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Benthic carbon is inefficiently transferred in the food webs of two eutrophic shallow lakes

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Abstract

1. The sum of benthic autotrophic and bacterial production often exceeds the sum of pelagic autotrophic and bacterial production, and hence may contribute substantially to whole-lake carbon fluxes, especially in shallow lakes. Furthermore, both benthic and pelagic autotrophic and bacterial production are highly edible and of sufficient nutritional quality for animal consumers. We thus hypothesised that pelagic and benthic transfer efficiencies (ratios of production at adjacent trophic levels) in shallow lakes should be similar.
2. We performed whole ecosystem studies in two shallow lakes (3.5 ha, mean depth 2 m), one with and one without submerged macrophytes, and quantified pelagic and benthic biomass, production and transfer efficiencies for bacteria, phytoplankton, epipelon, epiphyton, macrophytes, zooplankton, macrozoobenthos and fish. We expected higher transfer efficiencies in the lake with macrophytes, because these provide shelter and food for macrozoobenthos and may thus enable a more efficient conversion of basal production to consumer production.
3. In both lakes, the majority of the whole-lake autotrophic and bacterial production was provided by benthic organisms, but whole-lake primary consumer production mostly relied on pelagic autotrophic and bacterial production. Consequently, transfer efficiency of benthic autotrophic and bacterial production to macrozoobenthos production was an order of magnitude lower than the transfer efficiency of pelagic autotrophic and bacterial production to rotifer and crustacean production. Between-lake differences in transfer efficiencies were minor.
4. We discuss several aspects potentially causing the unexpectedly low benthic transfer efficiencies, such as the food quality of producers, pelagic–benthic links, oxygen concentrations in the deeper lake areas and additional unaccounted consumer production by pelagic and benthic protozoa and meiobenthos at intermediate or top trophic levels. None of these processes convincingly explain the large differences between benthic and pelagic transfer efficiencies.
5. Our data indicate that shallow eutrophic lakes, even with a major share of autotrophic and bacterial production in the benthic zone, can function as pelagic systems with respect to primary consumer production. We suggest that the benthic

autotrophic production was mostly transferred to benthic bacterial production, which remained in the sediments, potentially cycling internally in a similar way to what has previously been described for the microbial loop in pelagic habitats. Understanding the energetics of whole-lake food webs, including the fate of the substantial benthic bacterial production, which is either mineralised at the sediment surface or permanently buried, has important implications for regional and global carbon cycling.

KEYWORDS

bacterial production, benthic food chain, pelagic food chain, quantitative food webs, trophic transfer efficiency

1 | INTRODUCTION

In many ecosystems, several spatial compartments can be distinguished, which may fundamentally differ with respect to resource availability, habitat structure and food web components. Perhaps, the most fundamental of such compartments distinguished in lakes are the pelagic and benthic compartments. Most previous studies have focused on the pelagic zone, and research simultaneously evaluating the significance of both compartments to whole-lake functioning is rare. However, recent research has increasingly found benthic habitats to contribute substantially to whole-lake processes (Althouse, Higgins, & Vander Zanden, 2014; Ask et al., 2009; Karlsson et al., 2012; Vander Zanden, Chandra, Park, Vadeboncoeur, & Goldman, 2006; Vander Zanden & Vadeboncoeur, 2002). Vadeboncoeur, Vander Zanden, and Lodge (2002) showed that the production of benthic autotrophs, heterotrophic bacteria and invertebrates typically approximates or even exceeds pelagic production, and thus demanded the reintegration of benthic pathways into lake food-web models.

The dominance of benthic over pelagic autotrophic production rates is expected to be especially common in shallow lakes. Shallow lakes can exhibit alternative stable states, featuring a dominance of either phytoplankton or submerged macrophytes (Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993), although epipelon production can prevail under both regimes (Brothers, Hilt, Meyer, & Köhler, 2013). Nevertheless, energetic pathways in benthic and pelagic food webs in shallow lakes are rarely quantified simultaneously, and few studies include both autotrophic and animal consumer production (Andersson & Kumblad, 2006; Jia, Hu, Hu, Liu, & Wu, 2012; Rowland, Bricker, Vanni, & Gonzalez, 2015). In addition, studies frequently examine only single processes in these habitats, either focusing on autotrophic producers (Althouse et al., 2014; Ask, Karlsson, & Jansson, 2012; Blindow, Hargeby, Meyercordt, & Schubert, 2006; Brothers, Hilt, Meyer, et al., 2013), autotrophic and heterotrophic producers (Ask et al., 2009), or on the habitat origin of diet items for top consumers (Karlsson & Byström, 2005; Vander Zanden & Vadeboncoeur, 2002). In all of these studies, benthic organisms or processes were quantitatively important for whole-lake patterns and processes. However, it is not clear whether the high contribution of benthic organisms to the diet of top consumers is the consequence of a similarly high contribution of benthic producers to the whole-lake autotrophic and heterotrophic production (Althouse et al., 2014; Brothers, Hilt, Meyer, et al., 2013). To better understand the energetic link between all trophic levels, the relative efficiencies of the energy transfer from producers to animal consumers have to be studied in both lake habitats.

High transfer efficiencies can be expected when prey are accessible, of sufficient quality, and edible for the consumers. Evidence for high transfer efficiencies has thus come primarily from the pelagic zone of lakes. For example, herbivore-to-primary (phytoplankton plus bacterial) production ratios were between 0.2 and 0.4 in the mesotrophic, pre-alpine Lake Constance (Gaedke & Straile, 1994). However, the pre-conditions for an efficient energy transfer are comparably good in benthic habitats. Benthic autotrophs and bacteria have access to a larger nutrient pool in the sediments than their pelagic counterparts (Sand-Jensen & Borum, 1991), potentially making them a high-quality resource (low carbon to nutrient ratios) for their consumers. Epipelon, the dominant benthic autotrophic group on muddy-bottomed lakes (Brothers, Hilt, Meyer, et al., 2013), and bacterial aggregates are of suitable size for invertebrate grazing (Hecky & Hesslein, 1995). The nutritional quality and edibility of the dominant pelagic and benthic autotrophs and bacteria are thus believed to be equivalent (Hessen, Elser, Sterner, & Urabe, 2013; Sand-Jensen & Borum, 1991). We therefore postulated that the transfer of benthic production to animal consumers should be as efficient as the transfer of pelagic production to animal consumers in a shallow lake. We thus expected comparable benthic and pelagic contributions to whole-lake processes at all trophic levels.

We tested this hypothesis by investigating the pelagic and benthic food webs of two shallow eutrophic lakes, one with and one without submerged macrophytes. Submerged macrophytes provide shelter and food for macrozoobenthos and may thus enable a more efficient conversion of basal production to consumer production, as compared with shallow lakes dominated by phytoplankton (Jeppesen, 1998). Our quantitative approach relied on detailed measurements of the biomass and production of all basal producers. In contrast to many previous studies this included pelagic (water column) and benthic (sediment) bacteria, as well as biomass and production measurements or estimates of various animal consumer groups. We calculated the trophic efficiencies of autotrophic and bacterial production to animal consumers for the whole lake, as well as separate calculations for the pelagic and benthic habitats of each lake. With this approach, we demonstrate that full-lake energetic fluxes can only be functionally understood if the benthic contributions to total autotrophic and bacterial production are quantified (Vadeboncoeur et al., 2002).

