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Received: 16 June 1998

Accepted: 14 June 1999

Limnol. Oceanogr., 44(8), 1999, 1999–2004
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Preferential recycling of nutrients—the ocean's way to increase new production and to pass nutrient limitation?

Abstract—Uptake of atmospheric CO₂ by the oceans and the export of carbon into deeper waters via the biological CO₂ pump is driven by the production of particulate organic matter (POM). The elemental ratios of carbon, nitrogen, and phosphorus within POM follow Redfield ratios, suggesting that the concentrations of dissolved inorganic carbon (DIC) and nutrients decrease during new production corresponding to these ratios. Subsequently, new production and the efficiency of the biological CO₂ pump are usually estimated using Redfield ratios. However, our observations in the Baltic Sea and observations elsewhere show significantly greater decreases in DIC during the productive season than that predicted from the decline in nutrients with reference to Redfield ratios. Using new DIC, nutrient, and oxygen data from the Baltic Sea, we discuss this discrepancy and provide evidence that preferential recycling of nutrients fuels the productive community with nutrients. Limiting nutrients are preferentially recycled and become available for new production. These findings derived from hydrochemical bulk data confirm the picture of the microbial loop but question the common description of new production and nutrient limitation. Finally, we argue for a carbon-based efficiency estimate of the biological CO₂ pump probably exceeding significantly nutrient-based estimates.

Uptake of atmospheric CO₂ by the oceans via the biological CO₂ pump is driven by the new production of particulate organic matter (POM) and its export into deeper waters (e.g., Eppley and Peterson 1979). Phytoplankton produces POM during photosynthesis consuming dissolved inorganic carbon (DIC) and mainly nitrate (NO₃) and phosphate (PO₄). The elemental ratios of carbon (C), nitrogen (N), and phosphorus (P) within freshly produced POM that are found to be similar all over the world's oceans (e.g., Copin-Monteguet and Copin-Monteguet 1983; Toggweiler 1993) are expressed by Redfield ratios, suggesting that the concentration changes of DIC and nutrients during production and remineralization of POM are in the same ratios (Redfield et al. 1963). With

reference to Redfield's idea of a coupling between DIC and nutrient concentrations and elemental ratios of POM, Dugdale and Goering (1967) deduced the widely accepted and applied description of new production and its limitation by nutrients: New production is defined as phytoplankton production based on nitrate uptake that can be converted to carbon units using the elemental ratios of POM. New production is limited by nutrient availability in the euphotic zone. Consequently, the export of CO₂ into the deeper waters via the biological CO₂ pump is estimated using the increases of nutrients.

However, several investigations on the relationship between the elemental composition of POM and changes of nutrients over depth show only weak consistency (Shaffer 1996, and review therein). There are even strong indications that the observed DIC decrease during production of POM is decoupled from the associated NO₃ decrease, because the ratio of DIC to NO₃ decreases, $\Delta\text{DIC}/\Delta\text{NO}_3$ is found to be significantly higher than predicted by the C/N ratio of POM. Here, we discuss some of these hydrochemical indications and refer to new DIC and NO₃ data from the Baltic Sea to provide evidence that the discrepancy between observed and predicted DIC decrease is caused by preferential recycling of nutrients within the euphotic zone. This mechanism enhances the efficiency of the biological CO₂ pump by allowing further net-CO₂ fixation, i.e., net community production, using recycled nutrients. We suggest that Redfield's idea of fixed elemental ratios of POM is consistent with this mechanism. However, in contradiction to this mechanism are (1) the assumption that the concentration changes of DIC and nutrients would reflect the Redfield ratios, (2) the application of the definitions of new production and nutrient limitation according to Dugdale and Goering (1967) to assess net community production, and (3) the description of the biological CO₂ pump with reference to nutrient concentrations and Redfield ratios.

Table 1. Particulate C/N ratios vs. concentration change ratios $\Delta\text{DIC}/\Delta\text{NO}_3$.

