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Small diversity effects on ocean primary production under environmental change in a diversity-resolving ocean ecosystem model

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Abstract

Marine ecosystem models used to investigate how global change affects ocean ecosystems and their functioning typically omit pelagic diversity. Diversity, however, can affect functions such as primary production and their sensitivity to environmental changes. Using a global ocean ecosystem model that explicitly resolves phytoplankton diversity within four phytoplankton functional types (PFTs) we investigate the model's ability to capture diversity effects on primary production under environmental change. An idealized scenario with a sudden reduction in vertical mixing causes diversity and primary-production changes that turn out to be largely independent of the number of coexisting phytoplankton types. The model provides a small number of niches with respect to nutrient use in accordance with the PFTs defined in the model, and increasing the number of phytoplankton types increases the resolution within the niches. The variety of traits and trade-offs resolved in the model constrains diversity effects such as niche complementarity, which operate between, but not within PFTs. The number and nature of the niches formulated in the model, for example via trade-offs or different PFTs, thus determines the diversity effects on ecosystem functioning captured in ocean ecosystem models.

1 Introduction

Ocean ecosystems are under pressure from global environmental change and an increasing human demand for natural resources. As a consequence of often ultimately anthropogenic perturbations, a loss of diversity has been observed in a variety of different ecosystems including marine environments (Butchart et al., 2010). Increasing evidence suggests that such a diversity loss coincides with a reduction in ecosystem functioning such as primary production or nutrient use (Cardinale et al., 2011; Reich et al., 2012). Losses in functioning are small in highly diverse systems and tend to

increase with decreasing diversity. Diversity might thus potentially aid in sustaining an ecosystem's established functioning through periods of environmental change.

Experimental evidence for effects of diversity on ecosystem functioning predominantly originates from terrestrial and benthic ecosystems, while studies on pelagic communities are still scarce (Cardinale et al., 2011; Ptacnik et al., 2010). Here we employ a novel global coupled ocean ecosystem modelling approach (Follows et al., 2007) which resolves phytoplankton diversity within four phytoplankton functional types and potentially allows investigating diversity effects on ecosystem functioning without observational and experimental limitations. We examine whether the magnitude of changes in primary production arising from environmental change depends on the level of phytoplankton diversity as indicated by the number of phytoplankton types in the model. We relate our findings to the underlying structure of ecological niches implicit in the model formulation, and thereby assess the model's inherent ability to capture diversity effects such as niche complementarity (Tilman et al., 1997; Loreau, 1998) and selection effects (Aarssen, 1997; Huston, 1997). Niches in the classical sense are created by variability in ecological factors and can be identified by the resource use along such a niche axis (Hutchinson, 1957; MacArthur and Wilson, 1967; Schoener, 1988). In plankton communities, in addition to this environmental dimensionality the traits of the species, for example regarding resource uptake, tolerance width to environmental conditions or mobility, shape further niches, thereby creating trait dimensionality (Ptacnik et al., 2010). Within this framework, diversity effects are thus constrained by both environmental and trait dimensionality.

One of the predicted consequences of global change on the upper ocean is an increased stratification and an associated reduction in mixing processes, and thus nutrient supply to the surface mixed layer (e.g., Sarmiento et al., 2004). Here we impose an instantaneous reduction in vertical mixing for nutrients and plankton as idealized environmental change to examine its consequences for diversity and productivity in a model ocean. We employ simulations with different levels of prescribed phytoplankton diver-

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sity and different numbers of plankton function types (PFTs) in order to examine if diversity and the way to resolve it affects the simulated primary production changes.

2   Methods

The model employed is the Darwin ocean ecosystem model coupled to the MITgcm general circulation model (Follows et al., 2007) in the configuration used by Prowe et al. (2012a). In the standard setup, the model simulates the dynamics of four nutrients (phosphorus, nitrogen, iron, silica), 78 phytoplankton types, two zooplankton types, dissolved and particulate organic matter. Phytoplankton types are assigned to one of four small or large plankton functional types (PFTs; diatom and *Prochlorococcus* analogs, other large and small phytoplankton). Cell size determines sinking speed, palatability, maximum growth rate and the basic level of the half-saturation concentration for nutrient uptake of the different types. Within each PFT, types are further distinguished by randomly assigned parameter values for nutrient-, light- and temperature-dependent growth. Half-saturation constants for phosphorus uptake are randomly assigned within a given range around a base value characteristic of the PFT. Corresponding half-saturation concentrations are adopted for the other nutrients using the same fixed stoichiometric ratios for all phytoplankton types. Temperature dependencies of individual types are characterized by different optimal temperatures chosen at random from a range of -2 to $30\,^{\circ}$C. Grazing on phytoplankton by a small and a large zooplankton type is formulated as a Holling type 3 functional response. Details can be found in Dutkiewicz et al. (2009) and Prowe et al. (2012a).

