Productivity and Energy Flows at All Trophic Levels in the River Thames, England: Mark 2

C.P. MATHEWS
Zoology Department
University of Reading
Whiteknights, Reading
England

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Abstract

The trophic model for the River Thames, England, developed by the International Biological Programme (IBP) is probably the most complete ever constructed for a riverine ecosystem. A Mark 2 model is presented here, constructed using ECOPATH II. The model reinforces many of the conclusions of the earlier study and exposes certain weaknesses. In particular, the trophic role of the main fish populations and of detritus is revised.

Certain improvements that could be made to the Mark 2 model are identified, relating to the inclusion of incoming solar energy and to the efficiency of the community in converting solar energy to animal and plant tissue.

Introduction

From 1966 to 1972, the International Biological Programme (IBP) funded a noteworthy study of the Dreadnought reach of the River Thames. This was the first attempt to study and quantify the energy flow through a whole riverine ecosystem.

The work carried out attempted to quantify: energy entering the ecosystem (as light) over the whole year; primary production by phytoplankton; primary production by periphyton; production by one year and older fish (1+ group); production by 0 group fish (including egg production and production by larval/fry stages); production by invertebrate predators; production by invertebrate browsers; production by invertebrate filter feeders; production by rooted macrophytes; input of material from terrestrial leaf litter; input of allochthonous matter into the ecosystem; and predation by 0 and 1+ group fish.

Mann et al. (1972) summarized all resulting estimates of production and provided descriptions of the methods used in obtaining them. Mathews (1971) summarized all estimates made during the IBP study of fish production and fish biomass, including his own work on 0 group fish and the observation of other workers (Williams 1963, 1965, 1967) and Mann (1964, 1965) on 1+ group fish.

Certain items were not addressed in these studies:

- primary production estimates of periphyton were never completed and the resulting data were not published;
- methodology and data on fish predation were not published;
- similarly, the only record of the estimates of invertebrate production is that published by Mann et al. (1972); and
- no attempt was made to study suspended organic matter.

In spite of these omissions, this work provided the first quantified picture of the energy flow through a riverine ecosystem. Since then, the methodology available for tackling complex ecosystem studies has become more sophisticated.

The object of this paper is to reanalyze the results of the Thames IBP study, using the ECOPATH II approach and to use the new technique to:

- reassess the results of the earlier analysis of Mann et al. (1972) and then place these

results on a firmer basis, making the output comparable with more recent studies of other ecosystems;
- identify areas which were tackled incompletely or not at all; and
- use ECOPATH as a heuristic tool and discuss how the IBP approach could be updated and strengthened if such a study were to be repeated.

There is an important methodological difference in the way that the two models account for flows. The IBP model counts each unit of energy or biomass once only (i.e., it may be harvested only once). The ECOPATH model for the calculation of energy or biomass throughput, as a measure of the "size" of an ecosystem *sums all flows* so that a unit of energy or biomass may be included several times. Therefore ECOPATH will usually produce a much larger estimate of the total flow through a system than the corresponding IBP model. Furthermore, matter may also be recycled several times through feces so that the role of detritus is described more realistically by the ECOPATH model. Total energy flows from the two models are therefore different and not strictly comparable.

Materials and Methods

The methods used to obtain and analyze data obtained during IBP are provided by Mann et al. (1972), Mathews (1971) and Mathews and Kowalczewsky (1969). Methods for the study of older fish are also given in Williams (1965, 1967) and in Mann (1965).

The ECOPATH II model is the version of Christensen and Pauly (1992a, 1992b, this vol.), a modification of the original ECOPATH model applied by Polovina (1984) to a coral reef ecosystem. The model is based on a single budget equation for each group in the system:

$$P_i - M2_i - M0_i - C_i = 0$$

where P_i is the production of species (i), $M2_i$ is the predation mortality, $M0_i$ is the nonpredation mortality and C_i is the fisheries catch of species (i).

Information on biomass (B), production (P), and consumption (Q) is thus needed; if some data are lacking, the program may provide estimates, based on an assumption of steady state for all groups. Even when information is lacking, ECOPATH II frequently allows the identification of a complete model of the ecosystem. The model in this case may not provide a unique solution. Nevertheless, the model does provide a clear working hypothesis, which may be compared with other models and so may be verified and be used as a guide for future research.

Mann et al. (1972) are the source of data unless otherwise indicated; Mathews (1971) is the source for all estimates of fish production and biomass used here. Jørgensen (1979) is used to provide estimates of variables where they were not available from the Thames study. Fig. 3 of Mann et al. (1972) is the source for data on diet composition. All estimates of production were converted to kcal·m^{-2}·year^{-1}, whereas biomasses are in kcal m^{-2}.

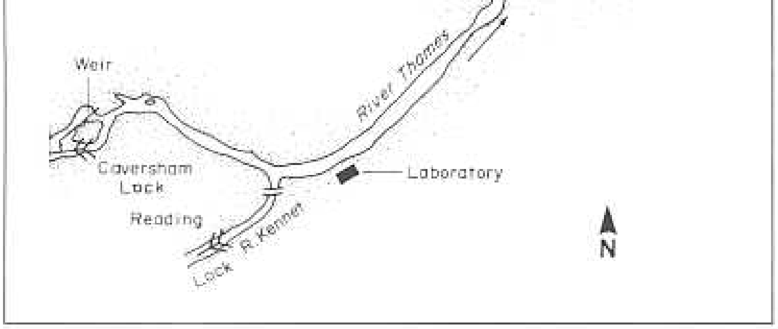

Fig. 1. Sketch map of the Dreadnought reach of the River Thames, near Reading, England. The locks at Caversham, Sonning, and on the River Kennet mark the limits of the study area.