2 | METHODS

2.1 | General overview

We studied two shallow lakes, Schulzensee and Kleiner Gollinsee (hereafter referred to as Gollinsee), both located in north-eastern Germany. The lakes were similar in size (3–4 ha), mean (about 2 m) and maximum depth (3–4 m), and nutrient and dissolved organic carbon (DOC) concentration (mean values of 32 and 33 μg total phosphorus L^{-1}, 16 and 15 mg DOC L^{-1} in Gollinsee and Schulzensee, respectively, Brothers et al., 2014) during the study period (April–October 2011). Approximately 25% of the surface area of Schulzensee contained submerged macrophytes (*Ceratophyllum submersum*: Ceratophyllaceae), whereas Gollinsee had no submerged macrophytes during the period of our investigation (Brothers, Hilt, Meyer, et al., 2013). Both lakes were occasionally unmixed below 1.5 m (Gollinsee) and 2 m (Schulzensee) in early and late summer, placing roughly 60% of their sediment areas below the mixing depth.

In 2011, we measured the biomass and production of bacteria and autotrophs, the biomass of consumers, and either measured or calculated consumer production rates in both the pelagic and benthic zones, to construct a fully quantitative food-web model for each lake. Samples were taken from the beginning of April to the end of October 2011 (213 days) to cover the majority of the annual production. We averaged the biomass measurements and summed the production values to obtain data for the whole growing season. Both lakes were divided by plastic curtains from October 2010 onwards, and maize leaves were added to one half of each lake as part of an unrelated experiment (Attermeyer, Premke, Hornick, Hilt, & Grossart, 2013; Scharnweber et al., 2014). We used only the data from the reference halves (which did not receive maize leaves) for this study, but refer to them as whole lakes given that the proportions of pelagic and benthic habitats were similar between the entire lakes and divided lake halves. Our overall intention was to compare pelagic and benthic transfer efficiencies. The results presented are raw data and we refrain from using inferential statistics to establish potential differences between the two habitats and lakes. Most of the biomass and production values rely on temporal or spatial replicates, which are not statistically independent. However, in agreement with Carpenter (1989), we argue that obtaining ecological knowledge about whole-lake ecosystems is a valid approach even in the absence of strict statistical tests.

2.2 | Autotrophs

Phytoplankton was sampled monthly in the pelagic zone at three depths and in the littoral zone at three locations between April and October 2011. Samples from each habitat were pooled, fixed with acidified Lugol's solution and analysed with inverted microscopy. The sizes of at least 20 cells of each morphotype were measured to calculate the cell volume and converted into the cell-specific individual carbon (C) content (Lischke et al., 2016). Submerged plastic strips were exposed to measure monthly epiphyton and epipelon biomass between April and October 2011, as described in Brothers, Hilt, Meyer, et al. (2013). We measured submerged macrophyte biomass in July 2010, at its annual maximum (Brothers, Hilt, Meyer, et al., 2013). Following visual observations, Schulzensee's submerged macrophyte abundance and biomass, and thus production and surface area available for epiphyton, did not appear to differ substantially between years. Values measured in 2010 were therefore applied to 2011.

The gross primary production (GPP) of submerged macrophytes was calculated from summer biomass measurements using a GPP-to-harvest ratio of 1.5 (Best, 1982; Brothers, Hilt, Meyer, et al., 2013). The GPP of phytoplankton was calculated every 2–4 weeks from the quantum yield of photosystem II (measured at 12 light intensities using a PhytoPAM, Walz, Germany), specific absorption cross section (Varian photometer with integrating sphere), the efficiency of carbon assimilation and the intensity of photosynthetically active radiation at 10 cm depth intervals (see Brothers, Hilt, Meyer, et al., 2013 for details). For periphyton (epiphyton and epipelon), submerged plastic strips were exposed in the open-water (pelagic) zone at 1.2 m below the surface to measure monthly periphyton biomass accumulation and production rates, which were then translated to epiphyton and epipelon production based on measurements of underwater plant surface area (estimated from 2010 values) and sediment surface area estimates respectively (Brothers, Hilt, Meyer, et al., 2013). This method is considered suitable for eutrophic lakes, where light replaces nutrients as the dominant factor limiting epiphyton and epipelon production (e.g. Eminson & Moss, 1980; Jones & Sayer, 2003). Due to a low biofilm thickness and the absence of vertical migration, this approach further avoids artefacts described for fluorometric measurements on natural sediments (e.g. Forster & Kromkamp, 2004). For epipelon production, we assumed the existence of a maximum "standing stock" biomass (estimated from littoral and off-shore plastic strips exposed from early May to mid-November, 2010) to which light attenuation and photosystem II quantum yield measurements made in 2011 were applied. Measuring the light attenuation inherently incorporated potential shading effects of DOC, and hence accounts for the effect of browning on primary production. To estimate net primary production, phytoplankton and submerged macrophytes were assumed to have lost, respectively, 40% and 60% of their GPP due to respiration (Best, 1982 for macrophytes; as described in Brothers, Hilt, Meyer, et al., 2013; following Platt, Bird, & Sathyendranath, 1991 for phytoplankton). Epiphyton and epipelon respiration rates were estimated using published summer (July) and autumn (September) relationships between periphyton biomass and respiration (from Brothers, Hilt, Meyer, et al., 2013; following Liboriussen & Jeppesen, 2006). Emergent (*Phragmites australis*: Poaceae) and floating-leaved macrophytes (*Nymphaea alba* and *Nuphar lutea*: Nymphaeaceae) were not considered to be autochthonous aquatic autotrophs, as they derive inorganic C directly from the atmosphere, although they were significant contributors to the lakes' organic C pool (following Brothers, Hilt, Meyer, et al., 2013, and see below).

2.3 | Bacteria

Pelagic and littoral water samples were taken every 4 weeks from April to October 2011. Samples included equal portions of water generally from 0.5, 1 and 2 m water depths (always within the mixed water volume, with precise sampling depths varying with mixing depths) in the pelagic zone and equal portions of water from three locations in the littoral zone (each 0.5 m). Samples were transported in glass bottles to the laboratory in a dark cooler and were analysed within 12–24 hr of sampling. Sediment samples were taken with a sediment corer (inner diameter 6 cm; Uwitec, Mondsee, Austria) in the lake centre (at *c.* 2–2.5 m water depth) and littoral zones (at *c.* 1.5 m water depth). Each sediment sample consisted of the first upper centimetre of three sediment cores (85 ml).

Total bacterial biomass was determined by epifluorescence microscopy after staining with SYBR Gold (Invitrogen, Darmstadt, Germany; Shibata et al. 2006). A subsample (500 μl) of well-homogenised sediment was diluted with 15 ml 0.1% (weight: volume) sodium pyrophosphate to detach cells from sediment particles, and both sediment and water samples were fixed with glutaraldehyde (0.9% final concentration) and stored at 4°C in the dark. In order to increase the recovery efficiency of attached bacteria, sediment samples were first sonicated prior to filtration in a sonication bath (Transsonic Digital Typ 790/H; Elma, Singen, Germany) at level 5 (50%) for 3 min and subsequently shaken on a horizontal shaker (Heidolph Reax2, Schwabach, Germany) at 40 rpm for 30 min. Then, 1–2 ml of the water and 40–50 μl of the fixed sediment samples were filtered with a 0.2-μm polycarbonate filter (Whatman, Dassel, Germany) and embedded in Citifluor (CITIFLUOR AF1, Science Services, München, Germany) with a SYBR Gold staining solution diluted to 1:1,000 (Molecular Probes, Eugene, Oregon, U.S.A.). Bacteria (>500 cells per filter) were counted with an epifluorescence microscope at 1,000× magnification (Zeiss, Axio Imager.Z1, Jena, Germany) and the biovolumes (V) of *c.* 100 cells per sample were measured. Bacterial V was converted to bacterial biomass using the conversion factor $89.9 \times V^{0.59}$ fg C per cell (Simon & Azam, 1989). Bacterial production rates were measured by incorporation of L-^{14}C-leucine into the protein fraction using the protocols of Simon and Azam (1989) for water and Buesing and Gessner (2003) for sediment. A detailed description of the procedure for water and sediment samples is available in Attermeyer et al. (2013). For each sample, bacterial production was determined in triplicates with one blank. Mean values were calculated from water samples collected in the littoral as well as pelagic zones of each lake, assuming horizontally well-mixed lakes, and sediment samples were scaled up to the whole lake by weighing according to the respective relative habitat size.

