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Trophic structure and interactions in Lake Ayamé (Côte d'Ivoire)

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ABSTRACT

Key-words: *trophic dynamic, transfer efficiency, Ecopath, Lake Ayamé, West Africa*

The Ecopath software with Ecosim and Ecospace was used to describe structure and trophic relationships in Lake Ayamé. The total biomass of fish is 8 t.km^{-2}. The trophic levels assessment revealed that the highest value (3.83) was observed in *Hepsetus odoe*. The mean trophic level of catch (2.94) indicates that fisheries are targeting mainly the fish groups of high trophic levels. Resources are not exploited properly. Competition between species occurs for *Sarotherodon melanotheron* and *Oreochromis niloticus* for the first group and *Chrysichthys* spp. and *Heterotis niloticus* for the second group. Transfer efficiency is high from producers.

RÉSUMÉ

Structure et interactions trophiques du lac Ayamé (Côte d'Ivoire)

Mots-clés : *lac Ayamé, retenue, relations trophiques, Ecopath*

Un modèle décrivant la structure et les relations trophiques du lac Ayamé a été construit à l'aide du logiciel Ecopath associé avec Ecosim et Ecospace. L'analyse de la dynamique de cet écosystème a été effectuée en termes de biomasse, niveau trophique, niveau moyen des captures et transfert d'énergie. La biomasse totale de poisson s'élève à 8 t.km^{-2}. L'estimation des niveaux trophiques attribue le plus haut niveau trophique à *Hepsetus odoe* avec une valeur de 3,83. La valeur de 2,94 pour le niveau trophique moyen des captures indique que les espèces cibles des pêches se trouvent au niveau supérieur de la pyramide trophique. Les ressources du lac n'ont pas encore atteint le seuil critique de surexploitation. Les compétitions interspécifiques sont peu marquées, notamment chez *Sarotherodon melanotheron* et *Oreochromis niloticus* d'une part, et chez *Chrysichthys* spp. et *Heterotis niloticus* d'autre part. Le rendement le plus élevé des transferts est enregistré chez les producteurs primaires.

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INTRODUCTION

Understanding the functioning of a complex ecosystem, and the possible impacts of different ecological changes on the system as a whole, calls for quantification of the trophic relationships between different groups in the system. This is one reason why Polovina (1984) developed Ecopath (modified by Christensen and Pauly, 1992; Walters *et al*., 1999; Christensen *et al.*, 2005), a steady-state model of trophic interactions in ecosystems. The relative simplicity of this model compared with other multispecies models, such as simulation models by Andersen and Ursin (1977), and Laevastu and Larkin (1981), is apparent in its application to several marine and continental ecosystems (Christensen and Pauly, 1993).

This study describes the situation of a tropical man-made lake, Ayamé, in West Africa. This reservoir has been studied by different researchers since its impoundment in 1959 (Daget and Iltis, 1965; Reizer, 1967) and more recently after several years of fishing (Kouamelan *et al.*, 1999; Diomande *et al*., 2001; Vanga *et al*., 2002; Ouattara *et al*., 2003, 2007; Dietoa *et al*., 2007).

Lake Ayamé presents a significant ichthyological richness. Fish fauna consists of 36 species (Gourène *et al*., 1999). There are endemic species with two introduced species: *Oreochromis niloticus* and *Heterotis niloticus* (Moreau *et al.*, 1988).

This diversity has favoured the development of intense fishing activity in the lake, which was one of the first water bodies where continental fisheries were developed in Côte d'Ivoire (Gourène *et al*., 1999). This resource exploitation has induced a decrease in catches of the principal species and modification of the fish community structure. For example, the contribution of *Oreochromis niloticus* to the catch has decreased from 50% to 3%, whereas the contribution of *Sarotherodon melanotheron* has increased simultaneously (Gourène *et al*., 1999).

With Ecopath, the structure and the trophic functioning of Lake Ayamé are presented.

MATERIAL AND METHODS

> *STUDY SITE*

The artificial Lake Ayamé (longitudes 3° and 3°5 west, latitudes 5°30 and 6° North) results from hydroelectric barrage construction on a coastal river (Bia) in Côte d'Ivoire (Figure 1). The average surface is 180 km^2; the lake is 80 km long and 27 km wide (at the maximum water level); the maximal depth is 30 m. Average annual precipitation in the region is about 1800 mm. The water level varies between 84.84 m and 88.44 m above sea level. The average surface water temperature is 28.4 °C.

Lake Ayamé fishery is predominantly artisanal. Fishermen operate various gears depending on the season, the investment level, the fishing areas and the species targeted. These gears are gillnets, cast nets, long-lines, seines and various kinds of traps (Reizer, 1967).

> *THE ECOPATH MODEL*

The Ecopath model is based on varied studies (Polovina, 1984; Polovina and Ow, 1985; Christensen and Pauly, 1992, 1996; Walters *et al*., 1997, 1999, 2000; Christensen *et al.*, 2005) and was used to construct a steady-state description of Lake Ayamé. The model, which has been used for quantifications of food webs in different ecosystems and impact of fisheries for management purposes, comprises a set of simultaneous linear equations, one for each group under consideration, and assumes a mass balance where the production of the considered group is equal to the sum of all predation, non-predatory losses and export:

$$\mathbf{B_i{*}P/B_i{*}EE_i} = \Sigma\, \mathbf{B_j{*}Q/B_j{*}DC_{ij}} + \mathbf{Y_i}.$$

B_i is the biomass of group *i* (in t.km^{-2} fresh weight); P/B_i is the annual production/biomass ratio of *i* equal to the total mortality coefficient (Z) in steady-state conditions (Allen, 1971);

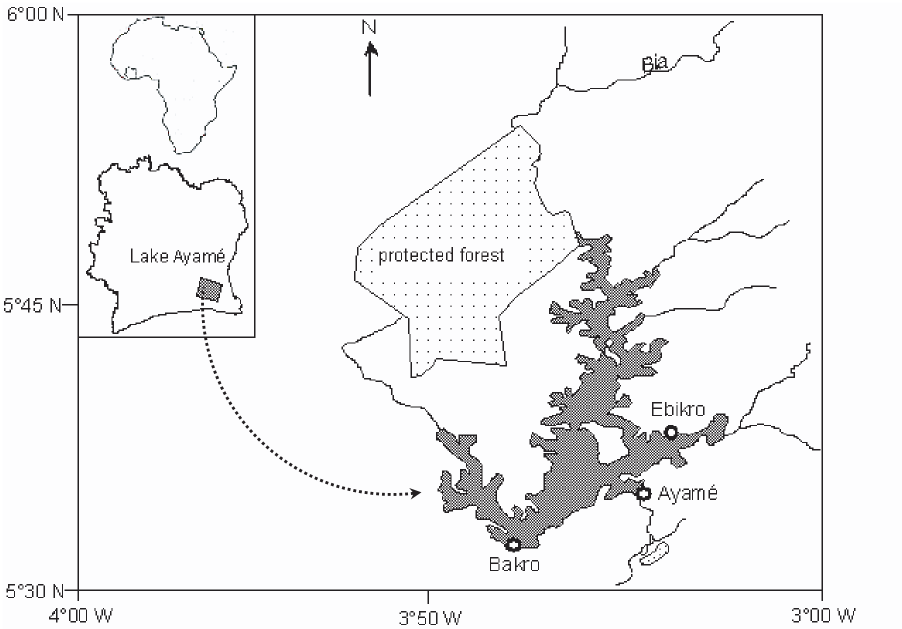

Figure 1
Lake Ayamé, situation map (from Ouattara et al., 2007).

Figure 1
Localisation du lac Ayamé (d'après Ouattara *et al.*, 2007).

EE_i is the ecotrophic efficiency representing the part of the total production consumed by predators or captured in the fishery or exported; B_j is the biomass of the predator group *j*; Q/B_j is the annual food consumption per unit biomass of the predatory group *j*; DC_{ij} is the proportion of the group *i* in the diet of its predator group *j* and Y_i is the export or catch in fishery of group *i*, that is assumed to be exploited in the fishery.

