The trophic position of dead autochthonous organic material and its treatment in trophic analyses

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1. The importance of the recycling of organic matter for the overall carbon and nutrient flow in a food web, e.g., by the microbial loop has been recognized for pelagic and other ecosystems during the last decade. In contrast, analyses of the trophic food web structure conducted, e.g., by network analysis based on mass-balanced flow diagrams (i.e., computation of, e.g., trophic positions and transfer efficiencies, organismal composition of trophic levels) which greatly contribute to our understanding of the flow and cycling of matter in food webs, have not yet responded adequately to this fact by developing coherent techniques with which dead organic matter and its consumers could be considered in the models.
2. At present, dead organic matter (measured in units of carbon or nutrients) is either allocated to a fixed trophic position (between zero and one), or the trophic position of dead autochthonous material depends on the trophic position of the organisms which released it. This causes partially ambiguous and inconsistent interpretations of key measures like trophic transfer efficiencies and trophic positions and greatly hampers cross-system comparisons.
3. The present paper describes and compares four different definitions of the trophic position of dead autochthonous organic material which have either been newly invented or already used. Their impact on the resulting trophic positions of individual groups is illustrated using a food web model from the pelagic zone of Lake Constance. The present analysis evaluates the partially far reaching consequences of the definition chosen, and suggests to allocate all dead organic material to the 'zeroth' trophic level irrespectively of its origin (allochthonous or autochthonous), chemical composition and the commodity used to quantify the food web model (e.g., units of carbon or nutrients). By this means trophic positions and trophic transfer efficiencies get a clear and consistent ecological interpretation, while inconsistencies between analyses conducted in units of carbon or nutrients and some operational problems can be overcome and cross-system comparisons and empirical verification are facilitated.

Keywords: trophic level, trophic position, dead organic matter, carbon recycling, trophic structure, nutrient cycling

1. Introduction

Describing the flow and cycling of carbon and nutrients and the trophic structure of food webs has long been a major aim of both theoretical and applied ecosystem studies, because it is regarded as a prerequisite for deeper insight into ecosystem functioning. The concept of trophic levels first introduced by Hutchinson (unpubl.) and Lindeman [18] was a key notion for this purpose. The original intention of this approach was to provide a tool for a static (i.e., non-dynamic) description of the flow of matter and energy in food chains. Further development of this idea led to powerful techniques like network analysis. The latter is based on mass-balanced carbon or nutrient flow diagrams which consist of various living and non-living compartments representing major functional groups of organisms, and the fluxes interconnecting the compartments. Given a sufficient data base, the mass-balance requirements (i.e., the inputs into each compartment and the entire system have to balance all respective outputs) enable consistency checks of the different bits of information used in order to quantify the fluxes (e.g., standing stocks, ingestion-, respiration-, and growth rates, diet compositions) which were derived from inevitably incomplete data sets. They may allow 'guesstimates' of a few fluxes which could not be measured at all. By this means, analyses of such flow models become

more powerful than the direct inspection of process rates of individual compartments. The food webs models may provide comprehensive descriptions of the flow and cycling of matter and the trophic structure of complex food webs (e.g., Ulanowicz [30]; Wulff et al. [32]; Christensen and Pauly [5]). They allow useful theoretical considerations which are hardly accessible to direct measurements as for instance a separate analysis of fluxes along the grazing chain (i.e., flows originating directly from primary production) and the detritus chain (i.e., flows starting from dead organic matter). In this context, the trophic levels do not necessarily have specific dynamic properties.

Additional attempts were made to analyze the dynamics and regulation of food webs with discrete trophic levels (e.g., Hairston et al. [13]; Fretwell [10]; Oksanen et al. [20]; Hairston and Hairston [14]). They led to concepts like trophic cascading (e.g., Carpenter and Kitchell [4]). The successful application of this approach, e.g., for biomanipulation of lakes, depends heavily on the fulfilment of numerous assumptions. Therefore, its utilization is restricted to a subset of the world's ecosystems which appears to be rather small according to actual knowledge (Reynolds [28]; Polis and Strong [26]). One of the essential prerequisites is that the trophic levels can be used as a surrogate for dynamic units. This requires each trophic level to be domi-

nated by functionally fairly similar groups of organisms and each group of organisms to belong to mostly one particular trophic level. These assumptions have to be tested by analyzing the system's energy flows using network analysis or related techniques. Thus, although analyzing the flow of matter and the organismal composition of trophic levels may appear as tiresome bookkeeping to those interested in food web regulation, the latter requires profound knowledge of the trophic structure of the community. The following evaluations are restricted to the first mentioned approach using the trophic level concept for static descriptions of energy flows. Critical evaluations and comparisons of the full range of definitions, uses, and concepts of trophic levels are given elsewhere (e.g., Pomeroy and Alberts [27]; Oksanen [21]; Polis and Strong [26]) and will not be reconsidered here.

