A size-spectrum zooplankton closure model for ecosystem modelling

MENG ZHOU1,2*, FRANCOIS CARLOTTI2 AND YIWU ZHU1
1 DEPARTMENT OF ENVIRONMENTAL, EARTH AND OCEAN SCIENCES, UNIVERSITY OF MASSACHUSETTS BOSTON, 100 MORRISSEY BDY, BOSTON, MA 02125, USA
2 LABORATOIRE D’OCEANOGRAPHIE PHYSIQUE ET BIOGEOCHIMIQUE, CENTRE OCEANOLOGIQUE DE MARSEILLE, CNRS, UNIVERSITE DE LA MEDITERRANEE, CAMPUS DE LUMINY, CASE 901, 13288 MARSEILLE CEDEX 09, FRANCE

*CORRESPONDING AUTHOR: meng.zhou@umb.edu

Received July 14, 2009; accepted in principle March 15, 2010; accepted for publication April 9, 2010

Corresponding editor: Roger Harris

A zooplankton closure model is developed by combining the size-based growth and mortality rates and size (biomass) spectrum theory. The new growth rate model, developed based on both Huntley and Boyd [(1984) Food-limited growth of marine zooplankton. Am. Nat., 124, 455–478.] and Hirst and Bunker [(2003) Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnol. Oceanogr., 48, 1988–2010.], avoids overestimating zooplankton growth at the high temperature and food concentration condition; the mortality rate model developed based on the slope of observed biomass spectra and assimilation efficiency; and the biomass spectrum theory is a conservation equation of biomass fluxes between size classes in terms of growth and mortality. The zooplankton closure model is applied to simulate particular organic carbon and mesozooplankton biomass concentrations from 5 January 1999 to 12 July 2007 forced by temperature and chlorophyll, all of which were observed at the Service d’Observation du Frioul du Centre d’Océanologie de Marseille (SOFCOM) long-term monitoring station in the Gulf of Lions, northwestern Mediterranean Sea. The modelled zooplankton biomass and size spectra imitate the seasonal variations and responses of zooplankton communities to phytoplankton blooms. The carbon fluxes of total grazing, grazing on phytoplankton, feeding on zooplankton and removal from the zooplankton community are analyzed equal to 78, 40, 38 and 14 mg C m$^{-3}$ day$^{-1}$, respectively. This zooplankton closure model is intended to provide a link between lower and higher trophic level models in ecosystem modelling.

KEYWORDS: size spectrum; growth; mortality; zooplankton model; biomass-carbon flux

INTRODUCTION

Many efforts have been made to synthesize understanding of fundamental biogeochemical and biological processes into models with significant success (Doney and Ducklow, 2006). Nutrient–phytoplankton–zooplankton–detritus (NPZD) models have been developed for more than 30 years (e.g. Steele, 1974; Wroblewski et al., 1988; Fasham et al., 1990). Within an NPZD model, zooplankton components are frequently treated as closure models taking a mechanistic approach (Steele and Henderson, 1992; Baird and Emsley, 1999; Edwards and Yool, 2000; Baklouti et al., 2006a, b). Realizing that it is not feasible to include all details in an ecosystem, a plankton functional group approach
has been proposed (Doney, 1999; Pomeroy, 2001; Moore et al., 2002; Le Quéré et al., 2005). Phytoplankton can be divided into, for example, diatoms and flagellates (Totterdell et al., 1993; Chai et al., 2002; Christian et al., 2002a, b), size-based groups (Silver and Platt, 1977; Platt and Denman, 1978; Moloney and Field, 1991; Chisholm, 1992; Armstrong, 1999; Baird and Suthers, 2007; Stock et al., 2008) and specific functional groups responding to nutrients (Leonard et al., 1999; Moore et al., 2002; Le Quéré et al., 2005; Buitenhuis et al., 2006; Mongin et al., 2006). Zooplankton have been divided into herbivorous, omnivorous and carnivorous groups (deYoung et al., 2004; Le Quéré et al., 2005; Batchelder and Kashiwai, 2007) and size spectra (Heath, 1995; Zhou and Huntley, 1997). At higher trophic levels, size-based fish models have been developed by specifying size relationships between prey and predators (Benoit and Rochet, 2004; Andersen and Beyer, 2006; Maury et al., 2007; Blanchard et al., 2008; Law et al., 2009). Though zooplankton models have been integrated into phytoplankton and nutrient models, not only are zooplankton results rarely compared with observations, but also zooplankton processes such as individual growth, respiration, mortality and biomass transfer between trophic levels are often not included. This makes it difficult to predict biomass fluxes from primary producers to higher trophic level organisms and carbon export.

Marine ecosystems and food webs are organized through complex prey–predator interactions among millions of individuals and thousands of species in a size range from tiny microbes of $10^{-1}$ $\mu$m to large top predators of 10 s meters in size. Many species change their feeding behavior in different geographic areas, seasons and during their life stages. Altering their behavior under pressure of food availability and competition leads to reorganization of the functional groups of a food web that is hard to predict and causes significant uncertainties in a plankton functional group approach (Huisman and Weissing, 1999). For example, Calanus finmarchicus, the most well-studied herbivorous copepod species, feeds on phytoplankton during spring blooms, but in post-bloom seasons, a significant fraction of food derives from the microbial loop (Eilertsen et al., 1981; Falkenhaug et al., 1997). Antarctic krill are herbivorous in spring, summer and early fall, and are omnivorous and carnivorous in late fall and winter (Atkinson and Snyder, 1997; Zhou et al., 2004). Uncertainties in these prey and predator relationships are the primary causes of uncertainties when considering ecosystem food web structure, and problems in ecosystem models to parameterize unpredictable prey and predator relationships (Mitra and Flynn, 2006).

The lack of general models for zooplankton processes has become a major obstacle for carbon flux models to simulate the effects of zooplankton grazing and fecal production on carbon storage and export flux, and for food-web models to simulate biomass transfer from lower to higher trophic level organisms including fish populations (deYoung et al., 2004; Le Quéré, 2005; Daewel et al., 2007). Recent studies indicate that zooplankton respiration contributes 13.0 $\pm$ 4.2 Gt C annually, approximately 17–32% of the primary production in the global ocean (Hernandez-Leon and Ikeda, 2005); and removing large fish from fisheries has significantly altered food-web structures and carbon storages, and led to instabilities of ecosystems (Frank et al., 2005, 2006, 2007; Beaugrand et al., 2009; Zhou et al., 2009). Such instabilities have been studied theoretically in fish population modelling based on size spectra and prey–predator size relationships (Maury et al., 2007; Law et al., 2009), and in selective fishing (Benoit and Rochet, 2004; Andersen and Beyer, 2006; Blanchard et al., 2008). Zooplankton models could play an important role in interpreting measurements of zooplankton rates and abundances at specific points to predict spatial and temporal distributions. However, there are still significant gaps in measuring rates and abundances of zooplankton, and determining biomass linkages from specific lower to higher trophic level organisms.

Despite the complexity in prey–predator relationships and their spatiotemporal variability, size spectra of plankton communities are continuous and often nearly linear (Sheldon et al., 1972; Rodriguez and Mullin, 1986; Sprules and Munawar, 1986; Zhou and Huntley, 1997; Titel et al., 1998; Quinones et al., 2003; Zhou et al., 2009). Measurements of size spectra using optical sensors over a short spatial scale of 1 km and a temporal scale of 5 min indicate similar continuity and linearity in pelagic ecosystems with a size resolution of approximately 0.1 on the log_{10} based body volume classes higher than that of the octave-based volume classes used traditionally (Huntley et al., 1995; Zhou et al., 2004; San Martin et al., 2006). The biomass spectra in coastal regions are more dynamic. In the spring season, a cohort of krill larvae contributed to a distinct peak on the biomass spectrum in the coastal area off Oregon, compared to that of the off-shelf area (Zhou, 2006), and in the coastal regions off northern Norway, Calanus finmarchicus contributed to a distinctive peak on the biovolume spectra in the spring season (Basedow et al., 2006; Edvardsen et al., 2002; Zhou et al., 2009). These peaks were produced by the seasonal pulse developments of some specific local zooplankton species. In contrast to these coastal upwelling zones, the magnitudes of size
spectra in zooplankton communities at low latitudes change seasonally, but their slopes remain similar (Huntley et al., 2006), as situation that is also found in the northwestern Mediterranean Sea.

