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Converting copepod vital rates into units appropriate for biogeochemical models

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Abstract:

The conversion of units is one of the difficulties of model parameterisation. Conversion errors may result not only from incorrect choices of conversion factors, but also from incorrect choices of the value itself. In biogeochemical models, mesozooplankton, is the highest trophic level of the food web, and it is very often reduced to a single variable generally considered as a representation of the copepod community, the dominant taxa in mesozooplankton. If this simplifies the information to be obtained for the stock, a correct parameterisation of the processes related to the copepod community is already a tricky task due to the wide range of copepod species, sizes, stages and behaviour. The goal of this paper is to improve the communication between experimentalists and modellers by giving indications for the conversion of copepod vital rates from experimental to biogeochemical model units. This includes the choice of values, conversion factors, terminology distinction and the scale transfer. To begin with, we briefly address the common problem of the conversion of a rate per individual to a rate per mass. Then, we focus on unit conversion problems for each specific rate and give recommendations. Finally, we discuss the problem of scale transfer between the level of organisation at which the rate value is measured at characteristic time and space-scales *versus* the level of representation of the corresponding process in the model, with its different characteristic time and space-scales.

1. Introduction

Modelling approaches suffer from a number of problems many of which are a result of the parameterization used (Scheffer, 1991; Lima et al., 2002). One of the reasons for the introduction of significant errors due to model sensitivity to parameterization, is the use of inappropriate conversion factors for a given model framework. The little commonality in units requires transforming experimental data into appropriate units for models to improve the communication among modellers and biologists (Flynn, 2005).

There are several types of error that may lead to incorrect conversions. Apart from simple direct errors due to initial incorrect values, like the initial decimal point error for the iron in spinach which took almost a century to be widely publicized (Hamblin, 1981), there are also indirect causes of errors such as wrong choices of values due to either a discrepancy in terminology between biologists and modellers (e.g. modellers include particulate matter into excretion or dissolved matter into egestion), or a transfer of a reference (e.g. a value initially from unpublished data that is transferred from one paper to the next), or a wrong application because of scale transfer (time, space, level of organisation at which the process or the value is measured *versus* the level of representation of this process or this value in the model).

Parameters of zooplankton have a large influence on the models sensitivity (Carlotti and Poggiale, this issue). In biogeochemical models, where mesozooplankton is often the highest trophic level of the food web explicitly represented and therefore being a closure term, its parameterisation is often difficult due to the mixture of different taxonomic groups, each one with a complex life cycle (developmental stages), a broad size spectrum, a variable behaviour and a different metabolism (Carlotti et al., 2000; Gentleman et al., 2003; Buitenhuis et al., 2006; Carlotti and Poggiale, this issue).

This paper aims to give general indications for the conversion of zooplankton rates, helping to build the bridge between modellers and biologists. Although it is much safer for biologists to make these transformations rather than modellers (Flynn, 2005) this paper intends to help both sides. Transformations will consider the choice of values, terminology distinction and transfer of scale that should be taken into account. To illustrate this, a comparison of the vital rates formulation and parameters of three largely distributed biogeochemical models will be presented in parallel from a biologist's point of view (Tables 1 and 2), and will serve as a reference for the detailed presentations of the different processes.

Although it would be more convenient for most biogeochemical models to consider the whole "mesozooplankton", it would be too extensive to give a common conversion guideline, due to the high diversity of this group (Anderson, 2005; Carlotti and Poggiale, this issue) so this paper will only focus on vital rates of copepods, the dominant mesozooplankton group. Copepods play an important role in marine ecosystems linking primary production to upper trophic levels and accounting for up to 80% of the metazoan biomass in the marine environment (Kiørboe, 1998). Their vital rates directly influence the amplitude of their role. These rates are considered here in a broad sense including physiological (i.e. ingestion, metabolic rates and growth) and demographic rates (e.g. mortality rates) and are defined as an amount of matter per amount of zooplankton per unit of time. In biogeochemical models, these rates are usually expressed in units of mass [M], and concern a flow of matter for a mass of organisms [M], per time unit [t], i.e. specific rate (e.g. mgC mgC^{-1} d^{-1} or %C d^{-1} or d^{-1}). The currency of mass unit in biogeochemical models is generally C, eventually N, P. Moreover, in several biogeochemical models some metabolic rates are expressed as a fraction of the assimilated (e.g. for excretion) or non-assimilated matter (for faecal pellet production) therefore with zero dimension (e.g. excreted mgC per assimilated mgC) (Table 1), i.e. assuming that at the time scale of the model resolution these rates could be supposed in a quasi steady state. These fractions values are used as parameters (Tables 1 and 2). To calculate such fractions (f), literature data of the metabolic rate (R), of ingestion rate (I) and of assimilation efficiency (ae) should be obtained in the same conditions, which is rarely the case. These fractions, also called "rates" in some

models, should not be confused with the former ones as they are of a different nature and have different units (e.g. R = I (1-ae) f ; with units for I: d^{-1} and for ae, f: zero dimension).