In addition to balancing the model, Ecopath can be used to compute parameters and indices corresponding to the food web characteristics:

The trophic level (TL) is represented as fractions (Odum and Heald, 1975) rather than integers (1, 2, 3, ...) as initially proposed by Lindeman (1942). A routine of Ecopath assigns a definitional trophic level of 1 to producers and detritus and a trophic level of 1 + [the weighted average of the preys' trophic level] to consumers.

The group-specific omnivory index (OI) is computed as the variance of the TLs of each predator's prey groups (Christensen and Pauly, 1993) while the system omnivory index (SOI) is computed as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake, Q (Christensen *et al*., 2000). It indicates the allocation of predator-prey interactions linking each trophic level (Christensen and Walters, 2004). Both OI and SOI indices vary from 0 to 1.

The connectance index (CI) is the ratio between the number of actual definite trophic associations among all the groups and the theoretical possible number of connections, $(N-1)^2$ for *N* groups, including consumption of detritus (Christensen *et al*., 2000; Christensen and Walters, 2004). This index is correlated with the maturity, *e.g.* the level of evolution of the ecosystem, as defined by Odum (1969), because the food chain structure changes from linear to web-like as a system matures (Odum, 1971).

Trophic aggregation per discrete TL, *sensu* Lindeman (1942), is based on an approach suggested by Ulanowicz (1995). This routine facilitates calculation of flows per TL based on diet compositions by reversing the routine for calculation of fractional trophic levels quoted above. More particularly, the transfer efficiencies between the successive discrete trophic levels are calculated as the ratio between the sum of the exports plus the flow that is transferred from one trophic level to the next, and the throughput at this trophic level (Christensen *et al*., 2000).

The total system throughput (TST) is defined as the sum of all flows in a system (Ulanowicz, 1986) and can be fractionated into import of TL1, export, respiration, consumption by predation and flows going back to detritus (Christensen *et al*., 2000).

The gross efficiency of the fishery (GEF) is computed as the ratio between the total catch and the total primary production in the system. The value will be higher for systems with a fishery harvesting fish belonging mainly to low TLs than for systems whose fisheries concentrate on high TLs. Therefore, this index may increase with fisheries' 'development' as defined by Pauly *et al*. (1998).

Primary production required (PPR) and Ecological footprint (EF). The PPR (primary production required) used in Ecopath corresponds to the ecological footprint (EF). For the catch the expression is EF = PPR/PP*C, where PP is the total flow out of trophic level I (from primary producers and detritus) and C the catch: this will give the size of the area in square kilometres (assuming the unit is km^{-2}) needed to sustain a catch of 1 ton for the given resource.

> *MODEL CONSTRUCTION*

The trophic model was constructed using mostly data collected from field surveys from 1995 to 1996 and complemented with information from the literature including FishBase (www.fishbase.org) (Froese and Pauly, 2007). A total of 23 groups (Table I) was considered and the ecological grouping of biological assemblages was made. Fish species were basically categorised and grouped according to their similarities in habitat, maximum body size, feeding habits and physiological behaviour, and ecological distribution in order to keep homogeneous characteristics among the species within each group (Yodzis and Winemiller, 1999; Christensen *et al.,* 2000). For each group, whenever possible, a representative species was selected based on its importance in the fisheries and available information.

> *BASIC PARAMETER VALUES*

Data required for the Ecopath model are: biomass (B), ratio production/biomass (P/B), consumption per unit of biomass (Q/B), catches (Y), diet composition and ecotrophic efficiency (EE).

Basic parameters of fish

The production/biomass (P/B) ratio

Whenever possible, the P/B ratio of the fish groups was estimated from recently-collected length-frequency distributions using the FiSAT software (Gayanilo *et al*., 2002). In a first step, this software was used to estimate the growth parameters of the Von Bertalanffy (1938) Growth Function, *i.e.*, the asymptotic length, L_∞, and the growth coefficient, K, which are needed for P/B computation (Gayanilo *et al*., 2002). Otherwise, the methods of Lévêque *et al.* (1977), Merona (1983), Pauly (1983) and the predictive models of Froese and Binohlan (2000) were employed to estimate these demographical parameters. Natural mortality, M, was computed using the predictive formula of Pauly (1980). Most of the P/B values were computed by Léonard Tah (personal data).

Relative food consumption (Q/B)

The food consumption per unit of biomass (Q/B) was estimated using the multiple regression formula of Palomares and Pauly (1998):

$$\mathbf{Log\ (Q/B) = 5.847 + 0.280 Log\ (P/B) - 0.152 Log W_\infty - 1.360T' + 0.062A + 0.510h + 0.390d}$$

Table I
Functional groups considered in Lake Ayamé.

Tableau I
Groupes des espèces considérées dans le lac Ayamé.

Ecopath group	Species concerned
Hepsetus odoe	*Hepsetus odoe*
***Hemichromis* spp.**	*Hemichromis bimaculatus* *Hemichromis fasciatus*
Clariidae	*Heterobranchus isopterus* *Clarias anguillaris*
Ichtyophagous Mormyrids	*Mormyrops anguilloides*
Insectivorous Mormyrids	*Marcusenius furcidens, Marcusenius ussheri* *Mormyrus rume*
***Chrysichthys* spp.**	*Chrysichtys nigrodigitatus* *Chrysichtys maurus*
***Synodontis/Schilbe* spp.**	*Synodontis bastiani* *Synodontis schall* *Schilbe mandibularis*
Heterotis niloticus	*Heterotis niloticus*
Small zoophagous organisms	*Chromidotilapia guntheri* *Ctenopoma petherici* *Micralestes elongatus* *Malapterurus electricus* *Petrocephalus bovei*
***Barbus* spp.**	*Barbus trispilos* *Barbus ablabes*
***Brycinus* spp.**	*Brycinus imberi* *Brycinus derhami, Brycinus nurse* *Brycinus macrolepidotus* *Brycinus longipinnis*
Labeo parvus	*Labeo parvus*
Sarotherodon melanotheron	*Sarotherodon melanotheron*
Oreochromis niloticus	*Oreochromis niloticus*
Tilapias	*Tilapia busumana* *Tilapia zillii* *Tilapia hybride*
Insects	
Annelids	
Molluscs	
Zooplankton	
Phytoplankton	
Macrophytes	
Benthic algae	
Detritus	

where:

$W\infty$ = fresh weight;

T' = 1000/Kelvin (Kelvin = T° C + 273);

A = the aspect ratio of the caudal fin, indicative of metabolic activity and expressed as the ratio of the square of the height of the caudal fin and its surface area, A, was obtained mainly from FishBase (www.fishbase.org) (Froese and Pauly, 2007).

The parameters h and d concern diet

h = 1, d = 0 for herbivorous;

h = 0, d = 1 for detritivorous;

h = 0, d = 0 for carnivorous.

Biomass (B)

The biomass (B) of each fish group was estimated assuming equilibrium conditions, such that:

B = Y/F

where Y is yield in $t.km^{-2}.yr^{-1}$ and F is the coefficient of fishing mortality. F is the difference between total and natural mortalities: F = Z – M, assuming that Z is equal to P/B as indicated by Allen (1971).

Annual fish yield

The evaluations of actual catches are usually based on landing statistics for each species or group of species included in a box. The total annual catch from the ecosystem concerned was estimated at 1061 t (1995–1996), which was split into two main categories of fishing gears: mesh gillnets and other gears for the multispecies consideration.

Diet composition (DC)

Diet composition is organised as a matrix. Data have been obtained from FishBase (Froese and Pauly, 2007) and studies from various authors: Kouamelan *et al.* (1999) for *Mormyrus rume*, Kouamelan *et al.* (2000) for *Mormyrops anguilloides,* Diomande *et al.* (2001) for *Synodontis bastiani*, Kone and Teugels (2003) for *Sarotherodon melanotheron*, and Dietoa *et al.* (2007) for *Brycinus longipinnis*. Other fish diet compositions come from VLIR (Vlaamse Interuniversitaire Raad) project unpublished data (Gourène and Ouattara, pers. comm.) (those are: *Heterotis niloticus*, *Marcusenius* spp.*, Synodontis schall, Brycinus* spp.*, Schilbe mandibularis* and Clariidae) and FishBase (Froese and Pauly, 2007) (*Tilapia* spp., *Chrysichtys* spp., *Hepsetus odoe, Hemichromis* spp., *Ctenopoma petherici, Micralestes elongatus, Malapterurus electricus, Barbus* spp., *Labeo parvus* and *Chromidotilapia guntheri*).

