Towards methodological approaches to implement the zooplankton component in "end to end" food-web models

F. Carlotti[a, *] and J.C. Poggiale[b]

[a] Laboratoire d'Océanographie Physique et Biogéochimique, UMR 6535, Station Marine d'Endoume, Observatoire des Sciences de l'Univers (OSU) – Centre d'Océanologie de Marseille (COM) C.N.R.S. – Université de la Méditerranée, Rue de la Batterie des Lions, F-13007 Marseille, France
[b] Laboratoire de Microbiologie, Géochimie et Ecologie Marines, UMR 6117, Observatoire des Sciences de l'Univers (OSU) – Centre d'Océanologie de Marseille (COM), C.N.R.S. – Université de la Méditerranée – Case 901, 163 Avenue de Luminy, 13288 Marseille cedex 9, France

[*] Corresponding author : F. Carlotti, Tel.: +33 4 91 04 16 44; fax: +33 4 91 04 1643, email address : francois.carlotti@univmed.fr

Abstract:

The modelling of marine zooplankton has made great progress over the two last decades covering a large range of representations from detailed individual processes to functional groups. A new challenge is to dynamically represent zooplankton within marine food webs coupling lower trophic levels to fish and to thereby further our understanding of the role of zooplankton in global change. In this respect, the "rhomboid strategy" (deYoung et al., 2004) has been suggested as a generic approach to model the various trophic levels of pelagic ecosystems and is deemed to be adaptable to different spatial and temporal frames of applications. The present paper identifies directions to develop zooplankton modelling by combining the skills of modellers, experimentalists, observers and theoreticians. In the first part, we present the main types of existing models, specifying the scientific issues, their characteristic time and space scales, across the ecological organization levels. In the second part, we focus on the strengths and weaknesses of parameterizations for the different processes. Finally in the last part, we make suggestions for improving these parameterizations by combining experiments and observations, using modelling techniques to transfer information across scales and testing theories which can themselves help to organize experimental and modelling research.

1. Introduction

Traditionally, two major issues have faced the marine biogeochemistry and ecosystem communities these being, (1) to evaluate the role of the pelagic ecosystem in the biogeochemical fluxes and particularly the carbon flux, and (2) to quantify the trophic fluxes through food web from the primary producers to the top predators and understand their contribution in the dynamics of exploited stocks. A new challenge stimulated by the IMBER program is to predict how global change will impact both marine food webs and biogeochemical cycles (IMBER, 2005; Legendre and Rivkin, 2005). In this respect, zooplankton play a pivotal role in the marine pelagic ecosystem at the interface of the so-called "lower" and "upper" trophic levels, influencing both the ocean biogeochemistry and productivity. Programmes such as JGOFS and GLOBEC have focused on biogeochemically based bulk and population models, respectively. A chronology of the development of different zooplankton models is clearly presented in Gentleman (2002). This evolution started with the development of ocean circulation and biogeochemical models which occurred during the last three and half decades within the framework of JGOFS (Steele, 1974; Fasham and Evans, 2000; Doney et al., 2004). In the last 15 years, GLOBEC stimulated the development of targeted zooplankton and fish models in connection to physical forcing. This fostered the first approach to coupled "end to end" food web models, the combination of biogeochemical and population models for zooplankton populations (Broekhuizen et al., 1995; Carlotti and Radach, 1996; Bryant et al., 1997; Slagstad et al.,1999) and then for fish populations (Megrey et al., 2007). However, coupling models between lower trophic levels, zooplankton and fish is still a major challenge (Travers et al., 2007). A major difficulty in implementing "end to end food web" models comes from the diversity of processes occurring at widely different temporal and spatial scales which need to be simultaneously addressed and integrated within a common frame. To this end, Steele et al. (2007) provide an example of an end-to-end model that addresses scaling issues by modelling the lower (bottom-up) and upper (top-down) webs separately and comparing their outputs at critical common nodes.

Organisms at trophic levels within and above mesozooplankton have fundamental biological and ecological differences compared to the lower trophic levels, inducing specific temporal and spatial variability in distribution patterns. This calls for a multifaceted approach to research, using a hierarchy of models, associated experimental and observational designs, and the identification of the appropriate scales for integration. The "rhomboid strategy" (de Young et al., 2004) has been suggested to develop a generic method for modelling various trophic levels of pelagic ecosystem The rhomboid strategy proposes that highest resolution is necessary at the trophic level or population of interest, and that resolution should decrease at progressively higher and lower trophic levels, as well as for in the case of specific target populations for other populations at the same trophic level. In their presentation of the rhomboid strategy, De Young and colleagues presented a few examples of model approaches but the challenge should not be restricted to modellers alone. Following this approach, the level of detail should be a trade-off based on the variables necessary to solve the specific scientific question, the biological knowledge on processes linking these variables, the field data corresponding to the variables, and the computer capacity. One goal of the present paper is to give direction based on the skills of modellers, theoreticians, experimentalists and observationalists (**Figure 1**). The need for combining these skills was pointed out by Mullin (1975) but despite Mullin's recommendations, interactions between modellers and experimentalists were limited within the framework of JGOFS, primarily because mesozooplankton were recognised as a secondary grazer of primary producers and used as a closure term in the majority of JGOFS models. In JGOFS, zooplankton core parameters (e.g. biomass size fractions) were mainly restricted to the integrated 200 upper meters biomass and as such were not sufficient for the parameterization of mesozooplankton models. The modellers issued a strong plea for additional zooplankton biomass data in a form where they could be used in models. In other words, broad community measurements expressed in terms of carbon and nitrogen", were needed (Lowry and Balino, 1999).

In recent decades, GLOBEC has stimulated the development and use of modern technologies for the estimation of field densities, parameters related to zooplankton dynamics and patterns s from bulk biomass to targeted populations (Wiebe and Benfield, 2003). Furthermore, GLOBEC fostered experimental studies in laboratory and mesocosms to quantify biological rates in interaction with physical and biological parameters   As a result, 0-D zooplankton models currently cover the full range of processes and scales from individuals to ecosystem: process models, individual budget models, structured or individual-based populations models, predator-prey models (see Carlotti et al., 2000; Gentleman, 2002; Runge et al., 2005; Fennel and Osborn, 2005). These models have reinforced cooperation between modellers, observers and experimentalists because of the focus on individual and population rates and behavior which were traditionally the domain of experimentalists (Marine Zooplankton Colloquium 2, 2001). Furthermore, new types of field data including species observations down to developmental stages at high spatio-temporal resolution have stimulated the coupling of zooplankton population and circulation models. As a result zooplankton population models are now currently dynamically embedded in the NPZ models (Gentleman, 2002). However, food-web models require information about the role of zooplankton species other than the target species such as competitors, predators and prey. Hence, many different processes occurring at widely different temporal and spatial scales inducing complex synergies and feedbacks (« *top down* » and « *bottom up* ») need to be simultaneously addressed and integrated in a common framework.

The application of population-based ecosystem models within a biogeochemical or trophic food web model structure remains problematic. Typically these approaches become too complex in terms of structure (variables and processes) and are too limited (they do not allow a sufficient representation of grazers and prey) with the addition of a population-based component. Furthermore, some variables and processes influencing food web dynamics at a specific scale may not be measurable (i.e. observable or resolved) at this scale but can be measured at larger or smaller scales. For instance, individual behavior takes place at short time and space scales and ultimately has an impact on the dynamics of the population, which takes place on longer time and larger space scales. The combination of new approaches (as indirect methods, transfer scales and theoretical concepts) coupled to datasets from new technologies for biological oceanography will help to define pathways across scales (spatial, temporal and organizational scales). Their analyses, performance and limitations require maintaining and further strengthening the mutual contact between observers, experimentalists and modellers started during GLOBEC.

In this paper, we will first present the main types of existing zooplankton models, specifying the scientific issues, their characteristic time and space scales, the ecological level of organisation represented and the associated processes. We then in the second section examine the strength of model parameterization of the different processes. In the third part, we will suggest approaches to improve parameterizations in zooplankton models based on increasing capabilities gained from experiments and observations as well as new modelling techniques. Concluding remarks will sum up the main recommendations.

2. Zooplankton models: model structure and questions to be solved

Zooplankton models cover a large range of representations from organism biology to functional groups of the pelagic ecosystem (**Table 1**). At any level of ecological integration (individual, population, etc.), the space and time scales need to be considered as a first step (**Figure 2**) followed by the variables and processes describing the system and finally availability of data required to implement the model (Steele, 1978; Mason and Brandt, 1999).

2.1. Bulk zooplankton in biogeochemical flux models

In the pelagic ecosystem, zooplankton consume primary producers, microzooplankton and detritus producing dissolved and particulate organic matter, actively contributing to the remineralisation of nutrients as well as to the export of matter to the ocean's interior with fast-

sinking faecal pellets, and via vertical migration. The initial NPZ representation of this complex interaction (Evans and Parslow, 1985) slowly evolved to a seven-compartment (nitrate, ammonium, phyto- and zoo-plankton, bacteria, detritus, DOM) nitrogen-based model of Fasham et al. (1990), which is widely used and currently coupled with physical models to study – lower trophic level dynamics on regional scale to basin scales. Recent versions of this model may have up to 12-15 variables.

Biogeochemical models usually distinguish two bulk categories of zooplankton, i.e. micro- and meso- zooplankton (Anderson et al., 1993; Buitenhuis et al., 2006), based on different feeding strategies and growth rates (**Figure 3**). Microzooplankton are strictly sized between 20 and 200 µm, dominated by ciliates, but "microzooplankton" is synonymous with "protozooplankton" in biogeochemical models, which includes heterotrophic flagellates in the size fraction of nanozooplankton (2-20 µm). Heterotrophic flagellates are the major grazers of small phytoplankton cells, while heterotrophic dinoflagellates specialize in feeding on diatoms, including chain-forming forms. Thus the microzooplankton component in these models can consume a high proportion of production on different size classes from bacteria, to pico- , nano- and micro phytoplankton. Mesozooplankton are typically dealt with strictly as heterotrophic organisms sized between 200 µm and 2 mm. This grouping includes crustaceans (in large part copepods but also decapods) which are herbivorous, omnivorous or carnivorous. Copepods, the major component of mesozooplankton, have been found to feed on larger microphytoplankton and proto-zooplankton, and several biogeochemical models consider predation of "mesozooplankton" on "microzooplankton".