2. Conversion of 'rate per individual' to 'rate per mass'

Experimental work on rates refers to a variety of mass units but even more frequently is the count of individuals per unit time. The convenience of counting number of individuals is that mortality of organisms during the experiments may be taken into account. The conversion of an amount of organism in mass can be presented in many forms: wet mass, dry mass, ash-free dry mass, C or/and N contents etc. Such conversions have been extensively reviewed by Postel et al. (2000) so the reader can refer to these authors' recommendations. This review and many other publications offer conversion values/equations for a specific area or at least for a specific copepod species. It should be kept in mind that although there are various transformations from dry weight, these are not as satisfactory as having raw data in C or N units.

3. Conversion from measurement units to specific units for biogeochemical models

3.1. Ingestion

Ingestion has a strong role on carbon and nitrogen cycles by affecting the stock of prey, and by affecting all other vital and demographic rates of copepods. Zooplankton models need to explicitly describe the flux of matter consumed per unit mass of the considered zooplankton category (bulk, functional group, population or individual) per unit time.

There are many direct and indirect methods to quantify the ingestion rate (see table 8.2 in Båmstedt et al., 2000) which make the comparison of results from different investigations difficult and, in addition, scientists commonly use conversions between weight measurements in carbon, nitrogen, or energy content, amplifying the difficulty in comparison. Classical indirect methods generally are based on measurements of the removal rate of individual prey or particles between experimental (with copepods) and control (without copepods) bottles. Initial values are obtained with a nominator in cells or Chl *a* (and a denominator of time unit and organisms expressed as individuals or mass unit). The conversion in mass in the currency of interest is a major source of variability in ingestion values. To convert cells to mass, a constant ratio of mass per cell should be avoided unless limited at the species level. In most studies, phytoplankton, bacterial and protistan mass in C (eventually N) is quantified by a combination of cell counts, cell size estimates and the use of conversion factors based on cell volumes. Cell counts and size will deliver a prey size-spectrum. As the carbon content depends on the size-frequency distribution of particles, the use of volume-carbon/nitrogen content should be more precise than with counting by microscope which then used a mean ESD. Choices during the cell sizing (i.e. choice of shape) but also in the choice of equation to convert volume to carbon are critical. Many papers use the empirical equations to convert volumes to carbon for phytoplankton (e.g. Strathmann, 1967; for bacteria Posch et al., 2001; for ciliates and for heterotrophic dinoflagellates Putt and Stoecker, 1989; Menden-Deuer and Lessard, 2000). However, when using laboratory cultures, particularly with phytoplankton, the experimental conditions have a strong impact on the cell content and should not be ignored (Brunet et al., 1996).

The most widely used direct method for studying ingestion of phytoplankton by copepods is the gut fluorescence method (Mackas and Bohrer, 1976). The interesting aspect

is that it provides information on *in situ* feeding rates immediately after collection. However, besides the high variability in the measurement, the C:Chl *a* conversion used to evaluate the carbon gut content is itself highly variable (Peterson and Festa, 1984). Moreover, the correction for taking into account gut pigment destruction varies from 0 to 90 % (Båmstedt et al., 2000), prompting Durbin and Campbell (2007) recent statement that "any correction for gut pigment destruction in calculating ingestion rate is inappropriate".

Ingestion measurements made on several stages of the same species clearly show differences in the specific (or intrinsic) ingestion. This specific rate is related to body weight in a curvilinear fashion following an allometric relationship with a body mass constant in exponent (generally between 0.7 and 0.8). Within a species the intrinsic ingestion rate may vary from a few tens of percent of the body weight for adults, to a few hundreds of a percent for nauplii (see table 21 in Mauchline, 1998). In this calculation, it is crucial to check that the relationships have been obtained with the same unit of reference for the rate and for body weight (i.e. µgC d^{-1} for ingestion and µgC for the body weight, instead of 10^{-6} gC). In general, this aspect is ignored when using the value of maximum ingestion rate in models. Better estimates of the carbon content of prey can be obtained from particle size analysis assuming the scaling of size to mass is well constrained for the currency of reference. When using chlorophyll content, the C:Chl *a* ratio should be measured. Body weight of copepods in the incubation bottles should be measured as well in the currency of reference.

The choice of any data of ingestion experiments for modelling purposes (i.e. fitting a functional response) should be made with caution for many reasons. Firstly, despite the large data sets on ingestion rate there is little information on early developmental stages (Calbet et al., 2007; Saiz and Calbet, 2007). In addition, biogeochemical models include prey preference by copepods (Table 1), although studies on food preferences have not delivered any general rules (e.g. Hansen et al., 1994; Straile, 1997; Calbet and Saiz, 2005), probably because other factors may influence this choice, such as the local turbulence (Caparroy and Carlotti, 1996; Caparroy et al., 1998). Most field data on feeding rates on phytoplankton often included autotrophic and heterotrophic forms (Calbet et al., 2007; Saiz and Calbet, 2007). In single prey conditions, the part of accessible cells may vary between 0 and 100% depending on the size selectivity by the predator. Consequently, data obtained on food mixtures are probably better for this aspect.