An average diet composition was calculated whenever several species constitute one group. Import to a system is the consumption of preys that are not a part of the system. Import is treated as a "prey" in the diet composition, and should be entered as a fraction of the total diet.

Ecotrophic efficiency (EE)

Ecotrophic efficiency was estimated by the software when B, Q/B and P/B were known. Its value is between 0.5 and 0.95 (Ricker, 1969).

Other communitie

Benthic fauna

Benthic macrofauna inventory showed 3 groups (oligochetes, molluscs and insects). Insects constitute the richest group in terms of biodiversity (29 taxons). Molluscs are more abundant; about 70% of the total biomass of the benthic fauna (Diomande and Gourène, 2005).

The biomasses are: 34.33 t.km^{-2} for molluscs, 16.85 t.km^{-2} for insects and 0.44 t.km^{-2} for annelids (oligochetes).

Annual P/B and Q/B values of 3 and 30 yr^{-1} were used for molluscs, 5 and 25 yr^{-1} for insects, and 10 and 65 yr^{-1} for annelids (Palomares, 1991).

Benthic macrofauna diet compositions were adopted from Lauzanne (1983).

Zooplankton

The zooplanktonic community includes copepods, cladocerans and rotifers. The average B is 12.8 t.km^{-2} (VLIR project unpublished data). Annual P/B and Q/B values, respectively, of 35 yr^{-1} and 140 were adopted from Moreau and Villanueva (2002). Zooplankton diet compositions were adopted from Lauzanne (1983).

Phytoplankton

The dominant groups are Chlorophytes (Ouattara *et al*., 2003). Chlorophyll-a concentration showed clear seasonal variations. The Chlorophyll-a content was on average 13 mg.m^{-3} or 3.9 mg.m^{-2} when it was extrapolated over 3 m (*i.e.* the euphotic zone). Chlorophyll-a concentration was converted into phytoplankton fresh weight following the conversion factor indicated by Ivan *et al*. (2007): 1 mg chlorophyll-a = 300 mg fresh weight. The resulting fresh biomass is 11.7 t.km^{-2}. The daily primary production was measured at 0.65 g.C.m^{-2} by Ouattara *et al*. (2007). The annual primary production was computed as 237.2 t.C.km^{-2}. Assuming one g.C is 10 g fresh weight (Christensen and Pauly, 1993), a value of 2372 t.km^{-2} was obtained. A P/B ratio of 203 yr^{-1} was used as an input in the model.

Benthic algae

Only limited information was available for this group. Benthic primary production estimations indicated by Dufour (1994) were adopted. Benthic algae production was calculated as 10% of phytoplankton production. The benthic algae biomass obtained was 1.17 t.km^{-2}. A P/B ratio of 203 yr^{-1} was used as an input in the model.

Macrophytes

Macrophyte communities were dominated by *Pistia stratiotes*, *Salvinia molesta* and Cyperacea.

An input value of 0.950 for EE was used to estimate the biomass based on intense predation noted from Macrophyte consumers. A P/B ratio of 5 yr^{-1} was adopted from Dufour (1994).

Detritus

A standing stock of 1 t.km^{-2} (fresh weight) was calculated using the empirical equation of Pauly *et al*. (1993) based on an annual primary production estimated in the Lake and a euphotic zone of 3 m. It is a required input when using Ecopath.

Balancing the model

The first step in verifying whether the model output was realistic was to check that the ecotrophic efficiency (EE) was < 1.0 for all compartments, as values > 1.0 are inconsistent (that is impossible, under conditions of steady state). The second step in verifying whether the model output was realistic was to check if the production/consumption ratio or gross efficiency (GE) was often between 0.1 and 0.3 (Christensen and Pauly, 1992). Diet composition of some groups was also modified, considering that these were of the highest uncertainty compared with other input variables, to achieve an EE less than 1.

RESULTS

The basic input for each of the 23 categorised ecological groups and the parameters computed with the software are presented in Table II, while the relative diet compositions are given in Table III.

> *RESOURCES EXPLOITED FOR HUMAN CONSUMPTION*

The total estimated fish biomass is 8.02 t.km^{-2}. *Sarotherodon melanotheron* (2.51 t.km^{-2}), *Heterotis niloticus* (1.28 t.km^{-2}) and *Chrysichtys* spp. (0.83 t.km^{-2}) contribute the most to biomass. On the other hand, Clariidae (0.022 t.km^{-2}) and *Hemichromis* spp. (0.099 t.km^{-2}) contribute the least. Small species' biomasses, *e.g.*, small zoophagous organisms (0.166 t.km^{-2}), *Barbus* spp. (0.192 t.km^{-2}) and *Labeo parvus* (0.327 t.km^{-2}), are only 8.55% of fish total biomass. EE values calculated for fish are between 0.745 and 0.967. Most values are high (EE > 0.85).

> *TOP PREDATORS*

The highest trophic levels (TLs) were estimated for *Hepsetus odoe, Hemichromis* spp., ichtyophagous Mormyrids, insectivorous Mormyrids, small zoophagous organisms, *Barbus* spp., Clariidae and *Chrysichtys* spp. (TL > 3.0) (Table II) due to their carnivorous feeding ecology (Table III). Most groups belong to TL3 and most are predatory carnivorous.

> *INTERMEDIATE PREDATORS*

Intermediate TLs (2 < TL > 3) were estimated for *Sarotherodon melanotheron*, *Heterotis niloticus*, *Synodontis/Schilbe* spp., *Brycinus* spp., Tilapias, *Labeo parvus* and *Oreochromis niloticus*.

> *LOWEST TL UTILISATION*

EE values for primary producers (phytoplankton, Macrophytes and benthic algae) are high (more than 0.80) for several groups which are targeted by predators. They are quite low (less than 0.60) for primary consumers. Molluscs and insects are highly consumed by fish. Zooplankton was not fully utilised due to the benthic fauna abundance.

The P/Q ratios (Table II) are low for *Hepsetus odoe*, *Oreochromis niloticus*, Tilapias, *Sarotherodon melanotheron* and *Labeo parvus*. The maximum value was obtained for small zoophagous organisms. The value for *Hepsetus odoe* is low for a top predator; this is in relation to its size and prey size.

> *STRUCTURE PER TROPHIC LEVEL*

Most of the fish biomass, catch and ecological production take place at TL3 (Table II and Figure 2). Fishers target mainly the highest TL fish (about 3 or more) as summarised in Table IV.

Moreover, Ecopath usually calculates trophic levels higher than 4 (Ulanowicz, 1995). In the present study, 7 TLs are counted (Table IV), which is due to cannibalism in the highest trophic levels.

Trophic aggregation revealed that transfer efficiency from TL1 (phytoplankton, macrophytes, benthic algae and detritus) to higher TLs is relatively high (about 11%), as shown in Table V.

The total flow originating from the first trophic level comes from primary producers (63%) and only 33% originates from detritus.

Detritus mainly constitutes primary producers' waste, as the most significant part (75%) originates from the primary producers and only 25% is directed into the system (Table VI).

Table II
Input values and calculated parameters (in bold) for the Ecopath model of the Lake Ayamé between 1995 and 1996. TL is the trophic level, B is the total biomass ($t.km^{-2}$), P/B is the production rate (yr^{-1}), Q/B is the annual food consumption per unit biomass (yr^{-1}), EE is the ecotrophic efficiency, P/Q is the production/consumption ratio and Y is the total catch ($t.km^{-2}.yr^{-1}$).

Tableau II
Paramètres entrés et paramètres estimés (en gras) par Ecopath pour les groupes considérés dans le lac Ayamé entre 1995 et 1996. NT est le niveau trophique, B est la biomasse en poids frais ($t.km^{-2}$), P/B est le rapport production/biomasse (an^{-1}), Q/B est la consommation relative de nourriture (an^{-1}), EE est le rendement écotrophique, P/Q est le rapport production/consommation, et Y est la capture par pêche ($t.km^{-2}.an^{-1}$).