The second major mesozooplankton component is gelatinous plankton which can be herbivorous (e.g. salps and appendicularians), or carnivorous (e.g. schyphomedusae, hydromedusae, ctenophores). Finally although rarely included in coastal areas, this component can also include meroplanktonic larvae of fish and benthic invertebrates. Hence, the "mesozooplankton" component of these models is complex, and challenging to model. Functional groups of zooplankton, based on large size fractions are not amenable to modelling for example, copepods cover a size from tens of µm (eggs) up to one cm (adults). Thus during their early life history stages are part of microzooplankton but as their growth rates e.g. nauplii are not comparable to those for example ciliates and they should be clearly separated (**Figure 3**). Thus, a first subdivision within the whole zooplankton community should be to distinguish between protozoan plankton (unicellular) and metazoans plankton (multicellular). Many characteristics of protozooplankton (protozoan plankton) are similar to those of phytoplankton, except heterotrophy. The life cycle of protozooplankton is quite complex, but in their growth phase, each mother cell produces two daughter cells, similar to the life history strategy of phytoplankton. The turnover rate of protozooplankton is high, allowing rapid response to their food dynamics, mainly blooms of phytoplankton.

 Typically in biogeochemical models, metazoan plankton are subdivided in mesozooplankton (200 µm-2 mm) and macrozooplankton (2-20 mm) which represents the highest trophic level of the food web that is explicitly modelled. The main processes related to mesozoopankton and macrozooplankton are grazing on larger microphytoplankton (20–200 mm), detrital particulate organic matter (POM) and on microzooplankton (Calbet and Landry, 1999). This group typically has growth rates slower than those of protozooplankton with some carnivorous species being cannibalistic thus adding a density dependent component to the modelling of this group. Metabolic transformation of particulate organic matter by this group follows two modes, the first similar to protozooplankton is into DOM which is remains in the surface layer while unlike protozooplankton their faecal pellets contribute to the vertical flux of organic material being species and size-dependent. Once again the criteria to distinguish meso- and macrozooplankton can be criticized because many species change feeding strategies and life form over ontogeny as well as increasing in size from meso- to macrozooplankton during their life cycle. Furthermore, prey size range may not be directly related to their body size. Salps, relatively large organisms are gelatinous filter feeders selecting small planktonic prey and having higher feeding and growth rates than crustaceans in the mesozooplankton component, Additionally, appendicularians produce mucus houses high in POM, while salps produce large faecal pellets, and pteropods a dense shell. Another area of high variability is in swimming rates which can be quite different between meso- and macrozooplankton and can have a significant impact on the

rate of flux of organic material. For example, salps also show strong diel vertical migration patterns like euphausiids and large copepods which transports organic material to depth.

Recent global ocean biogeochemistry models (e.g., Le Quéré et al. 2005) have explicit representation of different plankton functional types (i.e. groups are based on similar taxonomic types), which may be active or inactive depending on the scientific question addressed by the model. In recent models, the elemental stoichiometry of zooplankton and their prey is simulated, resulting in non-Redfield cycling of C, N, and P (Anderson, 1992; Touratier et al., 1999; Touratier et al., 2003; Mitra, 2006; Baklouti et al., 2006a and b, Mitra and Flynn, 2007).

Process parameterization of zooplankton functional groups based on functional types is still on going as the biological knowledge on biomass and processes for types other than copepods is still scarce (Anderson, 2005; Flynn, 2006; Irigoien, 2006; Buitenhuis et al., 2006). In general, biomass data for this component is insufficient in quantity and quality for validation (Buitenhuis et al., 2006). Even for copepods a major component of the mesozooplankton group, several studies have shown that the parameterization of the grazing function i.e. with or without a threshold, selectivity on different prey types, and mortality rate of the zooplankton are key processes for ecosystem model stability (Evans, 1977; Caswell and Neubert, 1998; Lima et al., 2002; Mitra and Flynn, 2006). Assimilation efficiency parameters which quantify the faecal pellet production, and their temperature-relationship, are also sensitive parameters (Tjiputra et al., 2007). The mathematical properties of the functions used to represent processes and their impact of the simulated dynamics are an area of development (Gentleman et al., 2003; Caswell and Neubert, 1998; Gentleman and Neuheimer, 2008). As well, new observations have initiated study and implementation of for instance mortality rates (Ohman and Hirche, 2001). Clearly, there is a need to incorporate these process parameterizations in the frame of the end-to end modelling approach and some suggestions are given below.

2.2. Zooplankton population models.

A number of zooplankton population models have been developed in the last two decades to describe changes in abundance, distribution, and production of targeted populations relative to the abiotic environment, food conditions and predation (see Carlotti et al. 2000; Fennel, 2001; Fennel and Neumann, 2003; Gentleman et al., 2003; Mitra and Flynn, 2007). The main goal of these models is to understand how oceanic variability and global climate change may influence population dynamics and distribution of key zooplankton species in oceanic areas (see figure 2: scales from local to basin scale, and from few days to years) both in terms of their coupling to the physical environment (e.g., stratification, retentive circulation features, frontal zone exchanges, climatic index) and to the biotic environment (e.g., predator/prey relationships, multi-species interactions).

Within these models of zooplankton population dynamics, it is necessary that two main phases of the life cycle included. The first phase is that of population growth during which individuals are actively feeding, growing and reproducing (and thus heavily sampled and studied)., The second phase is one of dormancy (or diapause) which generally occurs when trophic and/or temperature conditions in the upper layers become unfavourable for the species: extremes of temperatures (too warm or too cold), absence of preferable prey, etc. For shelf species, this dormancy phase corresponds to either a benthic stage such as dormant eggs in sea-bed sediments (for crustaceans) or a polyp form on the sea floor (for schyphomedusae and hydromedusae) or pre-adult or adult planktonic stage surviving in the deeper water layers of the bays. For shelf edge species, this pre-adult or adult planktonic stage can occur in the slope canyons or on the sea floor while for many oceanic species, these stages migrate to mesopelagic layers (crustaceans and gelatinous plankton). The capacity of a population to recruit each year requires a critical stock of individuals from the quiescent phase. Species unable to maintain this stock will disappear. Thus, the conditions of survival during this period of the life cycle have the potential to be a critical link between the climate-induced environmental changes and population long-term variations. Generally the habitat of the dormant phase is more stable in terms of environmental conditions, but advection or temperature changes may also affect the stock during this phase. The biological processes linked to the entrance into and exit from diapause (temperature or food threshold, or internal clock), their links with local and

temporal variations in environmental conditions, are generally not well understood. For example, the Trans-Atlantic Study of *Calanus* project and its initial modelling activities underlined the need to increase our understanding of the over-wintering period of *Calanus finmarchicus*. It is clear that copepodites IV and V leave the surface waters between mid-summer and autumn, and remain in deeper waters for several months before ascending to the surface during spring. This ascent typically coincides with the spring bloom (Tintensor et al., 2003; Heath et al., 2004; Edvardsen et al., 2006; Johnson et al., 2008). The timing of the re-emergence of these copepods in spring relative to the seasonal timing of the spring bloom is proposed to be critical for both the copepod population dynamics during the rest of the year, the dynamics of the phytoplanktonic and microzooplanktonic prey (Carlotti and Radach, 1996), and, for fuelling the first-feeding of many other organisms, such as larval fish (Cushing, 1990; Beaugrand et al., 2003).

During their active period of life in the surface layer, mesozooplanktonic organisms progress through a number of developmental stages during ontogeny which population models take into account as either developmental stages or size groups. During this active phase, the key processes for zooplanktonic organisms are the rates of feeding, growth, development, and reproduction, as well as vertical migration, and habitat selection. All these processes fluctuate with environmental factors (food availability, predation pressure including cannibalism, advection, temperature, etc.). Feeding and mortality of targeted zooplankton populations are two major processes for which model parameterization is a bottleneck (Gentleman et al., 2003; Mitra et al., 2007). Focus on patterns and causes of zooplankton mortality have been increasing in the last decade both from theoretical and empirical points of view. It has become clear that multiple factors account for mortality during the different life history stages of the zooplankton, These factors range from chemical compounds (i.e. toxins) to predators and parasites. To improve information on these processes, better linkages between experimental, theoretical and modelling approaches are needed. For example, population models for species other than copepods are scarce (e.g., salps, appendicularians, jellyfish, chaetognaths), as it is not simple to find demographic criteria to define model structure.

2.3. Models of zooplankton as links between lower and higher trophic levels

Marine zooplankton play a critical role in the structuring of higher and lower trophic levels, impacting upon the population dynamics of exploited species, as well as in the modification of the flux of organic materials to deep-ocean. Climatic and anthropogenic forcing on zooplankton vital rates, life cycles, population distributions and community structure moderate the role of zooplankton in transferring matter to other ecosystem components. Early models used simple box components to compute the flow of energy through marine food webs. These box components were either functional groups (Steele, 1970, 1974; Kremer and Nixon, 1978; Vézina and Platt, 1988) or fish populations (Ecopath approach by Christensen and Pauly 1992). The development of ecosystem models by coupling lower and higher trophic levels is still at its infancy, with open debates on the best approach to realise this coupling (Travers et al., 2007; Daewell et al. 2007; Fennel, 2008), i.e. to represent zooplankton. Trophic food-web models may be constructed following two different approaches. The first approach is to increase the complexity (i.e. the number of components) of ecosystem models (which can be qualified as top-down approach). Ecosystem models attempt to describe ecosystem behaviour as being the result of relations between functional groups variables and external driving variables. However, the fundamental change from "biogeochemical-based" interactions to "biochemical-biological-behaviour-based" interactions will necessitate a modification of the complexity of the higher trophic levels. Temporal and space scaling will be important as biochemical, biological and behavioural processes take place are different temporal-scale. The second approach (bottom – up) is to attempt to predict food-web dynamics on the basis of lower level processes (individual-based and population-based). Such models are deterministic mechanistic and process-based, explaining higher level system performance as being the outcome of systems on lesser spatial and time scales. That is the so called Rhomboid approach (De Young et al., 2004). This approach can, due to the increase in complexity of the models and the subsequent propagation of error, lead to spurious predictions of species and ecosystem dynamics.

The **table 1** gives examples of models, which use the two approaches. Several models use the bulk biomass of mesozooplankton from biogeochemical models as prey resource for fish (e.g., Nemuro fish model by Megrey et al., 2007). The use of existing biogeochemical models makes this approach quicker, although zooplankton bulk biomass is never globally selected by any predator (fish prey are selected on their size and behaviour). Daewell et al. (2007) suggest that zooplankton size structure could be derived from the simulated bulk biomass using observed size frequency distribution of zooplankton. However, the zooplankton bulk biomass in biogeochemical models is weakly validated (although the majority of existing zooplankton data are integrated bulk biomass). Feeding and mortality rates are difficult to parameterize (Arhonditsis & Brett, 2004). To avoid representing the dynamics of zooplankton, Lehodey et al. (this issue) proposes a transfer function which age the primary production up to a metric for tuna forage.

