Internat. Rev. Hydrobiol.	**88**	2003	5	433–452

DOI: 10.1002/iroh.200310666

RAINER POEPPERL

University of Muenster, Institute for Animal Evolution and Ecology, Department of Limnology, Huefferstrasse 1, D-48149 Muenster, Germany; e-mail: poepperl@uni-muenster.de

A Quantitative Food Web Model for the Macroinvertebrate Community of a Northern German Lowland Stream

key words: network analysis, consumption, connectance, mass-balance, trophic interactions

Abstract

Trophic interactions and cycling of organic carbon within the macroinvertebrate community of a Northern German lowland stream were analyzed based on a compartment model. The network model describes the structure of the food web quantifying biomass, production, and consumption of their elements, of the entire system and between trophic levels. System primary production is 153.7 g C m^{-2} yr^{-1} and invertebrate production 53.3 g C m^{-2} yr^{-1}. Invertebrate consumption amounts to 702.6 g C m^{-2} yr^{-1}. Main flows are identified between trophic level 1 and 2 and are connected with highly productive compartments. '*Anodonta* and *Pseudanodonta*' and *Dreissena polymorpha* show the highest consumption of all groups with 269.9 g C m^{-2} yr^{-1} and 114.1 g C m^{-2} yr^{-1}, respectively. System consumption is highest on the import from the upstream lake with 532.5 g C m^{-2} yr^{-1}, sediment detritus with 135.5 g C m^{-2} yr^{-1}, and primary producers with 25.7 g C m^{-2} yr^{-1}. The lowest predation pressure is observed for Bivalvia with an ecotrophic efficiency of <10% and highest for Chironomidae with 91%. Approximately 20% of organic matter entering the detritus pool are recycled to the living groups of the system. Transfer efficiencies between discrete trophic levels are generally low except for transfer of detrital material between level I and II.

1. Introduction

Few studies deal with the question, what a share imported material has in the total consumption of macroinvertebrate communities in streams (SCHÖNBORN, 1992; SCHWOERBEL, 1972, 1987; STATZNER, 1979). Lakes may supply large quantities of suspended particulate material to the outlet streams (ARMITAGE, 1977; CUSHING, 1963; GIBSON and GALBRAITH, 1975; ULFSTRAND, 1968) and therefore they may be responsible for high densities of filter feeding invertebrates (ARMITAGE, 1976; HYNES, 1970; ILLIES, 1956; OSWOOD, 1979; SHELDON and OSWOOD, 1977; SPENCE and HYNES, 1971; WOTTON, 1988). Compared to other studies (see BENKE, 1993; IVERSEN, 1988; SMOCK *et al.,* 1985, 1992) POEPPERL (1996) determined a very high secondary production for the investigated stream and the abundance, biomass, and secondary production of filter feeders decrease with increasing distance from the lake (POEPPERL, 1999). The study presented here investigated how much material was being consumed by the macroinvertebrate community of a northern German lowland stream.

The food web, presented here as a carbon mass-balance model, describes the trophic interactions and trophic impact of invertebrate groups. Along with the general objective to gain a more holistic understanding of structure and functioning of the community (comp. TOWNSEND *et al.*, 1998; POWER and DIETRICH, 2002) by quantitatively describing how matter and energy propagate along pathways of the food web (comp. OKEY and PAULY, 1999; THOMPSON and TOWNSEND, 2000; MOREAU *et al.*, 2001), the model was intended to yield the fol-

 1434-2944/03/509-0433

lowing more specific results: (1) to provide information on resource utilization and position of single ecological groups in the trophic web by quantifying consumption, number of predators, and amount of production consumed by predators, (2) to assess the importance of large ecological groups on the cycling of matter within the system, such as primary producers, detritus, and invertebrates, (3) to estimate size and efficiency of flows between trophic levels with respect to origin or destination, and (4) finally, to provide estimates of biotic parameters not measured *in situ* by extrapolation from model results.

Furthermore, for a quantitative characterization and classification of the overall system, system parameters and ratios, along with indicators of system performance and developmental stage, are obtained from model outputs.

2. Materials and Methods

2.1. Study Area

The investigated stream 'Alte Schwentine' is located in northern Germany 30 km south of Kiel at the outer margin of the Weichselian (= Wisconsinan) glaciation (54°06′ N, 10°15′ E; Fig. 1). The stream is the outlet of Lake Belau, a eutrophic, partly dimictic and mainly holomictic hardwater lake with a total surface area of 1.13 km^2 and a maximum depth of 26 m (POEPPERL *et al*., 2001). The straightened stream has a constant width of 6 m and flows through cultivated farmland. There is only a very small buffer zone at the bank where nitrophytes are the characteristic element in the herb layer. The discharge of the stream is regulated by a water mill (0.08 to 0.6 $m^3\ s^{-1}$) and current velocity ranges from 0.05 to 0.6 m s^{-1}. After a distance of 1.9 km the stream flows into Lake Stolpe. Chemical and physical properties of the water are strongly influenced by the upstream lake. Throughout the year water temperature varies from –1.4 °C to 24.9 °C. High amplitudes in conductivity, pH, N- and P-concentrations measured over the year are mainly caused by the biological activities of the plankton in the eutrophic lake (POEPPERL, 1996). Further information about hydrochemical and hydrophysical results can be found in POEPPERL (1991, 1996, 1999), POEPPERL and WITZEL (1991), POEPPERL *et al*. (2001), and SCHERNEWSKI (1992).

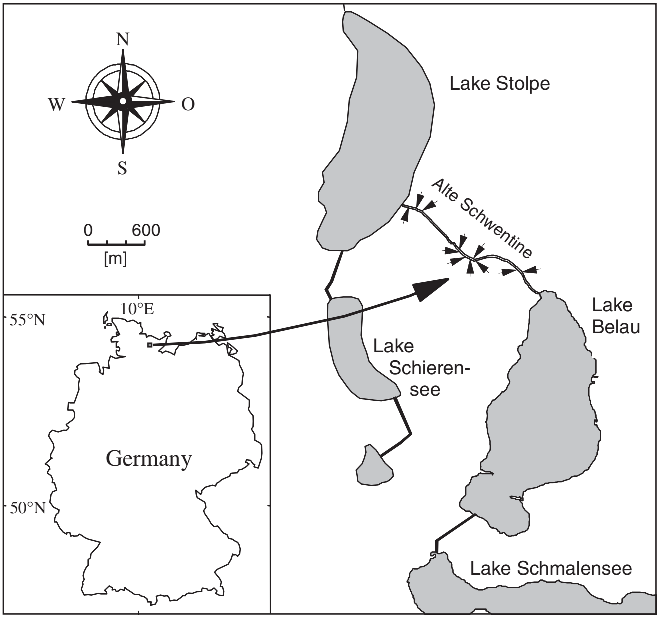

Figure 1. Map of the Bornhoeved Lake Region. The present study describes trophic interactions in the stream between Lake Belau and Lake Stolpe. Arrows mark the sampling sites.

2.2. Analysis of Data

The modelling approach used here for the macroinvertebrate community of a lake outlet assumed mass-balance, i.e. it balanced the flow to and from each ecological group or compartment in the model based on the equations:

$$P = PM + M + E + BA \tag{1}$$

with P: production, PM: predation mortality, M: other mortality, E: migration, BA: biomass accumulation. The predation mortality term PM was used to link predator and prey species, and the consumption Q is defined as

$$Q = P + NA + R \tag{2}$$

with P: production, NA: unassimilated food, R: respiration. A detritus compartment D served as recipient of flows originating from 'other mortality' M and 'non assimilated food' NA, so:

$$D = M + NA. \tag{3}$$

For calculations the following input parameters were used for all living groups: Biomass B, ratio of production to biomass (P/B), and gross efficiency rates GE (= P/Q). A fourth parameter, usually ecotrophic efficiency EE (= predation mortality expressed as percentage of production), was then calculated using a set of linear equations so as to ensure mass-balance. In addition to the previously mentioned parameters, the amount exported from the system by migration (E, i.e. emerged biomass), an estimate of the percentage of food that is not assimilated (%NA), and a diet composition estimate (DC), were required as inputs for each ecological group.

For constructing the trophic network, the concept of trophic levels has been adopted. Two different types of trophic levels were used: (1) The position of a functional group within the food web was determined by assigning a fractional trophic level to each compartment as suggested by ODUM and HEALD (1975) based on the quantitative composition of its diet: A trophic level TL of 1 was assigned to primary producers and detritus. TL of consumers were calculated as 'TL = 1 + (the weighted average of the preys' trophic level)'; (2) Prior to calculating quantity and efficiency of transfer of matter between trophic levels these fractional trophic levels have been reversed by an approach suggested by ULANOWICZ (1995) into discrete trophic levels sensu LINDEMAN (1942). Thus, when a group obtained 60% of its food as a herbivore and 40% as a first-order carnivore, the relevant fractions of the flow through the group were attributed to the herbivore level and the first predatory level.

Consumption per year was calculated starting from top predators, and then proceeding down the trophic chain. The annual intake of each predator, coupled with a diet composition estimate, determined the grazing quote on the lower level.

For model calculations the software package ECOPATH 3.0 was used, an approach for constructing ecosystem models (CHRISTENSEN and PAULY, 1992a, 1992b, 1993a). Ecopath 3.0 and previous versions are developed from the Ecopath model of POLOVINA (1984) and are designed for the construction and parametrization of mass-balanced ecosystem models. The program includes routines for balancing of flows in an ecosystem and for estimating indices for ecosystem characterisation. All parameters were entered as g carbon per m^2, expressing rates of exchanges on an annual basis.

2.3. Data Basis and Ecological Groupings

Sampling. POEPPERL (1996) investigated the abundance, biomass and secondary production of the macroinvertebrate community at eleven characteristic sampling sites of the outlet of Lake Belau. Samples were taken using a box sampler (500 cm^2) as described by HYNES (1971) and STATZNER (1979, 1981). The export of biomass by insects emerging from the stream was determined by POEPPERL (2000a) installing a total of 12 emergence traps above typical areas of the stream. Overall stream average biomass, production, and turnover of carbon within the benthic community was weighted according to the different substrate types along the stream bed. A detailed description of the sampling sites as well as field and laboratory methods can be found in POEPPERL (1996, 1999, 2000a, 2000b).

Ecological groupings. To describe the benthic food web of the lake outlet a vast number of taxonomic species and groups was assembled initially. In the stream 126 species of invertebrates were identified (POEPPERL, 1992, 1996; POEPPERL and MARTIN, 1995). With the objective to reduce the number of compartments to an amount that could be handled with some ease (comp. ABARCA-ARENAS and ULANOWICZ, 2002; OPITZ, 1996): and still represent typical features of the system, the original number of species was aggregated into 15 compartments by applying a series of ecologically relevant criteria such as (1) Type of biomass production (producer/consumer), (2) Type of food (plant, meat, detritus, mixed), (3) Mode of feeding (filter feeders, mixed feeders, predators), (4) Production and/or consumption rate, and (5) Standing stock.

