



Toward standard parameterizations in marine biological modeling

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Abstract

Biological modeling is an important investigation tool in oceanography, which can provide an insight into biological dynamics, integrate multi-disciplinary processes and predict ecological events. However, the lack of a common set of parameterizations of fundamental biological processes hinders progresses in simulation skill, reliability and predictability. There exist 13 functions for light forcing on phytoplankton growth, 5 for nutrient limitation, 6 for ammonium inhibition on nitrate uptake, 10 for temperature forcing on biological rates, 20 for zooplankton feeding on a single type of prey, 15 for feeding on multiple types of prey, 8 for mortality and 6 for respiration. All of these functions are actually in use in modeling applications. This paper presents an overview of the existing functions. Based on their functionality, flexibility and reliability, a subset of functions has been selected as an a priori set of parameterizations. I suggest to use these selected parameterizations when they can fit well the data. By doing this, we can reduce the number of biological parameters that need to be estimated and provide a better opportunity for intercomparison. © 2005 Elsevier B.V. All rights reserved.

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1. Introduction

After half a century from the early effort of Riley (1946, 1947a,b) and Riley et al. (1949), biological modeling has become a research method widely used in

ocean sciences. Ocean science is, by its nature, science of systems that integrates dynamics in various disciplines: physics, chemistry, biology and geology. Numerical modeling represents an essential and efficient tool to provide an insight into the interactions between different disciplines and integrate dynamics at a system level. Numerical modeling can help to predict ecological events over an appropriate time scale and provide strategies for marine resource management and exploitation. Certain fundamental processes are of particular importance in the function of marine

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ecosystems that numerical models need to adequately parameterize. Light and nutrients are two fundamental factors in determining the productivity of the ocean. Trophic dynamics are key energy links from primary production to high trophic levels.

Various mathematical formulations have been developed to describe fundamental biological processes and forcing functions, such as those of light, nutrient and temperature. Since the beginning of the 20th century when Blackman (1905) described CO₂ fixation as a rectilinear function of light intensity, 13 equations have been developed to describe the same relationship, i.e., the growth–light or μ – E function. All these equations have been used in modeling applications.

There are two basic functions of nutrient limitation on phytoplankton growth, the Michaelis–Menten function and the Droop function, but different formulations have been developed and used in numerical simulation, with 6 functions of ammonium inhibition on nitrate uptake. More confusing are parameterizations of zooplankton feeding, 20 equations for feeding on a single type of prey and 15 for feeding on multiple types of prey. Trophic dynamics are complex at the secondary production level and different feeding modes and functional responses may require different mathematical approaches. In numerical simulation, however, zooplankton are often represented by aggregated state variables, e.g., zooplankton, mesozooplankton and microzooplankton. Species and feeding modes are usually not specific. All these various equations have been used in the same way for the same purpose, i.e., trophic link and energy flow from low to high trophic levels. In addition to these various equations of zooplankton feeding, there exist eight functions describing zooplankton mortality and six functions describing respiration.

These various functions are mostly based on empirical relationships that express correlation between measurable variables. The real ecological or physiological processes underlying the observed correlation are not explicit. There is no sound statistical or physiological basis to reject one or another parameterization (Sakshaug et al., 1997), but the choice among them can be critical with respect to the model functionality (Gao et al., 2000; Gentleman et al., 2003). The lack of a common set of parameterizations of the most fundamental biological dynamics hinders intercomparison, adequacy and skills of simulation and prediction. Using

all of these equations is a confused practice that make doubtful the rigor and reliability of biological and ecological modeling.

Methodological standardization represents progresses in scientific research. Standardization has been achieved in many subdisciplines in marine science, such as standard sampling and analytical procedure, standard environmental criteria, standard seawater density functions and standard fish stock assessment models. The primitive equations are used in most physical circulation models with well-established controlling parameter values. Standardization can reduce ambiguity and redundant effort in scientific research, promotes working efficiency and applications, and provides a unique framework for communication and intercomparisons.

Standardization in ecological modeling has been suggested over the years. Cohen et al. (1993) called for standardization in food web studies. Effort has been conducted for standard model structure, parameterization and documentation (Kaluzny and Swartzman, 1985; Wilhelm and Brüggemann, 2000; Williams et al., 2002; Wilhelm, 2003, 2005; Hoch et al., 2005). However, the intrinsic complexity in trophic dynamics and diversity in ecosystem function prohibit the progress in standardizing parameterization in ecological and biological models. Trophic preferences, strength, omnivory, path length, trophic level and biodiversity all influence the trophic dynamics in marine ecosystems (Williams and Martinez, 2000; Montoya and Solé, 2003). Numerical models have the limitation in simulating and predicting the complexity of marine ecosystems. In practice the accuracy of numerical simulation depend on the quality of the data set used to constrain the model. Parameterizations are often selected according to the goodness-of-fit with the data set available. Standardization of biological parameterization resides in the development of mechanistic formulations based on physiological and biological dynamics instead of empirical forms from data fitting.

Although it may not be realistic nowadays to standardize biological parameterizations given the lack of physiological and mechanistic functions, it is necessary to give an overview of these functions and to evaluate their suitability for biological simulation. In this paper, I have reviewed the existing functions describing light and temperature forcing and nutrient limitation on phytoplankton growth, ammonium inhibition

on nitrate uptake, zooplankton feeding, mortality and respiration. Based on analyses of their functionality, a subset of functions has been selected as the a priori set of parameterizations. The selection was based on the correctness, flexibility and generality of the existing functions. For example, parameterizations of light forcing on phytoplankton growth rate with photoinhibition have been selected over that without photoinhibition. Functions with photoinhibition have the advantage to apply to a large range of ecosystems both with and without photoinhibition by assigning an appropriate value to the photoinhibition coefficient. Grazing functions which can simulate various functional responses have been selected over monotonous functions due to their large applicability. Mechanistic parameterizations have been selected over empirical relationships. Mechanistic functions are based on accepted knowledge about the mechanisms of a specific process. Their parameters are generally interpretable and their application can be extended further than empirical models. The purpose of this paper is not to reject certain of the existing functions, but to suggest an a priori set of parameterizations as a selection.

2. Light forcing on phytoplankton growth rate

Based on early experiments, Blackman (1905) described the relationship between phytoplankton growth and light (μ – E relationship) as a rectilinear function:

$$\mu(I) = \begin{cases} \alpha I & \text{for } \frac{I}{\alpha} < P_m \\ P_m & \text{for } \frac{I}{\alpha} > P_m \end{cases} \quad (1)$$

where P_m is the maximum phytoplankton growth rate and α is the slope between phytoplankton growth and light intensity (Blackman, 1905; Riley, 1946; Jassby and Platt, 1976; Platt et al., 1977). According to this equation, the phytoplankton growth rate increases linearly with light intensity up to a certain level (P_m/α) beyond which the growth rate ceases to increase. Blackman interpreted the saturation light level as a result of other limiting factors that overwhelmed the effect of light.

Field and laboratory observations later showed that the μ – E relationship follows a hyperbolic curve and can

be expressed by the Michaelis–Menten function (Baly, 1935; Tamiya et al., 1953; Caperon, 1967; Kiefer and Mitchell, 1983):

$$\mu(E) = P_m \frac{\alpha E}{P_m + \alpha E} \quad (2)$$

The Michaelis–Menten function was developed to describe enzymatic activities (Michaelis and Menten, 1913). Its application to light limitation was chosen to fit experimental results and is without fundamental physiological underpinnings. Smith (1936) used a modified Michaelis–Menten function while trying to improve the fitting of experimental data:

$$\mu(E) = P_m \frac{\alpha E}{\sqrt{P_m^2 + \alpha^2 E^2}} \quad (3)$$

Later, Bannister (1979) and Laws and Bannister (1980) proposed a more flexible form of the Michaelis–Menten function:

$$\mu(E) = P_m \frac{\alpha E}{(P_m^n + (\alpha E)^n)^{1/n}} \quad (4)$$

Changes in the power n can generate different responses of phytoplankton growth to light intensity. When $n = 1$, the Bannister formulation is equivalent to the Michaelis–Menten function (Eq. (2)), when $n = 2$, it is equivalent to the Smith function (Eq. (3)), and when $n \sim \infty$, this formulation approximates the rectilinear function.