	Group names	TL	B ($t.km^{-2}$)	P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q	Y ($t.km^{-2}.yr^{-1}$)
1	*Hepsetus odoe*	**3.83**	0.28	0.99	11.48	**0.745**	**0.086**	0.06
2	*Hemichromis* spp.	**3.61**	0.099	1.89	13.44	**0.898**	**0.141**	0.06
3	Clariidae	**3.07**	0.022	1.62	9.75	**0.932**	**0.166**	0.02
4	Ichtyophagous Mormyrids	**3.54**	0.437	0.93	7.77	**0.956**	**0.120**	0.12
5	Insectivorous Mormyrids	**3.34**	0.475	1.72	12.29	**0.916**	**0.140**	0.41
6	*Chrysichthys* spp.	**3.03**	0.827	2.20	13.33	**0.857**	**0.165**	0.94
7	*Synodontis/Schilbe* spp.	**2.61**	0.393	1.83	14.94	**0.808**	**0.122**	0.30
8	*Heterotis niloticus*	**2.93**	1.28	1.01	7.51	**0.851**	**0.134**	0.59
9	Small zoophagous organisms	**3.25**	**0.166**	3.72	17.81	0.950	**0.209**	0.03
10	*Barbus* spp.	**3.12**	**0.192**	4.83	28.78	0.950	**0.168**	0.01
11	*Brycinus* spp.	**2.56**	0.421	1.75	15.58	**0.967**	**0.112**	0.30
12	*Labeo parvus*	**2.14**	**0.327**	1.42	37.3	**0.950**	**0.038**	0.03
13	*Sarotherodon melanotheron*	**2.95**	2.505	2.30	43.25	**0.917**	**0.053**	3.01
14	*Oreochromis niloticus*	**2.06**	0.251	1.647	40.7	**0.952**	**0.040**	0.15
15	Tilapias	**2.19**	0.34	2.00	45.18	**0.909**	**0.044**	0.12
16	Insects	**2.37**	16.85	5.00	25	**0.567**	**0.200**	
17	Annelids	**2.35**	**2.096**	10.00	65	0.95	**0.154**	
18	Molluscs	**2.03**	34.5	3.00	30	**0.247**	**0.10**	
19	Zooplankton	**2.05**	12.85	35.0	140	**0.754**	**0.25**	
20	Phytoplankton	**1**	11.7	203	-	**0.964**	**-**	
21	Macrophytes	**1**	**23.14**	5.00	-	0.95	**-**	
22	Benthic algae	**1**	1.17	203	-	**0.936**	**-**	
23	Detritus	**1**	1	-	-	**0.82**	**-**	

Table III
Diet composition (fractional) of the groups considered in the Ecopath model of Lake Ayamé.

Tableau III
Régime alimentaire des groupes fonctionnels d'Ecopath considérés au Lac Ayamé.

	Preys\Predators	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	*Hepsetus odoe*	0.02	0.01	0.01	0.02															
2	*Hemichromis* spp.	0.02	0.02	0.005	0.005															
3	Clariidae	0.002	0.005	0.01																
4	Ichtyophagous Mormyrids	0.04	0.01	0.01	0.02			0.01												
5	Insectivorous Mormyrids	0.05	0.01	0.005	0.03			0.01												
6	*Chrysichthys* spp.	0.10	0.02	0.03	0.06			0.01												
7	*Synodontis/Schilbe*	0.03	0.01	0.03	0.05															
8	*Heterotis niloticus*	0.05	0.04	0.01	0.02		0.01	0.02												
9	*Small zoophagous organisms*	0.04	0.03	0.03	0.03		0.02	0.01												
10	*Barbus* spp.	0.06	0.05	0.01	0.03		0.02	0.005	0.02			0.01								
11	*Brycinus* spp.	0.04	0.05	0.03	0.03		0.005	0.10												
12	*Labeo parvus*	0.03	0.03	0.02	0.03		0.01	0.01												
13	*Sarotherodo melanotheron*	0.25	0.20	0.10	0.25		0.02	0.02												

Table III
Continued.

	Preys\Predators	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
14	*Oreochromis niloticus*	0.02	0.015	0.01	0.03		0.005													
15	Tilapias	0.03	0.02	0.02	0.06		0.01	0.01												
16	Insects	0.05	0.23	0.20	0.10	0.95	0.25	0.105	0.30	0.70	0.25	0.35	0.05		0.01	0.05	0.05	0.05		
17	Annelids	0.05	0.10	0.02	0.02		0.10	0.1	0.10	0.02	0.03	0.03	0.03		0.01	0.05	0.02	0.05		
18	Molluscs	0.01	0.03	0.05	0.02		0.21	0.03	0.18	0.05							0.05			
19	Zooplankton	0.05	0.10	0.05	0.05	0.04	0.10	0.05	0.12	0.20	0.70	0.02	0.03	0.90	0.03	0.05	0.20	0.20	0.03	0.05
20	Phytoplankton			0.03	0.01	0.01	0.05		0.05		0.02	0.07	0.20	0.10	0.70	0.30	0.04	0.15	0.15	0.85
21	Macrophytes			0.18	0.05			0.30	0.15			0.50	0.01			0.25	0.30		0.08	
22	Benthic algae			0.04	0.015		0.04	0.03		0.01			0.05		0.15	0.10		0.15	0.14	
23	Detritus	0.005		0.05	0.02		0.10	0.22	0.05	0.02		0.02	0.63		0.10	0.20	0.29	0.40	0.60	0.10
24	Imports	0.053	0.02	0.05	0.05		0.05	0.05	0.03								0.05			
25	Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

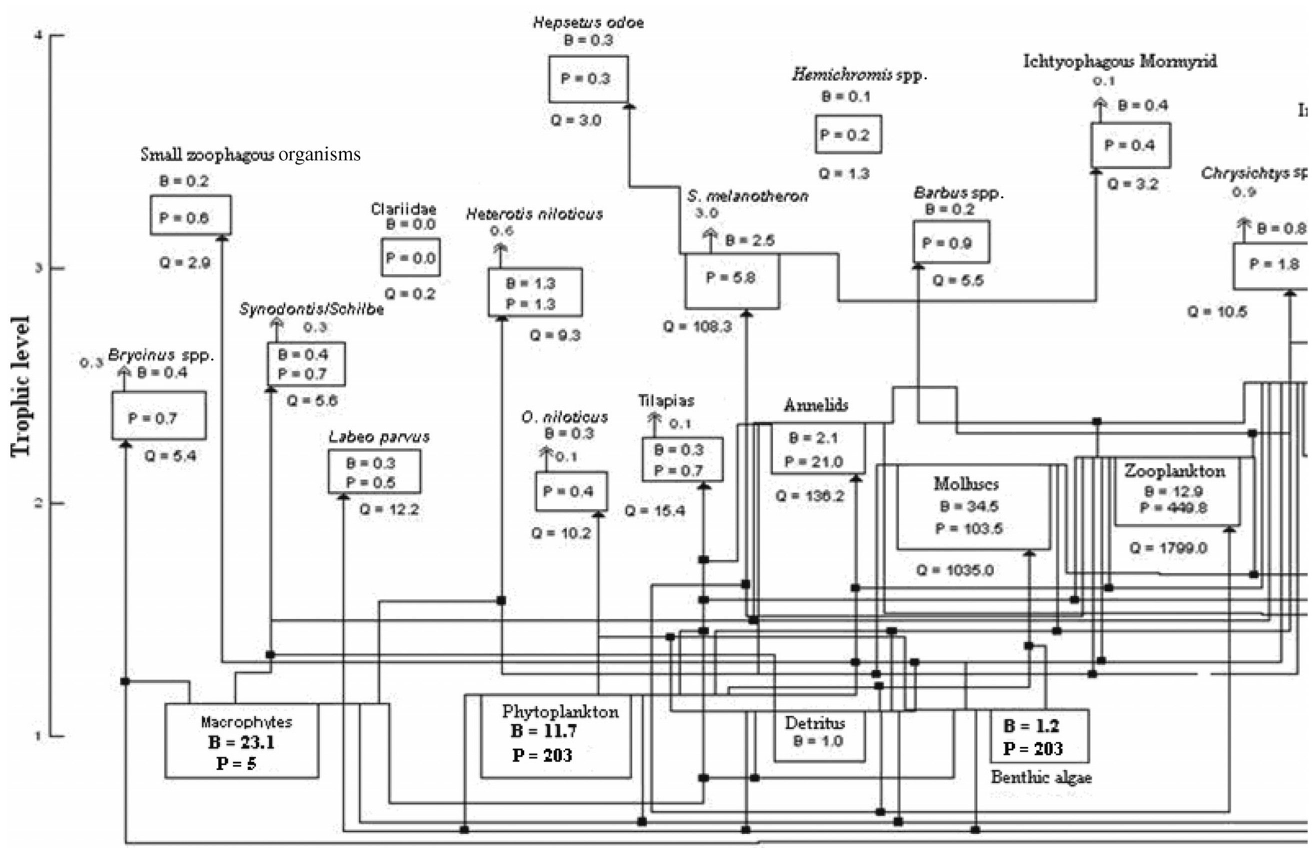

Figure 2
Schematic representation of trophic structure of Lake Ayamé ecosystem. B = Biomass, P = Production and Q = Food consumption. Flows are expressed in t.km^{-2}.yr^{-1}.