The resulting set of compartments consisted of 13 groups of benthic macroinvertebrates, one group of primary producers, and one of detritus. The model structure applied here focused on the macroinvertebrate community.

Data basis. Model inputs of B, P, P/B, Q/B, GE, E, and NA for compartments were estimated as described below. The underlying data base was assembled from 1988 to 1991. Inputs were prepared according to available data. Biomass and secondary production was presented by POEPPERL (1996, 1998, 2000b), functional feeding groups by POEPPERL (1999), and biomass of emerged insects by POEPPERL (2000a). Biomass values were rounded to 0.01 g C m^{-2} and P/B values to 0.1 (with the exeption of two Unionidae compartments where values were rounded to 0.01). GE, E and NA were rounded to 0.01.

Primary producer: LANDMESSER (1993) investigated the phytoplankton of Lake Belau. For modelling of the food web biomass was calculated by the phytoplankton carbon concentration and mean water depth. Phytoplankton biomass amounted to 0.48 mg C l^{-1} (LANDMESSER, 1993) and P/B was 67.8 (U. MÜLLER, pers. comm.) yielding a production of 13.02 g C m^{-2} yr^{-1}. The mainly occurring macrophyte was *Elodea canadensis* with a B of 90.25 g C m^{-2}. A P/B investigated by SCHIEFERSTEIN (1997) for the macrophytes of the littoral of the upstream lake was used. Compartment biomass was 90.44 g C m^{-2} and primary production 153.7 g C m^{-2} yr^{-1} (Table 1).

Theod, Ancyl, Acro, Valva: This group comprised grazing Gastropoda which consume similar food and use similar modes of feeding. The most important representative of this group was *Theodoxus fluviatilis* with a proportion of more than 95% of the compartment biomass (POEPPERL, 1996). DW was converted into C using a factor of 0.4 from JØRGENSEN (1979). GE was fixed at 0.18 and NA at 40%

Table 1. Basic input values of the food web analysis for the macroinvertebrate community of the outlet of Lake Belau. Acro: *Acroloxus*, Ancyl: *Ancylus*, Bithyn: *Bithynia* sp., C: collectors, Ceratop: Ceratopogonidae, Ephem: Ephemeroptera, GE: gross efficiency, Hirud: Hirudinea, Hydrachn: Hydrachnidia, Limon: Limoniidae, Lymn: *Lymnaea* sp., Mola: *Molanna* sp., NA: nonassimilated part of the food, Odo: Odonata, P/B: Ratio of production/biomass, Polycen: *Polycentropus*, Pot: *Potamopyrgus antipodarum*, Pseudanod: *Pseudanodonta complanata*, Theod: *Theodoxus fluviatilis*, Trich: *Trichoptera*, Valva: *Valvata* sp. A detailed description of the compartments and the origin of the values are found in the text.

	Compartment	Biomass g C m^{-2}	P/B yr^{-1}	Export E g C m^{-2} yr^{-1}	GE	NA
1	Primary producer	90.44	1.70	–	–	–
2	Theod, Ancyl, Acro, Valva	1.11	1.40	–	0.18	0.40
3	Potamo, Bithyn, Lymn	8.29	1.80	–	0.14	0.50
4	Anodonta, Pseudanod	35.99	0.15	–	0.02	0.80
5	Unio sp.	20.51	0.09	–	0.02	0.80
6	Sphaeriidae	4.18	2.00	–	0.18	0.35
7	Dreissena polymorpha	5.02	2.50	–	0.11	0.60
8	Oligochaeta	0.52	4.00	–	0.10	0.65
9	Chironomidae and Ceratop.	0.48	5.00	0.48	0.13	0.50
10	Hirud, Tricladida, Hydrachn	0.69	1.60	–	0.20	0.24
11	Trich and Ephem, c	0.20	3.00	0.13	0.12	0.58
12	Sialis, Odo, Mola, Polycen	0.34	2.70	0.07	0.35	0.22
13	Hydropsyche sp.	0.17	2.70	0.10	0.12	0.51
14	Asellus, Gammarus, Limon	0.40	2.10	–	0.10	0.65
15	Detritus, sed.	676.70	–	–	–	–

(comp. McNeill and Lawton, 1970; Streit, 1975a, b, 1976). Diet composition estimates were obtained from results in Schwenk and Schwoerbel (1973).

Potamo, Bithyn, Lymn: This compartment is composed of the gastropods which belong to the functional feeding group of collectors. As regards biomass, the most important species were *Bithynia tentaculata* and *Potamopyrgus antipodarum* followed by *Lymnaea auricularia* and *Gyraulus albus* (Poepperl, 1996). DW was transformed into C using a C/DW ratio of 0.4 indicated in Jørgensen (1979). A biomass of 8.29 g C m^{-2} and a production of 14.92 g C m^{-2} yr^{-1} was calculated for the compartment. GE was fixed at 0.14 (McNeill and Lawton, 1970), NA at 0.5 (comp. Fisher and Gray, 1983; Blandenier and Perrin, 1989, Wotton, 1994). DC estimates followed indications in Brown (1961); Frenzel (1979), Haynes and Taylor (1984), Tashiro and Colman (1982), and Wallace *et al.* (1987).

Anodonta, Pseudanodonta: This compartment included the species *Anodonta anatina*, *A. cygnea,* and *Pseudanodonta complanata* (Poepperl, 1992). *A. anatina* was the species with the highest biomass proportion of all macroinvertebrates and had a share of 90.1% of the compartment biomass (Poepperl, 1996). *P. complanata* had a share of 9.6%. According to Lewandowski and Stanczykowska (1975) NA was fixed at 0.8. Based on this NA value and the investigations of Statzner (1979) a GE of 0.02 was calculated (Table 1). Since these species incorporate their food by filtering particles out of the surrounding water body their DC roughly reflects the percentage of different fractions of particulate material in the water column (Table 2). Due to its mobility the percentage of animal plankton has been considerably reduced.

Unio sp.: Two species of *Unio* sp. lived in the stream. *Unio tumidus* had a share of 70% and *Unio pictorum* of 30% of the compartment biomass. As for *Anodonta* sp. and *Pseudanodonta complanata,* NA was fixed at 0.8 (Lewandowski and Stanczykowska, 1975). Combined with the investigations of Statzner (1979) a GE of 0.02 was estimated. DC was used as described for the compartment 'Anodonta, Pseudanodonta'.

Sphaeriidae: This compartment included *Sphaerium corneum* which had a proportion of over 90% of the biomass as well as 8 species of *Pisidium* sp.. DW was transformed into C by a factor of 0.4 (Jørgensen, 1979). According to Hornbach *et al.* (1984) NA was established at 0.35 and GE at 0.18. (McNeill and Lawton, 1970). A diet composition was used as described for the compartment 'Anodonta, Pseudanodonta'.

Dreissena polymorpha: *D. polymorpha* had a share of almost 5% of the biomass of the total macroinvertebrate community (Poepperl, 1996). DW was transformed into C by a factor of 0.4 (Jørgensen, 1979). NA was established at 0.6 (Walz, 1978a, b; Stanczykowska, 1977; Stanczykowska *et al.,* 1975). Based on this NA value and the investigations of Statzner (1979) a GE of 0.11 was calculated. A diet composition was used as described for the compartment 'Anodonta, Pseudanodonta'.

Table 2. Inputs of the diet composition [%] for the individual compartments used in the model calculation. Abbreviations of group names and the origin of values are described in text.

Prey	Predator	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Primary producer	0.50	0.15	–	–	–	–	0.10	0.05	–	0.35	–	0.05	0.05
2	Theod, Ancyl, Acro, Valva	–	–	–	–	–	–	–	–	0.02	–	0.03	–	–
3	Potamo,Bithyn,Lymn	–	–	–	–	–	–	–	–	0.40	–	0.08	–	–
4	Anodonta, Pseudanod	–	–	–	–	–	–	–	–	0.05	–	–	–	–
5	Unio sp.	–	–	–	–	–	–	–	–	0.03	–	–	–	–
6	Sphaeriidae	–	–	–	–	–	–	–	–	–	–	0.05	–	–
7	Dreissena polymorpha	–	–	–	–	–	–	–	–	0.03	–	0.03	0.01	–
8	Oligochaeta	0.01	–	–	–	–	–	–	–	0.20	0.01	0.15	0.03	0.01
9	Chironomidae and Ceratop.	–	–	–	–	–	–	–	0.02	0.12	–	0.15	0.05	0.01
10	Hirud, Tricladida, Hydrachn	–	–	–	–	–	–	–	–	0.02	–	–	–	–
11	Trich and Ephem, c	–	–	–	–	–	–	–	–	0.03	–	0.06	0.01	–
12	Sialis, Odo, Mola, Polycen	–	–	–	–	–	–	–	–	0.05	–	0.08	–	–
13	Hydropsyche sp.	–	–	–	–	–	–	–	–	–	–	0.07	0.03	–
14	Asellus, Gammarus, Limon	–	–	–	–	–	–	–	–	0.05	–	0.15	–	–
15	Detritus, sed.	0.49	0.80	–	–	–	–	0.85	0.90	–	0.63	–	0.20	0.93
	Import	–	0.05	1.00	1.00	1.00	1.00	0.05	0.03	–	0.01	0.15	0.62	–
	Total	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Oligochaeta: This compartment had a biomass of 0.52 g C m^{-2} (Poepperl, 1996). Carbon content of dry matter was fixed at 45% (Poepperl and Opitz, unpubl. data). Based on Ivlev (1953) for *Tubifex tubifex* and Brinkhurst and Austin (1979) NA was fixed at 0.65 of amount consumed. A GE of 0.10 was applied based on investigations of Schönborn (1987) with *Chaetogaster* and *Nais* sp. (comp. Schönborn, 1998) and of McNeill and Lawton (1970) with *Limnodrilus*. DC was provided by Loehlein (pers. comm.).

Chironomidae, Ceratopogonidae: B and E were determined in mg DW by Poepperl (1996, 2000a). Transformation into C was accomplished by applying a factor of 0.45 for C/DW after Salonen *et al.* (1976). GE was set equal to 0.13 following Tilly (1968) and McNeill and Lawton (1970) and a NA of 0.5 was used after Mathews (1993). DC followed Wallace *et al.* (1987) and Mayer (1934).