2.4 | Zooplankton

Epilimnetic mixed water samples (40 L) were taken monthly at pelagic and littoral sites in each lake. These were split into ciliate samples (50 ml) that were fixed with acidified Lugol's solution (Hoehn et al., 1998) and into rotifer/crustacean samples that were filtered (55-μm mesh) and fixed with 4% sugar formalin (Haney & Hall, 1973). Samples were quantitatively analysed, identified to the genus or species level, and size was determined as volume (ciliates, rotifers) or length (crustaceans) following Schmidt-Halewicz, Hoehn, Kasten, and Dembinski (2012). Individual C content was calculated using regressions with specific conversion factors for each zooplankton group (Dumont, Vandevelde, & Dumont, 1975; Müller & Geller, 1993; Telesh, Rahkola, & Viljanen, 1998) and assuming that 50% of the dry weight was C (Gaedke, 1992 and included references).

Maximum ciliate production was estimated following Montagnes, Lynn, Roff, and Taylor (1988), accounting for species biomass, cell volume and temperature. This approach provided values similar to those obtained using the equations of Hansen, Bjornsen, and Hansen (1997). These lab-derived maximum production rates are based on optimal prey concentrations and may thus not be achieved in natural systems. This likely holds true for our lakes as well, as the prey demand required by the maximum ciliate production surpassed the measured autotrophic and bacterial production when assuming a ciliate growth efficiency of 33% (Straile, 1997). We therefore calculated the maximum achievable ciliate production given the measured available prey production and a ciliate growth efficiency of 33%, reducing maximum production estimates by 66% and 70% in Gollinsee and Schulzensee, respectively. This ciliate production would be sufficient to maintain the measured ciliate biomass dynamics over the year. Previous studies using the same approach suggested a 75%–80% reduction of the calculated values (Barthelmeß, 1995; Straile, 1994). Rotifer production rates were estimated using a linear regression model which accounted for total biomass and temperature (Shuter & Ing, 1997). Production estimates for crustaceans considered the individual size and biomass of each species using two sets of specific parameters for a water temperature below and above 10°C (Stockwell & Johannsson, 1997). Zooplankton production was estimated for each sampling day, summed over the respective month, and subsequently summed to obtain growing season values. Whole-lake biomass and production were calculated as arithmetic averages of pelagic and littoral values as they were similar at both lake sites and these small lakes were assumed to be horizontally mixed.

2.5 | Macrozoobenthos

The biomass of macrozoobenthos (here defined as benthic organisms retained by a net with a 500 μm mesh size) was estimated from monthly samples taken from April to October 2011, as described in

Brothers, Hilt, Attermeyer, et al. (2013) and Mehner et al. (2016). Briefly, macrozoobenthos was collected from three depths 0–1, 1–2 and >2 m. For each habitat shallower than 2 m, an area of 0.63 m^2 was sampled using a kick-net (mesh size 500 μm). An area of 0.14 m^2 was sampled using an Ekman grab in deeper areas. The total sampled area was chosen to capture most of the species occurring at a given habitat, as evaluated at other lowland lakes in northern Germany (Schreiber & Brauns, 2010). The annual production (P, g DW m^{-2} growing per season) of macrozoobenthos in the three depths was estimated using the allometry-based approach of Plante and Downing (1989), as described in Mehner et al. (2016):

$$\text{Log}(P) = 0.06 + 0.79 \times \text{Log}(B) - 0.16 \times \text{Log}(M_{\text{max}}) + 0.05 \times T \quad (1)$$

where B is the mean annual biomass (averaged across the eight samples, g DW m^{-2}) and M_{max} is the maximum individual biomass (mg DW per individual) for each taxon in each habitat of each lake. Because calculations based on single maximum-sized individuals may overestimate production, we used the average length of the largest 10% of individuals of pooled Chironomidae for the maximum individual biomass (compare Bergtold & Traunspurger, 2005). T is the annual mean water temperature (14.3°C in Schulzensee, 13.6°C in Gollinsee), measured using a stationary weather station at each lake. DW was converted to C by multiplying by 0.45 (Wetzel, 2001). Whole-lake production was calculated as the weighted averages of production rates from the different depths, accounting for the relative areal contribution of each habitat (roughly 25% <1 m depth, 25% 1–2 m depth, 50% >2 m depth).

This macrozoobenthos production approach provided higher values than two alternative established approaches (Banse & Mosher, 1980; Brey, 2012) and may thus be considered as a high-end estimate. To explore the maximum macrozoobenthos production, we repeated the calculations following Equation 1 but applying the maximum biomass of each macrozoobenthos taxon from the eight sampling dates.

2.6 | Fish

To estimate the biomass and production of fish, abundance data were derived from a 5-day mark–recapture approach conducted in October 2011, as described in Brothers, Hilt, Attermeyer, et al. (2013) and Mehner et al. (2016). Briefly, we caught fish with an electrofishing device (Bretschneider Spezialelektronik, Breitenbrunn, Germany) and tagged them using coded wire tags (Northwest Marine Technology, Inc., U.S.A.) that were inserted into the snout region. Population abundance was estimated using the Schnabel multiple-census approach, adjusted by Chapman (Ricker, 1975). The fish community was dominated by omnivorous fish, with roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) (both Cyprinidae) comprising 95% of the total abundance in both lakes, whereas sunbleak (*Leucaspius delineates*, Cyprinidae), tench (*Tinca tinca*, Cyprinidae), perch (*Perca fluviatilis*, Percidae) and pike (*Esox lucius*, Esocidae) were much less abundant (Scharnweber, 2013).

A scale analysis of the predominant fish species (roach) was conducted to estimate individual growth in 2011. To accomplish this, roach were caught in September and the distances between the nucleus and the annuli of three scales were measured using a measuring microscope (Quick Scope Vision Measuring Machine, Mitutoyo Corporations, Japan), and mean values were calculated. Length at age was back-calculated following Fraser (1916) and Lee (1920). Biomass and weight increments of the different cohorts, and hence production in 2011, were estimated using our own length–weight regressions (K. Scharnweber, unpublished data).

Production for the whole fish community was extrapolated according to the proportions of roach age classes on total biomass. These were estimated from a standardised fishing campaign using four Nordic multimesh gillnets which were installed perpendicular to the shoreline from dusk until dawn, and additional standardised electrofishing (applying 15 dips for 15 s at randomly chosen locations) (see Brothers, Hilt, Attermeyer, et al., 2013; Mehner et al., 2016 for details). Young of the year (YOY) fish were likely abundant (Hilt et al., 2015), however, we were not able to quantify their biomass and production.

