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Scaling of growth rate and mortality with size and its consequence on size spectra of natural microphytoplankton assemblages in the East China Sea

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Abstract

Allometric scaling of body size versus growth rate and mortality has been suggested to be a universal macroecological pattern, as described by the Metabolic Theory of Ecology (MTE). However, whether such scaling generally holds in natural assemblages remains debated. Here, we test the hypothesis that the size-specific growth rate and grazing mortality scales with the body size with an exponent of $-1/4$ after temperature correction, as MTE predicts. To do so, we couple the dilution experiment with the FlowCAM imaging system to obtain size-specific growth rates and grazing mortality of natural microphytoplankton assemblages in the East China Sea. This novel approach allows us to achieve highly resolved size-specific measurements that could be hardly obtained in traditional size-fractionated measurements using filters. Our results do not support the MTE prediction. The size-specific growth rates scale positively with body size (with scaling exponent ~ 0.1), and the size-specific grazing mortality is independent of body size. Furthermore, results of path analysis indicate that size-specific grazing mortality is mainly determined by size-specific growth rate. We further investigate how the variation of size-specific growth rate and grazing mortality can interact to determine the microphytoplankton size structure, described by Normalized Biomass Size Spectrum (NB-SS). We test if the variation of microphytoplankton NB-SS slopes is determined by (1) differential grazing mortality of small versus large individuals, (2) differential growth rate of small versus large individuals, or (3) combinations of these scenarios. Our results indicate that the relative grazing mortality of small over large size category best explains the variation of NB-SS slopes across environments. These results suggest that higher grazing mortality of small microphytoplankton may release the large phytoplankton from grazing, which in turn leads to a flatter NB-SS slope. This study contributes to an understanding of the relative importance of bottom-up versus top-down control in shaping the microphytoplankton size structure.

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1 Introduction

Growth and mortality represents two key ecological processes of organisms. The phytoplankton population growth rate is determined by temperature and resource availability, together with physiological constraints of the biological machinery (Finkel et al., 2004). Temperature has been known to positively affect the maximum phytoplankton growth rate (Bissinger et al., 2008; Eppley, 1972). In terms of resource availability, light and nutrients receive most discussion (Key et al., 2010; Malone et al., 1993). Physiological constraints mainly base on the body size (Brown and Gillooly, 2003; Brown et al., 2000; Cermeño et al., 2006). The phytoplankton body size also determines the rate in which the phytoplankton uptake resources (Huete-Ortega et al., 2011; Moreno-Ostos et al., 2011). The body size and environmental conditions often interwoven in determine the competitiveness of a phytoplankton individual. For example, large phytoplankton expose competition advantage over small ones under sufficient light condition (Cermeño et al., 2005; Finkel et al., 2004). In addition, larger phytoplankton, though subject to lower size-specific nutrient uptake rate, could absorb nutrient with higher efficiency under nutrient sufficient condition (Maguer et al., 2009; Wang et al., 1997).

The Metabolic Theory of Ecology (MTE) was recently proposed to link the population growth rate with temperature and body size (Brown et al., 2004). According to MTE, the temperature-corrected size-specific population growth rate scales allometrically with its body size, with an exponent of $-1/4$ (Brown et al., 2000, 2004). Although this $-1/4$ scaling exponent has been observed in lab cultures (Finkel et al., 2004) and compiled data from freshwater and marine phytoplankton (Edwards et al., 2012; Litchman et al., 2007), other studies using natural assemblages from open ocean and coastal regions have showed that the phytoplankton growth rate scales isometrically with body size (Maranon, 2008; Maranon et al., 2007; Huete-Ortega et al., 2012) or exhibits a parabolic relationship with body size (Chen and Liu, 2010). Some study also suggests there is no constant scaling relationship between size and growth rates

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(Glazier, 2005). Indeed, linkage between growth rate and body size of phytoplankton needs further investigation.

In addition to growth rate, mortality is another important factor influencing phytoplankton dynamics. The mortality rate generally is determined by both intrinsic and extrinsic mechanisms. Intrinsic mechanism attributes to the individual metabolic rate, which is determined primarily by body size and temperature (Brown et al., 2000, 2004; Savage et al., 2008). The extrinsic mechanism refers to other death causes such as disease, predation, or accident (Ricklefs, 1998). According to MTE, mass-specific intrinsic mortality rate should scale with body size with a $-1/4$ exponent, because of metabolic constraints (Brown et al., 2004), and indeed, such a scaling relationship has been reported empirically (Hendriks, 2007; McCoy and Gillooly, 2008; Marba et al., 2007). However, the relationship between extrinsic mortality and body size is not well studied. Curiously, McCoy and Gillooly (2008) compiled a comprehensive empirical data and reported that the total mortality (i.e. the sum of intrinsic and extrinsic mortality) of organisms still scales with body size with a $-1/4$ exponent. This finding suggests that either extrinsic mortality also scales with body size with a $-1/4$ exponent, or extrinsic mortality is independent of body size.

For microphytoplankton, the major extrinsic mortality comes from microzooplankton grazing (Calbet and Landry, 2004). So far, two mechanisms have been proposed to explain the microzooplankton grazing behavior. The first mechanism proposes that microzooplankton select phytoplankton that grow faster (Lie and Wong, 2010), yet the second mechanism suggests microzooplankton prefer phytoplankton that are small in size (Zhang et al., 2005; Froneman and McQuaid, 1997). The debate could stem from the strong correlation between being small and being growing fast according to MTE (Brown et al., 2004). In addition, the confusion could result from the low resolution in defining the size class of phytoplankton (Montagnes et al., 2008). In order to shed light on the unclear pattern of phytoplankton grazing mortality, detailed and thorough size-specific studies are in need.