Under high light intensity, photosynthesis is photoinhibited, most likely through photo-oxidation reactions, i.e., over excited antenna chl a can be combined with oxygen to become chemically altered (Rabinowitch, 1945; Steele, 1962; Prezelin, 1981). None of the previous functions parameterize photoinhibition (Fig. 1A, curves 1–4). Consequently, Vollenweider (1965) and Peeters and Eilers (1978) further modified the Michaelis–Menten function to take into account photoinhibition:

$$\mu(E) = P_m \frac{\alpha E}{\sqrt{E_{\text{opt}}^2 + \alpha^2 E^2}} \frac{1}{(1 + (\beta E/E_{\text{opt}})^2)^{n/2}} \quad (5)$$

$$\mu(E) = P_m \frac{E}{E_{\text{opt}}} \frac{2 + \alpha}{1 + \alpha E/E_{\text{opt}} + (E/E_{\text{opt}})^2} \quad (6)$$

where E_{opt} represents the optimal light intensity under which phytoplankton growth rate reaches its maximum

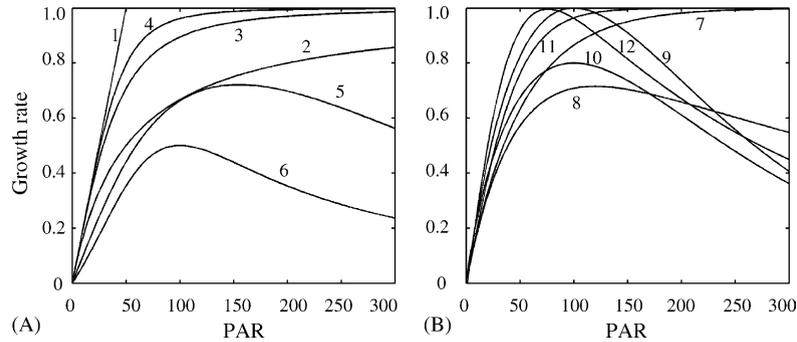


Fig. 1. Relationships between photosynthetically available radiation and phytoplankton growth rate: (1) rectilinear function (Eq. (1)), (2) Michaelis–Menten function (Eq. (2)), (3) Smith function (Eq. (3)), (4) generalized Michaelis–Menten function (Eq. (4) with $n=3$), (5) Vollenweider function (Eq. (5)), (6) Peeters and Eilers function (Eq. (6)), (7) Webb function (Eq. (7)), (8) Platt function (Eq. (8)), (9) Steele function (Eq. (9)), (10) Parker function (Eq. (10)), (11) hyperbolic function (Eq. (11)) and (12) Bissett function (Eq. (12)).

(Vollenweider, 1965; Peeters and Eilers, 1978; Parsons et al., 1984). Varying the parameters n , E_{opt} and α modifies the shape of the curve and thus the photosynthetic response to light intensity including photoinhibition in light ranges beyond the optimal intensity E_{opt} (Fig. 1A, curves 5 and 6).

Webb et al. (1974) used an exponential function to reproduce the observed data on light and CO_2 fixation used as a measure of photosynthesis:

$$\mu(E) = P_m(1 - e^{-\alpha E/P_m}) \quad (7)$$

Platt et al. (1980) added a second term to the Webb exponential function to represent photoinhibition observed in field studies:

$$\mu(E) = P_m(1 - e^{-\alpha E/P_m})e^{-\beta E/P_m} \quad (8)$$

where the exponential coefficient β determines the photoinhibition effect (Fig. 1B, curve 8). Steele (1962) combined the linear and exponential functions:

$$\mu(E) = P_m\alpha \frac{E}{E_{\text{opt}}} e^{1-E/E_{\text{opt}}} \quad (9)$$

where the exponential term determines the photoinhibition (Fig. 1B, curve 9). The shape of the curve of this equation is essentially fixed in high light intensity ranges. This rigid property makes it relatively difficult to fit this equation to data (Parsons et al., 1984). Parker (1974) modified the Steele function by adding a power parameter β to increase the flexibility for data fitting:

$$\mu(E) = P_m\alpha \left(\frac{E}{E_{\text{opt}}} e^{1-E/E_{\text{opt}}} \right)^\beta \quad (10)$$

Jassby and Platt (1976) suggested the hyperbolic tangent function to describe the μ – E relationship:

$$\mu(E) = P_m \tanh\left(\frac{\alpha E}{P_m}\right) \quad (11)$$

which does not include photoinhibition (Fig. 1B, curve 11). Bissett et al. (1999) modified this function by adding an exponential photoinhibition term:

$$\mu(E) = P_m \tanh\left(\frac{\alpha(E - E_0)}{P_m}\right) e^{\beta(E_{\text{opt}} - E)} \quad (12)$$

where E_0 represents the compensation light intensity under which the net growth rate of phytoplankton is null, i.e., photosynthesis and respiration neutralize each other and β determines the photoinhibition effect (Fig. 1B, curve 12).

Finally, Sakshaug et al. (1989) developed a mechanistic function for the μ – E relationship:

$$\mu(E) = \theta a \phi_{\text{max}} E \frac{1 - e^{-\sigma \tau E}}{\sigma \tau E} = \theta a \phi_{\text{max}} \frac{1 - e^{-\sigma \tau E}}{\sigma \tau} \quad (13)$$

where θ is the chlorophyll:carbon ratio (Chl:C), a represents the specific absorption coefficient for chlorophyll a , ϕ_{max} the maximum quantum yield, σ the mean absorption cross-section and τ is the minimal turnover time of the photosystem. The last exponential term represents the Poisson probability that a photosynthetic unit being hit is open.

Except for the last mechanistic function, all others are empirical and obtained from data fitting. All these formulations have been developed and used to simulate

the same μ – E relationship without specific environmental conditions or phytoplankton species. Given the diversity of the formulations that are used to describe the same biological process (i.e., the μ – E relationship) without specific environmental or biological conditions, it is desirable to select some of the functions according to certain criteria so that intercomparisons between models are feasible. Also this will reduce the number of biological parameters that need to be estimated for modeling applications.

Photoinhibition has been observed. This fact can allow us to rule out the functions, which do not include photoinhibition, i.e., functions 1–4, 7 and 11 in Fig. 1. Flexible functions can provide better fitting to data than functions with fixed forms, e.g., the Parker function (Eq. (10)) versus the Steele function (Eq. (9)). However, the flexibility of some functions requires more free parameters that are usually difficult to estimate and biologically uninterpretable. The Sakshaug–Kiefer mechanistic function (Eq. (13)) is the only one based on analysis of biological processes. However, it does not contain the photoinhibition term. This mechanistic function is equivalent to the Webb function. Assuming that the composite term $a\phi_{\max}$ represents the initial slope α of the μ – E curve and the composite term $\sigma\tau$ equals to $\alpha:P_m$, the Sakshaug–Kiefer function (Eq. (13)) becomes the Webb function (Eq. (7)). The Platt function (Eq. (8)) is based on the Webb function with a specific photoinhibition term. Its controlling parameters are interpretable and their values can be derived from measurable parameters such as the specific absorption coefficient, maximum quantum yield and the mean cross-section. Consequently, I propose the Platt function (Eq. (8)) as the a priori parameterization for the μ – E relationship.

3. Nutrient limitation on phytoplankton growth rate

Brandt (1899, 1902) first called attention to the importance of phosphate and nitrate as limiting factors for phytoplankton growth in the ocean and Ketchum (1939) established the relationship of hyperbolic nature between nutrient uptake and concentration. Based on a review of laboratory and field measurements, Caperon (1967) and Dugdale (1967) argued that nutrient uptake can be described by the Michaelis–Menten enzyme

kinetics:

$$\mu(N) = \frac{N}{N + K_S} \quad (14)$$

where N is the concentration of a nutrient element and K_S is the half-saturation constant (Fig. 2A, curve 1). The Michaelis–Menten function is thus an empirical formulation that can accommodate experimental data of nutrient uptake. Fennel (1995) modified the Michaelis–Menten function in a quadratic formulation:

$$\mu(N) = \frac{N^2}{N^2 + K_S^2} \quad (15)$$

and Flynn et al. (1997) proposed a more generic form:

$$\mu(N) = \frac{N^m}{N^m + K_S} \quad (16a)$$

Field observations and laboratory experiments sometimes showed a critical concentration of certain nutrients below which the uptake rate is virtually null (Caperon and Meyer, 1972; Paasche, 1973). Droop (1973, 1983) interpreted the phenomenon as the presence of an unreactive intercellular nutrient quota below which phytoplankton cease to grow. Consequently, Droop (1973, 1983) suggested the Droop function for nutrient uptake:

$$\mu_3(Q) = 1 - \frac{K_Q}{Q} \quad (16b)$$

where Q is the cell quota of nutrient and K_Q represents the critical cell quota below which phytoplankton growth is 0 (Fig. 2A, curve 3). Both the Michaelis–Menten function (e.g., Kiefer and Mitchell, 1983; Radach and Moll, 1993; Semovski et al., 1996; Davidson, 1996; Flynn, 1998; Backhaus et al., 1999; Napolitano et al., 2000; Chifflet et al., 2001; Franks and Chen, 2001) and the Droop function (e.g., Marra et al., 1990; Lange and Oyarzun, 1992; Oyarzun and Lange, 1994; Haney and Jackson, 1996) are in use in modeling application. Goldman and McCarthy (1978) argued that the Droop equation is applicable for minor nutrients such as iron, Vitamin B12 and phosphorus, but for major nutrients such as nitrogen and silicate, its applicability is limited.