The simplicity of biomass spectra found in pelagic ecosystems stimulates our approach to develop a simple zooplankton model explicitly including essential biological processes of individual growth, population mortality and biomass energy fluxes, and to compare model results with a time series of plankton observations at the SOFCOM Station (Service d’Observation du Frioul du Centre d’Océanologie de Marseille), a long-term monitoring station in the Gulf of Lions (GOL), northwestern Mediterranean Sea. To focus on the model development, the zooplankton closure model will be forced by observed total phytoplankton biomass, temperature and the slope of the biomass size-spectra, ignoring any physical process and lower and higher trophic level models. Though this zooplankton model will not be able to simulate any individual species or stages of zooplankton, it is aiming at the biomass fluxes from phytoplankton to zooplankton and to higher trophic levels, and internal biomass recycling through carnivorous grazing within a zooplankton community.

**METHOD**

**Biomass conservation model development**

We will use the terminology, variables and notations used in Zhou and Huntley (Zhou and Huntley, 1997) of which the definitions are similar to previous publications (Silvert and Platt, 1977; Platt and Denman, 1978; Maury et al., 2007). All size spectrum theories of plankton dynamics fundamentally assume that the number of plankton in a sampling water volume ($\Delta V$) is large enough so that their accumulative biomasses in different size intervals will form a continuous function of their body size. The accumulative biomasses ($mg$) in a size interval normalized by the width of the size interval ($mg$) and $\Delta V$ ($m^3$) are so-called normalized biomass spectrum in the unit of $m^{-3}$ (referred to hereafter as biomass spectrum). In the continuum model, the biomass fluxes between size classes can be exactly expressed by a partial differential equation, that is,

$$\frac{\partial b}{\partial t} + \frac{\partial (whb)}{\partial w} = (\mu + g)b, \quad (1)$$

where $w$ is the individual body weight in the unit of mg C, $g$ the specific individual growth rate in the unit of day$^{-1}$, $\mu$ the specific rate of net abundance change in the unit of day$^{-1}$ and $b$ the biomass spectrum in the unit of m$^{-3}$ at time ($t$). The specific rates of $g$ and $\mu$ are traditionally defined as $(1/w)(dW/dt)$ and $(1/N)(dV/dt)$, respectively, where $N$ is the number of plankton at $w$ in a unit water volume. Normalizing equation (1) by $b$, and rearranging after taking partial derivatives of the second term on the left side, we have

$$\frac{\partial \ln b}{\partial t} + g \frac{\partial \ln b}{\partial \ln w} = \mu - \frac{\partial g}{\partial \ln w}. \quad (2)$$

Equation (2) represents the actual biomass transfer between sizes through individual growth and population change processes represented by the second term on the left side and the first term on the right side, respectively. The second term on the right side is the size-dependent growth rate, which is typically small comparing to other terms (Zhou, 2006). To solve equation (2), growth rate ($g$) and mortality rate ($\mu$) must be determined.

**Growth and mortality model development**

The growth rates of zooplankton can be modelled by body-weight and temperature-dependent empirical formulae (von Bertalanffy, 1938; Mullin, 1963; Ikeda, 1977; Kato et al., 1982; Huntley and Boyd, 1984; Hirst and Bunker, 2003). We take the notations and approach used by Hirst and Bunker (Hirst and Bunker, 2003)

$$g(w, T, C_a) = 10^{aT}w^bC_a^c10^d, \quad (3)$$

where $T$ is the temperature in °C, $C_a$ is the food concentration in mg Chl-a m$^{-3}$, and $a$, $b$, $c$ and $d$ are empirical constants. Applying $a$, $b$, $c$ and $d$ equal to 0.0186, $-0.288$, 0.417 and $-1.209$, respectively, from summarizing all available data from Hirst and Bunker (Hirst and Bunker, 2003), equation (3) provides a good statistical fit except for small zooplankton at high temperature and high food concentrations. At food concentration of 10 mg C m$^{-3}$ and high temperature of 25°C, small zooplankton at a size of $10^{-5}$ mg C (approximately 0.14 mm in length assuming a length-to-width ratio of 2.5) will have the predicted growth rate of 1.8 day$^{-1}$. This model overestimates the growth of small zooplankton similar to those of Huntley and Boyd (Huntley and Boyd, 1984) and Huntley and Lopez (Huntley and Lopez, 1992). The approach by Hirst and Bunker (Hirst and Bunker, 2003) is purely empirical, while the approach by Huntley and Boyd (Huntley and Boyd, 1984) has many valid theoretical parts. Combining both approaches, we use the theoretical definition of growth rate in Huntley and Boyd (Huntley and Boyd, 1984) and

$$g(w, T, C_a) = \left\{ \begin{array}{ll}
10^{aT}w^bC_a^c10^d, & \text{for } w > \text{critical size} \\
0, & \text{for } w \leq \text{critical size}
\end{array} \right. \quad (4)$$

where the critical size is determined by the maximum growth rate in empirical studies. The mortality rate ($\mu$) is assumed to be temperature-dependent and can be expressed by

$$\mu(T) = 0.0186T^2 - 0.288T + 0.417 \quad (5)$$

where $T$ is the temperature in °C. This formula is based on the empirical study of Hirst and Bunker (Hirst and Bunker, 2003) and is assumed to be valid for small zooplankton at high temperatures (temperature range: 15°C-25°C).
and Boyd, 1984), that is,

$$\omega_g(w, T, C_s) = \alpha C_s F(w, T),$$  \hspace{1cm} (4)

where $\alpha$ is the assimilation coefficient and $F$ is the clearance rate of a zooplankter. The respiration term will not be treated as an independent term similar to the approach taken by Huntley and Lopez (Huntley and Lopez, 1992) and Hirst and Bunker (Hirst and Bunker, 2003) simply because there is no accurate in situ method to measure both respiration and growth rates independently at the same time. The clearance rate is theoretically proportional to the product of the body cross-section area ($s$) and its swimming velocity ($w$) as

$$F(w, T) = F_0(T)s(w)u(w),$$  \hspace{1cm} (5)

where $F_0$ is a function of temperature while $s$ and $u$ are body size dependent. The body cross-section can be scaled by individual body volume, or body weight ($w$), as follows:

$$s = s_0w^{2/3},$$  \hspace{1cm} (6)

where $s_0$ is an empirical constant. The swimming velocity of marine animals is proportional to their body size, and can be empirically written as

$$u = u_0w^{0.275},$$  \hspace{1cm} (7)

where 0.275 is an empirical constant with $r^2 = 0.95$ from experimental data (Huntley and Zhou, 2004). Combining equations (5)–(7), we have the clearance rate,

$$F(w, T) = s_0u_0F_{0}\omega^{2/3}w^{0.275} = F_w(T)w^{0.94},$$  \hspace{1cm} (8)

where $F_w(T) = s_0u_0F_{0}(T)$. Then substituting equation (8) into equation (4), we have

$$g(w, T, C_s) = \alpha C_s F_w(T)w^{-0.06},$$  \hspace{1cm} (9)

To make equation (9) deduced from Huntley and Boyd (Huntley and Boyd, 1984) and Huntley and Zhou (Huntley and Zhou, 2004) similar to equation (3) used in Hirst and Bunker (Hirst and Bunker, 2003), we assume that equation (3) has to be equal to equation (9) at a reference body size of 0.01 mg C under the food saturation concentration ($C_s^{0.01\text{mg C}}$). We choose this reference body size because all the rates in Hirst and Bunker (Hirst and Bunker, 2003) are corrected to the body size of 0.01 mg C at which the error is minimized.