Other models represent a dynamic size structure of zooplankton based on either different stages (e.g., Davis, 1984 a and 1984b; Fennel, 2008) or size classes (Zhou and Huntley, 1997, Maury et al. 2007 a and b). Following these approaches, dynamics is governed by demographic and physiological processes. The spatio-temporal observed variability in size or stage distributions in zooplankton is much lower than the variability in observed overall zooplankton biomass (Solow & Steele, 1995; Steele & Henderson, 1995). Consequently, development and growth are related to size and temperature with robust empirical formulations, which realistically simulate population structures (i.e. Henderson & Steele, 1995). Furthermore, feeding and mortality rates are also strongly linked to size structure (Peters, 1983, Zhou and Huntley, 1997). Increasing observations of size or stage-structure based on new tools such as Optical Particle Counters (OPC), and video systems including image analysis (Culverhouse et al., 2006) stimulate the development of zooplankton structured models. Clearly, as fish consumption of zooplankton is dependent of prey size spectrum, structured zooplankton models represent an interesting approach for coupling with fish models.

2.4. Other major issues related to marine zooplankton dynamics

Other issues related to zooplankton have emerged in the past few years, these being linked to the analysis of historical data from various time-series (Southward, 1995). Patterns in cyclic succession of zooplankton species have been very well studied and modeled for zooplankton in lakes (Sommer, 1989), where well documented observations and associated experimental manipulations have provided understanding of the underlying mechanisms of succession such as resource availability and predation. Even if such observations exist for marine systems, studies including experiments and modelling to understand the succession of the zooplankton assemblage are scarce, and are necessary for developing the "end to end approach".

Another key issue is the resolution of the biological consequences of climatic warming, and particularly the changes in the spatial distribution of species as a result of the shifts in the location of biogeographical boundaries (Beaugrand et al., 2002). These modifications will occur through changes of the phenology of the species, new interactions between species and changes in species dominance.

3. Strengths and weaknesses of existing model parameterizations

Significant advances have been made in our knowledge of many zooplankton processes including feeding rates, food selectivity, metabolism, life histories, fecundity, behaviour, mortality. However, as Miller (2004) states "*A good deal of very nice mathematics has been developed describing population dynamics. Unfortunately, for most organisms including zooplankton, the assumptions do not fit well enough to make the mathematics useful without long lists of ad hoc adjustments*.").

Most zooplankton models are readily available or rather easy to reproduce for application and testing in different systems. New applications of these models will help to support or falsify aspects as well as increasing their potential acceptance in a generic modelling structure.

Differences between systems will be introduced with new variables, new process formulations as well as new parameterization. These changes will be motivated by goal of the application itself. However, small differences in process formulation and parameterizations in particular in the functions linked to zooplankton may lead to extreme differences in simulated dynamics of the system (e.g. Caparroy and Carlotti, 1996; Myerscough et al. 1996; Gentleman et al. 2003; Arhonditsis and Brett, 2004; Fussman et Blasius, 2005; Buitenhuis et al., 2006; Mitra, 2006; Yoschie et al. 2007; Stegert et al., 2007).

As a rule of thumb, when researchers want to apply these different models, they should first define the scales of time, space and the ecological integration levels of the components (model structure) of the system that they wish to study. The most difficult task is to define the process formulation and the associated parameterization with respect to the scale of application. Typically the issue of scale of process parameterization is a critical and well appreciated issue. . For instance, rates obtained from experimental studies do not reflect *in situ* rates; rates obtained from laboratory or *in situ* measurements are obtained on individuals and do not represent the population or functional group dynamics. A rather more insipid problem is that parameters and mathematical formulations are imported from one model to another without any control criteria, i.e. without looking at the similarities between the modelled systems and their underlying assumptions (Flynn, 2006).

The predictive power of zooplankton models requires validation not only with large data sets (Buitenhuis et al., 2006) but also with information on the ecological level organisation (individual, population, community, functional groups) and the corresponding processes. In the following we will review the different processes imbedded in zooplankton models, as well as discuss their characteristics and mathematical representations at the different ecological levels of application.

3.1. Feeding – Grazing -Ingestion - Functional Response

The terminology of the intake of matter by zooplankton varies according to the ecological level of interest. For example, ingestion rate is the intake of matter per individual per time unit . The functional response is the relationship exhibited by an individual or a sub population between ingestion rate and food concentration. Feeding is a more general term used for individuals to include qualitative aspects such as food selectivity. Finally grazing refers to the impact of a zooplankton population feeding on a phytoplankton stock and is typically the terminology used in ecosystem models.

3.1.1. a) Relation to individual body weight and to biomass.

Allometric relationships provide links between various bioenergetic rates and weight or length (Peters, 1983). They typically read as follows:

$$R = aW^b \qquad (1)$$

where R is a rate and W is the weight, the dimension of R is per time $[t^{-1}]$ and the dimension of W is a mass $[M]$, a is an algometric coefficient and b is an algometric exponent. These algometric relations define empirical rules. The use of such relationships should only be applied within the ranges of weights at which they were obtained. However, this aspect is often ignored by modellers. Finally, they can lead to problems with the dimensions. For example, in equation 1, the dimension of a is $[t^{-1}][M]^{-b}$, which depends on the second parameter value b. This problem may be solved by considering a reference with a weight W_0 then the equation can be rewritten t as follows:

$$R = a\left(\frac{w}{w_0}\right)^b \qquad (2)$$

In this case, a has the same dimension as R and b is dimensionless. Hence the dimension problem is solved however, a new problem emerges: how can we define the reference W_0? This choice is important when we want to compare different situations. At the individual level, we can

choose the weight of individuals starting a for example a new stage. This implies that this weight at stage is constant in the species, a rather unrealistic assumption. Generally, the choice of W_0 is not obvious and critically even more important at population and community levels. From these remarks, it is clearly difficult to compare the different *a* and *b* values obtained across experimental conditions or in different ecosystems.

The parameters *a* and *b* depend on the ecological level of observation of the rate: they may vary between the different functional groups (Banse, 1982; Moloney & Field, 1989) as well as between different species in the same size range due to species specific adaptation (Frost, 1980). Usually modellers have used allometric relationships obtained on large data sets grouped by similar communities (e.g., Hansen et al., 1997; Blanco et al., 1998**).** As these are based on an empirical approach, there is not a clear way to link the parameters values obtained at a given organization level to those obtained at the community level.

In ecosystem models, the food intake related to the zooplankton bulk biomass is typically represented as proportional to the zooplankton biomass (b = 1). Values of b < 1 are used in various models ranging from individual to community models. The different scales associated with organization levels are not linked in these models and scale transfer methods should not aim to link these parameters. A consequence of the complexity of scale transfer for the allometric relationships is the controversy dealing with the "3/4-law" of metabolism. Approaches which permit avoidance of the use of such laws should be developed. We briefly give an example of such an approach in the "Theories" section.

3.1.2. b) Relation to food concentration.

Zooplanktonic organisms exhibit a functional response between ingestion rate and food concentration which follows a functional form e.g. Holling Type II, Type III or Type IV (Holling, 1966) with a saturation of ingestion rate at high prey concentrations. Several formulations exist (see Carlotti et al., 2000, and Gentleman et al., 2003, as review). Parameter values are usually obtained at a defined stage of development (adult or late stages generally) in classical grazing experiments (Båmstedt et al., 2000; Acuna and Kiefer, 2000). Functional responses are typical for each predator-prey pair due to differences in the predators' ability to perceive and capture specific prey and prey suitability. Prey concentration may however induce plasticity in predator behaviour. Such plasticity seems to play a major role in copepod capacity of switching responses between microplanktonic diets inducing emergent features in pelagic ecosystem dynamics, i.e. planktonic successions (Broglio et al. 2004). Unfortunately extrapolation to other stages is usually done without clear justification.

At the level of population, community and ecosystem models, modellers use individual-based functions. However, if the parameters are based on experimental results at the level of individuals (and possibly for populations), parameters used for bulk zooplankton biomass (total or for functional groups) in community and ecosystem models are not calibrated from ingestion data set at these integration levels, but mostly derived from parameters tuning to fit simulations to data.

There is no clear justification why the functional response established at the individual level, should stay valid for higher level of ecological integration (i.e. from population to bulk biomass levels). The changes in size of individuals in the various stages are associated with changes in parameterization of the functional response. The emergent ingestion response of the whole population might be a complex function of the sum of each individual response. And it is the same at the level of the whole bulk biomass of zooplankton or of functional groups.

3.1.3. c) Food quality- Grazing on several resources - Switching behaviour

One severe limitation of experimental results with single food prey is that the functional response on that prey may additionally be affected by the presence of other resources. At all levels of organisation (from individual to ecosystem), the issue of how to represent feeding of different food sources is a common question for modellers.

In their ecosystem model, Fasham et al. (1990) proposed to parameterize grazing on multiple prey with a preference function based on the relative proportion of the food using Hutson's (1984) switching expression. Steele (1974) and Evans (1988) emphasized that model predictions can be very sensitive to the parameter values used for this switching function. Critically for the modelling of zooplankton feeding there is little data on zooplankton feeding preferences to provide such values. Gentleman et al. (2003) have shown how subtle differences among formulations of feeding in copepods may exhibit dramatically different dynamics (see in details section 3.2.1). Therefore, accurate formulations are required to better understand the relative grazing impact of major planktonic groups. For example, information is missing for key groups such as salps (Deibel, 1982, Zeldis et al., 1995), appendicularians (Acuna and Kiefer, 2000; Scheinberg and Landry, 2005), ctenophores (Kremer, 1982), krill (Atkinson *et al.*, 2002), jellyfish (Hansson and Kiorboe, 2006), or ciliates (Fenchel, 1980, Calbet, 2008).

Hence, parameterization feeding interactions of these key zooplankton groups is an important issue for future experimental feeding studies. There is a clear need to deliver data for parameterization of selectivity and feeding rates of individuals and populations from cultures with various combinations of prey (including phytoplankton, microzooplankton from bacteria to copepod nauplii, and detritus).