The sigmoidal function (Eq. (15)) can provide certain simulation stability, but cannot theoretically ensure the parameterization of threshold (Fig. 2A, curve 2). Some authors suggested a simple combination of the

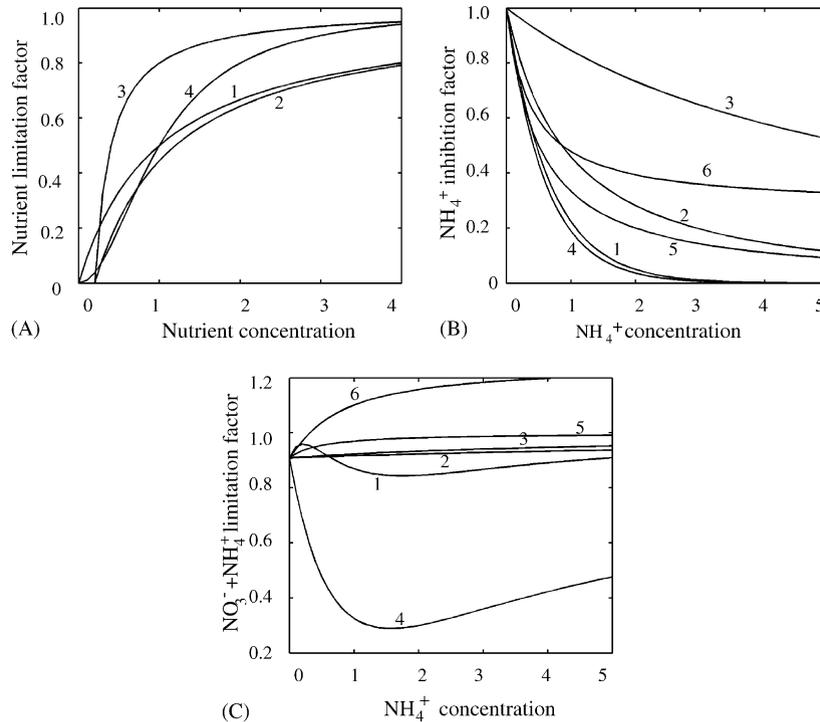


Fig. 2. (A) Relationships between nutrient concentration and nutrient limitation factor applied to phytoplankton growth rate: (1) Michaelis–Menten function (Eq. (14)), (2) quadratic Michaelis–Menten function (Eq. (15)), (3) Droop function (Eq. (16)), (4) combined Michaelis–Menten and Droop function (Eq. (17)). (B) NH_4^+ inhibition factor on NO_3^- uptake: (1) Wroblewski function (Eq. (18)), (2) Hurtt and Armstrong function (Eq. (19)), (3) O’Neil function (Eq. (20)), (4) Spitz function (Eq. (21)), (5) Parker function (Eq. (22)), (6) Yajnik and Sharada function (Eq. (23)). (C) NH_4^+ and NO_3^- total limitation factor on phytoplankton growth rate under NO_3^- replete condition ($10 \mu\text{M l}^{-1}$) with a half-saturation constant of $1.0 \mu\text{M l}^{-1}$. Function numbers are the same as that in panel (B).

Michaelis–Menten and the Droop functions (Caperon and Meyer, 1972; Paasche, 1973; Dugdale, 1977; Droop, 1983; Flynn et al., 1999):

$$\mu(N) = \frac{N - N_0}{N + K_S - N_0} \quad (17)$$

Martin (1992) demonstrated the threshold effect of dissolved iron concentration in seawater. When the concentration of dissolved iron is below a critical level (0.3–0.5 nmol in the open ocean), the diffusion of iron to the cell surface is so slow that phytoplankton growth is severely limited. It should be pointed out that the Droop equation models the relationship between phytoplankton growth rate and the internal cellular nutrient contents whereas the Michaelis–Menten function describes the relationship between phytoplankton growth rate and external nutrient concentrations in seawater. The threshold of nutrient concentration in sea-

water N_0 in Eq. (17) differs from the critical cell quota K_Q in the Droop function (Eq. (16)). In many cases, the threshold of nutrient concentration is below the detection limit of the currently used analytical methods so that N_0 can be assigned to 0 in modeling applications. Given the importance of iron limitation in ocean productivity and the diversity of phytoplankton species, the combined function with both a half-saturation constant and threshold (Eq. (17)) has the potential of wider application than the simple Michaelis–Menten function or the Droop function.

There are two main forms of dissolved inorganic nitrogen that can be taken up by phytoplankton, nitrate (NO_3^-) and ammonium (NH_4^+). NO_3^- assimilation requires reduction to NH_4^+ which is an energy-expensive process. Nitrate reductase activity (NR), which regulates the first step of NO_3^- reduction, is decisive in determining the rate of nitrate reduction and

assimilation (Solomonson and Barber, 1990). NO_3^- uptake induces NR whereas NH_4^+ uptake can repress NR and, thus, inhibits NO_3^- uptake (Dugdale and Goering, 1967; Eppley et al., 1969; Dortch, 1990; Flynn et al., 1997). Various functions have been developed to parameterize ammonium inhibition of nitrate uptake. Wroblewski (1977) proposed an empirical function with an exponential inhibition term:

$$\mu(N) = \frac{\text{NH}_4^+}{\text{NH}_4^+ + K_{\text{NH}_4}} + \frac{\text{NO}_3^- e^{-\psi\text{NH}_4^+}}{\text{NO}_3^- + K_{\text{NO}_3^-}} \quad (18)$$

where K_{NH_4} and K_{NO_3} are the half-saturation constants for NH_4^+ and NO_3^- uptakes and ψ is the exponential coefficient determining NH_4^+ inhibition for NO_3^- uptake. Hurtt and Armstrong (1996) proposed a formulation based on the argument that the sum of NH_4^+ and NO_3^- uptake should follow the Michaelis–Menten function $(\text{NO}_3^- + \text{NH}_4^+)/(\text{K}_N + \text{NH}_4^+ + \text{NO}_3^-)$:

$$\mu(N) = \frac{\text{NH}_4^+}{\text{NH}_4^+ + K_N} + \frac{K_N \text{NO}_3^-}{(\text{NH}_4^+ + K_N)(\text{NO}_3^- + \text{NH}_4^+ + K_N)} \quad (19)$$

O'Neill et al. (1989) deduced from molecular kinetics a substitution formulation between two nutrients that have been applied to NO_3^- and NH_4^+ uptakes:

$$\mu(N) = \frac{\text{NO}_3^-/K_{\text{NO}_3^-} + \text{NH}_4^+/K_{\text{NH}_4^+}}{1 + \text{NO}_3^-/K_{\text{NO}_3^-} + \text{NH}_4^+/K_{\text{NH}_4^+}} \quad (20)$$

Spitz et al. (2001) combined the Wroblewski and O'Neil functions for nitrogen uptake:

$$\mu(N) = \frac{\text{NH}_4^+/K_{\text{NH}_4^+} + \text{NO}_3^-/K_{\text{NO}_3^-} e^{-\psi\text{NH}_4^+}}{1 + \text{NO}_3^-/K_{\text{NO}_3^-} + \text{NH}_4^+/K_{\text{NH}_4^+}} \quad (21)$$

While taking into account nitrate reductase activity, Parker (1993) developed a formulation for nitrogen uptake based on the Michaelis–Menten function:

$$\mu(N) = \frac{\text{NH}_4^+}{\text{NH}_4^+ + K_{\text{NH}_4}} + \frac{K_{\text{NH}_4}}{\text{NH}_4^+ + K_{\text{NH}_4}} \frac{\text{NO}_3^-}{\text{NO}_3^- + K_{\text{NO}_3}} \quad (22)$$

Alternatively, Yajnik and Sharada (2003) proposed a modified Michaelis–Menten form in which a new free parameter was added to regulate the inhibition factor:

$$\mu(N) = \frac{\text{NH}_4^+}{\text{NH}_4^+ + K_{\text{NH}_4}} + \frac{1 + a\text{NH}_4^+}{1 + b\text{NH}_4^+} \frac{\text{NO}_3^-}{\text{NO}_3^- + K_{\text{NO}_3}} \quad (23)$$

where both a and b are constants which determine the NH_4^+ inhibition factor for NO_3^- uptake.

I have calculated the NH_4^+ inhibition factors for each formulation by assuming that nitrate uptake follows the Michaelis–Menten hyperbolic curve when no inhibition occurs (Fig. 2B). All these functions generate increasing inhibition factor with NH_4^+ concentration. The slopes of these curves can be adjusted by the corresponding parameters so that the different slopes do not necessarily mean different inhibition effects. However, the total nitrogen uptake rate (i.e., NH_4^+ uptake + NO_3^- uptake rates) is specific to each formulation (Fig. 2C). The Wroblewski function (Eq. (18)) generates a sigmoidal curve with the total nitrogen uptake rate increasing first, then decreasing with increase in NH_4^+ concentration. The Spitz function (Eq. (21)) generates high values of total nitrogen uptake rate when NH_4^+ approaches to zero and low value at intermediate NH_4^+ concentration (Fig. 2C, curve 4). This kind of irregular response of the total nitrogen uptake rate to increases in NH_4^+ concentration has not been reported and can lead to instability in numerical simulations.

The Yajnik function (Eq. (23)) generates a total nitrogen uptake factor >1 . According to the Michaelis–Menten and Droop functions, the maximum value of the limitation factor is 1 under nutrient replete condition, whereas the actual maximum value of phytoplankton growth rate is determined by the maximum growth rate of phytoplankton P_m (see Section 1). The Yajnik function can generate phytoplankton growth rate higher than the maximum growth rate and the simulation can be out of control. Moreover, the Liebig minimum law is applied when multiple nutrients are considered, i.e., the minimum of the uptake factor is applied among multiple types of nutrients. If the nitrogen uptake factor is >1 whereas that of other nutrients are <1 , the limitation effect of nitrogen will not be effectively taken into account and negative value can be simulated for this element.

The O'Neil, Hurrt and Parker functions all produce plausible total nitrogen uptake rate that slightly increases with respect to NH_4^+ concentration (Fig. 2C, curves 2, 4 and 5). The relatively high total nitrogen uptake rate at low NH_4^+ concentration ranges is due to the fact that nitrate is assumed replete so that the calculated total nitrogen uptake rate is not subject to nitrogen limitation. The O'Neil function (Eq. (20)) is a substitution formulation between two nutrients. It does not contain a specific inhibition factor and NH_4^+ can be equally substituted by NO_3^- under nitrate replete condition. The NH_4^+ inhibition on NO_3^- uptake is not a substitution phenomenon. It is governed by biochemical and physiological processes.