Finally, maximum ingestion rates must be taken cautiously as laboratory cultures are not necessarily the most suitable prey for a given species of copepod (Calbet et al., 2007; Saiz and Calbet, 2007). Many experiments present ingestion rates of copepods reaching their maximum at values over several hundred µgC per litre, which will not be comparable with *in situ* food availability. Few studies have measured demi-saturation coefficient and food concentration for maximal ingestion rate at natural conditions (Fransz et al., 1991 and references therein).

3.2. Assimilation

The assimilation efficiency is a key parameter in biochemical fluxes because it represents the proportions of ingested matter that will ultimately enter the secondary trophic level and that is lost via egestion of faecal pellets.

Conover (1978) made a review on the assimilation values produced from experiments and showed a very high variability. Båmstedt et al. (2000) clearly explained all sources of variability including the unit considered (carbon, nitrogen, organic matter, energy), because digestion efficiency depends on each food type. Direct and indirect measurements exist (see Båmstedt et al. 2000). For ecosystem modelling purposes, it would be recommended to use information obtained on long time step (day), measuring the production of faecal pellets against the ingested food (see Båmstedt et al. 2000 for all sources of error).

In most biogeochemical models, the assimilation rate is usually assumed to be a constant fraction (usually ranging between 0.6 and 0.8) of the ingestion rate (Table 1). This is certainly a simplification of the digestive process, as assimilation is linked to gut transit time

and faecal pellet production. Typically, it represents a budget of assimilated against ingested matter over time. However, on short time scales, this may not be the case. Franks et al. (1986) used a mathematical formulation of the grazing response that was derived from Mayzaud and Poulet (1978), and which simulated the change of feeding rate, and indeed assimilation, with food concentration. But even this formulation represents characteristics at the level of a given individual, which may be not important at the level of the population or community. Slagstad and Tande (1981) suggested a mathematical model of the assimilation process in copepods depending on the ingestion rate, the phytoplankton species composition and physiological state of the animal. This model predicts a decrease in assimilation efficiency with increasing ration. Assimilation efficiencies also will differ according to the currency being used in the model, because it focuses on different substrates to be assimilated (proteins, lipids…). When more than one element is modelled, inconsistencies can arise if prey and predator have different elemental ratios. Moloney (1992) showed how matter could be created in models where elemental ratio effects are not taken into account and constant assimilation efficiencies are used.

In general the literature gives a value without dimension. If the source is a calculation based on rates of feeding and faecal pellet production, it is important to check the consistency between the currencies, and eventually make the conversion (see sections on these two processes).

3.3. Respiration

Recent evaluations of mesozooplankton respiration on a global scale have shown that rates are considerably higher than previously thought, clearly identifying mesozooplankton as a major component of the carbon cycle in the ocean (Hernandez-Leon and Ikeda, 2005). This rate influences the budget of the total CO_2 produced by the secondary trophic level.

Respiration rates measurements are generally synonymous with oxygen consumption rate measurements (Ikeda et al., 2000). In fact, quantification of CO_2 directly is difficult to make with copepods under low animal density and reasonable incubation time. New techniques, such as coulometric determination have reduced these limitations (Mayzaud et al., 2005 and references therein).

The initial experimental units are expressed with a numerator of µl of O_2 (occasionally CO_2), a denominator of unit time and organisms expressed as individuals or unit mass (µg or µatg of DW, WW or protein or C or N). The conversion to carbon weight specific units is simple using direct CO_2 measurements and the weight of carbon in 1 mole of CO_2. However, as the large majority of respiration rate data obtained up to now correspond to oxygen consumption rate, the ratio of CO_2 produced to O_2 consumed (RQ) is needed to make conversions to carbon. This ratio was obtained until recently based on theoretical values related to the excretory end product (Gnaiger, 1983). Copepods are assumed to be primary ammonotelic (but are not always as discussed below) and a value of 0.97 is attributed (Ikeda et al., 2000). A recent study by Mayzaud et al. (2005) measuring RQ showed a mean value for copepods of 0.87. The study also highlights the paucity of RQ measurements, as well as the need to limit the pooling of RQ values up to the taxon level due to significant inter-specific variability.

Another aspect to consider is that some biogeochemical models distinguish basal and activity (or feeding) respiration (Table 1). Biologists distinguish basal (standard), routine and active metabolism (see Ikeda et al., 2001 for definitions). Methods used to measure respiration (or excretion) are considered to give estimates between basal and routine metabolism (Ikeda et al., 2001), and to be closer to a basal metabolism when done under starving conditions (filtered seawater) (Saiz and Calbet, 2007). For conversion purposes it may be useful to consider that routine and active metabolism is respectively, 1.9 and 6 times the basal metabolism, although these values should be used with caution as there are few studies concerning marine copepods (Buskey, 1998).