Hirud, Hydrachn, Tricladida: This compartment included five species of Tricladida, mainly *Polycelis tenuis* and *Dugesia polychroa*, eight species of Hirudinea, mainly *Helobdella stagnalis* and *Erpobdella octoculata* (Poepperl, 1992) and 15 species of Hydrachnidia (Poepperl and Martin, 1995). Transformation of B and P into C was realized based on Salonen *et al.* (1976) yielding for the compartment a B of 0.69 g C m^{-2} and a P/B value of 1.6. A GE of 0.2 was used indicated by Schönborn (1987) for *Erpobdella octoculata*. NA was fixed at 0.24 (comp. Schönborn, 1992; Manokov and Sorokin, 1972). DC estimates followed indications in Barton and Metcalfe (1986), Reynoldson and Bellamy (1975), Reynoldson and Young (1965), Schönborn (1987), and Seaby *et al.* (1996).

Trich and Ephem, c: This compartment consisted of Ephemeroptera, Trichoptera, and one species of Elmidae which belong to the functional feeding group of collectors. Most important species of Ephemeroptera were *Ephemera vulgata* with 29% and *Caenis luctuosa* with 9% of the compartment biomass. Within the Trichoptera *Athripsodes* sp. was most important with 15% of the compartment biomass, followed by *Silo nigricornis* with 11% and *Goera pilosa* with 10%. *Oulimnius tuberculatus* had a share of 12%. B, P, and E (by emergence) were adopted from investigations by Poepperl (1996, 2000a). After Salonen *et al*. (1976) DW was transformed into C using a factor of 0.49 for Ephemeroptera and 0.46 for Trichoptera and Elimidae. GE was fixed at 0.12 (Benke and Jacobi, 1994; Benke and Wallace, 1997; Jacobsen and Sand-Jensen, 1994; McNeill and Lawton, 1970; Wotton, 1994), NA at 0.58 (Blandenier and Perrin, 1989; Fisher and Gray, 1983; Jacobsen and Sand-Jensen, 1994; Otto, 1974). The diet was mainly detritus and aufwuchs algae (Benke and Jacobi, 1994; Benke and Wallace, 1997; Haynes and Taylor, 1984; Solem, 1983; Wallace *et al.*, 1987).

Sialis, Odo, Mola: This compartment included different predatory representatives of Megaloptera, Odonata and Trichoptera. Most important species was *Sialis lutaria* which had a share of 85% of the compartment biomass. C was calculated after Salonen *et al.* (1976). The export was investigated by Poepperl (2000a). From indications in Engelmann (1966), Lawton (1970), Manokov and Sorokin (1972), McNeill and Lawton (1970), and Schönborn (1992) a GE of 0.35 and NA of 0.22 were calculated. Diet composition was developed from investigations of individual taxonomical groups (i.e. Edington and Hildrew, 1981; Higler, 1978; Hildrew and Townsend, 1976; Jones, 1950; Lawton, 1970; Slack, 1936; Tachet, 1971; Thompson, 1978).

Hydropsychidae: Two species of Hydropsychidae lived in the stream. *Hydropsyche pellucidula* had a share of 66.8% and *H. angustipennis* of 33.2% of the compartment biomass (Poepperl, 2000a, b). The emerged biomass was determined by Poepperl (2000a). DW was transformed into C using a factor of 0.48 (Salonen *et al.*, 1976). GE was fixed at 0.12 (Benke and Wallace, 1997; McNeill and Lawton, 1970), NA at 0.51 (Schröder, 1988; Wotton, 1994). The diet composition was arranged after Benke and Wallace (1980, 1997), Schröder (1976, 1988), Wallace *et al*. (1987) and Xiang *et al*. (1984).

Asellus, Gammarus: This compartment incorporated benthic Crustacea and three families of Diptera based on their similar P/B and Q/B, their similar DC and their similar way of feeding. *Asellus aquaticus* was the most important species of this compartment with a share of 74% of biomass, followed by *Gammarus pulex* and the Diptera with respectively 13%. Conversion factors of 0.39 for C/DW (Jørgensen, 1979; Salonen *et al.*, 1976) yielded a B of 0.4 g C m^{-2}. A mean GE of 0.1 was assessed based on Adcock (1982), McNeill and Lawton (1970), and Pieper (1978), NA was fixed at 0.65 (Adcock, 1982; Marchant and Hynes, 1981; Pieper, 1978; Prus, 1971). The arrangement of diet composition resulted in accordance with Marcus *et al*. (1978) and Sutcliffe *et al*. (1981).

Detritus of sediment: Poepperl (1992) determined the amount of dead organic material based on samples from eleven sampling stations. DW was converted into C using a factor of 0.5 (Gessner *et al*., 1996; Jørgensen, 1979).

3. Results

3.1. The Trophic Web

The trophic network of the macroinvertebrate community shows a clear distinction into three levels (Fig. 2), with detritus and primary producers maintaining a broad variety of benthic and invertebrate consumers. These primary consumers in turn serve as food for the upper level of highly predatory invertebrates.

The compartments '*Sialis*, Odonata, Molanna, *Polycentropus*' (TL 3.31) and 'Hirudinea, Tricladida, Hydrachnidia' (TL 3.28) are acting as a top predator of the trophic network. They are followed by several compartments showing TLs ranging from 2.55 to 2.15 (Table 3): Oligochaeta, *Hydropsyche* sp., '*Asellus*, *Gammarus*, Limoniidae', and 'Chironomidae and Ceratopogonidae'. The majority of compartments has TLs ranging from 2.1 to 2.0 along with an increasing importance of detritus and primary producers (both TL 1) in their diet: '*Theodoxus*, *Ancylus*, *Acroloxus*, *Valvata*', Sphaeriidae, collecting Trichoptera and Ephemeroptera, '*Anodonta, Pseudanodonta*', *Unio* sp., *Dreissena polymorpha,* and '*Potamopyrgus, Bithynia, Lymnaea*'.

Mean annual macroinvertebrate biomass in the stream amounted to 77.9 g C m^{-2}, mean annual macroinvertebrate production 53.0 g C m^{-2} yr^{-1} (comp. POEPPERL, 1996). Annually 0.8 g C m^{-2} were exported by insects emerging from the system (comp. POEPPERL, 2000a). Apart from the sediment detritus with a content of 676.7 g C m^{-2} and the primary producers with 90.4 g C m^{-2} compartments with a biomass > 5 g C m^{-2} (Table 1, Fig. 2) were '*Anodonta* and *Pseudanodonta*', *Unio* sp., '*Potamopyrgus, Bithynia, Lymnaea*', and *Dreissena polymorpha*. Primary production amounted to 153.7 g C m^{-2} yr^{-1} and compartments with a secondary production between 15 and 2 g C m^{-2} yr^{-1} (Fig. 2) were '*Potamopyrgus, Bithynia, Lymnaea*', *Dreissena polymorpha*, Sphaeriidae, '*Anodonta, Pseudanodonta*', 'Chironomidae and Ceratopogonidae', and Oligochaeta. The ratio of production to respiration ranged between 0.11 for the compartments '*Anodonta* and *Pseudanodonta*' as well as '*Unio* sp.' and 0.81 for '*Sialis*, Odonata, Molanna, *Polycentropus*' (Table 3).

Table 3. Selected output parameters of the food web analysis. TL: Fractional trophic level, Q/B: Consumption/biomass ratio, EE: Ecotrophic efficiency, Prod*EE: Predation mortality, R: Respiration, A: Assimilation, R/A: Ratio of respiration/assimilation, P/R: Ratio of production/respiration, Det.flow: Flow to detritus. Abbreviations of ecological groups are explained in the text.

		TL	Q/B	EE	Prod*EE g C m^{-2} yr^{-1}	R g C m^{-2} yr^{-1}	A g C m^{-2} yr^{-1}	R/A	P/R	Det.flow g C m^{-2} yr^{-1}
1	Primary producer	1.00	0.00	0.17	25.67	0.00	–	–	–	128.01
2	Theod, Ancyl, Acro, Valva	2.02	7.78	0.12	0.19	3.63	5.18	0.70	0.43	4.82
3	Potamo, Bithyn, Lymn	2.10	12.86	0.16	2.42	38.37	53.29	0.72	0.39	65.80
4	Anodonta, Pseudanod	2.07	7.50	0.05	0.28	48.59	53.99	0.90	0.11	221.06
5	Unio sp.	2.07	4.50	0.09	0.16	16.61	18.46	0.90	0.11	75.52
6	Sphaeriidae	2.06	11.11	0.02	0.13	21.83	30.19	0.72	0.38	24.48
7	Dreissena polymorpha	2.07	22.73	0.02	0.28	33.09	45.64	0.73	0.38	80.72
8	Oligochaeta	2.55	40.00	0.88	1.83	5.20	7.28	0.71	0.40	13.77
9	Chironomidae and Ceratop.	2.15	38.46	0.71	1.70	6.83	9.23	0.74	0.35	9.45
10	Hirud,Tricladida,Hydrachn	3.28	8.00	0.10	0.11	3.09	4.20	0.74	0.36	2.32
11	Trich and Ephem, c	2.07	25.00	0.62	0.36	1.50	2.10	0.71	0.40	3.01
12	Sialis, Odo, Mola, Polycen	3.31	7.71	0.53	0.49	1.13	2.05	0.55	0.81	0.94
13	Hydropsyche sp.	2.36	22.50	0.65	0.30	1.42	1.87	0.76	0.32	2.01
14	Asellus, Gammarus, Limon	2.18	21.00	0.80	0.67	2.10	2.94	0.71	0.40	5.63
15	Detritus, sed.	1.00	–	0.21	–	–	–	–	–	–