Besides inhibition, preference is another factor controlling NO_3^- versus NH_4^+ uptakes (Dortch, 1990). NH_4^+ is generally preferred over NO_3^+ , most likely due to the low energy cost of NH_4^+ uptake. The preference for NH_4^+ over NO_3^- is believed to be accentuated at low light and low nitrogen conditions (Dortch, 1990). This preference is usually parameterized by a lower half-saturation constant or a higher preference coefficient for NH_4^+ uptake than that for NO_3^- uptake. The Hurrt and Armstrong function (Eq. (19)) does not contain parameters that control the preference between NH_4^+ and NO_3^- . The Parker function (Eq. (22)) appears thus more adequate than other functions with respect to inhibition effect, total nitrogen uptake rate and preference of NH_4^+ over NO_3^- . Flynn et al. (1997) presented a complete model to simulate NH_4^+ inhibition for NO_3^- uptake, which contains external and internal pools of NO_3^- and NH_4^+ , respectively, glutamine, amino acids, cellular nitrogen, nitrite reductase and nitrate reductase. The model is mechanistic, but its application in biological and ecological models is limited due to its complexity.

4. Temperature forcing on phytoplankton growth rate

Various formulations have been used to describe the relationships between biological growth rates and temperature:

- Linear function:

$$\mu(T) = a + bT \quad (24)$$

- Log linear function:

$$\mu(T) = a + b \log(T + c) \quad (25)$$

- Power function:

$$\mu(T) = a(T + c)^b \quad (26)$$

- Exponential function:

$$\mu(T) = e^{aT} \quad (27)$$

- Q_{10} function:

$$\mu(T) = Q_{10}^{T/10} \quad (28)$$

- Arrhenius function:

$$\mu(T) = e^{(E/R)((1/T_{\text{opt}})-(1/T))} \quad (29)$$

Most of these functions are empirical and their controlling parameter values are so determined to fit a specific data set (Eppley, 1972; Dam and Peterson, 1988). The exponential function is the most frequently used in marine biological modeling (e.g., Eppley, 1972; Dam and Peterson, 1988; Huntley and Lopez, 1992; Radach and Moll, 1993; Bissett et al., 1999; Leonard et al., 1999; Kawamiya et al., 2000; Tian et al., 2001, 2003). The Q_{10} function is an operational expression which can be measured as the change in biological rate over 10°C (Toda et al., 1987; Doney et al., 1996). The Arrhenius function is mechanistic for enzyme activities, with E presenting the activation energy of a reaction, R being the gas constant ($8.3 \text{ Pa m}^3 \text{ K}^{-1} \text{ mol}^{-1}$), and T being the absolute temperature (Raven and Geider, 1988). The activation energy can be determined from the corresponding Q_{10} value with $E = RT \ln(Q_{10})/10$ (Dixon and Webb, 1979, p. 175).

According to these functions, biological rates increase infinitely as a function of temperature (Fig. 3, curves 1–6). A major challenge to these monotonous functions is that, in many cases, biological rates show an optimal temperature above which rates decreases (Pomeroy and Deibel, 1986; Wiencke and Dieck, 1989; Zupan and West, 1990; Yager and Deming, 1999; Pomeroy and Wiebe, 2001). Different formulations have been developed to parameterize the optimal temperature, including:

- Thebault function:

$$\mu_i(T) = 2(1 + a) \frac{s}{s + 2as + 1}, \quad s = \frac{T - T_0}{T_{\text{opt}} - T_0} \quad (30)$$

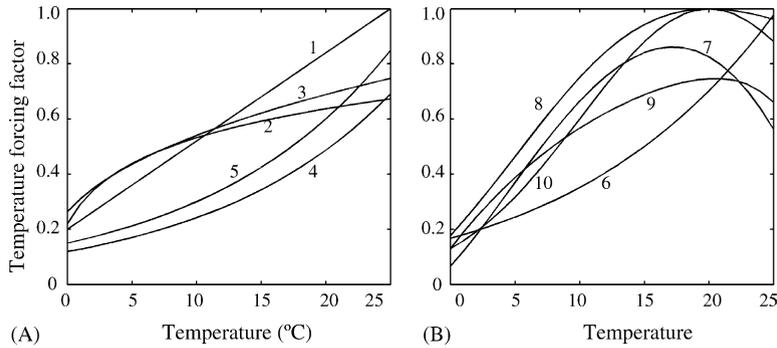


Fig. 3. Relationships between temperature and phytoplankton growth rate: (1) Linear function (Eq. (24)), (2) log-linear function (Eq. (25)), (3) power function (Eq. (26)), (4) exponential function (Eq. (27)), (5) Q_{10} function (Eq. (28)), (6) arrhenius function (Eq. (29)), (7) Thebault function (Eq. (30)), (8) Beta function (Eq. (31)), (9) exponential product function (Eq. (32)) and (10) modified exponential function (Eq. (33)).

where a is a constant, T_{opt} represents the optimal temperature and T_0 is the temperature under which the corresponding biological rate is zero (Thebault, 1985; Andersen and Nival, 1988; Skliris et al., 2001).

- Beta function:

$$\mu(T) = (T - T_{0L})^a (T_{0H} - T)^b \quad (31)$$

where a and b are constant and T_{0L} and T_{0H} are the low and high temperature under which the corresponding biological rate is zero (Carlotti et al., 2000).

- Exponential product (Kamykowski and McCollum, 1986):

$$\mu(T) = (1 - e^{-a(T-T_{0L})})(1 - e^{-b(T_{0H}-T)}) \quad (32)$$

- Modified exponential function:

$$\mu(T) = e^{-(T-T_{opt}/\Delta T)^2} \quad (33)$$

where ΔT is a constant determining the slope between biological rates and temperature (Lancelot, 2002).

There is no explicit biological interpretation of the temperatures at which biological rates are 0 in the Thebault, beta and exponential product functions. The values of these parameters are also difficult to evaluate. The modified exponential function has the optimal temperature and is flexible to produce different curves of temperature function. Moreover, the controlling parameter ΔT is readily determined from the measurable parameter Q_{10} .

5. Combination of light, temperature and nutrient forcing on phytoplankton growth

Temperature tends to influence the maximum growth rate so that its effect is multiplicative with the effects of light and nutrient (Steele, 1962; Webb et al., 1974). When multiple types of nutrients are considered, phytoplankton growth rate is generally determined by the availability of the nutrient in the shortest supply relative to the requirement by balanced growth, i.e., the Liebig Law. The Liebig Law of minimum was initially based on nutrient availability (Liebig, 1842). In addition to nutrient supplies, Blackman (1905) also considered light. Following Blackman’s suggestion, the minimum between light and nutrient limitation is often used as the combined effect on phytoplankton growth in modeling applications:

$$\mu_1 = \mu(T) \min(\mu(E), \mu(N(1, 2)), \mu(N(3)), \dots, \mu(N(nn))) \quad (34)$$

where $\mu_i(T)$, $\mu_i(E)$ and $\mu_i(N(j))$ are temperature, light and nutrient limiting factors on phytoplankton growth rate (Radach and Moll, 1993; Hurtt and Armstrong, 1996; Carbonel and Valentin, 1999; Napolitano et al., 2000; Oschlies et al., 2000; Denman and Pena, 2002). Alternatively, Baule (1918) expressed the combined effect of limiting factors by a multiplication. As a result, the product of light, temperature and nutrient forcing factors is also used in modeling applications (Goldman and Carpenter, 1974; Parsons et al., 1984; Andersen et al., 1987; Hofmann and Ambler, 1988; Moisan and Hofmann, 1996; Doney et al., 1996; Leonard et al.,

1999; Gao et al., 2000; Kawamiya et al., 2000; Tian et al., 2000, 2001; Chifflet et al., 2001; Fennel et al., 2002):

$$\mu_2 = \mu(E)\mu(T) \min(\mu(N(1, 2)), \mu(N(3)), \dots, \mu(N(nn))) \quad (35)$$

Both formulations are hypothetical. Experimental and field data often showed that the combined effect lies between the minimum and multiplication (Rhee and Gotham, 1981; Redalje and Laws, 1983). Consequently, I suggest to combine the minimum and multiplication forms:

$$\mu = \alpha\mu_1 + (1 - \alpha)\mu_2 \quad (36)$$

where $0 < \alpha < 1$.

6. Zooplankton feeding on a single type of prey

Zooplankton feeding modes can be broadly divided into filter feeding (e.g., herbivorous copepods), raptorial feeding (e.g., carnivorous copepods, euphausiids), and mucous net feeding (e.g., salps, doliolids, appendicularia). These feeding modes are not mutually exclusive, and examples of both filter feeding and raptorial feeding can often be found in one species, especially among planktonic crustaceans. On the basis of diet, zooplankton may be herbivorous, carnivorous, detritivorous, omnivorous, phytophagous, zoophagous or euryphagous (Parsons et al., 1984). There are two kinds of fundamental predator response to changes in prey density: “numerical response” (i.e., the number of predators changes as a function of prey density) and “functional response” (the ingestion rate of the predator changes as a function of prey density) (Solomon, 1949; Murdoch, 1969). Functional responses can be influenced by the predator’s ability to perceive and capture the specific prey, the time scales for handling and assimilating the prey and the nutritional content of the prey (Fenchel, 1980; Greene, 1986; Jonsson, 1986; Jonsson and Tiselius, 1990; DeMott and Waston, 1991). In general, there are three types of functional response of predators to prey density (Holling, 1959a, 1965, 1966; Real, 1977): linear and rectilinear, hyperbolic (curvilinear) and threshold (sigmoidal) responses.