Phytoplankton diversity or richness is measured at each grid point at each time step as the number of phytoplankton types exceeding a low threshold concentration of $P_{th} = 10^{-8}\,\mathrm{mmol\,P\,m^{-3}}$. As the standard simulation we select one member of the ensemble of simulations with $n = 78$ initial phytoplankton types used by Prowe et al. (2012a). Three simulations with reduced initial diversity are obtained by randomly selecting subpopulations of $n = 30$ types from this setup. A configuration with each PFT

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represented by only one phytoplankton type ($n = 4$) with the optimum-temperature function replaced with a simpler temperature dependence (represented by a factor of $1.04^{T[^\circ C]}$) allows simulating PFT-based ocean ecosystem models that do not resolve diversity within PFTs, comparable to models currently employed for global change sim-
5 ulations (e.g., Bopp et al., 2013). A companion simulation without the *Prochlorococcus* PFT (i.e. $n = 3$) reveals consequences of reducing PFT diversity, which indicates functional diversity in the model.

Simulations are run offline for 20 yr with physical forcing from the ECCO-GODAE state estimates (Wunsch and Heimbach, 2007). Environmental changes are prescribed
10 as a sudden reduction in mixing (vertical eddy diffusivity k_e reduced by 50 %) after 10 yr of simulation. The change in k_e in the offline model does not affect stratification or the depth of the mixed layer, but only the mixing of nutrients, phytoplankton and the other biogeochemical tracers. Excluding physical ocean changes allows us to separate direct effects on the ecosystem from more complex responses driven by physical feedbacks.
15 This idealized setup also allows us to simulate diverse phytoplankton communities explicitly without compromising spatial or temporal resolution. Annual average diversity and primary production in the upper 100 m are compared to simulations with no reduction in mixing after another 10 yr of simulation. Primary production is estimated from phosphate uptake using a fixed molar C : P ratio of 106 : 1.

20 **3 Results**

The reduction in k_e leads to an overall decrease in nutrient supply, and thus in primary production (PP) and net community production in the lower latitudes and increases in the Southern Ocean and the North Atlantic where PP is limited by light during large parts of the seasonal cycle (Fig. 1). Figure 2 shows the corresponding absolute and
25 relative differences of diversity and PP in year 20 between the simulations with reduced k_e and the respective simulations with unchanged k_e. For the standard setup with $n = 78$ phytoplankton types, diversity measured as the number of coexisting types overall

changes by less than 5–10 % upon reducing k_e, with increases at higher latitudes and decreases from roughly 40° S to 40° N. Relative PP changes are larger, with reductions around 10 % in the tropics and subtropics and reductions exceeding 20 % around 30° S and 30° N where PP is lowest. At higher latitudes, PP changes are generally small and, in the zonal average, positive only in the Southern Ocean.

Higher PP under global warming in this region has been inferred both from observations (Behrenfeld et al., 2006) and from coupled ocean ecosystem models (e.g., Bopp et al., 2001). In these studies, it can be explained by higher light availability for photosynthesis in a shoaling surface mixed layer. The effect of higher light availability at higher latitudes is reflected at least partly by lower phytoplankton losses due to mixing in the short-term simulations presented here. This increases PP (Fig. 1) and also the potential for export of organic matter to the deep ocean, particularly in regions that do not become nutrient depleted during the seasonal cycle. A PP decrease in the remaining ocean reflects aggravated nutrient limitation and closely corresponds to a decline in export production.

In the model, PP ($= \mu P$) may change because of changes in the growth rate (μ) or the biomass (P) of the individual phytoplankton types. Biomass changes in turn reflect both changes of total biomass as well as shifts in the community composition, i.e. the relative biomass of each type. In the oligotrophic low latitudes (about 30° S to 30° N; here shown for an Atlantic section), PP changes are almost entirely driven by a reduction in total phytoplankton biomass (Fig. 3). Community composition shifts and changes in the individual growth rates have only negligible effects. At higher latitudes, changes in growth rate dominate the PP signal. Biomass effects are evident from 40–50° S in the global average, and in the North Atlantic. Here, following the mixing reduction two dominating large phytoplankton types are partly replaced by two small types with lower growth rate, hence the negative composition effect in Fig. 3. The lower growth rate is more than compensated by an overall increase in biomass.

