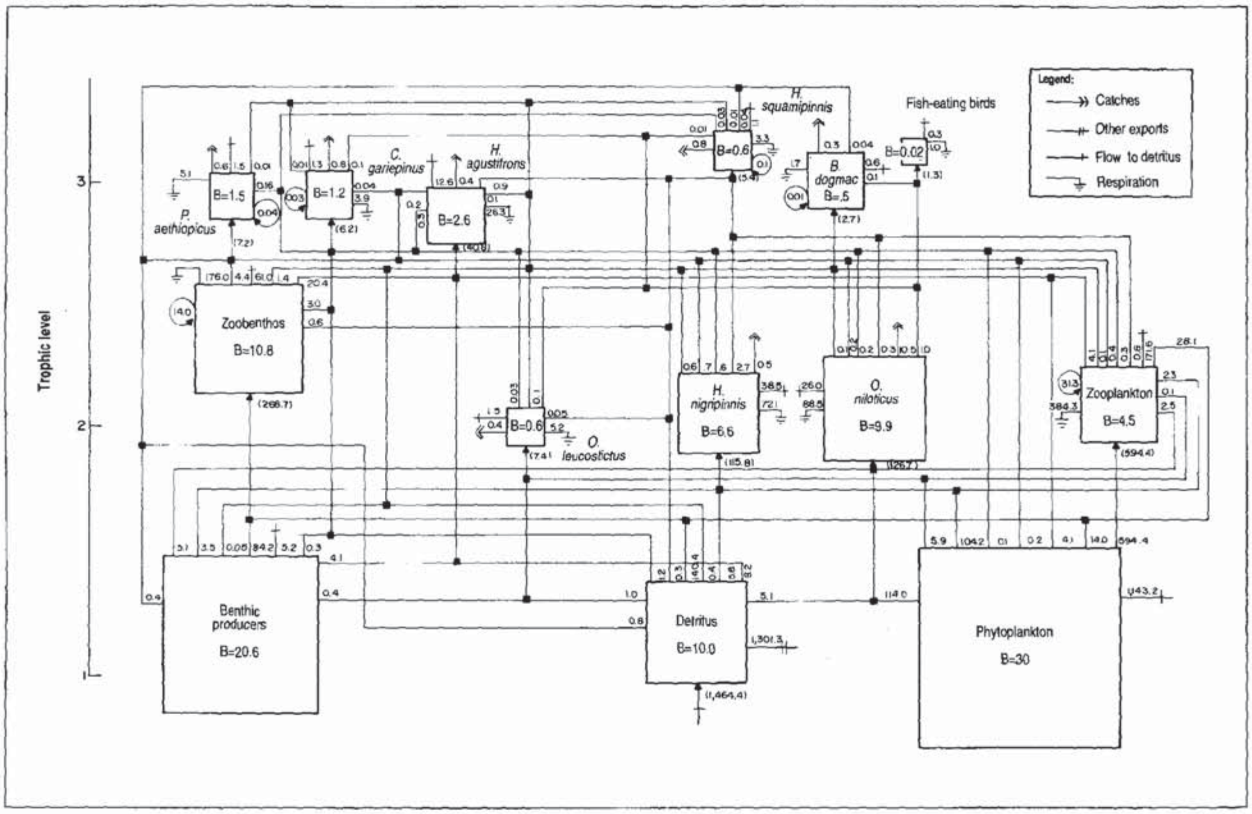

Fig. 2. ECOPATH II model of Lake George, indicating the biomasses (B in t·km⁻²) of the groups used for description of the ecosystem and the flows connecting these (t·km⁻²·year⁻¹).

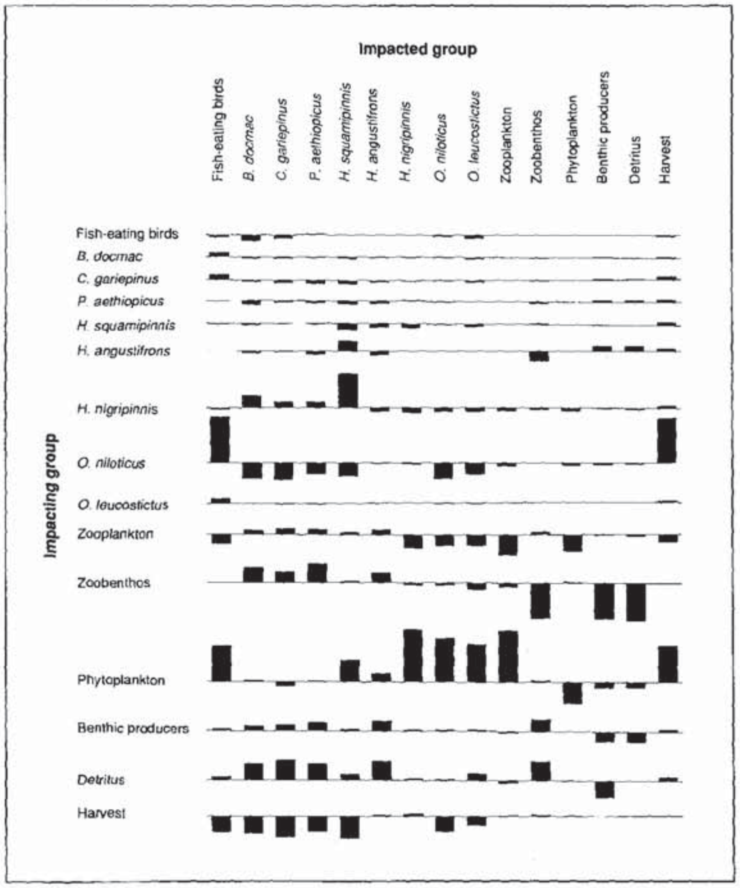

Fig. 3. Mixed trophic impacts of the groups included in the Lake George ecosystem model. The figure shows the direct and indirect trophic impacts on the groups mentioned on top from the groups given on the left. Positive impacts are shown above the baseline, negative below; the impacts are relative, but comparable between groups.

synthesis papers to make arbitrary assumptions on the relative importance of transfers of energy and biomass between the successive trophic levels (Burgis and Dunn 1978).

A short, and not exhaustive list of gaps in knowledge of Lake George includes:

- impact of predation by fish-eating birds;
- dynamics and ecological production of predatory fishes, haplochromines and zoobenthos;
- diet composition and food consumption of zoobenthos and benthophagous fishes;
- actual catch and its range of variations for each group of fishes;
- identification of the reason(s) why a large part of the primary production is not channelled into secondary production (as mentioned by several authors and confirmed by our low EE value for phytoplankton); and
- extent of the predation on zooplankton by young fishes (all species considered) in inshore areas.

Conclusion

ECOPATH II has allowed the authors to balance the biomass and production of several interacting groups in Lake George, based on data from the literature on the lake itself, or adapted from information from other lakes. The accuracy of several previous biomass and production estimates for major groups was demonstrated and the underutilization of some sources of food by fishes (especially phytoplankton) was confirmed. However, some gaps in our knowledge of the transfers of biomass between the groups have also been pointed out.

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