From equations (3) and (9), we have

$$g(10, T, C_s^{0.01\text{mg C}}) = \alpha C_s^{0.01\text{mg C}}F_w(T)0.01^{-0.06} = e^{a_T+b_T T},$$  \hspace{1cm} (10)

where $a_T$ and $b_T$ are two empirical constants equal to $-3.13$ and $0.09$, respectively, obtained by averaging the growth rates for both broadcasters and sac spawners at the body size of 0.01 mg C under food saturation in Hirst and Bunker (Hirst and Bunker, 2003). Solving the term of $\alpha F_w(T)$ from equation (10) and substituting it into (9), we have

$$g(w, T, C_s) = 0.033 \left( \frac{C_s}{C_s^*} \right)^{0.09 T}w^{-0.06},$$  \hspace{1cm} (11)

where $C_s^{0.01\text{mg C}}$ is replaced by $C_s^*$, food saturation concentration in mg C m$^{-3}$, and $w$ is in mg C.

To obtain a formula for food saturation concentration, we use the formula for clearance rates from Huntley and Boyd (Huntley and Boyd, 1984), that is,

$$F(w, T) = F_w^*(T)u^0(T),$$  \hspace{1cm} (12)

where

$$F_w^*(T) = 1.8e^{0.234T},$$  \hspace{1cm} (13)

and

$$n(T) = 0.681e^{0.0199T}.$$  \hspace{1cm} (14)

The units for clearance rate and $w$ are in mL h$^{-1}$ and dry weight used in Huntley and Boyd (Huntley and Boyd, 1984), respectively. The exponent of $n$ varies between 0.681 and 1.2 in the temperature range between 0 and 30°C, which is weakly dependent on the temperature. To simplify this formula in Huntley and Boyd (Huntley and Boyd, 1984), the term at the right side of equation (12), we simply take $n(T)$ equal to 0.94, the mean value between 0 and 30°C, which will make equation (12) consistent with equation (8), that is,

$$F_w(T)w^{0.94} = 1.8e^{0.234T}w^{0.681e^{0.0199T}} \approx 1.8e^{0.234T}w^{0.94}.$$  \hspace{1cm} (15)

Meanwhile converting the units of clearance and body weight to m$^3$ day$^{-1}$ and mg C in equation (12), respectively, we have

$$F_w(T) = 2.00 \times 10^{-4}e^{0.234T}.$$  \hspace{1cm} (16)

Using $\alpha$ of approximately 0.7 in equation (10) and

From equations (3) and (9), we have

$$g(10, T, C_s^{0.01\text{mg C}}) = \alpha C_s^{0.01\text{mg C}}F_w(T)0.01^{-0.06} = e^{a_T+b_T T},$$  \hspace{1cm} (10)

where $a_T$ and $b_T$ are two empirical constants equal to $-3.13$ and $0.09$, respectively, obtained by averaging the growth rates for both broadcasters and sac spawners at the body size of 0.01 mg C under food saturation in Hirst and Bunker (Hirst and Bunker, 2003). Solving the term of $\alpha F_w(T)$ from equation (10) and substituting it into (9), we have

$$g(w, T, C_s) = 0.033 \left( \frac{C_s}{C_s^*} \right)^{0.09 T}w^{-0.06},$$  \hspace{1cm} (11)

where $C_s^{0.01\text{mg C}}$ is replaced by $C_s^*$, food saturation concentration in mg C m$^{-3}$, and $w$ is in mg C.

To obtain a formula for food saturation concentration, we use the formula for clearance rates from Huntley and Boyd (Huntley and Boyd, 1984), that is,

$$F(w, T) = F_w^*(T)u^0(T),$$  \hspace{1cm} (12)

where

$$F_w^*(T) = 1.8e^{0.234T},$$  \hspace{1cm} (13)

and

$$n(T) = 0.681e^{0.0199T}.$$  \hspace{1cm} (14)

The units for clearance rate and $w$ are in mL h$^{-1}$ and dry weight used in Huntley and Boyd (Huntley and Boyd, 1984), respectively. The exponent of $n$ varies between 0.681 and 1.2 in the temperature range between 0 and 30°C, which is weakly dependent on the temperature. To simplify this formula in Huntley and Boyd (Huntley and Boyd, 1984), the term at the right side of equation (12), we simply take $n(T)$ equal to 0.94, the mean value between 0 and 30°C, which will make equation (12) consistent with equation (8), that is,

$$F_w(T)w^{0.94} = 1.8e^{0.234T}w^{0.681e^{0.0199T}} \approx 1.8e^{0.234T}w^{0.94}.$$  \hspace{1cm} (15)

Meanwhile converting the units of clearance and body weight to m$^3$ day$^{-1}$ and mg C in equation (12), respectively, we have

$$F_w(T) = 2.00 \times 10^{-4}e^{0.234T}.$$  \hspace{1cm} (16)

Using $\alpha$ of approximately 0.7 in equation (10) and
In equation (17), the food saturation concentration is weight-independent which is probably not correct, and should be determined as food sizes and compositions, temperature and predator size. Because of the lack of detailed data on these processes, equation (17) is only to set up the upper limit for food-dependent maximum growth in equation (11). Note that the growth rates in equation (11), Huntley and Boyd (Huntley and Boyd, 1984) and Hirst and Bunker (Hirst and Bunker, 2003) all support equation (17). Thus, we have the individual growth rate as

\[
C_a(T) = 410e^{0.125T}\text{ in mg C m}^{-3}. \tag{17}
\]

where \(C_a\) is the food saturation concentration in mg C m\(^{-3}\) as \(C_a\), we have

\[
g(w, T, C_a) = 0.033 \left(\frac{C_a}{C_a + 205e^{-0.125T}}\right)e^{0.09T}w^{-0.06} (C_a \leq C_w),
\]

\[
C_w(T) = 410e^{0.125T}
\]

(18)

where \(w\) is in mg C, \(g\) is in day\(^{-1}\), \(T\) is in °C and \(C_a\) is in mg C m\(^{-3}\). It is convenient to rewrite equation (18) in the Michaelis–Menten kinetics form by modifying the food-dependence term \((C_a/C_w)\) as \([C_a/(C_a + K_m)]\), where \(K_m\) is the half saturation concentration equal to 0.5 \(C_w\). Then we have

\[
g(w, T, C_a) = 0.033 \left(\frac{C_a}{C_a + 205e^{-0.125T}}\right)e^{0.09T}w^{-0.06}.
\]

(19)

The food concentration for zooplankton at a given size can be treated by, for example, the integrated biomass over a specified size range based on theoretical hypotheses (Benoit and Rochet, 2004; Andersen and Beyer, 2006; Maury et al., 2007; Blanchard et al., 2008; Law et al., 2009). Some studies have indicated that the selective grazing on phytoplankton species may significantly affect the ecosystem structure, while other studies have indicated that size spectra are dependent on physiological rates (Andersen and Beyer, 2006; Mitra and Flynn, 2006). However in most in situ cases, the detailed prey–predator relationships of sizes and species are unknown. Instead of giving any hypothetical prey–predator size relationships, we assume an animal can feed on all plankton smaller than its own size. This assumption can be justified because in our modelled zooplankton size range, large zooplankton such as copepods and krill feed on phytoplankton which are at the lowest zooplankton size range. This assumption can be expressed by

\[
C_a(w, t) = C_p + \int_{w_s}^w b(w, t)dw,
\]

(20)

where \(w_s\) is the smallest size of modelled zooplankton and \(C_p\) the phytoplankton biomass. The second term on the right side in equation (20) is the additional food provided by zooplankton in the size range between \(w_s\) and \(w\). Though the largest prey size can be set as a fraction of the predator’s body size, the biomass in that small fraction is negligible. Now equations (19) and (20) have formed the growth rate model linked with phytoplankton and zooplankton biomasses.