The first type of functional response is described by linear or rectilinear functions:

$$g = \alpha P \quad (37)$$

$$g = \begin{cases} g_{\max} \frac{P}{K} & \text{for } P < K \\ g_{\max} & \text{for } P > K \end{cases} \quad (38)$$

where g_{\max} is the maximum grazing rate and α and K are constants (Fig. 4A; Riley, 1946; Frost, 1972; Gamble, 1978; Dagg and Grill, 1980; Klein and Steele, 1985; Mayzaud et al., 1998). The rectilinear relationship is explained by continuous filtration of water unaffected by the concentration of phytoplankton, so that ingestion increases linearly with food concentration up to a critical concentration above which the rate of passage of food through the gut limits the rate of ingestion (e.g., mucous net feeding).

The second type of functional response is curvilinear, which is also called the “invertebrate curve”. While studying fish feeding dynamics, Ivlev (1955) found that the quantity of food ingested increases with the concentration of food available up to some maximum ration beyond which the ingestion ceases to increase with food concentration. Thus, the feeding rate at a given prey concentration P must be proportional to the difference between the actual and the maximal ration:

$$\frac{\partial g}{\partial P} = \alpha(g_{\max} - g) \quad (39)$$

The integration of the above equation yields the Ivlev function:

$$g = g_{\max}(1 - e^{-\alpha P}) \quad (40)$$

where α is a constant and P represents prey concentration (Fig. 4A, curve 2). A number of authors found that this formulation could be applied to zooplankton feeding (Parsons et al., 1984). Rashevsky (1959) explained the physical and biological meaning of the initial slope α as the ratio between the rate that the prey becomes available to the predator and the maximum rate the predator can feed. Consequently, the Ivlev function was modified as

$$g = g_{\max}(1 - e^{-\alpha P/g_{\max}}) \quad (41)$$

According to Rashevsky (1959), the Ivlev curve best describes situations in which a starved animal feeds for a relatively short period of time. Measurements of

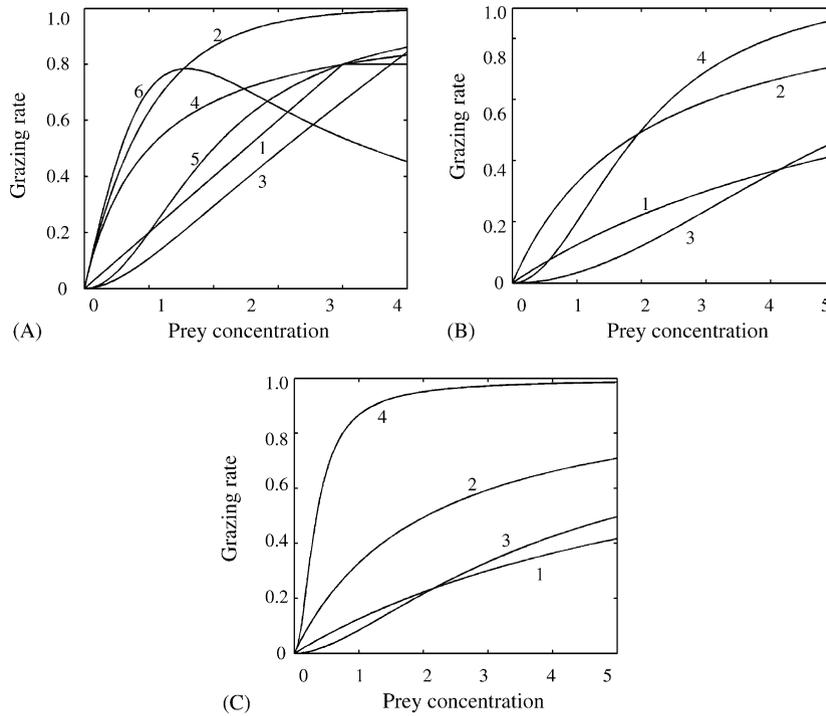


Fig. 4. (A) Zooplankton feed on a single type of prey: (1) rectilinear function (Eq. (38)), (2) Ivlev function (Eq. (40)), (3) combined linear and Ivlev function (Eq. (42)), (4) disc and Michaelis–Menten function (Eqs. (45) and (49)), (5) generalized Michaelis–Menten function (Eq. (53) with $n=2$), (6) inhibitory-substrate response (Eq. (55)). (B) Grazing on multiple types of preys based on the Michaelis–Menten function: (1) passive grazing with abundant prey of type 2 (Eq. (62) with $P2=100$), (2) passive grazing with limited prey of type 2 ($P2=1$), (3) active switching grazing with abundant prey of type 2 (Eq. (70) with $m=2, P2=100$), (4) active switching grazing with limited prey of type 2 ($P2=1$). (C) Grazing on multiple types of preys based on the disc function (Eqs. (60) and (67)). Function numbers are the same as that in panel (B).

well-nourished animals whose ingestion has reached equilibrium with food supply should generate a curve of different shapes. Mayzaud and Poulet (1978) combined the linear and Ivlev functions to simulate both Types I and II responses:

$$g = g_{\max} \alpha P (1 - e^{-\beta P}) \tag{42}$$

where α and β are constants (Fig. 4A, curve 3) (Mayzaud and Poulet, 1978; Franks et al., 1986). They attributed the increase in ingestion with increasing prey density to herbivore acclimation.

Holling (1959a) conducted a series of observations on predation dynamics using sawfly cocoons as prey and small mammals (shrew and deer mice) as predator. Based on these observations, he set up an artificial predator–prey scenario to analyze the mathematical relationship between prey density and predation rates

Holling (1959b). In his artificial predator–prey scenario, sandpaper discs served as prey and a blind-folded subject as the predator who removed the discs from the experiment table once found one. Assuming that N is the total number of discs and g is the number of discs removed (i.e., predation or grazing in modeling practice), it can be expected then:

$$g = aT_S N \tag{43}$$

where T_S is the time available for searching and a is a constant representing the rate of finding a disc in a unit time interval. T_S should be the difference between the total time interval T_T and the time used to remove discs found. If b represents the time to remove one disc (or handling time), then:

$$T_S = T_T - bg \tag{44}$$

Substituting Eq. (44) into Eq. (43) and adding the g_{\max} which is specific to a predator category results in the Holling's disc function:

$$g = g_{\max} \frac{aN}{1 + abN} \quad (45)$$

Fenchel (1980) deduced a similar equation for suspension feeding. Assuming that F is the clearing rate (i.e., the volume of water that the organisms can clear particles per unit time at low concentrations) and P is the concentration of particles (i.e., prey concentration), the feeding rate should be

$$g = FP \quad (46)$$

If each particle or unit volume of particles ingested blocks the mouth during τ time, then the feeding rate should be

$$g = FP(1 - \tau g) \quad (47)$$

and as a result:

$$g = g_{\max} \frac{FP}{1 + F\tau P} \quad (48)$$

In biological modeling, however, the most used formulation to describe feeding on a single prey type is the Michaelis–Menten function (also called the Monod function). While studying bacterial culture, Monod (1941, 1949) observed the hyperbolic nature of the bacterial growth rate as a function of substrate concentrations. Various functions can produce curves similar to that he had observed. By convenience, he had adapted the Michaelis–Menten function which was then widely used to describe the saturation of hemoglobin with respect to the partial pressure of oxygen. Following Monod, the Michaelis–Menten function is widely used to describe zooplankton grazing and predation:

$$g = g_{\max} \frac{P}{P + K_S} \quad (49)$$

where K is the half-saturation constant (Fig. 4A, curve 4) (Caperon, 1967; Walsh, 1975; Evans and Parslow, 1985; Radach and Moll, 1993; Strom and Loukos, 1998; Gao et al., 2000; Napolitano et al., 2000). Caperon (1967) explained the half-saturation constant as the ratio between the rate of freeing the absorption site and the rate of food uptake.

The third type of response, also called “vertebrate curve”, is characterized by a threshold of food den-

sity at which predation becomes negligible (Murdoch, 1969; Gismervik and Andersen, 1997; Strom, 1991). Holling (1959b) described the phenomenon as a “threshold of security” that stabilizes the prey population, others referred to a “refuge”, or “learning response”, i.e., zooplankton ignore low-density food (Holling, 1965; Mullin et al., 1975; Murdoch and Oaten, 1975). Another hypothesis for the threshold is that if the energy cost to zooplankton in searching and capturing food is high relative to energy gain, it is advantageous to cease feeding when foods are scarce (Mullin et al., 1975).

The Michaelis–Menten function has been modified with a specific threshold to simulate the Type III response:

$$g = g_{\max} \frac{P - P_0}{P - P_0 + K_S} \quad (50)$$

where P_0 represents the threshold (Walsh, 1975; Evans, 1988; Frost, 1993). Steele and Mullin (1977) modified the previous equation to take into account the predator weight in feeding dynamics:

$$g = g_{\max} \frac{P - P_0}{P - P_0 + K} W^\alpha \quad (51)$$

where W is the weight of the predator and α is a constant. Certain authors used sigmoidal functions for zooplankton predation (Fig. 4A, curve 5) (Denman and Pena, 2002; Oschlies et al., 2000):

$$g = g_{\max} \frac{P^2}{K_S^2 + P^2} \quad \text{or} \quad g = g_{\max} \frac{P^2}{K_S^2 + \alpha P + P^2} \quad (52)$$

Real (1977) and Steele and Henderson (1981) suggested a generalized Michaelis–Menten function which can parameterize both Types II and III responses:

$$g = g_{\max} \frac{P^m}{K_S + P^m} \quad (53)$$

where the power m determines the functional response of zooplankton feeding to prey density. With $m=1$, Eq. (53) is equivalent to the Michaelis–Menten function and thus corresponds to hyperbolic functional response. With $m=2$, Eq. (53) turns to be the sigmoidal function and thus corresponds to the vertebrate functional response. Note that the value of the half-saturation constant K_S also depends on m in Eq. (53).