Redfield ratio	North Atlantic Bloom Experiment		North Atlantic observations‡	Southern Ocean		Northeast Atlantic Ocean¶	
	POM*	Concentrations†		POM§	Concentrations	POM	Concentrations
C/N	C/N	$\Delta\text{DIC}/\Delta\text{NO}_3$	$\Delta\text{DIC}/\Delta\text{NO}_3$	C/N	$\Delta\text{DIC}/\Delta\text{NO}_3$	C/N	$\Delta\text{DIC}/\Delta\text{NO}_3$
6.6	6.7	10.7	8.5–14.2	6.6	14–21	6.6	5–15

* Ducklow et al. (1993).

† Chipman et al. (1993).

‡ Sambrotto et al. (1993).

§ Dehairs et al. (1997).

|| de Baar et al. (1997).

¶ Körtzinger et al. (in prep.).

Terminology—We define key expressions, in some cases from a chemical rather than a physiological point of view. New production, as a nitrogen-based term, comprises NO_3 uptake and nitrogen (N_2) fixation by biological processes within the euphotic zone. Originally, Dugdale and Goering (1967) focused their discussion on nitrate production. Both new and nitrate production can be converted to carbon units using Redfield ratios. However, we provide evidence that the new production simply converted to carbon units does not necessarily equal net community production, i.e., net DIC fixation by biological processes in the euphotic zone. Preferential recycling of nutrients comprises processes that enable a reuse of nutrients for further (net) DIC fixation. These may be genuine recycling processes in a physiological sense as well as processes that contribute to nutrient recycling in a more systemic sense.

Discussion follows of some observations from the oceans and the Baltic Sea, indicating a decoupling of DIC fixation from nutrient uptake. We then refer to hydrochemical observations of the Baltic Sea to provide evidence for preferential recycling of nutrients and suggest a solution for the discrepancy between the elemental composition of POM and the changes in hydrochemical properties.

Hydrochemical indications for decoupling of CO_2 fixation from nutrient uptake— $\Delta\text{DIC}/\Delta\text{NO}_3$ ratios vs. C/N ratios of POM: (1) During the North Atlantic Bloom Experiment (NABE), the C/N ratio of POM was determined to be C/N = 6.7/1 (Ducklow et al. 1993), which is close to Redfield's value. However, the observed $\Delta\text{DIC}/\Delta\text{NO}_3$ ratio during this productive period was almost twice as high as the associated C/N ratio of POM (Chipman et al. 1993) (Table 1). (2) Sambrotto et al. (1993) reported from the North Atlantic Ocean $\Delta\text{DIC}/\Delta\text{NO}_3$ ratios in the euphotic zone that also exceed the Redfield value (Table 1). (3) Observations from the Southern Ocean show the same pattern: the elemental ratio within POM reflects the Redfield ratio, whereas budget calculations show a significantly higher $\Delta\text{DIC}/\Delta\text{NO}_3$ ratio (Karl et al. 1991; de Baar et al. 1997; Dehairs et al. 1997) (Table 1). (4) The analysis of the carbon budget at the U.S. Joint Global Ocean Flux Study Bermuda Atlantic Time-series study (BATS) site indicates that biological DIC fixation takes place to a significant extent, although nutrient concentrations are below the detection limit during most of the year (Bates et al. 1996). (5) The CO_2 budget for the Baltic Sea (Thomas and Schneider 1999) shows that DIC uptake is decoupled