We find no pronounced difference in the response of simulated PP and diversity to a reduction of k_e between the simulations with $n = 78$ types and the three sim-

ulations with $n = 30$ types. Although the former simulation has overall higher PP at higher latitudes (cf. Prowe et al., 2012b), relative changes in both properties are of similar order of magnitude and display similar zonal patterns among the simulations. Global average PP changes vary by only 1 % among the model runs employing differ-

5 ent levels of diversity. Differences within the ensemble of three simulations with similar initial ($n = 30$) diversity are comparable with differences between simulations with different initial diversity (Fig. 2). "Diversity" in the generic simulation with $n = 4$ types assigned to four PFTs is affected by mixing changes only in the Southern Ocean. In all other regions all PFTs are present (i.e., they exceed the biomass threshold for diver-

10 sity of $P_{th} = 10^{-8}$ mmol P m^{-3}), although typically one or two PFTs dominate a region. Changes in PP in response to reduced mixing are generally comparable to changes predicted for the simulations resolving diversity within the PFTs. Southern Ocean PP increases more strongly in the simulation with low diversity (Fig. 2e, f). Here, surface nutrients tend to be higher in the low-diversity simulation compared to the more effi-

15 cient nutrient utilization in the high-diversity runs. This leaves more potential for a PP increase upon a mixing reduction in the lower-diversity simulations. In the oligotrophic lower latitudes, PP decreases more strongly in the low-diversity runs, although the essentially always complete drawdown of surface nutrients is not affected by the reduction in mixing. In contrast to the simulation with four PFTs, the simulation with three

20 PFTs shows higher relative PP changes between 20° N and 50° N, i.e. in regions where *Prochlorococcus* dominates in the other simulations.

The fact that all model communities with the same number of PFTs react in a similar way to the mixing reduction independent of diversity within the PFTs reflects the dimension of the trait space resolved by the assemblages, that is relevant in these

25 reduced-nutrient-supply simulations. The biogeography of each type is limited by the optimum temperature for growth, with defines suitable habitats on the global scale independent of PFT assignment. However, the half-saturation concentrations for nutrient uptake (e.g. K_{PO_4} for phosphate) are assigned randomly within each PFT so that lowest values distinguish *Prochlorococcus* analogues, slightly higher values characterize

other small types, and both large PFTs have high half-saturation concentrations. This pattern is the basis for PFTs in the generic $n = 4$ simulation, and is generally maintained in all other simulations (Fig. 4). The relative biomass fraction indicates that each assemblage fills only two main niches in terms of nutrient uptake traits with one or few dominant types, with low-K_{PO4} types at high temperatures (oligotrophic low latitudes) and high-K_{PO4} types mostly at lower temperatures. This demonstrates that the warm, oligotrophic regions select for types with lowest K_{PO4} ("gleaners"; Dutkiewicz et al., 2009) via resource competition, while in the colder seasonally mixed oceans high growth rates identify dominant "opportunist" types. The number of types per bin and fraction of total biomass emphasizes that all assemblages can by model design only resolve a few nutrient niches with similar characteristics (Fig. 5). In the low-K_{PO4} niche, the assemblage is strongly skewed towards types with lowest K_{PO4}, while in the high-K_{PO4} niche such a shift is not found.

Contrary to the simulation with four PFTs, omitting the *Prochlorococcus* PFT, which has lowest K_{PO4} levels, in the $n = 3$ simulation reduces the trait space resolved in the model. This reduction is most relevant in the oligotrophic regions, which now are populated by other types with higher K_{PO4}. Consequently, a reduction in nutrient supply caused by reduced mixing affects PP changes more strongly in the $n = 3$ run compared to the other simulations.

4   Discussion

Analysis of observations suggest a decline in ecosystem functions resulting from potential diversity losses and a stronger decline at lower overall diversity (Cardinale et al., 2011). Our model, in apparent contrast and for a relatively small diversity range tested so far, does not simulate such an effect of the diversity level on the magnitude of productivity changes under reduced mixing. Specifically, resolving phytoplankton diversity within plankton functional types does not affect the sensitivity of PP to environmental change, although explicitly resolving diversity can improve the representation of com-

munity structure and seasonal succession (Prowe et al., 2012a). As models currently employed for global change simulations often use setups similar to our simulation with four PFTs (e.g., Bopp et al., 2013), our results indicate that omitting diversity within PFTs as captured in our approach does not appear to compromise these predictions.

The model setup employed here provides two main niches for nutrient uptake, which agree with the characteristics of the two small and large PFTs: one low-nutrient high-temperature niche and one high-nutrient niche mostly realized at lower temperatures. These niches are resolved by different phytoplankton types characterized by a random combination of trait values for temperature, light and nutrient use within the boundaries of the niches according to the assigned PFT. The type 3 grazing will facilitate diversity within the two niches (Prowe et al., 2012b). Additional sensitivity experiments have shown that results are qualitatively similar for simulations employing a Holling type 2 grazing functional response which promotes competitive exclusion. This emphasizes that more diverse assemblages do not occupy more niches, because there are only two main global niches defined by nutrient use resolved in the model.

