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# Trophic Transfer Efficiency in Lakes

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## ABSTRACT

Trophic transfer efficiency (TTE) is usually calculated as the ratio of production rates between two consecutive trophic levels. Although seemingly simple, TTE estimates from lakes are rare. In our review, we explore the processes and structures that must be understood for a proper lake TTE estimate. We briefly discuss measurements of production rates and trophic positions and mention how ecological efficiencies, nutrients (N, P) and other compounds (fatty acids) affect energy transfer between trophic levels and hence TTE. Furthermore, we elucidate how TTE estimates are linked with size-based approaches according to the Metabolic Theory of Ecology, and how food-web models can be applied to study TTE in lakes. Subsequently, we explore temporal and spatial heterogeneity of production and TTE in lakes, with a particular focus on the links between benthic and pelagic habitats and between the lake and the terrestrial environment. We provide an overview of TTE esti-

mates from lakes found in the published literature. Finally, we present two alternative approaches to estimating TTE. First, TTE can be seen as a mechanistic quantity informing about the energy and matter flow between producer and consumer groups. This approach is informative with respect to food-web structure, but requires enormous amounts of data. The greatest uncertainty comes from the proper consideration of basal production to estimate TTE of omnivorous organisms. An alternative approach is estimating food-chain and food-web efficiencies, by comparing the heterotrophic production of single consumer levels or the total sum of all heterotrophic production including that of heterotrophic bacteria to the total sum of primary production. We close the review by pointing to a few research questions that would benefit from more frequent and standardized estimates of TTE in lakes.

**Key words:** stoichiometry; production rates; trophic position; fatty acids; land–water coupling; food-web models.

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## INTRODUCTION

Trophic transfer efficiency (TTE) is a unitless property, usually calculated as the ratio of production rates between two consecutive trophic le-

vels. In essence, TTE measures how efficiently energy is passed up the food chain. Although conceptually simple, estimating TTE demands high quantities of data (see below), and therefore only few reliable TTE estimates for freshwater systems are available. In marine environments, TTE has been studied particularly to understand the amount of primary production needed to generate the observed annual fisheries yield or fish production (Pauly and Christensen 1995; Stock and others 2017; Eddy and others 2021). Among several marine regions, fisheries yield can vary by two orders of magnitude, whereas primary production at the base of fish production varies only fourfold (Stock and others 2017). Originally, TTE in marine food webs was estimated to be around 10% per trophic step (Pauly and Christensen 1995), but more recent calculations report substantial variation (Barnes and others 2010; Stock and others 2017). According to a recent review, processes at the level of individuals, populations and ecosystem were identified as affecting TTE in marine systems (Eddy and others 2021).

In contrast, no such synthesis is available for freshwater systems. Here, we focus our attention on lakes, but would like to mention that studies of trophic efficiency and interaction strengths in lotic systems have likewise been conducted (for example, Bellmore and others 2015; Bumpers and others 2017; Siders and others 2021). Lakes and their food webs differ from oceans in two features at the ecosystem level, which are important for TTE. First, the contribution of benthic habitats to lake-wide processes is higher than in oceans, which except in coastal regions are usually dominated by pelagic processes. Second, the bidirectional connectivity of lakes with their terrestrial environments is likewise more intense. Both features are linked with the detritus pool and the microbial loop in lakes, and hence these processes are comprehensively covered in our review.

We start with a summary of the variables that must be measured for estimating TTE (production and trophic position) and briefly cover potential differences in TTE estimates with respect to ecological efficiencies and nutritional or compound-related constraints. We extend the perspective on TTE by elucidating how organismal size distributions and food-web models are linked with TTE. The next part of our review analyses the temporal and spatial heterogeneity of production and TTE estimates. In particular, we focus on primary and secondary production rates in benthic and pelagic lake habitats, and the potential subsidy of these production rates by terrestrially derived energy. In

this context, we discuss the range of TTE estimates for single trophic links or for lake food webs obtained from published studies. Finally, we elucidate the ambiguity with respect to the way TTE is calculated and interpreted, and we suggest that TTE can be seen as either mechanistic approach to reflect energy flows between groups of organisms, or as the food-chain and food-web efficiency by which ecosystems transform energy from primary into secondary production. Overall, we demonstrate that TTE might be a useful concept to link food-web structure and ecosystem functions of lakes. However, the estimation of TTE is far from simple, and several structures and processes in lakes have to be explored in more detail to understand whether TTE can be used for systematic comparisons between lakes.

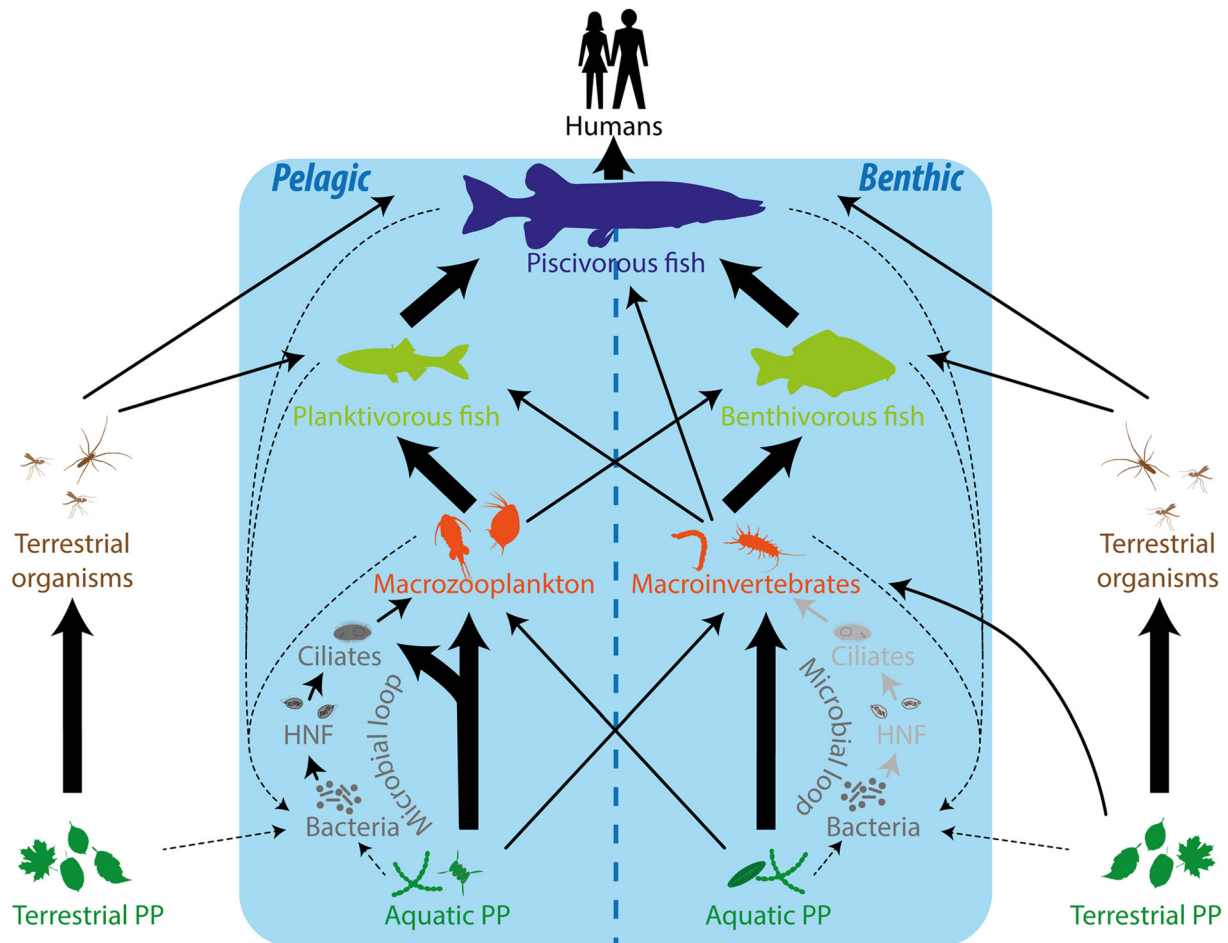
## ESTIMATING TTE: MEASURED PROCESSES AND MAJOR METHODOLOGICAL ADVANCES

Estimating TTE requires reliable estimates of production rates of two consecutive trophic levels, usually with units of biomass (or carbon (C) or energy) per area or volume per time. Trophic levels are here considered groups of primary producers or consumers of first, second, third or higher order (see Figure 1 for an overview). If production rates can be measured directly, estimates of population abundances or biomasses are not required. Accordingly, we briefly cover the methods to estimate primary and secondary production rates, and recent methodological advances that may contribute to ease quantifications of these estimates. Second, sufficient information on the quantitative food-web structure informing who eats whom (and to what extent) is required (Figure 1). This informs about the number of assimilation steps resource items have passed and thus about the precise trophic position (TP) of an individual consumer or consumer group. The importance of precisely estimating TP for estimating TTE has been underappreciated, and we cover a few developments in methodology that may help in overcoming this limitation.

### Measurement of Production

#### *Primary Production*

Primary production is the formation of biomass via photosynthesis. Gross primary production (GPP) rates in lakes are commonly measured using the diel oxygen curve technique (Staehr and others 2010; Hoellein and others 2013), though phyto-



**Figure 1.** Overview of the complex food webs of lakes, combining pelagic and benthic food webs including their microbial loops, their linkages by fishes, and the contribution of terrestrial primary production and organisms to the lake food web. Solid black/grey arrows indicate carbon/energy flow, with arrow thickness reflecting flow rate. Light grey arrows in the benthic microbial loop indicate that this pathway is not well described yet. Dashed arrows indicate recycling of carbon and nutrients via the microbial loop. PP = primary production, HNF = heterotrophic nanoflagellates.

plankton production was historically estimated using  $^{14}\text{C}$  with both methods yielding similar results (Lottig and others 2022). Littoral-benthic GPP is often under-represented in assessments of lake primary production rates (reviewed by Brothers and Vadeboncoeur 2021), but can be accounted for by measuring oxygen dynamics or  $^{14}\text{C}$  incorporation in sealed light/dark or multi-depth chambers (Devlin and others 2016) as well as modelling approaches (Vadeboncoeur and others 2008; Brothers and others 2016) incorporating fluorescence-based rapid light curve measurements (Jassby and Platt 1976).

