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The role of zoobenthos in energy flow in two shallow lakes

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Abstract

Net production of zoobenthos in two shallow and eutrophic lakes, *i.e.* the S-basin of Mývatn, Iceland (maximum depth 4.2 m, mean depth 2.3 m) and Hjarbæk Fjord, Denmark (maximum depth 6.5 m, mean depth 1.9 m) were calculated as 878 and 1093 kJ m^{-2} yr^{-1}, respectively. The zoobenthos in both lakes was dominated by Chironomidae (Diptera) living partly as filtrators feeding on suspended particles (phytoplankton) and partly as surface feeders foraging on benthic algae and/or seston. Respiration and consumption were estimated from the literature. Net production efficiency averaged 0.41 and 0.48 in Hjarbæk Fjord and Mývatn, respectively. Ingestion was dominated by herbivorous chironomids, while detritivorous tubificids were insignificant. Zoobenthic production made up 86% of total secondary production (zooplankton plus zoobenthos) in both lakes. The trophic efficiency between net primary production and benthic net secondary production was 8% and 11% in Hjarbæk Fjord and Lake Mývatn S-basin, respectively.

Introduction

Knowledge of population dynamics, production, respiration and feeding of the dominant species at all trophic levels is required to explain the structure and energy flow in ecosystems. Numerous studies (cited e.g. by Waters, 1977; Benke, 1984) have advanced understanding of the energetics of single species, but very few studies consider energy flow through entire communities. Particularly energy flow through benthic communities has been poorly investigated. It is extremely difficult and time consuming to estimate even the basic parameters of zoobenthic populations because of methodological problems. Therefore, most of the existing lacustrine ecosystem studies deal with a single depth zone only (references in Lindegaard, 1989, 1992a). Lindegaard & Jónasson (1979) and Lindegaard & Jónsson (1987) studied population dynamics and production ecology of zoobenthos in two shallow lakes: Mývatn in Iceland and Hjarbæk Fjord in Denmark. In these lakes the uniform soft bottom substrate covered about 95% of the total lake area and we assumed that the results reflected the energy flow of the whole lake ecosystem.

On the basis of this material, it was possible to construct, by indirect means, energy budgets for the entire zoobenthic community in both Mývatn and Hjarbæk Fjord.

The study areas

Lake Mývatn is situated in N-Iceland (65 °N and 17 °W) at 278 m a.s.l. The lake has two basins: the N-basin is 8.2 km^2 with a mean depth of 1.1 m, and the S-basin is 29.1 km^2 with a mean depth of 2.3 m and a maximum depth of 4.2 m. Inflow of water is mainly from cold and warm springs along the east shore. It is discharged to the west at a rate of 33 m^3 s^{-1}. Retention time in the S-basin is 24 days. The temperature of inflowing water ranged from 5.2–23.1 °C during 1972–73 and was thus considerably higher than the mean temperature of the area, 2.2°c. Water temperatures correlated well with air temperature, and the highest recorded water temperature was about 18 °C. However, highest average monthly temperature was 12.4 °C (Table 1). Average ice-cover was 190 d yr^{-1}, and an inverse thermocline developed in winter with short periods of oxygen depletion.

Phytoplankton gross production averaged 118 g C m^{-2} yr^{-1} in the S-basin during 1971–76 (Jónasson & Adalsteinsson, 1979). High production due to *Anabaena flos-aquae* (Lyngb.) Bréb. occurred during summer. Net phytoplankton production was estimated to 2500 kJ m^{-2} yr^{-1} (Jónasson, 1979). Net production of benthic diatoms amounted 9200 kJ m^{-2} yr^{-1} (Jónasson, 1979), while a dimlight adapted *Cladophora aegagropila* (L.) Rabenh. yielded a net production of 2100 kJ m^{-2} yr^{-1} (Hunding, 1979; Jónasson, 1979). Macro- and epiphytes were important only in the N-basin. A living substratum of *Cladophora* stabilizes the sediment in the S-basin and acts as a sieve for resuspended organic matter. A close relationship was found between substrate type and zoobenthos abundance and production. Chironomids dominated the *Cladophora* substrate making up about 90% of the total zoobenthic production of 878 kJ m^{-2} yr^{-1}. Zooplankton produced on an averaged 180 kJ m^{-2} yr^{-1}. Further details of Lake Mývatn are given by Jónasson (1979) and Jónasson & Lindegaard (1988).

