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Evolution of Trophic Relationships in Ubolratana Reservoir (Thailand) as Described Using a Multispecies Trophic Model

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Abstract

A multispecies trophic model called ECOPATH II, which can be used to describe trophic relationships in aquatic ecosystems on a quantitative basis, is briefly analyzed. When properly used, it can help explain the trophic relationships in ecosystems and the evolution of fish stocks several years after impoundment. An example is provided on an Asian man-made lake, Ubolratana reservoir (Thailand). It can be compared to African man-made lakes where similar conditions have been documented.

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, a steady state model of trophic interactions in ecosystems. ECOPATH partitions the system into boxes comprising species having a common physical habitat, similar diet and life history characteristics (Polovina 1984; Christensen and Pauly 1992). When necessary, the model estimates mean (annual) biomass, (annual) biomass production and (annual) biomass consumption for each of the boxes in the ecosystem. It assumes that the ecosystem is at equilibrium, which means that input to a group equals output from it for the period considered. This steady state condition allows a system of biomass budget equations which, for each group, is:

Production - all predation on this species (or group) - nonpredatory mortality - all exports = 0.

ECOPATH expresses each term in the budget equation as a linear function of the mean biomass. The resulting budget equations become a system of simultaneous linear equations. The relative simplicity of the ECOPATH model compared to 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).

The aims of this paper are to:

1. 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 and Pauly (1992), and
2. describe two different situations of a man-made ecosystem, Ubolratana reservoir (Fig. 1), which has been studied by different workers since its impoundment in the late 1960s (Bhukaswan 1980) and more recently in the 1980s after several years of stocking Asian carps and tilapiine fish (Baluyut 1983, 1992).

This paper will also contribute to studies on ecosystem modelling in various aquatic environments (Christensen and Pauly 1993).

The Ubolratana Reservoir

Ubolratana reservoir (latitude 0° 45' S; longitude 36° 20' E; altitude 182 m above msl; surface area approximately 410 km^2) is a large, shallow and eutrophic reservoir created by damming the confluence of the Pong and Chem Rivers in North East Province, Thailand, about 500 km from Bangkok (Bhukaswan 1980). It is located in a broad valley and is the largest reservoir in Thailand. The reservoir is drawn down yearly to 176 m msl and the area shrinks to about 160 km^2. At 182 m msl the mean depth is 12 m. Ubolratana is an "open water reservoir" with a large pelagic zone. The dam was closed in

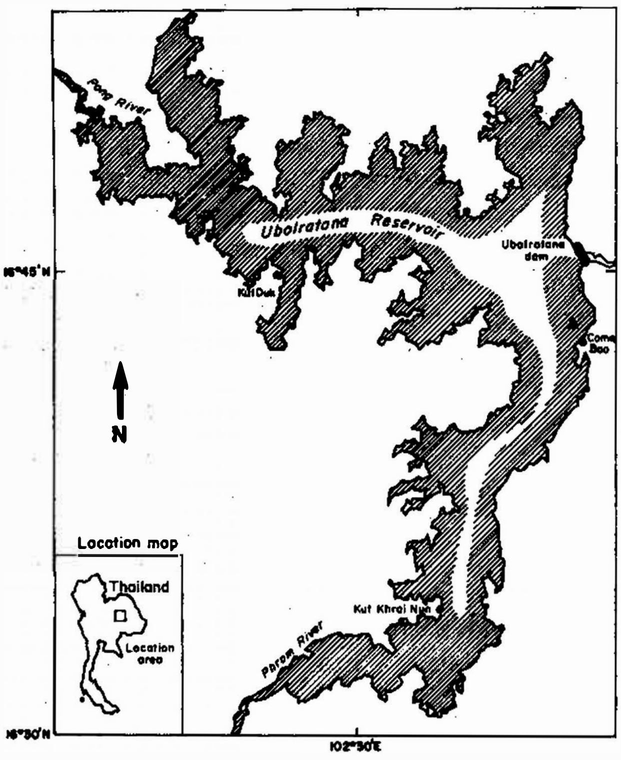

Fig. 1: General map of Ubolratana reservoir redrawn from Benchaken et al. (1989)