Alternatively, Wroblewski (1977) modified the Ivlev function to parameterize threshold response:

$$g = g_{\max}(1 - e^{-\alpha(P-P_0)}) \quad (54)$$

A fourth functional response that was not included in the Holling's definition is the inhibitory-substrate response: (e.g., grazing of toxic algae) in which the grazing rate decreases with increasing food density after an optimal food concentration:

$$g = g_{\max} \frac{P}{K_S + P + \alpha P^2} \quad (55)$$

where α is a constant determining the inhibitory effect (Van Gernerden, 1974; Gentleman et al., 2003). This equation does not generate monotonous increases in ingestion with increasing prey density. Instead, the ingestion rate reaches a maximum at an intermediate prey density (or optimal density) after which the ingestion rate decreases again (Fig. 4A, curve 6). Gentleman et al. (2003) interpreted this decrease as a result of toxicity (e.g., toxic algae) or predator confusion.

In the linear or rectilinear representation there is assumed to be no interference between particles in the capture–ingestion mechanisms until the critical concentration is reached. In most cases however, ingestion and assimilation occur within a time duration, which slow down the capture rate or the availability of the receptor sites. The linear and rectilinear functions can be valid only in the low range of prey density below the saturation. The modified Ivlev function (Eq. (54)) has the threshold of prey density, but it cannot mathematically ensure null intake below that threshold and in some circumstances, it can yield negative feeding unless another conditional equation is imposed.

The disc function (Eq. (45)), the suspension feeding function (Eq. (48)) and the Michaelis–Menten function (Eq. (49)) are almost equivalent, with the Michaelis–Menten function having fewer free parameters. Assuming $1/ab=K$ in the disc function and $1/F\tau=K$ in the suspension feeding function, these two forms become the Michaelis–Menten function. The sigmoidal function (Eq. (52)) cannot fully simulate the threshold of prey. The threshold has been interpreted as a “threshold of security” that stabilizes prey populations. Such a security threshold is also important in numerical simulation. If zooplankton grazing results in zero concentration of phytoplankton in a model, phytoplankton blooms will never be possible even with

abundant nutrient supply, i.e., a numerical extinction. The generalized Michaelis–Menten function (Eq. (53)) is attractive because it can simulate different functional responses, but it does not contain a parameter specifying the threshold. Following Eq. (50) in which a threshold is added in the Michaelis–Menten function, a threshold term can be added in the generalized Michaelis–Menten function:

$$g = g_{\max} \frac{(P - P_0)^m}{K_S^m + (P - P_0)^m} \quad (56)$$

In this form the half-saturation constant K_S is no more m -dependent as it is in the original formulation (Eq. (53)). This equation has the flexibility to simulate different functional response and can prevent numerical extinction of prey populations by the specific threshold. Consequently, I suggest this equation as the a priori choice for bask parameterization of predation on a single type of prey. This function does not include the inhibitory uptake which can be treated as a particular case using Eq. (55).

7. Zooplankton feeding on multiple types of prey

Many zooplankton species have been found to be omnivorous, i.e., they feed upon multiple types of prey instead on a single type of prey (Poulet, 1978; Landry, 1981; Gifford and Dagg, 1988; Stoecker and Capuzzo, 1990; Turner and Roff, 1993; Kiorboe et al., 1996). Mesozooplankton (e.g., copepods and dinoflagellates) can feed on phytoplankton, microzooplankton and detritus while microzooplankton (e.g., ciliates and heterotrophic nanoflagellates) can feed on picophytoplankton, bacteria and suspended particles.

When multiple types of prey are involved, feeding modes can be divided into three categories: non-selection feeding (i.e., the proportion of different types of prey in the diet is the same as in the food available), passive selection (i.e., the proportion of different types of prey in the diet differs from that of the food available, but with constant selectivity or preference), and switching selection (i.e., the preferences or proportion change as a function of prey density) (Teramoto et al., 1979; Goldman and Dennett, 1990; Strom, 1991; Wickham, 1995; Strom et al., 2000). Feeding selection depends on the abundance, size, shape, nutritional

status, motility, toxicity, and chemical composition of the prey (Andersson et al., 1986). Biological traits of the predators also influence their ability in food selection, such as size, mouth width, chemosensory and mechanosensory ability (Verity, 1991; Naoki et al., 2001). Predator switching can exert striking effects on the stability of prey populations by preventing extinction of rare species, preserving biodiversity and favoring coexistence of different predators (Murdoch, 1969; Murdoch, 1973; Murdoch and Oaten, 1975; Cousins and Hassell, 1976; Tansky, 1978; Hutson, 1984). Switching feeding has been showed even more important than trophic cascade in determining population dynamics of marine organisms (Wickham, 1995; Kiorboe et al., 1996).

Passive selection (no switching) feeding is usually parameterized by a constant preference coefficient for each type of prey. Based on the functions of predation on a single type of prey (see the preceding section), formulations for passive selection feeding include rectilinear, Ivlev, disc and Michaelis–Menten functions and their modified forms.

Armstrong (1994) developed a model of multiple food chains, with each food chain consisting of a size class of phytoplankton and zooplankton. Zooplankton of each food chain grazes only upon the specific type of phytoplankton. Following Moloney and Filed (1991), he allowed predation on zooplankton of the next smaller class so that two types of food were involved. He used a rectilinear function to determine feeding selection and trophic dynamics:

$$g_i = \begin{cases} g_{\max} \frac{p_i P_i}{K} & \text{for } R \leq K \\ g_{\max} \frac{p_i P_i}{R} & \text{for } R > K \end{cases}, \quad R = \sum_{j=1}^n p_j P_j \quad (57)$$

where g_i is the intake on prey P_i by a specific zooplankton category, p_i the corresponding preference coefficient, K represents the saturation constant (not the half-saturation constant) and R is the total food available to a specific zooplankton category.

Leonard et al. (1999) conducted a modeling study on a high-nitrate, low-chlorophyll ecosystem, the central equatorial Pacific. In their model, there are two categories of phytoplankton (nanoplankton and netplankton) and two categories of zooplankton (microzooplankton and mesozooplankton). Mesozooplank-

ton were allowed to feed upon netplankton and microzooplankton, i.e., two prey types. They used the combined linear and Ivlev function for each prey type:

$$g_i = g_{\max i} \beta_i P_i (1 - e^{-\beta_i P_i}) \quad (58)$$

In their application, all the controlling parameters (including the maximum grazing rate $g_{\max i}$) were specific for each type of prey and there is no interference between different types of prey.

Hofmann and Ambler (1988) proposed another form to compute grazing on multiple types of prey based on the Ivlev function. Zooplankton grazing on small and large phytoplankton was computed as

$$g_i = g_{\max} (1 - e^{-\psi R}) \frac{p_i P_i}{R}, \quad \text{with } R = \sum_{j=1}^n p_j P_j \quad (59)$$

where R represents the total effective food concentration and ψ is the Ivlev coefficient. The total ingestion is determined by the total effective food and the Ivlev exponential coefficient whereas the intake of each phytoplankton pool P_j is determined by its proportion in the total food and the preference coefficient p_i .

Murdoch (1973) and Holt (1983) extended the Holling disc function to feeding on multiple types of prey:

$$g_i = g_{\max} \frac{a_i N_i}{1 + \sum_{j=1}^n a_j \tau_j N_j} \quad (60)$$

where a_i and τ_i are the capture rate and handling time specific to the prey item N_i . Similarly, the Michaelis–Menten function applied to predation on multiple types of prey is usually written as

$$g_i = g_{\max} \frac{p_i P_i}{K + \sum_{j=1}^n p_j P_j} \quad (61)$$

where the preference coefficient p_i is specific for each prey type whereas the half-saturation constant is relative to the total prey concentration (Moloney and Filed, 1991). The Michaelis–Menten function was also used as

$$g_i = g_{\max} \frac{p_i P_i}{1 + \sum_{j=1}^n p_j P_j} \quad (62)$$

where the preference coefficients (p_i, p_j) correspond to that in Eq. (61) divided by the half-saturation constant K (Verity, 1991; Fasham et al., 1999; Strom and

Loukos, 1998; Tian et al., 2001). Alternatively, the Michaelis–Menten function was modified as

$$g_i = g_{\max} \left(\frac{R - P_0}{K + R - P_0} \right) \frac{p_i P_i}{R}, \quad \text{with} \quad (63)$$

$$R = \sum_{j=1}^n p_j P_j$$

where R represents the total food available and P_0 presents the threshold of total food below which feeding ceases (Evans, 1988; Lancelot et al., 2000; Leising et al., 2003). According to this equation, the total ingestion is determined by the total food available whereas the intake from each type to prey is determined by its relative abundance among total food and its preference coefficient.

All the above equations are characterized by the fact that the intake ratios among various types of prey differ from their ratios of abundance due to their specific preference coefficients. However, the preference coefficients do not change with the relative abundance of different types of prey, i.e., passive selection.