Figure 2
Représentation schématique de la structure trophique du lac Ayamé. B = Biomasse, P = Production et Q = Consommation de nourriture. Tous les flux sont exprimés en t.km^{-2}.an.

Table IV
Distribution of exploited production, fish biomass and ecological production between trophic levels in Lake Ayamé.

Tableau IV
Distribution entre différents niveaux trophiques de la production exploitée, de la biomasse et de la production écologique des poissons au lac Ayamé.

TL (entire number)	Catch ($t.km^{-2}.yr^{-1}$)	Biomass ($t.km^{-2}$)	Ecological production ($t.km^{-2}.yr^{-1}$)
VII	0.001	0.001	0.001
VI	0.008	0.015	0.021
V	0.078	0.147	0.216
IV	0.671	1.106	1.802
III	4.087	4.622	9.480
II	1.289	2.124	3.636

Table V
Transfer efficiency (%) at different trophic levels.

Tableau V
Variations des rendements des transferts (%) selon le niveau trophique.

	TL							
Sources	I	II	III	IV	V	VI	VII	Average
Producers	15.1	11.1	11.4	11.3	11.1	10.9	10.9	12.4
Detritus	7.3	11.5	11.5	11.2	10.9	10.9		9.9
Combined	12.6	11.2	11.4	11.3	11.1	10.9	10.7	11.7

Total flow proportion from detritus: 0.33.

The system omnivory index for Lake Ayamé is relatively high, 0.193. The omnivory index (OI) of each group in general is high with most of the values greater than 0.2 (Table VI). It means the diet of several organisms is diversified and that these organisms can adapt to environmental changes.

The TL of the fishery is 2.94, which is high. Predators are the most targeted groups. The gross efficiency of fishery (GEF) is quite low (0.002755), as shown in Table VII. This index increases with fisheries' development.

The primary production required (PPR) in order to support the fishery (Pauly and Christensen, 1995) is high, about 36.65% of the total primary production (Table VII); but a low ecological footprint, about 0.042 km^2, is observed.

The connectance index (CI) is higher (0.386) than the theoretical value (0.317), as presented in Table VII.

DISCUSSION

The total estimated fish biomass is acceptable (8.02 $t.km^{-2}$) when compared with other African inland waters. Indeed, these ecosystem biomasses are estimated at about 10 $t.km^{-2}$

Table VI
Transfer and flow (consumption) proportions from detritus to functional groups of Ecopath, flow transfer of groups to detritus and omnivory index of these groups.

Tableau VI
Transfert et proportions des flux (consommation) provenant du détritus vers les groupes fonctionnels d'Ecopath, transfert des flux des groupes vers le détritus et indice d'omnivorie de ces groupes.

Group names	Group detritus consumption ($t.km^{-2}$)	Detritus consumption proportion (%)	Flow to detritus ($t.km^{-2}$)	Omnivory index
Hepsetus odoe	0.016	0.002	0.713	0.226
***Hemichromis* spp.**	0	0	0.285	0.184
Clariidae	0.011	0.001	0.045	0.637
Ichtyophagous Mormyrids	0.068	0.007	0.697	0.443
Insectivorous Mormyrids	0	0	1.236	0.022
***Chrysichthys* spp.**	1.102	0.111	2.464	0.330
***Synodontis/Schilbe* spp.**	1.292	0.130	1.313	0.553
Heterotis niloticus	0.481	0.048	2.115	0.327
Small zoophagous organisms	0.059	0.006	0.62	0.067
***Barbus* spp.**	0	0	1.154	0.045
***Brycinus* spp.**	0.131	0.013	1.336	0.462
Labeo parvus	7.673	0.773	2.459	0.162
Sarotherodon melanotheron	0	0	27.563	0.100
Oreochromis niloticus	1.022	0.103	2.574	0.067
Tilapias	3.072	0.31	3.902	0.204
Insects	122.16	12.31	141.814	0.275
Annelids	54.493	5.491	35.106	0.286
Molluscs	621	62.57	336.668	0.032
Zooplankton	179.9	18.13	560.201	0.053
Phytoplankton		-	65.085	-
Macrophytes		-	11.57	-
Benthic algae	-	-	11.632	-
Detritus	-	-	-	-

(Christensen and Pauly, 1993; Mavuti *et al*., 1996; Thapanand *et al*., 2007). This acceptable biomass is due to favourable conditions for fish productivity. Lowe-McConnell (1987) indicated that lakes have more habitats and abundant feed such as plankton and benthos. The fish biomass in Lake Ayamé is low compared with those of lake Nokoué: 132 $t.km^{-2}$, lagoon Ebrié: 9.5 $t.km^{-2}$ and Bagré reservoir: 22.4 $t.km^{-2}$ (Villanueva *et al.,* 2005; 2006), but it is higher than the biomass recorded for Ubolratana reservoir (6.56 $t.km^{-2}$) by Villanueva *et al.* (2005) and Sri Lanka reservoirs (5.0 $t.km^{-2}$) by Haputhantri *et al*. (2008). The fish biomass in

Table VII
Summary statistics and flow network indices of Lake Ayamé.

Tableau VII
Statistiques globales et indices des réseaux de flux du lac Ayamé.

Parameters and index	Values
Sum all consumptions ($t.km^{-2}.yr^{-1}$)	3593.126
Sum of flow to detritus ($t.km^{-2}.yr^{-1}$)	1210.553
Mean trophic level of catch	2.94
Gross efficiency fishery (catch/PPnet)	0.002755
Calculated total net primary production ($t.km^{-2}.yr^{-1}$)	2226.248
Primary production required for catch ($t.km^{-2}.yr^{-1}$)	816.05
Total biomass (excluding detritus)	110.32
Total catches ($t.km^{-2}.yr^{-1}$)	6.133
Connectance index (IC)	0.386
System omnivory index (SOI)	0.193
Ecologic footprint (km^2)	0.042
Ascendancy (%)	26.40
Overhead (%)	73.60

the fresh water of Lake Ayamé is similar to what was computed by Christensen (1998) in marine water: 7.1 $t.km^{-2}$.

Ecotrophic efficiencies of fish groups are variable (but most are > 0.8). Groups for which EE is low suggest a limited exploitation, as these fishes have no significant predators in the lake and are poorly targeted by fishermen. On the other hand, the groups which display high EE values, *e.g.*, *Oreochromis niloticus*, ichtyophagous Mormyrid and *Brycinus* spp., are intensively exploited and suffer a high level of predation. Such high EE values of most groups (particularly fish EE values) were noted in other studies, *e.g.* in Bagré reservoir (Villanueva *et al*., 2005). Primary producers have a high EE value, indicating that these groups are the base food source in Lake Ayamé. They are fully utilised by organisms at higher trophic levels. This may be attributed to the abundance of fish consuming this group. The higher EE of primary producers means that the Lake Ayamé ecosystem has a bottom-up control. The important contribution of detritus in the food base was observed in Lake Nokoué (Villanueva *et al.*, 2006). This is not the case in Bagré reservoir (Villanueva *et al*., 2005). A high value of EE is also noted for zooplankton but is exploited by most zoophagous organisms (insects, small zoophagous organisms) and fish juveniles. Moreover, this resource also seems to be exploited by *Sarotherodon melanotheron*, usually regarded as herbivorous, which becomes zooplanktonophagous in Lake Ayamé. This possible adaptation of *Sarotherodon melanotheron* can be explained by feed flexibility (Pauly *et al*., 1988; Paugy, 1994; Blaber, 2000; Kone and Teugels, 2003).