from NO_3 uptake and/or NO_3 availability. The changes of DIC and NO_3 due to biological processes do not reflect the Redfield ratio and DIC uptake occurs, even if NO_3 is exhausted (Fig. 1A). The $\Delta\text{DIC}/\Delta\text{NO}_3$ ratio increases rapidly during the productive season from approximately 5.5 up to approximately 25, indicating that DIC uptake is decoupled from NO_3 uptake, even if NO_3 is still available in the surface waters (Fig. 1B). Consequently, the nitrate-based estimate of new production in the Baltic Sea (Fig. 1C) achieves only 65% of the carbon-based estimate, even taking into account the external nitrogen supply by nitrogen fixation as well as atmospheric and riverine input (Leppaenen et al. 1988; HELCOM 1997). (6) The above indications for decoupling of DIC and NO_3 uptake are supported by field data on the seasonal development of C/N ratios in the Northeast Atlantic Ocean (Körtzinger et al. in prep.) (Table 1) and (7) by data from mesocosm experiments (Banse 1994). Corresponding to Fig. 1A and B, both investigations provide evidence that, upon disappearance of NO_3 , net carbon production still occurs and the DIC/ NO_3 uptake ratio thus increases significantly.

Oxygen saturation vs. nutrient concentrations: An obvious feature that implies the decoupling of DIC fixation from nutrient uptake is the mismatch of the seasonal development of oxygen saturation and nutrient concentrations in surface waters of the Baltic Sea (Fig. 2). Oxygen supersaturation indicates net community production in the Baltic Sea from the beginning of March until September. The associated surface NO_3 is exhausted at the end of June, but net community production occurs, even if NO_3 is obviously exhausted from July to September (Fig. 2, shaded area), and there are no hints for exceptional high C/N ratios of POM within the euphotic zone of the Baltic Sea. Note that these observations underline the results of the carbon budget (Fig. 1A,B) and cannot be explained by regenerated production, because the release of oxygen indicates (net) DIC fixation.

Hydrochemical indications for preferential recycling of nutrients as internal nutrient source—The stratification of the Baltic Sea allows a detailed investigation of the seasonal hydrochemical changes within surface waters. During spring and summer, the Baltic Intermediate Water (BIW) is almost hermetically enclosed between the thermocline (≈ 25 m depth) and the permanent halocline (≈ 65 – 80 m depth) (Fig. 3, shaded areas). The air–sea exchange of CO_2 and other gases like, e.g., O_2 , cannot affect the BIW, because it is separated from the

