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SYNTHESIS AND EMERGING IDEAS

# A fresh look at the nutrient cycling in the oligotrophic ocean

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**Abstract** This paper aims at a synthesis of our conceptual views on the marine nutrient cycling. Based on selected biological, physical and geochemical aspects of the system, we present a framework for the description of the nitrogen cycling in oligotrophic regions of the ocean. Recent findings about the importance of the mesopelagic for remineralization are combined with ideas on the role of primary production, external input and fixation in nitrogen cycling. Instead of the usual distinction between euphotic and aphotic zones (i.e., with and without net primary production), our concept suggests a three-layer model featuring the *subsurface production remineralization layer* (SPRL) between the base of the surface mixed layer (SML) and the nutrient maximum at about 1000–1200 m depth, which can be used as a biogeochemical definition for the lower boundary of the mesopelagic. The approach leads to revised definitions of new and regenerated production, as well as export into the deep ocean, which are more adequate to characterize the biological pump, at least in the oligotrophic ocean. One of the main conclusions is that the steady state nitrogen export from the SPRL is fully determined by the sum of atmospheric deposition of nitrogen and $N_2$-fixation and can be best quantified at the depth of the nitrogen maximum. While the magnitude of primary production by non-diazotrophic phytoplankton is irrelevant for export into the deep ocean, biological processes are crucial in determining size, shape and density of sinking particles and the remineralization rate of detritus.

**Keywords** Stratified ocean · Nutricline · Subsurface biomass maximum layer · Primary production · Biological pump · Export · Remineralization length scale · Mesopelagic · Twilight zone · Conceptual model

## Introduction

Conceptual pictures of the marine “biological pump” are numerous and diverse (see, e.g., Ducklow et al. 2001; Sarmiento and Gruber 2006) based on various levels of abstraction of the complex coupled physical–biogeochemical system that involves the cycling of several elements. A common feature, however, is the separation of the euphotic from the aphotic zone. Within this approach, the region of net primary production is clearly identified, and “export production” can be defined as the part of the primary production that is not remineralized within this zone but transferred to deeper layers.

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This biologically motivated view comes with the so-called *f*-ratio, which relates the nitrate and fixed nitrogen based "new" production to the total, including also ammonium based regenerated production. Since in steady state new equals export production (Eppley and Peterson 1979) the *f*-ratio is used as a measure for the efficiency of the biological pump. This is so intuitively obvious that it has never really been challenged, even though some newer evidence is hardly integrable: First, the growing data base of particle flux measurements show that the export in 100 or 150 m depth is not well correlated with the primary production above these depths (Ducklow et al. 2001; Lutz et al. 2002). Second, a recent study on nitrification within the surface layers concludes that roughly half of the nitrate which is taken up by phytoplankton is remineralized above the local maximum winter mixed layer depth and that the standard use of the f-ratio as an indicator to distinguish nitrate based from ammonium based production is problematic (Yool et al. 2007). This reminds us that only the nitrogen from external pools are really "new" to the ocean (see, e.g., Duce et al. 2008), while upwelled and upwardly diffused nutrients have been cycled through the production layer before. Third, the vertical structure of particle fluxes has been found to be best describable by two detritus species with different remineralization lengths scales, one about 100–200 m, the other significantly longer (Lutz et al. 2002; Buesseler et al. 2007; Lamborg et al. 2008). This strongly suggests to conceptually separate the recycling in the mesopelagic (sometimes called the "twilight zone", e.g., Buesseler and Lampitt 2008) from the sinking that eventually can lead to deposition at the sea floor.

Considering these advances of our knowledge about the marine nutrient cycling, the usefulness of the "export from the euphotic zone" concept seems to be watered down enough to be almost useless; yet, for lack of an alternative, the majority of studies still tries to relate observations of primary production to export estimates at about 100–150 m depth (e.g., Lutz et al. 2002; Boyd et al. 2008). It seems that references to additional complexities of the system are more popular than a reconsideration of the underlying concept. Among these additional factors the potential role of lateral effects is sometimes mentioned as the main reason for inconsistencies between data and concept. Certainly, lateral advection is likely to play a significant role in many places (Sarmiento et al. 2004); it has, however, not been shown to which degree the overall structure of the nutrient fields is determined by three-dimensionality. In the meantime, budget calculations based on localized measurements usually adopt a one-dimensional (steady state) view. This is likely to be acceptable in some places, like the centers of the subtropical gyres, but less so along the continental margins.

We believe that an adequate view of the vertical processes is the first step toward the understanding of the system. We therefore try to combine the above findings into an advanced conceptual picture that may lead to new questions and approaches and help to reduce the confusion that exists in the literature on how to best analyse and interpret observations and how to describe production, export and the strength of the biological pump. In particular, clear definitions of the boundaries of different regimes seem helpful. We limit our considerations to oligotrophic regions, a significant portion of the ocean because we can initially ignore upwelling, lateral advection, and temporal variability. Instead we shall concentrate on vertical mixing, light penetration, and vertical nutrient distributions. The emerging conceptual view may turn out to be useful in other circumstances or other areas in the ocean as well.