3.4. Excretion

Copepod excretion products contribute directly to the nutrient recycling, the vertical flux of dissolved matter, the DOC pool (review by Frangoulis et al., 2005) and can indirectly influence primary production by affecting the water's optical characteristics (Steinberg et al., 2004).

Inorganic nitrogen excretion is measured by directly quantifying ammonia or indirectly by enzymatic methods (Ikeda et al., 2000). Organic nitrogen excretion, may concern a specific method for each product or total dissolved excretion after mineralization of the organic molecules (review by Le Borgne, 1986). Concerning excretion, several units have been used combining a numerator of µg or µatg (of N or C), a denominator of unit time and organisms expressed as individuals or unit mass (µg or µatg of dry weight or wet weight or C or N).

For conversion purposes, it is crucial to distinguish which forms of excretion products correspond to the rate data. Copepods produce dissolved matter via excretion, sloppy feeding and leakage from faecal pellets (Lampert, 1978). The term 'excretion' is being generally considered by biologists as the active release of liquid, metabolic by-products (from assimilated material). This distinction is important to make since some models include faecal pellet production and/or sloppy feeding into the term 'excretion' (Table 1). The leakage from faecal pellets can be consider as insignificant compared to excretion of liquid by-products (Steinberg et al., 2000), however, model formulation imposes a choice between the inclusion or exclusion of sloppy feeding into excretion (method with or without feeding). A distinction should also be made between data of rates corresponding to basal, routine or active metabolism. In addition, distinction between organic and inorganic excretion should be made.

If inorganic excretion rate data are used, the conversion to nitrogen weight-specific units is simple, since there is only one inorganic product (ammonia). However, in the case of organic excretion, the data may concern one or more products and/or the total dissolved nitrogen, the definition of the latter varying from one study to another. Most studies did not measure actual total dissolved nitrogen, but rather ammonia, urea, and amino acids (Steinberg et al., 2002 and references therein). Therefore, conversions should consider possible underestimation of total dissolved nitrogen. Some biogeochemical models use a constant ratio to convert from inorganic to organic excretion (Table 2), with the former exceeding the latter (ammonotelic animals). The limits of application of such a ratio should be carefully defined, as it may vary depending on the animal species (Dagg et al., 1980) and on the quantity and quality of consumed prey (Miller, 1992; Miller and Glibert, 1998). In some cases the amount of organic excretion may exceed the inorganic and this should also be considered when choosing a RQ ratio for respiration rate conversions.

3.5. Faecal pellet production (egestion)

Copepod faecal pellets can be important to carbon export and nutrient recycling, however, their importance can vary greatly, spatially and temporally (reviews by Turner, 2002; Frangoulis et al., 2005). A wide variety of methodologies is also used to measure the rate of faecal pellet production: time course or end-point method, duration from 1 to 24h hours, one copepod species (often adult females) or a mixed population, cultured or natural food (e.g. Carlotti et al., 1997; Daly, 1997, Huskin et al., 2000; Roy et al., 2000; Frangoulis et al., 2001; Olesen et al., 2005). However, no inter-comparison of methods currently exists (e.g. see lack of discussion in ICES Zooplankton Methodology Manual by Harris et al., 2000). In contrast with most other rates, the initial units obtained by all methods are often common (i.e. the number of pellets per copepod per unit time). In biogeochemical models, the rate of faecal pellet production is generally calculated from values of ingestion and assimilation rates (Table 1) and expressed in weight-specific units, generally in $C_{pellet}\, C_{copepod}^{-1}\, d^{-1}$. To convert to

such units the initial experimental units of faecal pellet production rate (pellets copepod^{-1} time^{-1}), pellets and copepods have to be converted to C or N. There are few direct measurements of C- or N-content of pellets (e.g. Gonzalez and Smetacek, 1994; Urban-Rich et al., 1998). For conversion purposes, data on pellets collected shortly after their production are preferred, as a large amount of dissolved and particulate matter is exuded respectively, within minutes and hours (review by Frangoulis et al., 2005; Olesen et al., 2005 and references therein).

Caution should be taken using literature values of faecal pellet content when they are expressed as amount of element per unit pellet (e.g. ngC pellet^{-1}) or per pellet volume (e.g. ngC mm^{-3}). Large variation (more than an order of magnitude) is found among these values (review by Frangoulis et al., 2005) due to many factors (e.g. copepod species, food type, assimilation efficiency, pellet compaction: Gonzalez and Smetacek, 1994; Urban-Rich et al., 1998). If such values are to be used, amounts of C, N per pellet volume should be preferred over element per unit pellet, when pellet volume measurements are available.

A second approach (when pellet volume data are available) is to use literature values of C, N per pellet dry weight (DW), pellet density and the ratio of pellet dry weight to wet weight (DW/WW). Despite the fact that this estimation approach uses more parameters (i.e. multiplies variability), these parameters have less variability than the amount of element per pellet or per pellet volume (see tables 1 and 4 in Frangoulis et al., 2005).

