# Theoretical considerations on factors confounding the interpretation of the oceanic carbon export ratio

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**Key points**

1. Mechanistic models of the export ratio integrated over various depths are developed based on the metabolic balance between photosynthesis and respiration
2. Discrepancies between studies on the relationship between the export ratio and taxonomy, temperature and productivity, may be explained by a variety of factors, including the depths of integration, biomass, and surface light availability
3. Seasonal variability in the export ratio in high latitudes is in great part controlled by mixed layer depth and photosynthetically active radiation
4. Our study demonstrates and discusses some of the mathematical and biogeochemical limitations of the export ratio, arguing for improvements or the development of new proxies



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**Abstract**

The fraction of primary production exported out of the surface ocean, known as the export ratio ($ef$-ratio), is often used to assess how various factors, including temperature, primary production, phytoplankton size and community structure, affect the export efficiency of an ecosystem. To investigate possible causes for reported discrepancies in the dominant factors influencing the export efficiency, we develop a metabolism-based mechanistic model of the $ef$-ratio. Consistent with earlier studies, we find based on theoretical considerations that the $ef$-ratio is a negative function of temperature. We show that the $ef$-ratio depends on the optical depth, defined as the physical depth times the light attenuation coefficient. As a result, varying light attenuation may confound the interpretation of $ef$-ratio when measured at a fixed depth (e.g., 100 m) or at the base of the mixed layer. Finally, we decompose the contribution of individual factors on the seasonality of the $ef$-ratio. Our results show that at high latitudes, the $ef$-ratio at the base of mixed layer is strongly influenced by mixed layer depth and surface irradiation on seasonal timescales. Future studies should report the $ef$-ratio at the base of euphotic layer, or account for the effect of varying light attenuation if measured at a different depth. Overall, our modeling study highlights the large number of factors confounding the interpretation of field observations of the $ef$-ratio.

**Key words**: Oceanic carbon export ratio, net community production, export production, net primary production

## 1. Introduction

The importance of relating oceanic carbon export to primary production has long been recognized. Building on *Dugdale and Goering* [1967] apportionment of primary production into "new" and regenerated production, *Eppley and Peterson* [1979] proposed to normalize new production to primary production ($f$-ratio). These seminal papers prompted complementary efforts to characterize the factors influencing the $f$-ratio, and the ratio of organic carbon export or particulate organic carbon (POC) export to total primary production (e-ratio and pe-ratio, respectively) [*Aksnes and Wassmann*, 1993; *Baines et al*., 1994; *Betzer et al*., 1984; *Dunne et al*., 2005; *Henson et al*., 2011; *Laws et al*., 2000; *Michaels and Silver*, 1988; *Murray et al*., 1996]. Whereas the $f$-ratio reflects the proportion of primary production fueled by "new" nutrients (or not fueled by regenerated nutrients), the e-ratio reflects the proportion of primary production exported (i.e., which has escaped respiratory processes). In a steady-state system with no change in elemental stoichiometry and no nitrification at the ocean surface, the $f$-ratio and e-ratio should be equal as export production should balance new production. Hereafter, we use the term "$ef$-ratio" following *Laws et al*. [2000] to describe the ratio of new or export production.

Among other things, the $ef$-ratio has been hypothesized to vary as a function of sea surface temperature (SST), net primary production (NPP), respiration and sinking rates of particles. The negative relationship between the $ef$-ratio and SST reported in some studies has been attributed to the stronger temperature dependency of respiration compared to photosynthesis [*Cael and Follows*, 2016; *Dunne et al*., 2005; *Henson et al*., 2011; *Laws et al*., 2000; *Laws et al*., 2011; *Rivkin and Legendre*, 2001]. A positive relationship between the $ef$-ratio and NPP and/or phytoplankton biomass concentration has also been reported in various regions of the world oceans [*Dunne et al*., 2005; *Eppley and Peterson*, 1979; *Huang et al*., 2012; *Laws et al*., 2011; *Laws et al*., 2000]. Conversely, the sinking rate of particles is

expected to vary as a function of their density and size [*Alldredge and Silver*, 1988], which are in turn related to the mineral content of the particles [*Armstrong et al*., 2002; *Francois et al*., 2002; *Klaas and Archer*, 2002], aggregation [*Burd and Jackson*, 2009; *Passow et al*., 1994], and plankton community structure [*Boyd and Newton*, 1995; *Boyd and Newton*, 1999; *Buesseler*, 1998; *Guidi et al*., 2016; *Michaels and Silver*, 1988]. These factors are often interconnected, which may explain the difficulty in identifying and quantifying the dominant factors. For example, some plankton types are generally associated with high production (NPP) and biomass regimes, which may also influence aggregation [*Jackson and Kiorboe*, 2008; *Passow et al*., 1994].

In this vein, *Britten et al*. [2017] attributed to confounding factors the recent report of a lack of dependency of the carbon export efficiency on temperature in the Southern Ocean [*Maiti et al*., 2013]. According to their "temperature-ballast" hypothesis, changes in ballasting masked the effect of temperature on the export efficiency [*Britten et al*., 2017; *Henson et al*., 2015]. An inverse relation of the export efficiency on NPP in the Southern Ocean as reported by *Maiti et al*. [2013] also prompted various hypotheses for mechanisms, including trophic structure, grazing and fecal pellet production, bacterial activity and recycling, and dissolved organic carbon (DOC) export [*Cavan et al*., 2015; *Laurenceau-Cornec et al*., 2015; *Le Moigne et al*., 2016; *Maiti et al*., 2013]. As importantly, a lack of steady-state, for example with export lagging production [*Buesseler*, 1998; *Buesseler et al*., 2009; *Henson et al*., 2015] would also bias estimates of the export ratio.

However, more fundamental factors, even at steady-state, may also explain the large scatter in the relation of the carbon export efficiency on predictors. For example, the depth of the measurements [*Boyd et al*., 1995; *Buesseler and Boyd*, 2009; *Palevsky and Doney*, 2018], and the depth of the mixed layer in absolute terms and in relation to the depth of measurement of the $ef$-ratio may also introduce noise. As stated by *Buesseler* [1998], "since

both production and particulate export are strongly depth dependent, the relative ratio of these will depend upon the depth of integration." The net production of organic matter, aka net community production (NCP) and which reflects the carbon export potential as presented in *Li and Cassar* [2017], is depth-dependent because it results from the balance between photosynthesis, which decreases with depth, and respiration. Conversely, POC export is depth-dependent because of remineralization and POC attenuation with depth. Such concepts are important but often overlooked when interpreting differences in $ef$-ratios between ecosystems and between studies.

In this study, we explore how some of these factors may confound the interpretation of the $ef$-ratio using a mechanistic model of the metabolic balance between photosynthesis and respiration. Using this model, we first compare $ef$-ratios at different depths of integration (i.e., euphotic depth (1% of surface irradiance), fixed depth, and mixed layer depth) and discuss factors regulating their relations to NPP. For example, two identical plankton communities may have diverging $ef$-ratios because of differences in mixed layer depth, with shallower mixed layers leading to higher $ef$-ratios. Similarly, our theoretical considerations predict that two ecosystems with differing autotrophic biomass and growth rates but equivalent NPP will display different $ef$-ratios, with the greater growth rates leading to a higher $ef$-ratio. Finally, we partition and examine the influence of the individual factors (i.e., mixed layer depth, surface irradiance, SST, nutrient concentration, and chlorophyll concentration) on the seasonality of the $ef$-ratio at the base of mixed layer of the world's oceans.

## 2. Model description

By definition, the volumetric NCP at depth $z$ ($NCP(z)$) is equal to the volumetric NPP ($NPP(z)$) minus the volumetric heterotrophic respiration ($HR(z)$) [*Li and Cassar*, 2017]:

$$NCP(z) = NPP(z) - HR(z)$$

$$= N_m \times I_m(z) \times \mu_{max} \times C - r_{HR} \times C \qquad (1)$$

where $C$, $\mu_{max}$, $N_m$, $I_m(z)$, and $r_{HR}$ represent the phytoplankton biomass concentration and maximum growth rate, the effects of nutrient concentration and light availability on the phytoplankton growth rate, and the heterotrophic respiration rate, respectively (see Table 1 for a list of acronyms and definitions). $N_m$, $\mu_{max}$, $r_{HR}$, and $C$ are assumed to be homogeneous above the depth of integration. Neglecting light inhibition, $N_m$ and $I_m(z)$ can be modeled to obey Michaelis-Menten kinetics [*Dutkiewicz et al*., 2001; *Huisman and Weissing*, 1994]:

$$N_m = \frac{N}{N + k_m^N} \qquad (2)$$

$$I_m(z) = \frac{I(z)}{I(z) + k_m^I} \qquad (3)$$

where $N$ and $k_m^N$ represent the nutrient concentration and half-saturation constant, respectively; and $I$ and $k_m^I$ stand for the photosynthetically active radiation (PAR) level and half-saturation constant, respectively. PAR at depth $z$ ($I(z)$) exponentially decays with depth according to the following equation:

$$I(z) = I_0 \times e^{-K_I \times z} \qquad (4)$$

where $I_0$ and $K_I$ represent PAR just beneath the water surface, and the light attenuation coefficient, respectively. In the open ocean, $K_I$ is modeled as an empirical function of the light attenuation coefficient at the wavelength of 490 nm ($K_d(490)$), which is in turn derived from the chlorophyll a concentration ($[Chl]$) [*Morel et al*., 2007]:

$$K_I = 0.0665 + 0.874 \times K_d(490) - \frac{0.00121}{K_d(490)} \qquad (5a)$$

$$K_d(490) = 0.0166 + 0.0773 \times [Chl]^{0.6715} \qquad (5b)$$

where the constant '0.0166' is the light attenuation at 490 nm due to pure seawater; and the second term on the right-hand side of equation (5b) represents the light attenuation

coefficient due to non-water components (e.g., phytoplankton and colored dissolved organic matter). $K_I$ and $K_d(490)$ increase with $[Chl]$ ($\frac{dK_d(490)}{d[Chl]} > 0$, and $\frac{dK_I}{d[Chl]} > 0$).