Ichtyophagous fish (*Hepsetus odoe*) have quite a low P/Q value. This unusual situation might come from the relatively small size of this fish, which cannot attack large fishes as prey. Somehow, when their small preys become less available due to predation and catch pressure, their ichtyophagous character could be modified. However, a high P/Q ratio is estimated for zoophagous organisms due to their carnivorous feeding habits, and this is in relation to their small size. This case was also observed in Lake Kivu for zoophagous *Haplochromis* (Villanueva *et al*., 2007). Benthophagous groups also have a high P/Q.

This situation is in relation to the abundant biomass of benthic organisms observed in Lake Ayamé. This significant biomass has been noted in various lakes such as Lake George (Moreau *et al.,* 1993), Lake Ihema (Mavuti *et al.,* 1996) and Lake Victoria (Villanueva and Moreau*,* 2001). The low P/Q ratios obtained for *Oreochromis niloticus* and Tilapias are in agreement with the low quality of their preferred preys, which are principally phytoplankton and decaying organic material.

The Lake Ayamé trophic chain is relatively longer, as indicated by the highest trophic level, which is > 3. Generally trophic level does not exceed 4 (Ulanowicz, 1995). Similar results are observed in other aquatic systems such as Lake Tchad (Palomares, 1991) and lagoon Ebrié (Villanueva *et al.*, 2006). This trophic chain is based on primary producers and organisms of trophic level II which constitutes zooplankton, molluscs, annelids, insects, *Oreochromis niloticus*, *Labeo parvus*, Tilapias and *Brycinus* spp. The trophic level II favours most flow transfers to the highest trophic level. Indeed, primary producers' abundance governs that of primary consumers, which constitutes the highest trophic level prey and supports fisheries (Pauly and Christensen, 1995). This situation could justify the importance of catch, biomass and ecologic production of *Sarotherodon melanotheron*, *Heterotis niloticus* and *Chrysichthys* spp. at trophic level III. These species are important for the functioning of the lake in terms of fish production. The regulation of this lake is clearly a "bottom-up" control; this concords with ecological theory, which states that bottom-up forces would dominate the ecosystem process (Platts and Ulanowicz, 1985; Dyer and Letourneau, 2003).

The average transfer efficiency is relatively high (11%). This is most probably due to the utilisation of the ecological production of the fish groups by fisheries and predation as revealed by the high EEs of several groups. This average transfer efficiency noted in Lake Ayamé is high when compared with those observed in lake Nakuru (< 8%) by Moreau *et al*. (2001), in Ria Formosa reservoir (< 6.0%) by Gamito and Erzini (2005) and in Pasak Jolasid reservoir (5.3%) by Thapanand *et al*. (2007). Other studies (*e.g.* by Villanueva *et al*., 2005, in Bagré reservoir: > 13%) showed the highest values when compared with the Lake Ayamé value. The high transfer efficiency in Lake Ayamé may be attributed to the high diversity of predators in this ecosystem. The significance of biodiversity in assuring ecosystem stability has been evoked by Naeem and Li (1997), and Loreau *et al*. (2001). Moreover, Christensen (1995) suggests that system ascendancy and overhead can be considered as possible measurements of ecosystem stability. The values obtained for our model (26% for ascendancy, 74% for overhead) indicate a good stability of the ecosystem of Lake Ayamé. This stability is due to the greater biodiversity of Lake Ayamé. Most authors (*e.g.* Castillo *et al.*, 2000; Perez-España and Arreguin-Sanchez, 1999; 2001) have promoted this idea.

The importance of relative total flow from detritus in Lake Ayamé can be explained by the significant decomposition of organic material. In other ecosystems, a high connectance index expresses detritus' important role in the trophic chain. That is why detritus is an alternative food in Lake Ayamé. It was shown by Moore *et al.* (2004) that plant decomposition allows mineralisation and releases nutritive salts and detritus with microbe fauna. This improves the detritus' nutritive value. Detritus is primary producers' additional food and also supports fish production.

The trophic level of the fishery is 2.94 as it targets mostly *Sarotherodon melanotheron* (which is at TL 2.95). This results in a situation of "immaturity" *sensu* Pauly *et al*. (1998) because this fishery exploits high trophic levels. This trophic level of the fishery is high when compared with other values obtained by Villanueva *et al*. (2005) and Villanueva *et al*. (2006), respectively, in Bagré reservoir and Ebrié lagoon which are, however, considered as immature ecosystems. Fish productivity is linked to primary production by many intermediate trophic links. The gross efficiency of the fishery is low as compared with what was observed for Lake George (Moreau *et al*., 1993), Lake Ihema (Mavuti *et al*., 1996) and Lake Victoria (Villanueva and Moreau, 2001) or other tropical inland water bodies (Christensen and Pauly, 1993). The primary production required (PPR) in order to support the fishery is high as compared with an average value suggested by Pauly and Christensen (1995) for tropical lakes and rivers (23.6%). This may be due to the high utilisation of food resources as expressed by the high EE of most groups.

The higher connectance index (0.396) than the theoretical value (0.317) computed using the regression model of Christensen and Pauly (1993) for Lake Ayamé can be regarded as the result of the diversity of the diets of some groups and it expresses a certain level of maturity *sensu* (Odum, 1971). This concords with an intermediate system omnivory index value which shows specialised and generalised groups existing in the lake in terms of diet. Guild diversification contributes to ecosystem stability. Functional groups which exhibit a certain degree of diet generalisation have trophic flexibility. This flexibility confers upon them larger possibilities of adaptation (Paugy, 1994). Moreover, the fish fauna of Lake Ayamé has several species which seem adapted to pressures such as environment changes and fisheries. This is the case of *Sarotherodon melanotheron*, which is probably adapted to environment changes because it integrates zooplankton in its diet. Lauzanne (1988) indicates that *Sarotherodon melanotheron* is filter microphagous. Moreover, Lowe-McConnel (1993) shows that in man-made lakes Tilapiine fish are most adapted. This biological plasticity enables them to survive and in most cases, to dominate in considerable abundance and productivity in most tropical waters (Lévêque, 2002). According to Polis and Strong (1996), resource utilisation and ecological interactions are highly dependent on habitat heterogeneity and may explain deviation in trophic guilds and behaviours of similar taxonomic groups in different ecosystems. This adaptation has reduced competition with *Oreochromis niloticus*. In other words, *Oreochromis niloticus* disappearance can be due to fish pressure. Similar low competition between endemic and alien tilapias is exhibited in Lake Kivu (Villanueva *et al*., 2007) and in Lake Victoria (Twongo, 1995). Competition is also not strong between *Chrysichtys* spp. and *Heterotis niloticus*. Lauzanne (1988) noted that both consume molluscs.

CONCLUSION

The use of Ecopath provided a conventional representation of ecosystems consisting of compartments connected by trophic links or flows which provides simplified quantitative descriptive organisation of aquatic communities. It has been a useful tool in describing and understanding the trophic structure in Lake Ayamé.

The highest trophic level is 3.82 and all trophic levels are represented in this ecosystem: primary producers, low trophic level consumers, intermediate trophic levels and top predators.

The Lake Ayamé ecosystem can be qualified as stable. This relative stability is based on trophic resource abundance, notably primary producers and detritus. However, these resources are not fully utilised. This situation involves little marked competition between various species considered as important in the lake ecosystem. Lake functioning is based on trophic levels 2 and 3. So organisms of these levels constitute key species for the lake.

The mean trophic level of catch (2.94) indicates that fisheries are targeting mainly the fish groups of high trophic levels. As a consequence, the lake resources have not yet crossed the critical threshold of overexploitation.

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 inland waters appears to be a way of increasing the productivity of the fisheries.

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REFERENCES

Allen K.R., 1971. Relation between production and biomass. *J. Fish. Res. Board Can., 28*, 1573–1581.