Table 1. Monthly average temperature (°C) and annual number of degree days (dd) in Lake Mývatn and Hjarbæk Fjord.

Month	Mývatn	Hjarbæk Fjord
January	0.6	0.0
February	0.7	0.5
March	1.4	1.7
April	3.2	6.0
May	7.9	8.9
June	10.1	18.1
July	12.4	15.9
August	9.8	17.2
September	7.2	15.5
October	2.5	8.1
November	0.4	6.0
December	0.5	2.0
Number of dd	1740	3050

Hjarbæk Fjord is situated in Jutland, Denmark (57°N, 9°E) and covers an area of 24.8 km^2. Maximum depth is 6.5 m, but more than 90% of the lake is shallower than 3 m resulting in an average depth of 1.9 m. Before 1966, the 'lake' was connected to the brackish Limfjord by a 200 m narrow strait. This communication was removed by the construction of a dam, and a sluice gate prevented intrusion of brackish water from the Limfjord. The dam construction resulted in reduced salinity; from 7–9‰ to less than 1‰ within a few years. A limited area (1.5 km^2) close to the sluice gate contained bottom water of higher salinity (up to 5‰), which was isolated from the outflowing freshwater by a stable chemocline. Recently the sluice gate has been locked open in order to reestablish the brackish water environment. This investigation considers the period 1981 to 1982, during the freshwater conditions.

Four large tributaries provided most of the water input to the lake, giving a renewal time of about seven weeks. Sewage and agricultural run off resulted in high concentrations of nutrients and gross phytoplankton production was estimated at approximately 400 to 500 g C m^{-2} yr^{-1} (Rasmussen, 1982; Lindegaard & Jónsson, 1987). Macrophytes were practically absent, and benthic periphyton was assumed to be of minor importance, as transparency during the growth season normally was less than 0.5 m. Dissolved oxygen was typically above 100% saturation throughout the water column, though it might fall below 10% saturation during windless periods. The saline bottom water, close to the sluice gate, was usually anoxic.

The bottom substrate, except in the deep area near to the sluice gate, consisted of sand with only a thin layer of detritus. This substrate provided stable conditions for a large population of invertebrates consisting primarily of chironomids. Total zoobenthic production was estimated to 1093 kJ m^{-2} yr^{-1}. The zooplankton production was estimated to about 200 kJ m^{-2} yr^{-1}. Further details on Hjarbæk Fjord are given by Lindegaard & Jónsson (1983, 1987), Olrik *et al.* (1984) and Rasmussen (1990).

Materials and methods

The estimates of energy flow through the zoobenthos of Mývatn and Hjarbæk Fjord are based on the calculation of biomass and production made by Lindegaard & Jónasson (1979) and Lindegaard & Jónsson (1987) assuming ash free dry weight has an energy content of 25 kJ g^{-1} (Cummins & Wuycheck, 1971). Respiration of the dominant taxa was calculated from equations obtained from respiration experiments on zoobenthos from Lake Esrom, Denmark (Hamburger & Dall, 1990), adjusted to actual temperatures measured in Mývatn and Hjarbæk Fjord, respectively (Table 1). Exceptions were the less numerous species (Tables 2–3), where respiration was estimated from net production efficiencies (NPE) found for similar species.

Table 2. Mean lakewide density (D, no. m^2), maximum individual weight (W, mg ash free dry weight), annual production/mean biomass ratio (P/$\bar{B}$), mean lakewide annual production (P), respiration (R), assimilation (A), net production efficiency (NPE), and ingestion (I) of 19 taxa in Lake Mývatn. All rates are given in kJ m^{-2} yr^{-1}. P/$\bar{B}$ and NPE ratios estimated from related species or taken from literature are marked with "*".