On regional scales, silicate requirements for diatoms and nitrate availability for other small phytoplankton (*Prochlorococcus* in these simulations are assumed to not be able to assimilate nitrate) can generate additional niches. Temperature creates geographical niches as the optimum temperature of each type determines whether positive net growth is possible or not under a given temperature regime. In any given region, however, the temperature traits do not create complementary niches in terms of nutrient uptake, as they do not involve a trade-off. Similarly, the Holling type 3 functional grazing response does not shape complementary niches because the susceptibility to grazing is, in our current model, not linked to any costs, for example related to grazing defenses. Consequently, one should pose the question of what actually defines different niches in an ocean ecosystem model, and how these relate to the PFTs and trade-offs resolved in the model.

Reducing PFT diversity corresponds to a reduction in the relevant trait space resolved and demonstrates that in current ocean ecosystem models the variety of PFTs

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determines the niches resolved. In the framework of Ptacnik et al. (2010), here it is the trait dimensionality resolved in the phytoplankton community that governs diversity effects on PP against the background of environmental dimensionality simulated by the model. Higher trait dimensionality might potentially allow larger diversity effects, if the traits give rise to coexistence or competition along an axis of environmental dimensionality. In any given location, i.e. in a given physical and ecological environment, this condition would require model formulations based on trade-offs between different traits. Furthermore, while niches may change dominance under changing environmental conditions, the rigid structure of this modelling approach does not allow for new niches to be populated.

Small diversity effects on PP changes are evident from the differences between simulations with $n = 30$ types, and are related to the identity of types present. The $n = 30c$ simulation reacts to the mixing reduction in a way more similar to the standard simulation with $n = 78$ types than to the other simulations with same nominal diversity. This indicates that type identity plays a more important role than overall diversity and raises the question whether the number of coexisting phytoplankton types is the most appropriate measure for relating diversity to ecosystem functions. While there is a higher probability in more diverse assemblages, that a specifically suited type is present (Aarssen, 1997; Huston, 1997), our experimental setup is not aimed at identifying this effect.

The similarity of responses among the simulations with different diversity also reflects the fact that the diversity of the phytoplankton community is formulated in terms of a small number of traits that might not include the most relevant traits under changing environmental conditions. Including, for example, nitrogen fixation as additional trait adding PFT diversity may become more relevant in future compared to current conditions, and alter our results. Also, our model setup does not take into account coexistence through trade-offs in stoichiometric ratios for nutrient requirements (Göthlich and Oschlies, 2012), and thus omits potential effects of stoichiometrically imbalanced nutrient supply on both diversity and productivity (Gross and Cardinale, 2007; Cardinale

et al., 2009). Future investigations covering an extended diversity range and employing a larger variety of traits, trade-offs and different random phytoplankton assemblages may help to confirm or revise our findings.

Reduced mixing due to enhanced stratification of the upper ocean and thereby lower
5 supply of nutrients into the surface layers is one of the predicted consequences of a warming climate (e.g., Sarmiento et al., 2004; Steinacher et al., 2010). Here we employ an idealized reduction in mixing to investigate the model's ability to capture phytoplankton diversity effects on PP related to environmental changes. The sudden reduction in nutrient supply implied by our idealized model setup is not realistic in terms
10 of expected time scales of real ocean change. A more realistic setup requires a model configured to perform climate change simulations over centennial time scales (e.g., Follows and Dutkiewicz, 2011; Dutkiewicz et al., 2013), possibly with lower spatial and temporal resolution, or fewer state variables. Our approach also excludes effects of deep ocean equilibration, which may increase the nutrient supply to the upper ocean
15 particularly in upwelling regions on longer time scales. Phytoplankton community structure and diversity adapts to the changed environmental conditions well within the 10 yr time scale. The reductions in PP observed in the 10th year after reducing mixing are of the same order of magnitude as predictions from century-scale simulations (Steinacher et al., 2010; Taucher and Oschlies, 2011). Thus the sensitivity experiments performed
20 here provide a reasonable framework for investigating model behaviour in terms of potential diversity effects. However, they do not take into account the temperature changes that will accompany the environmental change. Warming may enhance PP (Taucher and Oschlies, 2011; Dutkiewicz et al., 2013), possibly mitigating some of the decrease from a reduction in nutrient supply.