2.7 | Food web

We compiled the described measurements and estimates into a quantitative food web for each lake. The food-web structure was derived using information gained in previous studies on the community composition of zooplankton (Lischke et al., 2016), macrozoobenthos (K. Scharnweber, unpublished data), and stable isotope analyses of crustacean zooplankton, macrozoobenthos and fish (Mehner et al., 2016). The emerging fluxes were analysed for plausibility. Phytoplankton and pelagic bacteria were considered to be the pelagic basal producers, and macrophytes, epiphytes, epipelon and sediment bacteria the benthic basal producers. Ciliates, which dominated the zooplankton biomass in our lakes (Lischke et al., 2016), and rotifers relied on phytoplankton and bacteria, while crustaceans fed on phytoplankton and ciliates. The maintenance of the high ciliate biomass required the consumption of the majority of the phytoplankton production, implying that phytoplankton settling was of minor importance in these shallow lakes. The low crustacean biomass was dominated by nauplii and copepodites as a consequence of a severe predation pressure by YOY fish (Hilt et al., 2015; Lischke et al., 2016). Previous stable isotope analyses of the few adult crustaceans suggested a predominant pelagic reliance, whereas macrozoobenthos and fish strongly relied upon benthic basal production (Mehner et al., 2016; Appendix S1). Consequently, pelagic contributions to macrozoobenthos and benthic contributions to zooplankton were considered marginal in our lakes. Similar results were reported in a previous study of the same lakes, as based on H, N and C stable isotopes (Syväranta, Scharnweber, Brauns, Hilt, & Mehner, 2016). Accordingly, we depict the pelagic and benthic food chains of both lakes as separated, although we are aware that adult crustaceans and some macrozoobenthos can be sufficiently mobile to transfer C between habitats in small lakes (e.g. Mahdy, Scharfenberger, Adrian,

& Hilt, 2014). The pelagic and benthic food webs were linked by omnivorous fish, which fed on both pelagic and benthic organisms (Scharnweber et al., 2013).

The phytoplankton and ciliate production was shared by multiple consumers and distributed according to the relative production of each consumer group. Particulate and dissolved organic carbon (PDOC) originating from several sources (Figure 1) were pooled and assumed to be taken up by pelagic and sediment bacteria. PDOC results from the exudation of all autotrophs, which was assumed to account for 4% of macrophyte GPP (Wetzel and others, 1972 in Hough & Wetzel, 1975) and 15% of the GPP for all other autotrophs (Gaedke & Straile, 1994). We further assumed that all consumers assimilate 67% of the ingested prey, the remains being excreted and entering the PDOC pool (Figure 1; see also Gaedke, Hochstädter, & Straile, 2002). Our approach is insensitive to deviating assimilation efficiencies as the resulting differences in unconsumed and excreted C balance each other out (Figure 1). The trophic efficiencies are not sensitive towards the assimilation efficiencies as long as some C remains unconsumed. The assimilated C was assumed to fuel animal production (50%) and respiration (50%) equally. We thus estimated that the C demand of the consumers was triple to their production rate (Gaedke et al., 2002). The difference between the C available to the consumers (i.e. the sum of the respective prey production) and the consumers' C demand was labelled "unconsumed C," and was allocated to the PDOC pool (Figure 1). The fraction of rotifer and crustacean production which was left over by omnivorous fish was considered to be consumed by YOY fish (see Mehner & Thiel, 1999). In addition, allochthonous C originating from emergent and floating-leaved macrophytes, terrestrial leaf litter and DOC from groundwater input and precipitation contributed to the PDOC pool (Brothers, Hilt, Attermeyer, et al., 2013). These inputs were quantified in 2010, but we were unaware of any reason for systematic deviations in 2011, the year of this study.

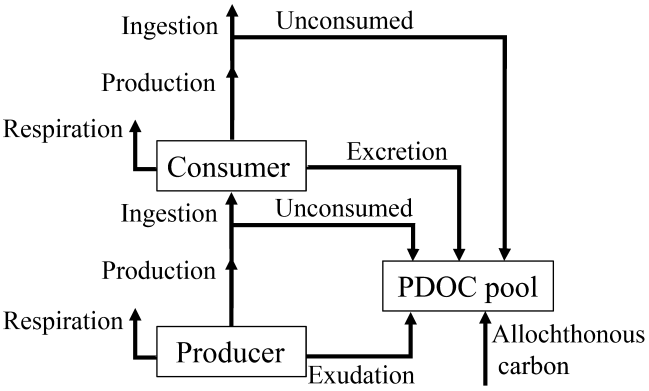


FIGURE 1 Fluxes to the pool of particulate and dissolved organic carbon (PDOC) originate from exudation by all primary producers, unconsumed primary producer and consumer production, consumer excretion and allochthonous carbon inputs

The trophic efficiencies were obtained by dividing consumer production by the sum of autotrophic and heterotrophic production separately for pelagic and benthic habitats. For comparative purposes, we also calculated trophic efficiencies exclusively between consumer production and autotrophic production. In order to compare pelagic and benthic trophic efficiencies, we defined metazooplankton (rotifers and crustaceans) as the pelagic and macrozoobenthos as the benthic top consumers of these restricted chains. Whole-lake trophic efficiencies were calculated relative to the lake-wide sums of autotrophic and bacterial production for three trophic consumer levels. Here, the production of primary consumers was thus the sum of metazooplankton and macrozoobenthos production, secondary consumers consisted of the production of omnivorous fish, and tertiary consumer production was represented by piscivorous fish.