## 3. Influence of the depth of measurements on the export production and export ratio

In order to evaluate how the depth of integration influences export production and the $ef$-ratio, we derive equations describing these properties at the base of the euphotic layer and at a fixed depth (Table 2). To that end, we use equations (1-5) and build on the model presented in *Li and Cassar* [2017]. For simplicity, we assume that $\mu_{max}$, $r_{HR}$, $N$, $k_m^N$, $k_m^I$, $[Chl]$, and $C$ in equations (1-5) are well mixed or constant within the depth of integration. We also assume that the ecosystem is at steady state, and thus that export production is equal to NCP and new production.

### 3.1. Export ratio at the base of euphotic layer

Based on equation (1), NCP integrated over the euphotic layer ($NCP(0, Z_{eu})$) may be expressed as follows [*Li and Cassar*, 2017]:

$$\begin{aligned} NCP(0, Z_{eu}) &= NPP(0, Z_{eu}) - HR(0, Z_{eu}) \\ &= \int_0^{Z_{eu}} NPP(z)dz - \int_0^{Z_{eu}} HR(z)dz \\ &= N_m \times I_m(0, Z_{eu}) \times \mu_{max} \times C - r_{HR} \times C \times Z_{eu} \end{aligned} \quad (6)$$

where $NPP(0, Z_{eu})$ and $HR(0, Z_{eu})$ represent NPP and HR integrated over the euphotic zone, respectively; $Z_{eu}$ denotes the euphotic depth where 1% of surface PAR remains; and $I_m(0, Z_{eu})$ is calculated from equations (3-4) as follows:

$$I_m(0, Z_{eu}) = \int_0^{Z_{eu}} I_m(z)dz = -\frac{1}{K_I} \times ln\left(\frac{I_0 \times e^{-K_I \times Z_{eu}} + k_m^I}{I_0 + k_m^I}\right) \quad (7)$$

where

$$Z_{eu} = -\frac{\ln(0.01)}{K_I} \quad (8)$$

The autotrophic carbon to $[Chl]$ ratio ($C$: $[Chl]$) influences how $NCP(0, Z_{eu})$, $NPP(0, Z_{eu})$, and $HR(0, Z_{eu})$ respond to changes in $C$ (Figure 1 and supplementary material). Intuitively, one would expect $NCP(0, Z_{eu})$, $NPP(0, Z_{eu})$, and $HR(0, Z_{eu})$ to monotonically increase with $C$, which is observed when $C$: $[Chl]$ ratio is a constant. However, when accounting for the varying $C$: $[Chl]$ ratio, $NCP(0, Z_{eu})$, $NPP(0, Z_{eu})$, and $HR(0, Z_{eu})$ plateau at high $C$. This can be explained by: (1) the shoaling depth of integration $Z_{eu}$ resulting from decreasing light availability with increasing $C$ and $[Chl]$ (equations 5 and 8); and (2) the balance between phytoplankton physiology ($C$: $[Chl]$) and the package effect on light attenuation (equation 5b). It is worth noting that the responses of euphotic-depth integrated NCP, NPP and HR to variations in $C$ are markedly different from the ones presented in Figure 2 of *Li and Cassar* [2017], where the rates where integrated to a fixed depth (e.g., mixed layer depth) as opposed to the euphotic depth.

The export ratio at the base of euphotic zone ($ef_{eu}$) can be derived from equation (6):

$$ef_{eu} = \frac{NCP(0, Z_{eu})}{NPP(0, Z_{eu})} = 1 - \frac{1}{\overline{I_{eu}}} \times \frac{1}{N_m} \times \frac{r_{HR}}{\mu_{max}} \qquad (9)$$

where $\overline{I_{eu}} = \frac{I_m(0,Z_{eu})}{Z_{eu}} = \frac{1}{Z_{eu}} \times \int_0^{Z_{eu}} I_m(z)dz$ represents the averaged effect of light availability on the phytoplankton growth rate in the euphotic zone which is independent of $[Chl]$ (equations 7-8). The right-hand side of equation (9) shows that $ef_{eu}$ is a function of the proportion of NPP not respired within the euphotic zone ($ef_{eu} = 1 - \frac{HR(0,Z_{eu})}{NPP(0,Z_{eu})}$). $\mu_{max}$ and $r_{HR}$ can be modeled to vary as a function of temperature ($T$) according to the following equations [*Eppley*, 1972; *Lopez-Urrutia et al*., 2006; *Rivkin and Legendre*, 2001]:

$$\mu_{max} \propto e^{P_t \times T} \qquad (10)$$

$$r_{HR} \propto e^{B_t \times T} \qquad (11)$$

and therefore:

$$\frac{r_{HR}}{\mu_{max}} = \beta \times e^{(B_t - P_t)\times T} \qquad (12)$$

where $P_t$ and $B_t$ represent constants; and $\beta$ is a parameter related to the community structure [*Lopez-Urrutia et al*., 2006]. See Table 1 for the values attributed to these parameters.

### 3.2. Export ratio at a fixed depth

To investigate how export production and the $ef$-ratio at a fixed depth $Z_z$ ($ef_z$) varies with $Z_{eu}$ and $[Chl]$, we consider the two cases when the measurement depth is deeper and shallower than the euphotic depth ($Z_z > Z_{eu}$ and $Z_z < Z_{eu}$, respectively).

#### 3.2.1. Measurement depth deeper than the euphotic depth

Assuming that particle flux below $Z_{eu}$ exponentially decays with depth [*Armstrong et al*., 2002; *Lutz et al*., 2002], export production ($F$) when $Z_z > Z_{eu}$ can be estimated as follows:

$$F(Z_z) = F(Z_{eu}) \times e^{-\frac{Z_z - Z_{eu}}{Z^*}} \qquad (13)$$

where $Z^*$ is the remineralization length scale; and $F(Z_{eu})$ is equal to $NCP(0, Z_{eu})$ at steady state. Equation (9) and equation (13) lead to $ef_z$:

$$ef_z = \frac{NCP(0, Z_{eu})}{NPP(0, Z_{eu})} \times e^{-\frac{Z_z - Z_{eu}}{Z^*}} = ef_{eu} \times e^{-\frac{Z_z - Z_{eu}}{Z^*}} \qquad (14)$$

Equation (14) suggests that $ef_z$ is smaller than $ef_{eu}$ and increases with deepening $Z_{eu}$ because of lower particle flux attenuation (Figure 2(A)). Since $Z_{eu}$ shoals with increasing $[Chl]$, $ef_z$ is expected to be negatively related to $[Chl]$. As the depth of measurement deepens (i.e., increase $Z_z$), $ef_z$ decreases because of the increasing contribution of remineralization processes. The general form of the relation between $ef_z$ and $Z_{eu}$ does not change if the particle attenuation in equation (14) is modeled using the Martin curve [*Martin et al*., 1987].