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The knowledge of size-specific responses, their growth rate and grazing mortality, would directly contribute to understanding the variations of phytoplankton size structure across environments. While this is intuitive, rarely were the studies of phytoplankton size structure carried out simultaneously with size-specific growth rate and mortality measurements. Rather, most studies focused on correlation analyses to link phytoplankton size structures with environmental variables. For instance, studies have shown that high nutrients generally lead to prevalence of large phytoplankton (Huete-Ortega et al., 2011; Juhl and Murrell, 2005; Cavender-Bares et al., 2001; Reul et al., 2005; Yvon-Durocher et al., 2011; Kiorboe, 1993); oligotrophic conditions, by contrast, result in predominance of small phytoplankton (Irwin et al., 2006; Li, 2002). In addition, high temperature favours the dominance of small phytoplankton (Agawin et al., 2000; Yvon-Durocher et al., 2011). These studies, however, focus on the size structure variations with respect to environmental factors instead of directly measuring the phytoplankton growth rate and grazing mortality (Moran et al., 2010). While other studies focused on the selective grazing behavior of microzooplankton and inferred their potential effects on the phytoplankton size structure, they did not measure the phytoplankton size structure together with feeding experiments (Calbet et al., 2008; Teixeira et al., 2011). Moreover, while size-specific phytoplankton responses were examined in modeling researches to explain the relative importance of small and large phytoplankton in different nutrient conditions (Verdy et al., 2009, Irwin et al., 2006), empirical studies on size-specific growth rate and grazing mortality would help clarify the mechanisms affecting the phytoplankton size structure.

Here, we developed a novel approach to measure the phytoplankton size-specific growth and grazing mortality using the Flow Cytometer And Microscope (FlowCAM). This new approach overcomes the deficiency in traditional size-fractionated chlorophyll measurements, which cannot provide satisfactory size resolution (Calbet et al., 2001, 2008; Lessard and Murrell, 1998; Reckermann and Veldhuis, 1997; Calbet, 2008).

We carried out our experiments in the East China Sea (ECS). The ECS is an ideal region to study microzooplankton-phytoplankton interactions, because of its strong environmental gradient. The ECS is influenced by the eutrophic discharge from the Changjiang River in the coastal region and the oligotrophic Kuroshio Current in the offshore area (Gong et al., 1996, 2003). Previous studies have indicated a declining gradient in nutrient concentration from the coastal area to offshore (Zhang et al., 2007). The phytoplankton community structure and the interactions between phytoplankton and zooplankton in the ECS have been shown to vary across this nutrient gradient (Chan et al., 2009; Chang et al., 2003; Jiao et al., 2002; Tsai et al., 2011). These studies focused on pico- and nano- phytoplankton rather than microphytoplankton. Microphytoplankton, however, would be more important under nutrient sufficient condition (Garmendia et al., 2011), and would be worthy studying in detail.

Here, we focus on microphytoplankton, the community that has never been studied for their size-specific growth rate and mortality in natural assemblage. We have two objectives. First, we test if the MTE is applicable to the natural microphytoplankton assemblage. Specifically, we test whether the size-specific growth rate and grazing mortality scales with the body size with an exponent of $-1/4$ after temperature correction. Secondly, we investigate how the microphytoplankton growth rate and grazing mortality interact to determine the microphytoplankton size structure across environments. To do so, we use the slope of Normalized Biomass Size Spectrum (NB-SS) to describe microphytoplankton size structure (Platt and Denman, 1977). We test the hypotheses that the variations of microphytoplankton NB-SS slopes are determined by (1) differential grazing mortality of large versus small individuals, (2) differential growth rate of large versus small individuals, or (3) combinations of these scenarios.

2 Methods

2.1 Sampling

We carried out 23 sets of dilution experiments in the East China Sea (Fig. 1) from May 2010 to October 2011 on board of research vessel in 6 cruises (Table A1). Temperature

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and salinity profiles were recorded with a SeaBird CTD profiler (SBE9/11 plus, SeaBird Inc., USA). Photosynthesis Active Radiation (PAR) profile was measured with a quantum scalar irradiance meter (4π collector; Biospheric Inc., USA) attached to the CTD. Nutrients (nitrate, phosphate, and silicate) and chlorophyll *a* (chl *a*) concentrations were measured from water samples collected with Go-Flo bottles at 4 to 6 depths depending on stations and stored in liquid nitrogen before analysis. Analytic methods for nutrients and chlorophyll *a* are described by Gong et al. (2000). These measurements for each station were calculated as the integrated average from the euphotic zone (Table A1). Note, these environmental data are presented in the Supplement A as background information of environmental conditions but not used in the data analysis, except for temperature. Because our experiments were carrried out with nutrient amendment and on board of research vessel where light is never limited, resource limitation is not a concern for phytoplankton growth and mortality.

2.2 Dilution experiments

To investigate the growth and mortality rate of microphytoplankton, dilution experiments were conducted following the method developed by Landry and Hassett (Landry and Hassett, 1982; Landry et al., 1995). For each set of experiments, 40 l of whole seawater (WSW) were collected at the 10-m depth using a CTD-rosette system with Go-Flo bottles. All incubation bottles, tubes, and carboys were acid rinsed with 10 % HCl and then distilled water. Carboys were rinsed with ambient sea water before each experiment. Another 20 l of seawater were filtered through a 0.2 µm filter membrane (millipore 144 mm) with a peristaltic pumping system to obtain particle-free sea water (FSW). We gently mixed the FSW and WSW in 2 l polycarbonate bottles to prepare the four dilution treatments, 25 %, 50 %, 75 %, and 100 % of WSW with artificial nutrient amendment and another 100 % WSW without amendment. The nutrient amendment consists of 6.2ml Guillard's (F/2) Marine Water Enrichment Solution (cat. No. G0154) and 20 µml NH_4Cl (the final concentration is 3 µM NO_3; 0.12 µM PO_4; 0.36 µM SiO_4; 3 µM NH_4). Three of five treatments of dilution series (25 %, 50 %, and 75 % WSW)

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were prepared in duplicate and the other two (100 % WSW with and without nutrient amendment) in triplicate. All the 2 l polycarbonate bottles were placed in a large opaque incubation tank with a lid for 24 h incubation on boat. Incubations tanks are filled with constantly circulating surface seawater along the cruise, with temperature measured periodically. During the incubation, we keep the natural light cycle, and thus the lid was unveiled before dawn and was veiled after dusk to avoid artificial light from the research vessel. Samples were collected from the WSW before incubation (T_0) and from each incubation bottles after incubation (T_{24}) for FlowCAM analyses. Note, as we ammended nutrients during experiments, the mortality of phytoplankton is presumably mainly due to grazing rather than intrinsic processes such as starvation.

