

An ECOPATH II Model of the Lake Chad System*

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Abstract

The trophic ecosystem modelling software, ECOPATH II, was used to analyze the Lake Chad system, Africa, during its "normal" phase, the period between 1969 and 1972. Reasonable estimates of population-related parameters for fish and invertebrate stocks were obtained, and an energy flow diagram for the whole lake is presented.

Introduction

Lake Chad (Fig. 1) is located between 12° and 14°20' N and 13° and 15°20' E, and occupies a 25,000-km² enclosed basin (Carmouze and Lemoalle 1983). The lake is supplied by two large river systems, the Shari-Logone in the south and the Yobe in the north; and has one outlet, the Chad Bahr-el-Ghazal in the southeast. The south basin of the lake sits at a higher altitude, 280-278.5 m, than the north basin, whose altitude varies between 277.5 and 275.5 m. Carmouze and Lemoalle (1983) explained how this difference in bottom basin altitudes affects the rise and fall of water level. The north basin completely dries up during extended dry periods and is filled only after several successive high river floods (from the Shari delta). High-water periods were recorded in the second half of the 19th century and in 1963-1964 when the entire basin was filled with floodwater. Dry periods so far recorded date back to the beginning

of the century and to 1973-1976 (Carmouze and Lemoalle 1983) when the area occupied by lake waters was reduced to 9,000 km².

Carmouze and Lemoalle (1983) described Lake Chad as "unstable in time and heterogenous in space". The lake has a mean depth of 4 m, with a high variance due to the irregular seasonal flow of the Shari and the other rivers, evaporation (which is responsible for 20% of water losses) and infiltration (responsible for 10% of losses). The resulting fluctuations of mean water depth lead to radical changes in the structure of the lake.

The nature of the lake bottom varies from zone to zone mainly as a function of the suspended particles brought by the inflowing waters of the Chari-Logone, by water movement within the lake itself and by the presence of aquatic vegetation. Thus, the open water of the lake is characterized by clay substrates, the zones around the archipelago with clay-muddy substrates. This results in very variable amounts of

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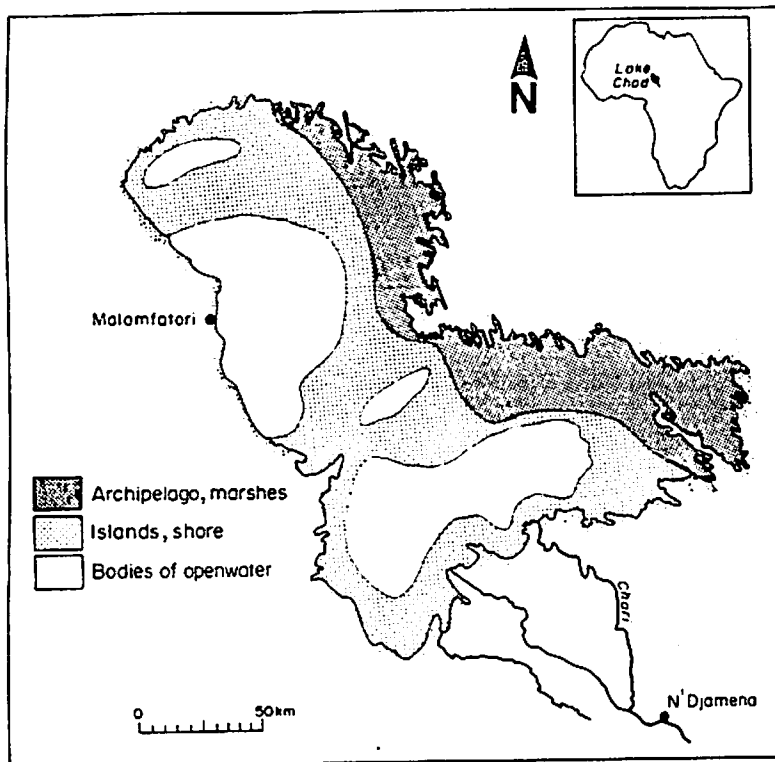


Fig. 1. The Lake Chad system in an intermediate phase, modified from Carmouze et al. (1983).

sediments being deposited on the lake bottom and in a spatially very heterogeneous environment (Carmouze and Lemoalle 1983).