## Secondary Production

Secondary production is the formation of heterotrophic biomass over time (Benke and Huryn,

2007) by unicellular microorganisms (bacteria, protists), fungi and animals.

### *Bacterial Production and the Microbial Loop*

Bacteria include a large variety of 'living styles' and energy sources with photoautotrophs (= primary producers included in the measurement of primary production, see above) and chemosynthetic bacteria. New basal biomass or energy comparable to that produced by autotrophic photosynthesis (fixation of  $\text{CO}_2$  by sunlight) is generated only by the group of chemoautotrophic microorganisms, which use  $\text{CO}_2$  as C source, and either inorganic (chemolithoautotrophs) or organic (chemoorganoautotrophs) compounds as electron donor. Production rates of these bacteria and archaea are measured as dark carbon fixation (DCF) using radioactive inorganic carbon ( $\text{H}^{14}\text{CO}_3$ ). If the

C source for chemosynthesis is organic (chemo-heterotrophs) and of autotrophic origin, this C is re-used or recycled by microorganisms within the lakes and hence does not represent a new basal C resource. If the C is from allochthonous sources (outside of the aquatic system, such as terrestrial primary production), it can substantially augment autochthonous (in-lake) C fixation, resulting in higher secondary production than what would be possible with only autochthonous primary production.

Although there are methods to count and measure bacterial biomass with epifluorescence microscopy after staining with DNA/RNA stains (Hobbie and others 1977), the classical (since the 1980s) and still most commonly used approaches to measure bacterial production are radioisotope techniques using thymidine or leucine ( $^3\text{H}$  or  $^{14}\text{C}$ ) incorporation into DNA or protein (Fuhrman and Azam 1980; Kirchman and others 1985). These techniques are used to measure production of pelagic (Simon and Azam 1989), sediment and periphytic bacteria (Buesing and Gessner 2003). To replace radioisotope tracers, alternative techniques have been developed, such as the incorporation of bromodeoxyuridine (BrdU) into DNA by means of immunological detection (Steward and Azam 1999), or bio-orthogonal non-canonical amino acid tagging (BONCAT) based on the *in vivo* incorporation of artificial amino acids that carry modifiable chemical tags into newly synthesized proteins (Beatty and others 2005).

The autochthonous and allochthonous dissolved organic matter (DOM) consumed by chemo-heterotrophic bacteria is re-integrated into the classical food web (that is, based on grazing of autotrophs by animals) via the microbial loop (Figure 1), linking heterotrophic nanoflagellates (HNF) with higher trophic levels, including ciliates and rotifers (Fenchel 1982; Azam and others 1983). Therefore, estimating production rates of HNFs, ciliates and rotifers is crucially needed to calculate the TTE of the microbial loop and the C transfer from the microbial loop to macroorganisms in pelagic or benthic habitats. However, this approach is laborious because all groups of microorganisms contain several trophic levels (Wieltschnig and others 2003; Work and others 2005). *In situ* growth rates of HNF, ciliates and other protozoans can be measured using diffusion chambers where predators are removed but light, nutrients and prey may enter (Weisse 1997). Additionally, in analogy to larger organisms, the production rates may be inferred from biomass measurements and laboratory-derived growth rates. This may, however, yield an

overestimation as food shortage may substantially reduce the growth rates realized *in situ*. Finally, the production rates of other heterotrophic microorganisms such as aquatic fungi are usually not considered in lake studies, even though they may be elevated and potentially ecologically significant (Grossart and others 2019; Hassett and others 2019).

#### *Secondary Production of Invertebrates and Vertebrates*

A comprehensive methodological overview on secondary production of aquatic invertebrates and vertebrates is provided by Dolbeth and others (2012). There are three methods that differ in data requirements and precision. If cohorts can be discerned for a given taxa, cohort approaches such as the increment summation method are the method of choice (Benke and Huryn 2010). The size frequency method (Hynes and Coleman 1968) is suitable if cohorts cannot be followed due to having multiple overlapping generations per year or taxonomic difficulties allowing for identification to genus level only. Finally, short-cut methods use regression analysis to examine the relationship between production, production-to-biomass ratio (PR/B) or growth rate and more easily measured variables, such as lifespan, temperature or body size (Benke and Huryn 2010). For zooplankton specifically, measurements on the moulting enzyme chitinase in the water may provide a powerful alternative to the methods mentioned above (Sastri and others 2013).

Estimates for fish production do not differ substantially from those described above for macroinvertebrates (Dolbeth and others 2012; MacLeod and others 2022). The major challenges are reliable estimates of fish densities and biomasses, because many passive fishing gears (gillnets, fyke nets) rely on fish activity to catch them and hence do not allow inference on the fished area or volume. In contrast, active fishing gear (midwater or bottom trawls, seine nets) is moved over defined distances and provide fish density estimates per area or volume (Winfield 2022). For cohort production methods, fish size (and age) must be determined. In cases where cohorts cannot be discerned from multi-modal length distributions, individual ageing of fish is required, usually based on annual increments of hard structures (otoliths, scales). A promising method to obtain reliable fish density and size estimates simultaneously is the application of hydroacoustics (Simmonds and MacLennan 2005), although these devices cannot distinguish between different species of fish and provide only

total community abundance, biomass and size distributions. However, species composition can be 'ground-truthed' with traditional capture methods (for example, Williamson and others 2018).

In essence, aquatic ecologists have made only modest progress with respect to estimating secondary production of invertebrates and vertebrates in aquatic food webs, and we must expect substantial uncertainty when applying production rates for TTE estimates. Measuring the heterotrophic production of unicellular organisms (bacteria, protozoa) is as uncertain as that of metazoans, but there seems to be more technological advancement that may pave the way for improvements. Estimating primary production might be more reliable, in particular for pelagic phytoplankton, but the contribution of macrophytes and periphyton to lake-wide primary production is still more difficult to obtain.

### Estimation of Trophic Position

Trophic position is the exact, non-integer value of an organism in the food chain, based on the diet composition of the organism. If PR denotes production, TP denotes trophic position, subscript *r* refers to resources, and *c* refers to consumers, TTE can be expressed as

$$\text{TTE} = \frac{\text{PR}_c/\text{PR}_r}{\text{TP}_c - \text{TP}_r} \quad (1)$$

In the context of TTE estimates, TP is expressed as integers in accordance with traditional food-web categories or trophic levels, that is, TP = 1 corresponds to primary producers, TP = 2 to primary consumers, TP = 3 to predators, and TP > 4 to higher-order predators that feed on other predators. In that case, the denominator of Equation (1) is exactly equal to one for consecutive trophic levels. However, a higher accuracy of TTE estimates can be achieved if non-integer TPs of the interacting trophic levels are estimated, in particular when consumers feed on more than one trophic level.

Trophic position can be quantified by gut content and stable isotope analysis. Gut content analysis works particularly well for predators and provides insight into short-term diets. However, gut content analysis is based on ingested prey and may not necessarily equate to assimilated prey (Traugott and others 2013). Because of its flexibility and utility, analysis of natural abundance stable isotopes (SIA) has become one of the leading techniques for assessing TP. Estimating TP using stable isotopes of nitrogen builds upon the principle that the heavier isotope ( $^{15}\text{N}$ ) becomes enriched

with each trophic transfer. Using  $\delta^{15}\text{N}$  as a tracer for TP comes with at least three assumptions that induce uncertainty in the TP estimate. First, SIA-based TP requires setting a trophic baseline, from which a given consumers' TP is inferred. Setting such baselines is notoriously difficult due to  $\delta^{15}\text{N}$  differences in the various pools of organic matter at the base of the food web. Moreover, the  $\delta^{15}\text{N}$  of primary producers can be highly variable in space and time (Syväranta and others 2008) due to differences in N sources for primary production (Finlay and Kendall 2007), but also taxonomic differences (Vuorio and others 2006). A way to reduce the spatio-temporal uncertainty is to set independent baselines for each food web and use primary consumers'  $\delta^{15}\text{N}$  as the baselines. Primary consumers integrate  $\delta^{15}\text{N}$  variation over larger spatio-temporal scales than primary producers and thus reduce baseline uncertainty (Kristensen and others 2016). Second, SIA-based estimates of TP rely on the assumption of a rather constant increase in  $\delta^{15}\text{N}$  between consecutive trophic levels, that is, the trophic discrimination factors (TDF). Recent reviews show that the variation around the average TDF of  $\delta^{15}\text{N}$  can be large (Brauns and others 2018) due to a variety of potentially co-occurring mechanisms such as resource quality, consumer identity and physiology and tissue type that are analysed (Caut and others 2009; Scharnweber and others 2021a). Third, there are several mathematical methods available to estimate TP from SIA measurements (Kjeldgaard and others 2021). Each method has its inherent assumptions, and the TP estimate may vary with the chosen model. Similar to the production estimates, we recommend propagating all uncertainties through the calculations and using methods that produce distributions of TP rather than integers (Quezada-Romegialli and others 2018).

Within the past decade, development of compound-specific stable isotopes, that is, the analysis of stable isotopes of specific amino acids, may overcome the inherent problems associated with variation in  $\delta^{15}\text{N}$  at the base of the food web. Trophic fractionation values vary among individual amino acids including those for which  $\delta^{15}\text{N}$  changes from one trophic step to another (for example, glutamic acid, valine, leucine, aspartic acid, isoleucine) and those that remain unchanged (for example, phenylalanine, lysine, methionine, tyrosine) and therefore provide an  $^{15}\text{N}$  baseline value that may allow an estimation of trophic position of consumers (McClelland and Montoya 2002; McMahan and McCarthy 2016). However, similar to the application of bulk  $\delta^{15}\text{N}$ , an estimate of the

amino acid-specific trophic fractionation factor is crucial to adequately allow the positioning of a consumer on a precise trophic position. Apparent differences, especially between vascular and non-vascular plants at the base of a more complex aquatic food web, may include uncertainties and great care should be applied when choosing the specific fractionation factors (Ramirez and others 2021).