5 Conclusions

One of the hypothetical diversity effects under environmental change is that less diverse communities show a larger decrease in primary production than more diverse

communities, because with more species present it is more likely that the existing niches can be filled also under different environmental conditions. Our simulations comprise diverse communities with up to 78 phytoplankton types grouped in four PFTs and distinguished by temperature, light and nutrient use. However, the less diverse communities occupy a similar trait space as more diverse communities, so that the model essentially only resolves two niches with respect to nutrient use. Consequently, primary production changes are independent of overall diversity within the PFTs, as more diverse communities do not occupy more niches. The magnitude and sign of these changes is affected by type identity, but is not linked to the number of types. Our results thus demonstrate that niches in typical ocean biogeochemical models are directly related to the PFTs defined. In such models it depends on the type and number of trade-offs between different PFTs, which effects of diversity on ocean ecosystem functioning under environmental change are captured. Capturing changes in the niches occupied under changing environmental conditions might thus require formulations allowing niche plasticity or niches not occupied under current conditions.

Appendix

Decomposition of primary production changes

The effect of a mixing reduction on total primary production (PP) can be decomposed into effects of changes in total biomass, biomass of individual types, or community composition (cf. Fig. 3) according to the following equations. Here, $\sum PP^{std}$ and $\sum P^{std}$ denote the total PP and total phytoplankton biomass, respectively, and pp_i^{std} is the specific growth rate (in d^{-1}) of phytoplankton type i in the standard run. Consequently, for example $\sum PP^{std} = \sum_i \left[pp_i^{std} P_i^{std} \right]$.

$$\Delta PP = \sum PP^{rm} - \sum PP^{std} \qquad \text{sum of all effects} \qquad (A1)$$

$$\Delta PP_{gro} = \sum_i \left[pp_i^{rm} P_i^{std} \right] - \sum PP^{std} \qquad \text{specific growth rate} \qquad (A2)$$

$$\Delta PP_{phy} = \sum_i \left[pp_i^{std} P_i^{rm} \right] - \sum PP^{std} \qquad \text{individual biomass} \qquad (A3)$$

$$\approx \Delta PP_{bm} + \Delta PP_{comp} \qquad \text{total biomass and composition} \qquad (A4)$$

$$\Delta PP_{bm} = \sum PP^{std} \frac{\sum P^{rm}}{\sum P^{std}} - \sum PP^{std} \qquad \text{total biomass} \qquad (A5)$$

$$\Delta PP_{comp} = \sum_i \left[pp_i^{std} \sum P^{std} \frac{P_i^{rm}}{\sum P^{rm}} \right] - \sum PP^{std} \quad \text{composition} \qquad (A6)$$

In the model simulations, the individual effects to very good approximation sum up to the total effect, so that

$$\Delta PP \approx \Delta PP_{gro} + \Delta PP_{phy} \approx \Delta PP_{gro} + \Delta PP_{bm} + \Delta PP_{comp}. \qquad (A7)$$

References

Aarssen, L.: High productivity in grassland ecosystems: effected by species diversity or productive species?, Oikos, 80, 183–184, 1997. 12573, 12580

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., Falkowski, P. G., Letelier, R. M., and Boss, E. S.: Climate-driven trends in contemporary ocean productivity, Nature, 444, 752–755, doi:10.1038/nature05317, 2006. 12576

Bopp, L., Monfray, P., Aumont, O., Dufresne, J., Le Treut, H., Madec, G., Terray, L., and Orr, J.: Potential impact of climate change on marine export production, Global Biogeochem. Cy., 15, 81–99, 2001. 12576

Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., and Vichi, M.: Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models, Biogeosciences Discuss., 10, 3627–3676, doi:10.5194/bgd-10-3627-2013, 2013. 12575, 12579

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., Galloway, J. N., Genovesi, P., Gregory, R. D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M. A., McRae, L., Minasyan, A., Morcillo, M. H., Oldfield, T. E. E., Pauly, D., Quader, S., Revenga, C., Sauer, J. R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S. N., Symes, A., Tierney, M., Tyrrell, T. D., Vie, J.-C., and Watson, R.: Global biodiversity: indicators of recent declines, Science, 328, 1164–1168, doi:10.1126/science.1187512, 2010. 12572

Cardinale, B. J., Hillebrand, H., Harpole, W. S., Gross, K., and Ptacnik, R.: Separating the influence of resource "availability" from resource "imbalance" on productivity–diversity relationships, Ecol. Lett., 12, 475–487, doi:10.1111/j.1461-0248.2009.01317.x, 2009. 12580

Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M. I., and Gonzalez, A.: The functional role of producer diversity in ecosystems, Am. J. Bot., 98, 572–592, doi:10.3732/ajb.1000364, 2011. 12572, 12573, 12578

Dutkiewicz, S., Follows, M. J., and Bragg, J. G.: Modeling the coupling of ocean ecology and biogeochemistry, Global Biogeochem. Cy., 23, GB4017, doi:10.1029/2008GB003405, 2009. 12574, 12578