2.3 FlowCAM analysis

Our method differed from the traditional dilution experiment in a way that we aimed to estimate size-specific growth rate and mortality of microphytoplankton. To do so, we incorporated the FlowCAM analysis into dilution experiments. FlowCAM is an automatic sampling device that has been shown to exhibit high accuracy and efficiency in measuring phytoplankton size structure (Alvarez et al., 2011) and in zooplankton grazing experiments (Ide et al., 2008). Combining the detailed size information acquired from the FlowCAM and dilution technique (Landry et al., 1995; Landry and Hassett, 1982), we are able to measure the size-specific growth and mortality rate of microphytoplankton with high resolution ranging from 10 to 300 µm.

We processed fresh samples with the FlowCAM on board of the research vessel. All fresh samples were taken from the bottles at the end of incubation and initial undiluted WSW. However, due to time limitation on boat, each sample was processed by passing water sample of 6 ml (or within 18 min limitation to save time). The objective used for on boat analysis is 4× and the flow cell used is 300 µm in thickness following the guidance of manual. This combination allows all the particles to pass through. The images of particle size ranging from 4 to 500 µm ESD (Equivalent Spherical Diameter)

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were captured by the FlowCAM automatically, while only those ranging from 10 to 300 µm ESD were extracted for further analyses.

In order to better estimate the biomass of microphytoplankton, particle were manually classified into 6 categories: chain forming diatom, single diatom, naked dinoflagellate, shelled dinoflagellate, colony small cells, and singletons smaller than 20 µm ESD. All microphytoplankton individuals biovolume (μm^3) were first automatically calculated by the FlowCAM. These biovolume were then converted into carbon biomass (pg) according to the category-specific conversion equation (Marquis et al., 2011). Throughout this paper, we use carbon biomass to represent body size of phytoplankton.

2.4 Data analysis

To estimate the size-specific growth and mortality rate of microphytoplankton, we first constructed the size spectrum of microphytoplankton at T_0 and T_{24} (Fig. 2). The Normalized Biomass-Size Spectra (NB-SS) of phytoplankton were employed in this study. We divided the total biomass of each $\log_2$ size class by the width of the respective size class as described by Platt and Denman (Platt and Denman, 1977; Sheldon et al., 1972). The microphytoplankton biomass within this range expands 12 orders under $\log_2$ scale. We implement $\log_2$ in size class in order to accord with the convention, as well as keep high size-resolution as possible. As such, we estimate the biomass of each size class at T_0 and T_{24}. This new method has advantage over traditional size-fractionated chl *a* measurements, which pertain difficulties in having data with high resolution (Zhang et al., 2005).

The growth and mortality rates were estimated following the classic method using a linear regression of realized phytoplankton growth rates of four dilution treatments versus the corresponding dilution factors. Thus, we could calculate the slope as the grazing mortality (m) and the intercept as the intrinsic phytoplankton growth rate (μ). The novel treatment here is that we carried out such calculation for each size class (Fig. 2); as such size-specific growth and mortality rates were estimated. In addition to μ, we also measured the size-specific growth rate without nutrient amendment (μ').

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Consequently, the size-specific growth rate with and without nutrient amendment (μ and μ') and grazing mortality (m) of microphytoplankton can be estimated.

To achieve the first objective, we examine the relationship between size-specific growth rate versus the microphytoplankton body size, using the Generalized Linear Mixed effect Model (GLMM) (Bolker et al., 2009). Here, cruises were considered as the random effect to account for strong variation in temperature, light, and other factors among cruises. Likewise, size-specific grazing mortality was analyzed following the same fashion. We further investigated the relationships between size-specific growth rate and body size for each cruise separately, using linear regression. Because of the rather fine scale in size class defined in our study and sampling error, it was possible for certain size classes to exhibit negative size-specific growth or grazing mortality. For each station, those negative values were removed from analyses. After removing negative values, 178 sets of data including both positive size-specific growth rate and grazing mortality were left. Prior to analysis, the temperature effect on growth rate and mortality was adjusted according to MTE (Brown et al., 2004). The temperature corrected rate (M_c) was calculated from the measurement (M) as following: $M_c = M \times e^{E/kT}$, where E is the activation energy (in electronic volts (eV)), k is the Boltzmann constant ($8.617 \times 10^{-5}\,\mathrm{eV\,K^{-1}}$) and T is the absolute temperature in K. In this study, the activation energy is set to be 0.32 eV (Allen et al., 2005; Lopez-Urrutia et al., 2006).

To further clarify the relationship among microphytoplankton body size, size-specific growth rate, and size-specific grazing mortality, we conducted path analysis (Kline, 2011) to determine the relationships among the three. Here, we considered only biologically plausible models. In the path model design, we always fix the microphytoplankton body size as an exogeneous variable, which means that growth rates and mortality does not affect body size. Besides, we consider that size-specific grazing mortality does not affect size-specific growth rate, because there has been no empirical support to this possibility under the nutrient sufficient condition (as was the case in our epxperiments). Under this prerequisit, we designed three path models (Fig. 3).