#### 3.2.2. Measurement depth shallower than the euphotic depth

When $Z_z < Z_{eu}$, export production and $ef$ at $Z_z$ may be expressed as follows:

$$NCP(0,Z_z) = NPP(0,Z_z) - HR(0,Z_z)$$

$$= \int_0^{Z_z} NPP(z)dz - \int_0^{Z_z} HR(z)dz$$

$$= N_m \times I_m(0,Z_z) \times \mu_{max} \times C - r_{HR} \times C \times Z_z \qquad (15)$$

$$ef_z = \frac{NCP(0,Z_z)}{NPP(0,Z_z)} = 1 - \frac{1}{\overline{I_z}} \times \frac{1}{N_m} \times \frac{r_{HR}}{\mu_{max}} \qquad (16a)$$

$$ef_z = \frac{NCP(0,Z_z)}{NPP(0,Z_z)} = 1 - \frac{\overline{I_{eu}}}{\overline{I_z}}(1 - ef_{eu}) \qquad (16b)$$

where $\overline{I_z} = \frac{I_m(0,Z_z)}{Z_z}$ represents the averaged effect of light availability on the phytoplankton growth rate above a fixed depth $Z_z$. $\overline{I_z}$ decreases with increasing $[Chl]$. $I_m(0,Z_z) = \int_0^{Z_z} I_m(z)dz = -\frac{1}{K_I} \times ln\left(\frac{I_0 \times e^{-K_I \times Z_z} + k_m^I}{I_0 + k_m^I}\right)$ denotes the integrated effect of light availability on phytoplankton growth rate above the depth $Z_z$. The term $\overline{I_z}$ in equation (16) is a function of the optical depth of $Z_z$ (i.e., $Z_z \times K_I$). $ef_z$ decreases with increasing $Z_z$, $[Chl]$, and optical depth ($Z_z \times K_I$ ) as schematically shown in Figure 2(B). As equation (16) can be rewritten as $ef_z = \frac{NCP(0,Z_z)}{NPP(0,Z_z)} = 1 - \frac{HR(0,Z_z)}{NPP(0,Z_z)} = 1 - \frac{\frac{HR(0,Z_z)}{C}}{\frac{NPP(0,Z_z)}{C}}$, these results can be alternatively explained by the biomass-normalized NPP ($\frac{NPP(0,Z_z)}{C}$) (i.e., the autotrophic growth rate) decreasing with increasing $[Chl]$ due to light attenuation while the biomass-normalized HR ($\frac{HR(0,Z_z)}{C}$) is insensitive to changes in $[Chl]$.

### 3.3. Comparison to other export ratio algorithms

Rearranging and taking the natural logarithm of equation (9) yields:

$$ln(1 - ef_{eu}) = (B_t - P_t) \times T + ln(\beta) + ln\left(\frac{1}{\overline{I_{eu}}}\right) + ln\left(\frac{1}{N_m}\right) \qquad (17)$$

In sum, the controls on the export efficiency can be decomposed into four components: (1) the temperature dependence of the balance between autotrophic and heterotrophic processes

($(B_t - P_t) \times T$), (2) the community structure ($ln(\beta)$), (3) the effect of light availability on the phytoplankton growth rate, and (4) the effect of nutrient availability on the phytoplankton growth rate. Missing or misrepresenting one of these components may impair the accuracy of satellite export production estimates. Equation (17) may be further simplified to:

$$ef_{eu} = -(B_t - P_t) \times T - ln(\beta) + ln(\overline{I_{eu}}) + ln(N_m) \quad (18)$$

based on the rough first-order approximation ($ln(1 - ef_{eu}) \approx -ef_{eu}$ with increasing errors as $ef_{eu} \to 1$). If $(B_t - P_t)$ in equation (18) is a constant, $ef_{eu}$ is a negative linear function of temperature, consistent in form with the empirical model of *Dunne et al*. [2005]: $pe_r = -0.0081 \times T + 0.0668 \times ln\left(\frac{Chl}{Z_{eu}}\right) + 0.426$, where $pe_r$ is the particulate export ratio and $Chl$ in this case reflects the chlorophyll inventory over the euphotic zone. Alternatively, if the temperature dependence $(B_t - P_t)$ relates to NPP, equation (18) is more in line with the empirical equations in *Laws et al*. [2011]: $ef = -\frac{0.0165 \times tp}{51.7 + tp} \times T + \frac{0.5857 \times tp}{51.7 + tp}$ and $ef = -\frac{0.43 \times tp^{0.307}}{30} \times T + 0.04756 \times 0.78 \times tp^{0.307}$, where $tp$ is defined as NPP in *Laws et al*. [2011]. The term $-ln(\beta)$ in equation (18) may correspond to the $ln\left(\frac{Chl}{Z_{eu}}\right)$ term in *Dunne et al*. [2005] because $\beta$ is associated with phytoplankton community structure, which is in turn correlated with $[Chl]$ [*Agawin et al*., 2000; *Brewin et al*., 2010; *Sathyendranath et al*., 2001]. The term $ln(\overline{I_{eu}})$ varies as a function of $I_0$, but also depends on $[Chl]$ when integration is to a fixed depth (equations 14 and 16). The terms $ln(\overline{I_{eu}})$ and $ln(N_m)$ are not directly taken into account by some earlier models, but are indirectly taken into account through NPP and $[Chl]$ as in *Dunne et al*. [2005] and *Laws et al*. [2011].

### 3.4. Comparison of the export ratio at the base of the euphotic layer and at 100 m

As an example of the effect of the depth of integration, we derive a functional relationship between $ef_z$ at 100m ($ef_{100}$) and at the euphotic depth ($ef_{eu}$) using equations (9, 14, and 16), noting that our conclusions are valid for any other depths of integration. We select a

remineralization length scale of $Z^* = 100$ m, a half-saturation constant for radiation of $k_m^I = 4.1$ Einstein $m^{-2}$ $d^{-1}$, and the monthly climatology of $ef_{100}$ estimated using the algorithm of *Dunne et al*., [2005]. Monthly climatology of sea surface temperature, chlorophyll a concentration, and photosynthetically active radiation were downloaded from the ocean color website (https://oceancolor.gsfc.nasa.gov/). We use these data products to calculate the euphotic depth and $ef_{100}/ef_{eu}$ based on equations (7-8).

When $Z_{eu}$ is deeper than 100 m ($Z_{eu} > 100$), $\frac{1-ef_{100}}{1-ef_{eu}} = \frac{\overline{I_{eu}}}{\overline{I_{100}}} < 1$ can be obtained by reorganizing equations (9 and 16), where $\overline{I_{100}}$ is the averaged effect of light availability on the phytoplankton growth rate above 100 m. This relationship suggests that $\frac{ef_{100}}{ef_{eu}}$ is greater than 1 ($\frac{ef_{100}}{ef_{eu}} > 1$) and rapidly decreases with increasing $[Chl]$ (due to decreasing $\overline{I_{100}}$ but no change in $\overline{I_{eu}}$), as shown in the schematic diagram in Figure 3. In the subtropical gyres, where $Z_{eu}$ is often deeper than 100 m due to extremely low $[Chl]$ (e.g., $[Chl] = 0.01\ mg\ m^{-3}$ leads to $Z_{eu} = 192.66\ m$), $ef_{100}$ could be as much as seven times larger than $ef_{eu}$ (Figure 4).

When $Z_{eu}$ is shallower than 100 m ($Z_{eu} < 100$), a simple reorganization of equation (14) yields $\frac{ef_{100}}{ef_{eu}} = e^{-\frac{100-Z_{eu}}{Z^*}}$. This equation suggests that $\frac{ef_{100}}{ef_{eu}}$ is smaller than 1 ($\frac{ef_{100}}{ef_{eu}} < 1$), and that an increase in $[Chl]$ again decreases $Z_{eu}$ and hence $\frac{ef_{100}}{ef_{eu}}$ (Figure 3). However, $\frac{ef_{100}}{ef_{eu}}$ is less sensitive to changes in $[Chl]$ than when $Z_{eu} > 100$ (Figure 3). For example, $ef_{100}$ is less than half of $ef_{eu}$ in regions with very high $[Chl]$ (e.g., Southern Ocean and coastal regions; $[Chl] = 10\ mg\ m^{-3}$ gives $Z_{eu} = 11.66\ m$ and $\frac{ef_{100}}{ef_{eu}} = 0.41$ for $Z^* = 100\ m$).

These considerations may in part explain the large discrepancies between satellite algorithms in predictions of export production in the subtropical regions, the Southern Ocean, and the Arctic Ocean [*Li and Cassar*, 2016]. In these regions, extremely low and high $[Chl]$

regimes are observed. Some algorithms predict the $ef$-ratio at the euphotic depth [*Eppley and Peterson*, 1979; *Laws et al*., 2000; *Siegel et al*., 2014], while others at a given depth such as the mixed layer depth [*Li and Cassar*, 2016], or 100 m [*Dunne et al*., 2005; *Henson et al*., 2011; *Le Moigne et al*., 2016; *Maiti et al*., 2013]. Differing integration depths could also explain the reported inconsistent relationship between $ef$-ratio and GPP [*Hendricks et al*., 2004] and NPP [*Maiti et al*., 2013].

$ef$-ratios measured at different depths display similar functionalities (equations 9, 14, and 16); however, integrating to the euphotic depths may be preferable. First, as opposed to the euphotic depth which has a clear influence on phytoplankton physiology, a physical depth's influence on the $ef$-ratio changes with light attenuation, preventing the exploration of controls (e.g., plankton community structure) on the $ef$-ratio across regions with different $[Chl]$. An $ef$-ratio measured shallower than the euphotic depth misses parts of the particles produced. Conversely, an $ef$-ratio measured deeper than the euphotic depth disproportionately reflects particle destruction processes.