January 1965 and reached its equilibrium level 2 years later. Because of its low altitude, the total electric power generated is low. Indeed, in some years, the total financial income from capture fisheries exceeded the income from electric power (Costa-Pierce and Soemarwoto 1990). The commercial fisheries are quite active and deal with many fish species among them some introduced: mostly Asian cyprinds stocked on a yearly basis (Baluyut 1983). From 1975 a pelagic clupeid species, *Clupeichthys aesarnensis* (previously known as *Corica goniognatus*), has had a continuously increasing importance in the fisheries (Costa-Pierce and Soemarwoto 1990).

Materials and Methods

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

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

The records available for use in this simulation effort describe two phases of the evolution of Ubolratana reservoir: the beginning of the fisheries in 1968-72 and more recent years (1985-88).

For each group the main assumption of ECOPATH II is:

Production = actual catch of the group + what is consumed of it by all its predators + the amount of production transformed into detritus.

For each group of organisms, the basic equation of ECOPATH II is given below.

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

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

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

Tables 1 and 2 present the groups used to describe the two different situations of Ubolratana reservoir.

All biomasses were estimated via ECOPATH II, i.e., via a system of linear equations, such as (1), for which estimates of parameters were provided, as follows. The estimated biomasses were then compared to estimates available in the literature.

Table 1. Key features of an ECOPATH model for Ubolratana reservoir (1968-72).

	Groups	Catches[b]	Biomass[a]	P/B[c]	Q/B[d]	EE[e]	Gross efficiency[f]	Flow to detritus[a]	Trophic level[a]
1 -	*Ophicephalus*	0.67	1.515	1.00	5.64	0.95	0.18	1.78	3.39
2 -	*Wallagonia* sp.	0.49	1.657	0.75	4.21	0.95	0.18	1.46	3.36
3 -	*Oxyeleotris*	0.31	0.670	1.50	8.90	0.95	0.17	1.24	3.21
4 -	*Kryptopterus*	0.24	0.470	1.80	11.90	0.95	0.15	1.16	3.24
5 -	*Notopterus* n.	0.43	1.643	1.05	7.70	0.95	0.14	2.67	3.02
6 -	*Mystus* spp	0.31	0.953	1.50	11.50	0.95	0.13	2.26	3.04
7 -	*Hampala* spp	0.18	0.588	1.50	10.70	0.95	0.14	1.30	3.03
8 -	*Morilis* sp	0.31	2.419	0.70	9.10	0.95	0.08	4.48	2.27
9 -	*Puntius* spp	1.53	4.708	2.00	24.40	0.95	0.08	23.45	2.34
10 -	*Osteochilus* sp	0.55	2.202	1.30	15.60	0.95	0.08	7.01	2.09
11 -	*Puntioplites*	0.12	0.449	1.60	16.20	0.95	0.10	1.49	2.37
12 -	*Cirrhinus* j.	0.61	1.492	2.10	40.00	0.95	0.05	12.09	2.16
13 -	Clupeids	0.06	0.060	4.00	38.00	0.90	0.10	0.48	2.59
14 -	Zooplankton	-	6.930	30.00	200.00[f]	0.50	0.15	384.32	2.05
15 -	Insects	-	10.960	7.00	50.00[f]	0.95	0.14	113.34	2.16
16 -	Crustaceans	-	3.877	5.00	40.00[f]	0.95	0.12	31.11	2.19
17 -	Phytoplankton	-	5.460	365.00	-	0.70	-	597.60	1.00
18 -	Benthic producers	-	54.942	4.50	-	0.95	-	12.38	1.00
19 -	Detritus	-	-	-	-	-	-	-	1.00

[a] Computed by ECOPATH II
[b] Chookajorn and Pawapootanon (1976), Bhukaswan and Pholprasith (1977), Pawapootanon (1987)
[c] Computed as P/B = Q/B Gross efficiency for fishes + Payne (1986) and Winberg (1971) for other groups
[d] Model of Palomares (1991)
[e] Fixed values
[f] Fixed values according to feeding habits (Moreau et al. 1993a, b)

Table 2. Key features of an ECOPATH model for Ubolratana reservoir (1985-88).