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To achieve the second objective, we examine how the variation of microphytoplankton size-specific growth rate and grazing mortality in different size classes affects their NB-SS slope across environments. The NB-SS slope is commonly used to represent the relative abundance of small versus large individuals in a community. To simplify the computation, we binned the smallest four size classes (2^6 to 2^{10} pg) into the small size category, the middle four size classes (2^{10} to 2^{14} pg) into the medium size category, and the largest four size class (2^{14} to 2^{18} pg) into the large size category, and calculated the average growth rate and grazing mortality for each category. Such binning is reasonable because the growth rate and grazing mortality of the large and small size category influence the NB-SS slope most, but the rates of medium size category show no influence. Therefore, only the size-specific growth rate under two nutrient conditions and grazing mortality of small and large size category (μ'_S, μ'_L, μ_S, μ_L, m_S, and m_L) were investigated. Meanwhile, considering the strong correlation between the growth rate and grazing mortality (Barnes et al., 2011; Chen et al., 2009; Landry et al., 2000; Murrell et al., 2002), we explored the univarate GLMM model instead of step-wise selection to avoide the issue of colinearity. We analyzed 15 univariate regression models. The independent variables of these 15 models included 4 growth rates and 2 grazing mortalities as described above (μ'_S, μ'_L, μ_S, μ_L, m_S, and m_L), 4 grazing impacts (I_S, I_L, I'_S, and I'_L where $I = m/\mu$ and $I' = m/\mu'$) designed to measure the grazing pressures of two size categories under two nutrient conditions, and 5 ratios (μ'_S/μ'_L, μ_S/μ_L, m_S/m_L, I_S/I_L, and I'_S/I'_L) of small over large category designed to explore the relative importance of small versus large size category in terms of the size-specific growth rate, grazing mortality and grazing impact. In these analyses, we focused on only biological plausible effect of each independent variable on the NB-SS slope. That is, we tested whether the relationship significantly follows the biological expectation using one-tail tests. For example, relatively higher growth rate of larger over smaller phytoplankton is expected to increase (flattern) the NB-SS slope, while relatively higher growth rate of smaller over larger phytoplankton is not possible to directly produce a flatter size spectral slope.

3 Results

3.1 Size-specific growth rates depend on body size

The size-specific growth rate scales with body size in $\log_2$ scale with a slightly positive scaling exponent (Fig. 4a, b). Under nutrient amendment condition, temperature-corrected logarthmatic size-specific growth rates are positively related with body size (biomass) with a slope of 0.099 ± 0.017 (mean ± SE; $p < 0.001$) (Fig. 4a). When examined for each cruise separately, such positive relationship still exists with a slope close to 0.1, except in June and August 2011 (Table 1). In addition, under the condition without nutrient amendment, temperature-corrected logarthmatic size-specific growth rates also positively relate with body size with a slightly elevated slope of 0.155 ± 0.026 (mean ± SE; $p < 0.001$); such a positive relationship remains significant when each cruise was analyzed individually, except in June and July 2011 (Table 1).

3.2 Size-specific grazing mortality does not depend on body size but depends on growth rate

The size-specific mortality rate, by contrast, shows no significant relationship with microphytoplankton body size, according to the results of GLMM (Fig. 5). We further examine the correlation between phytoplankton size-specific growth rate and grazing mortality, as motivated by the suggestion that the phytoplankton growth rate could be an alternative factor affecting zooplankton grazing (Lie and Wong, 2010; Safi et al., 2007). The correlation between the size-specific growth rate and mortality is significant when the whole microphytoplankton community across size range is considered (Fig. 6).

We subsequently conducted path analysis to clarify the relationship among body size, size-specific growth rate and size-specific grazing mortality. The results of path analyses unveil the dependence of grazing mortality on growth rate as well as the dependence of growth rate on body size (Table 2). The best fitting model is the Path

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model 2 in Fig. 3 (AIC = 11.397, Table 2). The path coefficient from size to size-specific growth rate is 0.154 ± 0.027 (mean ± SE; $p < 0.001$), and path coefficient from size-specific growth rate to size-specific grazing mortality is 0.610 ± 0.085 (mean ± SE; $r = 0.222$; $p < 0.001$). The other comparable model is the Path model 3 in Fig. 3 (AIC = 12, Table 2). The Path model 3 includes a directional effect from body size to size-specific grazing mortality, yet the path coefficient of this directional effect is nonsignificant ($p = 0.237$). Consequently, the Path model 2 is the most parsimonious model explaining the relationship among body size, growth rate and grazing mortality. Our results indicate that body size affects phytoplankotn size-specific growth rate, which in turn determines their grazing mortality in the ECS.

3.3 The relative size-specific grazing mortality (m_S/m_L) explains the variation of the Normalized Biomass-Size Spectrum (NB-SS) slope

The results of our 15 univariate GLMM indicate that only relative grazing mortality (m_S/m_L) is significantly related with the NB-SS slope and the relationship is positive ($p < 0.05$, Table 3). That is, when the relative grazing mortality rate for small individuals is higher, the spectral slope flattens (i.e. the proportion of larger individuals would increase). We note that, if we had considered two-tail tests, under two nutrient conditions, the relative size-specific growth rate (μ'_S/μ'_L and μ_S/μ_L) and size-specific growth rate of small size category (μ'_S and μ_S) would show a significant positive relationship with NB-SS slope; that is, a higher growth rate of small individuals causes the size spectral slope to flatten. However, this is not possible biologically. Such spurious correlation simply arises due to the significant relationship between growth rate and mortality (Fig. 6). (See also Sect. 4.3.)

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4 Discussions

4.1 Size-specific Isometric size-scaling of phytoplankton size-specific growth rates

We observe a positive relationship between logarithmatic size-specific growth rate and body size for the microphytoplankton assembalge in the East China Sea (Fig. 4). This finding supports a positive scaling relationship between size-specific growth rate and body size, which has also been observed in several recent studies focusing on unicellular organisms (Chen and Liu, 2010; Maranon, 2008; Maranon et al., 2007; Huete-Ortega et al., 2012). Here, our observed scaling exponent of 0.099 for size-specific growth rate could be converted to 1.099 for individual-specific growth rate; and this value is comparable with the reported values of individual-specific metabolic rates ranged from 0.9 to 1.2 (Maranon, 2008; Maranon et al., 2007; Huete-Ortega et al., 2012). Together with other studies showing isometric scaling between individual respiration and body in other phytosynthetic plants (Reich et al., 2006; Kiorboe, 1993), our resluts cast doubts on the plausibility of a ubiquitous negative one-quarter scaling rule (Brown et al., 2000; Cermeño et al., 2006; Niklas and Enquist, 2001) between size-specific rate and body size in natural phytoplankton assemblages.