Despite its large impact on system ecology, the original concept of trophic levels has been heavily debated during the last decades for various operational and theoretical reasons (e.g., Cousins [7] and literature cited therein). Two disputable issues and the subjects of our discussion are how to consider omnivory and how to treat dead organic matter when calculating and interpreting trophic positions, transfer efficiencies, and related measures. Nowadays, the problem of omnivory has largely been solved in static food web analysis by splitting omnivores over several trophic levels (see below), whereas a coherent solution to the classification of dead organic matter in trophic analyses is still lacking. At present, the definition of the trophic level of dead organic matter differs strongly among investigations, largely without reasoning on the legitimation and consequences. At first sight, this may appear as an insignificant question of definition, hardly influencing overall results. Depending on the questions asked, this may occasionally be true for individual studies conducted in either units of carbon or nutrients (but not both). However, the most commonly used definition at present involves, next to serious operational problems, inconsistencies in the interpretation of important measures like trophic positions and trophic transfer efficiencies. In addition, cross-system comparisons of, e.g., trophic pyramids are severely hampered or become impossible when using different definitions for the trophic level of dead organic material, which mostly represents a major component of the flow model. The trophic position of the dead organic matter determines the trophic positions of all organisms belonging exclusively to the detritus chain, and in complex food webs most consumer groups of the entire food web will be affected, since the grazing chain and detritus chain are strongly interconnected by omnivores. The significance of the detritus chain for the overall carbon flow has been recognized for pelagic and other ecosystems during the last decade. Thus, a seemingly minor question of definition may have a substantial impact on our potential to arrive at generalizations about the energy flow in ecosystems. We require further development of the methodology to compute measures describing the trophic food web structure which consider dead organic matter in a coherent way.

This study presents advantages and drawbacks of mainly four potential definitions concerning the trophic position of dead material, two of which have been used previously, whereas the others are suggested by us. The objective is to stimulate discussions and attempts for standardization in order to facilitate cross-system comparisons, and to clarify interpretations of analyses of the overall energy flow and related measures in ecosystems.

Trophic analyses distinguish three forms of biologically exploitable energy: light (combined with CO_2), dead organic matter, and living organisms. Each may represent a limiting resource but differs with respect to its metabolic activity. In most ecosystem studies, conditions of mass-balance are applied to carbon and/or nutrients within the food web model, and a closed budget for biologically exploitable energy is sought. CO_2 exchanges with other systems are generally not traced explicitly. This procedure is justified by the observation that gaseous CO_2 is in general non-limiting and its rate of exchange between ecosystems tends to be higher than those of living and dead organic carbon and nutrients. Export of matter and energy still usable by other systems is frequently included in flow diagrams (e.g., sedimentation, fish yield). If physical ecosystem boundaries are chosen in such a way that species immigrating from other systems constitute major prey items, we suggest that they maintain the trophic position they had in their previous food web, and that this number is included into the calculations. Further evaluations are restricted to the consideration of *dead* material. When considering the effective trophic position of many (multicellular) detritivores it should be kept in mind that they may receive substantial amounts of energy not directly from the dead material itself but from bacteria and other microorganisms colonizing the substrate.

2. Original concept of trophic levels based on a linear food chain

The original concept of trophic levels perceived the natural food web primarily as an acyclic chain of successive trophic levels consisting of autotrophs (first trophic level), herbivores (second level), primary predators (third level), and so on (figure 1a). The trophic levels represented functional, taxonomic aggregations of organisms according to the number of times the energy embodied in the organisms had previously been assimilated since it was fixed by autotrophs. The ratios between outputs of adjacent trophic levels represented trophic transfer efficiencies. Spatial system boundaries were delineated, enabling the definition of exports from the system. The uptake of CO_2 by autotrophs in the presence of light energy was regarded as system input. Despite (severe) limitations (e.g., Peters [22] and see below), this concept serves as a starting point in the present analysis because it forms the basis for all subsequent attempts of improvement.

Figure 1.