The rate of net abundance change can be generally modelled by

\[
m(w, t) = \text{birth rate} - \text{natural death} - \int_{w_s}^w r_m(w, w', t)b(w', t)dw',
\]

(21)

where \(r_m(w, w', t)\) is the per capita predation rate on class \(w\) by some other class \(w'\) (Zhou and Huntley, 1997). In past studies, a feeding kernel is applied for a given size relationship, and the grazing loss due to this feeding kernel leads to the predation mortality rate (Benoit and Rochet, 2004; Maury et al., 2007; Law et al., 2009). The advantage of such an approach is to have a closed loop between prey and predation using the feeding kernel. Because the ecosystem is an open system with fluxes of biomass into the system through primary production and out of the system by respiration and removal (or burial), in such a mechanistic approach, the loop between prey and predators cannot be closed without knowing assimilation efficiencies, in situ size relationship between prey and predators and size-dependent removal. The uncertainties associated with these prey–predator relationships lead to high uncertainties in model results. To avoid these unknown stochastic prey and predator relationships, we will use both theoretical approaches and observations to simplify equation (21).

Integrating equation (2) over a period of \(T\), and then taking the average, we have

\[
\frac{1}{T}\int_{t}^{t+T} \frac{1}{g} \frac{\partial \ln b}{\partial t} dt + \frac{1}{T}\int_{t}^{t+T} \frac{\partial \ln b}{\partial \ln w} dt = \frac{1}{T}\int_{t}^{t+T} \left(\frac{\partial \ln \mu}{\partial g}\right) dt - \frac{1}{T}\int_{t}^{t+T} \left(\frac{\partial \ln g}{\partial \ln w}\right) dt.
\]

(22)

In equation (22), \(b\) can vary about 10–20 times from lower to higher in a season that leads to the scale of
\[ \ln[b(t + T)/b(t)] \approx 2.3 - 3 \ (Zhou \text{ et al.}, \ 2004, \ 2009). \]

Considering \( g^{-1} \) on the order of 10 days and \( T \) on the seasonal scale of 100 days, the first term on the left side is on the order of \( 10^{-1} \). Because the slope of a biomass spectrum is on the order of \( 10^3 \), the second term is on the order of \( 10^0 \). On the right, because the mortality rate is on the same order of growth rate, the first term is on the order of \( 10^0 \). The last term is the weight-dependent growth. Taking the natural logarithms of equation (19), and the derivative relative to \( \ln w \), we have this term equal to \(-0.058\) on the order of less than \( 10^{-1} \). Ignoring these two high-order terms, we have

\[ \frac{1}{T} \int_1^{t+T} \frac{\partial \ln b}{\partial \ln w} \, dt = \frac{1}{T} \int_1^{t+T} \left( \frac{\mu}{g} \right) \, dt. \tag{23} \]

Taking the mean growth and mortality rates in equation (23) within a period of \( T \), we have

\[ \mu(w, t) = g S, \tag{24} \]

where \( S \) is the mean slope of biomass spectra within the period of \( T \), given by

\[ S = \frac{1}{T} \int_1^{t+T} \frac{\partial \ln b}{\partial \ln w} \, dt. \tag{25} \]

The advantage of using equation (24) for mortality estimates is not only its simplicity, but also that the \textit{in situ} slope of biomass spectra in a plankton community can be easily observed. Slopes observed in many parts of the ocean and lakes are linear varying around \(-1\), which implies the dominance of mortality in the mean specific rate of net abundance change (Sheldon \textit{et al.}, 1972; Rodríguez and Mullin, 1986; Sprules and Munawar, 1986; Sprules \textit{et al.}, 1988; Heath, 1995; Huntley \textit{et al.}, 1995; Tittel \textit{et al.}, 1998; Quinones \textit{et al.}, 2003; San Martin \textit{et al.}, 2006; Zhou \textit{et al.}, 2009).

**Numerical zooplankton model setup**

Considering a zooplankton community within a size range between the smallest size \( w_S \) and the largest size \( w_L \), to solve equation (2) requires a boundary condition at \( w_S \) and no boundary condition at \( w_L \) because equation (2) is a wave equation (Marchuk, 1975). To avoid any complications in phytoplankton and higher trophic level models during testing the zooplankton model, the boundary condition will be specified based on observations. We choose 60 \( \mu m \) in equivalent spherical diameter (ESD) as the smallest size which is close to the average size of copepod eggs and the upper limit of phytoplankton sizes. The largest size can be chosen arbitrarily because there is no boundary condition required. We choose 10 mm as the upper limit to cover large zooplankton. From the observations, the size spectra from bacteria, phytoplankton and zooplankton are continuous (Sheldon \textit{et al.}, 1972; Rodríguez and Mullin, 1986; Sprules and Munawar, 1986; Tittel \textit{et al.}, 1998; Quinones \textit{et al.}, 2003). Taking this fact, we use the observed chlorophyll as the boundary condition, which will also make the integration easy with phytoplankton models in the future. In order to use carbon units, we assume the conversion ratio of chlorophyll to carbon equal to 50, and the ratio of biovolume to zooplankton carbon equal to 0.03 mg C mm\(^{-3}\) (Estrada, 1996). We have the boundary condition as:

\[ b(w_S, t) = \frac{50 \text{ (mg C/mg Chl) } \times \text{ observed chlorophyll (mg m}^{-3}\text{) } \times 3.4 \times 10^{-6} \text{ (mg C) }}{b(w_L, t)}, \tag{26} \]

where \( w_S \) defined as the lowest zooplankton size modelled is equal to \( 3.4 \times 10^{-6} \text{ mg C equivalent to 60 } \mu m \) in ESD. The zooplankton closure model consists of equations (2), (19), (20), (24) and (26) in the size range between 60 \( \mu m \) \( (3.4 \times 10^{-6} \text{ mg C}) \) and 10 mm \( (15.7 \text{ mg C}) \) representing the governing equation, growth rate, food concentration, net abundance change rate and boundary condition, respectively.

An upwind finite difference scheme is employed for solving equation (2), as follows:

\[ \ln(b_{i+1}) = \ln(b_i) + \Delta t \left\{ \mu_{i,S} - \frac{g_{i,S} - g_{i-1,S}}{\Delta \ln(w)} \ln(b_{i}) - \ln(b_{i-1}) \right\}, \tag{27} \]

where the subscript \((i, n)\) represents \((w_i, \ t_n)\), \( w_i = w_S \ e^{i \Delta \ln(w)} \), \( t_n = n \Delta t \ (i = 1, 2, \ldots, 50; \ n = 0, 1, 2, \ldots) \), and \( \Delta \ln(w) \) is the size interval equal to 0.31 by taking 50 size intervals between \( \ln(w_S) \) and \( \ln(w_L) \). The stability of an upwind scheme associated with the growth term is determined by the Courant–Friedrich–Lewy (CFL) condition (Marchuk, 1975), i.e. the time step \( \Delta t \) must be satisfied with

\[ \Delta t \leq \frac{\Delta \ln(w)}{g_{max}}. \tag{28} \]

where \( g_{max} \) is the maximum growth rate expected. The damping term of \( \mu \) is unconditionally stable. The differential growth term is negligible in equation (2).
If zooplankton growth rates are less than 1 day\(^{-1}\), the time step of 0.3 day should be taken for the stability of the upwind finite difference scheme.

### Biomass budget and fluxes

To understand the biomass fluxes between size classes of a plankton community, we integrate equation (1) from \(w_S\) to \(w_L\),

\[
\frac{d}{dt} \int_{w_S}^{w_L} \mu dw + \int_{w_S}^{w_L} \mu dw, = \int_{w_S}^{w_L} \mu dw + \int_{w_S}^{w_L} \mu dw. \tag{29}
\]

In this equation, the first term on the left side is the rate of change in total biomass within the size range between \(w_S\) and \(w_L\) and the second and third terms are the biomass flux terms in and out of the size range. On the right side, the first term is the mortality primarily due to predation and the second term is the individual body growth through grazing. At a steady state, if all the mortality is balanced by the body growth through grazing, we have the right side of equation (29) equal to zero, and \(\mu dw\) at \(w_S\) equal to \(\mu dw\) at \(w_L\) that means the biomass propagates through the size spectrum without any loss. When the mortality is not balanced by the body growth through grazing, the difference between these two terms is the net removal of plankton to dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and particulate organic carbon (POC) pools due to respiration, grazing loss and excretion.