There are practical reasons to measure the $ef$-ratio at depth. For example, shallow sediment traps are notoriously unreliable [*Buesseler*, 1991]. However, as shown in equation (14), export at depth can be modeled as a function of $ef_{eu}$ and flux attenuation below the euphotic depth, albeit with significant uncertainties. Because controls on the $ef_{eu}$ and the transfer efficiency are likely different [*Buesseler and Boyd*, 2009; *Lima et al.*, 2014], this two-step approach likely improves predictions of the strength of the biological pump. Our results also underscore *Buesseler and Boyd* [2009] recommendation to account for variations in $Z_{eu}$ when reporting export or $ef$-ratios.

**4. Influence of environmental properties on the export ratio**

In order to gain some quantitative intuition into how $N$, $I_0$, $T$, $[Chl]$, and $MLD$ influence the $ef$-ratio, we take the partial derivative of $ef_z$ at the base of the mixed layer ($ef_{ml}$) relative to each property in equation (16):

$$\frac{\partial ef_{ml}}{\partial N} = N_m \times \frac{k_m^N}{N^2} \times (1 - ef_{ml}) \quad (19)$$

$$\frac{\partial ef_{ml}}{\partial I_0} = \frac{I_m(MLD) \times (e^{K_I \times MLD} - 1)}{I_m(0, MLD) \times K_I} \times \frac{k_m^I}{(I_0 + k_m^I) \times I_0} \times (1 - ef_{ml}) \quad (20)$$

$$\frac{\partial ef_{ml}}{\partial T} = -(B_t - P_t) \times (1 - ef_{ml}) \quad (21)$$

$$\frac{\partial ef_{ml}}{\partial [Chl]} = -\left(1 - \frac{I_m(MLD)}{\overline{I_{ml}}}\right) \times \frac{1}{K_I} \times \frac{dK_I}{d[Chl]} \times (1 - ef_{ml}) \quad (22)$$

$$\frac{\partial ef_{ml}}{\partial MLD} = -\left(1 - \frac{I_m(MLD)}{\overline{I_{ml}}}\right) \times \frac{1}{MLD} \times (1 - ef_{ml}) \quad (23)$$

where $I_m(MLD) = \frac{I_0 \times e^{-K_I \times MLD}}{I_0 \times e^{-K_I \times MLD} + k_m^I}$ represents the influence of light availability on phytoplankton growth rate at $MLD$; $\overline{I_{ml}} = \frac{I_m(0,MLD)}{MLD}$ represents the averaged effect of light availability on the phytoplankton growth rate within the mixed layer; $I_m(0, MLD)$ is the integrated effect of light availability on the phytoplankton growth rate over the mixed layer; and $\frac{dK_I}{d[Chl]}$ can be derived from equation (5) and is positive ($\frac{dK_I}{d[Chl]} > 0$). The derivations of equations (19-23) are presented in the supplementary material. $ef_{ml}$ increases with $N$ ($\frac{\partial ef_{ml}}{\partial N} > 0$) and $I_0$ ($\frac{\partial ef_{ml}}{\partial I_0} > 0$) due to increasing phytoplankton growth rate. $ef_{ml}$ decreases with $T$ ($\frac{\partial ef_{ml}}{\partial T} < 0$) because of the higher temperature sensitivity of heterotrophic respiration compared to phytoplankton growth rate ($B_t > P_t$), in line with multiple previous studies [*Cael and Follows*, 2016; *Dunne et al*., 2005; *Henson et al*., 2011; *Laws et al*., 2011; *Laws et al*., 2000]. $ef_{ml}$ decreases with $[Chl]$ ($\frac{\partial ef_{ml}}{\partial [Chl]} < 0$) and $MLD$ ($\frac{\partial ef_{ml}}{\partial MLD} < 0$) due to decreasing average light availability. In reality, a deepening of the mixed layer may also entrain nutrients

from the subsurface, leading to an increase in $ef_{ml}$ (equation (19)). This effect is not directly taken into account in our model. The balance of the effects of $MLD$ deepening on nutrient and light availability ultimately determines how $ef_{ml}$ varies with $MLD$. Equations (19-23) can be applied to $ef_{eu}$, with the exception that $ef_{eu}$ is independent of $[Chl]$ and the depth of integration ($\frac{\partial ef_{eu}}{\partial [Chl]} = \frac{\partial ef_{eu}}{\partial Z_{eu}} = 0$). In some studies, $ef_z$ is derived from taking the ratio of export (or NCP) measurements integrated to a certain depth (e.g., 100m or MLD) to NPP integrated over the euphotic depth. Under such circumstances, the sign of $\frac{\partial ef_z}{\partial [Chl]}$ varies, with $ef$-ratio displaying a bell-shaped relation to $[Chl]$ (see Figure S1 in supplementary material).

**4.1. Relation between the export ratio at a fixed depth and net primary production**

Recent studies have reported a negative relation between NPP and $ef_{100}$ in the Southern Ocean [*Le Moigne et al*., 2016; *Maiti et al*., 2013], in contrast to earlier studies [*Dunne et al*., 2005; *Eppley and Peterson*, 1979; *Laws et al*., 2011; *Laws et al*., 2000]. Relating the $ef$-ratio to NPP could lead to spurious negative correlations of the type x vs. (a/x) where "a" is a constant. This is especially the case for deep depths of integration because geographical variability in export production decreases with increasing depth [*Antia et al*., 2001; *Henson et al*., 2012]. While we cannot rule out that the negative correlation between the $ef$-ratio and NPP results from a mathematical tautology, others have hypothesized that it results from grazing and fecal-mediated export [*Cavan et al*., 2017; *Le Moigne et al*., 2016], temperature [*Henson et al*., 2015], and DOC export [*Hansell et al*., 2009; *Maiti et al*., 2013]. Many of these factors are encapsulated in the $\beta$ term relating $r_{HR}$ to $\mu_{max}$ in equation (12). $\beta$ reflects community structure that is in turn related $[Chl]$ and NPP [*Lopez-Urrutia et al*., 2006]. While the cause remains unknown, our models provide an additional explanation for the reported discrepancies in the relationship between $ef_{100}$ and NPP. NPP is the product of phytoplankton biomass ($C$) and growth rate ($\mu$). All other factors equal, euphotic-depth

integrated NPP is a positive function of $C$ (Figure 1). Since $ef_{100}$ is a negative function of $[Chl]$, an increase in NPP due to high $C$ will decrease $ef_{100}$ (Figure 2). Conversely, if the increase in NPP stems from other factors such as increasing nutrient and light availability (i.e., higher autotrophic growth rate), $ef_{100}$ is expected to positively correlate with NPP.

**4.2. Seasonal variability in the export ratio at the base of the mixed layer**

Based on equations (19-23), we decompose the seasonal controls on $ef_{ml}$ as the sum of partial differentials:

$$\Delta ef_{ml} = \frac{\partial ef_{ml}}{\partial N} \times \Delta N + \frac{\partial ef_{ml}}{\partial I_0} \times \Delta I_0 + \frac{\partial ef_{ml}}{\partial T} \times \Delta T + \frac{\partial ef_{ml}}{\partial [Chl]} \times \Delta [Chl] + \frac{\partial ef_{ml}}{\partial MLD} \times \Delta MLD \quad (24)$$

where $\Delta ef_{ml}$ denotes the total differential of $ef_{ml}$; and $\Delta N$, $\Delta I_0$, $\Delta T$, $\Delta[Chl]$, and $\Delta MLD$ represent changes in $N$, $I_0$, $T$, $[Chl]$, and $MLD$, respectively. As $1 - ef_{ml}$ appears in all the individual equations (19-23), it is not required to estimate the relative contribution of each term in equation (24). We estimate $I_0$, $T$, and $[Chl]$ from satellite data, $MLD$ from the climatology of *de Boyer Montegut et al*. [2004], and $N$ from World Ocean Atlas monthly climatologies [*Garcia et al*., 2014]. Details on data and the derivation of seasonal changes in nutrient availability are presented in the supplementary material [*Boyd et al*., 2000; *Boyd and Ellwood*, 2010; *Cassar et al*., 2007; *Deutsch et al*., 2007; *Johnson et al*., 1997; *Martin et al*., 1990; *Mitchell et al*., 1991a, *Mitchell et al*., 1991b; *Moore et al*., 2013; *Nelson et al*., 1991; *Sarmiento and Gruber*, 2006]. Figure 5 shows how seasonal variations in $ef_{ml}$ are impacted by $I_0$, $MLD$, $T$, $[Chl]$, and $N$. Among these factors, $I_0$ and $MLD$ dominate seasonal variability in $ef_{ml}$ at high-latitude. In the spring, $ef_{ml}$ sharply increases with increasing $I_0$ and shoaling $MLD$ ($\frac{\partial ef_{ml}}{\partial I_0} \times \Delta I_0 > 0$ and $\frac{\partial ef_{ml}}{\partial MLD} \times \Delta MLD > 0$). In contrast, decreasing $I_0$ and deepening $MLD$ in the autumn lead to a decrease in $ef_{ml}$ ($\frac{\partial ef_{ml}}{\partial I_0} \times \Delta I_0 < 0$ and $\frac{\partial ef_{ml}}{\partial MLD} \times \Delta MLD < 0$). Our

results are consistent with the dominant controls of $MLD$ and $I_0$ on NCP in the Southern Ocean on seasonal timescales [*Li*, 2017].