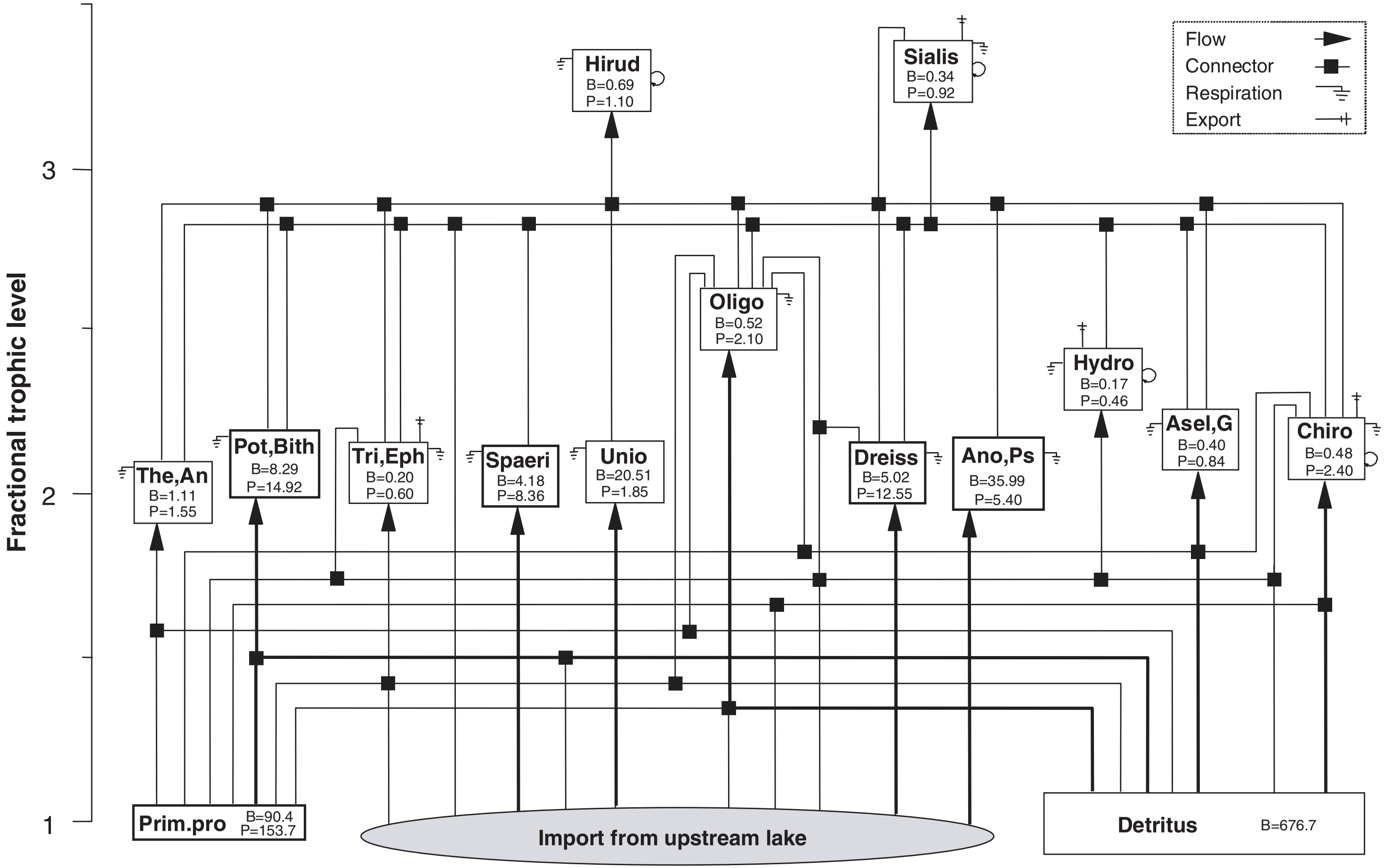

Figure 2. Trophic interactions and carbon fluxes within the benthic macroinvertebrate food web of the northern German stream 'Alte Schwentine'. The area of each box is proportional to the logarithm of the biomass [in g C /m^2] of each group. B: Biomass, P: Production, Ano,Ps: *Anodonta*, *Pseudanodonta*; Asel,G: *Asellus*, *Gammarus*, Limoniidae; Chiro: Chironomidae and Ceratopogonidae; Dreiss: *Dreissena polymorpha*; Hirud: *Hirudinea*, *Tricladida*, *Hydrachnidia*; Hydro: *Hydropsyche* sp.; Oligo: Oligochaeta; Pot,Bith: *Potamopyrgus*, *Bithynia*, *Lymnaea*; Prim.pro: Primary producer; Sialis: *Sialis*, *Odonata*, *Molanna*, *Polycentropus*; Sphaeri: Sphaeriidae; The, An: *Theodoxus*, *Ancylus*, *Acroloxus*, *Valvata*; Tri, Eph: collecting Trichoptera and Ephemeroptera. Thick lines mark flows > 5 g C m^{-2} yr^{-1} and compartments with a thick bordering have a production > 5 g C m^{-2} yr^{-1}.

3.2. Tansfer of Matter between Compartments of the Food Web

Total consumption of the macroinvertebrate community amounted to 702.6 g C m^{-2} yr^{-1}: 135.5 g C m^{-2} yr^{-1} originated from the detritus of stream sediments, 25.7 g C m^{-2} yr^{-1} from the autochthonous primary production, 532.5 g C m^{-2} yr^{-1} from the upstream lake, and 8.9 g C m^{-2} yr^{-1} from the macroinvertebrates themselves.

Main flows (>5 g C m^{-2} yr^{-1}, Fig. 2) occured between trophic level 1 and 2 and they are connected with highly productive compartments of P > 5 g C m^{-2} yr^{-1}. Inflows to compartments of greatest importance were (in g C m^{-2} yr^{-1}) '*Anodonta, Pseudanodonta*' (269.9), *Dreissena polymorpha* (114.1), '*Potamopyrgus, Bithynia, Lymnaea*' (106.6), and the filter feeding *Unio* sp. (92.3). Inflows of intermediate importance were evident for the Oligochaeta (20.8), 'Chironomidae and Ceratopogonidae' (18.5), '*Theodoxus*, *Ancylus*, *Acroloxus*, *Valvata*' (8.6), and '*Asellus*, *Gammarus*, Limoniidae' (8.4). All other functional groups had inflows lower than 6 g C m^{-2} yr^{-1} (Table 4).

Inflow to large ecological groups was 637.5 g C m^{-2} yr^{-1} to detritus and 702.6 g C m^{-2} yr^{-1} to secondary producers, with 522.8 g C m^{-2} yr^{-1} (74.2%) to filter feeding Bivalvia, 115.2 g C m^{-2} yr^{-1} (16.4%) to the Gastropoda, and 64.6 g C m^{-2} yr^{-1} (9.2%) to the remaining invertebrates. Only 29.9 g C m^{-2} yr^{-1} (4.3%) were consumed by larval insects of the stream.

Most important food resources with regard to the number of predators were the import from the upstream lake (10), detritus of sediment (7), primary producers (7), Oligochaeta (6), and the compartment of Chironomidae and Ceratopogonidae (5). 98.7% of the biomass consumed by the system originated from the compartments import (532.5 g C m^{-2} yr^{-1}), sediment detritus (135.5 g C m^{-2} yr^{-1}), and primary producers (25.7 g C m^{-2} yr^{-1}) (Table 4). Only 8.6 g C m^{-2} yr^{-1} originated from secondary producers.

The system exerted a high predation pressure (EE > 80%) only on the compartments Oligochaeta (EE = 88%) and '*Asellus* and *Gammarus*' (EE = 80%). A very low predation pressure (EE < 10%) was observed for the following groups: Sphaeriidae (EE = 2%), *Dreissena polymorpha* (EE = 2%), '*Anodonata* and *Pseudanodonta*' (EE = 5%), *Unio* sp. (EE = 9%), and 'Hirudinea and Tricladida' (EE = 10%). More than 90% of the production of these groups were recycled to the detritus pool. All other compartments showed intermediate values of EE (Table 3). 21% of material entering the detritus pool were recycled to the living groups of the system. Almost 80% (502.0 g C m^{-2} yr^{-1}) were accumulated and/or exported out of the system. Dead macrophytes contributed 20% of the material flowing back to the detritus pool from the living groups of the system. '*Anodonata* and *Pseudanodonta*' contributed 35% to the detrital pool, *Dreissena polymorpha* 13%, *Unio* sp. 12%, and '*Theodoxus*, *Ancylus*, *Acroloxus*, *Valvata*' 10%. All other groups together contributed 10% to the detrital pool.

3.3. Transfer of Matter between Discrete Trophic Levels

Because the concept of fractional trophic levels has not been used frequently for food web analyses until now (Carrer and Opitz, 1999; Heymans and Baird, 2000; Heymans and McLachlan, 1996; Monaco and Ulanowicz, 1997; Rosado-Solórzano and Guzmán del Próo, 1998) and the concept of discrete trophic levels is rather well known and widespread, fractional trophic levels (as presented in Fig. 2), have been reversed into six discrete trophic levels TL_D *sensu* Lindeman (1942) by an approach suggested by Ulanowicz (1995). Flows have been separated according to origin or destination (Fig. 3). As expected biomass is decreasing continuously with increasing trophic level. The same effect can be observed for flows. The backflow to detritus of 637.5 g C m^{-2} yr^{-1} from trophic level I to VI corresponds to the amount given previously for backflow from single compartments.

Table 4. Flow matrix of the food web analysis. Predation on a prey group is the sum of consumption values in the rows. Intake of a predator group is the sum over the corresponding column. All flows are in g C m^{-2} yr^{-1}. Abbreviations of group names are explained in the text.

Prey	Predator	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
1	Primary producer	4.32	15.99	–	–	–	–	2.08	0.92	–	1.75	–	0.19	0.42	25.67
2	Theod, Ancyl, Acro, Valva	–	–	–	–	–	–	–	–	0.11	–	0.08	–	–	0.19
3	Potamo, Bithyn, Lymn	–	–	–	–	–	–	–	–	2.21	–	0.21	–	–	2.42
4	Anodonta, Pseudanod	–	–	–	–	–	–	–	–	0.28	–	–	–	–	0.28
5	Unio sp.	–	–	–	–	–	–	–	–	0.16	–	–	–	–	0.16
6	Sphaeriidae	–	–	–	–	–	–	–	–	–	–	0.13	–	–	0.13
7	Dreissena polymorpha	–	–	–	–	–	–	–	–	0.16	–	0.08	0.04	–	0.28
8	Oligochaeta	0.09	–	–	–	–	–	–	–	1.10	0.05	0.39	0.12	0.08	1.83
9	Chironomidae and Ceratop.	–	–	–	–	–	–	–	0.37	0.66	–	0.39	0.19	0.08	1.70
10	Hirud, Tricladida, Hydrachn	–	–	–	–	–	–	–	–	0.11	–	–	–	–	0.11
11	Trich andEphem, c	–	–	–	–	–	–	–	–	0.16	–	0.16	0.04	–	0.36
12	Sialis, Odo, Mola, Polycen	–	–	–	–	–	–	–	–	0.28	–	0.21	–	–	0.49
13	Hydropsyche sp.	–	–	–	–	–	–	–	–	–	–	0.18	0.12	–	0.30
14	Asellus,Gammarus,Limon	–	–	–	–	–	–	–	–	0.28	–	0.39	–	–	0.67
15	Detritus, sed.	4.23	85.27	–	–	–	–	17.68	16.62	–	3.15	–	0.77	7.81	135.52
	Import	–	5.33	269.93	92.30	46.44	114.09	1.04	0.55	–	0.05	0.39	2.37	–	532.49
	Total	8.64	106.59	269.93	92.30	46.44	114.09	20.80	18.46	5.51	5.00	2.61	3.84	8.39	702.60