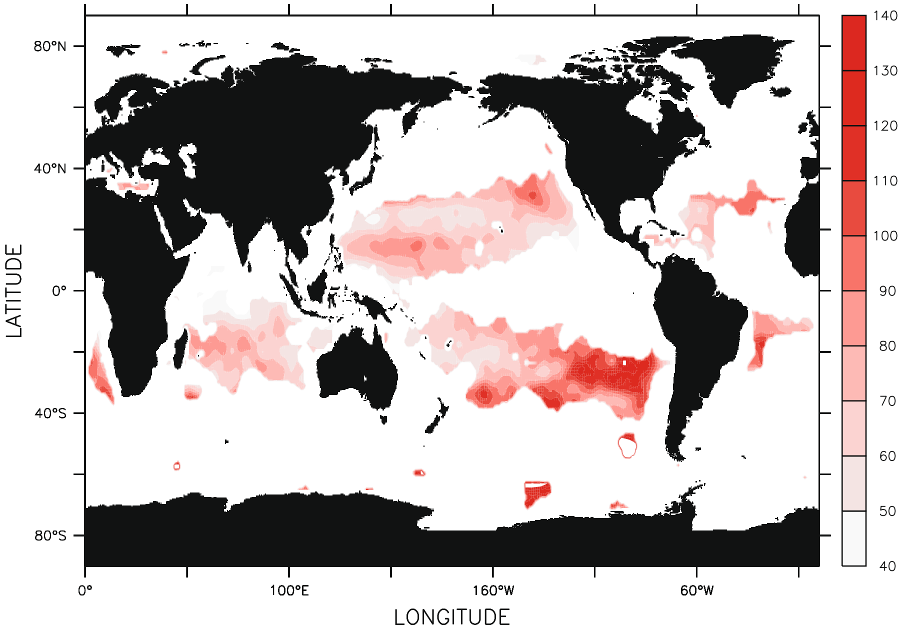
This paper collects the relevant data (section: Some characteristics of the surface nutrient depleted water column) to support an updated view (section: An updated concept for nutrient cycling in the oligotrophic ocean) for the oligotrophic ocean and considers some of the consequences (Discussion section). It concludes with suggestions for future investigations.

## Some characteristics of the surface nutrient depleted water column

Oligotrophic conditions (as defined by a surface chlorophyll concentration of less than 0.1 mg Chl *a* $m^{-3}$, see, Carr et al. 2006) are found in the central gyres in the North and South Pacific and Atlantic, as well as in most of the Indian Ocean, away from coastal areas (see Fig. 1). The total areal extent is about 100 million $km^2$, almost 30% of the ocean.

In addition to the low chlorophyll concentrations at the surface, several other features are common to

**Fig. 1** Climatological winter mixed layer depth $z_{ML}$ in areas with surface chlorophyll *a* concentrations of <0.1 mg Chl *a* m$^{-3}$, derived from the WOA01 data set (Conkright et al. 2002)



most of the oligotrophic areas: these are related to vertical mixing, light penetration and nutrient distributions. This is not to say that temperature, salinity, lateral and vertical advection play no role at all; they are, however, comparatively less important.

## Vertical mixing

Vertical mixing plays a prominent role for the structure of the oligotrophic ocean, as it separates a well-mixed near surface layer from a stratified (non well-mixed) regime below. The surface mixed layer (SML) is characterized by vertically quasi-homogeneous distributions of dynamically active and passive tracers, except those that sink or rise. Ideally determined from the level of turbulence that generates and maintains vertical homogeneity, the mixed layer depth $z_{ML}$ can only approximately be deduced from tracer observations, and the exact value will depend on the criterion used. We follow de Boyer Montégut et al. (2004) in their definition based on a 0.2° C temperature difference from a reference depth of 10 m.

Directly in contact with the atmosphere (wind, temperature), depth and water mass properties of the SML are seasonally varying (Fig. 2). In the oligotrophic parts of the ocean maximum values range from 50 to 80 m, with higher values in the eastern South Pacific (Fig. 1). During summer, values of about 20 m are not uncommon. Since the depth of the deepest penetration is most important for our considerations, we shall look at the climatological winter mean (Table 1).