3.6. Moulting

Exuvial production is generally not implicitly considered in models, although it is a contributor of losses to POM. Few papers present the contribution of exuvial production in copepods. Mullin and Brooks (1970) found the C content of the exoskeleton to be 10% of the total body C of *Rhinocalanus nasutus*. Vidal (1980) found a carbon content in exoskeletons of stages CII to CVI of *Calanus pacificus* ranging from 2.8 to 5.1% of the body carbon content of the preceding development stage.

3.7. Growth

Biogeochemical models have no term corresponding to zooplankton growth as it corresponds to the simulated secondary production of the whole community. The zooplankton functional group in ecosystem models is a black box, not considering intra- and inter-specific growth. Empirical relationships linking measured growth rate data compilation with environmental parameters (temperature, biomass, Chl *a*) (Hirst and Bunker, 2003) may be considered as more robust to derive food parameterisation in biogeochemical models, because individual growth integrates the impact of environmental conditions on a larger time scale than ingestion.

Measurements of growth by experimentalists are been mostly made at species level with a variety of approaches. Copepod females egg production has become one of the most common methods of estimating their growth rate (Sekiguchi et al., 1980; Berggreen et al., 1988; Poulet et al., 1995; Runge and Roff, 2000), because it is easier measured in comparison to younger and smaller stages and was considered as sufficient to estimate population growth rate (somatic growth rate of all stages) (Berggreen et al., 1988). However, several authors consider growth obtained from egg production rate may be less than somatic growth rate (Peterson et al., 1991; McKinnon and Ayukai, 1996), due to the fact that egg production is frequently related to food conditions and temperature (Hopcroft and Roff, 1998). Moreover, there is a high variability in egg production between females (Carlotti et al., 1997). If egg production rate is an easy measurement to obtain and a key demographic parameter, we should be careful deriving growth rates from it. After an expended research in measuring growth and development in copepods Hirst and McKinnon (2001) concluded that egg production rates may not reflect the growth of adults because this stage continues to

lose or gain weight while producing eggs. Also, weight-specific fecundity rates are often dissimilar to juvenile somatic growth rates in nature and the latter are more food limited in warmer waters (Hirst and Bunker 2003). Thus, if we wish to estimate copepod growth and production in future, juvenile growth rates must be examined directly. The main methods to measure field juvenile growth rates are the moult rate method (MR) and artificial cohort method (AC). These methods have been used for over 30 years and results from the > 45 papers using these approaches comprise the bulk of our understanding of mesozooplankton growth *in situ* (Kimmerer et al., 2007). However, none of the methods is perfectly suited to all conditions. Recently, the MR method has been shown to be in error by up to an order of magnitude, and a corrected method, the Modified Moult Rate method (MMR) established (Hirst et al. 2005). More recently the AC method has been critically examined, and again shown to have significant (order of magnitude) errors (Kimmerer et al. 2007). New method and equations have now been developed in this paper (the direct AC), and will need to be used if we are to improve the accuracy of growth measurements in future.

3.8. Mortality

Dead copepods also play a role in the transport of matter in the carbon and nutrient cycles and in the nutrition of marine organisms. Copepod mortality supports most food webs of the open sea, directly affecting pelagic fish populations and the biological pump of carbon into the deep ocean (Wheeler, 1967*;* Zhang and Dam, 1997; Yamaguchi et al., 2002).

Mortality is a demographic process which affects the abundance of a population by withdrawing individuals. Mortality rate corresponds to the intrinsic rate of the number of dead individuals among an initial stock over a given time step. There are several causes of mortality (see Ohman and Wood, 1995 for details) and as a consequence, there are a variety of formulations to represent mortality.

Mortality rate can be estimated by following populations over time in their environment or in controlled conditions (Aksnes, 1996). The major problem in the field is to define the fluxes of individuals in and out of the sampled volume, resulting from advection and diffusion fluid processes as well as the behaviour of the individuals. Mesocosms allow studying of the natural internal causes of mortality separately, but the main problem is that sampling itself reduces the number of individuals. Consequently, direct estimates of copepod mortality rates are scarce as this is inherently time consuming and made difficult by ocean circulation and mixing. (Aksnes et al., 1997; Hirst and Kiørboe, 2002; Ohman et al., 2004). Several indirect methods exist from body mass, temperature or depth, based on empirical relationships (e.g. Hirst and Kiørboe, 2002), or by following a field demographic approach (review by Aksnes et al., 1997; Ohman et al., 2004 and references therein) but no standard estimation technique has emerged up to now.

In biogeochemical models the central importance of zooplankton mortality patterns has become clear as it represents a model closure term and the used mathematical formulations may have a large influence on the model (e.g. Fasham, 1993; review by Carlotti et al., 2000; Edwards and Yool, 2000). The choice of the parameter values can have an influence greater than the closure term formulation itself (Edwards and Yool, 2000).