Fig. 1 shows the Dreadnought reach of the River Thames, on which this study concentrated. The Thames attains a maximum depth of 4.5 m in this reach and has very steep banks being maintained and dredged regularly to keep it open for navigation by pleasure boats. A mean depth of 4.0 m was assumed for the purpose of converting phytoplankton and trypton (suspended organic matter) from volume to area basis.

The mean biomass of suspended organic matter for the River Thames below Kennet Mouth was 6.0 g·m^{-3}, of which 1.0 g·m^{-3} was phytoplankton, the remainder being trypton (Mann et al. 1972, Fig. 3).

Jørgensen's (1979) value of 5 kcal·g^{-1} fresh weight for suspended organic matter and the mean depth of the Thames of 4.0 m were used to estimate a phytoplankton biomass of 20.0 kcal·m^{-2}.

Planktonic primary production was estimated by means of the oxygen light/dark bottle method, adjusted by a factor of x1.38 to reflect the difference between primary production in stationary experimental bottles and in the river, where currents ensure a well-mixed water column. The derived estimate of primary production by phytoplankton was 1,907 kcal·m^{-2}·year^{-1}.

Mann et al. (1972) noted the presence of substantial amounts of periphyton and their results indicate substantial periphyton production in depths up to 1 m, beyond which light is severely limiting. Since only 15% of the river surface lies at less than 1 m, it is likely that periphyton production is considerably less than phytoplankton production. A minimal estimate of periphyton production was obtained from analysis of stomach contents and the estimates of consumption rates by roach (*Rutilus rutilus* (L.)) and bleak (*Alburnus alburnus* (L.)) and was included by Mann et al. (1972) in their analysis of the ecosystem (their Fig. 3). For this study their estimate was increased to allow for consumption by all the species of fish and was regarded as a minimal estimate of production: it is unlikely that 95% of periphyton production is consumed by other organisms as assumed here.

Periphyton in the Thames was composed largely of filamentous algae and diatoms and was arbitrarily assumed to have a P/B ratio of half that of the much smaller phytoplankton.

Two species of macrophytes occur in the Dreadnought reach of the Thames, *Acorus calamus* and *Nuphar lutea*. Production of these was estimated to be 16.4 and 27.6 kcal·m^{-2}·year^{-1}, respectively, giving a total macrophyte primary production of 44 kcal·m^{-2}·year^{-1}.

Mathews and Kowalczewsky (1969) estimated the input of leaf litter from overhanging trees. A total of 79 kcal·m^{-2}·year^{-1} was estimated to fall into the Thames.

Mathews (1971) provided estimates of fish production, including the contribution of eggs and fry to production during the first year of life. Fry production was estimated from surveys aimed at age-group 0 and older. "Prefry", i.e., fish between the egg and the fingerling stages were fully vulnerable to fisheries, and their production was estimated using the algebraic method of Ricker (1946). Estimates of 1+ group fish production obtained from Allen (1951) curves were also provided. Detailed production estimates were carried out in this way for bleak (*A. alburnus* (L.)), roach (*R. rutilus* (L.)), dace (*Leuciscus leuciscus* (L.)) and gudgeon (*Gobio gobio* (L.)). Table 1 (from Table XX, Mathews 1971) shows the resulting estimates of production.

For this study it was decided to combine all fish production into 0 group and 1+ group boxes. Therefore the data in Table 1 were regrouped as in Table 2 and a conversion factor of 1 g live weight = 1.154 kcal (R. Britton, pers. comm.) was applied.

Mathews (1971) provided estimates of annual total instantaneous mortality rates (Z) from the egg stage to the end of the first year of life, for each of the four major species, for 1967 and 1968. The mean value was Z = 7.21 year^{-1}. This value was assumed to be an estimate of the P/B ratio (Allen 1971) for all 0 group fish. Applying

Table 1. Production (P, g·m^{-2}·year^{-1}), biomass (B, g·m^{-2}) and production/biomass ratios (P/B, year^{-1}) for four abundant fish species in the River Thames.

Species		Age group 0	1	2	3	4	5	6	7	8	9	Total
Bleak	P	24.2	5.3	10.8	9.0	2.6	0.7	-	-	-	-	52.8
	B	6.85	8.98	10.80	12.32	7.43	1.23	-	-	-	-	47.7
	P/B	3.56	0.59	1.00	0.73	0.35	0.53	-	-	-	-	1.11
Roach	P	8.2	1.6	1.9	2.2	1.8	0.6	0.7	0.4	0.3	0.1	17.8
	B	2.77	1.20	2.32	4.15	4.39	3.33	3.33	2.22	1.03	0.39	25.13
	P/B	2.96	1.33	0.82	0.53	0.41	0.18	0.21	0.18	0.29	0.26	0.71
Dace	P	1.16	0.35	0.29	0.27	0.23	0.17	0.09	0.04	-	-	2.60
	B	0.43	0.22	0.33	0.48	0.53	0.52	0.47	0.28	-	-	3.26
	P/B	2.70	1.59	0.88	0.56	0.43	0.33	0.19	0.14	-	-	0.80
Gudgeon	P	3.7	2.1	3.2	2.3	0.4	-	-	-	-	-	11.7
	B	1.40	2.44	3.37	4.60	3.08	-	-	-	-	-	14.9
	P/B	2.64	0.86	0.95	0.50	0.13	-	-	-	-	-	0.79

Table 2. Production (kcal·m^{-2}·year^{-1}) of fish in the River Thames and the ratio of roach and bleak production to total production (Mathews 1971; Mann et al. 1972).