3.1.4. d) Relation to small-scale hydrodynamics

At the individual scale, turbulence is known to affect trophic interactions, either directly by increasing the encounter rates between predators and prey (Rothschild and Osborn, 1988) or indirectly by changing properties of food (Kiørboe, 1993). The consequences of turbulence have been shown on zooplankton grazing (Marassé et al., 1990) and fish predation (Visser and MacKenzie, 1998), metabolism (Alcaraz, 1997), on development rates of marine copepods (Alcaraz et al., 1988), and on communities and ecosystems dynamics (see review in Petersen et al. 1998). Several models have been developed to simulate the different steps of the feeding process of a swimming organism catching prey in the natural environment. The original models were developed for fish larvae (e.g., Werner et al., 2001), and then applications were extended to zooplanktonic organisms in relation to turbulence. In these formulations, the amount of food ingested is a function of the number of prey encountered, captured and eaten, the levels of turbulence, light and prey aggregation. The number of prey encountered and prey ingested are functions of the local prey concentration modified by local turbulence (Rothschild and Osborn, 1988; MacKenzie and Kiørboe, 1995).

Different models have represented simple swimming behaviour and encounter rate expressions for linear swimming (Gerritsen and Strickler, 1977) or random-walk swimming (Evans, 1989; Yamazaki *et al.*, 1991). Kiørboe and Saiz (1995) introduced several types of swimming in their model. Some models have attempted to represent the effect of micro-scale turbulence on the ingestion of copepods (Davis *et al.*, 1991; Saiz and Kiørboe, 1995; Caparroy and Carlotti, 1996). In particular, Caparroy and Carlotti (1996) have shown how processes at short time scales (millisecond to second) could be parameterized at larger scales (hours to daily budget).

Many models directly use the information obtained at the individual level for targeted species, to parameterize the effect of turbulence on the interaction of different functional groups in ecosystem models (e.g., Metcalfe et al. 2004). Once again, the effect of turbulence on predator-prey interactions should not be studied in isolation from other factors, which simultaneously influence the trophic interactions, i.e. concomitant effects of small scale patchiness in planktonic distributions (biological, chemical and physical interactions between species, specific reaction to fluid motion, etc.). Most if not all of the modelling approaches assume a homogeneous prey environment whereas plankton patchiness has been observed for a number of years (Incze et al., 2001; Holliday et al., 2003) and induces non-linear grazing interaction between phytoplankton and zooplankton. Recently, Lévy-type searching behaviour has been pointed out as relevant in plankton movements to localize patchy distribution of prey (Viswanathan et al., 1999; Rhodes and Reynolds, 2007).

3.1.5. e) Relation to temperature

Temperature has an important and direct effect on the enzyme activities and thus on all physiological functions. This effect is crucial at the individual level and consequently at higher levels of organisation. However, the representation of the temperature effect is not similar between the population and the community level. At the individual and population levels, the temperature impact on ingestion rate follows a classical dome-shaped function, assuming that energy and other resources are not limiting. Physiological rates usually increase with temperature within the range normally encountered by the organism until a sudden decline near the upper limits when enzyme systems become damaged (lethal temperature). Temperature-specific physiological rates might be subject to adaptation to changing temperature conditions in zooplankton species, as shown for fish (Pörtner & Knust, 2007).

The thermal limitations in physiological and growth rates of dominant zooplanktonic species as well as the potential plasticity deserve further investigations. Although experimental protocols are available on how to get this information (Thébault, 1985; Robins and Bellan, 1986; Andersen, 1986; Durbin and Durbin, 1992; Sell et al., 2001; Broms and Tiselius, 2003), relatively few laboratory studies present ingestion (or clearance) rates within the normal range of temperatures that a given species experiences in the field (see for instance reviews by Bonnet et al. (2005) on *C. helgolandicus*, or Calbet et al. (2007) on *Centropages typicus*). Typically, relationships are extracted from field data examining ingestion versus local temperature, which are biased by factors such as prey type, micro-scale patchiness, predators' avoidance. Interestingly, temperature is considered as a key factor for species succession (Calbet et al., 2001; Halsband et al., 2002, 2004), however there are few studies that examine how changes in temperature affect the dynamics of interacting populations. There is a paucity of studies examining succession in marine systems however examples exist for lake ecosystems. Based on lake observations Adrian and Deneke (1996) put forward the hypothesis that zooplankton species rather than functional groups are the nexus between environmental stress, such as temperature, and ecosystem changes, a hypothesis which needs to be examined in marine systems.

Typically in ecosystem models including a zooplankton functional group, an exponential function is used to represent the temperature effect on physiological rates: $Y_T = A\,B^T$ (Carlotti et al., 2000) with an "averaged" Q10 value ($=B^{10}$) slightly above 2 (Ikeda, 1985; Dam and Peterson, 1988). Zooplankton population models typically employ a dome shaped temperature effect on ingestion. For example, Sourriseau (2002) used a dome shaped temperature effect on ingestion for 5 copepod populations. The result was an integrated average ingestion response of the whole zooplankton community to temperature which did not exhibit an exponential response. Clearly, the influence of the different formulations of temperature effect on ingestion rate as employed in population models (dome shape function) and in functional groups of ecosystem models requires further examination.

3.1.6. f) Combined effects of external factors on ingestion

Most of the parameterizations utilized above come from experiments dealing with the variation of a single factor. Modellers typically combine them in their models, assuming no interaction between the various parameters. Such combinations should be made with caution as biological responses to combined factors can differ from their effects studied separately. For example, Thébault (1985) showed that the effect of temperature can differ with food concentration. Clearly experimental studies examining a combination of external effects on the feeding require further investigation.

3.2. Assimilation and faecal pellets

There is a glaring lack of information on assimilation of ingested material for zooplankton. Typically, assimilation rates are based on gut contents (gut fluorescence) or faecal pellet production. Gut content has been employed extensively to infer feeding rates of aquatic herbivorous copepods (see Durbin and Campbell, 2007) and various models have attempted to

simulate the processes involved in the change in gut content (Dam *et al.* 1991; Jansen and Wolf-Gladrow, 2001; but see Durbin and Campbell, 2007). However these models have not been incorporated in zooplankton population or ecosystem models. In most models, the assimilation rate is assumed to be a constant fraction (usually ranging between 0.6 and 0.8) of the ingestion rate. There is an implicit assumption that assimilation is related to food content, food quality, temperature and weight in the same way as ingestion. This certainly is not true as during the assimilation process through the epithelial tissue of the gut, organic components are selected from the ingested prey. This selection may vary based on the quality of the prey and the physiological state of the predators it grows or develops energetic reserves. There are underlying assumptions when considering assimilation rate as proportional to ingestion rate. For example, the impact of temperature on enzyme activity in gut is similar to the impact of temperature on ingestion processes, and a similar relationship to weight as the ingestion (Touratier et al. 1999) These relationships should be tested with data. Assimilation efficiencies will also differ according to the currency being used in the model (Mitra and Flynn, 2005). When more than one element is modelled, inconsistencies can arise if prey and predator have different elemental ratios. In this regard, Moloney (1992) showed how matter could be created in models where element-ratio effects are not taken into account and constant assimilation efficiencies are used.

3.3. Metabolic rates respiration and excretion

Excretion and respiration represent the metabolic losses of nitrogen, phosphorous and carbon when parameterizing zooplankton models. These metabolic activities can be divided into several components due to the heterogeneous nature of catabolism. These costs include those associated with locomotion activity, basic metabolism, assimilation, synthesis of somatic and gonad tissue, matter transformation for storage, etc. (see Clarke, 1987). One major difficulty with modelling these costs is the possibility that each of these components may vary with season and temperature.

In their model, Steele and Mullin (1977) identified three main components of respiration of marine copepods: the basal or routine metabolism, the costs associated with foraging and capturing food and the cost of assimilating and biochemically transforming the food. The last two components are often grouped as active metabolism.

In individual and population models, the simplest formulation of basal respiration or excretion rates is related to weight (see Gurney and Nisbet, 1998) typically employing an allometric relationship based on a regression of metabolic rate versus weight (Corkett and McLaren, 1978; Peters, 1983; Vidal and Whitledge, 1982; Ikeda, 1985). The scaling exponent employed is usually close to 0.75. However, the variable to be used as an index of body size (i.e. biovolume, dry weight, etc.) in scaling studies deserves careful consideration (Anderson, 1992; Anderson and Hessen, 1995). Dry weight is the traditional measure for ecological variables such as growth. However, Vidal and Whitledge (1982) have suggested that dry weight-based scaling relationships may be biased if animals have large proportions of metabolically inactive tissue, such as lipid stores. This bias is illustrated by the scattered relationships observed when weight is used as index of body size instead of length (e.g. Kooijman, 2000).

Others have chosen to express body size in terms of carbon (e.g., Ikeda and Skjoldal, 1989; Schneider, 1990). Schmidt-Nielsen (1984) and Cammen *et al.* (1990) and have recommended the use of body nitrogen content as a mass variable; protein content provides an easily determined measure of body nitrogen. Critically metabolism-size relationships can change with the size index selected (Berges *et al.*, 1990), and metabolic measurements based on different mass variables are not easy to compare, and need careful consideration before inclusion in models. Basal metabolism is also temperature-dependent. Most of the papers (see for instance, Buitenhuis et al., 2006) refer to data compilation by Ikeda (1985) and Ikeda et al. (2001) and use a Q10 value higher than 3.

Active metabolism is usually represented in models by using a linear relationship with ingestion and is commonly grouped (and mistaken) with the assimilation process. As outlined earlier this implicitly assumes that active metabolism is related to food content, the food quality, temperature and weight in the same way as ingestion and is potentially wrong. Generally Q10

values for metabolic rates are usually larger than for ingestion which means that the temperature functions and/or their parameterisation should be different between ingestion and metabolic rates. All these simple representations are questionable due to a lack of experimental studies with appropriate protocols to parameterize the various factors influencing metabolic rate.

3.4. Population Vital rates (development, egg production and mortality)

Population vital rates are usually linked directly to external parameters (e.g., temperature, food concentration) which are experimentally easy to control. These rates can be obtained from cohort development studies either in laboratory controlled conditions, mesocosms, or in situ under various environmental conditions of temperature, food, salinity, etc. (Hopcroft et al., 1998; Campbell et al., 2001). Furthermore, Aksnes *et al.* (1997) discuss the possibility of obtaining of data for life tables from cohort analyses of populations of copepods and inverse methods to estimate vital rates by fitting simulations of a population model to data.

Indeed, population vital rates depend on physiological states (growth, reserves, etc.) of the organisms which vary with external factors. The modelling of functional biological properties which modify vital rates (e.g., Carlotti and Sciandra, 1989, their Figure 1) results in more realistic simulation of the dynamics of the modelled organisms if the external conditions of temperature and food are highly variable.