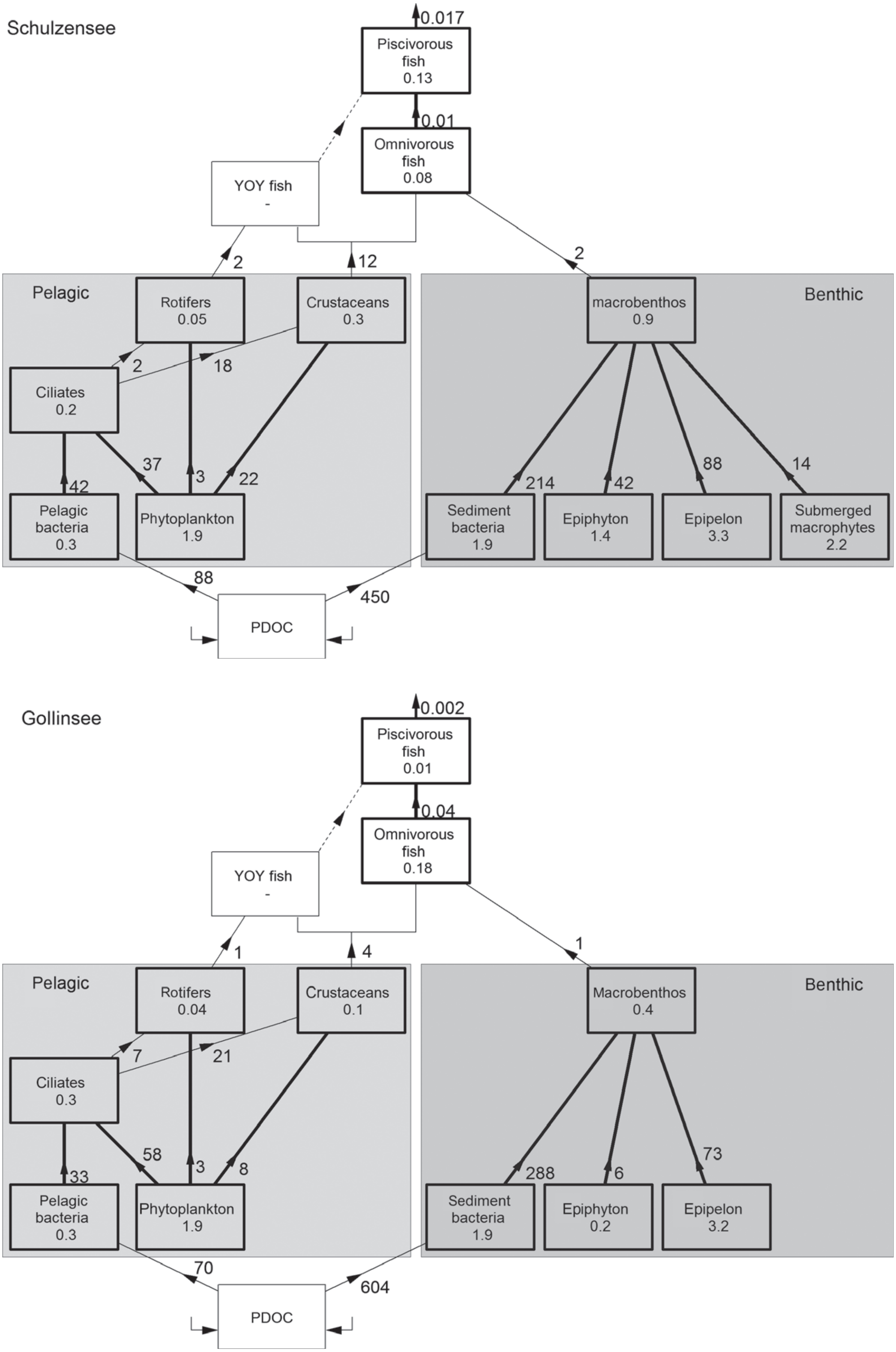
3 | RESULTS

3.1 | Biomass patterns and carbon fluxes between food-web components

The food webs compiled from the different measurements and estimates were mass-balanced in the sense that autotrophic and bacterial production (AP and BP, respectively) were sufficient to sustain the production of the animal consumers (numbers next to the arrows in Figure 2). Furthermore, the amount of C entering the PDOC pool via exudation, excretion, C unconsumed by animal consumers and allochthonous inputs was sufficient to balance the measured BP.

The overarching patterns in absolute biomasses and C fluxes between organismal groups were similar in both lakes (Figure 2). Within the pelagic food web, phytoplankton dominated the total biomass, having about seven times more biomass than pelagic bacteria and roughly four times more biomass than the zooplankton, which was dominated by ciliates. Phytoplankton production was roughly

FIGURE 2 Quantitative food webs including pelagic and benthic habitats of Lakes Schulzensee and Gollinsee for the period from April to October 2011 (213 days). Pelagic and benthic habitats were treated separately up to the zooplankton and macrozoobenthos level (grey boxes), while fish receive production from both habitats. Each organismal group is represented by a box including its average biomass (g C m^{-2}). The respective production data (g C m^{-2} growing per season) are shown next to the arrows which indicate that this production is potentially available to the subsequent consumer level. The phytoplankton and ciliate production was shared by multiple consumers and distributed according to the relative production of each consumer group. Bold boxes and arrows indicate measured biomasses and production rates, whereas values for boxes and arrows in thin lines were calculated. All fluxes to the particulate and dissolved organic carbon (PDOC) pool are indicated by the arrows entering the PDOC pool (cf. Figure 1). The presumably high biomass and production (dashed line) of young of the year (YOY) fish could not be estimated (see Section 4)


Schulzensee
0.017
Piscivorous fish 0.13
0.01
Omnivorous fish 0.08
YOY fish -
2
12
2
Pelagic
Rotifers 0.05
Crustaceans 0.3
Ciliates 0.2
2
18
37
3
22
42
Pelagic bacteria 0.3
Phytoplankton 1.9
Benthic
macrobenthos 0.9
214
42
88
14
Sediment bacteria 1.9
Epiphyton 1.4
Epipelon 3.3
Submerged macrophytes 2.2
88
450
PDOC
Gollinsee
0.002
Piscivorous fish 0.01
0.04
Omnivorous fish 0.18
YOY fish -
1
4
1
Pelagic
Rotifers 0.04
Crustaceans 0.1
Ciliates 0.3
7
21
58
3
8
33
Pelagic bacteria 0.3
Phytoplankton 1.9
Benthic
Macrobenthos 0.4
288
6
73
Sediment bacteria 1.9
Epiphyton 0.2
Epipelon 3.2
70
604
PDOC

twice the pelagic BP (Figure 2, numbers next to arrows). Ciliate production dominated consumer production of the entire zooplankton community. If split according to the estimated consumer production rates, the majority of the phytoplankton production (60% and 84% in Schulzensee and Gollinsee, respectively) was consumed by ciliates, while 46% and 72% (respectively) of the C available to metazooplankton (rotifers and crustaceans) originated from ciliates (Figure 2).

Benthic autotrophs (epiphyton, epipelon and submerged macrophytes) had the highest biomass of any group in the food webs of both lakes, whereas benthic (sediment) bacteria dominated the food webs of both lakes when considering production rates (numbers next to arrows in Figure 2). The biomass of macrozoobenthos was three times higher than the metazooplankton biomass, but metazooplankton production exceeded that of macrozoobenthos roughly by a factor of five in both lakes. Accordingly, more than 80% of the produced C available to fish originated from the pelagic pathway (Figure 2).

The food webs differed between both lakes in some details. In Schulzensee, the benthic AP was almost twice as high as in Gollinsee, in part due to the presence of submerged macrophytes and epiphyton, whereas the benthic BP in Gollinsee exceeded that of Schulzensee by 35%. Crustacean and macrozoobenthos biomasses, and thus production estimates, were at least twice as high in Schulzensee as in Gollinsee. Omnivorous fish biomass and production measurements were about three times higher in Gollinsee than in Schulzensee, while piscivorous fish biomass and production were roughly an order of magnitude lower in Gollinsee than in Schulzensee (Figure 2).

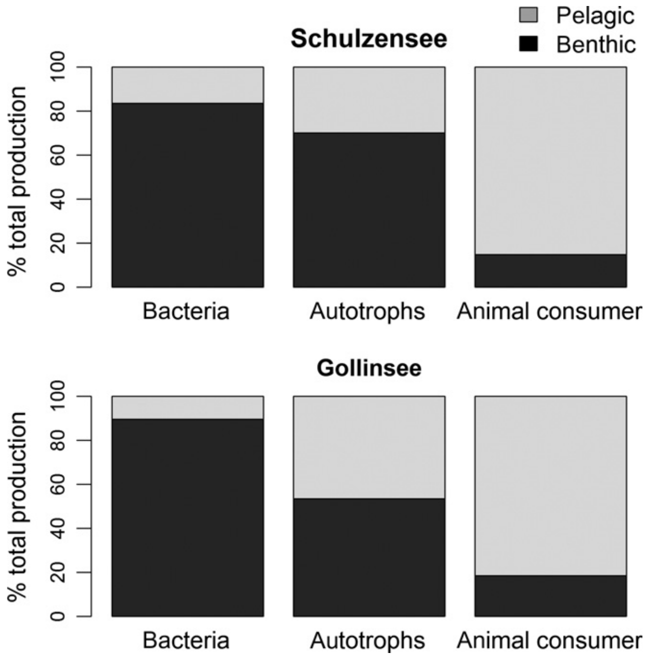


FIGURE 3 Relative contribution (in %) of benthic (black) and pelagic production (grey) to the total production of bacteria, autotrophs and animal consumers (metazooplankton and macrobenthos) in Schulzensee (top) and Gollinsee (bottom)

3.2 | Pelagic versus benthic carbon fluxes

Benthic bacteria contributed 84% and 90% to the entire bacterial production in Schulzensee and Gollinsee, respectively, and benthic autotrophs dominated the total AP (70% and 53%, respectively) (Figure 3). In contrast, primary consumer production (the sum of metazooplankton and macrozoobenthos) was mainly pelagic (85% and 82% in Schulzensee and Gollinsee, respectively, Figure 3). When the large ciliate production was included, the pelagic contribution to the whole-lake primary consumer production was raised to 94% and 97% in Schulzensee and Gollinsee, respectively.