	0-	1+
(a) Roach and bleak	94.0	43.0
Other major species	28.7	11.7
Minor species	13.6	6.0
(b) Total fish	136.3	60.7
(b):(a)	1.4	1.4

the P/B ratio of 7.21 to the annual production of 0 group fish (Table 2) the biomass of 0 group fish was estimated as 136.3/7.21 = 18.9 kcal·m^{-2}.

Mann et al. (1972) estimated consumption by fish of 0 group and 1+ group bleak and roach, using R. Britton's (unpublished) data on diet, digestion times and the calorific value of different components of the stomach contents.

Mann et al.'s (1972) predation estimates were adjusted to provide estimates of the predation by all species of fish (Table 3). The assumption that the mean diet composition of Thames fish is similar to the mean composition for bleak and roach seems acceptable: dace and bleak tend to be surface feeders, while roach and gudgeon tend to be bottom feeders. Amongst the minor species, perch (*Perca fluviatilis* (L.)) is zooplanktivorous when young and piscivorous when older, while bream (*Abramis brama* (L.)) is a bottom and detritivorous feeder. Other species provide only a very small component of predation.

Jǫrgensen (1979) provided estimates of the P/B ratios for various invertebrate predators, which were weighted by the production estimates provided by Mann et al. (1972). This provided a weighted mean P/B ratio for the invertebrate predators of the Thames of 3.5 year^{-1}.

A similar procedure was used to provide weighted mean P/B ratios for invertebrate browsers and invertebrate filter feeders, of 1.6 and 1.2 year^{-1}, respectively.

A value of P/B = 5.0 year^{-1} was provided by Mann et al. (1972) for young chironomids, similar to values for Chironomidae provided by Jǫrgensen (1979). An "export" of 180.5 kcal·m^{-2}·year^{-1} of young chironomids was used to produce the adult chironomids in the model.

A P/B ratio of 37.4 year^{-1} was obtained by combining appropriate values from Jǫrgensen (1979) for Thames zooplankton.

The production of macrophytes and trees was 44 and 79 kcal·m^{-2}·year^{-1} (Mann et al. 1972), respectively, all of which enters the detritus box.

A value of Q/B = 0 was assigned to adult Chironomidae, as they do not feed. After reproducing they fall into the water where they are subject to heavy predation by fish.

Values of 0.95 were assigned to the ecotrophic efficiencies of invertebrate predators, browsers and filter feeders, young and adult chironomids, and zooplankton. Such values imply that 95% of the production of these taxa is consumed by predators and 5% is reduced to detritus by decomposers.

The following values were assigned to the gross efficiencies (production/consumption ratios) for invertebrate browsers (20%), invertebrate predators (20%), filter feeders (15%), zooplankton (15%) and young chironomids (10%). These values complete the data requirements of the model and are consistent with general knowledge of the gross efficiencies for these groups observed in other areas (V. Christensen, pers. comm.). Values of Q/B in Table 5 were derived from these gross efficiencies.

Table 4 shows the diet composition for the consumers. The diet is based on the contributions of different types of organisms to 0 group and 1+

Table 3. Predation by Thames fish: quantities consumed by bleak and roach only (Mann et al. 1972) and by all species (data adjusted x1.40, Table 2).

Food item	Roach and bleak only		All Thames fish		
	0	1+	0	1+	Total
Fish 1+ group	0	0	0	0	0
Fish 0- group	0	4	0	5.6	5.6
Invertebrate predators	0	1	0	1.4	1.4
Invertebrate browsers	0	15	0	21.0	21.0
Filter feeders	0	11	0	15.4	15.4
Young chironomids	28	20	39.2	28.0	68.6
Adult chironomids	26	126	36.4	176.4	214.1
Zooplankton	97	23	135.8	32.2	172.8
Periphyton	3	155	4.2	217.0	221.4
Detritus	32	307	44.8	429.8	476.2
Total			260.4	926.8	1,187.2
Allochthonous	0	215	0	301.0	301.0
Grand total			260.4	1,227.8	1,488.2

Table 4. Input data on diet composition for the Thames Mark 2 model. Predator 1 is the fish 1+ group.

Prey	Predator 1	2	3	4	5	6	8
2. Fish 0 group	.004	-	-	-	-	-	-
3. Invertebrate predator	.002	-	-	-	-	-	-
4. Invertebrate browser	.017	-	.33	-	-	-	-
5. Filter feeders	.013	-	.33	-	-	-	-
6. Young chironomids	.023	.151	.34	-	-	-	-
7. Adult chironomids	.144	.140	-	-	-	-	-
8. Zooplankton	.026	.522	-	-	-	-	-
11. Phytoplankton	-	-	-	-	.5	-	.5
12. Periphyton	.177	.016	-	.33	-	-	-
13. Detritus	.350	.171	-	.67	.5	1.0	.5
- Import	.244	-	-	-	-	-	-

group roach and dace (Fig. 3 in Mann et al. 1972) and a general knowledge of the diet composition for other constituents of the ecosystem.

An assimilation rate of 80% was assumed for all food types except detritus. For detritus the assimilation rate (Mann et al. 1972) for roach (6.92%) was accepted as a general value. The egestion rate for 0 group and 1+ group fish was then obtained by weighing these two values by the composition of the food ingested.