Typically development times, egg production rates and mortality rates measured in mesocosms should serve to validate population models with mechanistic coupling of physiology and development, rather than be directly used in the model building. However, functions and parameterisation relating vital rates to internal factors are difficult or impossible to obtain experimentally.

3.5. Swimming behaviour and vertical migrations

described following a phenomenological approach, where a set of environmental signals can be mapped onto a set of reactions applied to individual, population or zooplankton bulk biomass models (Carlotti et al., 2000). This approach has been followed in models dealing with small scale interactions between predator – prey (Visser 2007) to represent the effect of microscale turbulence on the ingestion of copepods or escape of predators (Davis *et al.*, 1991; Saiz and Kiørboe, 1995; Caparroy and Carlotti, 1996). Encounter rate is related to the relative distance between prey and predator, which is a consequence of swimming dynamics and the microscale fluid motion (Rothschild and Osborn, 1988). Different models have represented simple swimming behaviour and derived encounter rate parameterizations for linear swimming (Gerritsen and Strickler, 1977) random-walk swimming (Evans, 1989; Yamazaki et al., 1991) and Levy motions (Viswanathan et al., 1999). Kiørboe and Saiz (1995) introduced several types of swimming in their model.

Swimming behaviour can be easily introduced in lagrangian individual-based models, which describe population dynamics by simulating a large number of individuals in the population. As powerful computers become more accessible, numerous IBMs of zooplankton populations have been developed, mainly to couple them with circulation models (see Grimm et al., 2006, for review). These approaches offer a large range of sophisticated representations of swimming behaviour related to internal and external factors (Carlotti and Wolf, 1998). This simulation approach allows the assessment of trade-off rules based on life history theory, as suggested by Tyler and Rose (1994). Lagrangian IBMs coupled with 3D hydrodynamical models allow studying the effects of the spatial distributions combining the physical transport and the individual behaviour along the life of each individual (Miller et al., 1998). However, an obvious disadvantage of these models is that they become extremely large, and are unmanageable for three-dimensional ecosystem model simulations.

In eulerian population or ecosystem models, the swimming behaviour of organisms is represented by the addition of a term for the swimming velocities on the vertical axis, usually related to temperature, salinity, light or depth in population. Because swimming rates are very

dependant on the size of the organisms, vertical swimming applied to bulk zooplankton biomass should be considered very cautiously.

Vertical migration of zooplankton refers to a pattern of large movements (> 10s to several 100s m) in the vertical axis which occurs at different temporal scales: diel vertical migrations are undertaken each day by organisms, whereas ontogenic migrations occur seasonally as a change of living habitat. Diel vertical migration is thought of as being primarily determined by a compromise between predator avoidance and foraging opportunities. This behaviour has been studied for nearly two centuries (Lampert, 1989) but it is still crudely represented in many models. Vertical migrations depend on the influence of absolute light intensity, on the rate of irradiance change, on the presence of predators, and on individual characteristics such as size, shape, weight and development stage (Carlotti & Wolf, 1998). Most of the models present scenarios of the influence of zooplankton migrations either on zooplankton distribution itself (i.e. Carr et al., 2008) or on related matter fluxes (i.e. Putzeys and Hernandez-Leon, 2005).

4. Future directions and suggestions to improve parameterization in zooplankton models

4.1. Towards an integrated approach between laboratory field experiments, observation and modelling.

When defining an experimental setup in order to develop a model for a given process, the researcher should always think about the data which correspond to the mechanism underlying the studied process. For the sake of simplicity, we can separate experimental data in two types. The first type includes variables or parameters linked to the mechanisms represented in the model (we shall call them input data). The second type includes the quantities affected by the process and which will be results of the model (output data). For instance, let us assume that we are interested in the functional response of a phytoplankton – zooplankton system. We can estimate it directly by comparing a predator – prey model (in which the functional response appears as one term) to the densities of the populations (output data). However, we could also have some information on the phytoplankton spatial distribution (camera and image analysis) and on the zooplankton individual behaviour (movement, consumption, etc.). This information provides the input data which are also suitable for the determination of the functional response and as a result, the output data.

These two data types should not be confused. Using output data in order to build a model imposes a strong constraint on the model and leads to a mathematical formulation only able to simulate what the researcher already knows. A best approach would consist of comparing the simulation of a model made on the basis of input data to a set of output data (such as in Steele et al., 2007). A good agreement from this comparison permits an improvement of our knowledge on the process. Optimally, models should be built in parallel with experimental studies that examine the response of various physiological and vital rates to external parameters (e.g., food, temperature) and quantify the consequences in terms of weight (structural and reserves, reproduction rates). Not only are experiments needed to derive parameterizations of functional feeding responses, metabolic and assimilation responses, but also the individual variability for each of these processes. This variability is critical since there is the possibility for genetic shifts or plasticity in these responses due to natural selection or adaptation in response to environmental change.

In support of modelling activities, field studies should collect information on easily measurable variables (body weight, reserve, reproductive state) with additional information on *in situ* processes (such as grazing, respiration and egg production rates) as well as abiotic variables such as temperature turbulence etc. Field data should mainly serve as validation of models and not to parameterise the model. Furthermore, long-term field studies combined with experimental studies should be employed to validate modelled dynamics and rate parameterisations.

Studies of population dynamics consists essentially of estimating mortality, reproduction, development times and stage-specific weights in field and in experimental conditions. Depending on the zooplanktonic species of interest, experimental studies can be conducted in micro- or mesocosms (from a few liters to 10 m^3) for the determination of parameters relevant to the population dynamics of target species (Aksnes et al., 1997). Most of the typical mathematical formulations of processes used in population and ecosystems models have been initially suggested and validated in laboratory experiments, usually at steady state, *i.e.* when the experimental system reaches equilibrium, or over a very short temporal period in order to avoid accounting with the changes of variable values. However, in population dynamics or in ecosystems, steady state situations are rare. Most of the demographic and biological processes are dependent on the short-, mid- and long- term variations of the environment. Furthermore, in the marine ecosystem, it is particularly difficult or impossible to know the historical conditions of life of sampled organisms. However, some biological characteristics are indicators of this history (weight, size, larval fish otoliths, gonad structure in reproductive organisms, etc.). Mesocosm studies are still not used enough to simultaneously combine demographic and vital rates estimates, in various stable and unstable conditions and thereby better calibrate population models. Similarly field studies should not restrict information to biomasses or numbers, but also include individuals characteristics (size structure, body weight, gonad structure; see **figure 4**) as better indicators of the status of the population structure.

For this reason, more and more experimental designs aim to study controlled systems (mesocosms) in order to represent the environmental variability and its effects on process formulation (Hansen et al. 1997; Caparroy et al., 1998). This approach must be supported as it permits us to understand individual or population responses to rapid environmental changes and then to improve the mathematical process formulation which are then implemented in ecosystem models.

In the support of parameterisation development, the need and desire for more rapid methods to count and size zooplankton in situ has led to the development of an impressive array of acoustic, optical, and physical sensors (Wiebe and Benfield, 2003). Development of future models at the level of population, community and ecosystem should be able to exploit the resultant different data types. Size spectrum modelling of zooplankton in connection with *in situ* optical counters, video, and scanners is one major direction.

With respect to field observations of a given process these should be performed at the characteristic space and time scales of the process. However, it is also useful to obtain information on process variability at other time and space scales. Indeed, each process can interact with other processes at different scales and the impact of these interactions can be seen at various scales. Moreover, by using scale transfer methods, it should be possible to anticipate the variability of a given process at different scales with relevant data needed to test the methods validity.

Typically model formulations are copied and used to examine species or population dynamics outside the scale at which the original formulation was developed. There is a real need to define different key levels of experiments and observations to explore scale-related questions of processes (both ecological levels and time and space scales) and evaluate scale-dependent responses. Robust empirical relationships at defined scales are better alternatives, than misuse of mechanistic relationships. **Figure 4** suggests the links between models at different ecological levels, and the experiments and field observations at the appropriate scales to deliver adequate data to calibrate and validate these models.

4.2. Models predicting transfer of mass incorporating spatial and temporal scales

In ecological models, there are three major dimensions which a scale can be defined: (i) the level of ecological organization (ii) time and (iii) space; each dimension has two properties: its range and its resolution. For marine zooplankton models, there are two major ecological levels of organisation at which models have been built: functional groups and population (including individual-based models).

The intrinsic complexity of ecosystem dynamics results from the interactions of a large number of components having themselves their own non linear dynamics, which take place at various

time and space scales. To deal with this complexity, we need to focus on specific tractable scientific questions. Then, we need to make assumptions in order to extract the variables and the relation between the variables which are expected to be the most important to solve this question. The choice of the mathematical formulations for describing the above defined processes may be crucial. The following paragraphs suggest approaches to help define these choices.

4.2.1. a) Empirical and mechanistic formulations

The relationship between variables can be either empirical (based on statistical relationships between observations and controlling factors) or mechanistic (process-based). Mechanistic models generally increase the number of components and relationships following a first principles approach. They allow the examination of responses outside of the domain where the initial data was collected. Even for so-called "mechanistic models", simplifications are made in order to keep the model numerically tractable. These simplifications are made on the basis of our partial knowledge on the system. Many mathematical formulations used in ecosystems models are established from data obtained in laboratory experiments. This procedure assumes that the scale transfer from the laboratory conditions to the ecosystem exploitation does not influence the mathematical formulations i.e. relationship.

In empirical approaches, parameters are estimated by fitting datasets which are obtained in a given set of conditions, either from laboratory or from natural environments. Usually, these relationships are strictly dependent on the experimental conditions from which they are extracted. The set of parameter values needs to be with the associated environmental conditions and the use of such relations from outside the range of observation should be excluded. With respect to scale transfer, mechanistic formulations are encouraged since they are designed to explain the variability of a given process at different scales. Moreover, if the mechanisms underlying a given process are sufficiently well described, it is possible to consider that a mathematical formulation based on this knowledge is more able to represent the process in variable and forced conditions. Indeed, there are some examples where different formulations having a very similar shape for the representation of processes can lead to very different dynamics (Fussman and Blasius, 2005). This paper finds its root in Myerscough *et al.* (1996), which provides an example of phytoplankton – zooplankton interaction model sensitive to the functional response mathematical formulation. In those papers, the authors consider three different mathematical formulations for the functional response in a predator – prey model. Each formulation contains two parameters and can thus be compared in a statistical sense. The parameters of these functions are chosen in such a way that the associated response curves are similar. In fact in this exercise a choice of functional response model cannot be made due to the variability in the observations. However, they show that the first formulation leads to extinction of the predator, the second function leads to predator – prey coexistence at steady-state and the third function leads to predator – prey oscillations. In this case, only the mechanisms underlying the functional response (swimming behaviour, searching time, capture and handling time, prey spatial distribution, ...) allows the selection between these functional responses. Such observations are not special cases and can be quite general (Wood and Thomas, 1999).