A novel approach to overcome the limitation described above is additions of  $^{15}\text{N}$  tracers with enrichment levels above 1000‰. Together with recent improvements in modelling approaches,  $^{15}\text{N}$  tracers allow for the simultaneous quantification of N fluxes and their uncertainty and facilitate model comparisons on the choice of consumers between particular resources as the baseline for estimating their TP. The conversion of N-fluxes into C-fluxes (the typical unit of TTE estimates) is unresolved; here stoichiometric constraints (for example, C:N ratio of consumer tissue) and the correlation between N-content and the content of essential fatty acids (FAs) may be important (see below).

## EFFECTS OF ECOLOGICAL EFFICIENCIES, STOICHIOMETRY AND FATTY ACID COMPOSITION ON TTE

### Ecological Efficiencies

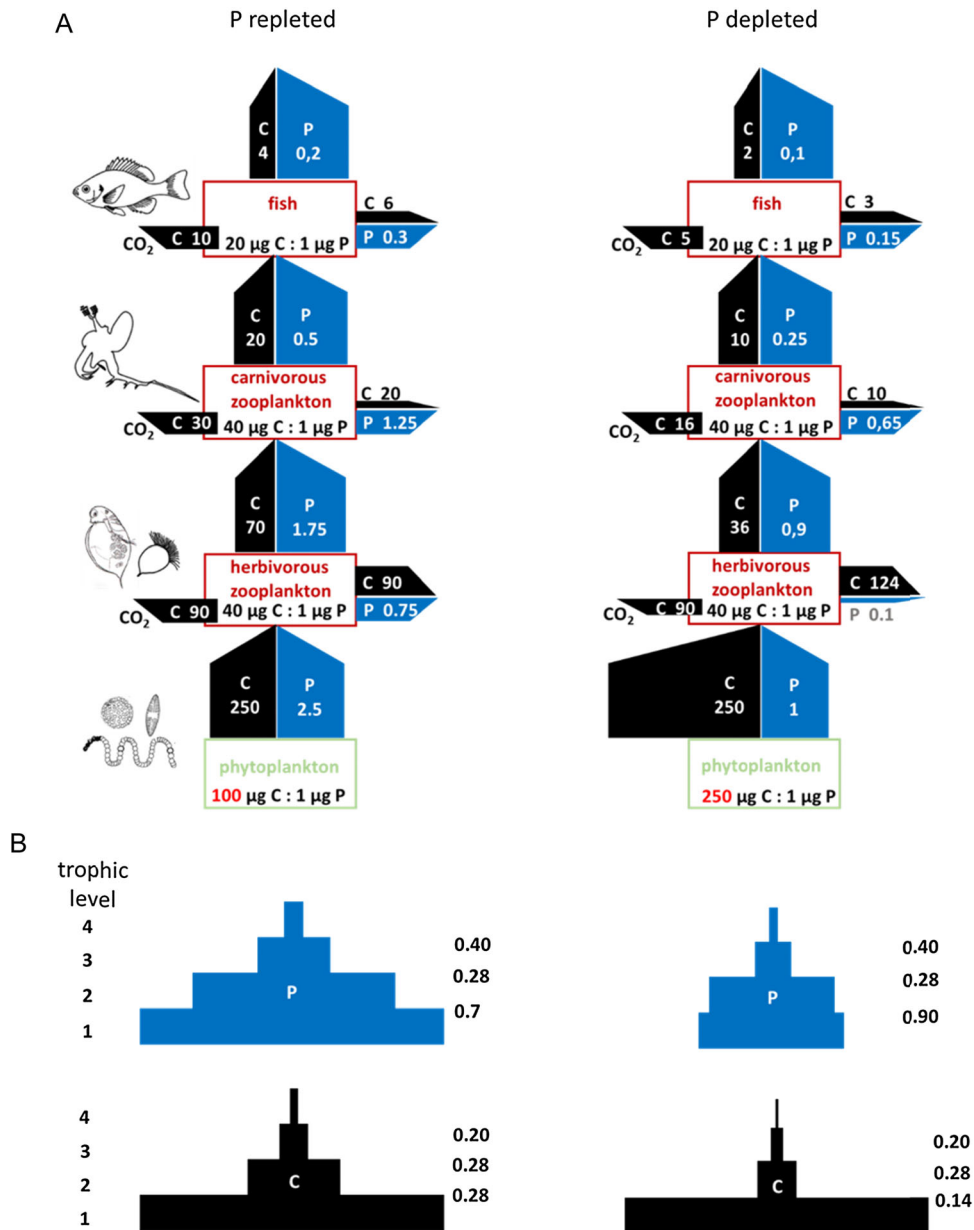
Quantification of TTE uses production rates. However, production rates of organisms are much smaller than their ingestion rates. Undigested parts of ingested food are egested (as faeces, at least in organisms with defined digestive, circulatory, and excretory systems), whereas assimilated substances are either excreted (as urine), used to cover the respiratory needs, or are converted into new consumer biomass, including somatic growth and reproduction (Figure 2A). Losses by egestion are typically high for organisms feeding on items that are difficult to digest, for example vascular plant tissue rich in complex substances such as lignin. Whereas most of this egested particulate material is channelled into the detritus pool, some compounds excreted by animals can be directly used by primary producers or microbes because they are soluble (for example, DOC and inorganic nutrients) (Sterner and Elser 2002). Respiration is the release of chemical energy from organic matter, used either to enable synthesis of new biomass or to maintain the basic metabolic functions that sustain life. This basal respiration is relatively low for unicells and invertebrates, increases for ectothermal vertebrates (fish, amphibians, reptiles), and is very

high for endotherms. Acquiring and digesting food is energy-consuming, and hence respiratory costs of activity are higher than basal metabolic costs for many animals. Proper consideration of activity respiration prevents modelling unrealistically high TTEs (Kath and others 2018). Furthermore, non-grazing mortality due to lethal environmental conditions, physiological death or inadequate nutrition, diverts energy from the transfer process and hence reduces TTE. Energy from non-grazing mortality is likewise channelled into the detritus pool.

Several ecological efficiencies commonly used in food-web analysis reflect the flow of energy through individuals and populations. The gross growth efficiency  $K_1$  is the ratio of biomass production to biomass ingested (PR/IN). For energy,  $K_1$  rarely exceeds 30–35% under natural conditions and often is considerably lower. The net growth efficiency of an organism ( $K_2$ ) is defined as the ratio of new biomass produced to the amount of assimilated biomass (PR/A). This efficiency has a maximum value of about 50% for small organisms but is much lower for large organisms (for example, ectothermic fishes, endothermic birds or mammals). Finally, the consumption efficiency represents the ratio between the amount of energy ingested by the upper trophic level and the total production at the next lower level (IN/PR<sub>-1</sub>). Thus, it accounts for the non-grazing mortality. This efficiency is low if the material produced is hard to ingest or digest or if there are few consumers which can exploit the prey production at that time and location.

### Stoichiometric Constraints

Tissue stoichiometry (essentially the ratios between carbon (C) and the nutrients nitrogen (N) or phosphorus (P)) may differ strongly between aquatic organisms and can be temporally highly variable. Bacteria are generally rich in nutrients but their stoichiometry may vary considerably (Hochstädter 2000). Depending on nutrient and light availability, autotrophs may have several fold higher C:nutrient ratios than heterotrophs (Elser and others 2000), which may vary seasonally by a factor of four in the same lake, and more than tenfold in laboratory cultures (Hochstädter 2000). In aquatic macrophytes, N content is a major determinant of food quality for herbivores, but secondary compounds may serve as anti-herbivore defences (Bakker and others 2016). Accordingly, TTE may be constrained by nutrients (N or P) rather than C in herbivores feeding on strongly



nutrient-depleted autotrophs (Figure 2) (Gaedke and others 2002). Nutrient limitation of herbivores may be substantially reduced by a small amount of omnivory, that is, the consumption of nutrient-rich heterotrophs, as frequently found in so-called herbivorous zooplankton, which may largely be on the second trophic level with respect to carbon/energy but on a higher trophic level with respect to nutrients (Gaedke and others 2002; Boit and Gaedke 2014). In contrast, carnivore invertebrates consume prey with a stoichiometry more similar to their own bodies, minimizing dietary mismatch and thus a reduction of the TTE due to food quality

constraints. In fishes, nutrient limitation is rare (Schindler and Eby 1997), but vertebrate bodies are more P-rich than those of invertebrates, and thus the C:P ratio between a vertebrate consumer and invertebrate prey can be somewhat mismatched (Figure 2). Recent work suggests that in particular young fish may be P-limited as they build P-rich bones but feed mainly on non-vertebrate prey (Schiettekatte and others 2020).