The use of mortality values from literature for models should be made with caution. Many models used a simple constant value for the mortality rate. In this case, the specific mortality rate appears to be expressed similarly in biogeochemical models and from field or laboratory studies, i.e. in d^{-1}. However, the mortality unit in biogeochemical models is in mass of dead organisms [M] over the mass of whole stock [M], per unit time [t] (biomass mortality), whereas, most mortality rates are estimated from abundances which is a number of dead organisms [Ind] over of the whole stock number [Ind], per unit time [t]. Few values exist concerning measurements of copepod biomass mortality rates which correspond to the parameters used in biogeochemical models (e.g. Kiørboe and Nielsen, 1994; Gries and Güde, 1999; Roman et al., 2002). Most measurements concern stage-specific mortality rates of a given species (ind ind^{-1} d^{-1}) that cannot be easily extrapolated to the whole copepod

population. Compilation of stage-specific mortality rates may give patterns of what biomass mortality looks like in copepods across the globe (Hirst and Kiørboe, 2002) that can be used only in large space scale models (Buitenhuis et al., 2006). Moreover, the "average" mortality rate from field and laboratory studies will depend on the stage structure of the sampled populations, both due to internal (e.g. development stages) or external (e.g. selectivity of predators) characteristics.

Some biogeochemical models use a specific mortality rate (μ_2) proportional to the biomass (μ_2=d x Z), as an additional or sole mortality measure. This implies that the growing zooplankton biomass contains predators which affect the mortality of the zooplankton biomass itself. The new parameter to be found (d) is a density-dependent intrinsic mortality rate thus in a different unit than μ_2, i.e. in $(gC\ m^{-3})^{-1}\ d^{-1}$ (Edwards and Yool, 2000 and references therein). Problems arise essentially from the differences in the nature of these values. These may correspond to the total mortality or only to one of its components (e.g. non-predational mortality). If biogeochemical models consider other functional groups feeding on copepods (i.e. macrozooplankton or fish), the representation of mortality on the mesozooplankton should be accordingly revisited due to the different representation of the ecosystem (i.e. explicit representation of the mesozooplankton predators).

4. Discussion

An issue that has to be considered during all conversions is the transfer of scale of time, space and level of organisation at which the rate value is measured *versus* the level of representation of the corresponding process in the model. Concerning the time scale, biogeochemical models are generally run over months to years, while few rate measurements cover seasonal to annual variations, with most generally run over minutes to days (Carlotti and Poggiale, this issue). Rate data originating from short term experiments (<24h) may not be representative of the daily metabolism as vital rates may show shorter variations (diel variations or other). If such data have to be used a correction could eventually be made after consulting the literature on rhythms of excretion rate (e.g. Checkley et al., 1992; Miller and Glibert, 1998), ingestion rate (e.g. Durbin et al., 1995 and references therein), respiration rate (Duval and Geen, 1976) etc. However, no general correction rules should be made, as diel rhythms may vary in space or time. For example, diel feeding rhythms may be absent during bloom conditions and develop after (Durbin et al., 1995).

Part of rate variability is included in biogeochemical models by considering a temperature and a food effect in the vital rate formulation. However, biogeochemical models do not consider other important sources of variability such as the variability of body size inside the copepod population (due to species variability and stage development). Although information on rates of different species is available, most of it is based on pre-adult and adult stages. Therefore, depending on the available information, some authors have limited relationships to late stages (e.g. for feeding: Saiz and Calbet, 2007) or different relationships has been established for adults and juveniles (e.g. growth: Hirst and Bunker, 2003). In other cases the extrapolation to naupliar stages of copepods has shown contradictory views (e.g. excretion and respiration: Ikeda et al., 2001). In addition, the transferring of values obtained from an individual to a population should not be done directly but through specific approaches (Pascual, 2005; Carlotti and Poggiale, this issue). Finally, caution should be applied when using vital rates values across different geographic locations, as those are likely to vary with environment even within the same species (e.g. Halsband-Lenk et al., 2002; Ohman et al., 2004; Gaudy and Thibault-Botha, 2007).

We can conclude with Båmstedt et al. (2000) discussion concerning conversion of units: "Because most of the dominant biochemical components included in zooplankton body constituents are not conservative, this practice can introduce considerable bias into the resulting estimates. The safest way to use such conversion is to investigate relationships on the same type of biological matter, for example same species and developmental stage,