$T$ also contributes to the seasonal variability in $ef_{ml}$. Interestingly, $\frac{\partial ef_{ml}}{\partial T} \times \Delta T$ is higher in polar regions. Similarly, $[Chl]$ affects the seasonality in $ef_{ml}$ north $45°N$ in March and April. However, $\frac{\partial ef_{ml}}{\partial [Chl]} \times \Delta [Chl]$ shows large spatial variability (see the supplementary material). Conversely, $N$ mostly impacts the seasonality of $ef_{ml}$ in the Southern Ocean. $\frac{\partial ef_{ml}}{\partial N} \times \Delta N$ leads to an increase in $ef_{ml}$ in late austral summer early autumn due to deepening mixed layers, in part counteracting the decreasing light availability associated with $I_0$ and deepening mixed layers. Additionally, our data support equation (19)'s prediction that $ef_{ml}$ is particularly sensitive to variations in nutrient availability when nutrient concentrations are low (see supplementary material). Because of the assumptions going into the derivation of $N$, it is likely the parameter with the most uncertain effect on $ef_{ml}$. Uncertainties, assumptions and simplifications associated with $\frac{\partial ef_{ml}}{\partial N} \times \Delta N$ are discussed in the section on caveats and limitations. Overall, our results emphasize that caution should be exercised when interpreting $ef_{ml}$ across regions and seasons because of varying $I_0$, $MLD$, $T$, $[Chl]$, and $N$.

**5. Caveats, limitations, additional considerations, and future improvements**

Below we enumerate some of the assumptions and simplifications that go into the construction of our model. While they introduce uncertainties, they do not change our main conclusions that fundamental factors confound the interpretation of the $ef$-ratio.

Photophysiology: Modeling the influence of light availability on phytoplankton growth assuming Michaelis-Menten kinetics does not account for light inhibition and photoacclimation [*Geider*, 1987; *Geider et al*., 1996; *Geider et al*., 1998; *Jassby and Platt*, 1976; *Pahlow and Oschlies*, 2009]. In addition, $K_I$ varies with depth due to the optional attenuation of PAR (see *Li and Cassar* [2017] and references therein), with the relationship

between $K_I$ and $[Chl]$ also being impacted by other factors, including detritus, colored dissolved organic matter, and solar zenith angle [*Gordon*, 1989]. We also note that defining the euphotic depth based on a percentage of surface irradiance has been shown to be of little physiological significance [*Banse*, 2004; *Laws et al*., 2014; *Letelier et al*., 2004; *Lorenzen*, 1976; *Marra et al*., 2014]. While our model can readily be adapted to reflect a depth more meaningful to photochemistry, for the purpose of this study, the definition in equation (8) is adequate.

Stoichoimetry: The elemental stoichiometry and half-saturation constants of marine phytoplankton are known to vary with seasonal changes in growth conditions and species [*Eppley et al*., 1969; *Moreno and Martiny*, 2018; *Smith et al*., 2009]. Our model does not account for this variability and assumes that the concentrations and half-saturation constants of limiting and non-limiting factors vary proportionally. All these simplifications and top-down controls on the phytoplankton growth rate (as opposed to nutrients) will need to be further evaluated.

Other biogeochemical and trophic processes: By design, our metabolism-based model prescinds complex biogeochemical processes represented in food-web models. While our modeling of autotrophy is on par with more complex food web models (e.g., NPZD), our representation of heterotrophy being a simple function of temperature and biomass does not reflect the panoply of biogeochemical and trophic processes influencing organic carbon loss from the system. For example, our model does not represent the process of particle aggregation, which is believed to be a first-order control on the $ef$-ratio [*Boyd and Trull*, 2007; *Burd and Jackson*, 2009; *Passow et al*., 1994]. Aggregation with rapid sinking would lead to lower surface respiration and higher $ef$-ratios than predicted based on the model's temperature parameterization. The temperature dependence of $r_{HR}$ and $\mu_{max}$ have large uncertainties (see *Li and Cassar* [2017] and references therein). Variations in the relative

proportion of POC and DOC production associated with NCP, attributed to food web processes and plankton's physiological status [*Emerson*, 2014; *Hansell and Carlson*, 1998; *Hygum et al*., 1997; *Thornton*, 2014], are also not included in our modeling effort.

Our model assumes steady-state. A lack of steady-state may lead to two types of biases, natural and methodological. First, export efficiency observations may be biased when export lags production [*Buesseler*, 1998; *Buesseler et al*., 2009; *Henson et al*., 2015], in which case the $ef$-ratio would be under(over)-estimated in the production (export) phase. This is particularly important in physically dynamic and biologically sluggish (low temperature) systems such as the Southern Ocean. Second, differences in integration timescales of export production and NPP bias estimates of the $ef$-ratio in systems that are not at steady-state. For example, export production measurements (~24 days based on $^{234}$Th) usually have longer integration timescales than NPP estimates (~1 day).

Vertical profiles: For simplicity, we assume that $\mu_{max}$, $r_{HR}$, $N$, $k_m^N$, $k_m^I$, $[Chl]$, and $C$ are well mixed or constant within the euphotic zone and mixed layer. However, these parameters may vary within the mixed layer, especially for water columns with limited turbulent mixing. In the subtropical regions where the water column is well stratified, low nutrient availability often leads to euphotic zones that are deeper than the mixed layer, and as a results some parameters (e.g., $N$, $[Chl]$, and $C$) beneath the mixed layer may differ from those within the mixed layer.

**6. Conclusions**

In this study, we developed a metabolism-based mechanistic model to explore how fundamental factors may confound the interpretation of field observations of the export ratio ($ef$-ratio). Our results show that the effect of trophic processes and community composition on the export efficiency may be masked by changes in temperature, biomass and light availability. As such, analyses of the impact of biological and biogeochemical processes on

$ef_{ml}$ should be interpreted with caution, especially in high latitudes where variations in $ef_{ml}$ are dominated by mixed-layer depth and surface radiation over seasonal timescales. Our approach also offers a new framework for relating phytoplankton size composition to field estimates, satellite algorithms and earth-system models of the $ef$-ratio. Finally, our theoretical considerations provide further support for reporting or normalizing field observations of the $ef$-ratio to the euphotic depth. While the best depth horizon for reporting $ef$-ratio may depend on the process under study, our modeling effort shows that estimating $ef$-ratios at a depth other than the euphotic depth (e.g., 100m or MLD) complicates the interpretation of the temporal and spatial variability in the $ef$-ratio.

More fundamentally, our study demonstrates that it may be time to revisit the export ratio proxy. In their classical paper, *Eppley and Peterson* [1979] first recommended normalizing new production to primary production (f-ratio) as the "total flux seems to be approximately proportional to the plankton production in the overlying water". While normalization by ratio correction is commonly applied in life sciences to account for the effect of a confounding variable, it is known to be flawed (*Karp et al*., [2012] and references therein). In addition to the issues associated with ratio corrections, our theoretical considerations above demonstrate that export is not a simple function of NPP. Identical NPP resulting from differing autotrophic biomass and growth rates may lead to differing export ratios. These mathematical and biogeochemical shortcomings with the export ratio thus argue for the development of more ecumenical proxies of the biological pump.

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**Table 1**. Model parameters, abbreviations, and units