	Groups	Catches[b]	Biomass[a]	P/B[c]	Q/B[c]	EE[c]	Gross efficiency[f]	Flow to detritus[a]	Trophic level[a]
1 -	*Ophicephalus*	0.10	0.165	1.00	5.64	0.80	0.18	0.22	3.23
2 -	*Wallagonia* sp	0.03	0.103	0.75	4.21	0.80	0.18	0.10	3.23
3 -	*Oxyeleotris*	0.12	0.138	1.50	8.90	0.80	0.17	0.28	3.14
4 -	*Kryptopterus*	0.03	0.047	1.80	11.90	0.80	0.15	0.13	3.17
5 -	*Notopterus* n.	0.21	0.319	1.05	7.70	0.80	0.14	0.56	2.94
6 -	*Mystus* spp	0.12	0.151	1.50	11.50	0.80	0.13	0.39	3.00
7 -	*Hampala* spp	0.04	0.065	1.50	10.70	0.80	0.14	0.16	3.00
8 -	*Morilius* sp	0.19	0.508	0.70	9.10	0.70	0.08	1.03	2.26
9 -	*Puntius* spp	1.53	1.732	2.00	24.40	0.70	0.08	9.49	2.28
10 -	*Osteochilus* sp	0.44	0.659	1.30	15.60	0.70	0.08	2.31	2.07
11 -	*Puntioplites*	1.30	1.543	1.60	16.20	0.70	0.10	5.74	2.36
12 -	*Cirrhinus* j.	1.36	1.354	2.10	40.00	0.70	0.05	11.68	2.11
13 -	Clupeids	0.72	0.338	4.00	38.00	0.80	0.10	2.84	2.58
14 -	Zooplankton	-	6.292	30.00	200.00	0.50	0.15	346.15	2.05
15 -	Insects	-	11.797	7.00	50.00	0.55	0.14	155.13	2.06
16 -	Crustaceans	-	3.898	5.00	40.00	0.55	0.12	39.97	2.10
17 -	Phytoplankton	-	4.900	365.00	-	0.70	-	536.50	1.00
18 -	Benthic producers	-	53.528	4.50	-	0.90	-	24.08	1.00
19 -	Detritus	-	-	-	-	-	-	-	1.00

[a] Computed by ECOPATH II
[b] From Benchaken et al. 1989
[c] See legend of Table 1

Fish Catches (Y)

Catch estimates were obtained for the fish groups in Tables 1 and 2 from records of the National Inland Fisheries Institute, Department of Fisheries of Thailand, or from published literature (Bhukaswan and Pholprasith 1977; Benchaken et al. 1989). They are expressed here, like all other flows, in t km^{-2} $year^{-1}$ (wet weight). The two periods of study are characterized by:

1. A similar total catch which is close to the maximum catch of about 2,300 t $year^{-1}$, e.g., about 6 t km^{-2} $year^{-1}$ was observed in both periods.
2. The importance of predatory fish in the catches just after impoundment (period one) and the collapse of these species in the middle of the 1980s (period two).
3. The increasing contribution to more than 10% of the total catch of the pelagic clupeid *C. aesarnensis.*

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 in the present instance), P/B is equal to total mortality Z as defined in fisheries science. Hence, some values could be obtained from the literature (Mekong Secretary 1982, 1984). When necessary, we estimated this parameter from length frequency data as outlined in Gayanilo et al. (1989). For a few fish groups, P/B was obtained from estimates of Q/B (see Table 1 for details) and reasonably selected values of gross efficiency (e.g., the ratio between P/B and Q/B) taking into account the kind of food ingested by those fish species. For groups other than fish, literature values were taken mostly from Winberg (1971) and Payne (1986). All values of P/B presented here are annual (Tables 1 and 2).