To estimate the amount of unconsumed C in the food webs, we compared the total AP and BP in the pelagic and benthic zones with estimates of the C demands of metazooplankton and macrozoobenthos (Table 1). Both the absolute amount and the contribution of unconsumed-to-total available C were much larger in the benthic (98% and 99% in Schulzensee and Gollinsee, respectively) than in the pelagic food webs (60% and 84%). The majority of the C unconsumed by metazooplankton was presumably utilised by pelagic ciliates (Figure 2).

3.3 | Pelagic, benthic and whole-lake food-web efficiencies

The trophic efficiencies (consumer production/autotrophic and bacterial production) of metazooplankton were much higher (5%–23%) than those for macrozoobenthos (0.3%–1.7%) in both lakes (Figure 4). They were lower when including BP in addition to AP, resulting in pelagic efficiencies (metazooplankton production [P]/pelagic AP + BP) of 13% (Schulzensee) and 5.4% (Gollinsee). These were more than an order of magnitude higher than the efficiencies calculated for the benthic zone (macrozoobenthos P/benthic

TABLE 1 Carbon (C) budget of pelagic and benthic animal consumers in the two studied lakes. We assumed consumer C demand to be three times the respective production in order to account for losses by excretion and respiration. The C demand was related to the total available C (autotrophic + bacterial production) separately for the pelagic and benthic habitats by calculating the difference between available and demanded C, named unconsumed C by metazooplankton (rotifers and crustaceans) and macrobenthos. Additional consumers such as pelagic ciliates, benthic protozoa and meiobenthos may have utilized parts of the unconsumed C (see Figure 2 and Discussion). All values in g C m^{-2} season^{-1}

Lake	C budget	Pelagic consumer (metazooplankton)	Benthic consumer (macrobenthos)
Schulzensee	C demand	5 + 37	7
	Available C	104	358
	Unconsumed C	62	351
Gollinsee	C demand	4 + 12	4
	Available C	102	367
	Unconsumed C	86	363

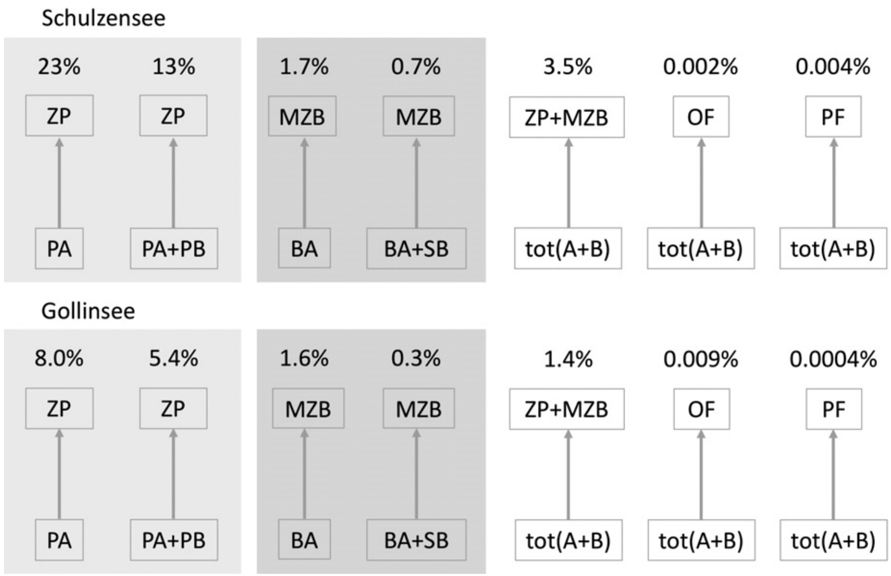


FIGURE 4 Trophic efficiencies (consumer production/prey production in %, numbers on top of food chain) for different pairs of producer and consumer groups. Efficiencies were calculated separately for the pelagic habitat up to the zooplankton level (left), for the benthic habitat up to the macrozoobenthos level (middle) and for the total food web up to the levels of primary, secondary and tertiary consumers (right) in Schulzensee (top) and Gollinsee (bottom). PA, pelagic autotrophs (phytoplankton); PB, pelagic bacteria; BA, benthic autotrophs (epiphyton, epipelon and submerged macrophytes; the latter only in Schulzensee); SB, sediment bacteria; ZP, metazooplankton (rotifers and crustaceans); MZB, macrozoobenthos; tot(A + B), total autotrophic and bacterial producers; OF, omnivorous fish; PF, piscivorous fish

AP + BP; Schulzensee 0.7%, Gollinsee 0.3%, Figure 4). When estimating macrozoobenthos production using maximum instead of mean annual biomass, rates of 3 and 7 g C m^{-2} growing per season were calculated for Gollinsee and Schulzensee, respectively. These maximum values increased benthic efficiencies from 0.3% to 0.8% in Gollinsee, and from 0.7% to 2% in Schulzensee, thus remaining substantially lower than pelagic efficiencies in both lakes.

Pelagic efficiencies were consistently higher in Schulzensee than in Gollinsee, whereas the benthic efficiencies were similar in both lakes if only AP was being considered. However, benthic efficiencies were likewise higher in Schulzensee than Gollinsee if BP was additionally included. The lake-wide trophic efficiency at the level of primary consumers (metazooplankton + macrozoobenthos P/whole lake AP + BP) was 3.5% in Schulzensee and 1.4% in Gollinsee. At the level of secondary consumers (omnivorous fish P/whole lake AP + BP), the efficiencies were low (0.002% and 0.009% in Schulzensee and Gollinsee, respectively), as were the overall food-web efficiencies at the level of tertiary consumers (piscivorous fish P/whole lake AP + BP), with Schulzensee at 0.004% and Gollinsee at 0.0004% (Figure 4).

4 | DISCUSSION

In contrast to our expectation, we demonstrated a striking discrepancy between the high contribution of benthic autotrophic and bacterial production (AP and BP, respectively) to the total basal production, and its low utilisation by macrozoobenthos in two eutrophic shallow lakes. The whole-lake AP and BP were dominated by benthic organisms in both lakes, in line with previous studies which have found benthic organisms to contribute substantially to whole-lake primary production (Althouse et al., 2014; Ask et al., 2009; Vadeboncoeur et al., 2002; Vander Zanden & Vadeboncoeur, 2002). In contrast, the dominant primary consumer production occurred in the pelagic zone, as metazooplankton (crustacean and rotifer) production was much higher than macrozoobenthos production. Benthic efficiencies (macrozoobenthos production/benthic AP + BP) were at least a factor of 10 lower than pelagic efficiencies (metazooplankton production/pelagic AP + BP), which implies that the vast majority of the benthic AP and BP remained unconsumed by macrozoobenthos. Our data thus indicate that these shallow lakes are essentially pelagic systems, at least when considering primary consumer production.

Our food webs, compiled from measured and estimated production values, were internally consistent with respect to the mass balances of both carbon pools as well as supply rates. First, the sum of AP and BP was sufficient to sustain the estimated animal consumer production. Second, the supply of autochthonous and allochthonous organic matter was calculated to sufficiently fuel the measured BP. Hence, we conclude that the disparity of pelagic and benthic efficiencies is a real phenomenon and not attributable to missing or imprecise data. When assuming a bacterial growth efficiency of 50% (Del Giorgio & Cole, 1998), about 30 g C m^{-2} growing per season of organic C would have remained unconsumed by sediment bacteria in both lakes. This value matches C burial rates measured in sediment cores in Schulzensee, but is lower than measured burial rates in Gollinsee (Brothers, Hilt, Attermeyer, et al., 2013), likely due to uncertainties in the measurements of BP, burial rates, or bacterial growth efficiencies themselves, which can range from 1% to 60% in natural systems (Del Giorgio & Cole, 1998).