| Parameter | Description | Units |
|---|---|---|
| MLD | Mixed layer depth | m |
| $Z_{eu}$ | Euphotic depth | m |
| $Z_z$ | A fixed depth | m |
| $z$ | Depth | m |
| NPP(z) | Net primary production at depth z | mmol C $m^{-3}$ $d^{-1}$ |
| NPP(0,z) | Net primary production above depth z | mmol C $m^{-2}$ $d^{-1}$ |
| HR(z) | Heterotrophic respiration at depth z | mmol C $m^{-3}$ $d^{-1}$ |
| HR(0,z) | Heterotrophic respiration above depth z | mmol C $m^{-2}$ $d^{-1}$ |
| NCP(z) | Net community production at depth z | mmol C $m^{-3}$ $d^{-1}$ |
| NCP(0,z) | Net community production above depth z | mmol C $m^{-2}$ $d^{-1}$ |
| $F$ | Export production | mmol C $m^{-2}$ $d^{-1}$ |
| $ef_z$, $ef_{eu}$, $ef_{100}$, $ef_{ml}$ | $ef_z$ is the export ratio at any depth z, which includes the specific cases of $ef_z$ at the euphotic depth ($ef_{eu}$), 100m ($ef_{100}$), and mixed layer depth ($ef_{ml}$). | unitless |
| $N$ | Nutrient concentration | mmol $m^{-3}$ |
| $k_m^N$ | Half-saturation constant for nutrient concentration | mmol $m^{-3}$ |
| $N_m$ | Nutrient effect on the phytoplankton growth $N_m = \frac{N}{N+k_m^N}$ | unitless |
| PAR | Photosynthetically active radiation | Einstein $m^{-2}$ $d^{-1}$ |
| $I_0$ | Photosynthetically active radiation just beneath water surface | Einstein $m^{-2}$ $d^{-1}$ |
| $I(z)$ | Photosynthetically active radiation at depth z | Einstein $m^{-2}$ $d^{-1}$ |
| $k_m^I$ | Half-saturation constant for PAR (4.1 einstein $m^{-2}$ $d^{-1}$, *Behrenfeld and Falkowski* [1997]) | Einstein $m^{-2}$ $d^{-1}$ |
| $I_m(z)$ | Light effect on the phytoplankton grow at depth z, $I_m(z) = \frac{I(z)}{I(z)+k_m^I} = \frac{I_0 \times e^{-K_I \times z}}{I_0 \times e^{-K_I \times z}+k_m^I}$ | unitless |
| $I_m(0,z)$ | Integrated light effect on phytoplankton growth above depth z, $I_m(0,z) = -\frac{1}{K_I} \times ln\left(\frac{I_0 \times e^{-K_I \times z}+k_m^I}{I_0+k_m^I}\right)$ | unitless |
| $\overline{I_z}$, $\overline{I_{eu}}$, $\overline{I_{100}}$, $\overline{I_{ml}}$ | $\overline{I_z}$ represents the averaged effect of light availability on the phytoplankton growth rate within the depth z, which includes the specific cases of $\overline{I_z}$ at the euphotic depth ($\overline{I_{eu}}$), 100m ($\overline{I_{100}}$), and mixed layer depth ($\overline{I_{ml}}$). | unitless |
| $\mu_{max}$ | Maximum phytoplankton specific growth rate | $d^{-1}$ |
| $r_{HR}$ | Heterotrophic respiration specific rate | $d^{-1}$ |
| $K_I$ | Diffusion attenuation coefficient | $m^{-1}$ |
| $K_I(490)$ | Diffusion attenuation coefficient at 490 nm | $m^{-1}$ |
| $C$ | Phytoplankton biomass concentration | mmol $m^{-3}$ |
| $[Chl]$ | Chlorophyll a concentration | mg $m^{-3}$ |
| POC | Particulate organic carbon | mg $m^{-3}$ |
| DOC | Dissolved organic carbon | mg $m^{-3}$ |
| $T$ | Sea surface temperature | ℃ |
| $P_t$ | Temperature dependence of phytoplankton growth rate (0.0663, *Eppley* [1972]) | $℃^{-1}$ |
| $B_t$ | Temperature dependence of heterotrophic respiration (0.08, *Rivkin and Legendre* [2001], *López-Urrutia et al.* [2006]) | $℃^{-1}$ |
| $\Delta ef_{ml}$ | Differential for $ef_{ml}$ | unitless |
| $\Delta N$ | Change in $N$ | mmol $m^{-3}$ |
| $\Delta I_0$ | Change in $I_0$ | Einstein $m^{-2}$ $d^{-1}$ |
| $\Delta T$ | Change in $T$ | ℃ |
| $\Delta[Chl]$ | Change in $[Chl]$ | mmol $m^{-3}$ |
| $\Delta MLD$ | Change in $MLD$ | m |

**Table 2**. Export ratios at different depths of integration, see Table 1 for acronyms.

| **Depth of integration** | | **Equation** | |
|---|---|---|---|
| Euphotic depth ($Z_{eu}$) | | $ef_{eu} = \frac{NCP(0,Z_{eu})}{NPP(0,Z_{eu})} = 1 - \frac{1}{\overline{I_{eu}}} \times \frac{1}{N_m} \times \frac{r_{HR}}{\mu_{max}}$ | (9) |
| Fixed depth ($Z_z$) | $Z_z > Z_{eu}$ | $ef_z = \frac{NCP(0,Z_{eu})}{NPP(0,Z_{eu})} \times e^{-\frac{Z_z - Z_{eu}}{z^*}} = ef_{eu} \times e^{-\frac{Z_z - Z_{eu}}{z^*}}$ | (14) |
| | $Z_z < Z_{eu}$ | $ef_z = \frac{NCP(0,Z_z)}{NPP(0,Z_z)} = 1 - \frac{1}{\overline{I_z}} \times \frac{1}{N_m} \times \frac{r_{HR}}{\mu_{max}}$ | (16a) |
| | | $ef_z = \frac{NCP(0,Z_z)}{NPP(0,Z_z)} = 1 - \frac{\overline{I_{eu}}}{\overline{I_z}}(1 - ef_{eu})$ | (16b) |

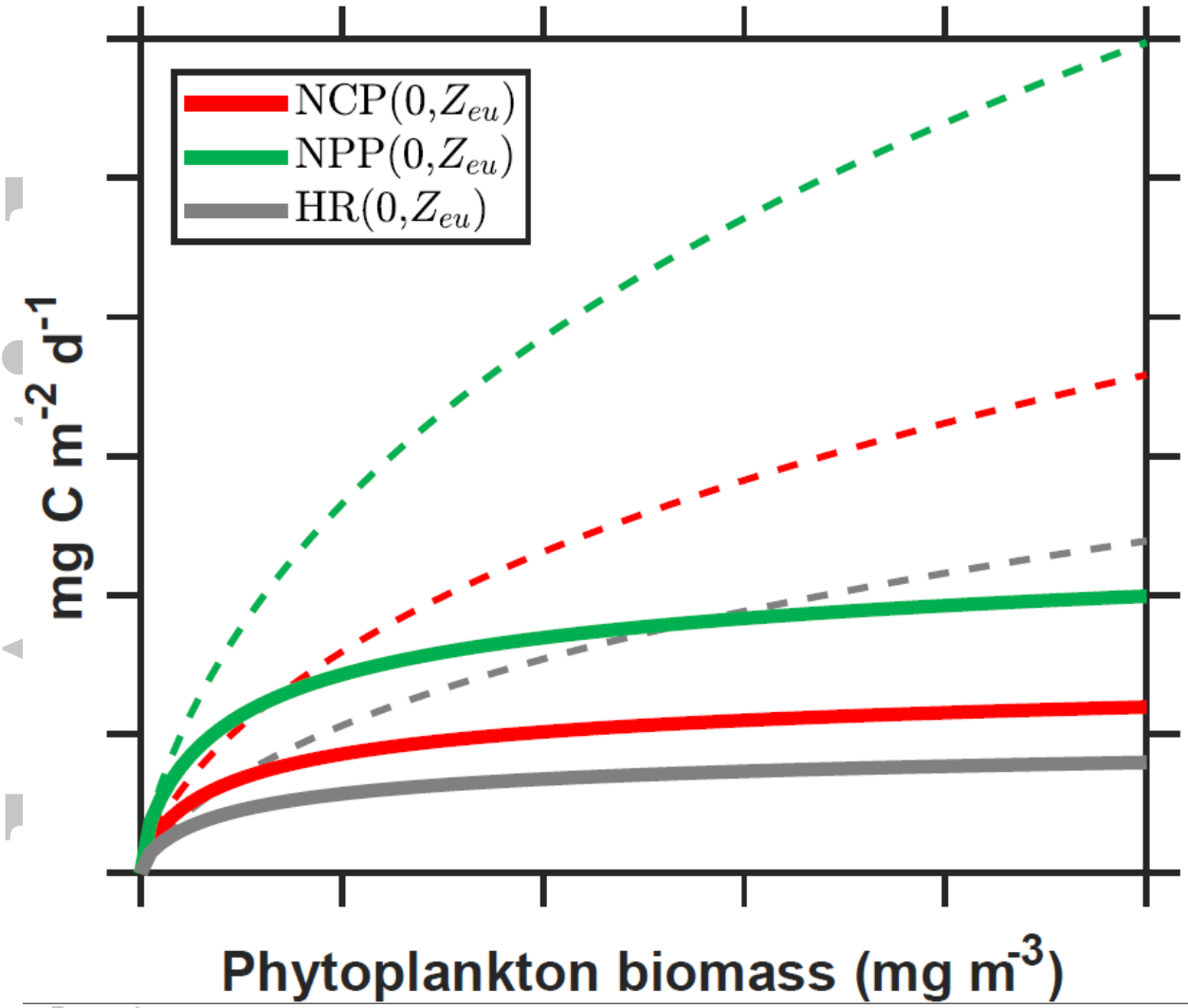


**Figure 1**. Schematic diagram of net community production (NCP), net primary production (NPP) and heterotrophic respiration (HR) integrated over the euphotic depth ($Z_{eu}$). Light attenuation coefficient ($K_I$) is a function of chlorophyll a concentration ($[Chl]$) [*Morel et al.*, 2007], which is in turn modeled as a function of phytoplankton biomass concentration ($C$) based on the autotrophic carbon to $[Chl]$ ratio ($C$: $[Chl]$). Dashed lines represent $NCP(0, Z_{eu})$, $NPP(0, Z_{eu})$, $HR(0, Z_{eu})$ derived using a constant $C$: $[Chl]$ of 90 [*Arrigo et al.*, 2008]. Solid lines represent $NCP(0, Z_{eu})$, $NPP(0, Z_{eu})$, $HR(0, Z_{eu})$ with variable $C$: $[Chl]$ estimated using the empirical relation between $C$ and $[Chl]$ derived by *Jakobsen and Markager* [2016].