Diet Composition (DC)

The average composition of the food of each consumer group in Tables 1 and 2 refers to wet weights, and was assembled from published information and personal observations by one of the authors. Tables 3 and 4 present the diet matrixes used for the two situations.

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 year (Pauly and Palomares 1987; Palomares and Pauly 1989). The estimates of Q/B used here were obtained via the predictive model of Palomares (1991) who showed that freshwater and marine fish have similar Q/B values when their shapes, size, food type and environmental temperature are equal, thus justifying the use of a common model for marine and freshwater fish. Estimates of Q/B are provided in Tables 1 and 2. A necessary input for the model of Palomares (1991) is the asymptotic weight of all fish considered here; this parameter was available from the literature (Sidthimunka 1973; Mekong Secretary 1984).

Table 3. Feeding matrix for Ubolratana reservoir (1968-71).

	Oph	Wal	Oxy	Kry	Not	Mys	Ham	Mor	Pun	Ost	Ppl	Cir	Clu	Zoo	Ins	Cru	Phy	Ben	Det
Ophicephalus	5	4	3	3	4	3	2	4	14	5	1	5	1	5	25	11	2	2	1
Wallagonia sp.	4	5	3	2	4	3	2	3	16	5	1	6	1	8	20	10	1	4	2
Oxyeleotris			3		4	3		3	15	5	1	5		4	25	25	2	2	3
Kryptopterus				3	4	3	2	4	16	5	2	6		10	20	20	1	2	2
Notopterus n.									1					10	66	11	2	8	2
Mystus spp.						1	1	2	10	4	1	4		1	47	15	1	10	3
Hampala spp.	1				2	2	2	2	15	6	2	6		18	2	22	1	2	17
Morilius sp.														25			53	18	5
Puntius spp.									1					5	20		10	30	34
Osteochilus sp.														5		2	65	18	10
Puntioplites												1		25	7	1	46	15	5
Cirrhinus j.														10			30	20	40
Clupeids														50	5		45		
Zooplankton														5			95		
Insects														1	4	1	1	25	68
Crustaceans														2	5	2	2	25	64

Quantitative data for fishes are derived from studies by Mekong Secretary (1984) Wongtirawatana (1981) and Sricharoendam (pers. observations unpubl.).
For other groups: suggestions by Christensen and Pauly (1993).

Table 4. Feeding matrix for Ubolratana reservoir (1984-87).

	Oph	Wal	Oxy	Kry	Not	Mys	Ham	Mor	Pun	Ost	Ppl	Cir	Clu	Zoo	Ins	Cru	Phy	Ben	Det
Ophicephalus	3	2	1	1	2	1	1	2	9	5	9	9	9	5	25	11	2	2	1
Wallagonia sp.	1	3	1	1	2	1	1	2	10	5	10	10	10	8	20	10	1	3	1
Oxyeleotris			2	1	1	1		1	10	2	9	5	7	4	25	25	2	2	3
Kryptopterus				2	2	2		1	10	2	10	9	7	10	20	20	1	2	2
Notopterus n.									1					10	66	11	2	8	2
Mystus spp.						1	1		5	2	5	5	4	1	47	15	1	10	3
Hampala spp.			1		1	1	1	2	8	3	7	8	6	18	2	22	1	2	17
Morilius sp.													25			53	17	5	
Puntius spp.									1					5	20		10	30	34
Osteochiles sp.														5		2	65	18	10
Puntioplites												1		25	7	1	46	15	5
Cirrhinus j.														10			30	20	

Quantitative data for fishes are derived from studies by Mekong Secretary (1984) Wongtirawatana (1981) and Sricharoendam (pers. observations unpubl.).
For other groups: suggestions by Christensen and Pauly (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) to 0.95 (Ricker 1969). ECOPATH II directs the fraction 1-EE of production towards detritus, a feature that is of relevance when attempts are made to equilibrate an ECOPATH II model. EE values differ from gross efficiency, GE = (P/B)/(Q/B), used here to check the inputs in Tables 1 and 2. In the present exercise, EE values have been chosen according to what is known of intensity of predation for each box.