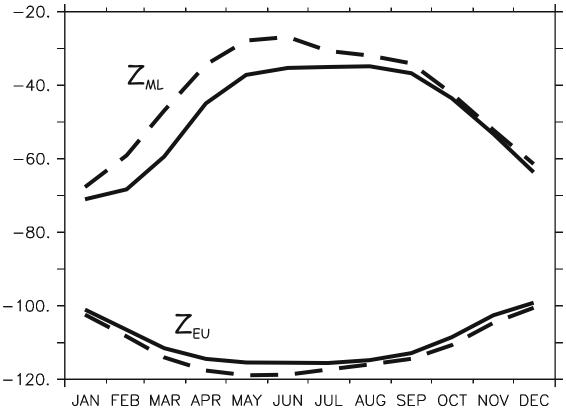


**Fig. 2** Seasonal cycle of mixed layer depth and community compensation depth in the oligotrophic part of the North Pacific (*solid lines*) and at ALOHA (*dashed lines*)

Below the SML we can assume relatively low (and uniform) levels of vertical mixing at the background level of a few times $10^{-5}$ m$^2$ s$^{-1}$, at least in regions of smooth topography (Polzin et al. 1997).

## Optical properties and the euphotic zone

With respect to the optical properties, the oligotrophic waters are generally classified as clear with

**Table 1** Characteristics (area, annual mean nitrate/nitrite maximum $N_{\max}$ and its depth $z_{N_{\max}}$, climatological winter mixed layer depth $z_{\mathrm{ML}}$ and annual mean depth of the euphotic zone $z_{\mathrm{eu}}$) of the five major oligotrophic regions in the world ocean, the global average and for station ALOHA (HOT) in the central North Pacific Ocean

| Region | Area ($10^{12}$m$^2$) | $N_{max}$ (mmol N m$^{-3}$) | $z_{N_{\max}}$ (m) | $z_{ML}$ (m) | $z_{\mathrm{eu}}$ (CCD) (m) |
|---|---|---|---|---|---|
| North Pacific | 32.3 | 42.3 ± 2.0 | 1170 ± 200 | 62 ± 18 | 101 ± 21 |
| South Pacific | 29.1 | 36.8 ± 1.7 | 1350 ± 210 | 75 ± 31 | 97 ± 22 |
| Indian Ocean | 20.5 | 35.8 ± 3.5 | 1320 ± 230 | 51 ± 24 | 91 ± 28 |
| South Atlantic | 5.6 | 35.7 ± 2.3 | 850 ± 230 | 62 ± 29 | 84 ± 31 |
| North Atlantic | 6.6 | 26.2 ± 5.1 | 970 ± 250 | 54 ± 27 | 79 ± 32 |
| global | 94.1 | 36.6 ± 6.1 | 1220 ± 270 | 61 ± 33 | 90 ± 30 |
| ALOHA (HOT) | – | 41.7 ± 0.33 | 950 ± 50 | 50 ± 13 | 96 ± 8 |

The standard deviations refer to spatial variations in each region, except for the ALOHA station where the temporal variability (including the seasonal cycle) is given

attenuation values not much larger than 0.03 m$^{-1}$ (Kirk 1994). This means that in 100 m depth, still 2–5% of the surface irradiance is available.

From the biological point of view, however, the euphotic zone is most adequately defined as the *community compensation depth* (CCD) (see, e.g., Ono et al. 2001), the depth in which phytoplankton gains and losses balance (this includes gross growth, respiration, mortality, and the divergence of the sinking flux). Like for the SML depth, the exact value of the CCD depends on the specification of several criteria and reference values. To calculate this depth we use (a) 45% (=PAR, photosynthetically active radiation) of the NCAR CORE annual mean surface irradiance $I_{\mathrm{o}}$ (Large and Yeager 2004), (b) a sea water attenuation coefficient of 0.03 m$^{-1}$ (Kirk 1994), and (c) the 3.6 Wm$^{-2}$ isolume as the minimum irradiance for net community production (following Siegel et al. 2002). For the oligotrophic areas in Fig. 1, the CCD ($z_{\mathrm{eu}}$ varies only little between 100 m in winter and 120 m in summer (Fig. 2). For our purposes, we assume it to be constant at 100 m. Net primary production should be possible within the EZ, unless the nutrient depletion causes severe limitation.

The upper part of the aphotic zone, where most of the remineralization takes place is sometimes referred to as "disphotic zone" or "twilight zone'" but no concrete definition for the depth of the interface has been proposed.

## Macronutrient profiles

Typical nutrient profiles (in this case nitrate+nitrite) in oligotrophic oceans are characterized by considerable depletion at the surface (within the euphotic zone, typically above about 80–100 m depth) and a mid-depth maximum at around 800–1400 m (Fig. 3). In the Atlantic, the large scale (overturning) circulation is more complex, leading to a second maximum at the bottom.

Analysis of the five large oligotrophic areas in the ocean yields that the typical nitrate maxima are found in about 1100 m below the base of the mixed layer, with a standard deviation of about 270 m, and a value of 36.6 ± 6.1 mmol N m$^{-3}$ (see Table 1). Additional data for ALOHA (HOT) have been obtained from http://hahana.soest.hawaii.edu/hot/hot-dogs/interface.html. They represent a situation not untypical for the North Pacific (see Table 1). Based on the WOCE data set, there is only a weak, statistically not significant correlation between maximum value and its depth (deep maxima tend to be larger than shallow ones).

