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Comment

Interactive comment on “Ecology and biogeochemistry of contrasting trophic environments in the South East Pacific by carbon isotope ratios on lipid biomarkers” by I. Tolosa et al.

I. Tolosa et al.

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Responses to Dr. Benthien

1) In order to estimate the growth rates from alkenone producing haptophytes the authors are applying equation 5 found in Bidigare et al., 1997 which is effectively (the calculation of) the b-value divided by 138. The authors should be extremely cautious to do so since this equation is based on the result of a nitrate-limited chemostat culture grown under continuous light conditions and cannot be simply extrapolated to field conditions with varying light and nutrient

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levels. This becomes evident by looking at the resulting growth rates listed in Table 5. For the sites upw and upx (both upwelling areas), the authors estimated growth rates of 1.5 to 1.7 d⁻¹ for alkenone producers in 40 to 100 m depth. This is more than unlikely! Even though there is no information about the light conditions at these locations one can assume that in an upwelling area the lower end of the euphotic zone (defined by 1% light level) is between 30 and 50 m, if at all. Thus, at these depths I would expect growth rates close to zero. The high growth rates presented here are mainly the result of the high CO₂ values at these depths inserted into Eq. 5 and, to a minor extend, of the low ϵ_p -values. Low ϵ_p -values in *E. huxleyi*, however, could not only be the result of high growth rates but also caused by low light levels which in turn cause low growth rates (cf., Rost et al., 2002, LO 47, 120-128). That changes in nutrient- and light-limited growth rates have opposite effects on certain patterns of isotopic fractionation in marine phytoplankton has also been shown in a theoretical model by Cassar et al. 2006 (GCA 70, 5323-5335).

We estimated the growth rates for alkenones following the equation (5) but applying also the corrections for the duration of the photoperiod and respiration (equation 6), in a similar way as Bidigare et al (1997) determined the growth rates of haptophytes in natural populations from different oceanic waters. Although we agree with the reviewer that we should be cautious with the use of equations derived from cultures, the estimates field values of Bidigare were well correlated with the strength of the upwelling, enabling us to compare our estimated values with their published data.

We absolutely agree that the reported growth rates are likely overestimated since they are valid only on the assumption that alkenone producing haptophytes obtain CO₂ (as the only carbon source) solely by passive diffusion, which may not be the case in the nutrient-rich waters of the upwelling zone. Moreover, alkenones may occur well below the euphotic zone (40-100 m) in fecal material derived from herbivorous zooplankton (Grice et al., 1998) and other particles, which have been transported down due to physical mixing and sinking. Through the continuous convective movement in the wa-

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ter column of this dynamic area, the phytoplankton cells are likely to encounter on an average lower CO_2 concentrations and higher irradiance than at the depths they were sampled. In this sense, if we consider that alkenones found at depths of 40-100m were produced in the upper layer where CO_2 concentration is lower ($28 \mu\text{mol kg}^{-1}$) and light is not limited, the estimated growth rate decreases to 1.2 d^{-1} , which is in the range of typical values found in field populations of nutrient rich waters (Bidigare et al, 1997). Consequently, we believe that the obtained value of 1.2 d^{-1} represents the maximum growth rates of the euphotic zone and is also the result of a rather extended photoperiod of the upwelling sites during the sampling period.

In the revised manuscript, we have only provided the b-values and growth rates for the euphotic layer of all sites, except for the UPW site where concentrations of CO_2 were not available (before they were assumed to be equal to the UPX site). The text was changed as (L 681-695):

“This is probably related to the strength of the upwelling as indicated by the higher nutrient and CO_2 concentrations of our samples and by the longer photoperiod. However, it is noteworthy that the calculated growth rates are maximum estimates and are valid only on the assumption that alkenone producing haptophytes obtain CO_2 (as the only carbon source) solely by passive diffusion, which may not be the case in the nutrient-rich waters of the upwelling zone. Moreover, alkenones may occur well below the euphotic zone (40-100 m) in fecal material derived from herbivorous zooplankton (Grice et al., 1998) and other particles, which have been transported down due to physical mixing and sinking. Through the continuous convective movement in the water column of this dynamic area, the phytoplankton cells are likely to encounter on an average lower CO_2 concentrations and higher irradiance than at the depths they were sampled. In this sense, if we consider that alkenones found at depths of 40-100m were produced in the upper layer where CO_2 concentration is lower ($28 \mu\text{mol kg}^{-1}$) and light is not limited, the estimated growth rate decreases to 1.2 d^{-1} , which is in the range of typical values found in field populations of nutrient rich waters (Bidigare et al, 1997).”

2) In the context of the comments above I suggest to avoid the use of equation 3 which is based on the assumption that marine phytoplankton obtain CO_2 (as the only carbon source) solely by passive diffusion. This was the state of knowledge 5-10 years ago. In the meantime, however, various laboratory studies as well as theoretical considerations have demonstrated that carbon isotopic fractionation is affected by a variety of factors, including growth rate and CO_2 concentration but also by the kind of growth limitation, active uptake of bicarbonate and CO_2 , various forms of CCMs and so on. As to my knowledge, there is no investigated marine phytoplankton species which does not use a CCM or take up bicarbonate. If the authors want to use an equation to describe the overall effect on carbon isotopic fractionation (ϵ_p), I suggest using the model of Sharkey and Berry 1985 which was later extended by Burkhardt et al. 1999 (GCA 63, 3729-3741). In this model ϵ_p is determined by the isotopic composition of the carbon source and the leakage (L) defined as the ratio of carbon efflux to carbon influx ($L = F_{\text{out}}/F_{\text{in}}$): $\epsilon_p = a \cdot \epsilon_s + \epsilon_f \cdot (F_{\text{out}}/F_{\text{in}})$ where a = fractional contribution of bicarbonate to total C uptake, ϵ_s = equilibrium discrimination between CO_2 and bicarbonate, F_{out} = carbon efflux, F_{in} = carbon influx.