3. Criticism to the original concept and potential solutions

3.1. Omnivory

The simplicity and unambiguity of the original model was achieved at the expense of ignoring two important characteristics of natural food webs: (1) omnivory (i.e., feeding of individual populations on different trophic levels), and (2) the energy input by dead organic material which is utilized by osmotrophs or detritivores. The dead organic matter may originate from sources external to the system considered (called allochthonous in the following), or may arise within the food web (autochthonous). Regarding static descriptions of energy flow, the problem of omnivory may be solved by distinguishing between trophic positions and trophic levels as described, e.g., by Odum [19], Levine [17], and Ulanowicz [30,31]. The trophic position of a population is in general a non-integer value which reflects the average number of trophic transfers its food items passed before being eaten by the given consumer. It is calculated as the weighted average of the lengths of a population's various feeding pathways. For example, a consumer satisfying two thirds of its energy demands by herbivory and one third by grazing on herbivores is assigned to a trophic position of $2/3 \cdot 2 + 1/3 \cdot 3 = 2\frac{1}{3}$. The biomass and

throughflow of conventional discrete trophic levels is established by distributing all omnivorous populations according to their diet compositions over the respective trophic levels. In the above mentioned example, two thirds of the biomass and metabolic activity of the consumer are assigned to the second, and one third to the third trophic level. This definition fully accounts for omnivory. The ecological meaning of trophic positions is identical to the original one given above for the trophic levels in a food chain. To conclude, given sufficient knowledge on diet, omnivory (including mixotrophy, conspecific cannibalism, etc.) can be acknowledged systematically in static analyses of the trophic food web structure (but not necessarily in dynamic approaches). Nowadays, the bottleneck is not the methodology or computer capacity but the biological data base indicating that the development of methodology kept up with empirical evidence.

3.2. Dead organic matter

The energy embodied in *allochthonous* dead organic import is commonly treated as a second external energy input like light energy used for gross primary production, i.e., organisms first assimilating this energy (e.g., autotrophs, bacteria, and detritivores) are allocated to the first trophic level. Being an external subsidy of biologically exploitable

energy, this seems to be the most logical way to proceed. For example, Burns et al. [2] argued that organisms utilizing dead allochthonous material bear only the costs for obtaining and assimilating it, but not for fixing the energy produced elsewhere, which is regarded as analogous to the autotroph's costs for using solar radiation. In contrast to the generally coherent assignment of dead allochthonous material to the 'zeroth' trophic level, different ways were suggested and used in order to include recycled *autochthonous* material into computations of trophic positions and transfer efficiencies.

4. First approach ('trophic unfolding')

Some scientists suggested keeping track of the origin of autochthonous non-living material and calculating the trophic levels of its consumers according to the trophic levels of the different sources of non-living material, i.e., osmotrophs and detritivores are one trophic level higher than the organisms which released the material (Burns et al. [2]) (figure 1b). For example, bacteria are allocated to the fifth trophic level if they consume material excreted by fish which belongs to the fourth level. This technique requires that one knows who produced the dead material which is generally hardly directly measurable but has to be inferred from food web models. Since carbon can recirculate for ever, it results in an unlimited number of trophic levels. For example, bacteria (at level 5) are consumed by some zooplankton (thus allocated to level 6) which is subsequently eaten by fish (at level 7). The fish in turn releases a part of its diet which serves some bacteria (assigned to level 8) as a nutritional basis, and so forth. Thus, bacteria (and most other groups) are spread over many trophic levels. To avoid an infinite assignment of trophic levels the food chains may be truncated, e.g., by an arbitrary threshold value for the minimum amount of energy passing through the highest trophic level.

This methodology provides condensed and abstract information on the energetic basis of individual compartments, e.g., to which extent they rely on which trophic level. This, however, is achieved at the expense of a very heterogeneous compartmental composition of the trophic levels aside from the lowest one(s) caused by mixing of many different functional groups (e.g., bacteria may contribute to each level) (figure 1b). This, in turn, may strongly complicate the analysis of the food web structure since trophic levels will often not represent groups of organisms with similar trophic histories. Based on such 'unfolded' food chains, the importance of recycled material cannot be assessed directly, and the total contribution of bacterial (or other detritivorous) production to the nutrition of larger consumers has to be calculated separately. Furthermore, indirect effects cannot be evaluated from such flow diagrams because losses to predators (representing a (+, -) interaction between predator and prey) cannot be distinguished from the release of organic substances (i.e., a (+, 0) interaction).