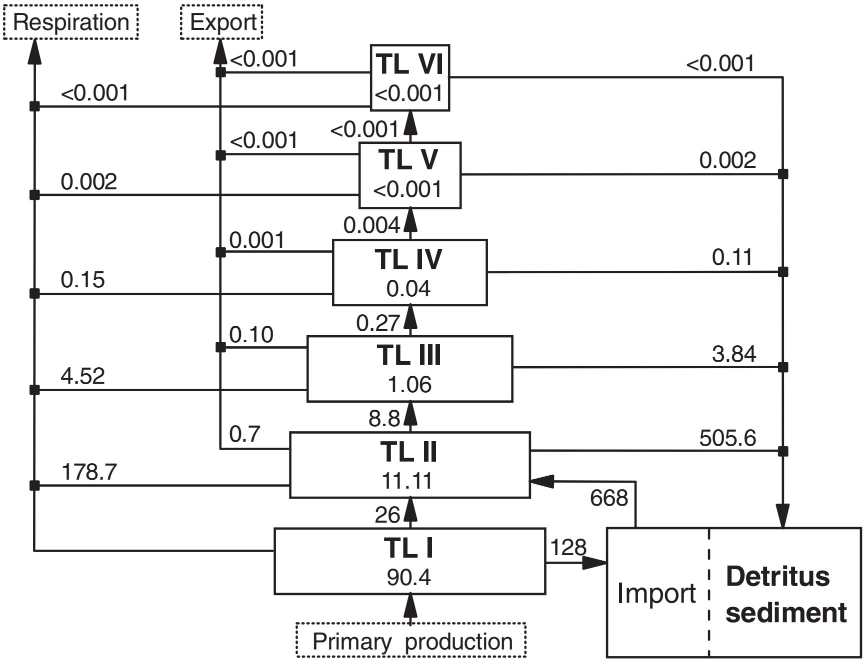

Figure 3. Transfer of matter between discrete trophic levels TL_D separated into the partial flows consumption by next trophic level, export from the system, respiration, and flow to detritus. All flows are in g C m^{-2} yr^{-1}, biomass in g C m^{-2}. The area of each box is proportional to the logarithm of biomass of each trophic level.

1,506 g C m^{-2} yr^{-1}, i.e. 98.8% of total system throughput (1,524 g C m^{-2} yr^{-1}, the sum of all flows within the food web, comp. Table 6) are confined to trophic levels I and II.

A transformation of absolute values into relative ones gives an indication of transfer efficiencies between discrete trophic levels. Efficiencies for flows originating from primary producers, from detritus, and for all flows are shown in Table 5. Transfer efficiencies between discrete trophic levels are generally low except for level II for transfer of detrital material originating from level I. After a sharp decline on TL_D IV efficiencies are constant with 2.1% and 2.2% before decreasing once again on TL_D VI. A low transfer efficiency in the grazing chain from TL_D I to II reflects the direct flow to detritus and is followed by low transfer efficiencies in higher trophic levels.

Table 5. Biomass decrease and transfer efficiencies (both in %) between discrete trophic levels. Values refer to transfer from the previous trophic level. * due to the small size of values no precise indication available.

	Discrete trophic level					
	I	II	III	IV	V	VI
Biomass	–	12.3	9.5	3.8	2.2	*
Flows originating from producers	–	3.6	1.3	2.9	0.4	–
Flows originating from detritus	–	6.7	5.8	2.1	2.3	0.2
All flows	–	6.0	5.2	2.1	2.2	0.2

4. Discussion

4.1. The Trophic Web

The secondary production exceeds considerably the values of other streams. An arrangement of macroinvertebrate biomass and secondary production living in 36 streams as well as a discussion of possible reasons for the high variation of values is found in POEPPERL (1999).

The ratio of production to respiration can be used as a check of the quality of input values. All values estimated by the model ranged between 0.11 (compartments '*Anodonta* and *Pseudanodonta*' and '*Unio* sp.') and 0.81 ('*Sialis*, Odonata, Molanna, *Polycentropus*') are in the order of magnitude reported by MCNEILL and LAWTON (1970) for 53 taxa.

4.2. Tansfer of Matter between Compartments of the Food Web

Main flows could be identified between trophic level 1 and 2 (Fig. 2; comp. PALOMARES *et al.*, 1993; ROSADO-SOLÓRZANO and GUZMÁN DEL PRÓO, 1998; MOREAU *et al.*, 2001) and are connected with highly productive compartments. The planktonic material from the upstream lake represents the most important source of food for the benthic macroinvertebrates of the investigated stream. Consequently the filter feeding '*Anodonta, Pseudanodonta', Dreissena polymorpha*, and *Unio* sp. belong to the four compartments of greatest importance concerning inflows. Inflow to primary producers, i.e. an uptake of carbon dioxide by primary producers was not considered here since the model is dealing exclusively with transfer of organic matter. With quantities lower than 6 g C m^{-2} yr^{-1} all other functional groups were of low to negligible importance in terms of size of inflow (Table 4). Only 4.3% of total consumption were consumed by larval insects of the stream whereas POEPPERL and OPITZ (unpubl. data) calculated for the littoral of the upstream lake that larval insects have a share of roughly 50% in total consumption. High biomass, secondary production, and food uptake of Bivalvia would seem to be responsible for these differences: In the stream Bivalvia contributed 74.2% to the total consumption whereas Bivalvia had a share of only 17.3% in total consumption in the upstream lake littoral.

Compared to other studies with maxima of nearly 95% (MATHEWS, 1993; PALOMARES *et al.*, 1993; POEPPERL and OPITZ, unpubl. data) the ecotrophic efficiencies of all macroinvertebrate compartments in the present model are low. Because only species composition of fish but no data on their biomass or production were available, this predatory group was left out of consideration. If fish species as top predators would be a part of the trophic model, values of ecotrophic efficiency EE of their prey compartments would be higher but would not exceed 1. Approximately 20% of carbon entering the detritus pool were recycled to the living groups of the system and almost 80% were accumulated and/or exported out of the system. This value of the EE of sediment detritus is much lower than the value for the river Thames (EE = 79%) calculated by MATHEWS (1993) and BERRIE (1972). It seems to be a result of the high density, biomass and secondary production of filter feeders which is charateristic for lake outlets (i.e., ARMITAGE, 1976; OSWOOD, 1979; POEPPERL, 1999; SHELDON and OSWOOD, 1977; WOTTON, 1988). At constant Q/B ratios the consumption of these filter feeding species accordingly has a high share of the total consumption.

The ecotrophic efficiency provides an immediate check for mass balance (CHRISTENSEN and PAULY, 1992a). If the model is not balanced, then there are negative flows to the detritus and EE are greater than one.

Based on a method developed by LEONTIEF (1951) for the economy and introduced to ecology by HANNON (1973) and HANNON and JOIRIS (1989), it becomes possible to assess not only the direct, but also the indirect effects any one compartment in the network has on any other (Ulanowicz and Puccia, 1990). In the macroinvertebrate community of the investigated stream the compartment with the highest trophic level ('Sialis, Odo, Mola, Polycen', TL = 3.31) has a negative impact on their preferred prey and a indirect, slight positive impact on the prey of their prey, such as 'Primary producer' or 'detritus, sed.' (Fig. 4). Most groups have a negative impact on themselves, reflecting increased within-group competition for resources. The mixed trophic impacts can also be regarded as a form of simple sensitivity analysis (Majkowski, 1982). Thus it can be concluded, e.g., that the impact of the mussels on any other group is negligible. Interesting is the effect an increase of 'Sialis, Odo, Mola, Polycen'-biomass and 'Hirud, Tricladida, Hydrachn'-biomass would have on other groups of the system.

Because some additional information synthesized in the model originated from literature and not from direct investigations at the stream, the sensitivity of the model was analyzed. The basic input parameters B, P/B, and Q/B were varied by –50% and +50% (in steps of

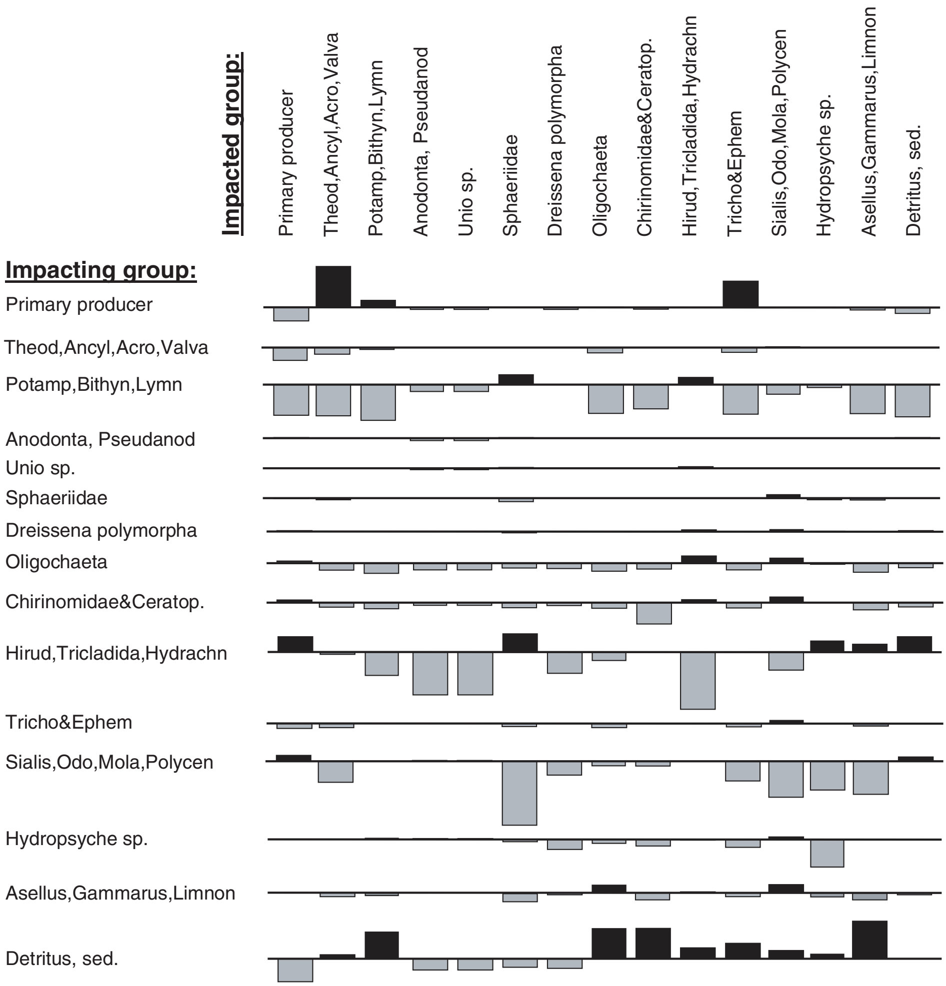

Figure 4. Representation of the direct and indirect impact that the group mentioned to the left of the histograms (rows) have on the other groups mentioned above the histograms (columns). Positive impacts are in black, negative ones in grey. The impacts are relative, but comparable between groups.