Dutkiewicz, S., Scott, J. R., and Follows, M. J.: Winners and losers: ecological and biogeochemical changes in a warming ocean, Global Biogeochem. Cy., 27, 463-477, doi:10.1002/gbc.20042, 2013. 12581

Follows, M. J. and Dutkiewicz, S.: Modeling diverse communities of marine microbes, Annu. Rev. Mar. Sci., 3, 427–451, doi:10.1146/annurev-marine-120709-142848, 2011. 12581

Follows, M. J., Dutkiewicz, S., Grant, S., and Chisholm, S. W.: Emergent biogeography of microbial communities in a model ocean, Science, 315, 1843–1846, 2007. 12573, 12574

Göthlich, L. and Oschlies, A.: Phytoplankton niche generation by interspecific stoichiometric variation, Global Biogeochem. Cy., 26, GB2010, doi:10.1029/2011GB004042, 2012. 12580

Gross, K. and Cardinale, B. J.: Does species richness drive community production or vice versa? Reconciling historical and contemporary paradigms in competitive communities, Am. Nat., 170, 207–220, 2007. 12580

Huston, M.: Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity, Oecologia, 110, 449–460, 1997. 12573, 12580

Hutchinson, G. E.: Concluding remarks, Cold Spring Harbor Sym., Quant. Biol., 22, 415–427, 1957. 12573

Loreau, M.: Biodiversity and ecosystem functioning: a mechanistic model, P. Natl. Acad. Sci. USA, 95, 5632–5636, 1998. 12573

MacArthur, R. and Wilson, E.: The Theory of Island Biogeography, Princeton University Press, Princeton, NJ, 1967. 12573

Prowe, A. E. F., Pahlow, M., Dutkiewicz, S., Follows, M., and Oschlies, A.: Top-down control of marine phytoplankton diversity in a global ecosystem model, Prog. Oceanogr., 101, 1–13, doi:10.1016/j.pocean.2011.11.016, 2012a. 12574, 12579

Prowe, A. E. F., Pahlow, M., and Oschlies, A.: Controls of the diversity–productivity relationship in a marine ecosystem model, Ecol. Model., 225, 167–176, doi:10.1016/j.ecolmodel.2011.11.018, 2012b. 12577, 12579

Ptacnik, R., Moorthi, S. D., and Hillebrand, H.: Hutchinson reversed, or why there need to be so many species, Adv. Ecol. Res., 43, 1–43, doi:10.1016/S0065-2504(10)43001-9, 2010. 12573, 12580

Reich, P. B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S. E., Flynn, D. F. B., and Eisenhauer, N.: Impacts of biodiversity loss escalate through time as redundancy fades, Science, 336, 589–592, doi:10.1126/science.1217909, 2012. 12572

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Sarmiento, J., Slater, R., Barber, R., Bopp, L., Doney, S., Hirst, A., Kleypas, J., Matear, R., Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S., and Stouffer, R.: Response of ocean ecosystems to climate warming, Global Biogeochem. Cy., 18, GB3003, doi:10.1029/2003GB002134, 2004. 12573, 12581

5 Schoener, T.: The ecological niche, in: Ecological Concepts: The Contribution of Ecology to an Understand of the Natural World, edited by: Cherrett, J., chap. 4, 79–113, Blackwell Scientific, Oxford, 1988. 12573

Steinacher, M., Joos, F., Frölicher, T. L., Bopp, L., Cadule, P., Cocco, V., Doney, S. C., Gehlen, M., Lindsay, K., Moore, J. K., Schneider, B., and Segschneider, J.: Projected 21st
10 century decrease in marine productivity: a multi-model analysis, Biogeosciences, 7, 979–1005, doi:10.5194/bg-7-979-2010, 2010. 12581

Taucher, J. and Oschlies, A.: Can we predict the direction of marine primary production change under global warming?, Geophys. Res. Lett., 38, L02603, doi:10.1029/2010GL045934, 2011. 12581

15 Tilman, D., Lehman, C., and Thomson, K.: Plant diversity and ecosystem productivity: theoretical considerations, P. Natl. Acad. Sci. USA, 94, 1857–1861, 1997. 12573

Wunsch, C. and Heimbach, P.: Practical global oceanic state estimation, Physica D, 230, 197–208, doi:10.1016/j.physd.2006.09.040, 2007. 12575