Taxa	D	W	P/$\bar{B}$	P	R	A	NPE P/A	I		
								Detritivores	Herbivores	Carnivores
Coelenterata										
Hydra sp. cf. *attenuata* Pallas	90	0.076	2*	0.3	0.3	0.6	0.50*	–	–	1.0
Mollusca										
Lymnaea pereger (Müller)	39	3.3	3.5*	4.9	4.3	9.2	0.53*	–	18.4	–
Pisidium spp.	547	1.35	1.3*	3.5	3.5	7.0	0.50*	35.0	–	–
Oligochaeta										
Chaetogaster diaphanus (Gruith.)	204	0.063	2*	0.6	0.4	1.0	0.60*	–	–	1.7
Nais spp.	202	0.043	2*	0.5	0.4	0.9	0.54*	–	1.8	–
Tubifex tubifex (Müller)	5422	1.0	2*	23.2	26.2	49.4	0.47*	247.0	–	–
Lumbriculus variegatus (Müller)	52	3.3	2*	4.4	1.5	5.9	0.75*	29.5	–	–
Hirudinea										
Helobdella stagnalis (L.)	5	4	3*	0.8	1.3	2.1	0.38*	–	–	3.5
Crustacea										
Benthic Copepoda & Cladocera	24500	0.005	15*	40.0	40.0	80.0	0.50*	–	160.0	–
Chironomidae										
Ablabesmyia monilis (L.)	22	1.0	7.5*	0.7	0.7	1.4	0.50*	–	–	2.3
Arctopelopia griseipennis (v.d. Wulp)	3	1.0	7.5*	0.1	0.2	0.3	0.37*	–	–	0.5
Macropelopia nebulosa (Meigen)	29	1.5	7.5*	2.1	1.1	3.2	0.65*	–	–	5.3
Procladius islandicus (Goetghebuer)	344	1.5	7.5*	11.4	11.4	22.8	0.50*	–	–	38.0
Cricotopus sylvestris (Fabricius)	85	0.4	7.5*	0.5	0.5	1.0	0.52*	–	2.0	–
Cricotopus tibialis (Meigen)	31	0.4	7.5*	0.2	0.2	0.4	0.52*	–	0.8	–
Orthocladius oblidens (Walker)	51	0.4	7.5*	0.5	0.3	0.8	0.59*	–	1.6	–
Pogonocladius consobrinus (Holmgren)	653	0.4	7.5*	8.2	5.9	14.1	0.58*	–	28.2	–
Psectrocladius barbimanus (Edwards)	295	0.7	7.5*	11.9	11.9	23.8	0.50*	–	47.6	–
Chironomus islandicus (Kieffer)	7068	3.0	3.4	199.6	354.8	554.4	0.36	–	1108.0	–
Tanytarsus gracilentus (Holmgren)	60323	0.24	7.5	564.9	481.2	1046.1	0.54	–	2092.2	–
Total 20 taxa	99965			878.3	946.2	1824.4	0.48	311.5	3461.4	52.3

Each taxon was assigned to a broad trophic group (detritivores, herbivores, and carnivores) based on observations of gut contents or on published sources. Published values of assimilation efficiency (A/I = assimilation/ingestion) vary greatly (e.g. Welch, 1968; Heal & MacLean, 1975; Berrie, 1976; Schroeder, 1981). Therefore, to estimate the ingestion, an assimilation efficiency of 50% for herbivores, 20% for detritivores, and 60% for carnivores was assumed as did Strayer & Likens (1986) in their computation of an energy budget for the zoobenthos of Mirror Lake.

Lindegaard (1992a) showed, that 95% C.L. varied from 20–40% of similar individual cohort production estimates. Therefore, the only reason for showing production (and consequently respiration, assimilation and ingestion) with up to five significant digits, is to show the size of these parameters for the less common species (Tables 2–3).

Results and discussion

Data for 20 taxa in Mývatn and 16 taxa in Hjarbæk Fjord are summarized in Table 2 and 3, respectively. Further, total annual net production, total annual respiration, total annual assimilation and total annual ingestion of the three trophic groups (detritivores, herbivores and carnivores) in the two lakes are shown in Table 4.