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). Since it was rather difficult to balance the model with a range of parameters in a set of simultaneous equations of the type (1), the equilibriun assumption which implies to equation (1) is extremely important. Thus, we accepted as realistic the solution which required the least modifications of our initial inputs (including the diet matrix) and yet generated biologically and thermodynamically possible outputs (i.e., all GE and EE values < 1).

Results

Estimates of biomass, gross conversion efficiency, food consumption and flow to detritus and trophic level obtained from the above-mentioned input parameters are presented in Tables 1 and 2. The trophic relationships are summarized in Figs. 2 and 3.

Just after the creation of the dam, the total fish biomass of Ubolratana reservoir was 18.8 t km^{-2}. The food sources are expected to be fully exploited except zooplankton (assumed EE=0.50) and phytoplankton (EE = 0.70). The computed ratio between predators and prey biomasses is 0.66. It was 0.5 in the rivers before the impoundment (Sidthimunka et al. 1978). The gross efficiency of the fisheries (actual catch/primary production), is 0.0029, which is low compared to other lakes and water bodies considered by Christensen and Pauly (1993).

For the 1980s, the total computed fish biomass was reduced to 7.2 t km^{-2}. An important feature is the increased biomass of the pelagic clupeid *C. aesarnensis*. The computed ratio between biomasses of predator and prey fish is 0.16, a remarkable decrease, most likely due to overfishing of predators which have high market demand. All food sources except the benthic producers are clearly underutilized. The gross efficiency of the fisheries is still low (0.0031).