Stoichiometric constraints on herbivore production must be accounted for if production rates are not directly measured, but rather are extrapolated from biomasses of organisms. This is especially

◀ **Figure 2.** Flow of carbon (C), and phosphorus (P) and trophic transfer efficiencies (TTEs) in units of C and P along a food chain comprising four trophic levels, TL, that is, phytoplankton, herbivorous and carnivorous zooplankton, and fish under P-repleted conditions (left, C:P ratio of phytoplankton 100  $\mu\text{g C}$ : 1  $\mu\text{g P}$ ) and under P-depleted conditions (right, C:P ratio of phytoplankton 250  $\mu\text{g C}$ : 1  $\mu\text{g P}$ ). We assumed the same primary production (here 250 units of C) for P-repleted and P-depleted conditions, a maximum growth gross efficiencies in units of C of  $K_1 = 0.28$  for invertebrates and  $K_1 = 0.20$  for fish, a maximum P retention efficiency (that is,  $K_1$ ) of 0.9, constant C:P ratios for consumers (40  $\mu\text{g C}$ : 1  $\mu\text{g P}$  for invertebrates and 20  $\mu\text{g C}$ : 1  $\mu\text{g P}$  for fish) and that C losses by respiration surpass C production, in particular for fish. C that cannot be used for new herbivore production due to a lack of P is released by excretion and respiration. **(A)** The width of the arrows reflects the C:P ratios of prey production equaling predator ingestion (that is, non-grazing losses are neglected, upwards arrows) and of egestion (arrows to the right). The arrows to the left symbolize respiration. The numbers provide the rounded absolute values of the fluxes. Organismal C:P ratios increase with TLs implying that at each trophic transfer (except from herbivorous to carnivorous zooplankton) consumers have to accumulate P compared to their diet, reducing P excretion. In fish, this is counteracted by the higher C loss via respiration compared to invertebrates. Thus, under P-repleted conditions most P is recycled by herbivorous and carnivorous zooplankton whereas under P-depleted conditions herbivores hardly contribute to P excretion, which is dominated by carnivorous zooplankton (compare Gaedke and others 2002). **(B)** Production pyramids with TTEs between adjacent TLs in units of C (black) and P (blue) for repleted (left) and depleted P conditions (right). They reveal that under P-repleted conditions the maximum TTE in units of C determines the flow of matter among all trophic levels whereas the TTE in units of P remains partly far below its maximum value, indicating energy limitation of all consumers. In contrast, under P-depleted conditions, herbivores lack P to convert the consumed C into own biomass with the maximum possible efficiency, which reduces by half the C available for the higher TLs (that is, TTE for C ( $K_1$ ) is 0.14, compared to 0.28 under P-repleted conditions). The TTE in units of P is maximal for herbivores feeding on prey with a much higher C:P ratio than themselves, minimal for carnivorous zooplankton grazing on prey with the same C:P ratio as themselves, and fish falling in between, having a higher C:P ratio than its prey but also higher C losses by respiration.

important if TTE relies on laboratory derived PR/B ratios, which may not reflect production rates during nutrient limitation. Mass-balanced flux models of the pelagic food web of large, deep Lake Constance during a mesotrophic period suggested

that the herbivorous production (ciliates, rotifers and predominantly herbivorous crustaceans such as daphnids), which was feasible according to the available prey production in units of C, was actually about 20% lower due to a lack of P during summer. Thus, the TTE was about 80% of that expected based purely on energetics. Such a moderate reduction of the TTE due to a single limiting factor is to be expected as organisms and food webs are highly complex and flexible systems, which can adjust to ambient conditions to reduce the impact of individual limiting factors by, for example, physiological mechanisms, alteration in diet choice, compensatory feeding or species shifts. Consequently, a co-limitation by food quantity (carbon) and quality (nutrients or other essential substances such as polyunsaturated fatty acids (PUFAs)) is more likely to occur in situ (Gaedke and others 2002). This is supported by field and laboratory measurements revealing that a PUFA was usually more limiting than P at a near-shore station in Lake Constance during the mesotrophic period (Wacker and von Elert 2001). Eleven years later, under more oligotrophic conditions and persistent P-limitation of phytoplankton, herbivores were driven into co-limitation by food quantity, P and PUFAs (Hartwich and others 2012). Such changes in co-limitation can result from changes in taxonomic composition (Hartwich and others 2012; Marzetz and others 2017) and physiological plasticity of phytoplankton communities (Marzetz and Wacker 2021). In general, seasonal changes in PUFA availability may influence the TTE of essential nutrients in aquatic food webs (Hartwich and others 2013).

Controlled experiments also reveal effects of algal stoichiometry on TTE. Specifically, laboratory (Malzahn and others 2007) and mesocosm (Dickman and others 2008) experiments showed that when phytoplankton C:P ratios were high (that is, phytoplankton are more P-limited), TTE for both herbivorous zooplankton and zooplanktivorous larval fish was lower than when algal C:P was low. The response of herbivorous zooplankton can be explained by a lower efficiency in converting primary production into their own biomass when food quality is low (that is, algal C:P is high). This reduces production of zooplanktivorous larval fish and therefore the ratio of zooplanktivore production to primary production (Figure 2). However, this is partly due to a 'carryover' effect whereby the ratio of zooplanktivore (fish) production to herbivore (zooplankton) production was lower when algal C:P was high. Thus, when zooplankton feed on low-quality food, they are lower quality food for



fish (larval clupeids in both experiments). However, a subsequent experiment (Rock and others 2016) showed no evidence for a 'carryover effect' of algal quality on herbivore quality when other carnivore species were used (the invertebrate *Chaoborus* or juvenile centrarchid fish). Thus, the response of TTE across multiple trophic levels, as well as specifically for the zooplankton to zooplanktivorous organism link, seems to vary among species (Rock and others 2016).

### Compound-Related Constraints

TTE also varies between different carbon compounds, for example between bulk or non-essential and essential PUFAs (Gladyshev and others 2011). There is a strong correlation between the amount of FAs and the energy content of organisms because lipids containing FAs have a high caloric value. However, the correlation between FA concentration and %C is less strong, and hence TTE expressed as C-transfer versus FA- (or even PUFA) transfer may differ. Consumers receive the majority of their PUFAs from primary producers, which synthesize these compounds (Bell and Tocher 2009); thus the availability and concentration of FAs at the base of the food web can regulate TTE (Müller-Navarra and others 2000; Müller-Navarra and others 2004). The PUFA pattern in primary producers is affected by several environmental factors that drive algal community structure and physiology, for example, nutrient concentration, temperature and light (Guschina and Harwood 2009). Generally, FAs are transferred more efficiently than C as they can be retained or accumulated by organisms (Hessen and Leu 2006; Gladyshev and others 2011; Feniova and others 2021). This is especially the case for the long-chain PUFAs eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Kainz and others 2004).

A recent meta-analysis demonstrated that PUFAs are not only stored, but also internally transformed (Jardine and others 2020). Thus, aquatic invertebrates and fish may synthesize PUFAs enzymatically from shorter chain precursors to meet metabolic and physiological requirements (Twining and others 2016). Accordingly, ignoring internal PUFA transformation may bias estimates of TTE if based on PUFA transfer rates. However, we are just beginning to understand the degree and extent of FA bioconversion in natural populations (Twining and others 2021). Bioconversion of FAs is key for estimates of TTE because the capability for bioconversion may come with a competitive advantage for single species or even individuals

(Scharnweber and others 2021b), but trade-offs might be involved to maintain the enzymatic machinery.

In essence, the partial equivalence between energy (the original unit of TTE), carbon, nutrients, and essential FAs challenges the assumption that there is a single superior unit for estimating TTE. Food quality may matter for strict herbivores but not for carnivores (or omnivores) feeding on prey with a composition very similar to their own biomass, and which are normally energy limited. For spatial and temporal comparisons of TTE, use of identical units is necessary. However, a mechanistic understanding of temporal or spatial TTE variation is achievable only if estimates consider TTEs in all commodities that can limit consumer growth (energy, nutrients or essential FAs) (Figure 2).

### TTE ESTIMATES AS BASED ON ORGANISM SIZE DISTRIBUTION AND MODELS

Although TTE can be estimated from empirically determined production rates and trophic positions, complementary approaches link TTE with the Metabolic Theory of Ecology (MTE) (Brown and others 2004). Furthermore, mass-balanced food-web modelling is an additional theoretical approach. These alternative or complementary approaches of TTE estimation are included to motivate comparisons between approaches and to facilitate mechanistic understanding of processes, which determine differences of TTE over time and between systems.

### TTE and the Metabolic Theory of Ecology

Estimates of TTE between two trophic levels emerge directly from the allometric relationships between size and abundance of organisms, as summarized by the MTE (Brown and others 2004). Following Reuman and others (2008), abundance of individuals sharing a common resource  $f(M)$  scales negatively with the individual size ( $M$ , mass) of organisms according to a power law with the exponent =  $-1.75$ .

$$f(M) \propto M^{-1.75} \quad (2)$$

If the size distributions of predator-prey pairs are combined, and larger organisms from higher trophic levels consume exclusively smaller organisms from lower trophic levels (as is the case in many pelagic food webs), the exponent declines and becomes more negative ( $< -1.75$ ). The exact dimension of the decline is determined by both the TTE and the predator-prey mass ratio (PPMR, the

ratio between the average masses of the predators and their prey) by

$$f(M) \propto M^{\frac{\log(\text{TTE})}{\log(\text{PPMR})} - 1.75} \quad (3)$$

Because biomass ( $B$ ) is the product of numbers and  $M$ , the community biomass distribution is

$$f(B) \propto M^{\frac{\log(\text{TTE})}{\log(\text{PPMR})} - 0.75} \quad (4)$$

From Equation (4), it becomes clear that the size distribution of trophic levels coupled by predation is determined by the opposing effects of PPMR and TTE. High PPMRs are normally associated with lower TTE, suggesting that for example in pelagic food chains, the link between phytoplankton and zooplankton is energetically more efficient than the link between zooplankton and zooplanktivorous fishes. The PPMR between zooplankton and phytoplankton tends to be smaller ( $\sim 500$ ; for example, zooplankton body size = 100  $\mu\text{g}$  fresh mass (fm), phytoplankton body size = 200 ng fm) than the PPMR between zooplanktivorous fish and zooplankton ( $\geq 100,000$ ; zooplanktivorous fish body size at least = 10 g fm, zooplankton = 100  $\mu\text{g}$  fm). This is illustrated by a graphical exploration of the effects of varying levels of the power law exponent of the biomass distribution or the PPMR on the TTE. A typical power-law exponent of the pelagic biomass distribution is  $-1.0$ , indicating that the equivalent slope of a linear regression between  $\log_{10}$  biomass and  $\log_{10}$  body size in logarithmic bins is  $-1.0 + 1 = 0.0$  (White and others 2008). By assuming a PPMR = 500, the resulting TTE = 21% (Figure 3, middle column). By varying the power-law exponent to either  $-0.9$  (shallower slope) or  $-1.1$  (steeper slope) at PPMR = 500, TTE changes to 39% or 11%, respectively (Figure 3, two left columns). While fixing the power-law exponent to  $-1.0$ , and varying the PPMR to either 100 or 100,000, TTE changes to 32% or 6%, respectively (Figure 3, two right columns). The variation of TTEs reflects the strong effect of PPMR on the efficiency to transfer energy from smaller to larger size classes, and this efficiency determines the slope of the size spectrum (Barnes and others 2010). As a consequence, the TTE of trophic links or entire food chains can be calculated from empirically determined size distributions of combined interacting trophic levels and the PPMR of the interacting trophic levels, facilitating comparison with TTEs directly estimated from production rates of trophic levels (Gaedke and Straile 1994b; Mehner and others 2018).