10%) for each group and the resulting percent change in each of the output parameters that are computed by the model were calculated for all other groups. The results of this analysis were summarized with a sensitivity index, which is the count of the parameters affected by ±30% or more for each group.

The mass-balance model was relatively insensitive to parameter values for most groups (Fig. 5). Varying the parameters for groups with a trophic level lower than 2.6 indicated low-medium model sensitivity. However, the analysis showed that changes in the parameters of the two groups with highest trophic level, 'Sialis, Odo, Mola, Polycen' and 'Hirud, Tricladida, Hydrachn', exert the greatest influence on the system (Fig. 5). This is the result of the wide variety of their food items whereas a cascading in the food web is only limited (CHRISTENSEN, 1995).

4.3. Transfer of Matter between Discrete Trophic Levels

98.8% of total system throughput are confined to trophic levels I and II. This value is comparable to the 98% for Palude della Rosa, a shallow water area in the Lagoon of Venice, Italy (CARRER and OPITZ, 1999), but considerably higher than the 90% calculated by POEPPERL and OPITZ (unpubl. data) for the littoral of the upstream Lake Belau. However the value calculated for the stream is still in agreement with other systems (CHRISTENSEN and PAULY, 1993a).

Summarizing the trophic situation of the stream reveals a large proportion of matter transfer in the lower levels. Carbon is scarcely passed up the trophic web. A large amount of it is recycled to the detritus pool directly from the first and second trophic level.

Since LINDEMAN (1942) it has often been assumed that trophic transfer efficiencies in ecosystems vary around 10%, so that one-tenth of matter or energy entering a trophic level is transferred to the next trophic level and that the trophic transfer efficiencies gradually decrease on higher trophic levels (CHRISTENSEN and PAULY, 1993b). Values between 6.0% and 0.2% presented here are generally low but they are in the same order of magnitude reported for the River Garonne (PALOMARES *et al.*, 1993) and the River Thames (MATHEWS, 1993). CHRISTENSEN and PAULY (1993b) compared the trophic transfer efficiencies for a number of ecosystem models (mainly marine ecosystems) and concluded, that the efficiencies are variable, because of both system- and model-specific characteristics. As described

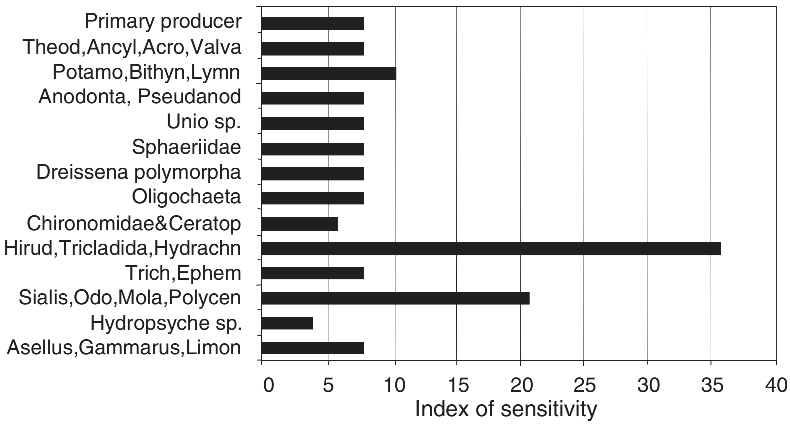

Figure 5. Sensitivity analysis results using an index of sensitivity (the count of parameters for other groups affected by 30% or more for each group).

for the investigated stream trophic efficiencies generally tend to be higher at lower trophic levels than at higher trophic levels.

4.4. System Summary Statistics and Conclusions

The selection of summary statistics for the macroinvertebrate community listed in Table 6 gives an impression of the size of total system flows such as consumption, exports, respiratory flows, flows into detritus, system throughput, and production. In addition the model provides information that may allow to assess the 'developmental status' of an ecosystem in terms of maturity and to compare different ecosystems (see CHRISTENSEN and PAULY, 1992a).

Of the total system throughput, 12% was due to respiratory processes and 42% passed through the detritus. The total carbon flow through detritus is larger than the net primary production. The community is therefore dominated by the carbon flow through detritus. MATHEWS (1993) reported a corresponding result for the River Thames (comp. BERRIE, 1972). System biomass, production and consumption is high compared to the River Thames (MATHEWS, 1993), the River Garonne (PALOMARES *et al.*, 1993), and the mountain stream Steina (POEPPERL and MEYER, 1999). Therefore the lake outlet can be classified as a very productive system. Summarising the trophic situation of the macroinvertebrate community of the outlet of Lake Belau it reveals a large transfer of matter in the lower levels. The overall system is to a large extent based on consumption of detritus and – in the present case particulary – imported organic material from the upstream lake. Matter is only moderately passed up the trophic web, a large amount of it being recycled to the detritus pool.

The ratio of primary production to respiration ($P_P/R = 0.84$) is relative low compared to other studies. CHRISTENSEN and PAULY (1993b) as well as LEWIS (1981) found P_P/R ratios for 25 and 41 ecosystems respectively ranging in the majority from 0.8 to 3.2. The P_P/R ratio of the lake outlet presented here is close to the lower limit of this range. ODUM (1969, 1971) described how this ratio would develop as systems become more mature: $P_P/R > 1$ in early stages of ecological succession (immature systems), $P_P/R < 1$ in cases of organic pollution, and $P_P/R = 1$ in mature systems. The primary production of immature system would grossly exceed total respiration (CHRISTENSEN and PAULY, 1993b) and therefore the investigated stream would be classified to be mature. Other parameters and ratios (Table 6) yield contra-

Table 6. Selected summary statistics for the macroinvertebrate community in the outlet of Lake Belau.

Sum of all consumption [g C m^{-2} yr^{-1}]	702.60
Sum of all exports [g C m^{-2} yr^{-1}]	0.78
Sum of all respiratory flows [g C m^{-2} yr^{-1}]	183.38
Sum of all flows into detritus [g C m^{-2} yr^{-1}]	637.54
Total system throughput [g C m^{-2} yr^{-1}]	1,524.30
Sum of all production [g C m^{-2} yr^{-1}]	206.71
Calculated total net primary production [g C m^{-2} yr^{-1}]	153.68
Total primary production/total respiration	0.84
Net system production [g C m^{-2} yr^{-1}]	29.70
Total primary production/total biomass	0.91
Total biomass/total throughput	0.11
Total biomass (excluding detritus) [g C m^{-2}]	168.30
Connectance Index	0.36
System Omnivory Index	0.01

dictory estimates about the developmental stage and maturity of the trophic web. This subject will be discussed in the future together with additional model applications. In this context the model presented here may be integrated into a model complex in the future describing trophic interactions between subsystems of the Bornhöved Lake Region such as littoral (Poepperl and Opitz, unpubl. data), pelagial, and lake outlet. The investigations may also lead to a detailed quantification of trophic interactions between aquatic subsystems.

5. Acknowledgements

The studies are supported by the Bundesministerium fuer Bildung und Forschung BMBF (Federal Ministry for Education and Research) and by the State of Schleswig-Holstein. The investigations were carried out at the Ecology Center of the Christian-Albrechts-Universität Kiel.

6. References

Adcock, J. A., 1982: Energetics of a population of *Asellus aquaticus* (Crustacea: Isopoda): respiration and energy budgets. – Freshwat. Biol. **12**: 257–269.

Abarca-Arenas, L. G. and R. E. Ulanowicz, 2002: The effects of taxonomic aggregation on network analysis. – Ecol. Model. **149**: 285–296.

Armitage, P. D., 1976: A quantitative study of the invertebrate fauna of the River Tees below Cow Green Reservoir. – Freshwat. Biol. **6**: 229–240.

Armitage, P. D., 1977: Invertebrate drift in the regulated River Tees, and an unregulated tributary Maize Beck, below Cow Green dam. – Freshwat. Biol. **7**: 167–183.

Barton, D. R. and J. L. Metcalfe, 1986: Life cycles, reproduction, and diets of *Dina dubia* and *Erpobdella punctata* (Hirudinea: Erpobdellidae) in Canagagigue Creek, Ontario. – Can. J. Zool. **64**: 640–648.

Benke, A. C. and J. B. Wallace, 1980: Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. – Ecology **61**: 108–118.

Benke, A. C., 1993: Concepts and patterns of invertebrate production in running waters. – Verh. Internat. Verein. Limnol. **25**: 15–38.

Benke, A. C. and D. I. Jacobi, 1994: Production dynamics and resource utilization of snag-dwelling mayflies in a blackwater river. – Ecology **75**: 1219–1232.

Benke, A. C. and J. B. Wallace, 1997: Trophic basis of production among riverine caddisflies: Implications for food web analysis. – Ecology **78**: 1132–1145.

Berrie, A. D., 1972: The occurrence and composition of seston in the River Thames and the role of detritus as an energy source for secondary production in the river. – Mem. Ist. Ital. Idrobiol. Suppl. **29**: 473–483.

Blandenier, P. and N. Perrin, 1989: A comparison of the energy budget of two freshwater Pulmunates: *Lymnaea peregra* (Müller) and *Physa acuta* (Drap.). – Rev. suisse Zool. **96**: 325–333.

Brinkhurst, R. O. and M. J. Austin, 1979: Assimilation by aquatic Oligochaeta. – Int. Revue ges. Hydrobiol. **64**: 245–250.

Brown, D. S., 1961: The morphology and functioning of the mouthparts of *Chloeon dipterum* L. and *Baetis rhodani* Pictet (Insecta, Ephemeroptera). – Proc. Zool. Soc. Lond. **136**: 147–176.

Carrer, S. and S. Opitz, 1999: Trophic Network Model of a Shallow Water Area in the Northern Part of the Lagoon of Venice. – Ecol. Model. **124**: 193–219.

Christensen, V. and D. Pauly, 1992a: A guide to the Ecopath II software system (version 2.1). – Int. Center Living Aquat. Resources Managem. Software **6**: 72 pp.

Christensen, V. and D. Pauly, 1992b: Ecopath II – A software for balancing steady-state models and calculation network charactersistics. – Ecol. Model. **61**: 169–185.

Christensen, V. and D. Pauly, eds., 1993a: Trophic models of aquatic ecosystems. – Int. Center Living Aquat. Resources Managem. Conf. Proc. **26**: 390 pp.

Christensen, V. and D. Pauly, 1993b: Flow characteristics of aquatic ecosystems. – Int. Center Living Aquat. Resources Managem. Conf. Proc. **26**: 338–352.