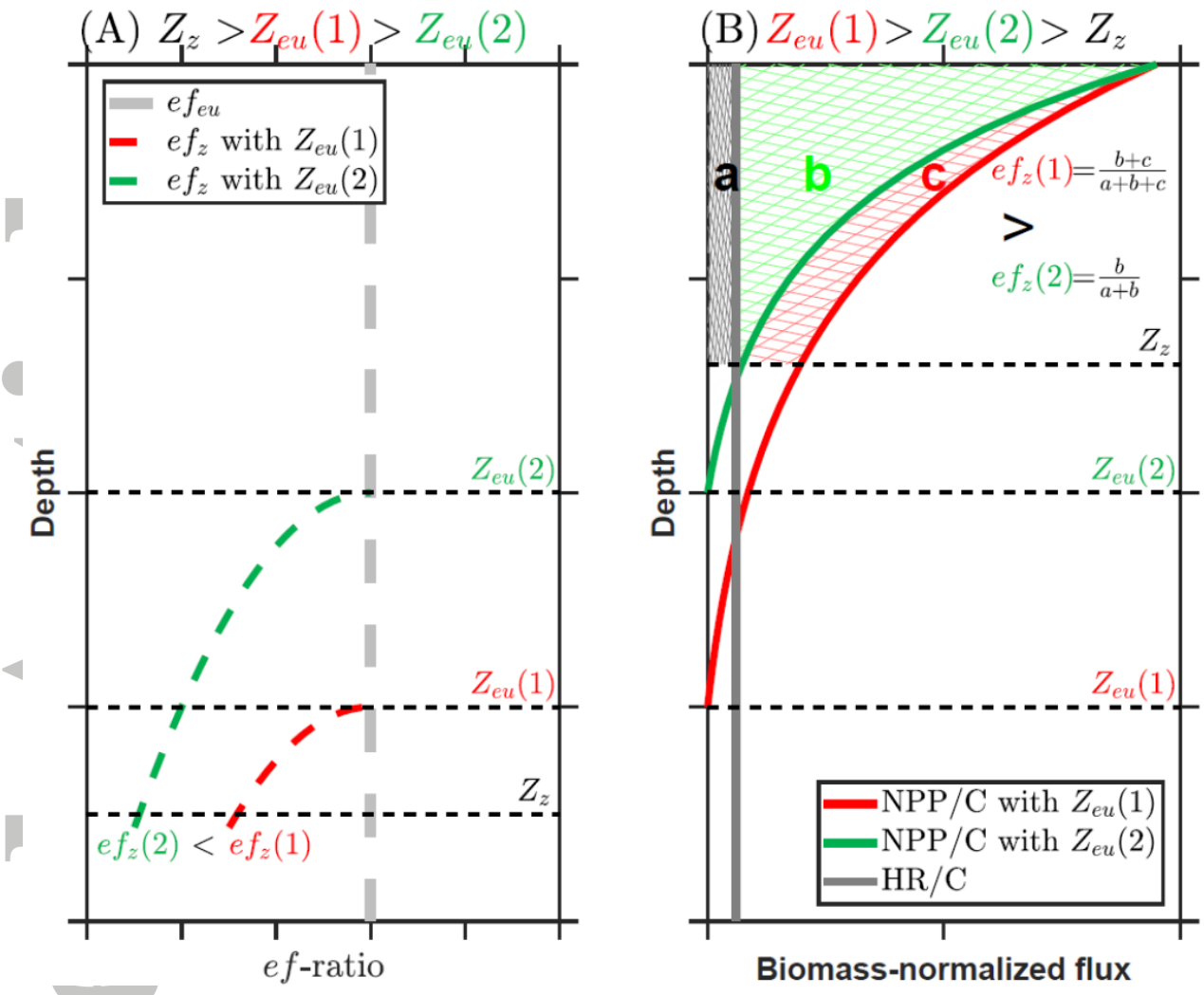


**Figure 2**. Schematic diagram of the export ratio as a function of the integration depth (i.e., depth horizon of measurement). (A) Case where the depth of integration $Z_Z$ is deeper than the euphotic depths and $Z_{eu}(1) > Z_{eu}(2)$. Particles are modeled to exponentially attenuate with depth (red and green dashed curves). Because $Z_{eu}(1) > Z_{eu}(2)$, the export production with $Z_{eu}(2)$ (green-dashed curve) has experienced more attenuation than the export production with $Z_{eu}(1)$ (red-dashed curve) at depth $Z_z$. (B) Case where $Z_{eu}(1) > Z_{eu}(2)$ and the euphotic depths are deeper than the depth of integration $Z_z$ for net community production (NCP), net primary production (NPP), and heterotrophic respiration (HR). Gray line represents the biomass-normalized HR. Red and green lines represent biomass-normalized NPP with $Z_{eu}(1)$ and $Z_{eu}(2)$, respectively. $Z_{eu}(1) > Z_{eu}(2)$ implies that light attenuation for the red line is weaker than for the green line. The export ratios for $Z_{eu}(1)$ and $Z_{eu}(2)$ are $ef_z(1) = \frac{b+c}{a+b+c}$ and $ef_z(2) = \frac{b}{a+b}$, where $a$, $b$ and $c$ represent the areas of the hatched regions. Geometrically, $ef_z(1) = \frac{b+c}{a+b+c} > ef_z(2) = \frac{b}{a+b}$.

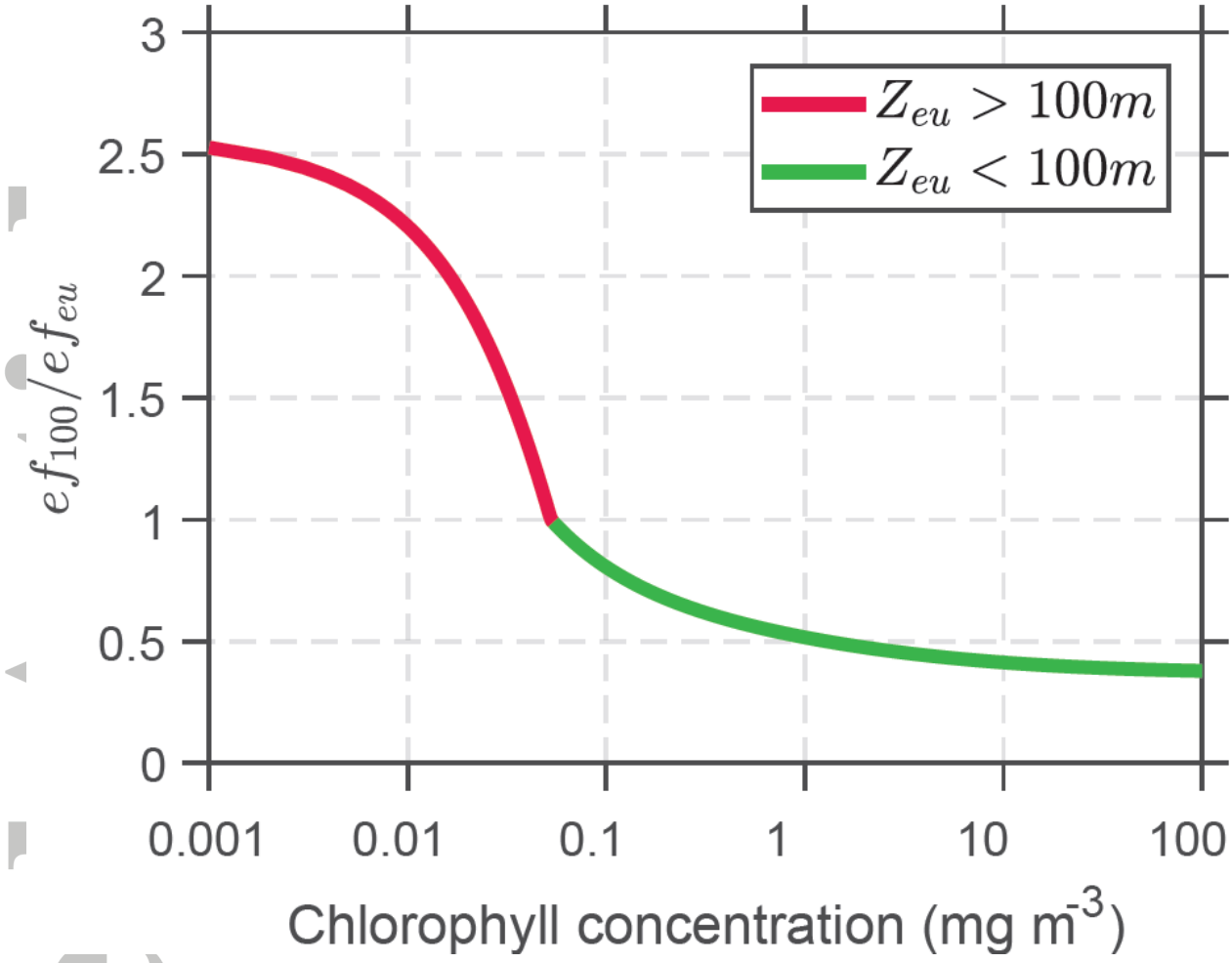


**Figure 3**. Export ratio at 100 m ($ef_{100}$) normalized to the export ratio at the euphotic depth ($ef_{eu}$) as a function of the chlorophyll a concentration. $ef_{100}$ is calculated from equations 14 and 16. $ef_{eu}$ is derived using equation (9). We select a remineralization length scale of $Z^* = 100$ m, a half-saturation constant for PAR of $k_m^I = 4.1$ Einstein m$^{-2}$ d$^{-1}$, and a surface radiation beneath the water surface of $I_0 = 50$ Einstein m$^{-2}$ d$^{-1}$. To calculate $ef_{100}/ef_{eu}$ when the euphotic depth is deeper than 100 m, we set $ef_{eu} = 0.2$ which is in line with the typical value for the global ocean. Note that the abscissa is on a logarithmic scale.