From a purely energetical point of view, it appears as one systematic and logical way to allocate the autochthonous material to the trophic levels of its sources. However, little can be learned about the trophic structure of complex food webs by this approach, since it does not provide a functional aggregation scheme. Aggregation should improve clarity and predictability. However, all higher trophic levels comprise in general all compartments of the food web model in this approach because, e.g., detritivores and thus also their subsequent consumers occur on all higher trophic levels. The trophic levels do not represent any kind of functional units suitable for further evaluations but abstract 'composites of those portions of the energy content of each compartment that have been assimilated an equal number of times' (Burns [1]). Consequently, trophic levels were put in contrast to trophic guilds, i.e., 'groups of species that exploit the same class of trophic resources in a similar way'.

Switching from units of carbon to units of nutrients leads to a heterogeneous composition of each trophic level and an unlimited length of the grazing chain as well (figure 1b). But this approach may not be suitable for the analysis of flow diagrams quantified in units of nutrients which can cycle for ever, because the trophic positions of conservative substances depend on the number of cycles taken into consideration, i.e., they are a function of time.

5. Second approach ('IBP-convention')

Alternatively, all autochthonous non-living organic matter may be assigned to the first trophic level like autotrophs independently of its origin (figure 1c). This definition (for simplicity called 'IBP-convention' in the following) is used in numerous studies (e.g., Pimm [24]; Wulff et al. [32]) and implies that decomposers are on the second level. According to this convention, carbon once fixed by autotrophs (i.e., entering the organic realm) remains at least on the first trophic level as long as it is contained in organic substances residing within the spatial system boundaries (table 1). Degradation to inorganic CO₂ is regarded as equivalent to an export of dead organic material from the system and implies an allocation to the 'zeroth' trophic level. In contrast, nutrients once assimilated always remain at least on the first level independent of being remineralized or not until they are exported across system boundaries. Thus, inorganic carbon and nutrients are treated differently in this approach, and spatial transport of dead material implies a change of trophic levels although the substances remain unchanged (table 1).

Bacteria are often perceived as secondary producers. In purely autochthonous systems (which do not truly exist in nature), this perception is reflected in the trophic positions of autotrophs (level 1) and bacteria (level 2) when allocating autochthonous material to the first trophic level. However, many systems receive a substantial fraction of labile allochthonous organic substances which reduces the difference in trophic positions between autotrophs and bacteria

Table 1

Summary of definitions of the trophic level of dead material used in the second approach ('IBP-convention', e.g., Wulff et al. [32]). In this case, the trophic level of dead material depends on its type (organic or inorganic), the commodity used (carbon or nutrients), and on the spatial origin of the material (residing within spatially defined system boundaries or in the outside world).

Substance	Trophic level	
	units of carbon	units of nutrients
dead organic substances within system boundaries	1	1
dead organic substances imported from outside	0	0
dead inorganic substances within system boundaries	0	1
dead inorganic substances imported from outside	0	0

to a value between zero and one, which is hard to interpret from a trophic point of view. In addition, following the train of thought of Burns et al. [2] bacteria are not only secondary but also tertiary, etc. producers if they consume material which has been assimilated more often than once since its fixation by autotrophs. Switching from units of carbon to units of nutrients implies that bacteria and autotrophs are now competitors for the same resource. This relationship is reflected in their trophic positions, as both belong to the second trophic level under these conditions, i.e., the trophic positions of autotrophs and all subsequent consumers of the grazing chain increase by one (figure 1c).

Assigning the autochthonous material to the first and allochthonous material to the 'zeroth' trophic level causes the dead organic material, its consumers and their predators each to be spread over two trophic levels if significant allochthonous imports are available (figure 1c). Thus, depending on their classification of being allochthonous or autochthonous, substances of potentially equal composition and exploitability, and organisms with identical trophic relationships may be assigned to different trophic levels. In such cases bacteria have a trophic position between one and two, which reflects the relative contribution of the recycled material to the total amount of dead material. If the analysis is performed in units of the limiting nutrient, the trophic positions of autotrophs and bacteria indicate the 'f-ratio' (Ducklow et al. [8]; Field et al. [9]).