Macrophytic and Phytoplanktonic Populations

The differences in bottom sediments together with the mean lake water level influence the nature of populations dominant in each zone. For example, during what is termed the "normal" Chad period around 1969-1972 when lake waters covered a total area ranging from 18,000 and 21,000 km², with a water level of 281 m, the bulk of the aquatic vegetation was concentrated in the deltaic zones, around the borders of the archipelago and floating islands that detach from it, and in the shallower areas of the eastern part of the lake (Iltis and Lemoalle 1983). These emergent and semisubmerged macrophytes then covered an area of about 2,400 km² or 12% of the total lake area (Carmouze et al. 1983) representing a total macrophyte biomass of 400 t·km⁻² dw (or 2,000 t·km⁻² ww assuming a 1 to 5 dry to wet weight conversion ratio).

During the drought of 1973, the north basin was isolated from the south basin by the "Great Barrier," and by the end of 1974, the lake was reduced to a few isolated small ponds in the north while the south basin was filled up to the level of 1972. These two periods saw the massive development of macrophytes in the areas which had dried up and were turned

into marshy, species-poor zones. These zones then covered 50% of the lake basin (Iltis and Lemoalle 1983): in 1974, the total water covered lake area was reduced to 1,500 km² and in 1976 after a slight flooding, the total inundated area reached about 9,000 km², with vegetation cover totalling 6,000 to 7,000 km² (Lemoalle 1983).

With respect to phytoplankton, Compère and Iltis (1983) concluded that Lake Chad is relatively rich in phytoplankton compared to other tropical lakes. This is further intensified during dry periods and particularly marked in the northern basin, which then more or less develops into a eutrophic pond. Compère and Iltis (1983) reported biomass estimates of 40,800 t over an area of about 18,000 km² in 1971 while for 1975, the biomass was 240,000 t over 11,000 km².

Zooplankton and Benthic Fauna

The zooplankton of Lake Chad was analyzed by Saint-Jean (1983) who found no radical changes in the biomasses between the "normal" Chad phase and the period of drought. Thus, it will have to be assumed that zooplankton biomass remained constant at 0.67 t·km⁻² dw (or 3.4 t·km⁻² ww at a 1:5 dry to wet ratio) over the seven-year period of study.

The benthic fauna of the lake can be assumed to have a high biomass because of the high sedimentation rates generally occurring in large tropical lakes. Furthermore, the high densities of emergent and semisubmerged plants in the deltaic region and the archipelago add periphyton biomass to the already considerable benthic biomass. However, Lévêque et al. (1983) reported biomass estimates of molluscs (3.3 t·dw·km⁻² or 16.5 t·ww·km⁻²), worms (0.29 t·dw·km⁻², 1.4 t·ww·km⁻²) and insects (0.12 t·dw·km⁻², 0.61 t·ww·km⁻²) which included only those invertebrates inhabiting the sediments. The box for benthic invertebrates, with a total biomass of 18.6 t·ww·km⁻² considered in this present modelling attempt refers only to the "normal" Chad period.

No biomass estimates were available for the periphyton associated with the macrophyte vegetation in the lake. Dejoux (1983) mentions that since the area covered by water during the "normal" Chad phase is considerable, it follows that the area of vegetational cover is large and so is the biomass of the periphyton. In general this consisted of insects (chironomids, hemipterids, odonatids, ephemeroptids, lepidoptids, entomostracids), ostracods and pulmonate molluscs. An estimation of the insect

biomass was attempted in the present work assuming that the references made by Lauzanne (1983) to "terrestrial insects" in the diet of fishes found in the lake (discussed later) refer to insects associated with the vegetation cover. A separate box was also attributed to shrimps (*Caridina* sp. and *Macrobrachium* sp.), for which no estimates of biomass are available. Shrimps are, however, included in the fish diet matrices reported by Lauzanne (1983).

Fishery

The complexity of the Lake Chad system is well reflected by its complex fish community. Bénech et al. (1983) summarize the changes in the lake which occurred between the "normal" phase in 1969-1972 and the dry phase in 1973-1977 as having three basic effects on the fish populations. The decrease in water level caused an obvious concentration of the fish biomass and thus resulted in an increase in inter- and intraspecific competition. This enabled the fishers to increase their efficiency, and thus to increase fishing mortality. Wave action on the shallow water resulted in resuspension of sediments which caused massive fish mortalities due to suffocation. (The high solubility of nutrients, however, caused a characteristic phytoplankton bloom leading to huge variations in daily dissolved oxygen and CO₂ levels which may have to a certain extent counteracted the impact of increased turbidity.) Anoxic conditions were then created as the lake dried up, further increasing natural mortality. These changes favored hardy species, with a capacity to modify their diet. Thus, the heterogenous fish community existing in 1971, and composed mainly of migratory species, was replaced by a more homogenous community of "marsh" species during the drought period of 1973-1977.