same season, etc. However, this is not always feasible" and the authors "recommend that the investigator uses direct measurements, or locate appropriate published values for material that is as similar as possible to the target material of investigation". Several important values for conversions in biogeochemical units are still poorly known/measured by experimentalists: determination of ingestion rate maximal value and demi-saturation coefficient under natural food conditions, assimilation efficiency over long time-step, CO_2 respiration direct quantification, RQ values, dissolved organic matter produced (composition, source and ratio to inorganic excretion), level of metabolism (basal, routine, active), fresh faecal pellets (C, N) content, rate of body (C, N) loss through moulting, new methods for growth measurements (e.g. direct AC) and direct measurements of biomass mortality (as well as its dependence to density and its fate). When the appropriate values are found, we suggest that these conversions (including the choice of values) should be done by (or with the assistance of) a biologist, after carefully considering the type and the scale of application of the model. For conversion purposes, it is essential to distinguish the different subcategories of vital rates (e.g. forms of excretion) and avoid terminology confusions (Table 1). Terminology used should be initially checked in order to convert the appropriate level of metabolism (e.g. see respiration and excretion). If a constant ratio is used, the underlying assumption should be verified depending on the model frame. The choice between the most appropriate methods of unit conversion depends on the availability of values needed for the conversion that were obtained at the most similar conditions to the ones of the model. When converting data, direct measurements are preferred, or otherwise the ratios should be carefully chosen (e.g. see respiration). Values chosen should not be limited to means but their range and associated parameters should be taken into account. If associated data (especially temperature, body size and food conditions) are not available, values should not be considered. On the other hand, even if vital rates data are judged appropriate, plugging them into models of questionable construction is insufficient (Flynn, 2006).

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Table 1. Comparison of the terminology for mesozooplankton vital rates generally used by biologists with the terminology and formulation in three models.

"Biologists"	ERSEM 2004 (Blackford et al., 2004)	PISCES (Buitenhuis et al., 2006)	Fasham et al. (1990)
Ingestion rate (I)	Uptake rate $I = I_{max}*f(food)*f(T)$ $f(food) = food_{tot}/(K + food_{tot})$ $food_{tot} = \sum[p*food^2/food+Z_{minfood}]$ $f(T) = Q_{10}^{((T-10)/10)} - Q_{10}^{((T-32)/3)}$	Grazing rate $I = I_{max}*f(food)*f(T)$ $f(food) = p*food/(K + \sum(p*food))$ $f(T) = (\sqrt[10]{Q_{10}})T$	Grazing rate $I = I_{max}*f(food)$ $f(food) = \sum[p*food^2/(K+ \sum(p*food^2)]$
Assimilation rate (A)	Assimilation $A = I*ae$	no equivalent (assimilation is included in GGE) $NG= I*GGE$ (GGE=NGE*ae)	Assimilation $A = I*ae$
Egestion rate (F)	Particulate excreted fraction of uptake $F = I*(1-ae)*e_u*(1-pDOM)$	Particulate egestion $F = I*unass$	Egestion $F = I* (1-ae)$
Basal respiration rate (R_b)	Basal respiration rate $R_b = r_{rest}*f(T)$ $f(T) = Q_{10}^{((T-10)/10)} - Q_{10}^{((T-32)/3)}$	Basal respiration $Rb = resp_{0°C}*f(T)$ $f(T) = (\sqrt[10]{Q_{10}})T$	Not included
Routine respiration rate (R_a)	Activity respiration rate $R_a = I*(1-ae)*(1-e_u)$	Feeding respiration producing DIC $R_a = I * (1-unass-GGE)*inorg$	Not included
Inorganic excretion rate (E_{inorg})	Not included	Feeding respiration producing nutrients $E_{inorg} = I * (1-unass-GGE)*inorg$	Ammonium excretion $Einorg = \mu_2* \varepsilon$
Organic excretion rate (E_{org})	Excretion going to DOM $E_{org} = I*(1-ae)*e_u*pDOM$	Dissolved egestion $E_{org} = I* (1-unass-GGE)*(1-inorg)$	DON excretion $E_{org} = \mu_2*(1-\varepsilon)$
Intrinsic mortality rate (M)	Oxygen dependent mortality $M = (1-f(O_2))*r_{mortox}+r_{mort}$	Temperature and biomass-dependent mortality $M+P = mort_{0°C}*f(T))* f(Z)$	Mortality staying in the mixed layer $M = \mu_5*(1-\Omega)$
Mortality rate by predation (P)	Not included	$f(T) = (\sqrt[10]{Q_{10}})T$ $f(Z) = Z/ Z_{ave}$ or $f(Z) = 1$	Mortality instantly exported from the mixed layer $P = \mu_5*\Omega$

$f(O_2)$, f(food), f(T), f(Z): oxygen, food, temperature or zooplankton dependent function. food: concentration of each food type. $food_{tot}$: total food concentration. inorg: inorganic. NGE: net growth efficiency. org: organic. p: food preference (w.d.). T: temperature. Z: zooplankton biomass. Z_{ave}: average zooplankton biomass. $Z_{minfood}$: lower threshold for feeding. For other terms see Table 2.

Table 2. Comparison of the terminology for mesozooplankton vital rates associated parameters generally used by biologists (for copepods) with terminology and units used in three models.