Results and Discussion

Table 5 presents input to the Mark 2 model of the Thames ecosystem, together with selected output for the model.

The Dreadnought reach of the Thames is characterized by high energy circulation through the detritus. This, as Mann et al. (1972) discussed, is probably associated mainly with high nutrient levels due to sewage effluents and mineralization of sewage solids, stimulating production and causing the exceptionally high levels of fish production that were observed in the Thames (197 $kcal \cdot m^{-2} \cdot year^{-1}$ being more comparable to production levels in aquaculture systems than to natural populations).

Primary Production and Energy Throughput

Primary production is dominated by the phytoplankton (1,907 $kcal \cdot m^{-2} \cdot year^{-1}$) and the periphyton production of at least 246 $kcal \cdot m^{-2} \cdot year^{-1}$, with a small contribution from macrophytes (46 $kcal \cdot m^{-2} \cdot year^{-1}$). Total primary production of the ecosystem is at least 2,172 $kcal \cdot m^{-2} \cdot year^{-1}$ but could be larger, because the estimate for periphyton was obtained by back calculation from stomach content analysis.

The total energy content of the incident light was 729,000 $kcal \cdot m^{-2} \cdot year^{-1}$, thus 0.3% of the incident light is fixed during photosynthesis by the Thames ecosystem.

Table 5. Data input (without brackets) for the Mark 2 Thames model. For macrophytes and trees only total production is known, and this is split arbitrarily between P/B and B as only the total production is used in the actual calculations. Estimates given in brackets are estimated by ECOPATH II.

Group	Biomass ($kcal/m^2$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	Unassimilated food	Trophic level
1. Fish 1+ group	101.7	0.597	9.158	(0.00)	0.47	(2.12)
2. Fish 0 group	18.9	7.210	14.269	(0.00)	0.33	(2.67)
3. Invertebrate predator	(0.4)	3.500	17.500	0.95	0.20	(3.00)
4. Invertebrate browser	(12.3)	1.600	(16.000)	0.95	0.50	(2.00)
5. Filter feeders	90.9	1.280	8.533	(0.12)	0.50	(2.00)
6. Young chironomids	(51.6)	5.000	(33.333)	0.95	0.50	(2.00)
7. Adult chironomids	(36.1)	5.000	0.000	0.95	-	(1.00)
8. Zooplankton	(4.7)	37.400	(187.000)	0.95	0.50	(2.00)
9. Macrophytes	10.0	4.400	0.000	(0.00)	-	(1.00)
10. Trees	10.0	7.900	0.000	(0.00)	-	(1.00)
11. Phytoplankton	20.0	95.350	0.000	(0.43)	-	(1.00)
12. Periphyton	(5.2)	47.700	0.000	0.95	-	(1.00)
13. Detritus	10.0			(0.79)	-	

Detritus: Its Role in the Thames

Detritus provides the single most important secondary energy flow with 61% of all possible energy flow pathways with ecosystem originating from circulating through or returning to the detritus. The "ecotrophic efficiency" of detritus is estimated to be 55%, indicating that more than half of the energy entering the detritus is reused in the system.

Mathews and Kowalczewsky (1969) studied the disappearance rate of leaf litter originating from trees (mainly willows) along the River Thames bank. The disappearance of leaf litter was not caused by benthos, but was caused principally by microorganisms. The litter disappearance was accompanied by an increase in total nitrogen content of the leaf litter, presumably due to nitrogen uptake from the environment by microorganisms. The total input of leaf litter was reduced to fine particles available to filter feeders and microorganisms, before the next year's leaf crop was added to the ecosystem. Benthic browsers found on litter were thought to feed on the microorganisms, which themselves fed on and digested litter. In this respect, the invertebrate litter browsers of the Thames carry out a function analogous to that of earthworms in soils on land.

No similar experiments were conducted in the Thames on other types of detritus. The main sources for flow to the detritus are 1+ fish, filter feeders, zooplankton, young chironomids and 0 group fish, with a total of 1,878 kcal·m^{-2}·year^{-1}, i.e., 59% of the total flow through detritus. This input will be mainly in the form of feces and should therefore be more easy to break down than the leaf litter experimented on by Mathews and Kowalczkewsky. In conclusion, it seems reasonable to assume that all detritus in the Thames ecosystem can be converted into more accessible energy within a year.

Unfortunately, no estimate of the biomass of microorganisms (bacteria and fungi: Mathews and Kowalczewsky 1969) is available with which to compare the estimated amount of detritus converted to more accessible energy nor is any estimate of microorganism production yet available.

Assuming that invertebrate browsers feed on the microorganisms as these consume litter, there is an extra trophic level involved in the reduction of litter to animal tissue. The trophic position of invertebrate browsers and fish is therefore open to discussion.

This may also explain the low assimilation ratio estimated by Mann et al. (1972) of 6.92% for detritus eaten by roach (which is close to the value of 8.35% reported by Jørgensen (1979, Table A256); this low value for roach occurs because the food consumed itself is produced by microorganisms, with an unknown assimilation ratio, from the digestion of detritus.

Because of the potential implications of the work of Mathews (unpubl. data) and Mathews and Kowalczewsky (1969) for the role of detritus in the Thames ecosystem and elsewhere, it is suggested here that the fungi and microorganisms are the true detritivores and that the roach and dace, considered detritivores by Mann et al. (1972) because of the large amounts of detritus in their guts, are actually "detritivore browsers".