Comparing the profiles with those averaged over the global ocean (see Sarmiento and Gruber 2006) it is obvious that the global mean is dominated by the signature from the oligotrophic regions.

A look at individual ocean basins reveals significant differences: the North Pacific has by far the largest nutrient maximum value (42.3 mmol N m$^{-3}$), the North Atlantic has the lowest (26.2 mmol N m$^{-3}$); the mean depth is largest in the South Pacific (1350 m) and shallowest in the South Atlantic (850 m). Generally, the oligotrophic areas in the Pacific are one extreme, those in the Atlantic are the other (Fig. 3, Table 1). For our purposes the most interesting feature of all these profiles is the mid-depth maximum, where the gradient changes sign and the diffusive fluxes vanish.

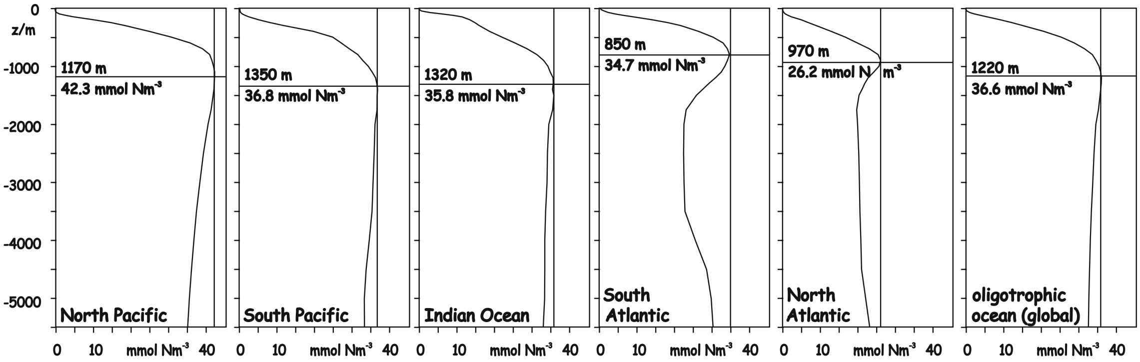


**Fig. 3** Average nitrate profiles for the various oligotrophic regions, showing the depth of the nitrate maximum and maximum values

## An updated concept for nutrient cycling in the oligotrophic ocean

Combining the biological, physical and geochemical characteristics of the oligotrophic ocean as presented in the preceding section, we can draw a conceptual picture that takes into account that the euphotic zone is not uniform in terms of vertical mixing and that the aphotic zone can be subdivided into two parts, above and below the nutrient maximum.

Known since Sverdrup (1953)'s seminal work, the depth of the SML and its relation to the CCD plays a crucial role for the dynamics of seasonal phytoplankton blooms. But while in meso- and euphotic areas this depth is (at least temporarily during late winter) deeper than the euphotic zone, this is different in the oligotrophic ocean. Figure 4 shows the difference between these two depths, with darker shading for cases where the euphotic depth is deeper than the climatological winter mixed layer depth. In a global average over oligotrophic areas this difference is 30 ± 11 m. See also the summer/winter profiles by Letelier et al. (2004) which indicate a year-round positive difference at station ALOHA (HOT).

Hence, the euphotic zone can and should be subdivided into (a) the SML and (b) the stratified region below, the latter featuring a subsurface biomass maximum layer (see, e.g., Hense and Beckmann, 2008) with net community production and little upward leakage of nitrate (see, e.g., Beckmann and Hense 2007, and references therein). Production in the SML can thus only rely on nitrogen fixation and regenerated nutrients.

Similarly, we propose to subdivide the *aphotic zone* into two sub-layers: (a) the upper part with downward increasing nutrient concentrations and (b) the lower part with a nutrient decrease down to the sea floor. This nutrient decrease can be explained by, e.g., lateral exchange, adsorption to sediment particles or, in case of dissolved inorganic nitrogen, denitrification and anammox. Note that the depth of the maxima for nitrate, phosphorus and several other (micro)nutrients is very similar (see Sarmiento and Gruber 2006). The nutrient maximum constitutes a singularity, because the vertical diffusive nutrient flux vanishes there and the only remaining flux at this depth is the sinking flux of detritus.

We propose to regard the water column between the base of the mixed layer and the nutrient maximum as a conceptual entity, distinct from the layers above and below, and hence to subdivide the water column into three layers. In particular, we give a precise definition for the what has sometimes been called "thermocline layer" (e.g., Duce et al. 2008) or "twilight zone" (e.g., Buesseler and Lampitt, 2008) and thought to be somehow related to the thermal stratification.

So what makes the intermediate layer an entity? In steady state (one of the basic assumptions in all similar concepts), it includes both the subsurface production (between SML base and CCD) and the subsequent remineralization of all this organic material, simply because the net fluxes at its top and base must balance. So whatever is produced in this layer, is also remineralized. Hence, an appropriate name for this layer is *subsurface production remineralization layer* (SPRL).