The 'IBP-approach' disperses allochthonous and autochthonous substances to different trophic levels and combines living and non-living material in the first one. This procedure complicates the ecological interpretation of the trophic food web structure and transfer efficiencies (it may clarify subsequent population dynamics in systems where living and dead plant material is used indiscriminately, but see discussion section). Bringing together autotrophs and dead substances in the first trophic level has two major drawbacks. First, it implies that the flux from autotrophs to the pool of dead organic substances which is often of quantitative importance, occurs *within* a trophic level. Second, the transfer efficiency between the first (comprising respiring and/or non-respiring material) and second trophic level (consisting only of living organisms) is difficult to interpret as it cannot be related to usual trophic transfer efficiencies occurring between living compartments. In an extreme case where the first level consists only of dead material, the in-

put into the second level may equal the input at the first one if no sedimentation occurs because metabolic losses at the first level are lacking. Thus, the transfer efficiency between the first and second level, defined as the ratio between the inputs into the two levels, may approach 100% (Ducklow et al. [8]).

Applying the 'IBP-convention', the trophic positions of members of the grazing chain reflect the number of *assimilation* events that took place since the energy was primarily fixed by an organism (most computer programs assume equal assimilation efficiencies for all resources of an omnivore, i.e., trophic positions of omnivores are computed based upon relative ingestion rates). In contrast, trophic positions of members of the detritus chain indicate the number of *transfer* events that occurred after the material entered the system or was released autochthonously (i.e., before it entered the pool of dead organic matter). These transfers may have occurred between living compartments and, thus, involve losses by, e.g., respiration and excretion, or may start at a dead compartment which avoids these losses, or start at a compartment comprising a mixture of dead and living material. Thus, it is difficult to assign an ecological interpretation to the number of *transfer* events. Since grazing and detritus chain are generally highly interconnected (e.g., Polis [25]) the overall meaning of trophic positions becomes troublesome in a food web applying this set of definitions.

Trophic positions of most groups reflect to some extent the degree of internal recycling as compared to external subsidies (see above). However, in highly connected food webs with many omnivores and strong links between the grazing and detritus chain, interpretation becomes extremely difficult for all secondary consumers. Thus, providing the ratio between allochthonous and autochthonous inputs directly may be more useful than inferring it roughly from trophic positions. Again, the compartmental composition of individual trophic levels may be very heterogeneous, rendering the trophic level concept as a functional aggregation scheme rather meaningless. This situation can only partially be improved by considering the grazing and detritus chain in the food web model separately (figure 1c).

Another major drawback of assigning different trophic positions to allochthonous and autochthonous material is that the classification into allochthonous and autochthonous depends entirely on the more or less arbitrarily chosen system boundaries and spatio-temporal scales. For example,

nutrients which are allochthonous to a system in the uppermost water layer of a thermally stratified lake may become autochthonous as soon as a larger fraction of the water column is considered, and some material may be refractory and removed from the system in the short run but may be utilized if a longer time period is considered. Coastal areas and Wadden Seas which are characterized by high flushing rates are examples where it is almost impossible to distinguish between allochthonous and autochthonous material. Thus, calculations of transfer efficiencies and of the quantitative importance and composition of trophic levels as well as trophic positions of individual organisms may be sensitive to the selection of spatio-temporal scales, which also complicates cross-system comparisons.

An alternative approach intermediate between the one first ('unfolding') and secondly ('IBP-convention') mentioned is to calculate the trophic position of the autochthonous dead organic matter as the *weighted average* of the trophic positions of all compartments releasing organic substances (Ebenhöh, unpubl.). Thus, rather than being spread over various trophic levels, all bacteria and detritivores and their subsequent consumers are allocated to specific trophic positions which reflect the average number of times the organic matter is transferred within the food web. This number is finite in open systems.

6. Third approach ('new definition')

Regarding the limitations of the two previously published approaches, we invented an alternative in which we change from an ecosystem to a biospheric point of view without defining artificial system boundaries abolishing the distinction between dead allochthonous and autochthonous material. From this point of view we may allocate all dead material to the 'zeroth' trophic level (or to the first one), or, according to Burns [1], to the respective trophic positions of its sources, or to their weighted average (Ebenhöh, unpubl.). The autochthonous mass balance and its contribution to the total energy input into the living system may be acknowledged separately (see below). Regarding *all dead* organic material as external energy input into the *living* system (i.e., allocating all decomposers to the first trophic level like autotrophs) largely circumvents the problems mentioned above (figure 1d). This definition relates the non-living inputs into the first living compartment of the grazing and detritus chain to each other, i.e., the energy embodied in dead organic material is treated like light energy used for autochthonous gross primary production. Trophic pyramids and comparative analyses of the grazing and detritus chain with autotrophs and decomposers at the lowest level may be more meaningful from a biomass and process point of view than relating autotrophs to the pool of dead organic matter which lacks dissipative costs and may have a lower nutritional value than living tissue.