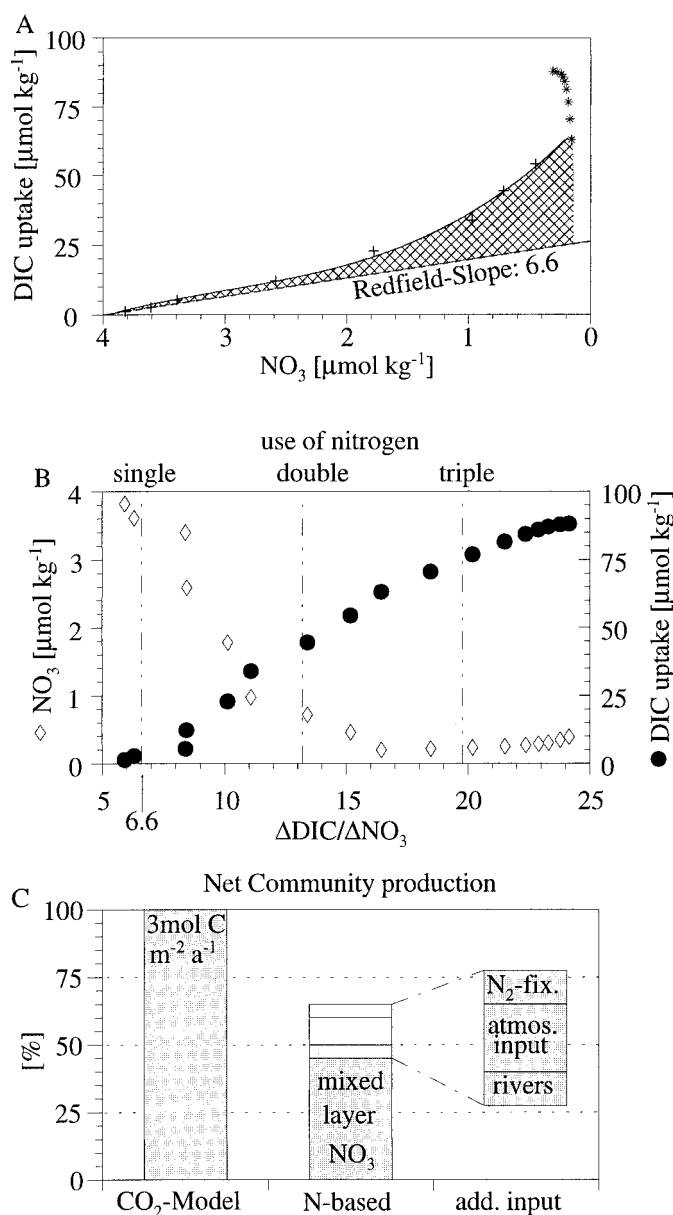


Fig. 1. (A) DIC changes due to net community production (DIC uptake) vs. NO_3 concentrations obtained for the surface waters at the central station in the Baltic Proper (57.30°N , 20.07°E) (Thomas and Schneider 1999). The crossed area indicates the mismatch between the expected relationship according to particulate C/N ratios (Redfield-slope) and the calculated DIC uptake. (B) $\Delta\text{DIC}/\Delta\text{NO}_3$ ratios as a function of surface NO_3 and DIC uptake. The lines mark the Redfield C/N ratio and its multiples to indicate recycling quota of nitrogen. (C) Mean annual net community production in the Baltic Proper obtained by the CO_2 model (Thomas and Schneider 1999) and obtained as new production with reference to available surface NO_3 of the winter mixed layer and external sources converted to carbon units using Redfield's C/N ratio (6.6/1). Data for the additional nitrogen inputs are compiled from Leppanen et al. (1988; N_2 fixation) and HELCOM (1997; riverine and atmospheric inputs).

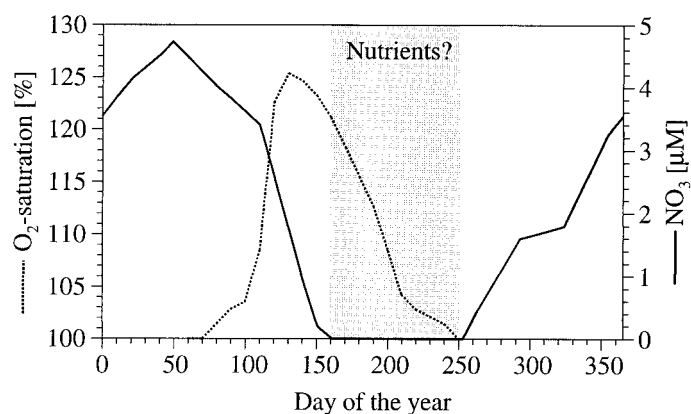


Fig. 2. Climatological annual cycles of oxygen saturation and NO_3 in the surface waters of the central Baltic Proper (HELCOM 1997). The shaded area indicates the period of net community production when NO_3 is already exhausted.