This concept is illustrated and contrasted to the more traditional view in Fig. 5. The euphotic zone comprises the high vertical mixing regime in the SML and the low vertical mixing regime below and

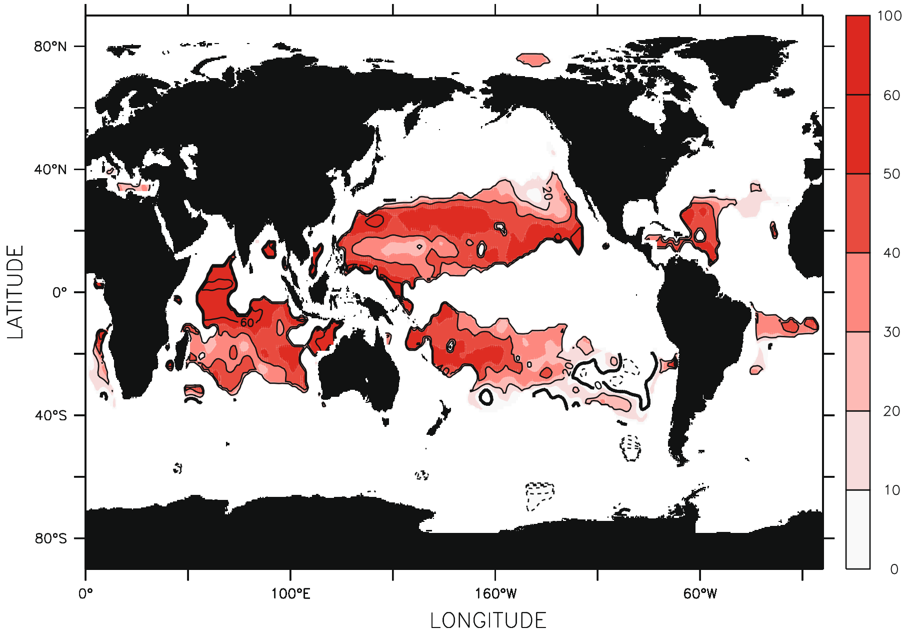


**Fig. 4** Map showing oligotrophic areas (defined by surface chlorophyll concentrations smaller than 0.1 mg Chl *a* $m^{-3}$; *colored*) of the global ocean derived from the WOA01 data set (Conkright et al. 2002). The difference between the climatological winter mixed layer depth $z_{ML}$; from de Boyer Montégut et al. 2004 and the annual mean of the base of the euphotic zone ($z_{eu}$; computed based on irradiance data from Large and Yeager 2004, see text) is color-coded. Average characteristics for each ocean basin are shown in Fig. 3 and listed in Table 1

so the production in this layer is proportional to both input at the surface, nitrogen fixation, upward diffusion and downward sinking. This complex interplay makes it particularly difficult to relate euphotic zone export to primary production; furthermore, the export at the base of the euphotic zone is not overly relevant for the transfer of nutrients to the deep ocean, because there is substantial remineralization below the base of the euphotic zone (see, e.g., Martin et al. 1987; Lutz et al. 2002).

With our focus on the SPRL, however, we consider the net downward flux at the base of the SML as the external driving of the nutrient cycling within this layer. Both diffusive and sinking fluxes across this interface are possible. For nitrate, upward diffusive and entrainment fluxes are small because there is little leakage of N through the subsurface production layer (Beckmann and Hense, 2007)[1]. Considering annual mean (=approximate steady state) conditions, these fluxes have to be balanced by equal fluxes into the SML (atmospheric deposition and nitrogen fixation). Note that in oligotrophic areas the upper nitracline (defined as the depth above which no net community production is possible due to nitrate limitation) is well below the SML. Hence, the net fluxes at the base of the SML are downward and the only sources are atmospheric deposition $F_{atm}$ and nitrogen fixation $F_{fix}$, irrespective of any regenerated production within the SML.

Thus, consideration of the SPRL reminds us that the nitrogen export into deeper layers (below the nutrient maximum) is identical to the input from atmospheric deposition and nitrogen fixation; the SPRL is self-contained. While profiles within the SPRL may vary substantially (due to the external forcing—nutrient fluxes and light, and internal mechanisms—mixing, phytoplankton physiology, grazing, and the microbial loop) the throughput of nutrients is fixed by the boundary conditions. This statement must seem trivial (and is certainly not very spectacular) but seems to have been often overlooked (or at least unappreciated) nevertheless.

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[1] For other nutrients, this may be different, see Duce (1986) who found substantial upward fluxes of phosphorus (and iron) into the surface waters in the central North Pacific Gyre and the Sargasso Sea.