The plausibility of negative one-quarter scaling rule from the MTE (Brown et al., 2004) critically relies on the geometrical constraints from surface to volume ratio and the pigment package effect for phytoplankton (Kiorboe, 1993). However, in natural phytoplankton assmeblage, the positive scaling exponent in our study suggests other mechanisms should be considered to offer explainations. From the perspective of individual, the difference in phytoplankton growth condition might explain why lab cultures follow the MTE, but natural assemblages do not. The scaling exponent between cholorophyll and cell volume in natural assemblage is reported to be close to 1 (Finkel et al., 2004; Maranon et al., 2007), while it is reported to range from 0.6 to 0.8 in lab culture (Finkel et al., 2004). Higher cholorophyll content might allow the large individuals to exhibit higher size-specific photosynthesis rate and thus higher size-specific growth

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rate. Besides, larger phytoplankton have been demostrated to be able to utilize several strategies to elevate their size-specific growth rate, including increasing their vacuole size to have higher storage ability (Thingstad et al., 2005; Latasa et al., 2005; Stolte et al., 1994) and attaining higher photosynthesis efficiencies (Cermeño et al., 2005). In addition, the taxonomic composition shifting could be another factor overiding the size effects (Maranon, 2008; Maranon et al., 2007; Huete-Ortega et al., 2012).

For the MTE to be implemented in phytoplankton, resource availibility such as light must be sufficient for organisms to grow without limitation (Brown et al., 2000, 2004). To avoid the issue of ligh limitation in testing MTE on phytoplankton growth, phytoplankton samples were collected from surface or near surface water layer to prevent light limitation in most of the in situ studies (Chen and Liu, 2010; Huete-Ortega et al., 2011; Maranon, 2008; Maranon et al., 2007). Among those, Maranon et at. (2007) was the only study discussing the difference between two distinct stations with different light intensity. They found that the scaling exponent of individual photosynthesis rate versus body size is significantly lower in coastal area (0.96) than in open ocean (1.14); however, the author accounted this difference to nutrient availability instead of light. In our study, the phytoplankton samples were also collected from the surface layer (10 m depth) and then incubated on deck to allows sufficient light intensity for phytoplankton growth. Thus, the effect of light on phytoplankton growth should be regarded as minor in our study.

4.2 Size-specific growth rate instead of body size mainly affects the size-specific mortality

In our study, the microphytoplankton size-specific grazing mortality mainly depends on the size-specific growth rate, according to our regression anaysis (Fig. 6) and path model (Table 2), but not on body size (Fig. 5). These results are cosnsitent with previous studies indicating that the microphytoplankton extrinsic size-specific mortality rate (grazing mortality) is size independent (McManus et al., 2007; Gutiérrez-Rodríguez et al., 2009, 2011). Nevertheless, meta-analysis on phytoplankton total mortality rate

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(including both intrinsic and extrinsic mortality) still shows a −1/4 power relationship between size-specific mortality and body size (McCoy and Gillooly, 2008). Combining these evidence, we suggest that the −1/4 scaling of total mortality versus body size of phytoplankton is to a large extent determined by the intrinsic processes. The extrinsic processes are independent of body size and do not contribute significantly to affecting the scaling in microphytoplankton.

Our study also suggests that microphytoplankton growth rate might be the most essential characteristic influencing the microzooplankton prey selection behavior (Burkill et al., 1987; Gaul and Antia, 2001; Strom, 2002; Strom and Welschmeyer, 1991; Lie and Wong, 2010), at least in the ECS. However, we caution our interpretation because it is clear that body size and size-specific growth rates show a significant positive relationship (Fig. 4). One might argue that since grazing mortality relates positively with growth rate (Fig. 6) and growth rate scales positively with body size (Fig. 4), a positive scaling relationship between grazing mortality and body size is expected. However, we note that the scaling exponent of growth rate versus body size is very small (∼ 0.1) and does not result in a significant positive scaling relationship between grazing mortality versus body size.

4.3 The relative grazing mortality of small to large microphytoplankton (m_S/m_L) determines the microphytoplankton NB-SS slope

The NB-SS slopes in the ECS were mainly determined by the relative higher grazing pressure on the small over the large microphytoplankton (m_S/m_L) (Table 3). Although the Model 1, 3, 4 and 5 in Table 3 could be significant if we had considered two-tail tests, their positive coefficients are contradictory to biological anticipations. Biologically, the raised growth rate of small individuals (Model 4 and 5 in Table 3) or relatively higher growth rate of small versus large individuals (Model 1 and 3 in Table 3) should have promoted the abundance of small individuals and consequently steepen the NB-SS slope, which is exactly opposite to our observations. Thus, the estimated positive coefficients of these four models are a spurious correlation resulted from the covariance

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between size-specific growth rate and grazing mortality (Fig. 6). In short, we suggest that the raised grazing pressure on small microphytoplankton should be responsible for flatter NB-SS slopes.

In fact, the raised grazing pressure on small microphytoplankton (i.e. grazing mortality) could be due to their higher growth rate (Fig. 3). Recall that growth rate and grazing mortality is coupled together (Fig. 6). The elevated growth rate of small microphytoplankon could provoke grazing mortality on themselves. Accordingly, this raised grazing mortality either directly reduced the abundance of small microphytoplankton or released the large ones from grazing. The NB-SS slope is consequently flattened. In other words, relatively higher growth rate of small versus large individuals serves as a trigger for higher grazing mortality of small than large individuals, which in turn decreases the abundance of the small microphytoplakon and results in a flatter NB-SS slope. This mechnaism could link the microphytoplankton growth rates to graizng mortality, and finally to the shape of microphytoplakon size structure.