Zooplankton grazing (FG) with an assimilation efficiency (\(\alpha\)) is equal to

\[
FG(t) = \int_{w_S}^{w_L} \frac{1}{\alpha} g(w, T, C_p) dw. \tag{30}
\]

Meanwhile the grazing on phytoplankton (FP) is equal to

\[
FP(t) = \int_{w_S}^{w_L} \frac{1}{\alpha} g(w, T, C_p) dw. \tag{31}
\]

The grazing on zooplankton (FZ) in addition to phytoplankton is the difference between equations (30) and (31), that is,

\[
FZ(t) = \int_{w_S}^{w_L} \frac{1}{\alpha} \left[ g(w, T, C_p) - g(w, T, C_p) \right] dw. \tag{32}
\]

The biomass grazed by predators remains in the community, and predators can become the prey of others. Thus, mortality biomass can be recycled within different trophic levels without leaving the community. We note this as

\[
FZ(t) = R_z \int_{w_S}^{w_L} S_g(w, T, C_p) b dw, \tag{33}
\]

where \(R_z\) is the biomass-recycle index representing the percentage of zooplankton biomass due to carnivorous grazing. The recycling of zooplankton biomass in the system is critical to retain the biomass balance, especially in oligotrophic regions where phytoplankton biomass will not support zooplankton grazing alone. When the value of \(R_z\) is greater than 100\%, it means that the zooplankton biomass grazed is recycled more than once. If the food required for zooplankton growth (FG) is balanced by grazing on the phytoplankton biomass (FP) and on zooplankton (FZ), we combine equations (32) and (33) as follows:

\[
\int_{w_S}^{w_L} \frac{1}{\alpha} g(w, T, C_p) dw - \int_{w_S}^{w_L} \frac{1}{\alpha} g(w, T, C_p) dw = R_z \int_{w_S}^{w_L} S_g(w, T, C_p) b dw, \tag{34}
\]

where we have ignored the fluxes of small zooplankton growing into and out of the size range between \(w_S\) and \(w_L\) which are small and will be discussed in the next sections. We can solve for the biomass-recycle index \(R_z\) after rearranging equation (34) as follows:

\[
R_z(t) = \frac{1}{\alpha S} \left( \int_{w_S}^{w_L} S_g(w, T, C_p) b dw \right) - 1. \tag{35}
\]

Comparing with the recycle estimate in Zhou (Zhou, 2006), equation (35) is a modified estimate by dropping the flux into the smallest size class, and including the grazing on phytoplankton. Taking the difference between total mortality loss and predation mortality for growth (FZ), we have the export of zooplankton as the zooplankton removal rate (ZEx),

\[
ZEx(t) = -S(1 - R_z) \int_{w_S}^{w_L} g(w, T, C_p) b dw. \tag{36}
\]

The positive value of ZEx represents the net export of zooplankton biomass removed from their pool and a negative value represents zooplankton biomass recycling.
Field data

The SOFCOM Station is located at 43°14'30"N and 5°17'30"E along the 60 m isobath, a long-term monitoring station in the Golfe du Lion, northwestern Mediterranean Sea, operated by the Centre Océanologique de Marseille (Fig. 1). The monitoring program started from 5 January 1999 with a biweekly sampling program for standard variables of the Joint Global Ocean Flux Study (JGOFS), including water column temperature, salinity, chlorophyll and POC. Since 1 January 2004, a zooplankton sampling program has been added by taking vertical net tows.

A Seabird 911plus CTD (SeaBird Electronics, Inc., Bellevue, WA, USA) has been used for temperature, salinity and depth measurements. Niskin bottles were used for collecting water samples at 5 m, chlorophyll maximum and 55 m for chlorophyll and POC analyses. If the chlorophyll maximum was not present, water samples were taken at 30 m. A volume of 250 mL was filtered using a GF/F filter. Particles concentrated on the filter were extracted in methanol and the fluorescence concentrations were measured based on the method in Raimbault et al. (Raimbault et al., 1988). For POC, samples were filtered through pre-combusted glass fiber filters (Whatman GF/F, 25 μm), dried and measured based on Raimbault et al. (Raimbault et al., 1999).

Zooplankton were collected using a 0.25 m² ring net with a 200 μm mesh. Zooplankton samples were preserved in buffered seawater-formalin (4%), and then analyzed in the laboratory using a laboratory Optical Plankton Counter (OPC, Focal Technologies, Dartmouth, NS, Canada). Because a vertical net tow naturally integrates zooplankton samples in the water column, we averaged chlorophyll and POC measurements in the upper 55 m. The laboratory OPC was set similar to that described in Beaulieu et al. (Beaulieu et al., 1999), and has been used in previous studies (Riandey et al., 2005; Sourisseau and Carlotti, 2006). Organisms were gently introduced into the water circulation system. To avoid coincidence, we imposed a maximum count rate at 20 particles min⁻¹ and a constant flow rate at 18 L min⁻¹. The size spectrum of a tow was obtained by counting at least 1000 particles.

The digital sizes of OPC measurements were converted to ESD sizes based on the standard formula provided by the manufacturer. The ESD within 0.287 and 10 mm ESD was converted to biovolume as a sphere. Assuming the ratio of wet weight to volume equal to 1 mg mm⁻³ and the ratio of wet weight to carbon equal to 0.03 (Fryd et al., 1991), zooplankton measurements were further converted to carbon unit in mg C. The OPC measurements were binned into 50 equal Δlog₁₀(w) size intervals between 3.7 × 10⁻¹ μg C (0.287 mm) and 15.7 mg C (10 mm).

RESULTS

Growth rate

The growth rates at 0°C for zooplankton size with a body size of 0.1 mg C, at 15°C for zooplankton size of 0.01 mg C and at 30°C for zooplankton size of 10⁻⁵ mg C are predicted by equation (19) in Fig. 2, and superimposed with the observed growth rates of marine copepods synthesized at the global scale and the predicted growth rates for broadcasting and sac-spawning copepods based on Hirst and Bunker (Hirst and Bunker, 2003). The predictions by equation (19) agree well with the predictions of Hirst and Bunker (Hirst and Bunker, 2003) at 15°C. At the low temperature, the estimates from equation (19) are higher than those of Hirst and Bunker (Hirst and Bunker, 2003), whereas at the high temperature the estimates from equation (19) are lower than those of Hirst and Bunker (Hirst and Bunker, 2003). Though all growth rate models converge at Cₒ equal to zero, the largest differences in both models and observations are at low Cₒ. At high food concentrations, observed values show the food saturation, and estimates from equation (19) provide a better upper limit of growth rates than those of Hirst and Bunker (Hirst and Bunker, 2003) for both broadcasters and sac spawners. The predictions of equation (19) vary within a narrower range and provide a closer envelop over observed data than that of Hirst and Bunker (Hirst and Bunker, 2003). The highest growth rate predicted by equation (19) is 0.97 day⁻¹ while the prediction from
Hirst and Bunker (Hirst and Bunker, 2003) is \( \approx 3 \text{ day}^{-1} \) in Fig. 2.

**Time series of temperature, chlorophyll, POC and zooplankton size spectra**

The time series of observed surface temperature, and depth-mean phytoplankton and POC within the water column at the SOFCOM Station between January 1999 and 2007 are shown in Fig. 3. The temperature reached the highest and lowest values in July–August and January–February, respectively. Upwelling events can be seen from sharp temperature drops in spring and summer seasons. The spring blooms of phytoplankton occurred in February and March. After a spring bloom phytoplankton concentrations generally declined, though small short blooms occurred associated with upwelling events indicated by surface temperature fluctuations. The fall blooms were small compared to the spring blooms. The peaks of phytoplankton concentration reached 50–150 mg C m\(^{-3}\), but the mean was only 16 mg C m\(^{-3}\). POC concentrations varied correspondingly to the phytoplankton seasonal variations with different magnitude which may imply different timings and growth of organisms at different trophic levels. The standing stock of POC was approximately one order of magnitude higher than that of phytoplankton.