Table 6 shows that the total energy flow through detritus is greater than the net primary production. The Thames ecosystem is therefore dominated by the energy flow through the detritus. Detritus, however, does not appear in Fig. 2 except as input from trees and macrophytes into the periphyton and detritus box (and therefrom to 1+ fish), and as a small contribution to 0 group fish. The important detritus contributions from all other components were underestimated and the dominant position of energy flows through detritus was not realized. Insofar as I can recollect the team's discussions accurately, this was because:

- it was difficult then as it is now to address the question of detritus using trophic level analysis: the empirical observations needed to address the question are almost entirely lacking; and
- more detailed data, e.g., on P/B ratios, gross efficiencies and the various other efficiencies of energy transfer (Jørgensen 1979) used here to carry out estimates of the whole trophic structure and especially of the role of detritus in the ecosystem were not then available (indeed, it was the objective of IBP to produce such data).

Berrie (1972) discussed the role of detritus in the Thames and suggested that there is a dynamic interaction between the trypton flowing

Table 6. Summary statistics for the Thames Mark 2 model (kcal·m^{-2}·year^{-1}); see Christensen and Pauly (1992a) for further explanation and references.

Sum of all consumption	=	4,769.0
Sum of all exports	=	989.8
Sum of all respiratory flows	=	1,694.2
Sum of all flows into detritus	=	3,854.2
Total system throughput	=	11,307.2
Sum of all production	=	3,222.8
Calculated total net primary production	=	2,197.0

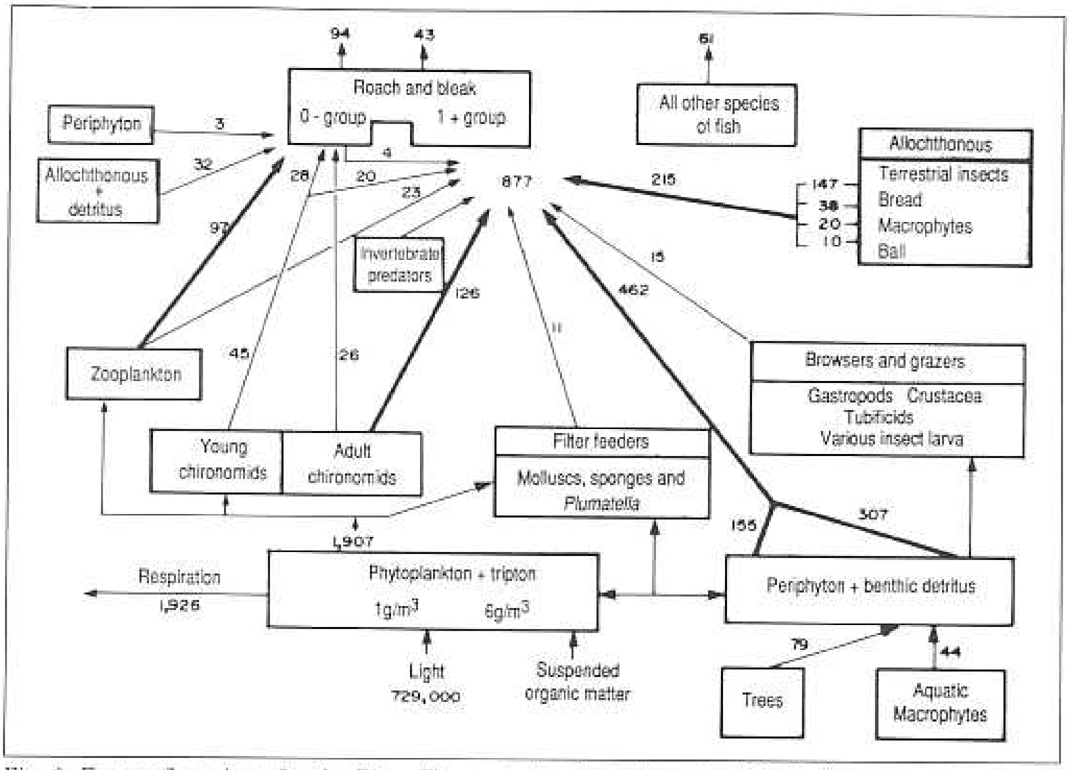

Fig. 2. Energy flow chart for the River Thames below Kennet mouth ("Mark 1"). In general, primary producers are shown at the bottom, invertebrate animals in the center and fish at the top, but to avoid complex networks of arrows, sources of periphyton, detritus and allochthonous materials are shown in two places. Heavy arrows indicate the largest of energy flows (from Fig. 3 in Mann et al. 1972).

through the ecosystem and the detritus being generated *in* the ecosystem by various populations. He also suggested that there was a dynamic relation between the trypton, benthic detritus, epiphytic detritus, and benthic and periphytic detritivores. The "ecotrophic efficiency" of detritus generated by the Thames model (Table 5) implies that 79% of the flow to detritus is recycled and that the rest is deposited as sediment within the system or else how exported, e.g., by being carried by the current downstream. This confirms Berrie's (1972) suggestion and identifies an important energy removal from the ecosystem not identified by the Mark 1 model.

It is clear that the precise role of the detritivores and the browsers needs to be studied in much more detail than was done in the Thames study. Scrutiny of the contents of this volume also suggests that the lack of critical work on detritus in aquatic ecosystems may be the single biggest omission of the IBP study and perhaps of most subsequent ecosystem analyses. Future ecosystem analysis should examine the relation between detritus, detritivores and detritivore browsers.