Andersen K.P. and Ursin E., 1977. A multispecies analysis of the efforts of variations of effort upon stock composition of eleven North Sea fish species, ICES Symposium of the Changes in the North Sea Fish stocks and Their Causes, *ICES Report*, *112*, 286–291.

Blaber S.J.M., 2000. Tropical estuarine fishes: ecology, exploitation and conservation. Fish and aquatic resources series *7*, Oxford: Blackwell, London, 372 p.

Castillo G., Li H.W. and Rossignol P.A., 2000. Absence of overall feedback in a benthic estuarine community: A system potentially buffered from impacts of biological invasions. *Estuaries 23*, 275–291.

Christensen V., 1995. Ecosystem maturity: towards quantification. *Ecol. Modell.*, *77*, 3–32.

Christensen V., 1998. Fishery induced changes in a marine ecosystem, insight from models of the gulf of Thailand. *J. Fish Biol.*, *53A*,128–142.

Christensen V. and Pauly D., 1992. ECOPATH II: a software for balancing steady state ecosystem models and calculating network characteristics. *Ecol. Modell., 61*, 169–185.

Christensen V. and Pauly D., 1993. Trophic Models of Aquatic Ecosystems, ICLARM Conference Proceedings, ICLARM Manila, Philippines.

Christensen V. and Pauly D., 1996. Ecological modelling for all. *Naga the ICLARM Quarterly, 19*, 25–26.

Christensen V. and Walters C., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Modell., 172*, 109–139.

Christensen V., Walters C.J. and Pauly D., 2000. Ecopath with Ecosim: A user's guide, October 2000, Fisheries Centre, University of British Columbia, Vancouver, Canada et ICLARM, Penang Malaysia [available on website URL: http://www.ecopath.org/].

Christensen V., Walters C. and Pauly D., 2005. Ecopath with Ecosim: a User's Guide. Fisheries Centre Report, 130 p., Fisheries Center, University of British Columbia, Vancouver, Canada and www.ecopath.org

Daget J. and Iltis A., 1965. Poissons de Côte d'Ivoire (Eaux douces et saumâtres). *Mémoire de l'Institut Fondamental d'Afrique Noire*, *74*, 385 p.

Dietoa Y.M., Gourène G. and Ouattara A., 2007. Habitudes alimentaires de *Brycinus longipinnis* dans le complexe fluvio-lacustre de la Bia, Côte d'Ivoire. *Belg. J. Zool.*, *137*, 3–9.

Diomande D. and Gourène G., 2005. Premières données sur la macrofaune benthique de l'hydrosystème fluvio-lacustre de la Bia (Côte d'Ivoire). *Sciences et Nature*, *2*, 167–176.

Diomande D., Gourène G. and Tito de Morais L., 2001. Stratégies alimentaires de *Synodontis bastiani* (Siluriformes : Mochokidae) dans le complexe fluvio-lacustre de la Bia, Côte d'Ivoire. *Cybium, 25*, 7–21.

Dufour P., 1994. Les microphytes. *In*: Durand J.R., Dufour P., Guiral D., Zabi S.G.F. (eds.), Environnement et ressources aquatiques de Côte d'Ivoire, Tome II – Les milieux lagunaires, ORSTOM, Paris, 109–136.

Dyer L.A. and Letourneau D., 2003. Top-down and bottom-up diversity cascades in detrital vs. living food webs. *Ecol. Lett., 6*, 60–68.

Froese R. and Binohlan C., 2000. Empirical relationships to estimate asymptotic length, length at first maturity and yield at maximum yield per recruitment in fishes, with a simple method to evaluate length frequency data. *J. Fish Biol., 56*, 758–773.

Froese R. and Pauly D., 2007. FishBase [available on website URL: http://www.fishbase.org/].

Gamito S. and Erzini K., 2005. Trophic food web and ecosystem attributes of a water reservoir of the Ria Formosa (south Portugal). *Ecol. Modell.*, *181*, 509–520.

Gayanilo F.C. Jr., Sparre P. and Pauly D. (eds.), 2002. The FAO-ICLARM Stock Assessment Tools II (FiSAT II Ver. 1.0), FAO [available on website URL: http://www.fao.org/fi/statist/fisoft/fisat/].

Gourène G.G., Teugels G., Hugueny B. and Thys Van Den Audernaerde D.F.E., 1999. Évaluation de la diversité ichtyologique d'un bassin ouest africain après la construction d'un barrage. *Cybium*, *23*, 147–160.

Haputhantri S.S.K., Villanueva M.C. and Moreau J., 2008. Trophic interactions in the coastal ecosystem of Sri Lanka: an ECOPATH preliminary approach. *Estuarine Coastal Shelf Sci.*, *76*, 304–318.

Ivan E., Silva L. and Schiemer F., 2008. Regulation of primary production in Sri Lankan reservoirs, *In*: Schiemer F., Simon D., Amarasinghe U.S. and Moreau J. (eds), Aquatic ecosystems and development comparative Asian perspectives. *Hydrobiology* (in press).

Kone T. and Teugels G.G., 2003. Food habits of brackish water tilapia *Sarotherodon melanotherodon* in riverine and lacustrine environment of a West African coastal basin. *Hydrobiologia, 490*, 75–85.

Kouamelan E.P., Teugels G.G., Gourène G., Ollevier F. and Thys Van Den Audernaerde D.F.E., 1999. The effect of man-made lake on the diet of the African electric fish *Mormyrus rume* Valenciennes, 1846 (Osteoglossiformes; Mormyridae). *Hydrobiologia, 380*, 141–151.

Kouamelan E.P., Teugels G.G., Gourène G., Thys Van Den Audenaerde D.F.E. and Ollevier F., 2000. Habitudes alimentaires de *Mormyrops anguilloides* (Mormyridae) en milieux lacustre et fluvial d'un bassin Ouest-africain. *Cybium*, *24*, 67–79.

Laevastu T. and Larkin H.A., 1981. Marine fisheries ecosystem. Its quantitative evaluation and management, Fishing News Books, Farnham.

Lauzanne L., 1983. Trophic relations of fishes in Lake Chad. *In*: Carmouze J.P, Durand J.R., Lévêque C. (eds.), Lake Chad: Ecology and productivity of a shallow tropical ecosystem, Junk Publ., The Hague, 489–518.

Lauzanne L., 1988. Les habitudes alimentaires des poissons d'eau douce africains. *In*: Lévêque C., Bruton M., Ssentongo G. (eds.), Biologie et écologie des poissons d'eau douce africains, ORSTOM, Paris, 221–242.

Lévêque C., 2002. Out of Africa, the success story of Tilapias. *Environ. Biol. Fishes*, *64*, 461–464.

Lévêque C., Durand J.R. and Ecoutin J.M., 1977. Relation entre le rapport P/B et la longévité chez les organismes. *Cahiers de l'ORSTOM, série Hydrobiologie, 11*, 17–32.

Lindeman R.L., 1942. The trophic dynamic aspect of ecology. *Ecology, 23*, 399–418

Loreau M., Naeem S., Inchausti P., Bengtsson J., Grime J.P., Hector A., Hooper D.U., Huston M.A., Raffaelli D., Schmid B., Tilman D. and Wardle D.A., 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science 294*, 804–808.

Lowe-McConnell R.H., 1987. Ecological studies in tropical fish communities, Cambridge University Press, Cambridge, UK, 382 p.

Lowe-McConnell R.H., 1993. Fish Faunas of the African Great Lakes: Origins, Diversity, and Vulnerability. *Conservation Biology*, *7*, 634–643.

Mavuti K., Moreau J., Munyandorero J. and Plisnier D., 1996. Analysis of trophic relationships in two shallow equatorial lakes: Lake Naivasha (Kenya) and Lake Ihema (Rwanda) using a multispecifies trophic model. *Hydrobiologia*, *321*, 89–100.

Merona B., 1983. Modèle d'estimation rapide de la croissance des poissons d'eau douce d'Afrique. *Revue d'Hydrobiologie Tropicale*, *16*, 103–116.