Zooplankton abundances within a size range between 0.287 and 10 mm ESD varied from 300 to 7000 individuals m\(^{-3}\) with biomass between 1 and 30 mg C m\(^{-3}\) in the period from January 2002 to January 2004 (Fig. 4A and B). There were only very few counts of zooplankton larger than 1 mm ESD, which might be caused by avoidance due to the small opening of the ring net (0.25 m\(^2\)) (Fig. 5A). Both the abundance and biomass peaked in both March–April and September–October after the spring and fall blooms, implying responses of zooplankton to food availability and their longer growth time scales compared to that of phytoplankton. The biomass spectra of zooplankton were nearly linear. The slopes of biomass spectra from linear regressions have a mean and standard deviation equal to \(-0.95\) and \(0.16\) (Fig. 4C; Table I), respectively.

**Modelled zooplankton growth, mortality and size spectra**

The modelled size-dependent growth rates are shown in Fig. 6A and Table I. They vary from the lowest at
0.01 day\(^{-1}\) in winter to the highest at 0.58 day\(^{-1}\) in late summer and fall. The highest peaks occur in August and September when fall blooms occur at high temperature. After their peaks, the growth rates decline sharply due to food limitation. Population mortality loss is represented by the first term \((\mu b)\) on the right side in equation (1) shown in Fig. 6B with the unit of \((\text{mg C m}^{-3}\text{day}^{-1})\), or simply \((\text{m}^{-2}\text{day}^{-1})\). Higher mortality losses are expected for smaller zooplankton while lower mortality losses are expected for larger zooplankton.

The seasonal variations of modelled size spectra in the period between January 1999 and January 2007 are driven by spring and fall blooms and temperature (Fig. 7). Biomass propagates from small to large zooplankton through growth while the value decreases due to mortality. A close comparison between modelled and observed biomass spectra between January 2002 and January 2004 is shown in Fig. 5. The modelled biomass spectra have very similar seasonal variations responding to phytoplankton blooms and temperature as the observed ones. The magnitudes of modelled zooplankton are approximately 10 times higher than those observed. The differences between modelled and observed biomass spectra can be caused by model approximations, sampling errors due to zooplankton

**Table 1: Rate estimates in the model**

<table>
<thead>
<tr>
<th>Rate</th>
<th>Mean ± STD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean zooplankton growth rate</td>
<td>0.15 ± 0.07 day(^{-1})</td>
</tr>
<tr>
<td>Mean zooplankton mortality rate</td>
<td>-0.14 ± 0.07 day(^{-1})</td>
</tr>
<tr>
<td>Mean slope of biomass spectra</td>
<td>-0.95 ± 0.16</td>
</tr>
<tr>
<td>Biomass recycle of mortality biomass</td>
<td>88 ± 30%</td>
</tr>
</tbody>
</table>
extrusion and avoidance and decoupling due to physical advection and mixing processes which will be addressed in the discussion section.

**Time series of modelled zooplankton biomass**

To compare with observed variables, the modelled biomass spectra are integrated into a small size range between 60 and 100 μm close to the biomass of phytoplankton, total zooplankton biomass between 60 μm and 10 mm compared to POC measurements, and zooplankton biomass between 287 μm and 1.5 mm compared to OPC analysis (Fig. 8). The size classes are clearly driven by phytoplankton biomass while the total zooplankton biomass responds to phytoplankton biomass variations, but both amplitudes and timings are modified due to grazing and development time. The comparison between total zooplankton biomass and POC shows similar seasonal and annual variations. Because POC measurements were made from water samples of 250 mL in which mesozooplankton were certainly under-sampled, the comparison between total zooplankton biomass and POC will be relative. The temporal variations of predicted zooplankton biomass are compatible with those of observed biomass estimates from net tow samples though the predictions are approximately 10 times higher than the observed ones similar to the biomass spectrum predictions (Figs 5 and 8C).

**Biomass flux estimates**

The biomass flux estimates from grazing and growth processes are shown in Fig. 9 and Table II. The grazing on zooplankton is often greater than the grazing on phytoplankton. In our modelled size range, the zooplankton biomass balance is between the growth into and out of the size range \([w_S, w_L]\), growth by grazing and loss due to mortality [equation (2)]. Within these biomass flux terms, the fluxes due to growth into and out of the size range \([w_S, w_L]\) are 10–100 times less than growth and mortality; this means that both growth and mortality are primarily contributed by carnivorous grazing (Fig. 9A and B). In the case that carnivorous small grazers are grazed by large grazers, the zooplankton biomass will be grazed (or recycled) more than once, i.e. \(R_c > 1\). The biomass-recycle index in Fig. 9C shows that the recycling of biomass mortality fluxes in winter and summer is more than 100% \((R_c > 1)\) while in the spring and fall bloom periods less than 100% zooplankton mortality fluxes are recycled \((R_c < 1)\) that leads to rate of zooplankton biomass. The positive net zooplankton biomass removal (or export burial) flux estimates are shown in Fig. 9B (a negative value means recycling). The removal occurs during phytoplankton bloom periods when the demands to recycle zooplankton biomass are less; and the recycling is highest in post-bloom periods.

**DISCUSSION**

**Stability of the zooplankton model**

Size-based model approaches have demonstrated the advantages in estimating biomass fluxes between size classes for understanding basic biomass balance and functioning of an ecosystem (Moloney and Field, 1991;
Han and Straskraba, 1998; Gin et al., 1999; Armstrong, 1999; Baird and Suthers, 2007). A mechanistic approach can be taken by specifying links between sizes as the prey–predator relationships. However in a size-based model, theoretical studies show the sensitivity of prey-size selection and instabilities associated with the selections (Edwards and Yool, 2000; Benoît and Rochet, 2004; Andersen and Beyer, 2006; Maury et al., 2007; Blanchard et al., 2008; Law et al., 2009). The first question for this zooplankton closure model is its stability if an introduced error decreases as a function of time.

The zooplankton closure model consisting of equations (2), (19) and (24) has the characteristic of a wave equation within which the mortality term damps oscillations. Instabilities of this closure model can be introduced from both rates [equations (19) and (24)] and numerical methods used to solve the partial differential equation [equation (2)]. For the upwind scheme [equation (27)], the limitation on the time step is determined by the CFL condition [equation (28)], which is inversely proportional to the growth rate. Thus, it is important to have an estimate of maximum growth based on the highest temperature and saturation food concentration for determining the CFL condition so that any potential numerical method instability can be eliminated.

The general characteristics of equation (2) can then be analyzed assuming both \( g \) and \( m \) are size-independent (Zhou, 2006). The general solution of equation (2) is equal to a general solution for the homogeneous equation plus a special solution of equation (2), that is,

\[
\ln(b) = f[\ln(w) - g] + \mu t, \tag{37}
\]

where \( f \) is an arbitrary function. Because \( f \) is arbitrary, we can rearrange equation (37) as

\[
b(w, t) = F[\ln(w) - g]e^{\mu t}, \tag{38}
\]

where \( F \) is equal to the initial biomass spectrum \( b_0 \) at \( t = 0 \), given by

\[
b_0(w) = F[\ln(w)]. \tag{39}
\]

Combining equations (38) and (39), the solution of equation (2) can be written as

\[
b(w, t) = b_0(w)e^{-gt}e^{\mu t}. \tag{40}
\]

The first term of the product on the right side of equation (40) represents the propagation of biomass from growth of body weight, and the second term