The trophic efficiencies calculated in this study cannot be easily compared with those of other studies which either considered fewer groups of producers and consumers (Jonasson, 1992; Lindegaard, 1994; Vander Zanden et al., 2006), or used artificially assembled communities (Rowland et al., 2015). The pelagic efficiencies in both our study lakes were lower than in other studies (Gaedke & Straile, 1994) due to low crustacean biomasses (Lischke et al., 2016). Adult fish biomass was reduced by 16%–43% following partial fish winterkills the 2 years prior to our study period, reducing competition and predation for YOY fish, and consequently increasing predation pressure on crustaceans (Hilt et al., 2015; Lischke et al., 2016). Therefore, higher crustacean biomasses and production rates leading to increased fluxes of the basal production to crustaceans may be assumed once the adult fish biomass has again reached pre-winterkill levels. The low food-web efficiencies for secondary and tertiary consumers (fish production/whole-lake AP + BP) were also attributable to low fish biomasses (*c.* 0.2 g C m^{-2} equivalent to *c.* 20 kg fresh weight ha^{-1}) following the partial winterkills. In a subalpine lake, fish preferentially utilised large-sized macrozoobenthos over the smaller metazooplankton (Vander Zanden et al., 2006). High benthic contributions to fish diets seem to be common (Scharnweber et al., 2013; Vander Zanden, Vadeboncoeur, & Chandra, 2011; see also Appendix S1; Vander Zanden & Vadeboncoeur, 2002), but no study has compared this contribution with the relative share of benthic AP and BP to whole-lake production rates. To our knowledge, our study is the first to quantify natural pelagic and benthic efficiencies within the same ecosystem, considering the production of nearly all trophic groups including bacteria. Benthic BP was equal to or four times greater than the benthic AP in our systems, and we would not have detected these large differences between pelagic and benthic efficiencies had benthic BP not been explicitly considered.

To evaluate the robustness of our finding that the benthic transfer efficiency is much lower than the pelagic one against potential errors in our empirically determined production rates, we compared the empirically estimated trophic pyramids with theoretical pyramids assuming a 10% transfer efficiency (Lindeman, 1942). The empirical pelagic efficiencies largely corresponded to the theoretical 10% efficiency (Figures 4 and 5), the measurements differing only by a factor of less than two from the theoretically possible basal and primary consumer production (Figure 5). In contrast, again assuming a theoretical efficiency of 10%, the measured benthic basal production allowed for a 15–30 times greater macrozoobenthos production than that which was empirically determined. In turn, only 3%–7% of the measured benthic basal production would have been required to maintain the lakes' macrozoobenthos production (Figure 5) at an

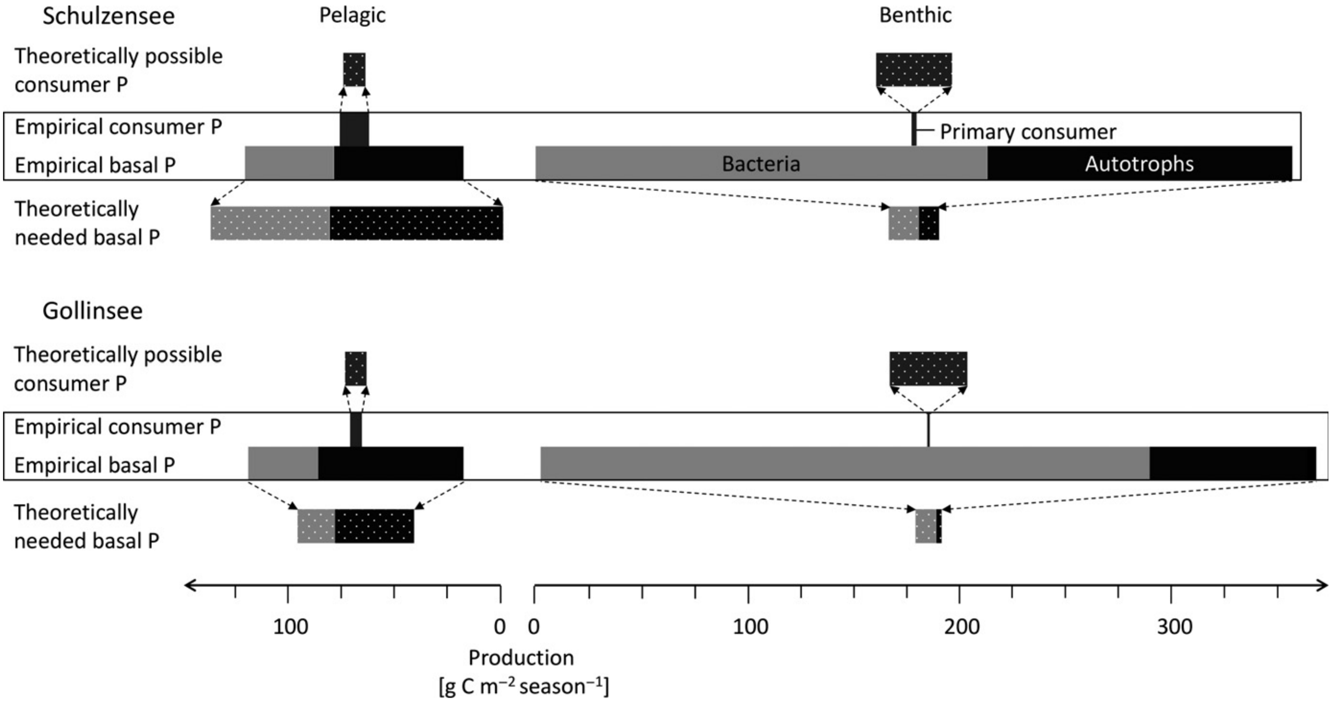


FIGURE 5 Trophic pyramids of the empirically determined production (P) (framed, cf. Section 2) compared to the theoretical P which assumes a 10% transfer efficiency (hatched bars) to evaluate the robustness of empirical data against potential errors in production estimates. The framed trophic pyramids represent the empirically determined basal (bacteria and autotrophs) and primary consumer (metazooplankton and macrobenthos) P in the pelagic and benthic habitats of Schulzensee (top) and Gollinsee (bottom). The theoretically possible consumer production was inferred from the measured basal production (above empirical pyramids) and the theoretically needed basal production from the calculated consumer production (below empirical pyramids) assuming a 10% transfer efficiency. Arrows indicate the necessary enlargement or shrinking of the empirically determined production to correspond to the 10% transfer efficiency

efficiency of 10%. As such, a large difference between theoretical and empirical benthic production rates is unlikely to be solely caused by sampling errors, we argue that the large difference between calculated pelagic and benthic trophic efficiencies represents a robust pattern in these two eutrophic shallow lakes. These calculations also indicate that uncertainties in biomass and production estimates of producers and consumers must be large to account for the strong deviations between the theoretical and empirically observed trophic transfer efficiencies in the benthic habitat.