atmosphere by the surface layer and the diffusive transport of dissolved compounds from below the halocline into the BIW is of minor relevance for this discussion. Therefore, the physical conditions of the winter mixed layer are maintained within the BIW. The changes of the hydrochemical properties between winter and summer (Fig. 3) contribute to biological processes that are induced by the export of organic matter from the euphotic zone. A rather homogeneous concentration of 4–5 μM NO_3 is detectable within the winter mixed layer down to the halocline. At the end of the productive season in summer, NO_3 is almost completely exhausted down to the halocline due to NO_3 uptake by new production (Fig. 3). DIC is expected to decrease correspondingly, because it is consumed during new production. However, instead of a DIC decrease, an increase of DIC occurs from winter to summer within the BIW (Fig. 3). Because the DIC concentrations within the BIW are not affected by CO_2 air-sea exchange and diffusive transport through the halocline is of minor relevance, the DIC increase indicates remineralization of organic matter. The corresponding oxygen consumption is indicated by the apparent oxygen utilization (Fig. 3). Given the remineralization of organic matter within the BIW, an increase of NO_3 still has to be expected, assuming that the elemental composition of POM settling into the BIW reflects the Redfield ratio. Roughly estimated, the DIC increase of $\sim 80 \mu\text{mol kg}^{-1}$ compared to the winter value (50 m depth, Fig. 3) should be associated with an increase in NO_3 of $\approx 12 \mu\text{M}$, i.e., the summer value should be $\approx 16 \mu\text{M}$, which is however found to be $\approx 1 \mu\text{M}$. This rough estimate underpins a lack of NO_3 within the BIW that accordingly has to be contributed to a lack of nitrogen in the organic matter remineralized there. These observations suggest that the C/N ratio of the POM settling out of the euphotic zone significantly exceeds the C/N ratio of freshly produced POM. Organic nitrogen is recycled earlier, i.e., within the euphotic zone, whereas the residual carbon tissue is exported to the BIW. Nitrogen fixation and atmospheric input of nitrogen compounds may counteract the high $\Delta\text{DIC}/\Delta\text{NO}_3$ ratios to a certain extent, the hydrochemical changes within the BIW, however, imply an export of carbon-enriched material from the surface layer that would not be

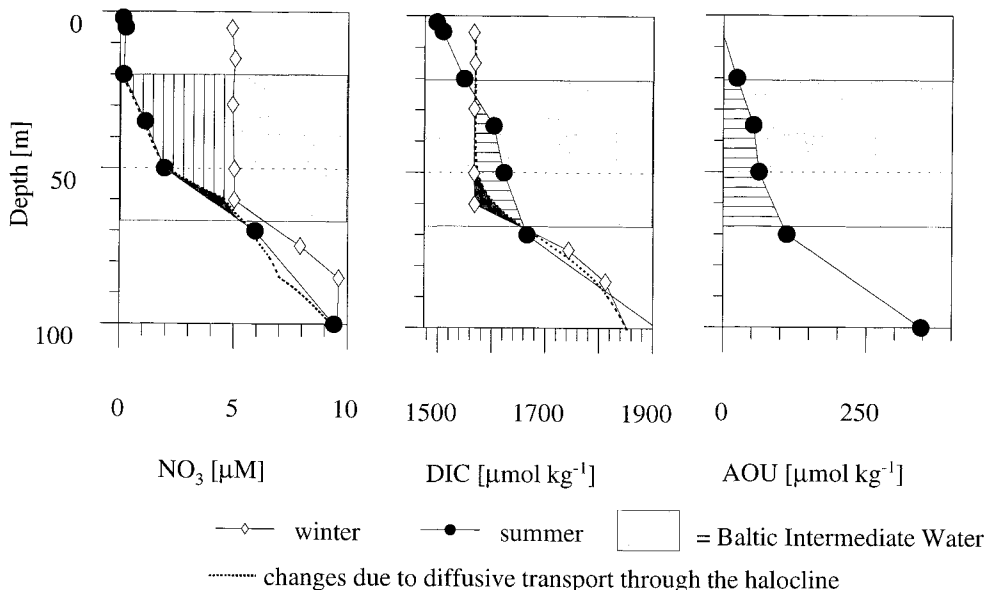


Fig. 3. Seasonal changes of the hydrochemical properties within the Baltic Intermediate Water shown for the central station within the Baltic Proper (57.30°N, 20.07°E). The samples were taken in early March and early September covering the beginning and the end of the productive season, respectively (Fig. 2). The changes caused by diffusive transport through the halocline are estimated with reference to changes of density. Vertically hatched areas indicate a decrease from winter to summer; horizontally hatched areas indicate an increase.

expected if these nitrogen sources provide all the missing nitrogen.