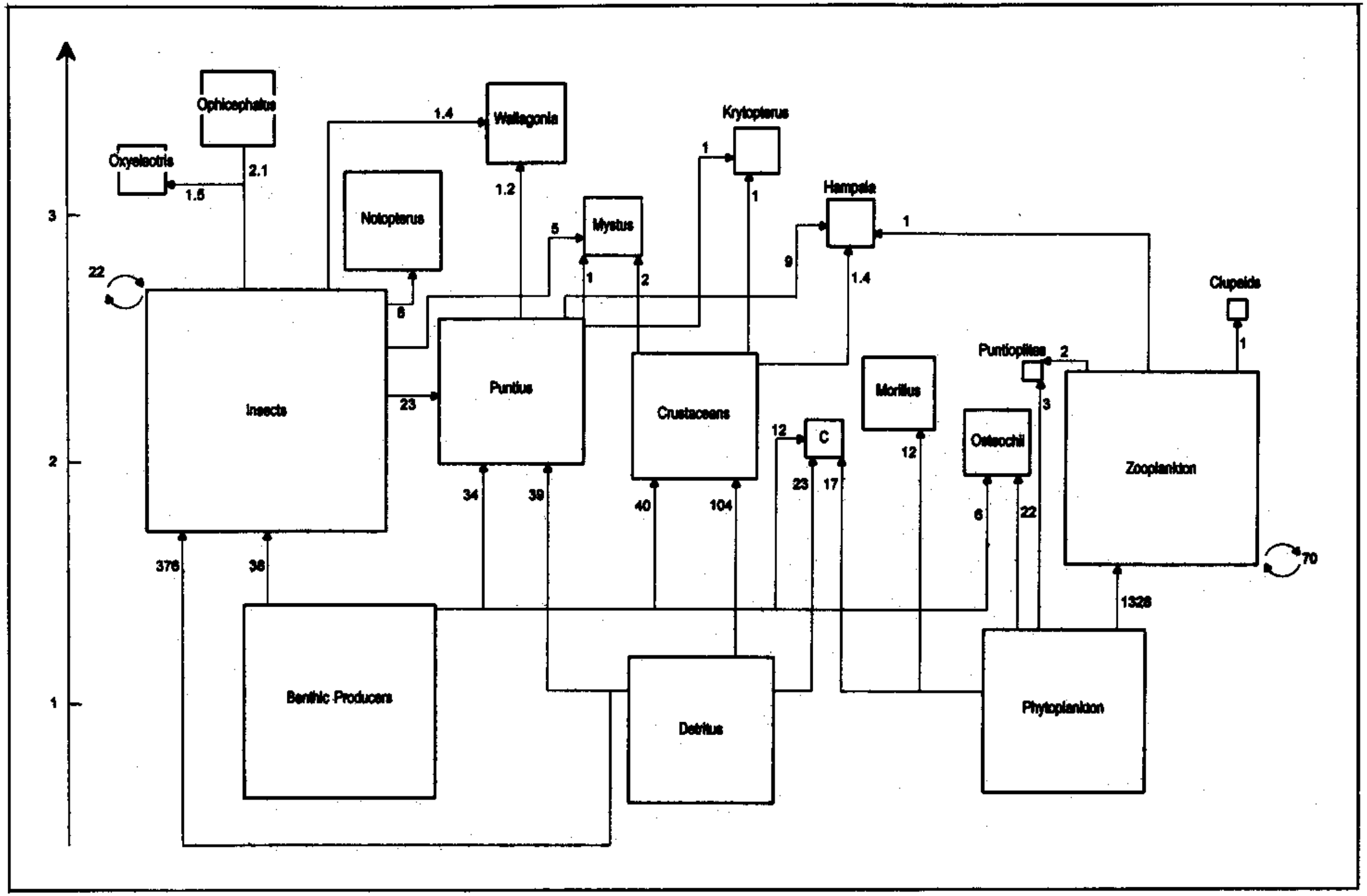

Fig. 2: ECOPATH II model of Lake Ubolratana for 1968-70, indicating the relative biomass of each group (area proportional to log B in t km^{-2}) and the major flows connecting them. For clarity, less important flows are omitted as are backflows to the detritus box and fishery catches. The horizontal axis of symmetry of each box is aligned with the functional trophic level of this box (see Christensen and Pauly 1992 for details).