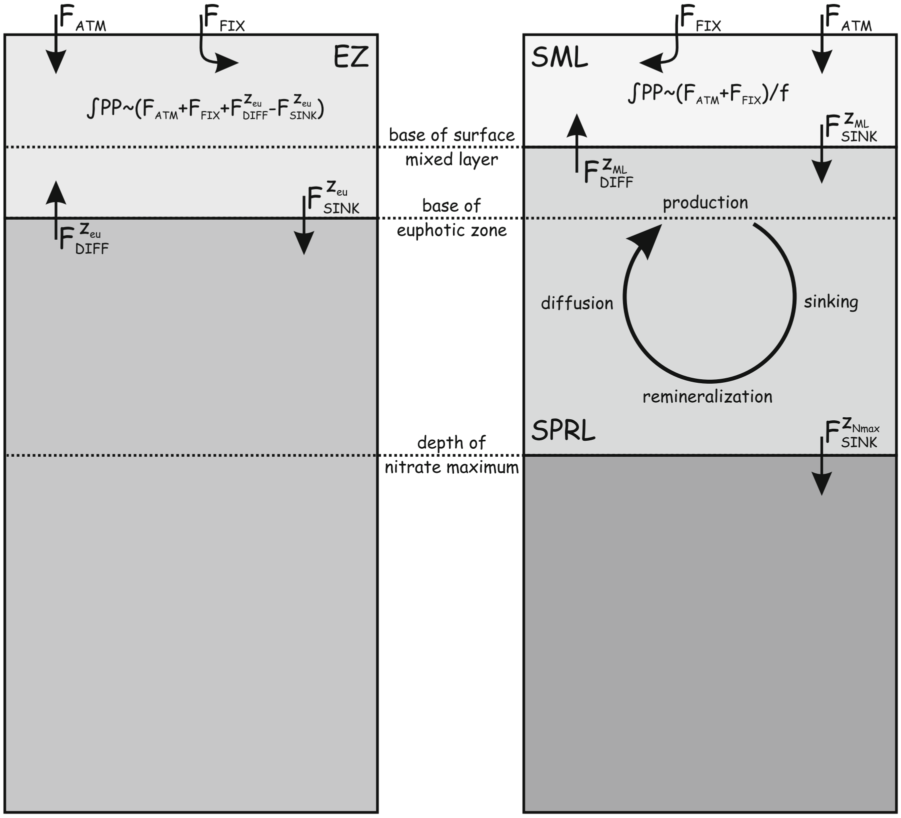

**Fig. 5** Schematic differences between the EZ concept (*left*) and the SPRL concept (*right*) for the oligotrophic ocean, where $z_{\rm eu}$ is deeper than $z_{\rm ML}$. The euphotic zone receives nitrogen from the atmosphere, by fixation and from upward diffusion while it loses sinking material. The vertically integrated primary production is proportional to these fluxes and the (generally unknown) effect of differential mixing between the upper mixed layer and the subsurface layer. In contrast, for the SPRL concept the SML production can conceptually be determined from atmospheric deposition and fixation; also, the total flux entering the SPRL at the top and leaving it at the bottom is given by $F_{\rm sink}^{z_{N_{\max}}} = F_{\rm diff}^{z_{z_{\rm ML}}} + F_{\rm sink}^{z_{z_{\rm ML}}} = F_{\rm atm} + F_{\rm fix}$ , where $F_{\rm diff}^{z_{z_{\rm ML}}}$ includes detrainment losses due to a shallowing mixed layer. It is assumed that no net upward nutrient diffusion occurs at the depth of the mixed layer base, because the subsurface production layer maintains permanent depletion at its top. The amplitude of nutrient cycling within the SPRL is inconsequential for the fluxes at its upper and lower boundaries

Below the SPRL, loss processes like lateral exchange processes and denitrification reduce the downward flux, ultimately leading to some deposition at the sea floor, the magnitude of which can only be determined with specific knowledge of the deep ocean processes (which is beyond the scope of this paper).

## Discussion

Studies of the biological pump in the ocean have so far relied exclusively on a biologically motivated distinction between the near surface layer where production can take place (i.e., the euphotic zone) and the ocean below. A simultaneous look at the prevailing chemical (nutrient distributions) and physical (vertical mixing) conditions, however, immediately suggests a three layer structure of the ocean, in which we distinguish the SML and the deep ocean from the SPRL in between. This approach has certain advantages for the investigation of marine biogeochemical cycling in the oligotrophic ocean.

The main consequence, i.e., that the steady state export at the depth of the nutrient maximum equals the import at the base of the SML, provides us with the opportunity to derive specific properties of the ecosystem dynamics within this layer, making use of recent advances in our understanding of the dynamics in weakly mixed water columns (Beckmann and

Hense 2007). In areas where our assumptions are met reasonably well (i.e., oligotrophic regions with weak lateral effects and an approximate steady state), the four elements of vertical nitrogen cycling are:

- This flux is handed down to the SPRL, irrespective of any fast remineralization within the SML, which might increase the total primary production leading to a small *f*-ratio there. Note that within this framework, the term "new nitrogen" refers only to the fixed and deposited nitrogen, not to the nitrate diffused upward (if any), because that is not new to the water column (cf. the term "completely new nitrogen" by Duce et al. 2008.)
- Within the SPRL, any additional production (and its conversion to detritus) is re-converted to dissolved nitrogen above the depth of the nitrogen maximum, where the diffusive flux of dissolved nitrogen vanishes and the export is maintained solely by sinking detritus (in steady state, this occurs at the same rate as the input at the top of the SPRL).
- Further down, denitrification and other loss processes (including lateral exchange) will decrease the DIN concentrations; ultimately some of the sinking detritus will be buried at the sea floor.