Furthermore, light intensity does not offer extra explaination to the size spectral slope variation in our analysis. The PAR variable does not significantly explain the variation of size spectal slopes. Indeed, if we add PAR into the 15 models in Table 3, the coefficients of the PAR variable were never significant. In addition, no clear pattern (either linear or Monod function) could be observed when plotting the size spectral slope across environments against the PAR values. Thus, the effect of light does not significantly afftect our results.

5 Conclusions

We developed a novel appraoch to measure size-specific growth rate and mortality for microphytoplankton. We found that size-specific growth rate of micrphytoplankton assemblages in the ECS scales positively with body size (however the slope is very small) and that size-specific motality exhibits no relationship with body size. These results differ from the prediction of MTE. Whether MTE is generally applicable in natural

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phytoplankton assemablages remians to be tested. Furthermore, our results indicate that body size affects phytoplankotn size-specific growth rate, which in turn determines their grazing mortality in the ECS. As a consequence, relatively higher growth rate of small versus large individuals serves as a trigger for higher grazing mortality of small than large individuals, which in turn decreases the abundance of the small microphytoplakon and results in a flatter NB-SS slope. Our findings provide a mechanistic linkage between rates measurements with biomass size specturm.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/9/16589/2012/ bgd-9-16589-2012-supplement.pdf.

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Table 1. Results of generalized linear mixing effect model (GLMM) and univariate regression analyses linking microphytoplankton size-specific growth rate (μ or μ') with microphytoplankton body size (biomass). In GLMM, all data were pooled and cruises were considered as random effects. μ and μ' represents size-specific growth rates measured with and without nutrient amendment, respectively.

Cruise	Coefficient	SE	p-value	r-square
GLMM:	**$Log_2(\mu) \sim Log_2$(phytoplankton biomass) + random effect (cruise)**			
Over all	0.099	0.017	< 0.001	
Linear model:		**$Log_2(\mu) \sim Log_2$(phytoplankton biomass)**		
May 2010	0.223	0.072	< 0.001	0.325
Dec 2010	0.174	0.032	< 0.001	0.501
Jun 2011	–0.009	0.029	0.763	0.003
Jul 2011	0.090	0.033	< 0.05	0.189
Aug 2011	0.047	0.034	0.177	0.053
Oct 2011	0.152	0.058	< 0.05	0.230
GLMM:	**$Log_2(\mu') \sim Log_2$(phytoplankton biomass) + random effect (cruise)**			
Over all	0.155	0.026	< 0.001	
Linear model:		**$Log_2(\mu') \sim Log_2$(phytoplankton biomass)**		
May 2010	0.291	0.100	< 0.001	0.299
Dec 2010	0.287	0.069	< 0.001	0.365
Jun 2011	0.113	0.057	0.06	0.127
Jul 2011	0.082	0.056	0.151	0.063
Aug 2011	0.085	0.026	< 0.01	0.241
Oct 2011	0.186	0.088	< 0.05	0.163

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Table 2. Results of path analyses of the path models presented in Fig. 3. The endogenous variables are italic. Path model 2 is considered as the best model describing the relationship between body size, size-specific growth rate, and grazing mortality according to AIC.

Path	AIC	Unstandardized path coefficient	SE	*p*-value	*r*-square for endogenous variable
Path model 1	53.492				
Body size → *size-specific growth rate*		0.154	0.027	< 0.001	0.157
Body size → *size-specific grazing mortality*		0.058	0.038	0.123	0.013
Path model 2	11.397				
Body size → size-specific growth rate		0.154	0.027	< 0.001	
size-specific growth rate → *size-specific grazing mortality*		0.610	0.085	< 0.001	0.221
Path model 3	12				
Body size → size-specific growth rate		0.154	0.027	< 0.001	
Body size → *size-specific grazing mortality*		−0.043	0.036	0.237	0.230
size-specific growth rate → *size-specific grazing mortality*		0.654	0.093	< 0.001	

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Table 3. Results of GLMM examining the relationship between NB-SS slopes (dependent variable) versus size-specific growth rates, mortality, grazing impacts, and the ratio of small versus large size category for these variables. The subscript (S or L) indicates the size category (small or large). μ and μ' represents size-specific growth rates measured with and without nutrient amendment, respectively; m represents size-specific grazing mortality; I and I' represents grazing impact measured with and without nutrient amendment ($I = m/\mu$ and $I' = m/\mu'$). Biological antipation represents the expected positive (+) or negative (−) relationship between each variable versus size spectral slopes, according to biological reasoning. The effect (coefficient) of each independent variable on NB-SS slopes was tested against the biological antipation using one-tail tests. Cruises were considered as random effects in GLMM.

	Independent variables	Biological anticipation	Coefficient	*p*-value
Model 1	μ'_S/μ'_L	−	0.129	0.995
Model 2	m_S/m_L	+	0.153	0.036*
Model 3	μ_S/μ_L	−	0.123	0.970
Model 4	μ'_S	−	0.166	0.992
Model 5	μ_S	−	0.255	0.993
Model 6	m_L	−	−0.006	0.079
Model 7	m_S	+	0.070	0.107
Model 8	I'_L	−	−0.058	0.155
Model 9	I_L	−	−0.049	0.170
Model 10	I_S/I_L	+	0.029	0.259
Model 11	μ_L	+	−0.099	0.884
Model 12	μ'_L	+	−0.053	0.814
Model 13	I'_S	+	−0.027	0.720
Model 14	I_S	+	−0.007	0.566
Model 15	I'_S/I'_L	+	−0.009	0.581

* Indicates the model that gives biologically reasonable and significant result.