Materials and Methods

The different states that can be taken by a complex variable system like the Lake Chad system cannot be summarized by one single ecosystem model. However, the important biological parameters needed in the construction of a box type ecosystem model for Lake Chad are not available for all the periods of change experienced by the lake. This limits modelling attempts that would eventually enable comparisons between critical periods, such as described above.

The Lake Chad model presented here was based on the "normal" period 1970-1972 and constructed using the ECOPATH II model described by Christensen and Pauly (1992), itself based on a

preliminary model (ECOPATH) described by Polovina and Ow (1983). These models describe systems at equilibrium. They assume for each trophic group in a model that

$$\text{consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad \dots 1)$$

where production is expressed as the sum of all exports resulting from biomass consumed by predation and all flows to detritus. In ECOPATH II, this is expressed as

$$B_i \cdot \left(\frac{P_i}{B_i} \right) \cdot EE_i - \left(\sum_{j=1}^n B_j \cdot \left(\frac{Q_j}{B_j} \right) \cdot DC_{ji} \right) - EX_i = 0 \quad \dots 2)$$

where B_i is the biomass of species i ; P_i/B_i its production/biomass ratio, equivalent to total mortality (Z); EE_i the ecotrophic efficiency; where B_j is the biomass of predator j ; Q_j/B_j the predator's relative food consumption and DC_{ji} the fraction of species i in the diet of predator j . EX_i represents the exports (including catches) of group i .

The bulk of the information used here on the production and biomass estimates for fish, invertebrate and plant populations in the lake refers to the "normal" Chad in 1970-1972 (Carmouze et al. 1983). Studies conducted by Lauzanne (1983) provide quantitative estimates of the food chain flows from detritus to the top predator, *Lates niloticus*.

Estimates of relative consumption rates (Q/B) of all but three fish populations considered here were obtained from the multiple linear regression model proposed by Palomares (1991) in the form

$$\log Q/B = -0.261 \log W_{\infty} + 0.759 \log T + 0.405 \log A + 0.530h + 0.466d - 0.294p \quad \dots 3)$$

where Q/B is the food consumption (% day⁻¹) per unit of biomass of the fish population in question, W_{∞} their asymptotic weight in g, T the mean annual water temperature in °C, A the aspect ratio of the caudal fin (see also Palomares and Pauly 1989; Pauly 1989), and where h , d and p are dummy variables representing herbivores, detritivores and pellet-fed fish. Equation (3) explains 58% of the variation of the data set of Palomares (1991), which comprised 96 different fish populations.

Tables 1 and 2 summarize the data used as inputs for ECOPATH II. The fisheries catches and the Q/B estimates, as obtained using equation (3) for the fish species represented in Table 1, were assembled together with biomass and P/B estimates for invertebrates, insects and primary producers

obtained from the various contributions in Carmouze et al. (1983). The top predator considered here, *Lates niloticus*, is separated from the medium-sized predators (*Bagrus* sp. and *Hydrocynus* sp.) and the smaller predators (*Eutropius* spp. and *Schilbe* sp.). The box, represented by *Alestes macrolepidotus*, includes fish species more or less strongly associated with macrophytes and which thus ingest periphyton. Benthivores include *Synodontis* spp., *Heterotis* spp. and *Hyperopisus* sp. The zooplanktivores include *Alestes baremoze*, *Brachysynodontis* spp. and *Hemisynodontis* sp. The box represented by *Sarotherodon galileus* refers to exclusive phytoplanktivores. Detritivores are *Citharinus* sp., *Oistichodus* sp. and *Labeo* spp.

Results and Discussion

Table 1 and Fig. 2 present results from ECOPATH II. The overall fish biomass estimates of 26 t·km⁻² obtained by this model are reasonable given the overall catch value of 6.4 t·km⁻². These results reflect the observations made by Durand (1983) on the relative dominance of *A. macrolepidotus* and of zooplanktivores, which amount to 8.8 t·km⁻². A relatively high biomass of 5.2 t·km⁻² for *S. galilaeus*

was obtained. No reference to the abundance of this group was made for the period of "normal" Chad. However, Durand (1983) states that *S. galilaeus* successfully survived the drought period, and even experienced an important increase in its biomass by the end of 1974. Reasonable biomass estimates of 2.9 and 9.3 t·km⁻² were obtained for the groups representing shrimps and macrophyte-associated insects, respectively.