CHRISTENSEN, V., 1995: A model of trophic interactions in the North Sea in 1981, the year of stomach. – Dana **11**: 1–28.

CUSHING, C. E., 1963: Filter-feeding insect distribution and planktonic food in the Montreal River. – Trans. Am. Fish. Soc. **92**: 216–219.

EDINGTON, J. M. and A. G. HILDREW, 1981: Caseless caddis larvae of the British Isles with notes on their ecology. – Freshwat. Biol. Ass. Sci. Publ. **43**: 91 pp.

ENGELMANN, M. D., 1966: Energetics, terrestrial field studies, and animal productivity. – Adv. Ecol. Res. **3**: 73–115.

FISHER, S. G. and L. J. GRAY, 1983: Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. – Ecology **64**: 1217–1224.

FRENZEL, P., 1979: Untersuchungen zur Biologie und Populationsdynamik von *Potamopyrgus jenkinsi* (SMITH) (Gastropoda: Prosobranchia) im Litoral des Bodensees. – Arch. Hydrobiol. **85**: 448–464.

GESSNER, M. O., B. SCHIEFERSTEIN, U. MÜLLER, S. BARKMANN and U. A. LENFERS, 1996: A partial budget of primary organic carbon flows in the littoral zone of a hardwater lake. – Aquatic Bot. **55**: 93–105.

GIBSON, R. J. and D. GALBRAITH, 1975: The relationship between invertebrate drift and salmonid populations in the Metamek River, Quebec, below a lake. – Trans. Am. Fish. Soc. **104**: 529–535.

HANNON, B., 1973: The structure of ecosystems. – J. Theor. Biol. **41**: 535–546.

HANNON, B. and C. JOIRIS, 1989: A seasonal analysis of the southern North Sea ecosystem. – Ecology **70**: 1916–1934.

HAYNES, A. and B. J. R. TAYLOR, 1984: Food finding and food preference in *Potamopyrgus jenkinsi* (E. A. SMITH) (Gastropoda: Prosobranchia). – Arch. Hydrobiol. **100**: 479–491.

HEYMANS, J. J. and A. MCLACHLAN, 1996: Carbon budget and network analysis of a high-energy beach/surf-zone ecosystem. – Estuar. Coast. Shelf Sci. **43**: 485–505.

HEYMANS, J. J. and D. BAIRD, 2000: Network analysis of the northern Benguela ecosystem by means of NETWRK and Ecopath. – Ecol. Model. **131**: 97–119.

HIGLER, L. W. G., 1978: Observations on caddis larvae in Stratiotes vegetation. – Proc. 2nd Int. Symp. Trichoptera **1977**: 309–315.

HILDREW, A. G. and C. R. TOWNSEND, 1976: The distribution of two predators and their prey in an iron rich stream. – J. Anim. Ecol. **45**: 41–57.

HORNBACH, D. J., T. E. WISSING and A. J. BURKY, 1984: Energy budget for a stream population of the freshwater clam, *Sphaerium striatinum* LAMARCK (Bivalvia: Pisiidae). – Can. J. Zool. **62**: 2410–2417.

HYNES, H. B. N., 1970: The ecology of running water. University of Toronto Press, Toronto, Ontario, 555 p.

HYNES, H. B. N., 1971: Benthos of flowing water. – *In:* W. T. EDMONDSON and G. G. WINBERG (ed.), A manual on methods for the assessment of secondary productivity in freshwaters: IBP Handbook **17**: 66–74.

ILLIES, J., 1956: Seeausfluss-Biozönosen lappländischer Waldbäche. – Ent. Tidskr. **77**: 138–153.

IVERSEN, T. M., 1988: Secondary production and trophic relationships in a spring invertebrate community. – Limnol. Oceanogr. **33**: 582–592.

IVLEV, V. S., 1953: Transformation of energy by aquatic animals. Coefficient of energy consumption by *Tubifex tubifex* (Oligochaeta). – Int. Revue ges. Hydrobiol. **38**: 449–458.

JACOBSEN, D. and K. SAND-JENSEN, 1994: Growth and energetics of a trichopteran larva feeding on fresh submerged and terrestrial plants. – Oecologia **97**: 412–418.

JONES, J. R. E., 1950: A further ecological study of the river Rheidol: the food of the common insects of the main-stream. – J. Anim. Ecol. **19**: 159–174.

JØRGENSEN, S. E., 1979, ed.: Handbook of environmental data and ecological parameters. – Pergamon Press, Oxford, England. (= Environmental Science and Applications **6**) 1162 pp.

LANDMESSER, B., 1993: Untersuchungen zur Struktur und zur Primärproduktion des Phytoplanktons im Belauer See. – PhD thesis Hamburg, 181 pp.

LAWTON, J. H., 1970: Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (SULZ.) (Odonata: Zygoptera). – J. Anim. Ecol. **39**: 669–698.

LEONTIEF, W. W., 1951: The structure of the U.S. economy. – 2nd ed., Oxford University Press, New York.

LEWANDOWSI, K. and A. STANCZYKOWSKA, 1975: The occurence and role of bivalves of the family Unionidae in Mikolajskie Lake. – Ekol. pol. **23**: 317–334.

LEWIS, J. B., 1981: Coral reef ecosystems. – *In*: A. R. LONGHURST (ed.), Analysis of marine ecosystems (ed): Academic Press, New York: 127–158.

Lindeman, R. L., 1942: The trophic-dynamic aspect of ecology. – Ecology **23**: 399–418.
Majkowski, J., 1982: Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. – Int. Center Living Aquat. Resources Managem. Conf. Proc. **9**: 149–165.
Manokov, A. V. and Y. I. Sorokin, 1972: Some results on investigations on nutrition of water animals. – *In*: Z. Kajak and A. Hillbricht-Ilkowska (ed.), Productivity problems of freshwaters: Polish Scientific Publishers, Warszawa, Poland: 765–773.
Marchant, R. and H. B. N. Hynes, 1981: Field estimates of feeding rate for *Gammarus pseudolimnaeus* (Crustacea: Amphipoda) in the Credit River, Ontario. – Freshwat. Biol. **11**: 27–36.
Marcus, J. H., D. W. Sutcliffe and L. G. Willoughby, 1978: Feeding and growth of *Asellus aquaticus* (Isopoda) of food items from the littoral of Windermere, including green leaves of *Elodea canadensis*. – Freshwat. Biol. **8**: 505–519.
Mathews, C. P., 1993: Productivity and energy flows at all trophic levels in the River Thames, England: Mark 2. – Int. Center Living Aquat. Resources Managem. Conf. Proc. **26**: 161–171.
Mayer, K., 1934: Die Nahrung der Ceratopogonidenlarven (Dipt.). – Arch. Hydrobiol. **27**: 564–570.
McNeill, S. and J. H. Lawton, 1970: Annual production and respiration in aminal populations. – Nature **225**: 472–474.
Monaco, M. E. and R. E. Ulanowicz, 1997: Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. – Mar. Ecol. Prog. Ser. **161**: 239–254.
Moreau, J., K. Mavuti and T. Daufresne, 2001: A synoptic Ecopath model of biomass flows during two different static ecological situations in Lake Nakuru (Kenya). – Hydrobiol. **458**: 63–74.
Odum, E. P., 1969: The strategy of ecosystem development. – Science **104**: 262–270.
Odum, E. P., 1971: Fundamentals of Ecology. – Saunders, Philadelphia, USA.
Odum, W. E. and E. J. Heald, 1975: The detritus-based food web of an estuarine mangrove community. – *In*: L. E. Cronin (ed.), Estuarine research. Vol. 1: Academic Press, New York: 265–286.
Okey, T. A. and D. Pauly, 1999: A mass-balanced model of trophic flows in Prince William Sound: Decompartmentalizing ecosystem knowledge. – Ecosystem Approaches for Fish. Managem. **99–01**: 621–635.
Opitz, S., 1996: Trophic interactions in Caribbean coral reefs. – Int. Center Living Aquat. Resources Managem. Techn. Rep. **43**: 1–341.
Oswood, M. W., 1979: Abundance patterns of filter-feeding caddisflies (Trichoptera: Hydropsychidae) and seston in a Montana (U.S.A.) lake outlet. – Hydrobiologia **63**: 177–183.
Otto, C., 1974: Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph.) (Trichoptera) in a south swedish stream. – J. Anim. Ecol. **43**: 339–361.
Palomares, M. L., B. Yulianto, L. Puy, D. Bengen and A. Belaud, 1993: A preliminary model of the Garonne River (Toulouse, France) ecosystem in spring. – Int. Center Living Aquat. Resources Managem. Conf. Proc. **26**: 161–171.
Pieper, H.-G., 1978: Ökophysiologische und produktionsbiologische Untersuchungen an Jugendstadien von *Gammarus fossarum* Koch 1835. – Arch. Hydrobiol. Suppl. **54**: 257–327.
Poepperl, R., 1991: Die Biozönose eines durch Stauhaltung geregelten Seeabflusses – dargestellt am Beispiel der benthischen Makroinvertebraten in der Alten Schwentine zwischen Belauer und Stolper See (Schleswig-Holstein). – PhD thesis Univ. Kiel, 188 pp.
Poepperl, R. and K.-P. Witzel, 1991: Ökosystemforschung Bornhöveder Seenkette: Stand der Grundlagenerfassung im Belauer See. – Verh. Ges. Ökol. **20**: 137–147.
Poepperl, R., 1992: Die Besiedlung und Vergesellschaftung der Makroinvertebraten in einem Seeabfluß des Norddeutschen Tieflandes, der Alten Schwentine zwischen Belauer und Stolper See (Schleswig-Holstein). – Drosera **92**: 186–209.
Poepperl, R. and P. Martin, 1995: Die Wassermilben (Hydrachnidia, Acari) eines norddeutschen Seeabflusses (Belauer Sees, Schleswig-Holstein). – Faun.-ökol. Mitteil. **7**: 61–72.
Poepperl, R., 1996: The structure of macroinvertebrate community in a Northern German lake outlet (Lake Belau, Schleswig-Holstein) with special emphasis on abundance, biomass and secondary production. – Int. Revue ges. Hydrobiol. **81**: 183–198.
Poepperl, R., 1998: Biomass determination of aquatic invertebrates in the Northern German lowland using the relationship between body length and dry mass. – Faun.-ökol. Mitt. **7**: 379–386.
Poepperl, R., 1999: Functional feeding groups of a macroinvertebrate community in a Northern German lake outlet (Lake Belau, Schleswig-Holstein). – Limnologica **29**: 137–145.
Poepperl, R. and E. I. Meyer, 1999: Ein quantitatives Nahrungsnetz-Modell für einen Mittelgebirgsbach (Steina, Schwarzwald). – Tagungsbericht Dt. Ges. Limnol. (1988), 858–860.