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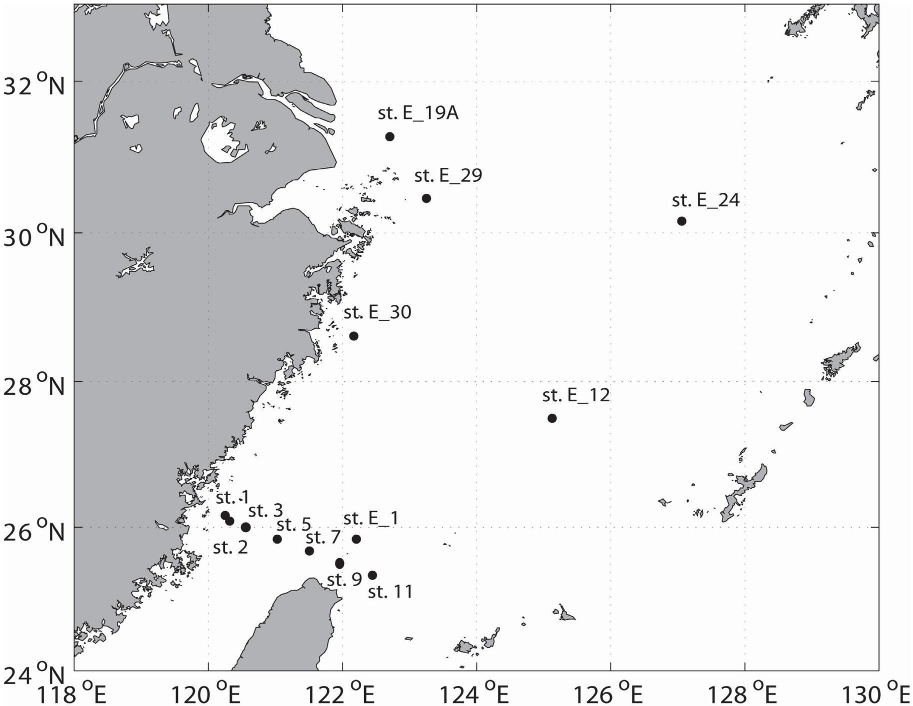

Fig. 1. Map illustrating experimental stations in the East China Sea.

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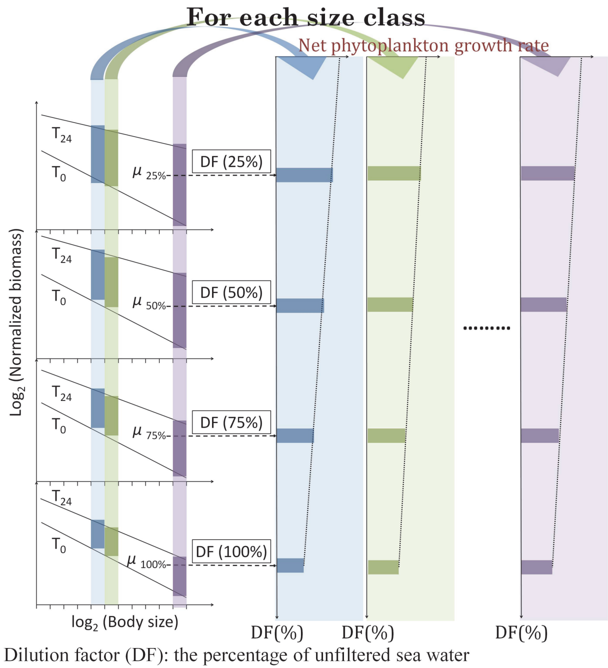

Fig. 2. Schematic illustrating how the size-specific growth rate and grazing mortality for each size class was calculated. Left panel shows the relationship between phytoplankton biomass versus size at T_0 and T_{24} (black lines) for each dilution factor. Dilution factor (DF) represents the percentage of unfiltered sea water. Right panel illustrates the regression analysis of realized phytoplankton growth rate (x-axis) versus the corresponding dilution factors (y-axis) for each size class. Colors indicate different size classes. By comparing the phytoplankton biomass at T_0 and T_{24} under different dilution factors for each size class, one can estimate size-specific growth rate and grazing mortality using the regression approach commonly employed in dilution experiments for each size class.

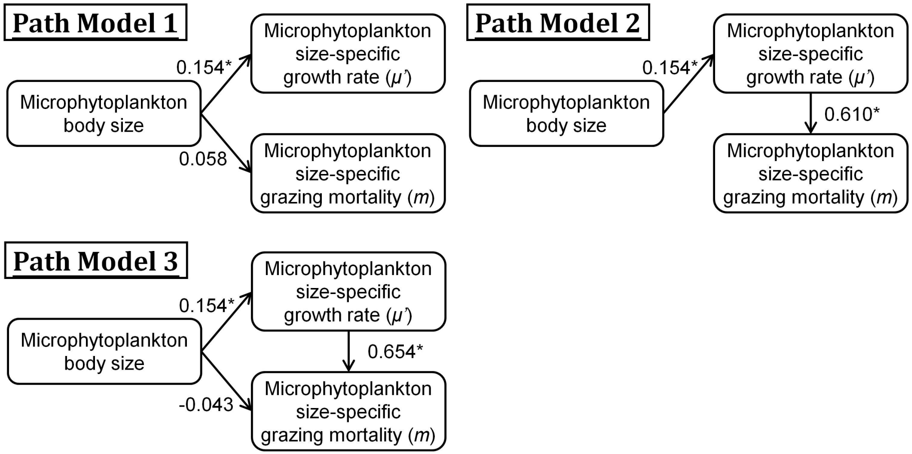

Fig. 3. Schematic indicating the three path models for path analyses to further clarify the relationships among microphytoplankton body size, size-specific growth rate, and grazing mortality. The effect from body size to size-specific growth rate was always fixed. The path coefficients denoted with a asterisk are significant.