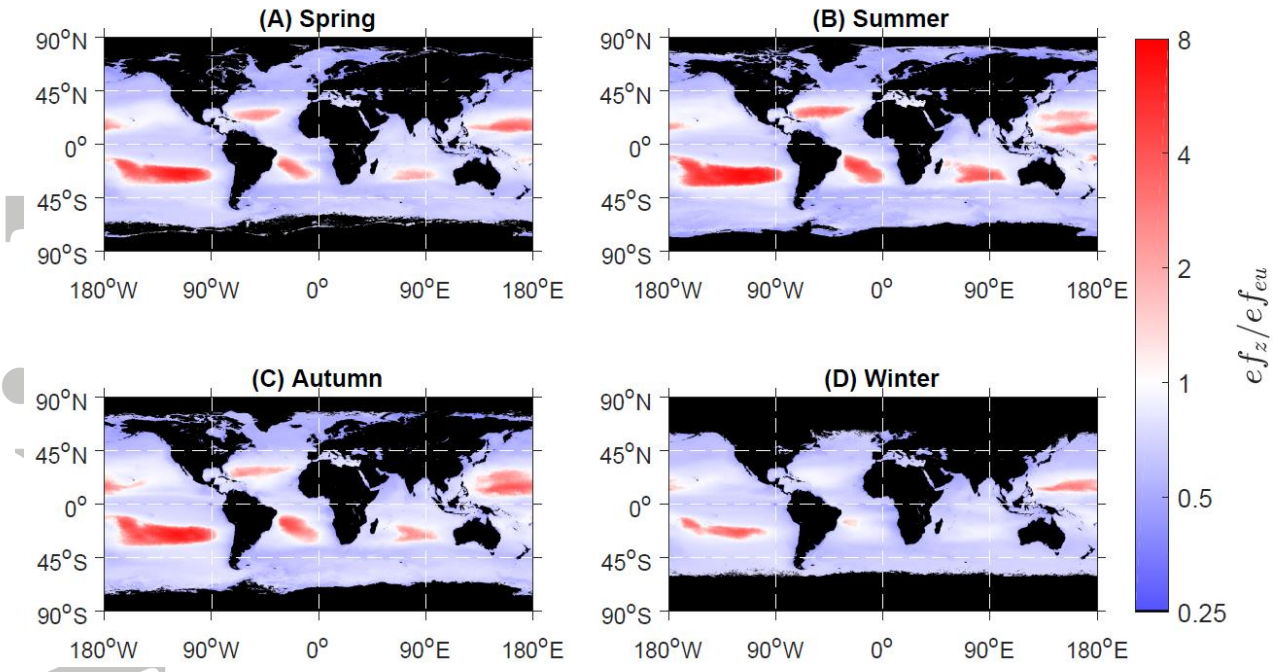


**Figure 4**. Global distribution of seasonally-averaged $ef_{100}/ef_{eu}$. $ef_{100}$ is calculated from equations 14 and 16. $ef_{eu}$ is derived using equation (9). In the Northern Hemisphere, seasons are defined as: spring (March–May), summer (June–August), autumn (September-November), and winter (December-February). In the Southern Hemisphere, seasons are defined as: spring (September–November), summer (December–February), autumn (March-May), and winter (June-August). Note that the ratio is shown on a logarithmic scale.

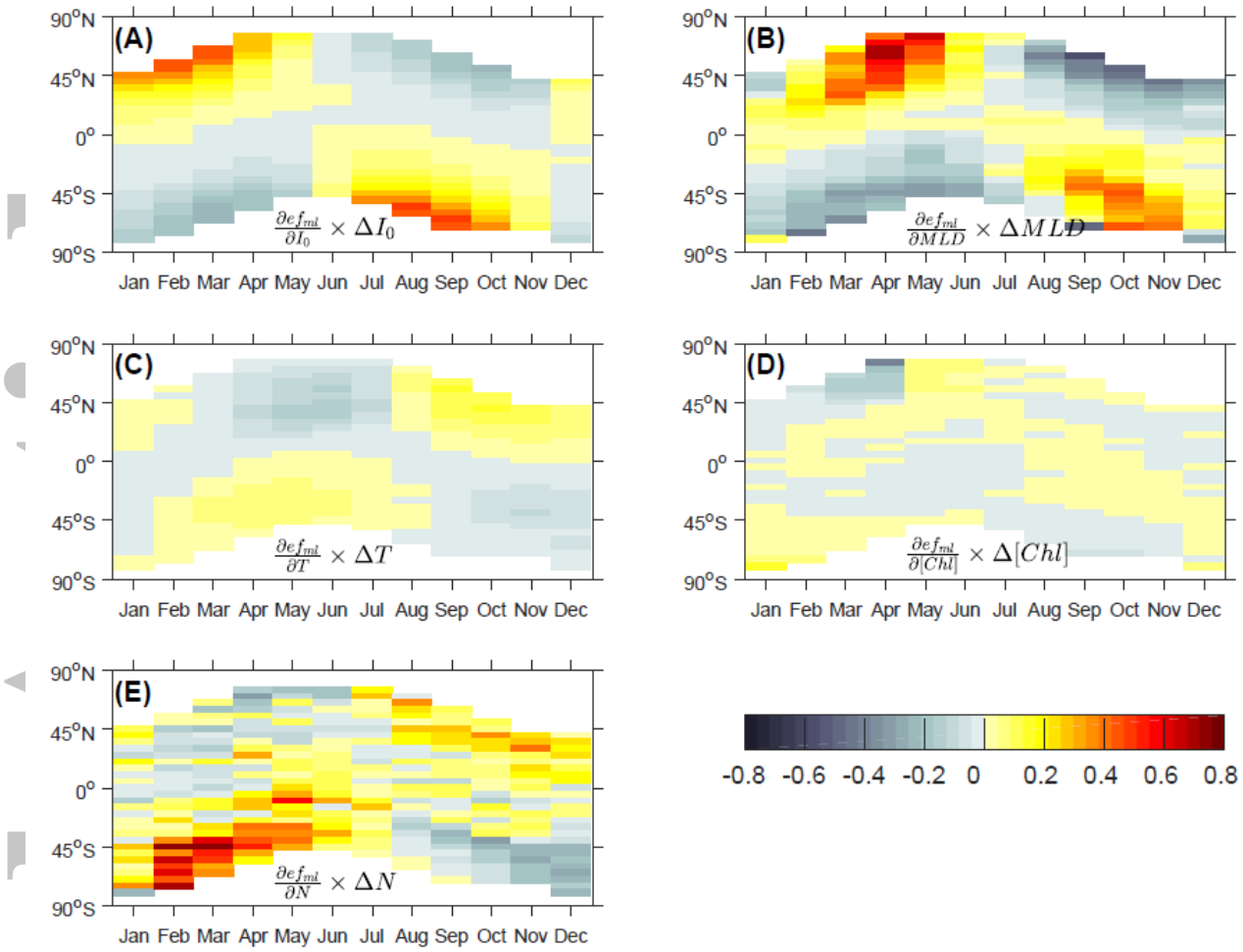


**Figure 5**. Hofmøller plots of the climatology of seasonal variations in the export ratio at the base of the mixed layer due to (A) photosynthetically active radiation just beneath water surface ($I_0$), (B) mixed layer depth ($MLD$), (C) sea surface temperature ($T$), (D) chlorophyll a concentration ($[Chl]$), and (E) nutrient concentration ($N$). Horizontal and vertical axes represent months and latitudes, respectively. Each row reflects a zonal average for each month. White areas represent missing values. Calculations are based on equation (24), noting that since $1 - ef_{ml}$ is included in equations (19-23) describing all individual parameters, it is normalized in the derivation. See the supplementary material for the spatial distribution of each (A-E) contribution.