Suggested solution of the discrepancies—The hypothesis of preferential recycling of nutrients has been suggested by Sambrotto et al. (1993) to explain the discrepancy between $\Delta\text{DIC}/\Delta\text{NO}_3$ uptake ratios and the elemental composition of freshly produced POM. This line of argument has been adopted among others by Bates et al. (1996) to resolve the misfit between observed net community production and missing nutrients in the euphotic zone in the Sargasso Sea. Our screening of preferential recycling of nutrients in the Baltic Sea (Fig. 3) underpins this hypothesis. We suggest a comprehensive explanation of the observations and discrepancies discussed above by comprising both cell–internal and cell–external processes of nutrient recycling to enhance net community production, i.e., net CO₂ fixation.

Redfield's idea of connecting changes in DIC and nutrient concentrations to elemental ratios of POM and the deduced description of new production and its nutrient limitation by Dugdale and Goering (1967) imply that growth of cells, i.e., net community production, is coupled to the uptake of nutrients. Thus, if there are no nutrients available in the environment of a phytoplankton cell, CO₂ fixation cannot occur (systemic nutrient limitation; Thingstad and Rassoulzadegan 1995). Following this view, all discrepancies discussed above arise because they do not provide non-Redfieldian, decoupled uptake of DIC and nutrients.

However, the observations discussed above seem to confirm a different view of net community production and nutrient limitation, earlier suggested by Droop (1973, 1974; see also Baratta-Bekker et al. 1997). He provided evidence that the internal

state of a phytoplankton cell acts as an additional factor controlling cell growth, i.e., net community production. Accordingly, growth of a phytoplankton cell is possible, if the cell can maintain its internal elemental ratio, even if uptake of nutrients is impossible. The phytoplankton cell grows maintaining the major features of cell growth, while carbon-rich organic matter is released to conserve the internal elemental ratio. Following this line of argument, cell growth is limited, if internal or external resources cannot be exploited any longer to maintain the cell's internal elemental ratio (physiological limitation; Thingstad and Rassoulzadegan 1995). The release of carbon-enriched organic matter (Fogg 1983), which is implied by exploiting internal nitrogen sources while maintaining the internal elemental ratio, is in fact observed as accumulation of dissolved organic carbon (DOC) with high C/N ratios during the productive season within the euphotic zone in the Baltic Sea (Matthäus et al. 1998) and in other regions as well (e.g., Toggweiler 1993; Williams 1995). The description of microbial dynamics by models achieves significantly better results using Droop's (1973, 1974) approach (e.g., Baratta-Bekker et al. 1997) and the increase of the $\Delta\text{DIC}/\Delta\text{NO}_3$ during the productive season indicates that a decoupled DIC and nutrient uptake occurs, even if indigenous NO₃ is available (Fig. 1B). Thus, in this case the essential nutrients are maintained—i.e., recycled—within the cells enabling further net-CO₂ fixation. The nitrogen overconsumption indicated by $\Delta\text{DIC}/\Delta\text{NO}_3$ uptake ratios being lower than the Redfield ratio (Fig. 1B; Körtzinger et al. in prep.) probably can be explained as luxury consumption (Droop 1973, 1974) that occurs if an essential compound is available in excess. This luxury consumption serves as a buffer to maintain the cell's internal ratio, if this compound is no longer available in the environment.