Functions of active selection feeding are characterized by varying effective preferences according to the relative abundance of prey. Fasham et al. (1990) developed a biological model in which zooplankton feed upon phytoplankton, bacteria and detritus, parameterized by a switching feeding function among the three types of prey. They parameterized the effective preference as a function of the relative abundance of each prey among the total food available:

$$p'_i = \frac{p_i P_i}{\sum_{j=1}^n p_j P_j} \quad (64)$$

where p'_i represents the effective preference coefficient of the prey P_i and p_i is the nominal preference, i.e., the effective preference when all the types of prey have equal abundance. Substituting p_i in the Michaelis–Menten function for multiple types of prey (Eq. (61)) with p'_i in Eq. (64), the switching feeding function is then:

$$g_i = g_{\max} \frac{p_i P_i^2}{K \sum_{j=1}^n p_j P_j + \sum_{j=1}^n p_j P_j^2} \quad (65)$$

In a similar way, Chesson (1983) deduced a switching feeding function based on the Holling disc function. Instead using a constant capture rate, he assumed that

the capture rate is linked to the relative abundance of each type of prey:

$$b_i = \frac{a_i N_i}{1 + c_i N_i} \quad (66)$$

Assuming $c_i = a_i \tau_i$, this relationships is similar to the disc function (Eq. (45)). Substituting the constant capture rate a_i in Eq. (60) by the varying effective capture rate b_i in Eq. (66), the switching disc function is then:

$$g_i = g_{\max} \frac{a_i N_i^2}{(1 + c_i N_i)(1 + \sum_{j=1}^n (a_j \tau_j N_j^2 / (1 + c_j N_j^2)))} \quad (67)$$

Meanwhile, some authors developed generalized forms by which the degree of selection or switching among various types of prey can be simulated. Tansky (1978) and Matsuda et al. (1986) developed the following formulation for predation on multiple types of prey:

$$g_i = g_{\max} \frac{(p_i P_i)^m}{\sum_{i=1}^n (p_i P_i)^m} \quad (68)$$

and Vance (1978) suggested a similar equation:

$$g_i = g_{\max} \frac{(p_i P_i)^m}{(\sum_{i=1}^n (p_i P_i)^m)} \quad (69)$$

where the power m determines the degree of selection among various types of prey. Both equations apply to feeding on multiple types of prey, but when only a single type of prey is involved, these equations result in independent feeding from prey densities. Alternatively, Gismervik and Andersen (1997) developed a more generalized formulation:

$$g_i = g_{\max} \frac{(p_i P_i)^m}{1 + \sum_{i=1}^n (p_i P_i)^m} \quad (70)$$

which can simulate various switching predation and functional responses. When $m = 1$, this equation becomes the Michaelis–Menten function for passive selection feeding (Eq. (62)). When $m = 2$, it is similar to the Fasham’s function for switching feeding (Eq. (65)). The higher the power m is, the higher the degree of switching occurs among various types of prey. When $m \sim \infty$, Eq. (70) generates exclusive or unique selection among various types of prey, i.e., feeding only on the most abundant prey and ignoring all other types of prey. This equation also applies to a single type of prey. When the number of types of prey n equals to 1,

Eq. (70) is equivalent to the generalized function for feeding on a single type of prey (Eq. (56)).

Feeding threshold is an observed fact (Frost, 1975; Strom, 1991; Strom et al., 2000) which is not specifically included in Eq. (70). As in the generalized Michaelis–Menten function for feeding on a single type of prey, a specific threshold for each type of prey can be added in Eq. (70), which results in the following form:

$$g_i = g_{\max} \frac{(p_i(P_i - P_{0i}))^m}{1 + \sum_{i=1}^n (p_i(P_i - P_{0i}))^m} \quad (71)$$

where P_{0i} represents the threshold of the prey P_i .

Passive and active selection feeding described by using the Michaelis–Menten function and the disc function are illustrate in Fig. 4B and C, respectively. Four scenarios of ingestion of a type of prey are simulated by each function with the presence of a second type of prey: passive selection under low and high density of the second type of prey (Eq. (62) for Michaelis–Menten function and Eq. (60) for the disc function) and active selection under low and high density of the second type of prey (Eq. (70) for Michaelis–Menten function with $m = 2$ and Eq. (67) for the disc function). For passive selection, both functions simulated much higher intake of the prey 1 under low density of prey 2 (Fig. 4, curves B2 and C2) than under high density of prey 2 (Fig. 4, curves B1 and C1). Even without specific parameterization of switching feeding, both functions simulates intake shift from the preys 2 to 1 when prey 2 becomes scarce. This simulated shifting is due to the changes in the relative abundance between the two types of prey while the half-saturation constants or preference coefficients remain unchanged. However, the active-switching forms simulated more important shift from preys 2 to 1 (Fig. 4, curves B3 and B4 and C3 and C4) than the passive-selection equations. The switching functions generated sigmoidal curves (Fig. 4, curves B3 and B4 and C3 and C4) which correspond to the Type III functional response (Fig. 4, curve A5), whereas passive-selection functions generated hyperbolic curves (Fig. 4, curves B1 and B2 and C1 and C2) which correspond to the Type II functional response (Fig. 4, curves A2 and A4).

Zooplankton have various feeding behaviors and can shift from one feeding mode to another. For example, Kiorboe et al. (1996) found that copepod *Acartia tonsa* shifted from suspension feeding mode by creat-

ing a feeding current when presented with diatoms to raptorial feeding mode by ambushing when exposed to ciliates. The various feeding behaviors may require different mathematical description. In modeling practice, however, zooplankton are usually represented by aggregated state variables such as zooplankton compartment or mesozooplankton and microzooplankton. Different feeding behaviors among various species are not explicitly considered. Various mathematical functions have been used for the same purpose. In this context, narrowing down the mathematical choices is plausible.

The disc function and the Michaelis–Menten function are almost equivalent. Given that the later has fewer free parameters than the former, it has been widely used in modeling applications. The Ivlev function has been successfully applied for feeding on a single type of prey. However, its flexibility and adaptability for feeding on multiple types of prey show certain limitation. On the other hand, the generalized form of the Michaelis–Menten function (Eq. (71)) can simulate various feeding behaviors and functional responses. It applies to feedings on both a single type and on multiple types of prey. Given its generality and flexibility, I suggest this parameterization as the a priori selection for trophic dynamics.

8. Mortality

Zooplankton mortality usually represents the model closure term. Zooplankton mortality consists of natural mortality, which may be caused by disease and starvation, and mortality due to predation by predators and cannibalism within the same compartment. Different parameterizations of plankton mortality have been used in modeling applications:

- Linear function (e.g., Evans and Parslow, 1985; Tian et al., 2000):

$$\frac{\partial Z}{\partial t} = -mZ \quad (72)$$

- Quadratic function (e.g., Steele and Henderson, 1981; Denman and Gargett, 1995; Fasham, 1995):

$$\frac{\partial Z}{\partial t} = -mZ^2 \quad (73)$$

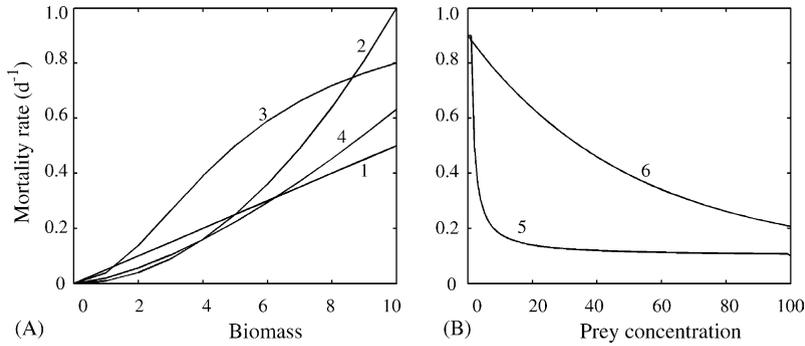


Fig. 5. (A) Biomass-dependent mortality: (1) linear function (Eq. (72)), (2) quadratic function (Eq. (74)), (3) sigmoidal function (Eq. (75)), (4) generalized function (Eq. (79) with $n = 1.5$). (B) Food-dependent mortality: (5) reciprocal function (Eq. (76)) and (6) exponential function (Eq. (77)).

- Hyperbolic function (e.g., Frost, 1987; Ross and Gurney, 1994; Tian et al., 2004):

$$\frac{\partial Z}{\partial t} = -m \frac{Z^2}{K + Z} \quad (74)$$

- Sigmoidal function (e.g., Malchow, 1994; Edwards and Yool, 2000):

$$\frac{\partial Z}{\partial t} = -m \frac{Z^2}{K^2 + Z^2} \quad (75)$$

- Food-dependent rectilinear function (Andersen and Nival, 1988):

$$\frac{\partial Z}{\partial t} = \begin{cases} -mZ & \text{for } P \geq P_0 \\ -\left(\frac{\alpha}{P} + m_0\right)Z & \text{for } P < P_0 \end{cases} \quad (76)$$

- Food-dependent exponential function (Andersen et al., 1987):

$$\frac{\partial Z}{\partial t} = -(m e^{-\alpha(P/Z)} + m_0)Z \quad (77)$$

- Temperature-dependent quadratic function (Kawamiya et al., 2000):

$$\frac{\partial Z}{\partial t} = -m_0 e^{\alpha T} Z^2 \quad (78)$$

- Generalized formulation (Edwards and Yool, 2000):

$$\frac{\partial Z}{\partial t} = -mZ^n \quad (79)$$

In the above equations, Z represents the zooplankton, P the prey, T the temperature, m , m_0 , K , P_0 , and n are constants. Eqs. (76) and (77) link zooplankton mortality to food availability to represent starvation. Eq. (76) generates more rapid increase in mortality than Eq. (77) at low ranges of prey density (Fig. 5B). The assumption behind these food-dependent parameterizations is that zooplankton do not have important lipid storage. In many cases, however, adult zooplankton have lipid storage that can be used for diapause and reproduction. Kawamiya et al. (2000) linked the zooplankton mortality to temperature by an exponential function, but they did not provide the rationale and assumption underpinning. The linear function means that zooplankton mortality is not influenced by its density. In modeling practice, however, the mortality includes several terms, such as natural mortality, predation and cannibalism (both true cannibalism and intratrophic predation because zooplankton in models usually aggregate a large number of species of different sizes). Predation and cannibalism are most likely density-dependent. The generalized form (Eq. (79)) is more flexible in which the power n determines the dependency of mortality on population density. It can be used as linear, quadratic or in between (which is closer to the hyperbolic and sigmoidal function in high density ranges, Fig. 5A). I propose this generalized form as the a priori parameterization of mortality which can approximate other formulations. It can be used for both zooplankton and phytoplankton. In the case of phytoplankton, aggregation which leads to the formation of large sinking particles justifies the usage of density-dependent functions.