These surprisingly low benthic trophic efficiencies emerged from detailed empirical measurements and calculations, but contrast many recent studies on strong benthic contributions to lake food webs (Vadeboncoeur et al., 2002; Vander Zanden & Vadeboncoeur, 2002). Our data do not offer unequivocal explanations for the underlying mechanisms. Therefore, we discuss subsequently, and in part speculatively, four processes which may have contributed to lower efficiencies in the benthic versus pelagic habitats:

1. The quality of benthic prey might be lower than that in the pelagic habitat because bacteria, which comprise the majority of the benthic basal production, are of inferior biochemical quality (in terms of polyunsaturated fatty acids) compared to eukaryotes, despite their high nutritional quality (high P:C ratios) (Fagerbakke, Heldal, & Norland, 1996; Müller-Navarra, 2008). However, the benthic autotrophic production alone, comprised mainly of diatoms and green algae in the periphyton (following detailed pigment analyses from Gollinsee in 2013, S. Hilt, unpublished data), was about 70 times higher than the macrozoobenthos production and was thus alone sufficient to fulfil the biochemical requirements of macrozoobenthos. Pelagic and benthic autotrophic producers were expected to be of equal nutritional quality (average weight C:N ratios: epipelon and epiphyton 7.3:1, seston 7:1; unpublished data). Consequently, we assume food quality was unlikely to limit the conversion of benthic basal to macrozoobenthos production, but nevertheless acknowledge the lack of detailed measurements.
2. Pelagic and benthic habitats may be energetically linked, and this may bias the habitat-specific efficiencies. High benthic contributions to pelagic metazooplankton were unlikely as juvenile stages dominated the crustacean community. In turn, macrozoobenthos feeding on pelagic autotrophs and bacteria would have further increased the discrepancy between pelagic and benthic efficiencies. Omnivorous fish species in both lakes relied more on benthic than on pelagic production (Scharnweber et al., 2013), but due to overall low fish biomasses (Hilt et al., 2015), their top–down control on macrozoobenthos was low and thus their feeding would not explain the low benthic efficiencies.
3. The larger benthic consumers have lower biomass turnover rates than their pelagic counterparts (Banse & Mosher, 1980), which may in principle be compensated for by higher macrozoobenthos biomasses to achieve similar efficiencies in both habitats. However, the macrozoobenthos biomass only exceeded the metazooplankton biomasses by a factor of three. Nevertheless, the observed macrozoobenthos biomasses were comparable to those in other lakes in northeast Germany (Brauns et al., 2011; O. Miler, personal communication, IGB Berlin) and in the northern U.S.A. (Craig, Jones, Weidel, & Solomon, 2015) and hence are likely not caused by incomplete sampling. The low macrozoobenthos production rates in both lakes were substantially below the amount required to achieve equally efficient pelagic and benthic food webs, although they were not likely limited by food availability or quality. Low benthic oxygen concentrations and sediment texture may have limited the available habitat for macrozoobenthos (Craig et al., 2015; Lindegaard, 1994), as indicated by the absence of macrozoobenthos in the deeper lake areas, representing roughly 50% of the total lake area. Indeed, sediments were muddy throughout the lakes and the oxygen concentration immediately above the sediments in deeper areas dropped to anoxic levels in both lakes several times in 2011 (Brothers et al., 2014 and S. Brothers, unpublished data). In line with this, the submerged macrophytes in Schulzensee facilitated higher oxygen concentrations and potentially provided shelter and food for macrozoobenthos (Jeppesen, 1998), resulting in a twofold higher macrozoobenthos biomass and higher benthic efficiencies than in Gollinsee, albeit the between-lake difference was minor compared to the large discrepancy between the pelagic and benthic efficiencies. Accordingly, benthic efficiencies still remained a tenth of the pelagic efficiencies even when considering solely autotrophic, bacterial and macrozoobenthos production in the more oxygenated littoral zone of Schulzensee.
4. Potential additional trophic levels, such as benthic protozoa and meiobenthos, were not quantified. For pelagic habitats, it is well established that ciliated protozoa are key grazers of pelagic AP and BP (Sommer et al., 2012). Our calculated pelagic carbon fluxes and efficiencies confirmed that metazooplankton derived a substantial proportion of the pelagic AP and BP via ciliates. Additional intermediate trophic levels such as ciliates can lower the overall food-web efficiency by providing further losses via excretion and respiration. In turn, benthic food webs may appear inefficient due to the exclusion of potential additional trophic levels, such as benthic protozoa and meiobenthos, whose production is difficult to quantify. However, potential intermediate production is incorporated automatically when comparing pelagic and benthic efficiencies at the level of metazooplankton and macrozoobenthos. For example, a linear benthic food chain would consist of bacteria and autotrophs, protozoa, meiobenthos and macrozoobenthos. This trophic chain would have one trophic level more than the pelagic food chain, which may partially explain why benthic trophic efficiencies are lower than those in the pelagic zone. Nevertheless, in our lakes the majority of the macrozoobenthos production arose from organisms, such as Gastropoda and Diptera, which feed directly on autotrophic producers, and potentially any protozoa associated with them. Accordingly, a predominantly short benthic food chain with two to three trophic levels is more likely, as has been suggested for a Wadden Sea ecosystem (Evrard et al., 2010). Alternatively, potentially neglected consumer biomasses at the same trophic

level as macrozoobenthos would enhance the calculated benthic efficiency. The few available studies of lake and stream ecosystems (Appendix S2) suggest that the sum of additional benthic protozoan and meiobenthos production would roughly double the macrozoobenthos production. Accordingly, total benthic consumer production would be three times greater than the rates estimated for macrozoobenthos alone. Applying this ratio to our lakes would triple our benthic efficiencies (2.1% in Schulzensee and 0.9% in Gollinsee, assuming that all benthic consumers occupy the same trophic level). Accordingly, the overall benthic efficiencies would remain low, and substantially below the pelagic efficiencies. We thus strongly encourage future studies to specifically measure biomass and production rates along with feeding links and transfer efficiencies within the benthic food web, with a particular focus on understudied groups of protozoa and meiobenthos.

The previously discussed four processes do not convincingly explain why the benthic efficiencies in both lakes were much lower than the pelagic ones. However, in contrast to several previous studies (Jia et al., 2012; Rowland et al., 2015), we included the benthic BP into our quantitative lake food webs. Together with the benthic AP, it provided a large amount of basal production, which was not efficiently consumed by macrozoobenthos. Consequently, benthic autotrophs and bacteria accumulated the majority of the whole-lake biomass (roughly two-thirds in both lakes) and likely large amounts of nutrients. Benthic bacteria are able to cope with low oxygen concentrations and hence may have efficiently utilised the benthic AP and freshly settled organic carbon in both lakes. Furthermore, grazing losses of bacteria may be low because the abundance of most benthic bacterivores is reduced at low oxygen concentrations (Auer, Kiertucki, & Arndt, 2003). Likewise, the grazing impact on bacteria by benthic protozoans is generally low (Starink, Bär-Gilissen, Bak, & Cappenberg, 1996), which points to an inefficient microbial loop in the benthic zone. Alternatively, viral abundances were reported to be high in freshwater and marine sediments, and could thus potentially cause a high bacterial mortality (Danovaro et al., 2008; Rastelli et al., 2016) and internal C cycling in sediments (Pan et al., 2014). Therefore, although not measured in detail, the evidence accumulated from our data suggests that the previously neglected benthic bacterial production and the interactions within the benthic microbial loop may play a key role in understanding the energetics of shallow lake food webs. This includes the processes determining the fate of the organic carbon fraction which was not consumed by the macrozoobenthos. Whether it is immediately recycled or buried in the sediments, is highly relevant for the role of shallow lakes in the global carbon cycle (Tranvik et al., 2009).

5 | CONCLUSION

We quantified the C fluxes in the pelagic and benthic food webs in two lakes and demonstrated that the pelagic energy transfer was substantially more efficient than the benthic one. From a theoretical perspective, this remains true when considering the food quality, pelagic-benthic links, the oxygen concentration and additional benthic consumer groups as determinants of the benthic efficiency. Our study is one of the first studies to incorporate benthic bacteria into lake food-web models. Sediment bacteria were important at the producer level, but their high production was very inefficiently transferred to macrozoobenthos. The discrepancy between the pelagic and benthic efficiencies was a consistent phenomenon in both studied lakes, while between-lake differences were minor. Testing the generality of these findings requires follow-up studies in a variety of aquatic ecosystems with differences in the pelagic and benthic food-web structure and autochthonous productivity.

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