Table 3. Mean lakewide density (D, no. m^2), maximum individual weight (W, mg ash free dry weight), annual production/mean biomass ratio ($P/\bar{B}$), mean lakewide annual production (P), respiration (R), assimilation (A), net production efficiency (NPE), and ingestion (I) of 16 taxa in Hjarbæk Fjord. All rates are given in kJ m^{-2} yr^{-1}. $P/\bar{B}$ and NPE ratios estimated from related species or taken from literature are marked with "*".

Taxa	D	W	$P/\bar{B}$	P	R	A	NPE P/A	I		
								Detritivores	Herbivores	Carnivores
Oligochaeta										
Tubificidae	1681	1.00	3*	38.3	38.3	76.6	0.50*	383.0	–	–
Hirudinae										
Helobdella stagnalis (L.)	4	2	2.4*	0.4	0.4	0.8	0.50*	–	–	1.3
Mollusca										
Theodoxus fluviatilis L.	2	11	1.5*	0.6	0.6	1.2	0.50*	–	2.4	–
Pisidium spp.	6	1.35	1.3*	0.9	0.9	1.8	0.50*	9.0	–	–
Trichoptera										
Oecetis ochrecea Curtis	17	4	4*	11.2	11.2	22.4	0.50*	–	44.8	–
Chironomidae										
Procladius spp.	739	0.6	3.2	19.0	51.4	70.4	0.27	–	–	117.3
Psilotanypus spp.	23	0.6*	3.2*	0.7	1.9	2.6	0.27*	–	–	4.3
Psectrocladius spp.	63	0.4*	5*	2.3	4.3	6.6	0.35*	–	13.2	–
Chironomus plumosus L. f. *semireductus* Lenz	1572	2.1	5.6	238.9	329.9	568.8	0.42	–	1137.6	–
Cryptochironomus redekei Kruseman	567	2.0	6.6	113.1	108.7	221.8	0.51	–	–	369.7
Fleuria lacustris Kieffer	7871	1.0	9.9	434.5	531.1	965.1	0.45	–	1931.2	–
Glyptotendipes sp.	65	2.0*	5*	9.5	13.1	22.6	0.42*	–	45.2	–
Polypedilum bicrenatum Kieffer	3431	0.18	6.7	43.1	87.5	130.6	0.33	–	261.2	–
Polypedilum nubeculosum (Meigen)	892	0.70	6.3	43.1	48.6	91.7	0.47	–	183.4	–
Cladotanytarsus spp.	17126	0.06	6.0	137.0	370.4	507.4	0.27	–	1014.8	–
Tanytarsus sp.	65	0.10	6*	0.8	2.2	3.0	0.27*	–	6.0	–
Total 16 taxa	34124			1093.4	1600.5	2693.9	0.41	392.0	4639.8	492.6

Production and trophic composition of the zoobenthic communities

Diversity indices in both lakes were low, because of the total dominance of a few species. In Mývatn two species, *Chironomus islandicus* and *Tanytarsus gracilentus*, accounted for 87% of total benthic net production (878 kJ m^{-2} yr^{-1}), while in Hjarbæk Fjord four taxa, *Fleuria lacustris*, *Chironomus plumosus* f. *semireductus*, *Cladotanytarsus* spp. and *Cryptochironomus redekei*, made up 85% of total production (1093 kJ m^{-2} yr^{-1}). The herbivores contributed 95% and 84% of these values, while the contribution from detritivores were insignificant (3–4% in both lakes). The carnivores were also insignificant in Lake Mývatn (2%), but in Hjarbæk Fjord they made up 12%. The production of carnivores in Mývatn seems very low compared with other lakes, where predators accounted for up to 20% of the total community (Strayer & Likens, 1986). A similar sparsity of carnivores was found by Lindegaard (1992b) in another Icelandic lake, the 114 m deep Lake Thingvallavatn. In spite of the low numbers of invertebrate carnivores in Thingvallavatn predation on the littoral zoobenthos was heavy, due to a large population of arctic charr (*Salvelinus alpinus* L.). This fish was also present in Mývatn, but in low numbers only. However, in this lake a large population of diving ducks exploited the chironomids as important food items (Jónasson, 1979). In Hjarbæk Fjord a large stocking of whitefish (*Coregonus lavaretus* L.) was carried out in order to reduce the amount of chironomids. In spite of establishment of a self-reproducing population with a high growth rate, Rasmussen (1990) estimated that only 2–5% of the chironomid production was consumed by whitefish.