Besides this cell-internal recycling, external processes enable the recycling of essential elements within the community, increasing its productivity. Studies on phytoplankton bloom decay showed that during lysis of cells, organic nitrogen is recycled faster than organic carbon (e.g., Azam 1998 and references therein). Moreover, the metabolism of organic carbon compounds at the different trophic levels of the microbial loop may contribute to a nutrient recycling in a rather systemic way: because bacteria have a lower C/N ratio than both phyto- and zooplankton, carbon-enriched compounds settle out of the euphotic zone as residue from bacterial degradation of phytoplankton. On the other hand, if bacteria are grazed by zooplankton, these grazers release nitrogen-enriched organic compounds in order to maintain their higher C/N ratio. Both the fractionation of C/N ratios between different trophic levels and the fast lysis of organic nitrogen compounds finally fuel phytoplankton with recycled nitrogen compounds. The consequential increase of carbon relative to nitrogen in sinking POM can be seen in analogy to the above accumulation of DOC and has been shown by increasing C/N ratios with depth and rapidly decreasing organic nitrogen contents in sinking particles trapped below the euphotic zone in the Baltic Sea and elsewhere (e.g., Knauer et al. 1979; Wakeham et al. 1984; Olesen and Lundsgaard 1995). The weak consistency in estimates of the relationship between the elemental composition of POM and changes of nutrients over the depth could reflect that there might be only a minor relationship being controlled by several, hardly assessable factors. Thus, in this case the essential nutrients are maintained, i.e., recycled, within the productive community enabling further net CO₂ fixation.

Preferential recycling of nutrients acts as an additional—internal—nutrient source allowing further (net) CO₂ fixation within the euphotic zone while maintaining the elemental ratios of freshly produced POM. Recycled nitrogen components are rapidly used again and cannot be traced by nutrient measurements causing high Δ DIC/ Δ NO₃ ratios. From the physiological point of view, some processes mentioned here may not be accounted for by genuine recycling; however, from a more chemical or overall point of view, all processes allow further net CO₂ fixation, because the productive community is supplied with (regenerated) nutrients while organic carbon is left over. Its export from the euphotic zone consists both of released DOC being adsorbed to particles and of carbon-enriched residuals from fractionated lysis and cell degradation. Net community production, i.e., net CO₂ fixation, can significantly exceed (N-based) new production and is limited rather by physiological than by systemic nutrient availability or by other factors such as light.

Recently, Hoppema and Goeyens (1999) argued in favor of a Redfieldian behavior of carbon and nutrient depletions during the vegetative season in the western Weddell Sea. These observations fit in the picture we present here, because the Weddell Sea is supposed to be a high-nutrient low-chlorophyll (HNLC) region, where shortages of N- and P-nutrients are not generally observed. Thus, the nutrient demand of new production can be fuelled sufficiently by indigenous nutrients available within the euphotic zone and recycling processes are not required because other factors, e.g., light or iron, are limiting new production. Furthermore, there are hints that in the case of P-limitation similar recycling fea-

tures may occur. In the subtropical North Pacific Ocean, which appears to be P and/or N limited, N/P ratios of POM within the euphotic zone are close to the Redfield value; however, the N/P ratios of exported POM trapped below the euphotic zone are significantly higher (Karl et al. 1997; Emerson and Karl 1999). These observations might be analogous to the increasing C/N ratios discussed above.

Conclusions—Using hydrochemical bulk data like DIC, nutrients, and oxygen, we provide strong evidence that the preferential recycling of nutrients can force the efficiency of the biological CO₂ pump due to increased new production and subsequently due to increased export of POM to the deeper waters. The available light is used more efficiently because systemic nutrient limitation can be overcome temporarily. Net community production is underestimated if based on nutrient concentrations and Redfield ratios only because the contributions of recycled nutrients cannot be taken into account. In the Baltic Sea this contribution amounts to 50% of the new production, emphasizing that carbon-based estimates of new production should be used to assess the efficiency of the biological CO₂ pump in regional as well as in global contexts.

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BARETTA-BEKKER, J. G., J. W. BARETTA, AND W. EBENHOEH. 1997.

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Acknowledgments

Valuable discussions with Dietwart Nehring, Piet Ruardij, and Gerhard Herndl are gratefully acknowledged. This work was supported by the German Research Council (DFG).

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Received: 16 February 1999

Accepted: 10 August 1999

Amended: 25 August 1999