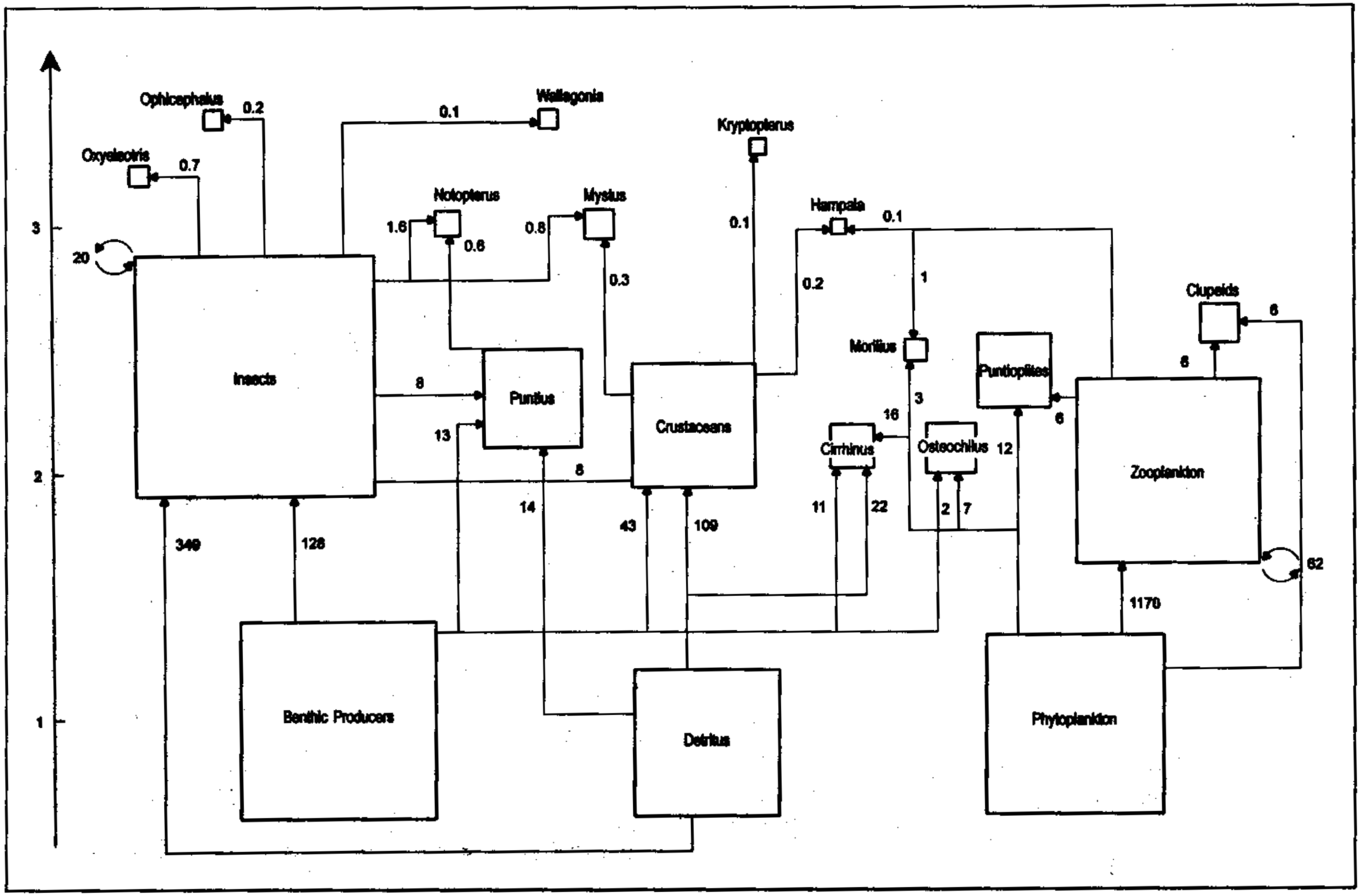

Fig. 3: ECOPATH II model of Lake Ubolratana for 1985-88. See Fig. 2 for details of the legend.

Discussion

Polovina (1984) and Polovina and Ow (1985) described the sensitivity of ECOPATH, in its first version, to variations of P/B values, mainly for groups at high trophic level (predators). In the present simulation efforts, the importance of the feeding matrix and of EE for accurate evaluations of biomass should be emphasized. One must properly quantify the available qualitative information on the diet composition of each group. This has been possible by taking into account several sources of information available from the literature following previous quantifications as suggested by Palomares (1991). Cannibalism, when it occurs, must be very low (often less than 5% of the diet) as proposed by Christensen and Pauly (1992) otherwise the biomass estimates of the group under consideration and its preys become, in an unrealistic way, too high.

As mentioned, the ECOPATH model was developed for static situations under general equilibrium conditions. We assumed that this holds true for the two situations of the ecosystem analyzed 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 and Pauly (1992) designed the mixed trophic impact routine of ECOPATH II based on Ulanowicz and Puccia (1990). However, it is not an instrument for predictions (Christensen and Pauly 1992).

Some parameters are known from direct measurements for Ubolratana reservoir or for some nearby man-made lakes. For instance, the biomass of zooplankton fluctuates between 4.5 and 14.5 t km^{-2} (Sidthimunka et al. 1978). The estimates provided here (6.2-6.9) are within this range. Similarly, according to Junk (1974) and Sidthimunka et al. (1978), the biomass of benthos including insects, crustaceans, annelids and molluscs can fluctuate seriously between 6 and 16 t km^{-2}. Again, our estimates (which should be assumed as average annual values) are within this range. Sidthimunka et al. (1978), Bhukaswan (1980) and Costa-Pierce and Soemarwoto (1990) provided several estimates of the standing crop obtained by rotenone sampling in the littoral areas. These estimates were quite high just after impoundment (11-48.5 t km^{-2} with an average of 17.7 t km^{-2}), as also suggested by our estimates (18.8 t km^{-2}). After several years, the reservoir has been characterized by overfishing of predatory fish, and strong variations of the standing crop are documented by Bhukaswan and Pholprasith (1977) and LIFDS (1985). Moreover, the ratio between prey and predatory fish has been declining as observed in the present study.