The equations presented above also demonstrate problems when the biomass ratio between con-

secutive trophic levels (units g biomass per area or volume) is applied as an approximation for production rates and hence for TTE (for example, Garcia-Comas and others 2016). If BMR = biomass ratio of consecutive trophic levels, and  $n$  = exponent of the power law of consumption with body size ( $\sim 0.75$ ) (Jobling 1994), BMR and TTE are not identical because

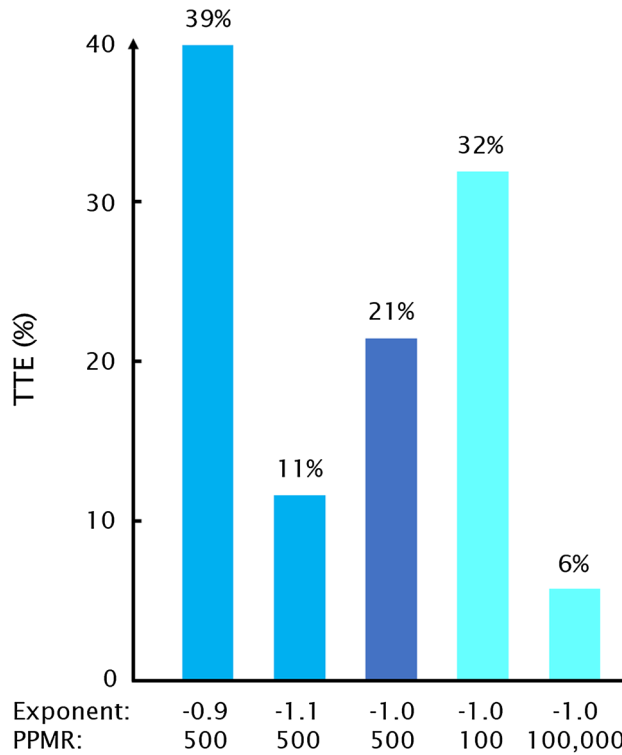
$$\text{BMR} = \text{TTE} \times \text{PPMR}^{1-n} \quad (5)$$

Accordingly, BMR = TTE only when PPMR = 1, which is very unlikely given that predators are usually substantially larger than their prey. (Kerr 1974; Sheldon and others 1977).

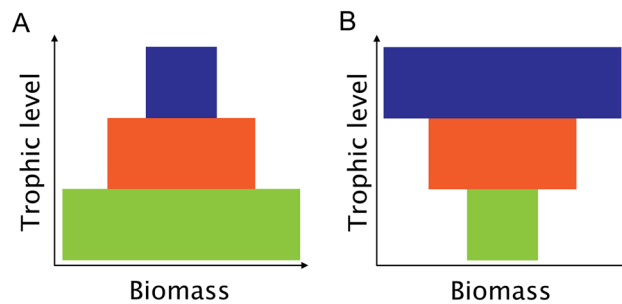
The link between size-based theory and TTE also suggests that the classical graphical expression of food webs in form of a biomass pyramid (Lindeman 1942) is just another depiction of the same relationships (Trebilco and others 2013). Bottom-heavy pyramids of organismal biomass have been used to explain the concept of TTE as being dominated by about 90% of energy losses per trophic link (Figure 4A). However, top-heavy biomass pyramids (Figure 4B) have also been found empirically and, indeed, may be common in food webs dominated by benthic resources (Vadeboncoeur and Power 2017). From the relationships between biomass ratios and PPMR outlined above, it is clear that consumer biomass can be higher than resource biomass for reasonable TTEs, if the consumer body mass is substantially higher than the average mass of the resource (= high PPMR), and hence the turnover times of both trophic levels differ strongly. Furthermore, inverted biomass pyramids may form if higher trophic levels are subsidized by energy not being basal to the local food web under consideration (Trebilco and others 2013). Examples are huge biomasses of whales, which may migrate over large distances and hence integrate spatially discrete primary production temporally, or strong but temporal pulses of terrestrial organisms falling into aquatic systems, like periodical cicadas that are then used by aquatic predators (Nowlin and others 2007).

## TTE and Mass-Balanced Models

Mass-balanced food-web models are static food-web representations of the fluxes of C and sometimes also nutrients among the major groups of organisms (compartments) of the food web and the exchange with the environment (for example, C fixation by photosynthesis, losses by sedimentation) during a distinct period of time. Models that are truly mass balanced must include the recycling



**Figure 3.** Effects of varying the power-law exponent of the biomass distribution between  $-0.9$  and  $-1.1$  (intermediate blue columns), and varying the predator-prey mass ratio (PPMR) between 100 and 100,000 (light blue columns), relative to the standard values with exponent =  $-1.0$  and PPMR = 500 (dark blue column in the middle), on the trophic transfer efficiency (TTE).



**Figure 4.** Examples of classical bottom-heavy (**A**) and inverted top-heavy (**B**) biomass pyramids, in which the energy loss between two trophic levels is inherently reflected by the declining area of the trophic level (**A**). Top-heavy pyramids (**B**) do not violate energy losses per trophic link but suggest that consumers are either much larger than their prey (for example, observed during the clear-water phase when daphnids graze on small algae resulting, for example, in a positive slope of the biomass size spectra Gaedke 1992a; Boit and Gaedke 2014), or being subsidized by resources from outside the system, often combined with high PPMR, which cause low TTEs.

of dead organic matter (detritus) via the microbial loop. Mass-balanced food-web models may be established as annual averages (resulting in webs, which may never exist in this form) or, better, for different parts of the season revealing the dynamics in food-web rewiring. Especially in this case, changes in standing stocks should be accounted for in the mass balance.

Appropriate computer programs such as Ecopath (Christensen and Walters 2004) or the food-web explorer (Hart and others 1997) are used to ensure that mass balance is constrained, including (1) the energy entering each compartment via, for example, ingestion equals the sum of all loss factors (for example, excretion, respiration, predation and changes in biomass), (2) the summed production of

the prey is identical with the summed ingestion of the predators, (3) the sum of the dead organic material released by all compartments balances the metabolic needs of bacteria, (4) the primary production covers all losses from the system (for example, via respiration, and sedimentation) and the temporal changes in standing stock biomasses are accounted for. Such mass-balanced flux models may be obtained by assuming distinct TTEs (DeRuiter and others 1995; Li and others 2021) or TTE may be a model outcome resulting from the above-mentioned mass-balance constraints (for example, Gaedke and Straile 1994b).

For deriving reliable TTE estimates, mass-balanced food web models provide a tool to integrate and check the internal consistency of the numerous types of information on which they are based such as direct production measurements, diet compositions and TPs inferred from stable isotope measurements, production estimates based on measured biomasses and laboratory-based (maximum) production rates. Often, consumer production and thus TTE depend not only on available food quantity but also food quality, which may also influence the diet choice. For example, as discussed above, a lack of P may prevent a consumer from converting ingested biomass into its own biomass production with the efficiency that would be feasible from an energetic point of view because it cannot synthesize sufficient RNA and ATP, or bones in the case of vertebrates (Figure 2). Hence, the excess carbon will be excreted or respired, thereby reducing TTE unless changes in diet composition can overcome nutrient limitation. Consequently, mass-balanced (and other) food web models should account for nutrients or other essential substances (for example, FAs) as well, in case they may limit secondary production (for example, Gaedke and others 2002).

For the plankton food web of large, deep, mesotrophic Lake Constance, absolute values and seasonal changes of TTE estimates obtained independently from biomass size spectra and mass-balanced food web models agreed well (Gaedke and Straile 1994b). The slope of the biomass size spectra relied on almost weekly measurements of all eukaryotic plankton including the microbial loop, and estimates of the PPMR based on the underlying food web structure (Gaedke 1992b, 1993; Gaedke and Kamjunke 2006). The food web models were additionally based on direct measurements of primary and bacterial production, and elaborate estimates of temperature-dependent production, diet composition, exudation and sedimentation

(Gaedke and Straile 1994a; Gaedke and others 1996).

## FOOD WEB STRUCTURE AND PROCESSES AFFECTING TTE

Sufficient knowledge of food web structure is one of the crucial preconditions to achieve a proper understanding about the mechanisms that determine TTE in lakes. However, it must be noted that TTE can be considered and estimated from at least two different perspectives. First, TTE can be seen as a mechanistic variable informing about energy and matter flows through the food web, and hence how efficiently resources are converted by a consumer into new biomass. From that perspective, all resources flowing into the consumer must be included in estimates of efficiencies. In contrast, TTE can also be considered as an integrative variable and ecosystem property, informing about the efficiency of conversion of ecosystem primary production into ecosystem secondary production (food-web efficiency). From this perspective, the baseline is only the new energy generated by C fixation, whereas all recycling processes become integrated while calculating the total heterotrophic production rates relative to primary production rates. We will explore this differentiation in more detail subsequently. To understand the difference between both approaches, we summarize spatial and temporal variability of production and TTE, explore how habitat-specific food chains are linked, focus on the links between lakes and the terrestrial landscape and discuss how the detritus food chain integrates pelagic and benthic food chains and links to the terrestrial landscape.