<table>
<thead>
<tr>
<th>Flux</th>
<th>Mean ± STD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total food demand for zooplankton grazing (FG)</td>
<td>78 ± 81 mg C m(^{-3}) day(^{-1})</td>
</tr>
<tr>
<td>Grazing on phytoplankton (FP)</td>
<td>40 ± 56 mg C m(^{-3}) day(^{-1})</td>
</tr>
<tr>
<td>Grazing on zooplankton (FZ)</td>
<td>38 ± 33 mg C m(^{-3}) day(^{-1})</td>
</tr>
<tr>
<td>Zooplankton mortality</td>
<td>51 ± 54 mg C m(^{-3}) day(^{-1})</td>
</tr>
<tr>
<td>Zooplankton removal rate (ZEx)</td>
<td>13 ± 31 mg C m(^{-3}) day(^{-1})</td>
</tr>
</tbody>
</table>

Fig. 9. (A) Modelled zooplankton grazing on phytoplankton biomass (FP in blue) mg C m\(^{-3}\) day\(^{-1}\), zooplankton grazing on zooplankton (FZ in black) in mg C m\(^{-3}\) day\(^{-1}\) and zooplankton total grazing (FG in red) in mg C m\(^{-3}\) day\(^{-1}\); (B) modelled zooplankton influx (IF in blue) and outflux (OF in red) in mg C m\(^{-3}\) day\(^{-1}\) growing into and out of the size range \([w_1, w_2]\), respectively, and zooplankton removal rate (ZEx in black) in mg C m\(^{-3}\) day\(^{-1}\) of which negative values are removed; and (C) the biomass-recycle index \(\mathcal{R}_c\).
represents the damping due to mortality. Any error \( \varepsilon(t, \ t_0) \) introduced at \( t_0 \) will propagate along the weight axis as \( \ln(w) - gt \) and diminish exponentially, that is,

\[ \varepsilon(t, t_0) \sim e^{\mu(t-t_0)}. \]  

The characteristics of equation (2) should be the same as equation (40) when \( g \) and \( \mu \) are size-dependent.

**Semi-theoretical and semi-empirical approaches to growth and mortality rates**

Growth and grazing mortality dominate the biomass flux in equation (2). There are neither any accurate theories nor enough empirical estimates to predict these rates. The approaches taken by Huntley and Lopez (Huntley and Lopez, 1992) and Hirst and Bunker (Hirst and Bunker, 2003) are purely empirical similar to many other studies (Roman et al., 2000, 2002; Richardson et al., 2001; Peterson et al., 2002; Ikeda and Motoda, 1978; Calbet et al., 2002). Their statistical regression models are valid and work well in the ranges their data collected, while predictions of these models become erroneous outside of their data ranges. As indicated by Hirst and Bunker (Hirst and Bunker, 2003), the Hirst–Lampitt and Huntley–Lopez models overestimate growth rates for oligotrophic areas, which is primarily the result of their bias toward data from food-rich areas and periods. The Huntley and Boyd model including food is only applicable over a very restricted body weight range due to available data. Because a regression model will be always biased by the distribution of data, our theoretical approach provides an upper limit based on an animal size and its capability of locomotion. In most cases, equation (19) provides similar estimates of zooplankton growth to those of Huntley and Boyd (Huntley and Boyd, 1984; Huntley and Lopez, 1992) and Hirst and Bunker (Hirst and Bunker, 2003) in the range of most empirical data; it also avoids overestimating growth rates in the range with few empirical data (Fig. 2).

Equation (19) is developed by taking the strengths from different model approaches (Huntley and Boyd, 1984; Hirst and Bunker, 2003). It uses the temperature-dependence relationship from Hirst and Bunker (Hirst and Bunker, 2003) which is obtained over a broader temperature range expecting to have a better regression relationship than that of other studies. The food dependence of equation (19) is linearly proportional to \( C_m \) similar to that of Huntley and Boyd (Huntley and Boyd, 1984). We keep this linear relationship till reaching saturation concentration. To measure clearance rates of zooplankton is not a trivial task (Frost, 1972). The empirical approach by Huntley and Boyd (Huntley and Boyd, 1984) can also be biased by data distributions and errors. The theoretical approach based on equation (5) simply adds a limitation to the regression based on the physical capability of a zooplankter. This physical capability, that is the capability of locomotion, can be measured more accurately compared to indirect measurements of filtration rates (Strickler, 1975; Huntley and Zhou, 2004). Thus, equation (19) is the product of maximum growth determined by temperature-dependent physiology, clearance capability limited by physical dimensions and food availability.

The growth rates estimated from the model based on both equation (3) (Hirst and Bunker, 2003) and the model based on equations (19) and (20) are shown in Fig. 10 using the observed temperature and Chl-a and modelled biomass spectra during the modelling period. The differences between these two models are significant within all low, intermediate and high values. Especially, the maximum growth estimated by equation (19) is approximately 0.58 day\(^{-1}\) while the maximum growth estimated by equation (3) is approximately 0.85 day\(^{-1}\). For the modelling period, the mean and standard deviation of growth rates based on equation (19) are 0.15 and 0.07 day\(^{-1}\), respectively, while the mean and standard deviation of growth rates based on equation (3) are 0.13 and 0.13 day\(^{-1}\), respectively. It is obvious that if we did not have a good estimate of zooplankton growth rates and their assimilation efficiencies, we would not have good estimates of biomass fluxes to...
higher trophic levels through growth. Thus, we cannot overemphasize the importance of accurate regional and global growth models similar to those developed by Huntley and Boyd (Huntley and Boyd, 1984) and Hirst and Bunker (Hirst and Bunker, 2003).

Mortality rate estimates are even rarer than the growth rate estimates because of the difficulties to sample a cohort over a certain period. The mortality estimates inferred from egg fecundity, development time and adult sex ratios of copepods, deduced from horizontal or vertical life tables, and inversely solved from repeated observations elucidate the efforts, variability and difficulties in mortality rate estimates (Huntley et al., 1994; Ohman et al., 1996; Ohman and Wood, 1996; Hirst and Kiørboe, 2002; Edvardsen et al., 2002). The mortality estimates from equation (24) provide an approximation for seasonal mean mortality based on the slope of measured biomass spectra (Zhou and Huntley, 1997; Zhou, 2006). The slope of our measured biomass spectra has the mean and standard deviation equal to 0.016 and 0.015 m$^3$ day$^{-1}$, respectively, which is very close to the mortality of $-0.19$ day$^{-1}$ at 25°C predicted for copepods in Hirst and Kiørboe (Hirst and Kiørboe, 2002). If equation (24) truly represents the seasonal mortality, it will be a significant achievement in zooplankton modelling providing a practical solution for much needed mortality estimates, and in turn fluxes between trophic levels.

Flux from phytoplankton to zooplankton

The phytoplankton biomass flux into zooplankton depends on the clearance rate of zooplankton. The modelled clearance rates vary between 0.003 and 0.146 m$^3$ day$^{-1}$ individual$^{-1}$ with a mean and standard deviation equal to 0.016 and 0.015 m$^3$ day$^{-1}$ individual$^{-1}$, which are closely comparable with the values in the literature [see the summary in Huntley and Boyd (1984)]. Using the estimated clearance rates, the mean daily grazing rate on phytoplankton is $\sim 40$ mg C m$^{-3}$ day$^{-1}$ meaning that 250% of the mean phytoplankton standing stack in the water column is grazed in a day at the SOFCOM Station in the GOL (Fig. 9; Table II). The phytoplankton concentration has to be maintained by primary production, or will decline. The in situ primary production measurements were between 166 and 401 mg C m$^{-2}$ day$^{-1}$ within the upper 100 m in the GOL (Gaudy et al., 2003). The depth-integration of zooplankton grazing is certainly higher than the measured primary production. It can be argued that not all zooplankton graze on phytoplankton, and our modelled grazing rates may overestimate the grazing on phytoplankton. Compared to the total food demand by zooplankton growth, total phytoplankton contribute only 51% (Table II). The remaining 49% will be contributed by zooplankton which is integrated into the food term ($C_0$) [equation (20)]. On the size spectrum, the zooplankton portion of food increases as the size of grazers increases, which indicates an increase in omnivorous and carnivorous feeding. The phytoplankton concentrations in the GOL were very low which limits higher trophic level organisms (Morel and André, 1991; Estrada, 1996).