The estimates of biomass of fish are within the range of available estimates for Ubolratana reservoir (Bhukaswan and Pholprasith 1977). However, these estimates have to be compared to those of Duangsawasdi (1990) for two other man-made lakes in Thailand, Bhumipol reservoir (24-30.6 t km^{-2} and only 5% of fish biomass was predatory) and Sirikit reservoir (8.4 t km^{-2} and 13% predatory fish). The reasons for such differences between reservoirs with similar species compositions in the same region are yet to be identified.

Table 5 summarizes the main features of Ubolratana reservoir and two other useful ECOPATH models for man-made lakes of similar importance in Africa. The biomasses and ecological productions of top predators are similar

Table 5. Comparison of some key features of ECOPATH in Ubolratana reservoir and in two other man-made lakes of similar area and draw-down (data from Baijot and Moreau, unpubl.)

Features	Ubolratana (Phase 1)	Ubolratana (Phase 2)	Tapoa ($200\ km^2$)	Sourou ($120\ km^2$)
Predators				
Biomass	7.49	0.99	9.74	7.88
Production	8.63	1.97	12.42	10.49
Prey fish				
Biomass	11.33	6.14	28.42	20.18
Production	18.06	11.34	34.87	24.64
Zooplankton				
Biomass	6.93	6.29	3.33	3.36
Production	207.90	188.76	93.24	94.19
EE	0.50	0.50	0.95	0.95
Zoobenthos				
Biomass	14.84	15.69	19.99	20.45
Production	96.10	102.07	89.99	92.02
EE	0.95	0.55	0.95	0.95
Phytoplankton				
Biomass	5.46	4.90	2.41	1.81
Production	1,992.90	1,788.50	880.74	657.36
EE	0.70	0.70	0.95	0.95
Benthic producers				
Biomass	54.94	53.53	37.62	37.76
Production	247.24	240.88	188.12	188.82
EE	0.95	0.90	0.95	0.95
Actual catch	5.81	6.19	20.09	9.60
Gross efficiency of fisheries	0.0029	0.0035	0.023	0.015

irrespective of prey populations for the first phase of this reservoir. However, the biomasses and productions of the prey fish are much lower in Ubolratana reservoir. It could be due to higher diversity. Zooplankton is much more abundant in Ubolratana reservoir than in the two other lakes; however it is clearly underutilized. The biomass, production and utilization of zoobenthos are similar in the three reservoirs, except recently in Ubolratana reservoir (assumed value of EE = 0.55). The primary limnetic production (phytoplankton) is low and fully exploited in Lakes Tapoa and Sourou, but high and poorly exploited in Ubolratana reservoir. The production and utilization of benthic producers are similar in the three lakes. The GE of the fisheries is exceptionally low in Ubolratana reservoir even if it appears to be overexploited (Costa-Pierce and Soemarwoto 1990). This seems to come mainly from the underutilization of most food sources as illustrated by their low EE values.

In fact, this ECOPATH exercise on two different phases of the evolution of a man-made lake has shown that increasing potential production of inland reservoirs is possible by effective utilization of all food sources. This has been the aim of some introductions and restocking in this lake and in other man-made lakes in Asia (Baluyut 1983, 1992). ECOPATH is a useful tool for the purpose.

Conclusion

Two different situations in the evolution of an "old" Asian man-made lake have been successfully described by the ECOPATH software and model, and this reservoir has been compared with reservoirs in Africa. Differences in biomasses and productions for some groups have been pointed out, mostly for food sources and some of these resources appear to be underexploited. Therefore, the optimal use of all the food sources in tropical inland waters appears to be a way of increasing yields. ECOPATH can contribute to the development of fisheries in tropical inland waters by identifying such misutilization of food sources in the ecosystems.

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