## Spatial and Temporal Variability of TTE in Lakes

Estimating TTE requires the estimation of production rates, which are rates expressed per unit of area (or volume) and per unit of time. Accordingly, it can be expected that several processes affect spatial and temporal differences in production rates and hence TTE. Whereas the seasonal succession of phytoplankton and zooplankton, and the changes in abundances and size structures in temperate lakes are well conceptualized (Sommer and others 2012), there are a very limited number of studies on the variability of TTE during seasonal succession. Schulz and others (2004) observed a gradual increase of pelagic TTE in an oligotrophic, stratified lake as obtained from monthly samples from April to November, for links from phytoplankton to

zooplankton, and from zooplankton to zooplanktivorous fish. Several studies (Gaedke 1992a, b; Gaedke and Straile 1994a; Gladyshev and others 2011) demonstrated strong seasonal variations of TTE between phytoplankton and zooplankton depending on the match (or mismatch) between prey production and predator consumption and food quality constraints (Gaedke and others 2002; Boit and Gaedke 2014). Accordingly, TTE estimates can be compared only if sampling for estimates of production and TPs have been conducted at similar temporal scales.

Overall, there are surprisingly few empirical studies estimating TTE in pelagic lake habitats (Table 1). Furthermore, to our knowledge, there are even fewer studies assessing the TTE strictly for benthic (either littoral or profundal) habitats in lakes (Vander Zanden and others 2011; Lischke and others 2017). A direct comparison of the range and variability of TTE between pelagic and benthic lake habitats based on empirical results is therefore difficult. For marine environments, a higher TTE for benthic compared to pelagic food webs has been suggested, based on the observation that predator-prey interactions in 2D benthic habitats are energetically more efficient, and the PPMR in benthic food webs is smaller than in 3D pelagic food webs (Stock and others 2017). Some lake studies also show higher efficiency in benthic compared to pelagic food chains (Vander Zanden and others 2011), but there are other studies showing no systematic differences between benthic and pelagic efficiencies (Vander Zanden and others 2006; Lischke and others 2017).

Most of the available studies estimate TTE only between two adjacent trophic levels, primarily between pelagic phytoplankton and zooplankton, with a range of TTE between 0.25% (Ersoy and others 2017) and greater than 30% (Gaedke and Straile 1994a) for this trophic link (Table 1), corresponding to the range of TTEs as based on the size-biomass relationships explored above. In a comparative study in 12 Polish lakes, the TTE between zooplankton and phytoplankton production was very low (range 0.0005–0.14%), because of high percentages of inedible algae and cyanobacteria in the phytoplankton communities (Karpowicz and others 2020).

Estimates of fish production (or catch) relative to primary production as usually calculated in marine systems (Pauly and Christensen 1995; Stock and others 2017) are rare from lakes. We found only two studies, with these food-chain TTEs ranging between < 0.01% from pelagic and benthic primary plus heterotrophic bacterial production to

omnivorous fish production in two productive shallow lakes (Lischke and others 2017), and 1% between phytoplankton and planktivorous fish in the pelagic habitat of a deep, oligotrophic lake (Schulz and others 2004).

## Trophic Links Between Food Web Compartments

### *Coupling of Lake Habitats by Mobile Organisms and Passive Matter Movement*

Although the organisms that primarily fix inorganic carbon are essentially habitat specific (pelagic phytoplankton, benthic macrophytes and epiphyton, benthic chemoautotrophic bacteria), there are no physical barriers in lakes that would prevent access of consumers to production from either habitat. Therefore, all organisms that can actively move between habitats potentially link the trophic chains between habitats. Above all, fishes have been considered as integrators of pelagic and benthic food chains (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002, 2020), with their diet often being composed of prey mixed from both habitats (Figure 1). In a similar way, but on more discrete temporal scales, ontogenetic habitat shifts of invertebrates (for example, the emergence of terrestrial adult insects from benthic larval over pelagic pupal aquatic stages) or fishes (habitat switches between pelagic and benthic habitats during the transition from larval to juvenile and then to adult stages) may link the energy consumption of certain trophic levels between lake habitats.

Regular mass movements of organisms, for example diel horizontal migrations of fishes or zooplankton (Brabrand and Faafeng 1993; Burks and others 2002), link littoral and pelagic habitats. In a similar way, diel vertical migrations of fishes (Mehner 2012) or zooplankton (De Meester and others 2022) link pelagic and profundal habitats. However, it is not clear whether diel migrations induce an energetic link between habitats because organisms feed in both habitats, or whether the link is primarily established via nutrient recycling because organisms may feed mostly in one habitat and excrete and egest nutrients in the other habitat (Schindler and Scheuerell 2002; Vanni 2002).

Finally, there may be passive translocation by gravity and lake-internal currents of DOM and particulate organic matter (POM) (detritus) from near-shore habitats to the deepest part of the lake (Bloesch 1995; Cyr 1998). In that way, littoral and profundal habitats may become linked, and al-

**Table 1.** Overview of Trophic Transfer Efficiency (TTE) Estimated in Either Pelagic or Benthic Habitats or for Entire Lake Food Webs (FW), Specifying the Method to Estimate TTE and the Trophic Groups Included

Habitat	FW	TTE measured	Trophic groups compared	TTE estimate	References
Pelagic, large, deep mesotrophic lake	Yes	Biomass spectra, C production of bacteria and algae (and consumers) and their C:P ratios, mass-balanced flow models	Phytoplankton-herbivorous zooplankton (ciliates, rotifers, herbivorous crustaceans)	20–25% (seasonal average) (5–38% seasonally resolved); 2–10% from TL 1–3, that is, carnivorous zooplankton	Gaedke 1992b, Gaedke and Straile 1994b, Gaedke and others 1996, Gaedke, 1992a
Pelagic	No	TTE from C production	Phytoplankton-zooplankton	< 1–13% (range of monthly means)	Gladyshev and others 2011
Pelagic (in mesocosms)	No	Predator-prey biomass ratio	Phytoplankton-zooplankton	0.2–14%	Ersoy and others 2017
Whole lake (small and shallow, 2 lakes divided in halves)	No	TTE from production	Primary (bacterial and autotrophic)—secondary (macroinvertebrates, ciliates, rotifers and crustaceans)	1.85% (lake half mean, ranging 1–3.5%)	Mehner and others 2018
Pelagic	No	TTE from C production	Phytoplankton-zooplankton	0.4%	Grosbois and others 2020
Pelagic	No	TTE from C production	Phytoplankton-zooplankton	2.9%	Grosbois and others 2022
Pelagic (12 lakes)	No	TTE from C production	Phytoplankton-zooplankton	0.0005–0.14%	Karpowicz and others 2020
Pelagic (30 lakes)	No	TTE from C production	Phytoplankton-zooplankton	6.5% (lake mean, ranging 0.3–26%)	Feniova and others 2021
Pelagic	No	TTE from production	Phytoplankton—zooplankton	18%	Schulz and others 2004
Benthic and pelagic	No	Ecological efficiency from production	Zooplankton—planktivorous fish Phytoplankton—zooplankton	5.5% 3%	Schulz and others 2004 Vander Zanden and others 2006
Benthic and pelagic	No	Ecological efficiency from production	Periphyton—zoobenthos	0.5–1%	Vander Zanden and others 2006
Benthic and pelagic	No	Ecological efficiency from production	Phytoplankton—zooplankton	6.5%	Jonasson 1992
Whole lake + benthic and pelagic	Close as	TTE from Ecopath model	Periphyton—zoobenthos Zooplankton/zoobenthos—fish	6.5% 10%	Jonasson 1992 Jonasson 1992
Whole lake or benthic and pelagic separately	Close as	TTE from production	Detritus up to fish (trophic level 1–7) Pelagic autotrophs-zooplankton	14% (mean lake wide)	Matthias and others 2021
				23%; 8%	Lischke and others 2017

Table 1. continued

Habitat	FW	TTE measured	Trophic groups compared	TTE estimate	References
TTE for two small shallow eutrophic lakes each			Pelagic autotrophs and bacteria—zooplankton	13%; 5.4%	Lischke and others 2017
			Benthic autotrophs—macroinvertebrates	1.7%; 1.6%	Lischke and others 2017
			Benthic autotrophs and sediment bacteria—macroinvertebrates	0.7%; 0.3%	Lischke and others 2017
			Total autotrophic and bacterial producers—zooplankton and macroinvertebrates	3.5%; 1.4%	Lischke and others 2017
			Total autotrophic and bacterial producers—omnivorous fish	0.002%; 0.01%	Lischke and others 2017
			Total autotrophic and bacterial producers—piscivorous fish	0.004%; 0.0004%	Lischke and others 2017

lochthonous C may be channelled into the pelagic food web via the microbial loop.

#### *Spatial Links Between Lake and Terrestrial Environment*

Carbon fixed by terrestrial primary production can enter lakes in dissolved (tDOM) or particulate (tPOM) form (Figure 1), and tPOM can be either dead matter (detritus) or living (terrestrial prey available to aquatic consumers) (Cole and others 2006). The contribution of terrestrial OM to lakes can be expressed as C input rates, similar to production rates of aquatic organisms that input organic C to the rest of the food web. tDOM becomes available for the lake food web primarily via consumption by heterotrophic bacteria, but usually only a small fraction of the C reaches higher trophic levels (Kritzberg and others 2004; Jones and others 2012). The tPOM forms a resource for benthic invertebrates, heterotrophic bacteria and fungi, but it usually contributes only a minor fraction to the lake-wide availability of C, in particular in productive lakes where C fixation by autochthonous producers is high (Attermeyer and others 2013; Mehner and others 2016).

For proper estimates of lake wide TTE, allochthonous organic C has to be included as another primary energy source, in addition to autochthonous inorganic C fixation. The fraction of allochthonous C used for production of a lake consumer can be termed allochthony (or allochthony) and indicates how strongly consumer secondary production depends on the terrestrial primary production (Grosbois and others 2020). Although allochthony is usually low because of the low nutritional quality of allochthonous C sources, tDOC and tPOC may accumulate in lakes and become available to bacterial consumption after further degradation in the long-term. Therefore, the contribution of allochthonous C to lake C budgets should be considered while estimating TTE in lakes. However, the quantification is complicated by the fact that allochthonous C can either be a subsidy, stimulating extra heterotrophic production, or a 'subtractive' interaction if consumers simply switch from autochthonous to allochthonous resources or if terrestrial organic C shades algae and reduces in-lake primary production (Jones and others 2012). The distinction between subsidy and replacement also applies to secondary production of benthic macroinvertebrates. tPOM may subsidize secondary production if macroinvertebrate production is resource limited. The higher C availability then leads to higher abundances and subsequently to higher production rates of benthic macroinverte-

brates than those achievable based on autochthonous C alone. Subsidized secondary production may result in an overestimation of TTE between primary producers and consumers if based only on autochthonous production (see below).