This approach results in clear and consistent meanings of the various measures. The trophic position reflects coherently the number of assimilation (not transfer) events

the material passed since it entered the living system (figure 1d). The comparability of the transfer efficiencies between trophic levels is improved as each step includes metabolic losses. The homogeneity of the composition of trophic levels and, thus, their value as a functional aggregation scheme increases by avoiding a combination of living (i.e., metabolizing) and dead material in one trophic level. For major systems (e.g., pelagic ones where trophic positions roughly correlate with body size under these assumptions), further improvement may be achieved by separating the grazing and detritus chain in the food web model which may largely prevent physiologically very different organisms from being combined in one trophic level. The mathematically unambiguously defined trophic levels will roughly correspond to trophic guilds as defined above (i.e., real biological entities) under these circumstances (e.g., Gaedke et al. [12]). This correspondence and the tendency towards a more homogeneous composition of individual trophic levels with respect to, e.g., feeding history, size, physiology, and taxonomy facilitates food web analyses and the empirical verification of the underlying flow diagrams. For example, calculated trophic transfer efficiencies may be compared with measured growth efficiencies and life history features of dominant groups. However, this option does not exist for all types of ecosystems. Regarding, e.g., terrestrial systems with plants of very varied structures and consequently very different sets of herbivores we are still left without functionally or dynamically meaningful categories (cf. introduction).

Treating all dead organic substances as system inputs implies that the trophic positions are largely independent of the commodities in which the flow diagrams are quantified. For example, primary producers and bacteria are on the first trophic level in carbon and nutrient flow diagrams (figure 1d). (Trophic positions of omnivores may depend in a meaningful way on the commodity used if the ratio of the different elements differs among prey groups. For example, bacteria having higher nutrient:carbon ratios than algae may contribute more to the nutrition of crustaceans in respect to phosphorus and nitrogen than to carbon.)

The significance of the recycling of matter can be easily deduced by computing directly the ratio between the dead autochthonous and allochthonous fluxes entering the living system, and by computing a recycling index, R , which reflects the contribution of autochthonous flows of dead organic matter to the total input of non-living substances into the living system:

$$R = \frac{\text{autochthonous flows}}{\text{gross primary production} + \text{allochthonous} + \text{autochthonous flows}}$$

The ratio between decomposer and autotrophic net production represents a corresponding measure at the next higher trophic level for autochthonous systems. It has frequently been used independently of network analysis to evaluate the importance of the recycling via the microbial loop in pelagic ecosystems. In addition, computations of dependency coefficients (as defined by Wulff et al. [32]) allow

Table 2

Comparison of trophic positions of eight living and one non-living compartment calculated according to the 'IBP-approach' and the 'new definition'. Computations are based on a carbon food web model of the pelagic zone of Lake Constance which neglects allochthonous imports (annual mean 1987, Gaedke and Straile [11]). Computations are also performed in units of phosphorus based on the new definition (Hochstädter [15]). The potential effect of variable carbon:nutrient ratios is omitted in the middle column (N^1) and accounted for in the third one (N^2) (for details see text). The compartment of heterotrophic flagellates comprises small flagellates which rely on bacteria and small algae. Herb. crustaceans stands for predominantly herbivorous crustaceans like daphnids and carn. crustaceans for predominantly carnivorous ones (for details see Gaedke and Straile [11]).

Compartment	'IBP-approach'	'New definition'	
	units of C	units of C or N^1	units of N^2
dead POM/DOM-pool	1	0	0
autotrophs	1	1	1
bacteria	2	1	1
het. flagellates	2.4	2	2
ciliates	2.1	2.1	2.1
rotifers	2.2	2.1	2.2
herb. crustaceans	2.2	2.2	2.3
carn. crustaceans	2.7	2.7	2.9
fish	3.6	3.6	3.8

one to trace the contribution of individual compartments to the input of any other one, e.g., the share of bacteria to the nutrition of larger consumers.

7. Fourth approach

Finally, we may also define that all dead organic material is allocated to the first trophic level, i.e., all nutrients and the carbon which once entered the living realm remain at least on trophic level one until it is degraded to CO_2 . Under this definition heterotrophs are always at least on the second trophic level (secondary producers), i.e., they are never lumped together with autotrophs. However, this implies that the trophic positions of members of the detritus chain do not reflect the number of assimilation but transfer events which severely complicates the interpretation of trophic positions in the entire food web (see above). Otherwise, respective arguments presented in the context of the second approach ('IBP-convention') apply which will not be repeated here.