4.2.2. b) Scale transfer and process formulation

A common approach in ecosystem modelling consists of the use of mathematical process formulations established at a given organisation level for another organisation level. A typical example is the functional response in trophic interactions. The functional response is often very difficult to measure in the field, whatever the organisation level. However, in laboratory experiments, it is possible to get quantitative measurements on the ingestion rate of selected individuals. The mathematical formulation derived from such experiments is a consequence of individual properties and should not be directly applied for a community or a functional group in an ecosystem model. The consequences of the scale transfer on the mathematical formulation, and not only on the parameter values, have to be investigated. A nice example of such an

approach is given by Englund and Leonardsson (2008), where the authors use the Transition Scale Theory do deal with the formulation of a functional response and spatial heterogeneity.

Laboratory experiments based on steady state designs, a case where processes compensate, can lead to formulations which are only available in homogeneous environments, similar to culture systems in laboratories. However, in some cases it is not correct to take these formulations to the ecosystem level. In Morozov *et al.*, (2008), the authors show that even if Holling type I or II functional responses are often found in experiments in laboratories, fields data are much more represented by a Holling type III functional response. Hence, Morozov and Arashkevich (2008) show, by a change of scale, that a mechanistic approach can explain this change of functional response formulation.

4.2.3. c) Scale transfer and model - data confrontation.

We can easily imagine two ways for the comparison of data to ecosystem models. The first consists of developing a model able to represent the data and then making a direct comparison using data upon which the model was not parameterised. The second approach consists of focusing on a given organisation level at a given scale and the associated observational data, then using scale transfer methods in order to build a model at another organisation level based on the results from the previous model. Finally, the observational data corresponding to the new organisation level is used for comparison with the model output for the new organisation level. The goal of this second approach is to improve the knowledge at the organisation level with a limited set of assumptions.

There are two components to the problem of scaling: firstlto identify the scales that are important, and second to produce an algorithm for relating process across scales (**Figure 5**). The scale at which the pattern of interest (zooplankton distribution and fluxes) is observed, is often much larger than the scale at which the associated processes are studied. For example, zooplankton physiological responses at the individual level are directly used to parameterise the mesozooplankton functional group in biogeochemical models.

The problem of scaling across ecological integration levels from an existing low level model can be addressed by different approaches (**Figure 6**). "Lumping" is probably the simplest and most common approach to change in scale. It involves retaining the original mathematical model, but selecting new parameter values applicable to the larger scale. An example of this is the grazing function in which an upscaling is made from the response of a single individual feeding on given prey to the feeding response of the zooplankton functional group to functional groups of prey. This is the ecosystem modelling approach often chosen for upscaling of zooplankton organisms. The premise behind this method is that the response of the specific ingestion rate (i.e. by biomass unit) is similar across the scales. An "average" individual may be sufficient to represent this individual. However, for many processes, the response of an average individual may not be easily transferred to an upper level. For instance, Poggiale *et al.*, (1998) show an example where a ratio-dependent functional response emerges at a global scale while a prey-dependent functional response is assumed at local scale. This illustrates that in a system, even if all individuals have similar properties, non-linear characteristics associated to a variable environment lead to emergent properties at global level which are not jut an average of local functions. Based on these outcomes it is clear that a model parameterized on a particular mean individual is unable to reproduce the dynamics of a zooplankton community a different scales. .

A second method employed is to replicate a sub-model a sufficient number of times to provide the larger scale information and material flow at the upper level. Population models based on individual-based models represent this type of direct replication (Carlotti & Wolf, 1998; Batchelder et al., 2002; Woods *et al.*, 2005). The cumulative performance of a large number of individuals determines the dynamics of a population. The justification for this approach is that the behaviour of a given system level is the sum of the behaviours of sub systems. An important aspect is that the number of replicated sub-units be statistically sufficient to reproduce the properties at the upper level.

A step forward of the aforementioned approach concerns the aggregation of variables and associated combined processes. It consists in defining (global) variables at a level of organization which should be, in theory at least, a function of (local) variables describing the

system at a lower organization level. The global variables describe the system as a whole while the local variables describe the system with lots of details. One problem with this approach is that of defining which of the local outputs to use and how to combine them to form an aggregated variable. In order words, the problem is the choice of the global variables and the way they rely to local variables. Some mathematical methods have been developed and may be applied for this purpose. For instance singular perturbation techniques provide tools which allow building mathematical formulations at a given level based on formulations at a lower organization level if the dynamics at each organization level can be associated to different characteristic time scales (Michalski *et al.,* 1997, Poggiale, 1998, Poggiale *et al.*, 1998, Auger *et al.*, 2006, and see Auger *et al.* 2008 for a general review in various ecological applications). The previous papers focus on time scales. In order to deal with space scales, an example of technique is the operator homogenization (Ainseba et al., 2002): it aims to build spatial operators at a large scale on the basis of detailed information at small scales.

Making some assumptions, these methods can be used to define Eulerian formulations on the basis of Lagrangian dynamics. Indeed, Lagrangian models are based on individual properties, associated to small space and short time scales. Eulerian models aim to describe the spatio – temporal dynamics at population or community levels, at larger space and longer time scales.

If slow and fast dynamics are linked in a formal context, as can be the case with the previous methods, we obtain mathematical relationships between variables describing detailed processes and variables for global description. This helps to understand how dynamics at the global level emerge from detail. Moreover, it can also illustrate how the global system dynamics acts on sub-systems thereby furthering the understanding of feed-back effects on system dynamics.

Finally, the formal relations between organization levels give mathematical conditions which can be used to define the most appropriate variables to be used in order to describe the system at the global level.

4.3. Theories as a framework to essential parameters.

It has been argued that as a science approaches maturity theories emerge. A large part of experimental works in ecology in the 70's – 80's were hindered by the traditional, phenomenological Lotka – Volterra model. As a result, recent publications have stressed the importance of considering the mechanisms underlying competitive interactions, (e.g. plankton Rothhaupt, 1988).

A theory aims to provide some tools for generalizing ideas with a set of recommendations for the validity and the limit of the generalization. In the biological context, a theory can provide a solid framework to understand how a given experiment should be set in order to extend the results as much as possible. Various theories are available in the literature and others will be developed. Experimentalists and modelers have to work together to improve our knowledge on the role and function of zooplankton populations in ecosystems and it seems unavoidable that it shall be done in a theoretical context. Theories reveal the basis for pattern and provide a framework for prediction where historically inexplicable variability appeared to prevail.

In the last decade, the input of new zooplankton data from modern instrumentation as well as our capacity to compile data as fostered by the development of global analysis, has contributed to development of general hypothesis and the evolution of theories. Among them, several theories related to the dynamics of individual, population, community or functional group have been developed and applied in the field of zooplankton ecology.

a)   Individual   and   population   level:
The Dynamic Energy Budget (DEB) theory (Kooijman, 2000) has been developed and used since the early 80's. This theory attempts to describe the rates at which individual organisms assimilate and utilize energy from food for maintenance, growth, reproduction and development. These rates depend on the state of the organism (age, size, sex, nutritional status, etc.) and the state of its environment (food density, temperature, etc.). Solutions of the model equations represent the life history of individual organisms in a potentially variable environment. DEB theory makes testable predictions about the performance of organisms in any given environment

and thereby helps to identify the mechanisms responsible for observed patterns in experimental data.

A simple and rather interesting characteristic of this theory is that it does not assume any allometric relationships. However, it produces relationships which can be in turn compared to datasets. Thus the DEB theory can provide formal relations between processes (e.g. respiration rate) and individuals properties (e.g. length). For example, respiration rate is the weighted sum of the square length (surface) and cubic length (volume). The weights are the energy conductance (v) and the maintenance rate (kM). This relationship comes from the theory and is based on the assumption that respiration is linked to loss of energy by a surface and to maintenance of volume. The energy conductance and the maintenance rate may be determined separately (see Kooijman, 2000, p. 88 for instance).

4.3.1. b) Community level.

The metabolic theory of ecology (MTE) proposed by Brown and colleagues (Brown et al., 2004) derives an emergent rule on the metabolism at the level of a community based on metabolic rates at the level of the organisms. As body size increases, metabolic rate increases with the exponential power of ¾ with body size. Metabolic rate also varies with temperature according to a well-known relationship between temperature and enzyme reaction rates. Combining these relationships gives a general expression that describes the metabolic rates of practically any organism: $B = b_o M^{3/4} e^{-E/kT}$

where B is the metabolic rate, b_o is a constant independent of body size and temperature, M is body mass, and the ¾ power scaling exponent reflects the fractal-like distribution network supplying resources to individual cells within the organism's body that adds a 4th dimension to a 3-dimensional being. The Boltzmann factor, $e^{-E/kT}$ describes the temperature-dependence of metabolic rate, where E is the average activation energy of metabolism or of photosynthesis and k is Boltzmann's constant, 8.62×10^{-5} eVK^{-1}.

López-Urrutia et al. (2006) compiled data on respiration of individual plankton species and showed that respiration rates follow the predictions of the metabolic theory, as function of body size and temperature. From their analysis, the respiratory rates of planktonic organisms from heterotrophic bacteria to zooplankton and the production rates of phytoplankton follow metabolic theory. The temperature-corrected respiration rates of heterotrophs (bacteria and zooplankton) scale with body carbon allometrically with an exponent higher 0.87 than the expected 3/4 power. They explain that this difference is mainly because planktonic organisms do not have a uniform constant density.

4.3.2. c) Size structured population:

The essence of biomass spectrum theory is that trophic interactions between predators and their prey are governed by allometric, or body-size-dependent, processes such as metabolic rate and specific production (production/biomass). A key and unique feature of the theory is the proposition that energy transfers in aquatic ecosystems occur at two different scales. At the physiological scale, energy fluxes *within* individuals are limited by size-dependent metabolic processes. At the ecological scale, energy transmission *between* individuals is governed by the hunt for spatially varying prey of appropriate size to support energy demands of predators that steadily increase in mass but decline in concentration. A review is given in Kerr and Dickie (2001).