9. Respiration and excretion

Respiration and excretion represent the metabolic losses of carbon and nitrogen, respectively. Metabolic processes consist of different components such as basic metabolism, locomotion, assimilation, synthesis of somatic and gonad tissue, material transformation, etc. (Clarke, 1987; Carlotti et al., 2000). Total metabolism is two to three times higher than the basic metabolism at resting (Steele and Mullin, 1977; Parsons et al., 1984). In general, respiration can be divided into basic respiration and active respiration (the later includes all respiration resulting from biological activities). The simplest formulation of respiration and excretion is a linear function of biomass (Eq. (72); Fasham et al., 1990). Walsh (1975) and Tian et al. (2001) linked respiration to ingestion instead to biomass by considering that active respiration dominates over basic respiration:

$$\frac{\partial Z}{\partial t} = -ag(P) \quad (80)$$

where a is a constant and $g(P)$ is the ingestion. Steele (1974) and Carlotti and Sviandra (1989) combined biomass- and ingestion-dependent functions by considering both basic and active respiration:

$$\frac{\partial Z}{\partial t} = -ag(P) - bZ \quad (81)$$

Alternatively, Hofmann and Ambler (1988) linked the active respiration to prey concentration instead of ingestion:

$$\frac{\partial Z}{\partial t} = -(aP + b)Z \quad (82)$$

where a and b are constants and P and Z represent prey and predator abundance, respectively. Moloney and Field (1989) expressed respiration as a function of zooplankton weight:

$$\frac{\partial Z}{\partial t} = -aW^b \quad (83)$$

where W represents zooplankton weight or individual biomass. Andersen et al. (1987) and Hirst and Shearer (1997) scaled respiration as an exponential function of temperature T :

$$\frac{\partial Z}{\partial t} = -ab^T Z \quad (84)$$

Among these various respiration functions, the combination between the linear function of biomass and ingestion (Eq. (81)) appears to be the most explicit description of respiration processes. The linear function of biomass represents the basic respiration whereas that of ingestion represents the active respiration. Body weight and temperature influence ingestion rate so that their effects on respiration can be included in the ingestion. This equation has also been applied to phytoplankton exudation of dissolved organic matter, i.e., DOM exudation has been parameterized as a combined linear function of both phytoplankton biomass and primary production:

$$\frac{\partial \text{DOM}}{\partial t} = (a + b\mu)P \quad (85)$$

where a and b are the constants, μ the phytoplankton growth rate and P is the phytoplankton biomass (Bannister, 1979; Spitz et al., 2001).

10. Conclusion

Standardization of biological parameterization resides in the development of mechanistic formulations based on physiological and biological dynamics instead of empirical forms from data fitting. However, few mechanistic functions have been developed in marine biological modeling. Sakshaug et al. (1989) have developed a mechanistic formulation of the μ - E relationship based on photosynthetic processes (Eq. (13)), but they did not consider photoinhibition phenomenon. The disc function for zooplankton grazing is based on feeding dynamics on a single type of prey (Eq. (45)), but it does not include omnivorous feeding and preference. Based on the correctness, functionality and generality of the existing empirical function, I have selected 10 parameterizations as the a priori set of parameterizations (Table 1). In most cases, these selected parameterizations can reproduce other functions by adjusting the controlling parameters. The Platt function (Eq. (8)) appears to be the most adequate to describe the μ - E relationship. The first term of this function is the same as the mechanistic function (Eq. (13)) and its photoinhibition term allows it to apply to a large range of different ecosystems. When the photoinhibition coefficient β is assigned to 0, the photoinhibition effect will be removed from the simulation

Table 1
Selected a priori parameterizations for marine biological modeling

Function	Symbols	Reference
(1) μ - E relationship $\mu(E) = P_m(1 - e^{-\alpha E/P_m})e^{-\beta E/P_m}$	μ : phytoplankton growth rate, E : PAR, P_m : theoretical maximum of μ , α : initial slope, β : photoinhibition coefficient	Platt et al. (1980)
(2) Nutrient limitation: $\mu(N) = \frac{N_j - N_0}{N + K - N_0}$	N_j : nutrient concentration, K : half-saturation constant, N_0 : threshold	Caperon and Meyer (1972), Paasche (1973), Dugdale (1977) and Droop (1983)
(3) NH_4^+ inhibition on NO_3^- uptake: $\mu(N) = \frac{\text{NH}_4^+}{\text{NH}_4^+ + K_{\text{NH}_4}} + \frac{\text{NO}_3^-}{\text{NH}_4^+ + K_{\text{NH}_4} \text{NO}_3^- + K_{\text{NO}_3}}$	NH_4^+ : NH_4^+ concentration, NO_3^- : concentration, K_{NH_4} : half-saturation constant of NH_4^+ , K_{NO_3} : half-saturation constant of NO_3^-	Parker (1993)
(4) Temperature forcing: $\mu(T) = e^{-((T - T_{\text{opt}})/\Delta T)^2}$	T : temperature, T_{opt} : optimal temperature, ΔT : constant	Lancelot et al. (2002)
(6) Feeding on a single type of prey: $g = g_{\text{max}} \frac{(P - P_0)^n}{K + (P - P_0)^n}$	G_{max} : maximum feeding rate, P : prey concentration, P_0 : prey threshold, K : half-saturation constant.	Real (1977), Steele and Henderson (1981) and this work for P_0
(7) Feeding on inhibitory prey: $g = g_{\text{max}} \frac{P}{K + P + \alpha P^2}$	P : prey concentration, K : half-saturation constant, α : constant	Van Gernerden (1974) and Gentleman et al. (2003)
(8) Feeding on multiple types of prey: $g_i = g_{\text{max}} \frac{(p_i(P_i - P_{0i}))^m}{1 + \sum_{i=1}^n (p_i(P_i - P_{0i}))^m}$	P : prey concentration, P_0 : prey threshold, p : preference coefficient, m : constant	Gismervik and Andersen (1997); This work for P_0 .
(9) Mortality: $\frac{\partial Z}{\partial t} = -mZ^n$	Z : zooplankton biomass, m , n : constants	Edwards and Yool (2000)
(10) Respiration: $\frac{\partial Z}{\partial t} = -ag(P) - bZ$	Z : zooplankton biomass, $g(P)$: ingestion, a , b : constants	Steele (1974) and Carloti and Sviandra (1989)

for ecosystems in which photoinhibition has not been observed. This parameterization has been widely used in modeling applications (Moisan and Hofmann, 1996; Leonard et al., 1999; Tian et al., 2000, 2004; Lancelot et al., 2000; Chifflet et al., 2001). The combination of the Michaelis–Menten and Droop functions (Eq. (17)) is selected to describe nutrient limitation on phytoplankton growth rate. This formulation has the advantage to parameterize both the half-saturation constant and the threshold of nutrient, whereas other functions parameterize only the half-saturation or the threshold of nutrients, but not both. It should be pointed out that the initial threshold of nutrient in the Droop equation was used for internal nutrient cell quota whereas in Eq. (17), it is designated for external nutrient concentration in seawater. Even though the threshold can be assigned to zero for major nutrients (e.g., NO_3^- , $\text{Si}(\text{OH})_4$), thresholds are necessary to simulate minor nutrient (e.g., Fe) limitation of phytoplankton growth rate (Martin, 1992). The modified exponential function (Eq. (33)) can simulate the optimal temperature at which biological growth rates reach a maximum value. The parameter ΔT determining the initial slope between biological rates and temperature in Eq. (33) can be readily esti-

mated from observed values of Q_{10} . A new formulation has been put forward to combine temperature, light and nutrient forcing on phytoplankton growth, i.e., to use an intermediate value between the minimum and production of light and nutrient limitation factors (Eq. (36)). For zooplankton feeding on a single type of prey and multiple types of prey, the generalized forms (Eqs. (56) and (71)) were selected over other relatively rigid and monotonous forms. These generalized functions allow simulating different functional responses and variable degrees of switching feeding among various types of prey. Also, a generalized form of mortality was chosen as the a priori parameterization (Eq. (79)). The combined linear function of both biomass and ingestion simulates the basic and active respiration together, whereas other forms parameterize only one fraction of respiration. Most of these a priori parameterizations have been widely used in previous modeling applications. They are subject to further tests in modeling practice and can be replaced by more advanced parameterizations in the future. I suggest to use these selected parameterizations when they can reproduce well the observations. By doing this, we can reduce the number of biological parameters that need

to be estimated and provide a better opportunity for intercomparison.

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