PP difference (mg C m^{-2} d^{-1})
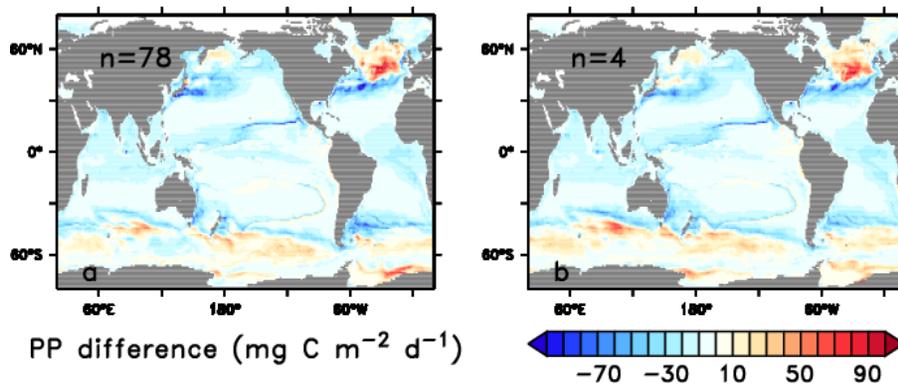
Fig. 1. Difference in primary production (PP; 0–100 m) between scenarios with and without reduced mixing 10 yr after mixing reduction for the simulation with $n = 78$ **(a)** and $n = 4$ **(b)** phytoplankton types.
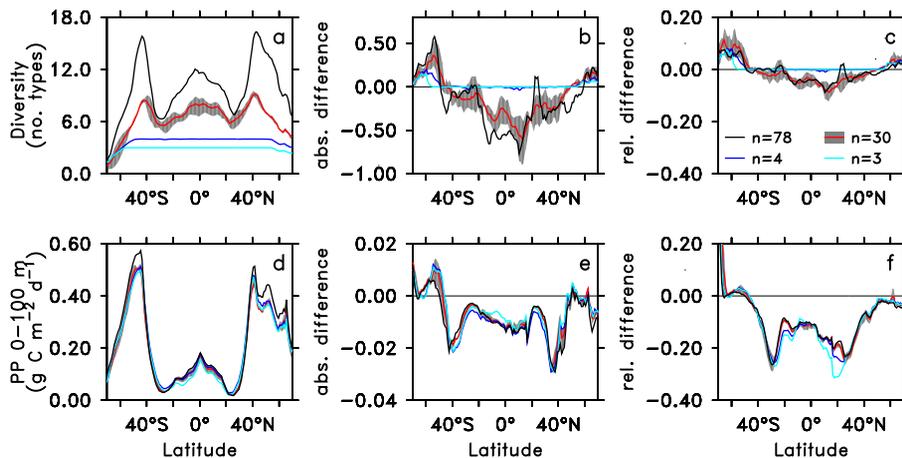
Fig. 2. Zonal averages of diversity as number of types exceeding threshold biomass P_{th} (**a**–**c**), and of primary production (PP; **d**–**f**) in the simulations without reduction in mixing (**a**, **d**), and as absolute (**b**, **e**) and relative (**c**, **f**) difference between scenarios with and without reduced mixing 10 yr after mixing reduction. Results are shown for one simulation with $n = 78$ phytoplankton types, the average of three simulations using different subpopulations of the $n = 78$ simulation with $n = 30$ types with minimum and maximum values indicated by the grey shaded area, and two simulations with four and three generic phytoplankton functional types ($n = 4$ and $n = 3$, respectively). See panel **(c)** for colour code.