Table 2 summarizes the conceptual differences of the traditional (euphotic/aphotic zones) and alternative (SML/SPRL) view.

Admittedly, the concept devised here is simplified in several respects: The assumed one-dimensionality requires either a sufficiently large and uniform area for horizontal averaging or weak lateral advection/diffusion. Similarly, the steady state is an abstraction, representing an average over a sufficiently long time scale (averaging out at least the seasonal cycle). Issues of climate variability and change can be considered by looking at trends in external forcing [i.e., deposition (Galloway et al. 2004, 2008) and nitrogen fixation (Karl et al. 1997)]. Temperature variations in the upper ocean might lead to different remineralization rates; changes in species composition can affect the sinking speeds. All these effects are likely to be seen most easily in the detrital flux across the depth of the nitrate maximum. Systematic monitoring of these variables seems advisable. With respect to the lateral effects we note that the meridional overturning circulation in the Pacific is confined to depths below 1000 m (see, e.g., Sarmiento and Gruber, 2006), which suggests that a one-dimensional view may be justified there.

**Table 2** Comparison of the EZ and SPRL concepts. $z_o$ is the ocean surface, $z_{eu}$ the base of the euphotic zone (i.e., the community compensation irradiance), $z_{ML}$ the depth of the mixed layer base, and $z_{N_{max}}$ the depth of the nutrient maximum

| | Two layer concept (focus on EZ) | Three layer concept (focus on SML/SPRL) |
|---|---|---|
| *Steady state fluxes* | | |
| across $z_o$ | $F_{atm} + F_{fix} = F_{ext}$ | $F_{atm} + F_{fix} = F_{ext}$ |
| across $z_{ML}$ | | $F_{diff}^{z_{ML}} + F_{sink}^{z_{ML}} = F_{ext}$ |
| across $z_{eu}$ | $F_{sink}^{z_{eu}} - F_{diff}^{z_{eu}} = F_{ext}$ | |
| across $z_{N_{max}}$ | | $F_{sink}^{z_{N_{max}}} = F_{ext}$ |
| *"New production" and f-ratio* | Applied also to $NO_3$ from below | To be applied only to $F_{ext}$ in the SML |

Returning to the regional differences noted in section "Some characteristics of the surface nutrient depleted water column" the concept is probably best applicable to the North Pacific (Fig. 3), which is likely to be closest to a steady state (Fig. 3) with little lateral advection. The Indian Ocean profile with its two nutriclines may indicate different areas averaged together. Our model seems to be least applicable to the Atlantic basins with their near-bottom increase in nitrate and the relatively shallow and (for the north) small magnitude of the nitrogen maximum. One might even argue that the Atlantic should be left out of this analysis, as the Atlantic profiles differ significantly in shape from the other oceans. These two basins are likely to be farthest from undisturbed central subtropical gyre steady states.

We have originally formulated our concept in terms of nitrogen, but one may wonder about the consequences for other macronutrients like phosphorus. Looking at phosphorus profiles in the oligotrophic ocean, we find that the depth of the phosphorus maximum coincides well with that of nitrate+nitrite (except for the Atlantic, where maximum N and P depths agree less well). The globally averaged maximum phosphorus concentrations are $2.6 \pm 0.48$ mmol P $m^{-3}$, larger than the Redfield ratio would suggest (Fig. 6, typically 16:1.13. Furthermore, the SML seems to be less severely P depleted than N depleted (Fig. 6).

As atmospheric deposition of P is small ($<0.03$ mmol $m^{-2}$ $a^{-1}$), the main phosphorus source is upward diffusion through the SBML, which is N-limited. Under steady state conditions the net sinking flux of P out of the SML has to balance the sinking flux of N at the average N:P ratio for SML species. Assuming a near-Redfield ratio, nitrogen fixation by diazotrophic organisms is required to close the budget (Table 3). Note that the resulting upward fluxes of P lie in the range of Duce (1986)'s open ocean estimates, and that the negligible sinking flux of phosphorus at the base of the SPRL indicates faster remineralization or slower sinking of P compared to N (see Lamborg et al. 2008).