Moore J.C., Berlow E.L., Coleman D.C., De Ruiter P.C., Dong Q., Hastings A., Collins Johnson N., McCann K.S., Melville K., Morin P.J., Nadelhoffer K., Rosemond A.D., Post D.M., Sabo J.L., Scow K., Vanni M. and Wall D., 2004. Detritus, trophic dynamics and biodiversity. *Ecol. Lett., 7*, 584–600.

Moreau J. and Villanueva M.C., 2002. Exploratory analysis of possible management strategies in Lake Victoria (Kenyan sector) using the recent Ecosim software. *In*: Pitcher T., Cochrane K. (eds.), On the use of ecosystem models to investigate multi-species management strategies for capture fisheries. *Fisheries Centre Research Reports*, *10*, 150–154 [available on website URL: www.fisheries.ubc.ca].

Moreau J., Arrignon J. and Jubb R., 1988. Les introductions d'espèces étrangères dans les eaux continentales africaines, Intérêt et limites. *In*: Lévêque C., Bruton M.N., Ssentongo G.W., (Eds.), Biologie et écologie des poissons d'eau douce africains, ORSTOM, Paris, 221–242.

Moreau J., Christensen V. and Pauly D., 1993. A trophic ecosystem model of Lake George, Uganda. *In*: Christensen V. and Pauly D. (eds.), Trophic Models of Aquatic Ecosystems, ICLARM Conference, 124–129.

Moreau J., Mavuti K. and Daufresne T., 2001. A synoptic Ecopath model of biomass flows during two different static ecological situations in lac Nakuru (Kenya). *Hydrobiologia*, *458*, 63–74.

Naeem S. and Li S., 1997. Biodiversity enhances ecosystem reliability. *Nature 390*, 507–509.

Odum E.P., 1969. The strategy of ecosystem development. *Science*, *104*, 262–270.

Odum E.P., 1971. Fundamentals of ecology, W.B. Saunders Co, Philadelphia, 574 p.

Odum W.E. and Heald E.J., 1975. The detritus-based food web of an estuarine mangrove community. *In:* Cronin L.E. (ed.), *Estuarine Research* Academic, Press, Inc., London.

Ouattara A., Podoor N. and Gourène G., 2003. Études préliminaires de la distribution spatio-temporelle du phytoplancton d'un système fluvio-lacustre (Bia, Côte d'Ivoire). *Hydroécologie appliquée*, *73*, 1–20.

Ouattara A., Podoor N. and Gourène G., 2007. Activité photosynthétique du phytoplancton dans le barrage hydroélectrique d'Ayamé I (Côte d'Ivoire). *Agronomie Africaine, 19*, 63–70.

Palomares M.L., 1991. La consommation de nourriture chez les poissons, étude comparative, mise au point d'un modèle prédictif et application à l'étude des réseaux trophiques. Thèse de doctorat, Institut National Polytechnique de Toulouse, France.

Palomares M.L.D. and Pauly D., 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Mar. Freshw. Res.*, *49*, 447–453.

Paugy D., 1994. Écologie des poissons tropicaux d'un cours d'eau temporaire (Baoulé, haut bassin du Sénégal au Mali): adaptation au milieu et plasticité du régime alimentaire. *Revue d'Hydrobiologie Tropicale*, *27*, 157–172.

Pauly D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature. *In*: 175 fish stocks, *Journal du Conseil International pour l'Exploration de la Mer*, *39*, 175–192.

Pauly D., 1983. Some simple methods for the assessment of tropical fish stocks. *FAO Fisheries Technical Paper, 234*.

Pauly D. and Christensen V., 1995. Primary production required to sustain global fisheries. *Nature*, *374*, 255–257.

Pauly D., Palomares M.L.D. and Moreau J., 1988. Detritus and energy consumption and conversion efficiency of *Sarotherodon melanotheron* (Cichlidae) in a West African lagoon. *J. Appl. Ichthyol., 4*, 190–193.

Pauly D., Palomares M.L.D. and Froese R., 1993. Some prose on a database of indigenous knowledge on fish. *IK and Development Monitor, 1*, 26–27.

Pauly D., Christensen V., Dalsgaard J., Froese R. and Torres F.C. Jr., 1998. Fishing down marine food webs. *Science*, *279*, 860–863.

Perez-España H. and Arreguin-Sanchez F., 1999. A measure of ecosystem maturity. *Ecol. Modell.*, *119*, 79–85.

Perez-España H. and Arreguin-Sanchez F., 2001. An inverse relationship between stability and maturity in models of aquatic ecosystems, *Ecol. Modell.*, *145*, 189–196.

Platts T. and Ulanowicz R.E. (eds.) 1985. Ecosystem theory for biological oceanography. *Can. B. Fish. Aquat. Sci., 213*, 260 p.

Polis G.A. and Strong D.R., 1996. Food web complexity and community dynamics. *Am. Nat., 147*, 813–846.

Polovina J.J., 1984. Model of a coral reef ecosystem, The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs, 3*, 1–11.

Polovina J.J. and Ow M.D., 1985. An approach to estimating an ecosystem box model. *Fisheries Bulletin*, *83*, 457–460.

Reizer C., 1967. Aménagement piscicole du lac artificiel d'Ayamé. Publication n° 30 du C.T.F.T., 108 p.

Ricker W.E., 1969. Food from the sea. *In:* Treeman W.H. (ed.), Resources and Man, A Study and Recommendations by the Committee on Resources and Man, San Francisco, 87–108.

Thapanand T., Moreau J., Jutagate T., Wongrat P., Lekcholayut T., Meksumpun C., Janekitkarn S., Rodloi A., Dulyapruk V. and Wongrat L., 2007. Towards possible fishery management strategies in a newly impounded man-made lake in Thailand. *Ecol. Modell.*, *204*, 143–155.

Twongo T., 1995. Impact of fish species introductions on the tilapias of Lake Victoria and Kyoga. *In*: Pitcher T.J., Hart P.J.B. (eds.), The impact of species changes in African Lakes, Fish and Fisheries Series *18*, Chapman and Hall, London, 45–57.

Ulanowicz R.E., 1986. Growth and development: ecosystem phenomenology, Springer Verlag, New York, 203 p.

Ulanowicz R.E., 1995. Ecosystem trophic foundations: Lindeman exonerate. *In*: Patten B.C., Jorgensen S.E. (eds.), Complex Ecology: The Part-whole Relation in Ecosystems, Prentice-Hall, Englewood Cliff, 549–560.

Vanga A.F., Gourène G. and Ouattara M., 2002. Impact de la pêche sur la disponibilité en poissons dans les régions des lacs d'Ayamé et de Buyo (Côte d'Ivoire). *Archives Scientifiques,* CRO/ORSTOM, Vol. *XVII*, 1–12.

Villanueva M.C., Isumbisho M., Kaningini M., Moreau J. and Micha J.C., 2008. Modelling trophic interactions in Lake Kivu, what role do exotics play? *Ecol. Modell.*, *212*, 422–438.

Villanueva M.C., Laleye P., Albaret J.J., Lae R., Tito de Morais L. and Moreau J., 2006. Comparative analysis of trophic structures and interactions of two tropical lagoons. *Ecosystem Modelling, 197*, 461–477.

Villanueva M.C, Ouedraogo M. and Moreau J., 2005. Relationship in the recently impounded Bagré reservoir in Burkina Faso. *Ecol. Modell.*, *191*, 243–259.

Villanueva M.C. and Moreau J., 2001. Recent trends of evolution in Lake Victoria fisheries as assessed by Ecopath 4 (with Ecosim) software, *In*: Cowx I.G. (ed.), Lake and Reservoirs Fisheries Management, UK, The University of Hull, 96–110.

von Bertalanffy L., 1938. A quantitative theory of organic growth. *Human Biology, 10*, 181–213.

Walters C., Christensen V. and Pauly D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass balanced assessments. *Rev. Fish Biol. Fisher., 7*, 139–172.

Walters C., Pauly D. and Christensen V., 1999. Ecospace, prediction of meso-scale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems, 2*, 539–554.

Walters C., Pauly D., Christensen V. and Kitchell J.F., 2000. Representing density dependent consequences of life history in aquatic ecosystems, Ecosim II. *Ecosystems, 3*, 70–83.

Yodzis P. and Winemiller K.O., 1999. In search of operational trophospecies in a tropical aquatic food web. *Oïkos, 87*, 327–340.