Table 4. Annual net production, respiration, assimilation and ingestion (kJ m^{-2} yr^{-1}) of the three trophic groups of zoobenthos in Mývatn and Hjarbæk Fjord.

	Detritivores	Herbivores	Detritivores + Herbivores	Carnivores
Mývatn				
Production	31	831	862	16
Respiration	31	900	931	15
Assimilation	62	1731	1793	31
Ingestion	312	3461	3773	52
Hjarbæk Fjord				
Production	39	921	960	133
Respiration	39	1399	1438	162
Assimilation	78	2320	2398	296
Ingestion	392	4640	5032	493

The high proportion of herbivores is remarkable. This could be due to incorrect classification of species into herbivores and detritivores. In fact, most surface feeders ingest both algae and detritus, but gut content analyses has shown that many species are able to feed selectively, and chironomids (except Tanypodinae and species belonging to some Chironomini genera (e.g. *Cryptochironomus*)) were found to be mainly herbivores (e.g. Armitage, 1968; Kajak & Warda, 1968; Mason & Bryant, 1975; Titmus & Badcock, 1981; Berg, 1993). Some less dominant groups (e.g. Trichoptera) were also considered herbivorous although, more correctly, they may be omnivorous. The main group of detritivores was oligochaetes (except Naididae), which are known to feed on cultures of bacteria in the sediment (e.g. Ivlev, 1937; Brinkhurst *et al.*, 1972).

I consider the fraction of 80 to 90% of production assigned to herbivores to be correct. This value is very high compared to other lake studies, where detritivores were found to dominate (e.g. Johnson & Brinkhurst, 1971; Strayer & Likens, 1986). However, in Mirror Lake the herbivores made up 32% and Strayer & Likens (1986) suggested, that in clear lakes much of zoobenthic production may be supported by benthic algae rather than detritus. In accordance with this Lindegaard (1992b) found 60% of the benthic secondary production was herbivorous invertebrates in Thingvallavatn, which has a photic zone reaching 20–30 m depth. The very high benthic diatom net production (9200 kJ m^{-2} yr^{-1}) in Mývatn (Jónasson, 1979) may easily explain the total dominance of herbivorous chironomids in this lake. Hjarbæk Fjord, however, may be considered as a very turbid lake with practically no benthic primary production. In this lake primary production is totally dominated by phytoplankton making up a rather 'thick' suspension normally circulated in the whole water column, which would favour filtrators. Of the chironomids found in Hjarbæk Fjord only *Chironomus plumosus* is known to live – at least partially – as a filtrator (e.g. Walshe, 1951; McLachlan, 1977; Johnson *et al.*, 1989). The other dominant species are considered to be merely surface browsers collecting newly deposited algae. In highly eutrophic shallow lakes the substrate often consists of unstable soft mud exposed to repeated resuspensions and consequently being unsuitable as habitat for invertebrates (e.g. Jónasson & Lindegaard, 1979; Moss & Timms, 1989). In Mývatn a living substrate of *Cladophora* stabilized the substrate, increased the surface area available to tube building chironomids and acted as a sieved for suspended organic matter. In Hjarbæk Fjord a sandy sediment provided the necessary stable conditions.

Respiration and assimilation efficiency

Total annual zoobenthic respiration was calculated at 946 and 1601 kJ m^{-2} yr^{-1} resulting in a net production efficiency (NPE) of 0.48 and 0.41 in Mývatn and Hjarbæk Fjord, respectively (Tables 2–3). However, a range in NPE from 0.27 to 0.54 was found within the specific taxa, where respiration was calculated according to the equations found by Hamburger & Dall (1990). NPE varied without any general correlation to body mass or length of life cycles. The parameters influencing NPE most were temperature and population biomass during periods with high water temperature.