POEPPERL, R., 2000a: Benthic secondary production and biomass of insects emerging from a lake-outflow stream. – Freshwat. Biol. **44**: 199–211.

POEPPERL, R., 2000b: The filter feeders *Hydropsyche angustipennis* and *H. pellucidula* (Trichoptera: Hydropsychidae) in a northern German lowland stream: Microdistribution, larval development, emergence pattern, and secondary production. – Limnologica **30**: 65–72.

POEPPERL, R., W. KLUGE, G. SCHERNEWSKI, C.-D. GARBE-SCHÖNBERG and W. NELLEN, 2001: Spatio and temporal variabilities of limnological processes in the Bornhöved Lake Region. – *In*: TENHUNEN, J. D.; LENZ, R. and R. E. HANTSCHEL (eds.), Ecosystem approaches to landscape management in Central Europe: Ecological Studies 147, Springer-Verlag, Berlin, Heidelberg, New York: 117–161.

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

POWER, M. E. and W. E. DIETRICH, 2002: Food webs in river networks. – Ecol. Res. **17**: 451–471.

PRUS, T., 1971: The assimilation efficiency of *Asellus aquaticus* L. (Crustacea, Isopoda). – Freshwat. Biol. **1**: 287–305.

REYNOLDSON, T. B. and J. O. YOUNG, 1965: Food supply as a factor regulating population size in freshwater triclads. – Mitt. Internat. Verein. Limnol. **13**: 3–20.

REYNOLDSON, T. B. and P. BELLAMY, 1975: Triclads (Turbellaria: Tricladida) as predators of lake-dwelling stonefly and mayfly nymphs. – Freshwat. Biol. **5**: 305–312.

ROSADO-SOLÓRZANO, R. and S. A. GUZMÁN DEL PRÓO, 1998: Preliminary trophic structure model for Tampamachoco lagoon, Veracruz, Mexiko. – Ecol. Model. **109**: 141–154.

SALONEN, K., J. SARVALA, I. HAKALAND and M.-L. VILJANEN, 1976: The relation of energy and organic carbon in aquatic invertebrates. – Limnol. Oceanogr. **21**: 724–730.

SCHERNEWSKI, G., 1992: Raumzeitliche Prozesse und Strukturen im Wasserkörper des Belauer Sees. – EcoSys Suppl. **1**: 160 pp.

SCHIEFERSTEIN, B., 1997: Ökologische und molekularbiologische Untersuchungen an Schilf (*Phragmites australis* (CAV.) TRIN. ex STEUD.) im Bereich der Bornhöveder Seenkette. – EcoSys Suppl. **22**: 143 pp.

SCHÖNBORN, W., 1987: Secondary production and energy transfer in the polluted river Saale (Thuringia, Southern GDR). – Int. Revue ges. Hydrobiol. **72**: 539–557.

SCHÖNBORN, W., 1992: Fließgewässerbiologie. Fischer Verlag, Jena.

SCHÖNBORN, W., 1998: Changes of biological time patterns and of energy transfer on exposed slides and stone surface (boundary layers with fractel structures) by organic pollution in a oligotrophic stream (Ilm, Thuringia, Germany). – Limnologica **28**: 347–361.

SCHRÖDER, P., 1976: Zur Nahrung der Larvenstadien der Köcherfliege *Hydropsyche instabilis* (Trichoptera: Hydropsychidae). – Ent. Germ. **3**: 260–264.

SCHRÖDER, P., 1988: Quantitative Aspekte zur Ernährungsbiologie passiver Filtrierer (Larven der Simuliidae, Chironomiden und netzbauenden Trichopteren). – Arch. Hydrobiol. Suppl. **77**: 183–270.

SCHWENK, W. and J. SCHWOERBEL, 1973: Untersuchungen zur Ernährungsbiologie und Lebensweise der Flußmützenschnecke *Ancylus fluviatilis* (O. F. MÜLLER 1774; Gastropoda Basommatophora). – Arch. Hydrobiol. Suppl. **2**: 190–321.

SCHWOERBEL, J., 1972: Produktionsbiologische Aspekte in Fließgewässern. – Verh. dt. Zool. Ges. **65**: 57–64.

SCHWOERBEL, J., 1987: Einführung in die Limnologie. Stuttgart.

SEABY, R. M. H., A. J. MARTIN and J. O. YOUNG, 1996: Food partitioning by lake-dwelling triclads and glossiphoniid leeches: Field and laboratory experiments. – Oecologia **106**: 544–550.

SHELDON, A. L. and M. W. OSWOOD, 1977: Blackfly (Diptera: Simuliidae) abundance in a lake outlet: test of a predictive model. – Hydrobiologia **56**: 113–120.

SLACK, H. D., 1936: The food of caddis fly (Trichoptera) larvae. – J. Anim. Ecol. **5**: 105–115.

SMOCK, L. A., E. GILINSKY and D. L. STONEBURNER, 1985: Macroinvertebrate production in a southeastern United States blackwater stream. – Ecology **66**: 1491–1503.

SMOCK, L. A., J. E. GLADDEN, J. L. RIEKENBERG, L. C. SMITH and C. R. BLACK, 1992: Lotic macroinvertebrate production in three dimensions: channel surface, hyporheic, and floodplain environments. – Ecology **73**: 876–886.

SOLEM, J. O., 1983: Identification of the Norwegian larvae of the genus *Potamophylax* WALLENGREN, 1891 (Trichoptera, Limnephilidae), with data on life histories, habitats and food in the Kongsvoll area, Dovrefjell mountains, Central Norway. – Fauna norv. Ser. B. **30**: 69–76.

SPENCE, J. A. and H. B. N. HYNES, 1971: Differences in benthos upstream and downstream of an impoundment. – J. Fish. Res. Bd. Canada **28**: 35–43.

Stanczykowska, A., W. Lawacz and J. Mattice, 1975: Use of field measurements of consumption and assimilation in evaluation of the role of *Dreissena polymorpha* Pall. in a lake ecosystem. – Pol. Arch. Hydrobiol. **22**: 509–520.

Stanczykowska, A., 1977: Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. – Pol. Arch. Hydrobiol. **24**: 461–530.

Statzner, B., 1979: Der Obere und Untere Schierenseebach (Schleswig-Holstein). Strukturen und Funktionen in zwei Norddeutschen See-Ausflußsystemen, unter besonderer Berücksichtigung der Makroinvertebraten. – PhD thesis Univ. Kiel, 551 pp.

Statzner, B., 1981: A method to estimate the population size of benthic macroinvertebrates in streams. – Oecologia **51**: 157–161.

Streit, B., 1975a: Experimentelle Untersuchungen zum Stoffhaushalt von *Ancylus fluviatilis* (Gastropoda – Basommatophora). 1. Ingestion, Assimilation, Wachstum und Eiablage. – Arch. Hydrobiol. Suppl. **47**: 458–514.

Streit, B., 1975b: Experimentelle Untersuchungen zum Stoffhaushalt von *Ancylus fluviatilis* (Gastropoda – Basommatophora). 2. Untersuchungen über Einbau und Umsatz des Kohlenstoffs. – Arch. Hydrobiol. Suppl. **48**: 1–46.

Streit, B., 1976: Energy flow in four different field populations of *Ancylus fluviatilis* (Gastropoda – Basommatophora). – Oecologia **22**: 261–273.

Sutcliffe, D. W., T. R. Carrick and L. G. Willoughby, 1981: Effects of diet, body size, age and temperature on growth rates in the amphipod *Gammarus pulex*. – Freshwat. Biol. **11**: 183–214.

Tachet, H., 1971: Aspects descriptifs du comportement alimentaire chez la larve de *Plectrocnemia conspersa* (Trichoptera, Polycentropodidae). – Z. Tierpsychol. **28**: 175–184.

Tashiro, J. S. and S. D. Colman, 1982: Filter-feeding in the freshwater prosobranch snail *Bithynia tentaculata*: Bioenergetic partitioning of ingested carbon and nitrogen. – Amer. Midl. Nat. **107**: 114–125.

Thompson, D. J., 1978: The natural prey of larvae of the damselfly, *Ischnura elegans* (Odonata: Zygoptera). – Freshwat. Biol. **8**: 377–384.

Thompson, R. M. and C. R. Townsend, 2000: Is resolution the solution?: the effect of taxonomic resolution on the calculated properties of three stream food webs. – Freshwat. Biol. **44**: 413–422.

Tilly, L. J., 1968: The structure and dynamics of Cone spring. – Ecol. Monogr. **38**: 169–197.

Townsend, C. R., R. M. Thompson, A. R. McIntosh, C. Kilroy, E. Edwards and M. R. Scarsbrook, 1998: Disturbance, resource supply, and food-web architecture in streams. – Ecol. Letters **1**: 200–209.

Ulanowicz, R. E. and C. J. Puccia, 1990: Mixed trophic impacts in ecosystems. – Coenoses **5**: 7–16.

Ulanowicz, R. E., 1995: Ecosystem trophic foundations: Lindeman exonerata. – *In*: Patten, B. C. and S. E. Jørgensen (ed.), Complex ecology: the part-whole relation in ecosystems: Prentice Hall PTR, New Jersey: 549–560.

Ulfstrand, S., 1968: Benthic animal communities in Lapland streams. – Oikos Suppl. **10**: 1–120.

Wallace, J. B., A. C. Benke, A. H. Lingle and K. Parsons, 1987: Trophic pathways of microinvertebrate primary consumers in subtropical blackwater streams. – Arch. Hydrobiol. Suppl. **74**: 423–451.

Walz, N., 1978a: Die Produktion der *Dreissena*-Population und deren Bedeutung im Stoffkreislauf des Bodensees. – Arch. Hydrobiol. **82**: 482–499.

Walz, N., 1978b: Growth rates of *Dreissena polymorpha* Pallas under laboratory and field conditions. – Verh. Internat. Verein. Limnol. **20**: 2427–2430.

Wotton, R. S., 1988: Very high secondary production at a lake outlet. – Freshwat. Biol. **20**: 341–346.

Wotton, R. S., 1994: Particulate and dissolved organic matter as food. – *In*: R. S. Wotton (ed.), The biology of particals in aquatic ecosystems; CRC, Boston MA. 2nd edition: 235–288.

Xiang, J., P. Schröder and J. Schwoerbel, 1984: Phänologie und Nahrung der Larven von *Hydropsyche angustipennis* und *H. siltalai* (Trichoptera, Hydropsychidae) in einem Seeabfluß. – Arch. Hydrobiol. Suppl. **66**: 255–292.

Manuscript received January 9th, 2003; revised April 28th, 2003; accepted April 29th, 2003