We agree with the reviewer's comment that equation (3) is based only on pure diffusion uptake of CO_2 and we have accordingly specified this statement on the title "*Estimations of growth rates and intracellular carbon demand in haptophytes assuming purely CO_2 diffusion uptake*". We preferred to introduce the equation (3) derived from laboratory experiments and field observations, because it shows the parameters affecting the b-variable. Hence, equation (3) enabled us to estimate directly intracellular carbon demand in haptophytes assuming uptake of CO_2 only by diffusion. However, the theoretical model of Burkhardt et al., (1999), includes parameters which are difficult or impossible to obtain in situ or scarcely documented. We therefore preferred to use a simple model and discuss the results with respect to maximum calculated growth rates (L 680-685).

3) Regarding the calculation of ε_p it is unfortunate that the carbon isotopic composition of DIC has not been measured (p. 4661). To deal with this problem, the authors use a constant value of 2.2 per mill for the ^{13}C of bicarbonate. However, is it reasonable to assume a constant value for the different oceanographic regions (upwelling vs. oligotrophic) and different depths? I suggest that the authors discuss how the potential errors of this assumption would affect the calculated ε_p values. In the context of estimating ε_p , the authors should also take into account that the isotopic difference between the lipid biomarker and biomass is not always constant. Does this uncertainty have an effect on the interpretation of the results?

We have taken into account this comment and we have now discussed the variability on the calculation of ε_p including the potential variations of $\delta^{13}\text{DIC}$ as well as variations in the offset between bulk organic matter and $\delta^{13}\text{C}$ of the biomarker. Overall, as it has been carefully discussed in point 2 and 3 of reviewer 2, the potential variability of $\delta^{13}\text{DIC}$ between the upwelling and oligotrophic area, and the variability in the offset between lipid biomarkers and biomass might only accentuate the differences between the trophic environments, providing lower ε_p values for the upwelling sites and higher ε_p values for the oligotrophic sites. Therefore, the uncertainties associated with the calculation of ε_p do not affect the interpretation of the results. Concerning the specific comment on the variability of $\delta^{13}\text{DIC}$ with depth, this uncertainty should not be of concern because vertical profiles of $\delta^{13}\text{DIC}$ has shown very little $\delta^{13}\text{C}$ variability above 400m, and only becomes more depleted at higher depths (Kroopnick, 1985).

4) In Fig. 7 the authors show that the estimated temperatures based on the $U_{37}^{K'}$ index were overestimated by 2-3_C. They argue that this phenomenon might be the result of nutrient limitation as found by Epstein et al. 1998 in *E. huxleyi* batch cultures (p. 4669). Also using batch cultures, however, Prah1 et al. 2003 (Paleoceanography 18, doi:10.1029/2002PA000803) found the opposite effect, namely decreasing $U_{37}^{K'}$ values (0.11 units or 3.2_C) under nutrient limitation. But in the same study Prah1 et al. observed increasing $U_{37}^{K'}$ values in light-limited cultures

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of *E. huxleyi* (+0.11 units). Thus, according to the results of Prah et al. the observed overestimation by alkenone unsaturation in the present study might be the result of light limitation rather than nutrient limitation. These findings should be discussed in the context of the oceanographic conditions. In this regard I am wondering why the authors did not estimate or present values for the other sites of this study (mar, hnl, egy, upw, upx) since they were able to measure $\delta^{13}\text{C}$ on alkenones.

In our samples, the observed overestimation of temperatures can not be the result of light limitation because light is not a limiting factor of the growth rate of alkenones in the upper layer of the gyre, at least above 125 m depth (see PAR values in Table 2). This statement has been incorporated within the revised discussion. We did not provide the $U_{37}^{K'}$ values for the other sites because there was only one point in the euphotic layer. Moreover, the use of $U_{37}^{K'}$ proxy is limited in tropical areas with sea surface temperature (SST) above 26 °C, such as the MAR and HNL sites where the tri-unsaturated alkenones reached their detection limit, which complicated the reconstruction of $U_{37}^{K'}$.

Minor comments:

1) **Often in the text (e.g. p. 4663, l. 19; p. 4670, l. 27) *huxleyi* is capitalised.**

We have now changed.

2) **p. 4668, l. 21: $U_{37}^{K'}$ is not a growth index.**

We agree and it has been changed

3) **p. 4669, l. 19: fractionation instead of fixation**

OK

4) **p. 4670, 4695, and 4696: in the text the authors use the correlation coefficient *r*(uncapitalised), in the Figures (8, 9) they use R-squared.**

We have modified

5) **p. 4667/4668, l. 23ff: Alkenones are not a marker for haptophytes in general**

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but for very few haptophyte species, namely *E. huxleyi* and *G. oceanica* (at least in open marine environments). So, why should cellular alkenone concentrations vary with the species composition of the coccolithophorid assemblage

The family Gephyrocapsaceae or the Isochrysidales order are the potential sources of alkenones including the genera of *Crenalithus*, *Emiliana* and *Gephyrocapsa*, all of which have been detected in these Pacific waters (Beaufort et al., 2007). Therefore the composition of the coccolithophorid assemblage and consequently their cellular alkenone concentration might change across the water column depth.

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