**Table 3** Fluxes for nitrate and phosphate for ALOHA-HOT

| Flux | Nitrate (mmol $m^{-2}a^{-1}$) | Phosphate (mmol $m^{-2}a^{-1}$) |
|---|---|---|
| $F_{\mathrm{atm}}$ | 6 | $\varepsilon_P$ |
| $F_{\mathrm{fix}}$ | 50 | – |
| $F_{\mathrm{sink}}^{z_{\mathrm{ML}}}$ | $56 - \varepsilon_N$ | 3.5 |
| $F_{\mathrm{diff}}^{z_{\mathrm{ML}}}$ | $\varepsilon_N$ | $3.5 - \varepsilon_P$ |
| $F_{\mathrm{sink}}^{z_{N\mathrm{max}}}$ | 56 | $\varepsilon_P$ |

The symbols $\varepsilon_{N,P}$ indicate negligible non-zero fluxes for nitrate and phosphorus, respectively. N measurements are from Karl et al. (1997) for nitrogen fixation and Duce (1986) for atmospheric deposition. The phosphate fluxes at the base of the SML are inferred by assuming that the sinking export from the SML is approximately at the Redfield ratio. The direction of fluxes follows the arrows in Fig. 5

## Conclusions

One of the paradigms in the field of marine biogeochemistry is that both the total primary production within the euphotic zone and the export at its base can be taken as measures of the strength of the biological pump. The disconcerting fact that no clear relationship between both quantities is found, can be explained, at least for the oligotrophic ocean, by the inadequate assumption of a two-layer system. If we abandon the traditional separation of the euphotic zone from the interior ocean in favor of distinguishing the vertically quasi-homogeneous SML from the stratified upper ocean, and introduce another conceptual boundary located at the (macro-)nutrient maximum, we arrive at a fundamentally different view. First, we realize that the regenerated production in the SML does not contribute to the sinking flux at the base of the euphotic zone. Second, it becomes clear that export at the base of the euphotic zone is only a measure of the strength of the element cycling in the upper ocean (more specifically, the SPRL). Finally, we are reminded that in equilibrium (and for negligible lateral flux divergence), the export at the base of both the SML and the SPRL is identical to the input by atmospheric deposition and $N_2$ fixation.

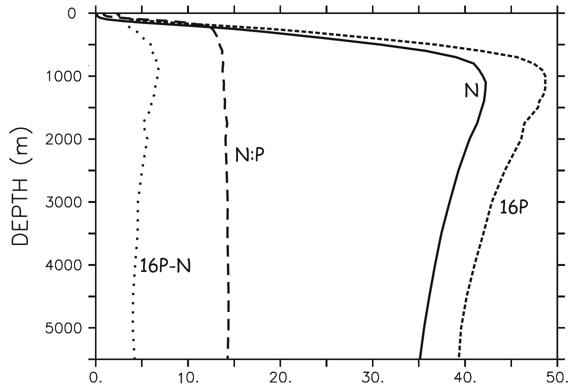

**Fig. 6** Profiles of N, P, excess phosphorus and the N:P ratio for the oligotrophic part of the Pacific Ocean

Within this framework it is then straightforward to infer the following characteristics of the biological pump in oligotrophic oceans:

- the steady state net downward flux of nitrogen is constrained only by atmospheric input and fixation of nitrogen (and hence the activity of nitrogen fixers);
- the exact magnitude of primary production by non-diazotrophic phytoplankton is irrelevant for export from the SML and subsequently from the SPRL;
- biological processes, however, are important for downward transport (by producing particles that are denser than sea water) and remineralization of organic matter, thus setting the vertical remineralization length scale (the ratio of sinking velocity to remineralization rate).

The first of these points is obviously true for the ocean as a whole. It would be interesting to know to what degree it is also a good approximation for the annual average at locations in the subtropic gyres. Annual or longer time means of nitrogen deposition and fixation in one location can be compared to the sinking flux at the depth of the nutrient maximum, and thus constitute a means to determine the accuracy of the assumption of one-dimensionality.

Finally, we conclude that the one-dimensional steady state SPRL framework suggests that, in order to maintain the flux through the level of the maximum in 1000–1200 m depth, the remineralization length scale of part of the detritus has to be significantly longer than a few hundreds meter. This, in combination with flux measurements in the upper 500 m, supports ideas about the remineralization being associated with two separate length scales (Lutz et al. 2002): one that will lead to rapid cycling in the upper part of the SPRL and one that maintains the sinking flux through the base of the SPRL. This means that we have to consider (at least) two species of dead organic matter which differ in remineralization rate (labile and refractory detritus) and/or sinking speed (see also Lamborg et al. 2008). Note that there are likely more falsifiable implications of this conceptual view, which might lead to progress in this area.

In a sense, the ideas laid out here call for a research programme – aimed at (i) the re-evaluation of existing data sets according to the proposed concept of export from the SPRL, (ii) the separation of mixed layer from subsurface production estimates, and (iii) additional measurements down to and including the nutrient maximum. These suggestions should be seen as a supplement to Boyd and Trull (2007)'s recommendations for future work on the export of biogenic particles in the ocean.

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