The difficulties identified here and the contrasts between Figs. 2 and 3 show some of the differences between models used during the IBP and more recent models. The evolution of new models came as a direct response to the creation of models such as the Thames Mark 1 model.

Energy Flow and Trophic Levels

The older model used discrete trophic "layers": Layer 1 (Fig. 2) included phytoplankton, trypton, periphyton, benthos, detritus. Layer 2 included zooplankton, chironomids, filter feeders and browsers with Layer 3, fish above. Such models deliberately refused to identify trophic levels because of the complex food webs.

The Mark 2 model shows the utility of the weighted mean trophic level generated by ECOPATH II, a concept easy to handle and understand. While the Mark 2 model also failed to tackle the trophic positions of detritus satisfactorily, this was because of a lack of data on the true detritivore (i.e., the microorganisms that digest detritus), not because of conceptual or analytical difficulties.

Fig. 3 shows the Mark 2 model's energy flows. The flows to the fish populations are essentially similar to the corresponding parts in Fig. 2. Table 6 shows a total production of 3,223 kcal·m^{-2}·year^{-1} for the Mark 2 model, of which 2,197 kcal·m^{-2}·year^{-1} is net primary production, showing that the primary production is, as expected, large compared to other production.

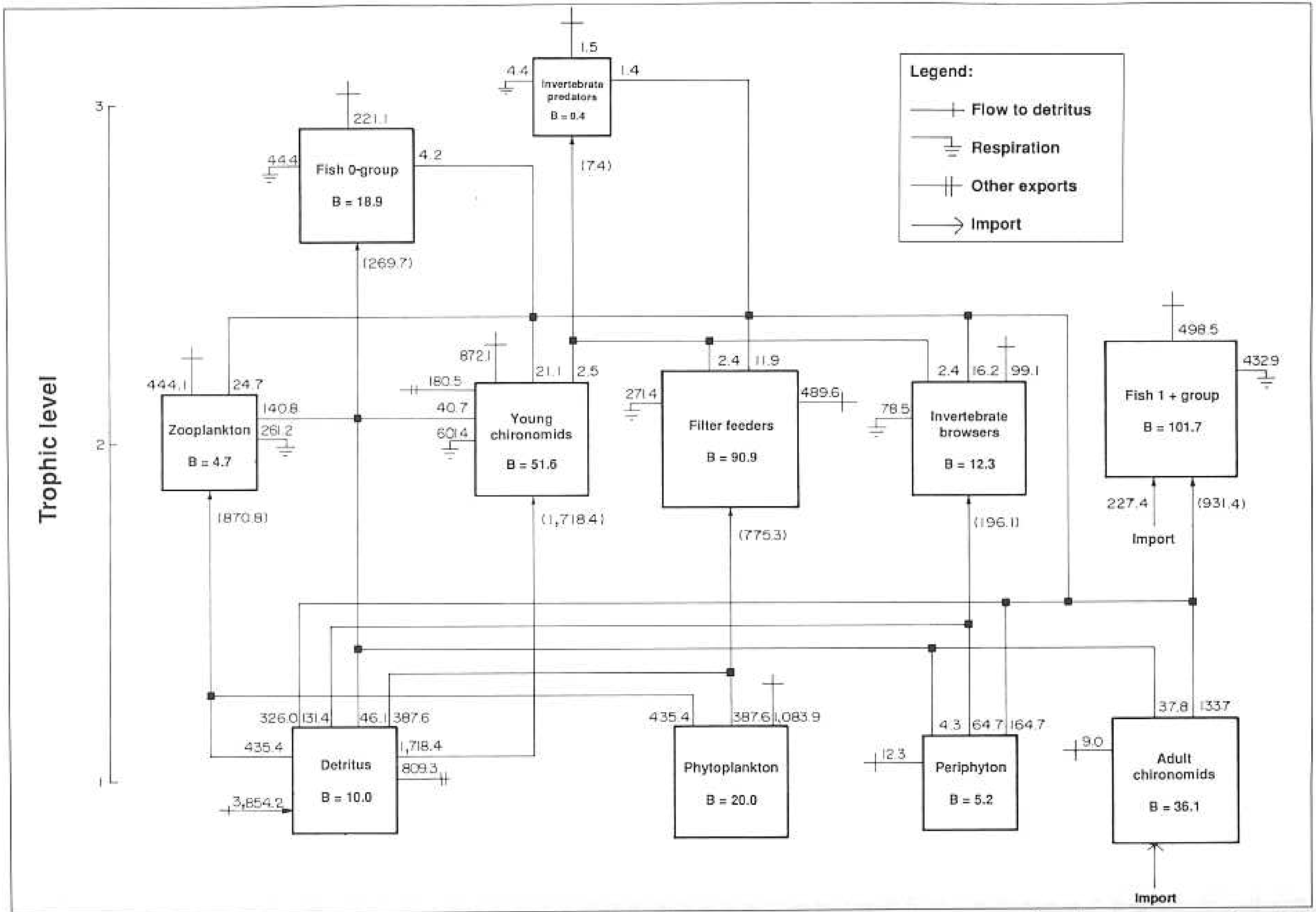

Fig. 3. Trophic flows in the River Thames below Kennet mouth ("Mark 2") constructed using the ECOPATH II model. Flows are in kcal·m^{-2}·year^{-1}. Flows from macrophytes (44.0 kcal·m^{-2}·year^{-1}) and trees (79.0 kcal·m^{-2}·year^{-1}) to the detritus are not shown. The "other export" of young chironomids is production of adult chironomids.