Carbon from terrestrial primary production can also enter lakes via organisms that are prey resources for aquatic predators. Examples are terrestrial insects with no aquatic life stage (Nowlin and others 2007). However, if these terrestrial insects have aquatic life stages, the distinction between in-lake and terrestrial carbon becomes blurred (Scharnweber and others 2014b). If terrestrial prey induces higher abundances of aquatic predators (Perkins and others 2021) and hence subsidizes their production, calculations of TTE for these predators relative to the consecutive trophic level must consider secondary production rates from both aquatic and terrestrial prey. Because terrestrial prey enters the lake food webs at a higher trophic level than leaves or DOC, this C flow is not directly comparable with autochthonous primary production.

#### *The Detritus Food Web in Lakes*

The pelagic microbial loop comprises heterotrophic bacteria, flagellates, ciliates and other microzooplankton. It describes a trophic pathway where DOC is made available for macrozooplankton via the assimilation into bacterial biomass (Figure 1). Ciliates may play a dual role and graze on both algae from fresh primary production and on smaller organisms like bacteria and heterotrophic flagellates, hence recycling old (primary) production via the detritus chain. Due to the number of trophic links involved, it has been concluded that only a limited amount of C in addition to that from autochthonous primary production reaches the macrozooplankton via the pelagic microbial loop (Koshikawa and others 1996; Havens and others 2000). However, especially under more oligotrophic conditions, feeding interactions of organisms from the microbial loop may contribute to the food supply of macrozooplankton. In pelagic habitats, bacterial C production typically amounts to approximately 20–30% of primary production. Ciliates often consume approximately half of the fresh primary production on annual average, adding an additional trophic level (which involves substantial losses by excretion and respiration) in the flow of energy from autotrophs to macrozooplankton. For example, production rates of cladocerans may rely on algal primary production, (part of the) bacterial production plus ciliate secondary

production (Lischke and others 2017). Furthermore, given the low C:nutrient ratio of bacteria compared to phytoplankton, the microbial loop typically contributes relatively more nutrients to the nutrition of large consumers compared to C (Gaedke and others 2002). Similar studies on the structure and efficiency of the benthic microbial loop are almost completely lacking (Findlay and Battin 2016).

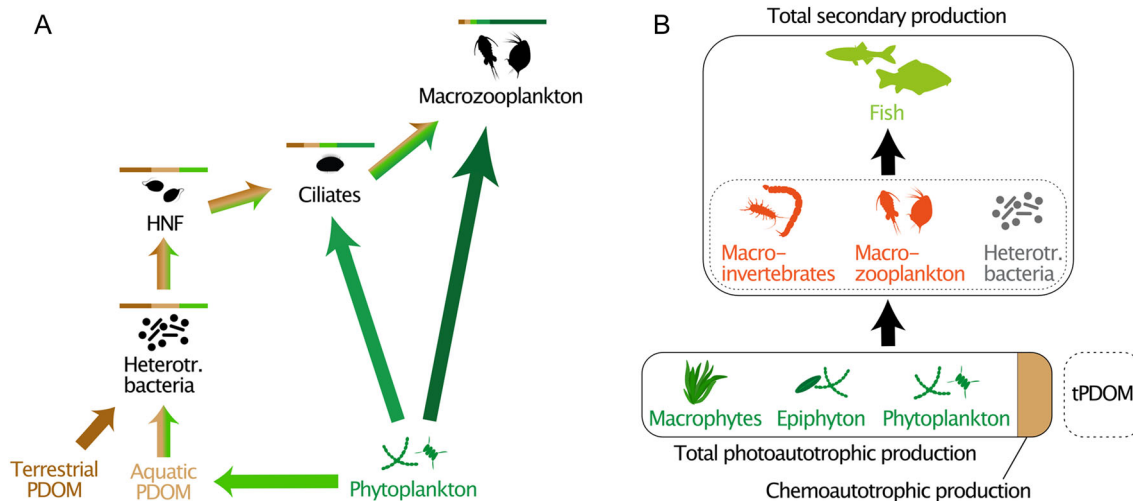
#### **Lake-wide TTE Estimates Integrating Pelagic, Benthic and Terrestrial Processes**

The structure of lake food webs and the complex links between lake habitats and lake and terrestrial environment constitute substantial challenges for estimating lake wide TTEs (Figure 1). In the majority of trophic links, only fractions of the production of one organismal group flow directly to the consecutive consumer, and many consumer groups receive C from a variety of sources (Figure 1). Furthermore, the pelagic (and probably benthic) microbial loops recycle parts of the C and nutrients from primary production leading to further heterotrophic production in addition to that of macroorganisms. Subsequently, we compare the mechanistic approach on TTE, which addresses all these links individually, with the alternative and simpler food-web efficiency, an ecosystem approach.

#### *TTE as a Mechanistic Approach*

If TTE is considered a mechanistic variable informing the production efficiency of an individual or of a group of similar organisms (a single population or a group of populations from the same trophic guild sharing the same prey groups), the C flow from any resource to that consumer group must be considered (Figure 5A). For example, macrozooplankton such as cladocerans receive C from feeding upon algae (primary production) and ciliates (secondary production) (Figure 5A), reflecting that macrozooplankton are omnivores. Finding the correct baseline production for calculating the TTE of omnivores is not easy. However, by using stable isotope analysis, the contribution of more than one resource to consumer production can eventually be resolved via consumer consumption, by assuming that the share of resource 1 to total consumer production equals  $\alpha$ , and the share of resource 2 equals  $(1-\alpha)$ . An expansion to more resources is possible. Consumer production can be used to estimate consumption via the gross growth efficiency  $K_1$ . Alternatively, instead of calculating consumption, assimilation of the con-





**Figure 5.** Two alternative approaches to calculate trophic transfer efficiency (TTE) in lakes. **(A)** The mechanistic approach compares secondary production of one consumer group with the sum of consumption obtained from all resources of that consumer group. Total resource production must be split according to the carbon flow to various consumer groups (for example, total primary production has to be split into proportions consumed by macrozooplankton, ciliates and (via detritus) to heterotrophic bacteria). Colours of arrows and organismal groups reflect contribution of various resources to consumer consumption. HNF = heterotrophic nanoflagellates. **(B)** The ecosystem approach (that is, food-chain or food-web efficiency) accumulates all net autotrophic production (photo- and chemotrophic organisms) and compares it with the secondary production of single consumer levels (food-chain efficiency) or with the sum of all secondary production (food-web efficiency) in the system. This approach compares energy availability with energy bound by secondary production. Terrestrial contributions (particulate and dissolved organic matter, summed as tPDOM) to lakes can be added to the basal energy availability, if the inputs are estimated as carbon flow rates similar to primary production.

sumer could be calculated via the net growth efficiency  $K_2$ , the difference between consumption and assimilation being the fraction of consumed C flowing into the detritus pool.

The total flow of resources (consumption, CO) from two sources to a consumer is then its production ( $PR_{\text{total}}$ ) split according to the share of resources by

$$CO = \frac{PR_{\text{total}} \times \alpha}{K_1} + \frac{PR_{\text{total}} \times (1 - \alpha)}{K_1} \quad (6)$$

$K_1$  can be identical, but also be different according to stoichiometric differences between the resources. For macrozooplankton, these quantities would be the consumption rates on ciliates and algae. In the same way, the consumption rates of ciliates can be split between algae and bacteria as resource, and the production of bacteria can be split into fractions coming from either autochthonous or allochthonous carbon (Figure 5A). A recent methodological paper suggested an approach to calculate cycling efficiency, by which the propagation of habitat-specific resources, as estimated by stable isotopes, could be traced through a food web (Baruch and others 2021). It needs to be explored whether this cycling efficiency is equivalent to the

consumption-based split of resources as discussed here and hence could be applied to estimate TTE.

For a balanced energy budget, the sum of consumption rates of one resource by all consumers would equal the production of this resource minus non-grazing losses (entering the detritus pool). In the example, the consumption of algae by ciliates and by macrozooplankton plus the flow of autochthonous production into the detritus pool must equal the total net primary production of algae. The correct TTE of macrozooplankton is then the ratio between the macrozooplankton production and the part of algal production flowing to macrozooplankton plus the ciliate production flowing to macrozooplankton. In a similar way, the production baselines can be calculated for the TTE of all omnivorous consumers, while omnivory can be attributable to resources from different trophic levels, from different lake habitats or even from lake and terrestrial habitats.

By this mechanistic approach, the production rates of consumers indirectly determine the contribution of resource production flowing into the microbial loop, because resources not used by any consumer will enter the detritus pool. Hence, mechanistic TTEs contribute to understanding of TTE variations between lakes as a consequence of

variations in food web structure and C flow. The required data can be readily obtained from mass-balanced food web models.

#### *TTE as an Ecosystem Approach—Food-Web and Food-Chain Efficiencies*

If TTE is alternatively considered as food-chain or food-web efficiency, the total C fixed by photoautotrophic or chemoautotrophic production has to be compared to the secondary production of any consumer trophic level (food-chain efficiency, FCE), but can even be summed across all consumer trophic levels (food-web efficiency) (Figure 5B). This perspective derives an integrative ecosystem variable that compares resources potentially available to consumers and the resources eventually bound by secondary production of consumers. At the base of the lake food web, autochthonous net primary production rates by pelagic phytoplankton and littoral epiphyton and macrophytes must be considered. In lakes receiving concentrated geochemical inflows, chemoautotrophs may fix additional organic C from CO<sub>2</sub> by oxidizing inorganic substances, and this C is additionally available for secondary production. If lakes are subsidized substantially by allochthonous DOC or POC, a part of the chemoheterotrophic bacterial production can be considered basal for the lake food web because this allochthonous C is not recycled within the lakes, but has been fixed by terrestrial primary production. Accordingly, we suggest that the C flow into lakes originating from terrestrial primary production (tPOM, tDOM) minus burial rates if they are substantial should be added to the sum of autochthonous primary and chemoautotrophic production as a baseline for C availability.