The basis size spectrum theory (Zhou and Huntley, 1997) is that the propagation of biomass along the axis of individual body weight can be written as

$$\frac{\partial b}{\partial t} + \frac{\partial (wgb)}{\partial w} = gb + \mu b$$

where t is the time, w is the body weight, g is the ensemble mean individual specific growth rate within the size class w, μ is the ensemble mean population specific mortality rate within the size class w, and $b(w, t)$ is the normalized biomass spectrum defined as the accumulative biomass within the size class interval $(w-\frac{1}{2}\Delta w, w+\frac{1}{2}\Delta w)$ normalized by Δw. Here Δw represents an

infinitesimal size class interval in the theory, or a finite size bin during sorting in field. Zhou (2006) developed a mathematical method to link the biomass spectrum slope ($\partial \ln b / \partial \ln w$), the community assimilation efficiency and the trophic levels.

Zhou and colleagues have applied their equations to estimate in situ zooplankton growth and mortality rates from Optical Plankton Counter measurements on size and abundance for different marine ecosystems. (Edvardsen et al., 2002; Zhou et al., 2004; Zhou, 2006). The large potential interest of the developed biomass spectrum theories intend to integrate the mathematical models and in situ observations from new observing tools.

4.3.3. d) Evolutionary perspectives.

The Adaptive Dynamics Theory (for instance Geritz *et al.*, 1997) aims to develop models allowing the study of phenotypic evolution. It provides simplified models on the basis of individual based underpinning. These models are powerful tools for investigating the implications of complex ecological settings. The theory gives a formal framework which is very useful for understanding the biodiversity evolutionary dynamics. This theory can be associated with theories of population dynamics, leading to a formal set of relations on parameters. These relations exhibit how the individual and population parameters evolve under evolutionary constraints. This theory has been used in zooplankton models to investigate for instance the evolution of some behavioural traits like feeding behaviour (Dercole and Rinaldi, 2002) or displacement behaviour (Bilton *et al.*, 2001). The theory assumes that after a mutation, the mutant density is rather low with respect to resident population density. On the basis of this assumption, a canonical equation is derived in which parameters of the population growth are involved. For instance, this equation allows us to identify the environmental conditions under which the mutant can invade the population.

These theories are beginning to be tested. As a first consequence, a theory permits reasonable extrapolations from one system to another with similar properties (e.g. comparison of plankton size spectra in different regions and/or seasons, or comparisons of metabolisms for different species with DEB theory). A second aspect of a theory is that it guides compilation of relevant and coherent data sets.

In a theoretical context, some models use variables which are very difficult or even impossible to measure (unattainable variables). The aim of such variables is to represent the mechanisms underlying the studied processes. Some authors consider that this approach should be avoided since it seems impossible to completely evaluate or validate such models. We here suggest another point of view by considering a qualitative validation. For instance, we can compare two models of the same processes: one with unattainable variables and the other based only measurable variables. Authors often compare the quantitative differences between models according to different kinds of measures. We can, however, compare them from a qualitative point of view: i.e. how well are they able to reproduce dynamics of a given system? Indeed, the mathematical study of a model can provide a so called bifurcation diagram which gives some of possible behaviors of the model according to a given set of parameters. In a situation where a model using unverifiable variables is the only one able to reproduce the observed dynamics, these variables cannot be avoided for a good understanding of the processes. Moreover, if it is done on the basis of a theory, this theory should provide some support for the validity of using these so-called unverifiable variables and should also allow us to extrapolate to get (indirect) information on these variables. For instance, Kooi and Kooijman (1994) provide an example of a three trophic level food chain for which the data can only be reproduced by the DEB model where some variables (reserves) are difficult to measure in practice. In their case, the model results from the Dynamics Energy Budgets theory (Kooijman, 2000).

A long term objective of theories is to foster the rigorous characterization of the inter-relationships that exist between theories (as robust properties or emergent properties) at different levels of ecological integration. It is not an issue in this paper to discuss the foundation

of these theories but to suggest that they could help to coordinate and orient experiments and data acquisition towards similar objectives, which means to take theories merely as motivation. This would also be a key step for these recent theories to test them from independent datasets.

5. Concluding remarks

As mentioned by de Young et al. (2004), "There is no single, fully integrated model that can simulate all possible ocean ecosystem states. The biological resolution of early attempts at marine trophic modelling was dictated more by the extent of knowledge rather than by conscious decision about the structure and function of the model". Whereas many efforts are made in the understanding of the physical-biological processes coupling zooplankton distribution and hydrodynamics both from observation and modelling, there are still large gaps of knowledge in the coupling between the lower and upper trophic levels of zooplankton. One reason is that up until now most research efforts concerning zooplankton (both for field and lab studies) have been made to understand its role as closure term of biogeochemical models. Recent research efforts focus on its role as prey for fish conducted with focus on a few targeted populations. These scientific questions have oriented research in directions which have minimized studies on a number of key biological processes (i.e. temperature-dependent response of rates at the species level). Regardless, zooplankton modelling has made great progress in the two last decades, but it has arrived at a bottleneck as the information necessary to advance these models is lacking or misused. Thus models should be now used as starting point to identify the information gaps upon which new experimental and field studies should be focused.

Aside from questions about the role of zooplankton in biogeochemical cycles and on their trophic role as fish food, other key questions should be addressed, such as the understanding (and modelling) of planktonic succession, their influence on other trophic levels (i.e. phyto- and zooplankton and fish), and on population survival during the "quiescent phase" versus "growth phase". Such objectives could re-stimulate process studies on key mechanisms of zooplankton dynamics which will be relevant for other ecological and ecosystem questions.

As proposed in this paper, zooplankton models should be specifically built at different level of organisation to answer precise questions. The building of any zooplankton model should start with a clear statement on the question to be addressed, the relevant time and space scales and biological structure (resolution and applications) at which the model will serve. Information obtained at smaller and larger scales may be then useful if adequate methods of transfer scales are used (Figure 7) both for the model structure and the associated processes.

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Table 1: Hierarchy of zooplankton models (or modules in ecosystem models)

Variables	Goal	Scales	Processes
Only a transfer function No variable	Transfer function through trophic chain to tuna's forage Ex SEPODYM model (Lehodey et al. 2003)	Basin Scale Annual to decadal	Transfer function
Global biomass $Z(x,y,z,t)$ (As zoo)	Biogeochemical fluxes induced by Z Ex: Fasham's model (Fasham et al. , 1990)	Regional to global ocean Annual to decadal	Grazing and faecal pellet production Metabolic rates Mortality and Predation Diurnal migration
$Z_i(x,y,z,t)$, Global biomass of i zooplankton functional Groups	Biogeochemical fluxes induced by different Z groups Ex: Moloney and Field's model Moloney and Field (1991)	Regional Scale to Basin Scale Seasonnal to Pluriannual	Grazing and faecal pellet production Metabolic rates Mortality and Predation Diurnal migration
$Z_i(x,y,z,t)$, Density and biomass size distribution i: continuous size-classes	Zooplankton size structure Prey field for fish Ex: Zhou'model Zhou and Huntley (1997)	Regional Scale Seasonnal to Pluriannual	Ingestion/ Egestion rates Metabolic rates Development/Growth rates Reproduction rate Mortality rate Interactions
$Z_{i, j}(x,y,z,t)$, Developmental stages or groups j of populations i Biomass or densities	Zooplankton target species dynamics, predator-prey dynamics and population successions Ex: Carlotti and Sourisseau'model Sourisseau (2002)	Regional Scale Seasonnal to Pluriannual	Ingestion/ Egestion rates Metabolic rates Development/Growth rates Reproduction rate Mortality rate Interactions
$Z_{ij}(x,y,z,t)$, Developmental stages or groups of stages for one population Biomass or densities	Zooplankton target species dynamics and life cycle Ex: Miller et al. (1998)	Regional Scale Seasonal to Pluriannual	Ingestion/ Egestion rates Metabolic rates Development/Growth rates Reproduction rate Mortality rate
Internal individual components in mass: structural weigh, reserves, gonads	Individual biology Trophodynamics, growth behaviour Ex: Caparroy and Carlotti (1996)	Local to Regional Scale Days to Months	Ingestion/ Egestion rates Metabolic rates Internal fluxes Egg production rates

Figure captions (all figures are originals, colour in electronic version and black/white in press**):**

Figure 1: Schematic representation of the combination of approaches required to implement the Rhomboïd strategy (see text).

Figure 2:   Typical time and space scales of marine systems.

Figure 3: Schematic representation of key differences in production, species numbers, life cycle and swimming behaviour between the different trophic levels in marine ecosystems.

Figure 4: Schematic representation of different processes and variables which could be obtained at the different levels of organisation in laboratory and field.

Figure 5: Scale transfer from one level where the information on processes is obtained at given time and space scales (see figure 1) to other levels where such information is used in models (Arrows).

Figure 6: Different approaches for scaling across ecological integration levels from an existing low level model. A. Lumping. B. Replication and aggregation.

Figure 7: Schematic representation of the different steps from a detailed model at the level of a single population to a community models considering several population but simplifying each population compared to step 1, and to an ecosystem models considering interaction of functional groups each of them based on simplification of community modules.