Table 6 also shows that the total energy throughput of the Thames ecosystem is 11,307 kcal·m^{-2}·year^{-1} compared to a total value of 2,907 kcal·m^{-2}·year^{-1} obtained by summing all production flows in Fig. 2 (Mark 1 model). The difference is mainly due to the inclusion of additional energy flows generated by the model for new knowledge about energy transfer efficiencies, as shown in Fig. 3. The Mark 1 model (Fig. 2), being the predecessor, anticipates problems addressed more completely by the Mark 2 model. The Mark 1 and 2 models also differ in the way they address energy flows and sum them (see below).

Zooplankton

Zooplankton are identified by both models as one of the most important groups in the Thames ecosystem. They have one of the largest food intakes and their respiration is exceeded only by that of 1+ group fish and filter feeders; their assimilation is second only to that of 1+ group fish.

The trophic position of Thames zooplankton is unclear: it has been included as a trophic level 2 organism in the ECOPATH II model (Fig. 3). But various zooplankton species may exist at different trophic levels. The great importance of the zooplankton arises from the unexpectedly high production and consumption rates of the prefingerling and fingerling fish: Mann et al. (1972) noted that this was perhaps the most unexpected result of the Thames ecosystem study.

Other Invertebrates

Other invertebrates channel large energy flows and include young chironomids, filter feeders, invertebrate browsers and invertebrate predators in decreasing order of importance. Mann et al. (1972) noted that filter feeders contributed little of their production to other living groups, and that most of the production was transferred to detritus. The Mark 2 model confirms this. They also noted that the large biomass (1 t per 100 m of river) was a major contribution to removal of excess organic matter from the river, and may have been a natural response to the increased organic level provided by municipal discharges into the Thames.

Production estimates of chironomids (Mann et al. 1972) for the Thames were very low (15.2 kcal·m^{-2}·year^{-1}) compared with the estimated amount of adults consumed (147 kcal·m^{-2}·year^{-1}, recorded as "allochthonous" by Mann et al. [1972, Fig. 3]). This was probably because of difficulty in obtaining good samples of young chironomids by any of the methods used: actual "allochthonous" input of adult chironomids may also have been higher.

Fish Groups

Compared to 0 group fish, the food intake, respiration and assimilation of 1+ group fish are high. This is remarkable because 0 group fish provide an average of 69% of total fish production, with an estimated trophic efficiency of 0.5. This high efficiency is reasonable because 0 group production includes that of larvae and prefingerlings.

Interestingly, 1+ group fish have a trophic level of only 2.12, considerably lower than that of 0 group fish (Table 5). This is so because of the very large contribution of detritus to the diet of 1+ group fish.

Mixed Trophic Impacts

Fig. 4 shows the direct and indirect impacts any of the groups have on all other groups in the system (Christensen and Pauly 1992a, 1992b). Some examples of how to interpret the results: 1+ group fish have a negative trophic impact on nearly all other groups in the system due to either predation or competition. Invertebrate browsers have a strong positive influence on invertebrate predators and phytoplankton has a strong positive effect on zooplankton, both of which are reasonable. The negative effect of detritus on adult chironomids is unexpected. Fig. 4, as a whole, shows that detritus is one of the most dynamic components, confirming the important role assigned by Berrie (1972) to detritus in the Thames.

It is difficult to compare the role played by detritus in the Thames with that in most other systems. The role of detritus is in the present applications based on general knowledge of ecological relationship only. Nevertheless it appears that detritus is more important in the Thames than in most other study areas where detritus is either very much less important relative to primary production (e.g., Lakes George [Moreau et al., this vol.]; Kariba [Machena et al., this vol.]; and Tanganyika [Moreau et al., this vol.]) or, while important relative to primary production still of lesser importance than in the Thames (Lakes Turkana [Kolding, this vol.]; Malaŵi [Degnbol, this vol.]; Kinneret [Walline et al., this vol.]). Possibly the relatively unimportant role of detritus in many other models reflects the lack of research on detritus rather than the underlying ecosystem structure.