The rich, relatively stable sediment bottom of the lake during the "normal" Chad period is favorable for the maintenance of a large biomass of benthic invertebrates. This, coupled with its high P/B ratio and the relatively low predation pressure exerted by benthivores (which have a biomass of only 2 t·km⁻²), seems compatible with the low EE value of 0.15 obtained by the model. High predation pressure by the important *Alestes* group on zooplankton reflects the high EE value of 0.93 of the later group whereas the moderate grazing of *S. galilaeus* on phytoplankton is reflected by an EE of 0.77. The bulk of the macrophyte biomass, which is underutilized by consumers, joins the detritus, as reflected by the rather low EE value of 0.10.

The Lake Chad model in Fig. 2 thus appears to present reasonable results. It is important to note, however, that this model represents only one phase

Table 1. Input data used with ECOPATH II for the Lake Chad "normal" period model, along with parameters estimated by ECOPATH II (in brackets). All flows are in t·km⁻²·year⁻¹; all biomasses in t·km⁻², all rates in year⁻¹.

Group	Catch ^a	Biomass	P/B	Q/B ^b	EE ^c	GE ^d
<i>Lates niloticus</i>	0.73	(2.43)	(0.43)	4.3 ^e	0.80	0.10
Medium predators	1.38	(3.00)	(1.58)	10.5	0.80	0.15
Small predators	0.90	(2.52)	(2.48)	16.5	0.80	0.15
<i>Alestes macrolepidotus</i>	0.06	(3.63)	(3.20)	16.0	0.90	0.20
Benthivores	0.35	(1.98)	(4.00)	20.0	0.90	0.20
Zooplanktivores	1.66	(5.16)	(4.00)	16.0	0.90	0.25
<i>Sarotherodon galilaeus</i>	0.38	(5.25)	(2.40)	16.0 ^e	0.90	0.15
Detritivores	0.52	(2.12)	(4.00)	40.0	0.90	0.10
Shrimps	-	(2.89)	5.00	30.0	0.90	-
Benthic invertebrates	-	18.60 ^f	36.4 ^g	120.0 ^h	(0.15)	0.30
Insects	-	(9.30)	15.0 ^h	45.0 ^h	0.80	0.33
Zooplankton	-	3.40 ⁱ	63.7 ^j	(182.0)	(0.93)	0.35
Phytoplankton	-	2.25 ^k	365.0 ^l	-	(0.77)	-
Macrophytes	-	2,000.00 ^m	1.0 ⁿ	-	(0.10)	-

^a Total catch = 6.4 t·km⁻² (Durand 1983) in 1971; species composition from Lauzanne (1983).

^b Q/B from equation (26) (Palomares 1991).

^c Assumed values from Moreau et al. (this vol.).

^d Assumed values.

^e Q/B obtained from experiments (Palomares 1991).

^f From Lévêque et al. (1983).

^g P = 600 t·km⁻²·year⁻¹ (Lévêque and Saint-Jean 1983).

^h Assumed from GE value.

ⁱ From Saint-Jean (1983).

^j P = 217 t·km⁻²·year⁻¹ (Lévêque and Saint-Jean 1983).

^k From Compère and Itis (1983).

^l Assumed value similar to that of Lake Victoria (Moreau et al., this vol.).

^m From Itis and Lemoalle (1983).

ⁿ From Carmouze et al. (1983).