8. Illustration of the consequences of different definitions using a case study

Mass-balanced carbon flow diagrams were established for the pelagic food web of Lake Constance which were analyzed in detail using network analysis (Gaedke and Straile [11]; Straile [29] and in prep.; Gaedke et al. [12]). Primary production is regarded as the only system input (i.e., allochthonous imports in units of carbon (energy) are neglected, but see below) in this food web model consisting of eight living compartments and one non-living one

comprising the pool of dead organic matter. The trophic positions of the various compartments are computed based on the 'IBP-approach' and the 'new definition' in units of carbon (table 2). In this case study, only trophic positions of bacteria and predominantly bacterivorous compartments (i.e., heterotrophic flagellates) are significantly affected by a change of definitions, because the detritus chain contributes only little to the nutrition of larger organisms with respect to carbon (Straile [29]; Gaedke et al. [12]). Trophic positions derived from flow diagrams quantified in units of nutrients (phosphorus in the present case study) were not calculated according to the 'IBP-approach', because this demands a distinction between allochthonous and autochthonous nutrients which appears to be unreliable in the present case. Based on the 'new definition', trophic positions are in principle always the same for carbon and nutrient flow diagrams. However as mentioned above, carbon:nutrient ratios may vary between organismal groups. Under these circumstances, an alteration of commodities affects in an ecologically reasonable manner the trophic positions of omnivores (Hochstädter [15]; third column table 2). The slightly higher trophic positions of most consumers obtained from nutrient flow diagrams indicate that the detritus chain has a larger importance for the supply of large organisms with nutrients than with carbon. Computations according to the 'trophic unfolding' approach (Burns et al. [2]) are not given because the specific values of the resulting trophic positions of all compartments – except autotrophs in a carbon flow network – depend heavily on individual assumptions (e.g., sedimentation rates) and exhibit pronounced seasonal changes.

9. A plea for a separate treatment of living and non-living components in network analyses

Independently of the definition of the trophic level of dead organic material, we strongly recommend treating non-living compartments differently from living ones in a trophic sense when performing a network analysis of a mass-balanced flow diagram as described, e.g., by Wulff et al. [32] (especially when computing measures which rely in any way on the number of trophic transfers or on the total sum of fluxes). For example, a food chain going from algae via ciliates to the POM/DOM-pool and further to bacteria (four transfer but only three assimilation events) has to be distinguished from a chain going from algae via ciliates and daphnids to fish (four transfer and assimilation events). Treating the POM/DOM-pool like a living compartment when computing trophic positions implies that one step of the trophic ladder is performed without dissipation of energy which is otherwise characteristic for all trophic transfers. Besides exports from the system, the input into the POM/DOM-pool equals the output since the POM/DOM-pool has no metabolism and no losses by, e.g., respiration. The flow of dead material should not be counted twice (e.g., as input in the POM/DOM-pool

and as input into the first consumer compartments) when evaluating a flow diagram with network analysis. Energy embodied in dead organic material should change trophic positions when it is assimilated by decomposers, but not when it is transferred to a non-living compartment (i.e., one ought to distinguish between enumerating transfer or assimilation events; cf. Burns et al. [2]). Otherwise, computations of the total fluxes along the detritus chain cannot be compared to those along the grazing chain in a meaningful way, and rather odd results may be obtained when calculating, e.g., average path lengths. As an extreme case, a food web model may be thought of where the dead organic matter is distributed over a number of compartments which range from very refractory to labile dead organic material and which are passed on successively as abiotic degradation proceeds until the material is sufficiently labile for consumption. Considering all transfer events and fluxes between these non-living model compartments like trophic interactions between living compartments would alter the results arbitrarily (e.g., the total system throughput or average path length).

Another argument in favour of considering only assimilation events involves the experimental verification. Originally the concept of trophic levels was purely theoretical and could hardly be tested empirically. This can be expected to change now with the development of techniques to measure stable isotope ratios of major food web components which allow one to estimate (relative) trophic positions from direct measurements (e.g., Peterson and Fry [23]). This approach takes advantage of the fact that animals discriminate between, e.g., ^{14}N and ^{15}N isotopes and are enriched in ^{15}N as compared to their diets. It allowed to trace seasonal and cross-system variability of trophic positions of various zooplankton and fish species (Kling et al. [16]; Cabana and Rasmussen [3]; Yoshioka et al. [33]). Thus, the number of trophic transfers between *living* compartments can be investigated with this approach.