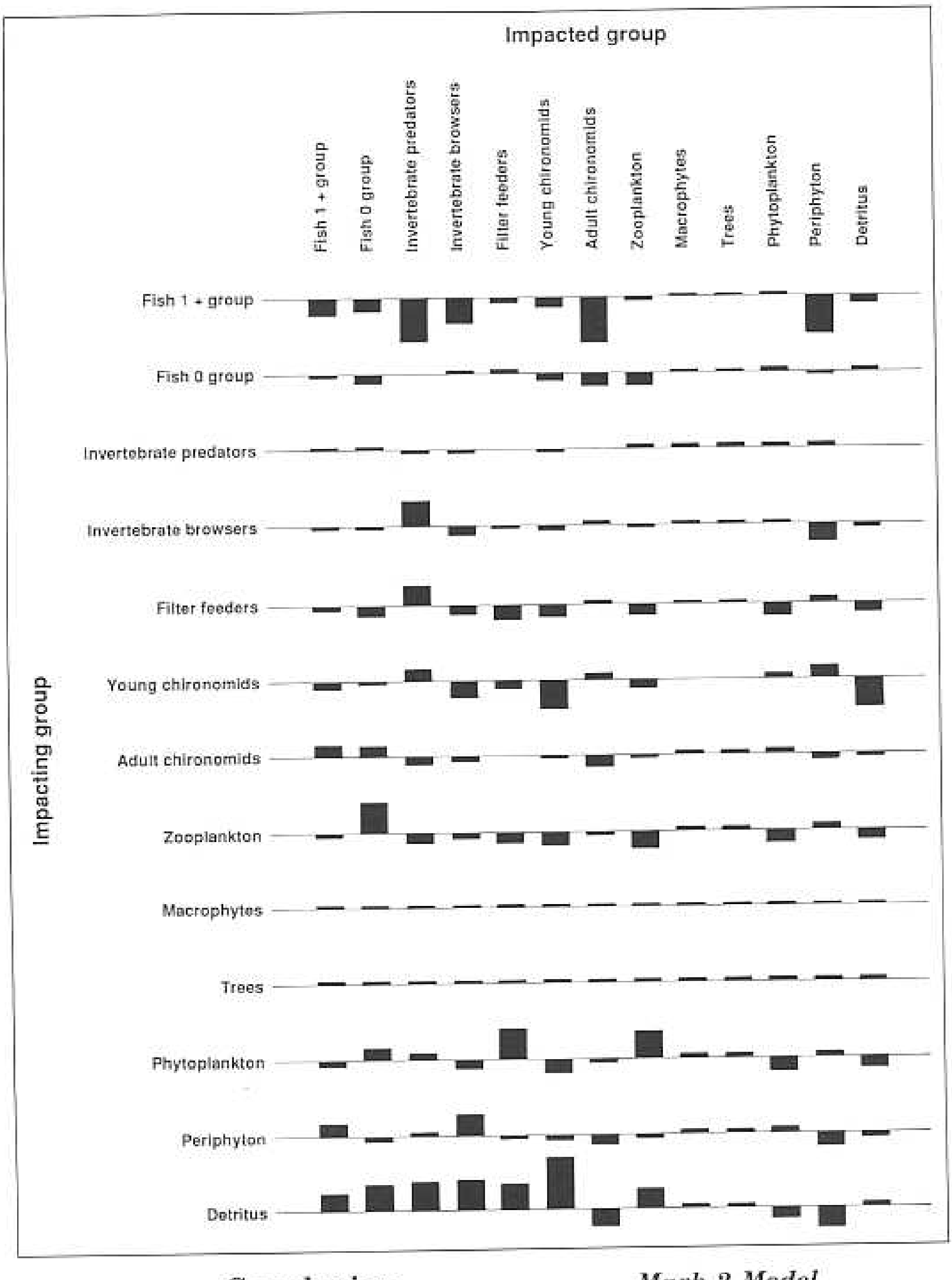

Fig. 4. Mixed trophic impacts in the River Thames below Kennet mouth ("Mark 2") constructed using the ECOPATH II model. The bars show the direct and indirect impact any of the groups have on all other groups in the system.

Conclusion

Mark 1 Model

Apart from the omission of the detritus from the Mark 1 model, the Mark 2 model of the Thames also exposes a major weakness in the original study: the only published biomass estimates were those summarized by Mathews (1971) for fish and that for the phytoplankton (Mann et al. 1972). Yet all of the Thames IBP studies provided biomass estimates.

Loss of the Thames data shows the difficulties of data conservation, a matter that should be considered a natural part of any project involving data collection (Mathews 1993).

Mark 2 Model

The Mark 2 model provides a similar picture of the Thames ecosystem to that provided by the Mark 1 model, but is more complete; it handles trophic levels and the foodweb easily and in more detail, and provides a much more complete picture of the ecosystem.

The Mark 2 model is weaker in one respect: it makes no reference to incident light and does not estimate the gross efficiency of primary production. This could, however, have been addressed in the present model by allocating a "consumption" to the primary producers. The transfer efficiency of sunlight deserves further attention: it is likely that some ecosystems will process light energy more efficiently than others and that those with large energy inputs from detritus may be different from those without.

Uniqueness

The Mark 2 model of the Thames is not necessarily a unique solution to the available data: many estimates of P/B ratios and various trophic efficiencies had to be introduced, either from Jφrgensen (1979) or on the basis of general knowledge of such values in other ecosystems. Still it is unlikely that other possible models will vary greatly from the one provided here.

Future Work

The Mark 1 model was an excellent stimulus to further analysis; likewise the Mark 2 model may be used as a heuristic device to stimulate further research into the Thames and other riverine systems, especially into:

- the role of detritus, detritivores and "detritivorous browsers" as defined above and in Figs. 3 and 4;
- the role of zooplankton;
- the roles of prefingerling production and consumption none of which has been investigated sufficiently in the Thames.

The lack of followthrough on the Thames work, in spite of the useful output produced, was characteristic of the whole IBP.

One reason for this has been the perceived difficulty in handling the large amount of data, and the complex analyses that extensions of the trophic approach required. It seems that ECOPATH II, with its analytical routines, may provide a tool that can encourage ecologists to attempt again to make holistic ecosystem models.

There is no doubt in this context that any trophic modelling, including ECOPATH II, is insufficient to describe an ecosystem completely. A fully predictive ecological model needs to take more into account than trophic interactions. Nevertheless it is equally certain that a clear understanding of the transfer of energy (and information) through an ecosystem is a *sine qua non* for comparing its structure with other ecosystems.

The ECOPATH II approach is the most complete as yet available; its application leads to a rich variety of hypotheses for future research and it is perhaps the best hope for identifying a research program leading towards a combined ecosystem engineering/management approach. The ability to manage our ecosystems in the future will certainly be an important factor in successful conservation of the environment. ECOPATH II offers a useful approach for tackling this question.

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