The sum of photoautotrophic or chemoautotrophic carbon fixation is then compared with the secondary production of one consumer trophic level (for example, macrozooplankton or fish) (food-chain efficiency), or with the total sum of secondary production of all consumers, including the production rates of chemoheterotrophic bacteria that recycle autochthonous C (food-web efficiency) (Figure 5B). For this approach, the exact origin and amount of C flowing to each consumer group is unimportant. Ecosystems characterized by long food chains with high total respiration rates would have a lower food-web efficiency than ecosystems with fewer trophic levels. This approach needs only estimates of production rates and is therefore less data hungry than the mechanistic approach mentioned before but requiring also knowledge on food web structure. Calculating TTE

as food-web efficiency facilitates across-ecosystem comparison of energy conversion between primary and secondary production, but does not contribute to mechanistic understanding why food-web efficiency differs between them. Trophic transfer efficiency expressed as food-chain efficiency is strongly linked to the calculation of TTE via size distributions for which size and biomass of all organisms in a lake are plotted together into a lake-wide size spectrum (see above).

The calculation of lake-wide TTE between primary production and fisheries yield, similar to the approaches in the oceans (Pauly and Christensen 1995), is therefore a special case of the food-chain efficiency. This approach simply excludes all secondary production below the fish trophic levels, calculates only the ratio of production of the top trophic level (all fish or only piscivorous fish) to basal production, but still keeps the information whether C fixed in the system is efficiently or inefficiently converted into fish production and yield, respectively. However, the reasons for differences in food-chain efficiency between systems would remain unexplored, without additional information.

Most of the TTEs between zooplankton and phytoplankton available in the scientific literature (Table 1) are certainly variants of food-chain efficiencies because omnivory and recycling via the microbial loop are usually ignored. For an exploration of the dimension of efficiencies of entire food webs in lakes, data from a whole lake tPOM subsidy experiment (Scharnweber and others 2014a) can be re-used here. These data have been used to calculate quantitative food webs and TTEs for two experimentally divided shallow lakes (Lischke and others 2017) and to compare these data with the slope of lake-wide size-abundance relationships (Mehner and others 2018). This comparison revealed that the low TTEs estimated for the lakes (< < 10% between all trophic levels, see Table 1) were reflected by correspondingly steeper regression slopes of the size-abundance relationship (< - 1.0, or exponents of size-abundance power-law relationships < - 2.0) (Mehner and others 2018).

The basic production data (g C m<sup>-2</sup> y<sup>-1</sup>) from this experiment are assembled here again (Table 2, as based on Mehner and others 2016) and facilitate calculation of both food-chain and food-web efficiencies. For crustacean zooplankton and benthic macroinvertebrates in these lakes, food-chain efficiencies were substantially lower than 10% (0.3–4.8%, Table 2). Likewise, fish production was only 0.01% relative to basal C availability. The food-web

**Table 2.** Overview of Production Rates ( $\text{g C m}^{-2} \text{y}^{-1}$ , Estimated for the Year 2011) in Treatment and Reference Halves of Two Experimentally Divided Shallow Lakes (Schulzensee, Gollinsee) in Northeast Germany (Numbers from Mehner and others 2016)

	Gollinsee treatment	Reference	Schulzensee treatment	Reference
NPP phytoplankton, macrophytes, epiphyton	134.4	122.9	208.7	159.9
NPP reeds	214.0	214.0	92.0	92.0
Allochthonous C input	33.4	8.4	39.9	11.9
Bacterial SP	340.5	386.4	293.9	310.0
Crustacean SP	3.47	4.37	8.98	12.77
Benthic macroinvertebrates SP	1.19	1.25	1.84	2.40
Fish SP	0.047	0.044	0.023	0.028
FCE crustacean SP	0.91%	1.27%	2.64%	4.84%
FCE benthic macroinvertebrate SP	0.31%	0.36%	0.54%	0.91%
FCE fish SP	< 0.01%	< 0.01%	< 0.01%	< 0.01%
Food-web efficiency (– BP)	1.23%	1.64%	3.19%	5.76%
Food-web efficiency (+ BP)	90.4%	113.5%	89.5%	123.3%

Food-chain efficiencies (FCE) are calculated for the three consumer groups crustaceans, benthic macroinvertebrates and fish relative to total primary production of phytoplankton, macrophytes, epiphyton and reed plus allochthonous C sources. Food-web efficiency (+ BP) is the ratio between the sum of all known heterotrophic production including bacterial production but except ciliates, which occurred in high numbers (Lischke and others 2016) and total net primary plus carbon input from allochthonous sources. Food-web efficiency (– BP) is the same ratio as before, but excluding bacterial production. NPP = net primary production, SP = secondary production.

efficiency calculated as ecosystem property between basal C availability and all heterotrophic production excluding bacteria varied between about 1.2% and 5.8% among the four lake halves (food-web efficiency-BP, Table 2). However, we did not calculate the secondary production of ciliates, which dominated the phytoplankton consumption (Lischke and others 2016), and hence the food-web efficiency was underestimated. If we include bacterial secondary production and estimate the food web efficiency between animal plus bacterial secondary production and primary production plus allochthonous C input (+ BP, Table 2), food-web efficiencies increase substantially to range between 90 and 123%.

The high food-web efficiencies + BP, which even exceed 100%, demonstrate that bacterial production and the detritus food chain are the dominant secondary production processes in these shallow lakes with high primary production of macrophytes including reeds. The re-use of ‘older’ autochthonous or allochthonous primary production accumulated as DOM or POM (detritus) in benthic habitats over decades or centuries may explain why bacterial production was higher than the primary production in the same year. However, the detritus chain is energetically very inefficient and does not provide much extra energy for larger animal consumers because the animal secondary production is low even in comparison with the bacterial production. Food-web efficiencies -BP reflect the dominant effect of secondary production of

macrozooplankton and benthic macroinvertebrates on these numbers, while fish secondary production contributes marginally. However, if fish would have been subsidized by allochthonous C, their production might be more important for -BP food-web efficiencies.

## CONCLUSION

Conceptually, TTE is a seemingly simple measure that requires only production estimates of two consecutive trophic levels. However, the methods to estimate rates, in particular secondary production, have not developed much during the last decades and still bear enormous uncertainty. Furthermore, the feeding links between resources and consumers required to calculate TTEs are often only approximately known. Finally, whereas the consumer production is easily defined, the relevant resource production is difficult to standardize, in particular if consumer omnivory with respect to trophic levels and origin of resources from lake habitats has to be considered, and if recycling of carbon and nutrients via the microbial loop is properly accounted for. These linkages require marker systems that can precisely trace the resource-specific origin of carbon in the accumulated organismal tissue, a major methodological progress that is not yet achieved. However, comparing all primary with all secondary production estimates to obtain food-web efficiency is fairly straightforward.

These numerous difficulties associated with properly estimating TTE in lakes contrast to the potential importance of energetic efficiency of food webs for understanding ecosystem function. There is a close link between the calculation of TTE as average growth efficiency of individuals and the energy flux through food webs, a quantity that relates biodiversity and ecosystem functioning (Barnes and others 2018). Modifications of species dominance within trophic levels and subsequent changes in interaction strengths between zooplankton, diatoms and detritus in shallow lakes also change TTE and can induce massive erosion of food-web stability towards critical transitions (Kuiper and others 2015). A globally available indicator such as food-web efficiency would facilitate large-scale comparison of the efficiency of energy transformations in different biomes, ecosystems and habitats. Via the link between biomass-size distributions and TTE, all changes in numerical abundance or size of organisms induced by disturbance will affect the biomass and energy conversion efficiency in the ecosystem (Jacquet and others 2020). Reductions of individual growth rates in response to global warming affect interaction strengths (Gardmark and Huss 2020) and will reduce TTE (Barneche and others 2021). Similarly, proliferation of cyanobacteria blooms may also reduce TTE because these primary producers are lower-quality food compared to most eukaryotic algae. Hence, TTE may be an indicator for critically exposed ecosystems.

In turn, the amount of biomass production harvestable by humans may differ between ecosystems with similar primary production rates, reflecting differences in food web structure and hence TTE (Stock and others 2017). Knowing these energetic differences may facilitate more sustainable human use of natural resources. Understanding the effects of global change on oceanic primary production and TTE may help predict consequences for fish biomasses and annual fish catches (Lotze and others 2019; du Pontavice and others 2020). Finally, the contribution of lakes as C sources or sinks in the global C cycle depends on allochthonous inputs, in situ production and respiration, and burial rates in sediments. It would be interesting to compare the ratio between ecosystem respiration and production (lake heterotrophy or autotrophy) with food-web efficiencies. It can be hypothesized that high C burial in lakes corresponds to low mechanistic TTE because substantial amounts of primary production are not available to secondary producers, at least in short term. In turn, however, the food-web efficiency could be high in such systems,

as demonstrated above (Table 2). An effect of food web structure in lakes on CO<sub>2</sub> flux between lake water and the atmosphere has already been demonstrated experimentally (Schindler and others 1997).

Accordingly, comparative studies estimating mechanistic TTEs and food-web efficiencies in lakes should be encouraged, with particular emphasis on including more than the typically studied phytoplankton–zooplankton trophic link. Only by empirically and theoretically exploring which processes drive ecosystem functions such as resource production, consumption and transfer efficiency will we be able to predict the response of lake ecosystems to anthropogenic disturbance, for example from global warming, species invasion, chemical pollution and size-selective harvest of fish populations.

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