NPE values of 0.41 to 0.48 is within the range found for invertebrates (McNeil & Lawton, 1970; Heal & MacLean, 1975; Alimov, 1991), but as an average for the total community the value for Mývatn seems high. Humphreys (1979) suggested a NPE of 0.3–0.4 for invertebrates. Sarvala *et al.* (1981) used a NPE of 0.3 in computation of an energy budget for zoobenthos in the Finnish Lake Pääjärvi. Strayer & Likens (1986) found a NPE of 0.42 by using a variety of literature sources (compiled by Walter (1976)) to estimate community respiration in Mirror Lake. However, Lindegaard (1992b) found – by using the same equations as for Mývatn – a NPE of 0.50 for the zoobenthos community in the Icelandic Lake Thingvallavatn. He suggested that the high NPE was due to the use of respiration rates estimated for invertebrates living in a temperate lake on subarctic communities living at lower average temperatures. Thus, the number of degree days (dd) is 3200 in Lake Esrom, while Thingvallavatn and Mývatn have 1550 and 1740 dd, respectively. Hjarbæk Fjord has 3050 dd which is close to Lake Esrom; it has a lower NPE (0.41). Bullock (1955) and Ivleva (1980) pointed out that animals adapted to live at lower temperatures have higher respiration rates at low temperatures than animals adapted to higher temperatures.

Alimov (1991) calculated zoobenthos community production as net production of detritivores plus herbivores plus carnivores minus assimilation of carnivores (= net production of detritivores + herbivores – respiration of carnivores). Using this approach NPE (= K_2 or net growth efficiency of Alimov) is 0.47 and 0.32 for Mývatn and Hjarbæk Fjord, respectively. Carnivory has little effect on NPE in Mývatn, while the large numbers of invertebrate predators in Hjarbæk Fjord are responsible for a change from 0.41 to 0.32.

Ingestion and sources of food

Annual total ingestion of non-carnivorous organisms was estimated between 3773–5032 kJ m^{-2} yr^{-1}, and of carnivorous between 52–493 kJ m – 2 yr^{-1} in Mývatn and Hjarbæk Fjord, respectively (Table 4).

The sources of food in both Mývatn and Hjarbæk Fjord were assumed to be mostly autochthonous, because allochthonous inputs for large lakes are insignificant (Szczepanski, 1965; Jónasson, 1984). In Mývatn both phytoplankton and phytobenthos were important food sources, while in Hjarbæk Fjord phytobenthos was considered insignificant. Net primary production of phytoplankton in shallow lakes was arbitrarily estimated to 50% of gross phytoplankton production (e.g. Jónasson 1979; Jónasson & Lindegaard, 1979, 1988). In this way available food for the non-carnivorous invertebrates was estimated to 13800 and 10500 kJ m^{-2} yr^{-1} in Mývatn and Hjarbæk Fjord, respectively (Table 5). Available food for the invertebrate predators was estimated to be equivalent to net production of non-carnivorous invertebrates (Table 5).

When estimating the efficiency with which zoobenthos utilizes the available food, it is important that all fractions of secondary production are considered. The zoobenthos production estimates of Mývatn and Hjarbæk Fjord do not include the proper micro- and meiofauna elements, as sieves with a mesh size of 150 μm and 200 μm were used and manual sorting done at low power (2.5 × magnification). The same procedure was used by Lindegaard (1992a) in Thingvallavatn, and Lindegaard (1992b) suggested that production estimates for 'macrozoobenthos' was raised by 25% if total zoobenthic fauna were included. This factor was applied to the calculation for both lakes (Table 5).

The production of non-carnivorous benthos made up 8% and 11% of net primary production in Mývatn and Hjarbæk Fjord, respectively (Table 5). This is close to the commonly accepted trophic level productivity efficiency of 0.1 (e.g. Kozlovsky, 1986; Krebs, 1985). However, the trophic efficiency of the carnivores in Mývatn was only 0.02, while a much higher efficiency of 0.14 was found in Hjarbæk Fjord.