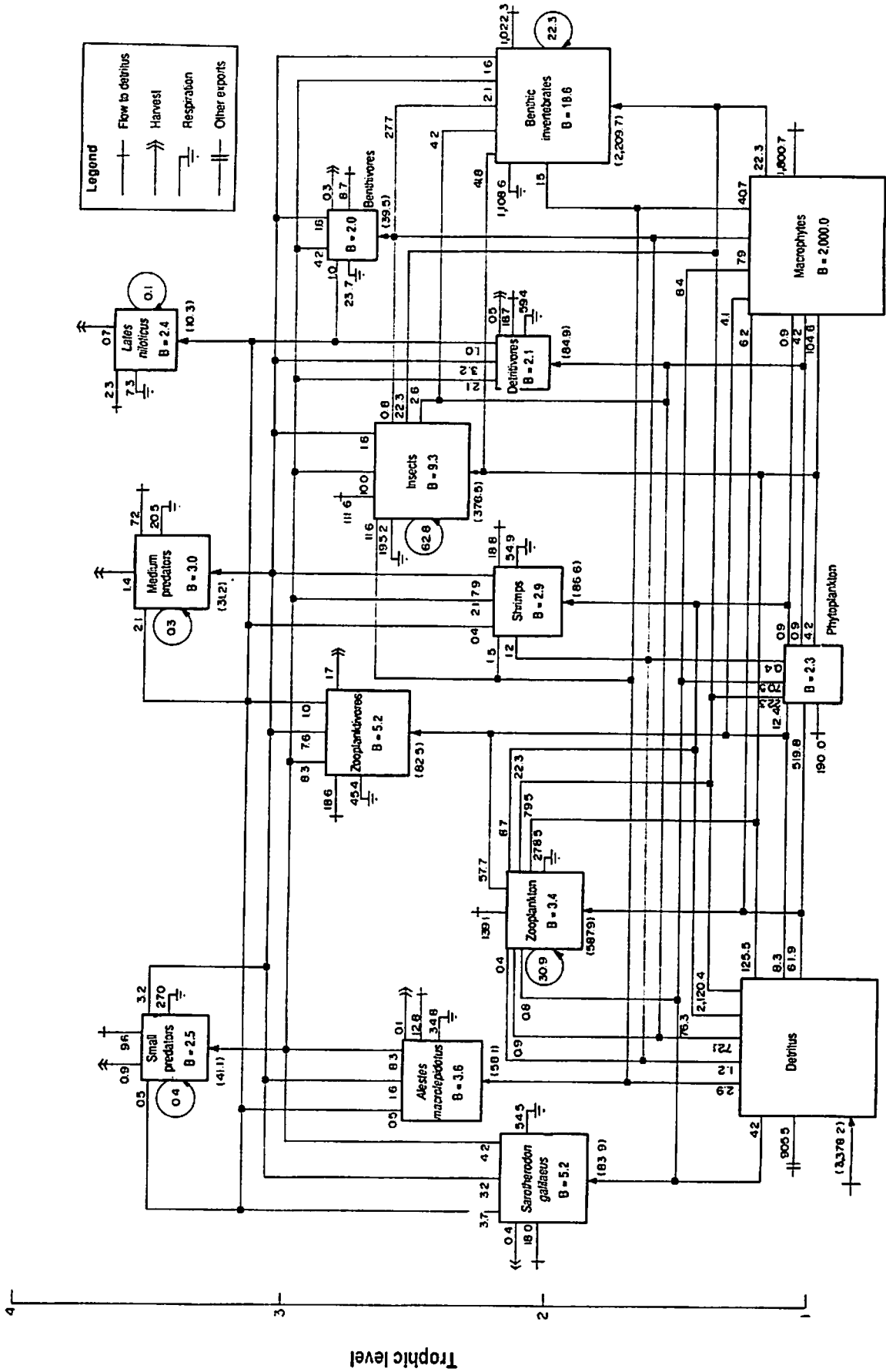


Fig. 2. ECOPATH II model of Lake Chad during the "normal" period.

Table 2. Feeding matrix of species groups in Lake Chad from Lauzanne (1983) in % (weight).

Prey	Predator												
	1	2	3	4	5	6	7	8	9	10	11	12	
1. <i>Lates niloticus</i>	1	-	-	-	-	-	-	-	-	-	-	-	-
2. Medium predators	20	1	-	-	-	-	-	-	-	-	-	-	-
3. Small predators	5	10	1	-	-	-	-	-	-	-	-	-	-
4. <i>Alestes macrolepidotus</i>	5	5	20	-	-	-	-	-	-	-	-	-	-
5. Benthivores	10	5	10	-	-	-	-	-	-	-	-	-	-
6. Detritivores	10	10	5	-	-	-	-	-	-	-	-	-	-
7. Zooplanktivores	10	24	20	-	-	-	-	-	-	-	-	-	-
8. <i>Sarotherodon galilaeus</i>	35	10	10	-	-	-	-	-	-	-	-	-	-
9. Shrimps	4	25	5	2.5	3	-	-	-	-	-	-	-	-
10. Benthic invertebrates	-	5	5	2.5	70	5	-	-	-	1	10	-	-
11. Insects	-	5	24	20	2	3	-	-	-	1	15	-	-
12. Zooplankton	-	-	-	-	1	1	70	1	10	1	19	5	-
13. Phytoplankton	-	-	-	-	1	1	15	84	1	1	1	84	-
14. Macrophytes	-	-	-	70	20	5	5	10	1	1	25	1	-
15. Detritus	-	-	-	5	3	85	10	5	88	95	30	10	-

in the evolution of Lake Chad; it would be interesting to compare this intermediate phase with the previous, more stable phase in the 1960s and the irregular dry phases from 1973 to 1985.

Also the model applies to a single ecosystem, whereas Lake Chad may be considered as element of "an ecological region" with its own functioning, which uses part of the production derived from the "adjacent river and floodplain" complex.

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