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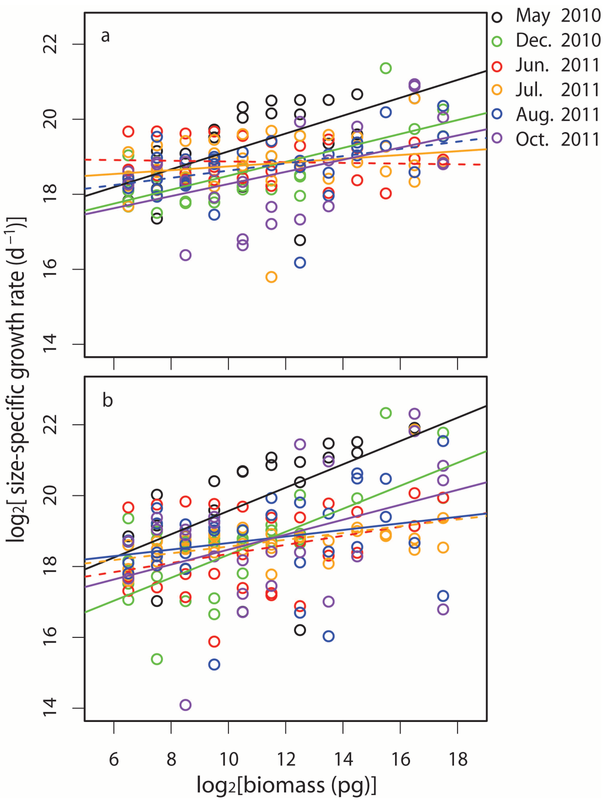

Fig. 4. Scatter plot of $\log_2$ transformed size-specific growth rate versus size (biomass). **(a)** indicates the size-specific growth rate measured with nutrient amendment (μ), while **(b)** indicates those measured without nutrient amendment (μ'). Both the estimated slopes from GLMM of **(a)** (0.10) and **(b)** (0.15) are significant. Different colors represent data from different cruises. Solid lines indicate significant correlations, while the dashed lines indicate nonsignificant correlations.

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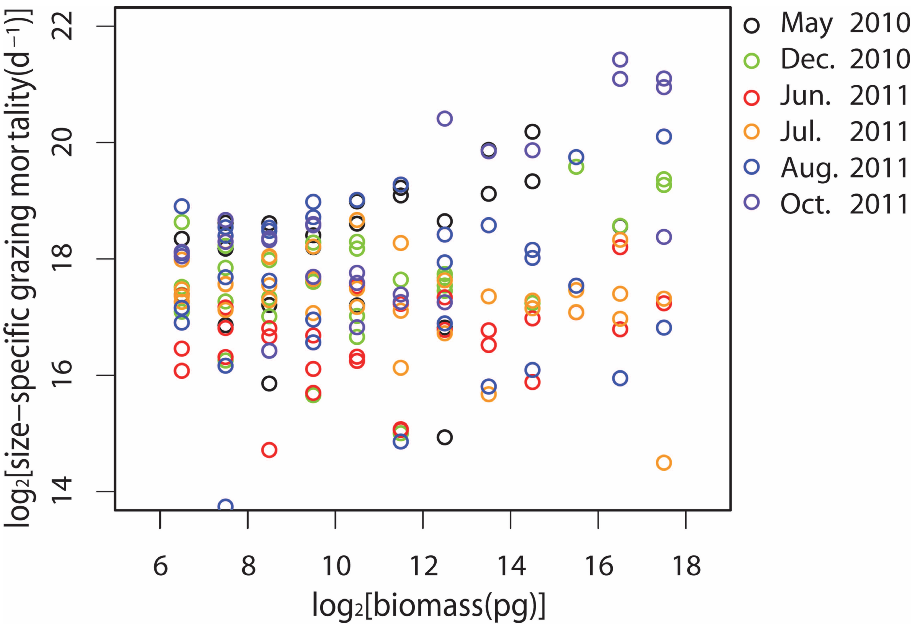

Fig. 5. Scatter plot of $\log_2$ transformed size-specific grazing mortality versus size (biomass). The regression is not significant in either GLMM or each cruise analyzed individually, except for August 2011 (-0.083 ± 0.035; $r = 0.119$; $p = 0.02$) and October 2011 (0.230 ± 0.099; $r = 0.155$, $p = 0.03$).

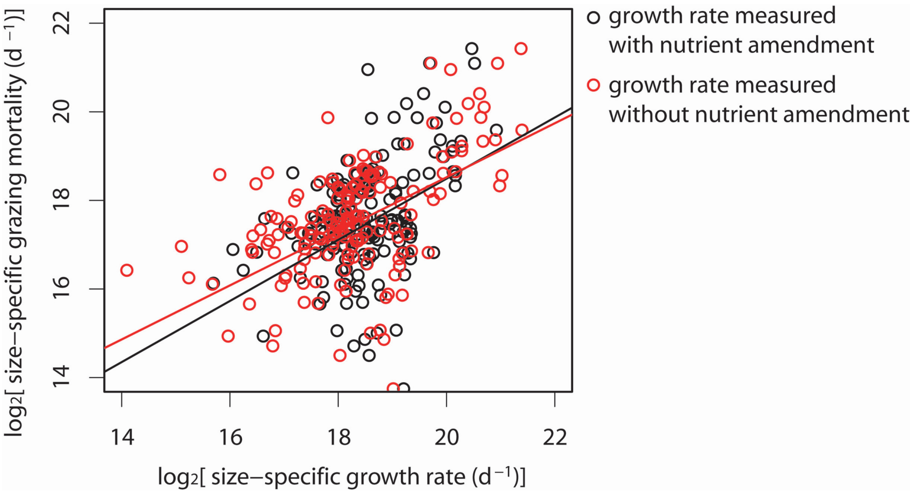

Fig. 6. Scatter plot of $\log_2$ transformed size-specific grazing mortality versus growth rate. The slope is significant either for the measurements with nutrient amendment (black, $p < 0.001$) or without nutrient amendment (red, $p < 0.001$).

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