"Biologists"			ERSEM 2004 (Blackford et al., 2004)			PISCES (Buitenhuis et al., 2006)			Fasham et al. (1990)		
Sym	Term (general units)	Range of values	Sym	Term	Value	Sym	Term	Value	Sym	Term	Value
K	Half saturation coefficient (mass V^{-1})	1-535mgC m^{-3} [a][b]	H	Food concentration where relative uptake is 0.5	40mgC m^{-3}	$K_{1/2}$	Half-saturation grazing	3.1mgC m^{-3} [b]	K	Half-saturation constant for grazing	79.3mgCm^{-3} [c]
I_{max}	Max ingestion rate (food $org^{-1}d^{-1}$)	0.03-2.65 d^{-1} [d]	r_{ass}	Assimilation rate at 10ºC	0.5 d^{-1}	$G_{0°C}$	Max grazing rate at 0 °C	0.31 d^{-1}	g	Max specific grazing rate	1.0 d^{-1} (N)
Q_{10}	Q_{10} for O_2 respiration	1.8-2.1[e]	Q_{10}	Q_{10} for respiration Q_{10} for uptake	2.0 2.0	Q_{10}	Q_{10} for respiration Q_{10} for grazing Q_{10} for mortality	3.16 1.77 1.99	-	-	-
ae	Assimilation efficiency	0.10-0.99[f]	a_e	Assimilation efficiency	0.6	1-unass	n.e. term	0.69	β_i	Assimilation efficiency	0.75 (N)
GGE	Gross growth efficiency	0.01-0.9[g]	-	-	-	GGE	Gross growth efficiency	0.26	-	-	-
-	egestion / ingestion	0.01-0.90[f]	$(1-a_e)e_u(1-pDOM)$	Particulate excretion	0.1	unass	Particulate egestion	0.31	1-βi	Egestion fraction	0.25 (N)
-	excretion+egestion / ingestion	>0.01 to >0.90[f]	e_u	Excreted fraction of uptake	0.5	-	-	-	-	-	-
-	organic excretion / egestion	0.05 - 12[h][m]	pDOM	Excretion fraction to DOM	0.5	-	-	-	-	-	-
-	Basal respiration rate (O_2 or CO_2 V)$org^{-1}d^{-1}$	0.02 - 0.12 d^{-1}[i][n]	r_{restr}	Basal respiration rate at 10ºC	0.02 d^{-1}	$resp_{0°C}$	respiration rate at 0°C	0.012 d^{-1}	-	-	-
$E_{inog}+E_{org}$	Total excretion rate (N or C mass)$org^{-1}d^{-1}$	0.01-0.48 d^{-1}(N)[h][m]	-	-	-	-	-	-	μ_2	Specific excretion rate	0.1 d^{-1} (N)
-	Inorganic excretion / Total excretion	0.11-0.93 [j] (N)	-	-	-		-		ε	Ammonium fraction	0.75 (N)
-	1- Organic excretion / CO_2 respir.+org. excr.	0.23-0.95 [i]	-	-	-	inorg	Inorganic fraction of excretion	0.68	-	-	-
-	n.e.	-	$Z_{minfood}$	Lower threshold for feeding	1 mgC m^{-3}	-	-	-	-	-	-
-	n.e.	-	r_{mort}	Background mortality rate	0.05 d^{-1}	-	-	-	μ_5	Specific mortality rate	0.05 d^{-1}
-	Intrinsic mortalityrate (d^{-1})	<0.01-0.63 d^{-1} [k]	r_{mortox}	Mortality rate at low O_2	0.25 d^{-1}	-	-	-	-	-	-
-	Intrinsic and predational mortality rate (d^{-1})	<0.01-1.9 d^{-1} [k]	-	-	-	$mort_{0°C}$	Mortality rate at 0 °C	0.053 d^{-1}	-	-	-
-	Mortality fraction exported from the mixed layer	Close to zero [l]	-	-	-	-	-	-	Ω	detrital fraction of mortality	0.33

To facilitate comparison, time units were converted to days and mass units to carbon unless when specified in nitrogen (N). food: cell number or mass in Chl*a* or C or N. n.e.: no equivalent. org: organisms units in individuals or mass. Sym: symbol. V: volume units. (a) Hirst and Bunker, 2003. (b) Converted using the C/Chl a used in Buitenhuis et al., 2006; Fasham et al., 1990. (c) converted using the Redfield N/C ratio used in Fasham et al., 1990; Blackford et al., 2004. (d) Saiz and Calbet, 2007. (e) Ikeda et al., 2001. (f) review by Conover, 1978; Besiktepe and Dam, 2002 and references therein. (g) Straile, 1997. (h) review by Frangoulis et al., 2005. (i) Steinberg et al., 2000 and references therein. (j) Steinberg et al., 2002. (k) Hirst and Kiørboe, 2002. (l) Roman et al., 2002; Yamaguchi et al., 2002 and references therein. (m) Range could be narrower as it was calculated using several ranges obtained separately. (n) Assumed as routine metabolism and corrected using a routine/basal metabolism ratio of 1.9 based on Buskey, 1998.