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Interactive Discussion
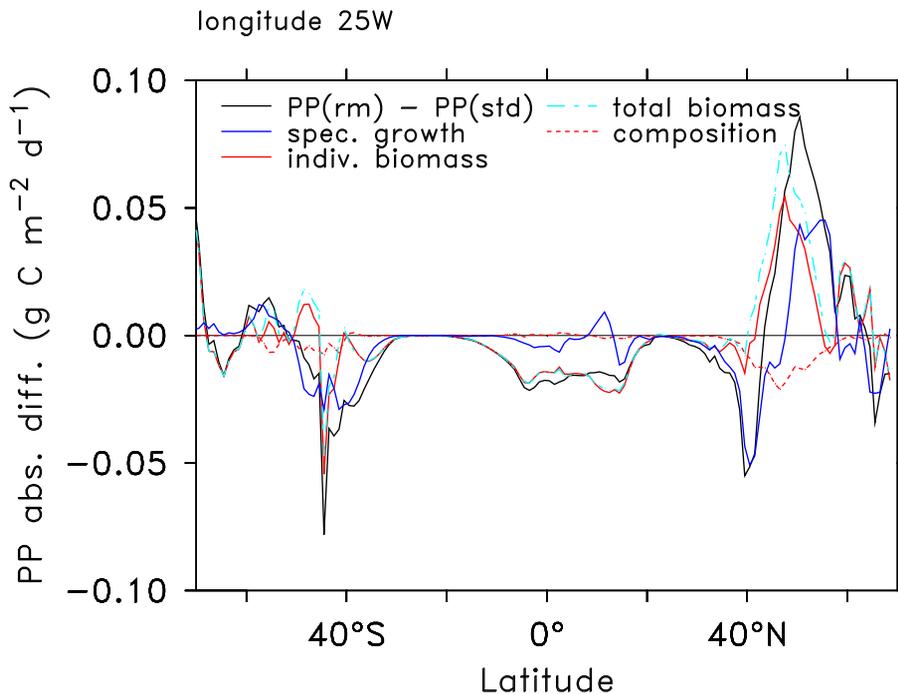
Fig. 3. Absolute primary production (PP) changes (black; cf. Fig. 2e) due to the reduction in mixing, and decomposition into effects of total biomass, growth rate, or composition changes along 25° W. The mixing reduction affects the specific growth rate (blue) via nutrient and light conditions as well as the individual biomass of phytoplankton types via effects on both total biomass and community composition (solid red). Effects on the individual biomass arise from changes in total biomass (dashed light blue) and shifts in community composition, i.e. the relative biomass of each phytoplankton type (dashed red). Displayed are zonal averages from the simulation with $n = 78$ types. See the appendix for details on the decomposition.
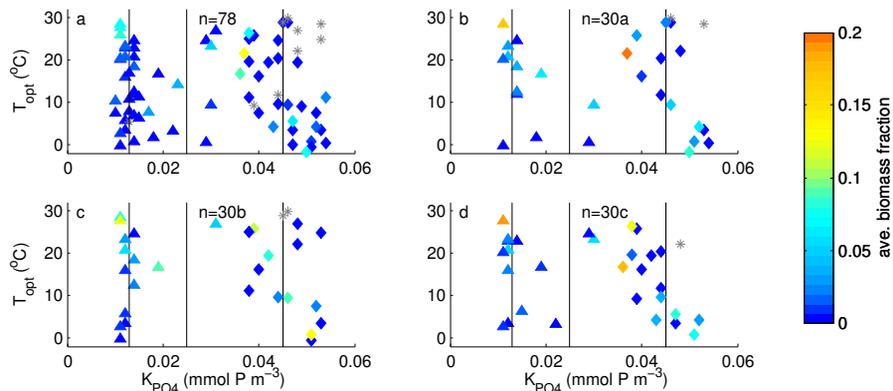
Fig. 4. Position of individual phytoplankton types in the trait space given by optimum temperature (T_{opt}) and half-saturation concentration for phosphate uptake (K_{PO_4}) for the simulation with $n = 78$ types **(a)** and the three simulations with $n = 30$ types **(b–d)**. Triangles and diamonds identify small and large types, respectively, and color shading indicates the global average fraction of total biomass for each type. Stars indicate types with 0 biomass fraction in the global average. Vertical lines indicate the PFTs in the $n = 4$ simulation, from lowest to highest K_{PO_4} *Prochlorococcus* analogues, other small phytoplankton, and other large phytoplankton/diatom analogues.
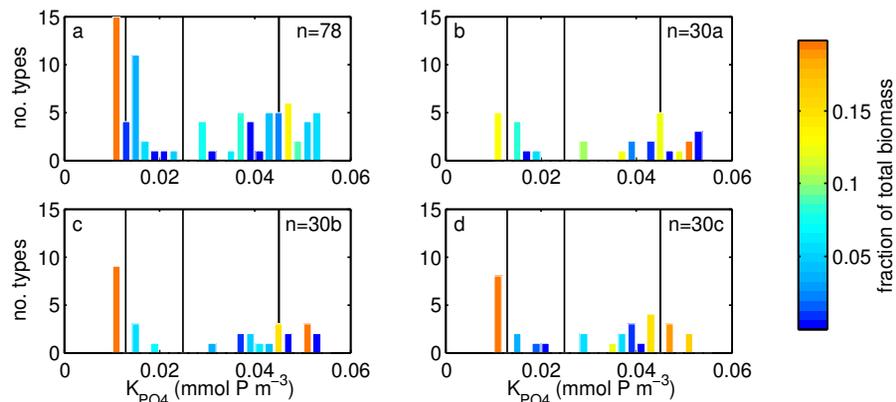
Fig. 5. Histogram of the number of phytoplankton types against half-saturation concentration for phosphate uptake (K_{PO_4}) for the simulation with $n = 78$ types **(a)** and the three simulations with $n = 30$ types **(b–d)**. Color shading indicates the fraction of total biomass for all types within a K_{PO_4} bin. Vertical lines indicate the PFTs in the $n = 4$ simulation (see Fig. 4 for details).