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Discussions

Interactive comment on "Rapid carbon cycling in the oligotrophic ocean" *by* C. M. Duarte and S. Agustí

Anonymous Referee #2

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This manuscript reports high rates of dissolved primary production (production of dissolved organic carbon, DOC) in oligotrophic waters, measured with the 14C technique over time scales of 15 minutes. This DOC, however, does not accumulate over longer time scales, which means that bacterial use rate must also be very rapid to account for its loss. Because typical measurements of phytoplankton primary production are conducted over time scales of 2 hours or longer, the authors conclude that 'conventional assessments of primary production in the oligotrophic ocean severely underestimate net phytoplankton production'. Failure to measure DOC production over short time scales would explain, following the authors' argument, the difficulties to reconcile estimates of bacterial carbon use with estimates of primary production in oligotrophic ecosystems.

The study is built upon the basis that the discrepancy between bacterial carbon demand (BCD) and phytoplankton dissolved primary production is paradoxical. However, there is nothing paradoxical in this discrepancy: 14C-based dissolved primary production need not be equal, or even close to, bacterial carbon demand. The reason is that the 14C-labelling technique only measures a fraction of all DOC production within the planktonic food web. Release of 'older' (e.g. not recently fixed, therefore unlabelled) phytoplankton carbon, excretion from protists, DOC production from zooplankton sloppy feeding, breakage of fecal pellets, and other processes, all contribute to the release of dissolved organic substrates that can be used by bacteria. This has been shown conceptually by Nagata et al (2000) and in a steady-state model by Anderson and Ducklow (2001), among others. These studies show that high values of BCD are compatible with low rates of primary production and moderate (e.g. 20-30%) PER values.

The rates of short-term primary production measured by the authors in oligotrophic waters (e.g. Figs. 2a,b,c) are extraordinarily high, and deserve further scrutiny. Let us examine these rates, calculating the resulting hourly and daily rates, and compare them to relatively well-known quantities pertaining to plankton standing stocks and metabolic activity in the open ocean.

In several oligotrophic locations (see Figs 2a,b,c) the amount of total organic carbon (TOC) produced during a 15-min period was in the range 10-28 mgC m-3. Assuming, conservatively, this activity is sustained during only 8 hours per day, the resulting daily rate of primary production would be ca. 320-900 mgC m-3 d-1. This rate exceeds the commonly reported rates of primary production by more than 1 order of magnitude. Typical rates of particulate primary production in surface waters of the oligotrophic ocean (excluding blooms) are around 2-6 mgC m-3 d-1 (Steinberg et al. 2001). Assuming a high PER of 50%, total primary production would be 4-12 mgC m-3 d-1.

Typical Chla concentrations in surface waters of the oligotrophic ocean are 0.1-0.2 mg m-3 or lower. Assuming surface Chla was 0.2 mg m-3 in the case of the samples

shown on Fig. 2, the resulting carbon fixation to chla ratios (assimilation numbers) would range between 200-560 mgC mgChla-1 h-1. The maximum theoretical value, calculated taking into account the composition and turnover of photosystems, is 25 mgC mgChla-1 h-1 (Falkowski 1981).

Typical values of phytoplankton C biomass in surface waters of oligotrophic regions are 5-15 mgC m-3 (Caron et al 1995, Buck et al 1996). Assuming a value of 10 mgC m-3 for phytoplankton C biomass, the rates reported here would imply biomass turnover times of 32-90 d-1. These values are clearly impossible: maximum biomass turnover rates for phytoplankton are 1-3 d-1.

The rates of TOC produced over a 15-min period are likely to be close to phytoplankton gross primary production (GPP). Converting C into O2 units by using a PQ of 1, the resulting GPP values are 27-75 mmolO2 m-3 d-1. Typical GPP rates in surface, oligotrophic waters, measured with the O2-evolution technique, are 1-3 mmolO2 m-3 d-1 (Robinson et al 2002, Williams et al. 2004).

The sharp decrease in accumulated DO14C, observed by the authors in oligotrophic waters, must be the result of bacterial respiration. The observed decrease, which is thus equivalent to bacterial respiration, is 8-25 mgC m-3 during a 45-min. period (Fig 2a,b,c). Even assuming that bacteria do not respire during the night, this rate translates (using a RQ of 1) into a daily rate bacterial respiration of ca. 7-22 mmolO2 m-3 d-1. For comparison, typical rates of total, community respiration (e.g. including the respiration of all heterotrophs) in the oligotrophic ocean are 0.5-5 mmolO2 m-3 d-1 (Robinson et al 2002, Williams et al. 2004).

In summary, it seems fair to conclude that the extraordinarily high values of primary production in oligotrophic waters reported here are not possible, which renders the authors' arguments and conclusions invalid.

Specific comments

Throughout the ms, the authors refer to bacterial use of carbon, rapid bacterial respiration, etc. However, none of these variables has actually been measured. Rather, they are inferred from the temporal dynamics of DO14C disappearance, which is attributed to bacterial use. This should be made clear throughout the ms.

The ms does not refer to previous measurements of DOC production over short-time scales (e.g. <1 h). However, in their seminal paper on phytoplankton DOC production, Mague et al. (1980) included a time-series experiment (conducted in relatively low production waters, Gulf of Maine in summer) which had measurements during the first 15 min. Lancelot (1979) and Jensen (1983), among others, also reported DOC production measurements over time scales of ca. 30 min. None of these studies reported major departures from linearity in DO14C accumulation over time.

Pages 11665-6. More details should be given regarding the 14C incubations, including sampling time, time elapsed between end of incubation and filtration, handling of DPMs from black bottles (e.g. were they subtracted from DPMs measured in the light bottles?), difference in DPM counts between light and dark bottles at each incubation time.

Page 11668, line 14. This sentence doesn't work – should be: '. . .shallower than that for TOC, at. . ..'

Page 11671 The model should be described with more detail – this description should be included in the Methods section.

Table 3. From the legend, it seems as tough there are missing columns in this table. P-values should have some decimal digits.

Fig. 3 The legend and the label to the Y-axis seem contradictory – please re-write.

Fig. 4. Y-axis labels are missing the micro- symbol.

References (not cited in the ms)

Anderson and Ducklow (2001) Aquat Microb Ecol 26: 37 Buck et al (1996) Aquat Microb Ecol 10: 283 Caron et al (1995) Deep-Sea Res 43: 943 Falkowski (1981) J Plankton Res 3: 203 Jensen (1983) Mar Ecol Prog Ser 11: 39. Mague et al. (1980) Limnol Oceanogr 25: 262 Nagata et al. (2000) In: Kirchman DL (ed) Microbial ecology of the oceans. Robinson et al (2002) Deep-Sea Res I 49: 787 Steinberg et al. (2001) Deep-Sea Res II 48: 1405 Williams et al. (2004) Deep-Sea Res I 51: 1563

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