Zooplankton mortality and internal biomass recycling

As phytoplankton contribute only 51% of the food required for zooplankton growth in the model results, grazing on zooplankton contributes 49% of the food required through predation. To meet this demand, 88% of mortality loss on average has to be recycled back to zooplankton (Fig. 9; Table II), which is similar to the estimate by Hirst and Kiørboe (Hirst and Kiørboe, 2002). The zooplankton biomass-recycle is higher prior to a phytoplankton bloom when zooplankton growth is limited by low phytoplankton. During a phytoplankton bloom, zooplankton growth will not be limited by food and zooplankton biomass increases. After a bloom, the phytoplankton biomass cannot provide the food required for the increased zooplankton biomass during the phytoplankton bloom, and zooplankton biomass recycling increases as the biomass declines. These processes represent the evolution of a zooplankton community from a herbivorous zooplankton-dominated community during a phytoplankton bloom to an omnivorous–carnivorous-dominated community in post-bloom periods. The maximum of biomass-recycle is 1.4 times indicating that the predators will be grazed by other higher level predators.

Comparing modelled and observed biomass spectra

Comparing modelled and observed biomass spectra in different size groups, the biomass predictions of small zooplankton between 60 and 100 μm in ESD are nearly in phase with observed chlorophyll because small zooplankton feed on phytoplankton directly (Fig. 8). Zooplankton biomass propagates from 0.06 to 0.1 mm ESD in 3 days taking the mean growth rate of small zooplankton 0.15 day$^{-1}$ (Table I). It will take more than 21 days for zooplankton biomass to propagate from...
0.06 to 1.5 mm ESD. The biomass in large-sized zooplankton can be out of phase with chlorophyll concentration because of this time lag.

Modelled mesozooplankton biomass values are approximately 10 times higher than the observed ones though both of them had similar seasonal variations (Figs 5 and 8). The model predictions of mesozooplankton biomass are also higher than the values in the literature in which similar net sampling methods were used (Gaudy et al., 2003). It has been long known that biomass and abundance estimates from net tow samples are typically 1–10 times less than other optical and acoustic measurements caused by extrusion or avoidance (Herman, 1992; Edvardsen et al., 2002; Lawson et al., 2008). Another potential error in the model forcing parameters is that we use the averaged phytoplankton concentrations in the water column to force the zooplankton closure model without considering zooplankton diel behavior and advection of phytoplankton and zooplankton. These processes can be included when the model is set to resolve the horizontal and vertical structure of zooplankton coupled with hydrodynamic and phytoplankton models.

These zooplankton abundance and biomass estimates at the SOFCOM Station should be treated as instantaneous measurements containing large spatial and temporal variability so that observed biomass spectra are more scattered than the modelled ones (Fig. 5). The scatter plots of paired biomass spectrum values from the observed and modelled are shown in Fig. 11. The regression between observed and modelled biomass spectra has a slope of 0.92, intercept of 1.22 and $R$ of 0.69. This slope and $R$ value implies that the modelled zooplankton biomass simulates the seasonal variations of both biomass and biomass spectra well. The intercept represents that the model estimates are on average 10 times more than that of observed zooplankton, implying potential errors in both observations and models. An effort has been made for improving the quality of zooplankton observations at the SOFCOM Station recently by deploying an in situ Laser Optical Plankton Counter (LOPC, Brooke Ocean Technologies, Dartmouth, NS, Can; Herman et al., 2004), and a ZOOSCAN (Grosjean et al., 2004) for analyzing live samples.

Zooplankton biomass removal
Zooplankton contribute significant carbon export in the ocean, and recent studies indicate that zooplankton respiration contributes $13.0 \pm 4.2$ Gt C annually, approximately 17–32% of global primary production in the global ocean (Hernanadez-Leon and Ikeda, 2005; Buitenhuis et al., 2006). It is assumed that 4.9% of body weight expires per day or a burial rate of 0.049 day$^{-1}$. In the model results, the mean mortality is 0.14 day$^{-1}$ of which 88% is recycled. The zooplankton biomass removal from equation (36) will be approximately 0.019 day$^{-1}$, which is lower than the respiration estimate in Hernanadez-Leon and Ikeda (Hernanadez-Leon and Ikeda, 2005). Considering the Mediterranean Sea as an oligotrophic ocean, our estimate should be less than the global mean.

The zooplankton removal exhibits pulse exports related to phytoplankton blooms instead of a constant fraction of zooplankton biomass (Fig. 9). Prior or after a phytoplankton bloom, the zooplankton biomass associated with mortality will be recycled back to zooplankton more than once through omnivorous and carnivorous grazing to meet zooplankton growth needs, and the net removal rate is zero. During a bloom period, small zooplankton increase first responding to increased phytoplankton that leads to a surplus of small zooplankton and increased removal rate before large zooplankton respond to the increased small zooplankton. As large zooplankton increase and graze down the surplus of small zooplankton, the removal rate decreases. Thus, we can expect a smaller removal rate in a stable physical and biological environment where large organisms can fully utilize small zooplankton and a higher removal rate in areas where phytoplankton blooms occur frequently.

Conclusion
The equation (19) provides a simple growth formula for applications similar to those provided by Huntley and
Boyd (Huntley and Boyd, 1984) and Hirst and Bunker (Hirst and Bunker, 2003). Because all empirical fitting is subjective, and very few data points cover broad ranges of body sizes, temperature, diet differences and behavior, the validation of equation (19) is questionable. However these weaknesses are the same for all species-stage or functional-based approaches, which is not unique only to size-based growth models. These weaknesses emphasize the need for more efficient and accurate methods to make more growth rate measurements.

The key approach in our model development is to use the slope of biomass spectra to approximate mortality without exploring detailed size relationships between prey and predators [equation (24)]. If the slope of a biomass spectrum is the end result of prey–predator size relationships and assimilation efficiencies, the product of the slope and growth rate should be a valid approach representing the predation mortality due to growth need and removal (Zhou, 2006). The relationships between slopes of biomass spectra and prey–predator size relationships have been explored in Benoît and Rochet (Benoît and Rochet, 2004; Maury et al. (Maury et al., 2007); Blanchard et al. (Blanchard et al., 2008) and Law et al. (Law et al., 2009). At the SOFCOM Station, the slope is nearly constant in all seasons (−0.95 ± 0.16) which means the use of the mean slope for mortality estimates may contain a relative error of ±17%. In the field, the slope of a biomass spectrum is easily measured while prey–predator size relationships are difficult to explore. Equation (24) can be used either directly to estimate mortality rates, or indirectly to guide development of prey–predator size relationships.

Equation (2) provides a core of a zooplankton closure model representing biomass flux conservation while equations (19) and (24) provide two model closure terms for zooplankton growth and mortality rates in a size range which can be defined arbitrarily. If these rates are known, a set of biomass flux terms defined in equations (30)–(33) and (35)–(36) can be solved including zooplankton carbon removal. This model can be applied between size-based lower trophic level and higher trophic level models (Mooney and Field, 1991; Chisholm, 1992; Armstrong, 1999; Benoît and Rochet, 2004; Baird and Suthers, 2007; Maury et al., 2007; Blanchard et al., 2008; Stock et al., 2008; Law et al., 2009). As the technologies based on acoustic and optical methods have been developed for measuring in situ sizes of organisms, all trophic levels can be plotted on a continuous size spectrum as has been done by Sheldon and Parsons (Sheldon and Parsons, 1967); Quinones et al. (Quinones et al., 2003) and San Martin et al. (San Martin et al., 2006). These technologies and in situ measurements provide us the basis for a set of size spectrum models from lower to higher trophic levels.

ACKNOWLEDGEMENTS

Authors would like to thank those contributing to the SOFCOM monitoring program, and making data available to the public. M.Z. acknowledges the thoughtful discussions on growth rates with A. Hirst.

FUNDING

M.Z. acknowledges the financial support from Le Centre National de la Recherche Scientifique of France, European Union Marie Curie People Fellowship and US National Science Foundation Grants (OCE0238653, OCE 0435581 and ANT0444040).

REFERENCES