10. Discussion

The trophic level concept was invented to support a macroscopic description (i.e., ignoring physiological details) of the flow of matter and energy in food webs. Its usefulness was discussed intensively during the last decades under various aspects (e.g., Cousins [7]; Pomeroy and Alberts [27]; Oksanen [21]; Polis and Strong [26]; and lit. cited therein). The present study was restricted to approaches which classify dead material and living organisms merely according to their trophic role ignoring other properties (e.g., degradability of detritus, size and type of herbivores; Cousins [6]), and focused on two aspects of the use of the trophic level concept as a static descriptive for trophic food web structures. Regarding such energetical analyses, the original problem of insufficiently accounting for omnivory may be overcome by introducing non-integer trophic

positions for individual compartments and allowing a population to spread over various trophic levels (i.e., thinking of trophic levels as fuzzy sets). A second specific problem concerned the way of how to include dead organic matter into computations of trophic levels and trophic transfer efficiencies. Allochthonous material is commonly treated as second external energy input like light energy, which implies that its consumers are assigned to the first trophic level like autotrophs. In contrast, different definitions were suggested for the trophic level of recycled autochthonous material.

The decision to select the best from a number of alternative concepts requires well considered selection criteria. Our main emphasis was placed on a straightforward, consistent ecological meaning of the trophic position and the transfer efficiency between trophic levels, as well as on the practicability of the definitions and the functionality of the aggregation scheme 'trophic level'.

The two first mentioned concepts ('trophic unfolding' and 'IBP-convention') rely on physically defined system boundaries, since the non-living material is classified according to its spatial origin into subsidies from the outside world and material generated within the system. Differentiating the dead organic material according to its spatial or biological sources may be useful for dynamic analyses (Polis and Strong [26]) but does not generally provide a suitable selection criterion from the viewpoint of biological exploitability, i.e., the history of energy does not matter to consumers. The third and fourth approach ('new definition') avoids such a distinction.

Previously it was tried to allocate dead organic material to a particular trophic level in order to obtain functionally similar consumer groups allocated to the same trophic levels. However, this train of thought does not provide an operational argument for a definition because it is not consistent throughout different types of ecosystems. The complication is given by the fact that the biological exploitability of POM and DOM varies greatly between systems and between labile and refractory substances, and that a large number of different organisms participates in this process. For example, equating herbivory and autochthonous detritivory in the trophic sense as done in the second approach ('IBP-convention') may be motivated by ecosystem studies where a large fraction of the autotrophs is consumed indiscriminantly before or after death (e.g., grass and hay by cows) (Ulanowicz [31]). However, in other systems, the exploitability of autotrophs and (dissolved) organic substances differs greatly, which largely prevents both resources from being utilized by similar organisms (e.g., herbivorous daphnids or elephants versus osmotrophic bacteria and fungi). Thus, profound cross-system comparisons representing a major aim of trophic analyses require consistent definitions which are independent of particular characteristics of specific ecosystems. Similarly, the degree to which some forms of biologically exploitable energy are limiting, varies greatly between systems, which again prohibits its consideration in the present definitions.

To conclude, it appears unlikely that a final definition exists which acknowledges the specifics of all types of ecosystems and all questions raised in computations of trophic measures in an optimal way. Keeping track of the origin of autochthonous material as suggested in the first approach ('trophic unfolding', Burns et al. [2]) appears logical from a purely energetical point of view but is empirically intractable and does not provide any functional aggregation scheme. The second approach, which allocates allochthonous material to the 'zeroth' and autochthonous matter to the first level (e.g., Wulff et al. [32]), appears as the least suitable one to us due to (1) the operational problems when defining material as allochthonous and autochthonous, (2) the inconsistent definitions of trophic levels of inorganic carbon and nutrients, and (3) the inconsistency of the interpretation of the transfer efficiencies and trophic positions between grazing and detritus chain. A number of arguments were put forward in favour of allocating all dead organic material to the 'zeroth' trophic level ('new definition'). By this means trophic positions and trophic transfer efficiencies have a clear and consistent ecological meaning, while inconsistencies between analyses conducted in units of carbon or nutrients and operational problems can be overcome and cross system comparisons and empirical verification are facilitated.

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