Figure 1

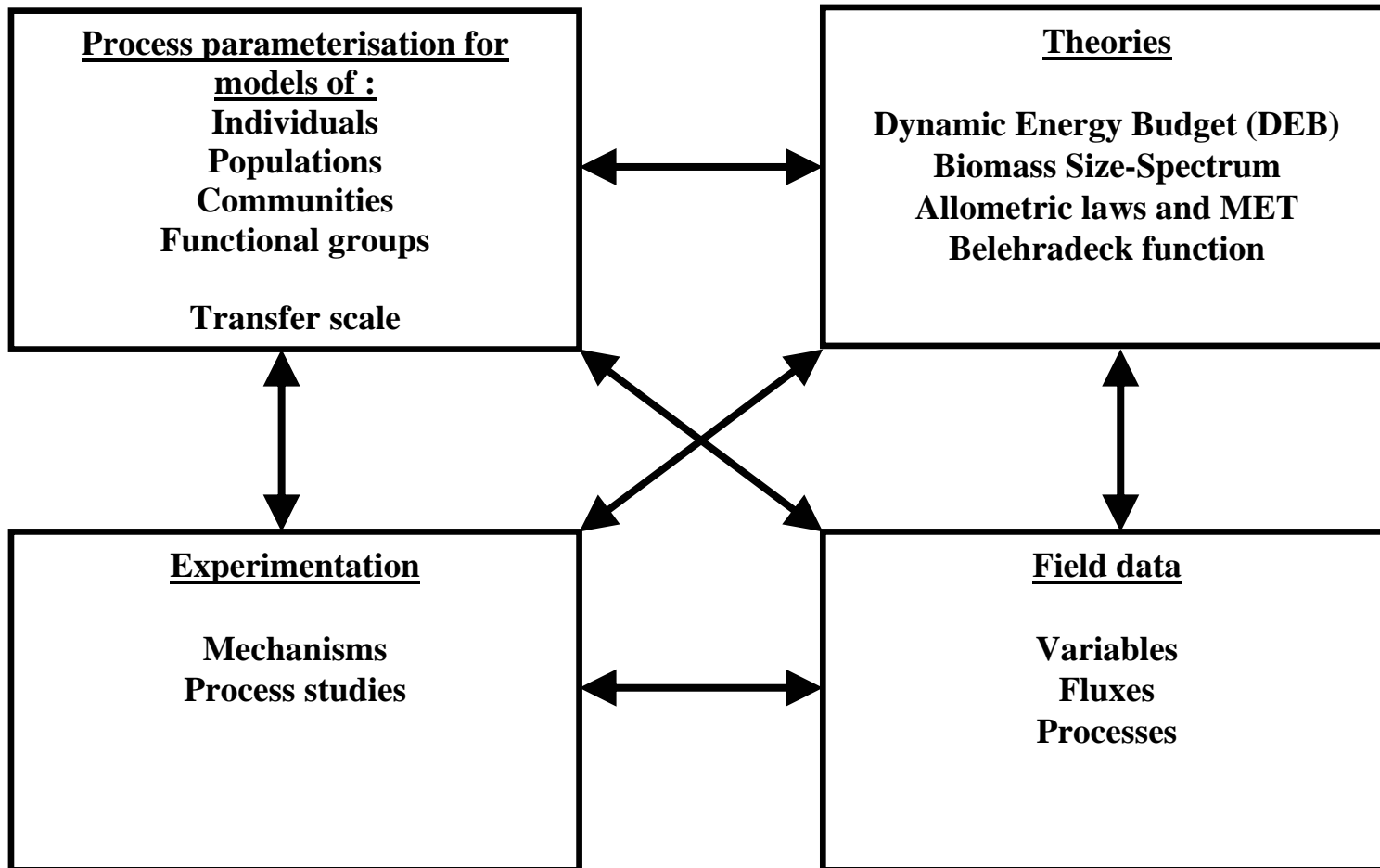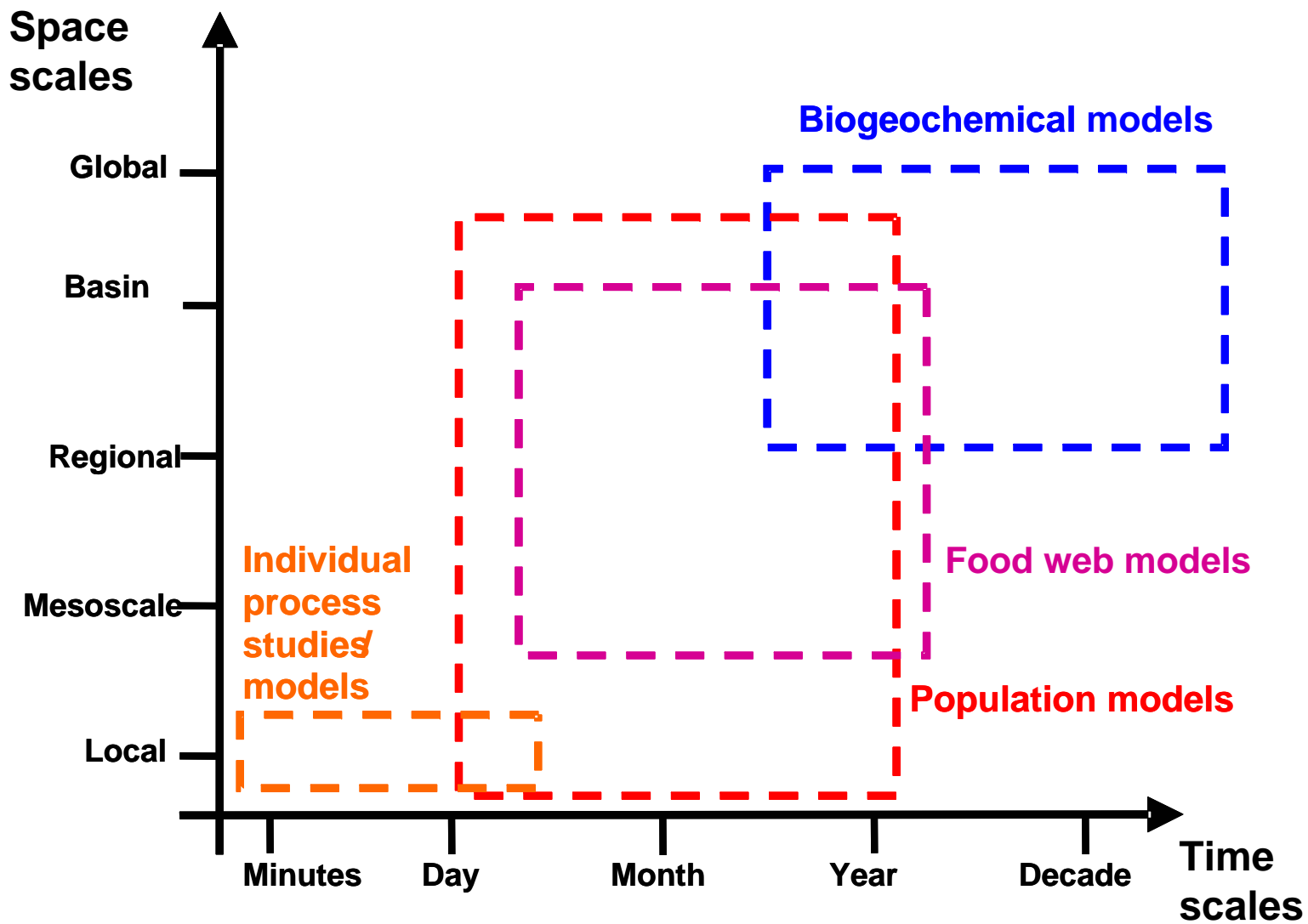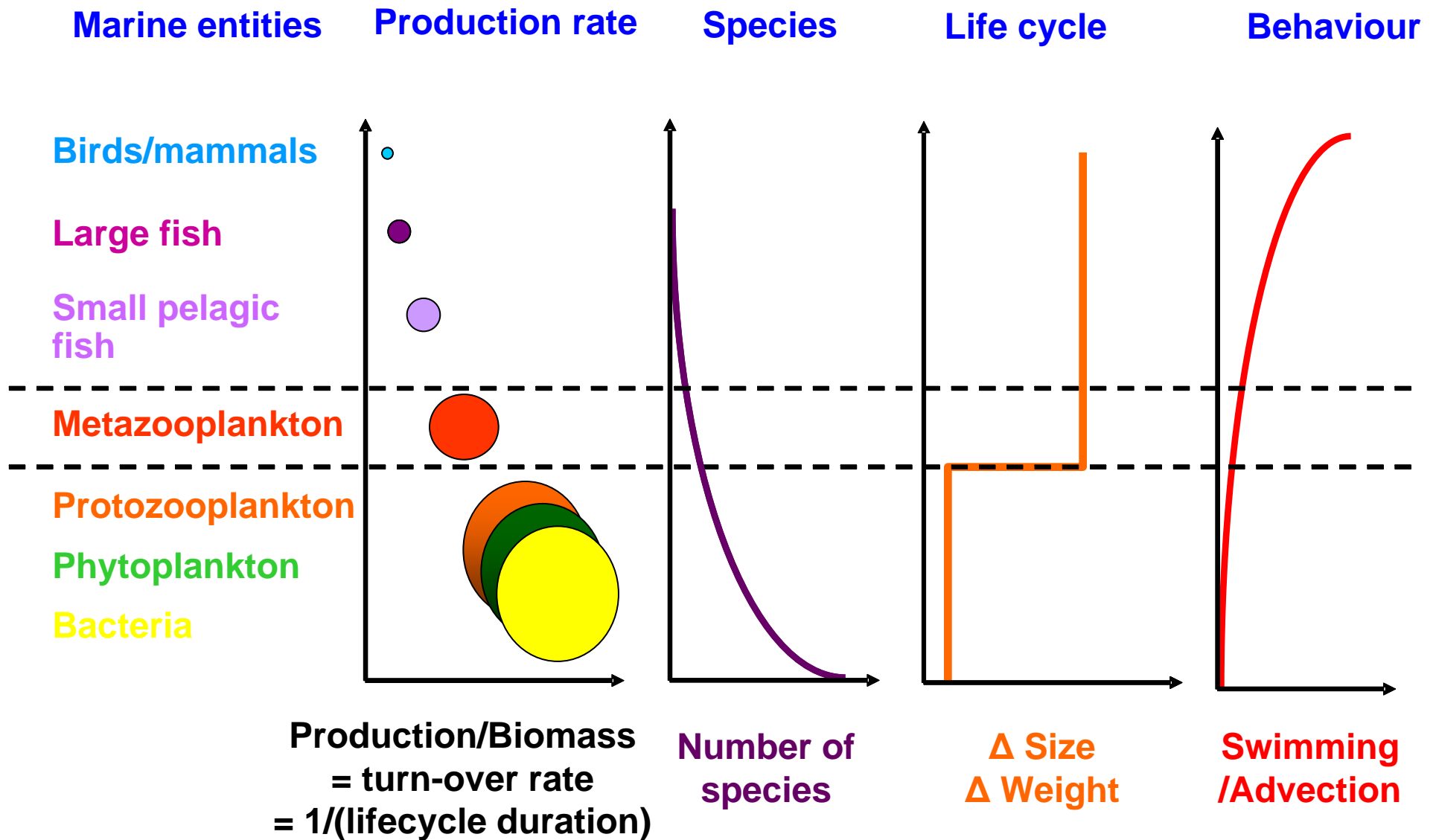| Process parameterisation for models of : Individuals Populations Communities Functional groups Transfer scale	Theories Dynamic Energy Budget (DEB) Biomass Size-Spectrum Allometric laws and MET Belehradeck function
Experimentation Mechanisms Process studies	Field data Variables Fluxes Processes

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

A

B

Individual

Individual

Population

Bulk biomass

Bulk biomass

Population

Life history

Predators

Key taxa

Prey

Community

Predators

Prey

Functional groups

Predators

Prey 1

Prey 2

Figure 7