The ingestion of detritivores and herbivores was only 34% of net primary production in Mývatn, but as much as 60% in Hjarbæk Fjord. This difference was even more pronounced for carnivores, which exploited only 6% of available food in Mývatn, but about 50% in Hjarbæk Fjord. Predation by fish in both lakes was only about 5–10% (Jónasson, 1979; Rasmussen, 1990) resulting in large amounts of biomasses leaving the lakes as adult midges (Lindegaard & Jónasson, 1979; Lindegaard & Jónsson, 1987). The ingestion rates found in Mývatn are almost identical to those found in Thingvallavatn, where on a mean lakewide basis, the non-carnivorous zoobenthos utilized about one third of the available food (Lindegaard, 1992b).

Energy flow

The zooplankton net production was estimated between 180–200 kJ m^{-2} yr^{-1} in Mývatn and Hjarbæk Fjord, respectively. This is 17% of the zoobenthos production in both lakes. Compared to phytoplankton net production (2500 kJ m^{-2} yr^{-1} in Mývatn (Jónasson & Adalsteinsson, 1979) and 10500 kJ m^{-2} yr^{-1} in Hjarbæk Fjord (Rasmussen, 1982; Lindegaard & Jónsson, 1987)) trophic level efficiencies of zooplankton were 7% and 2% in the two lakes, respectively. Total net production of non-carnivorous invertebrates (zoobenthos plus zooplankton) made up 9% and 13% of total net organic inputs in Mývatn and

Table 5. Estimated available food, production and ingestion by herbivorous, detritivorous and carnivorous invertebrates in Mývatn and Hjarbæk Fjord (all values in kJ m^{-2} yr^{-1}). Compared to values in Tables 2–4 production and ingestion are multiplied with 1.25 in order to include meio- and microfauna (further explanation in test).

	Available food	Zoobenthos		Trophic efficiency	
		Production	Ingestion	Production	Ingestion
Mývatn					
Detritivores + herbivores	13800	1078	4716	0.08	0.34
Carnivores	1078	20	65	0.02	0.06
Hjarbæk Fjord					
Detritivores + herbivores	10500	1200	6290	0.11	0.60
Carnivores	1200	166	616	0.14	0.51

Table 6. The trophic level efficiency and percentage contribution of zooplankton (ZP) and zoobenthos (ZB) to total annual net production of primary consumers (PC) compared to mean depth and net primary production (PP) in four lakes. Data from Lake Esrom and Thingvallavatn are from Jónasson *et al.* (1990a, b) and Jónasson (1992).

Lake	Mean depth m	Net PP kJ m^{-2} yr^{-1}	Net production			Trophic efficiency		
			PC kJ m^{-2} yr^{-1}	ZP % of PC	ZB % of PC	PC	ZP	ZB
Hjarbæk Fjord	1.9	10500	1400	14	86	0.13	0.02	0.11
Mývatn	2.3	13800	1258	14	86	0.09	0.01	0.08
Esrom	13.5	9400	1470	53	47	0.16	0.08	0.08
Thingvallavatn	34.1	4500	310	68	32	0.07	0.05	0.02

Hjarbæk Fjord, respectively (Table 6). This is well within the range from 14 lakes reviewed by Strayer & Likens (1986), who found that zooplankton plus zoobenthos production varied between 2.3% and 23% (average 11%) of total organic inputs.

Rough estimates of total zoobenthos and zooplankton grazing in the two lakes examined here leaves about 40% and 30% of net primary production available for direct decomposition by bacteria. Further the egestion from invertebrates makes up about 50% of ingestion or about 30% of net primary production. Thus, a sum of 60–70% of the net primary production energy should be processed in the bacterial loop, or be deposited in the sediment. This does not necessarily imply that bacterial production is limited by this amount, as organic carbon can recycle several times among consumers before total energy input is respired (Scavia, 1988; Strayer, 1988).

The high proportion (*ca.* 86%) of zoobenthic production in the two shallow lakes contrast with the findings in deeper lakes, where zooplankton constitute a larger proportion of total secondary production. Zoobenthos production in deeper lakes, Lake Esrom (maximum depth 22 m) and in Thingvallavatn (maximum depth 114 m), is 47% and 32% of total secondary production (Table 6).

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