PP

Net Primary Production in the Ocean

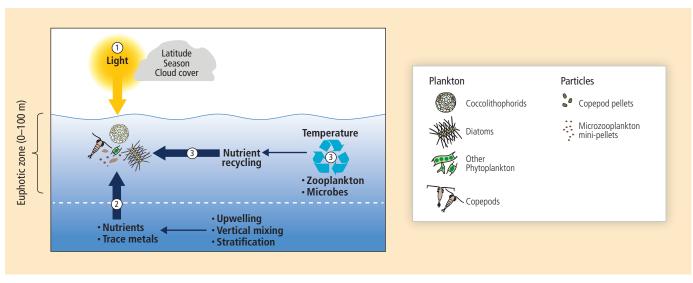
Philip W. Boyd (New Zealand), Svein Sundby (Norway), Hans-Otto Pörtner (Germany)

Net Primary Production (NPP) is the rate of photosynthetic carbon fixation minus the fraction of fixed carbon used for cellular respiration and maintenance by autotrophic planktonic microbes and benthic plants (Sections 6.2.1, 6.3.1). Environmental drivers of NPP include light, nutrients, micronutrients, CO₂, and temperature (Figure PP-1a). These drivers, in turn, are influenced by oceanic and atmospheric processes, including cloud cover; sea ice extent; mixing by winds, waves, and currents; convection; density stratification; and various forms of upwelling induced by eddies, frontal activity, and boundary currents. Temperature has multiple roles as it influences rates of phytoplankton physiology and heterotrophic bacterial recycling of nutrients, in addition to stratification of the water column and sea ice extent (Figure PP-1a). Climate change is projected to strongly impact NPP through a multitude of ways that depend on the regional and local physical settings (WGI AR5, Chapter 3), and on ecosystem structure and functioning (*medium confidence*; Sections 6.3.4, 6.5.1). The influence of environmental drivers on NPP causes as much as a 10-fold variation in regional productivity with nutrient-poor subtropical waters and light-limited Arctic waters at the lower range and productive upwelling regions and highly eutrophic coastal regions at the upper range (Figure PP-1b).

The oceans currently provide ~ 50×10^{15} g C yr⁻¹, or about half of global NPP (Field et al., 1998). Global estimates of NPP are obtained mainly from satellite remote sensing (Section 6.1.2), which provides unprecedented spatial and temporal coverage, and may be validated regionally against oceanic measurements. Observations reveal significant changes in rates of NPP when environmental controls are altered by episodic natural perturbations, such as volcanic eruptions enhancing iron supply, as observed in high-nitrate low-chlorophyll waters of the Northeast Pacific (Hamme et al., 2010). Climate variability can drive pronounced changes in NPP (Chavez et al., 2011), such as from El Niño to La Niña transitions in Equatorial Pacific, when vertical nutrient and trace element supply are enhanced (Chavez et al., 1999).

Multi-year time series records of NPP have been used to assess spatial trends in NPP in recent decades. Behrenfeld et al. (2006), using satellite data, reported a prolonged and sustained global NPP decrease of 190×10^{12} g C yr⁻¹, for the period 1999-2005—an annual reduction of 0.57% of global NPP. In contrast, a time series of directly measured NPP between 1988 and 2007 by Saba et al. (2010) (i.e., *in situ* incubations using the radiotracer ¹⁴C-bicarbonate) revealed an increase (2% yr⁻¹) in NPP for two low-latitude open ocean sites. This discrepancy between *in situ* and remotely sensed NPP trends points to uncertainties in either the methodology used and/ or the extent to which discrete sites are representative of oceanic provinces (Saba et al., 2010, 2011). Modeling studies have subsequently revealed that the <15-year archive of satellite-





PP

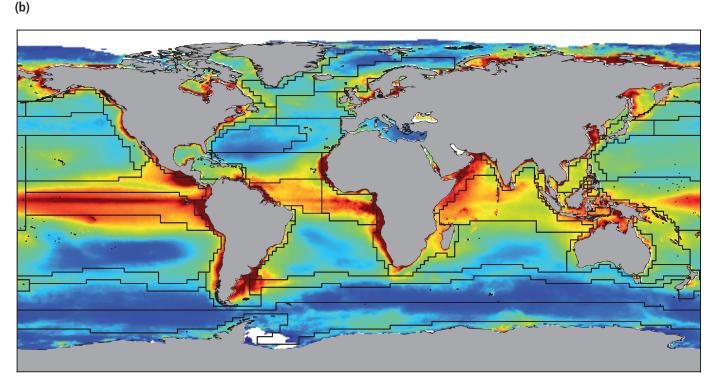




Figure PP-1 (a) Environmental factors controlling Net Primary Production (NPP). NPP is controlled mainly by three basic processes: (1) light conditions in the surface ocean, that is, the photic zone where photosynthesis occurs; (2) upward flux of nutrients and micronutrients from underlying waters into the photic zone, and (3) regeneration of nutrients and micronutrients via the breakdown and recycling of organic material before it sinks out of the photic zone. All three processes are influenced by physical, chemical, and biological processes and vary across regional ecosystems. In addition, water temperature strongly influences the upper rate of photosynthesis for cells that are resource-replete. Predictions of alteration of primary productivity under climate change depend on correct parameterizations and simulations of each of these variables and processes for each region. (b) Annual composite map of global areal NPP rates (derived from Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite climatology from 2003–2012; NPP was calculated with the Carbon-based Productivity Model (CbPM; Westberry et al., 2008)). Overlaid is a grid of (thin black lines) that represent 51 distinct global ocean biogeographical provinces (after Longhurst, 1998 and based on Boyd and Doney, 2002). The characteristics and boundaries of each province are primarily set by the underlying regional ocean physics and chemistry. White areas = no data. (Figure courtesy of Toby Westberry (OSU) and Ivan Lima (WHOI), satellite data courtesy of NASA Ocean Biology Processing Group.)

derived NPP is insufficient to distinguish climate-change mediated shifts in NPP from those driven by natural climate variability (Henson et al., 2010; Beaulieu et al., 2013). Although multi-decadal, the available time series of oceanic NPP measurements are also not of sufficient duration relative to the time scales of longer-term climate variability modes as for example Atlantic Multi-decadal Oscillation (AMO), with periodicity of 60-70 years, Figure 6-1). Recent attempts to synthesize longer (i.e., centennial) records of chlorophyll as a proxy for phytoplankton stocks (e.g., Boyce et al., 2010) have been criticized for relying on questionable linkages between different proxies for chlorophyll over a century of records (e.g., Rykaczewski and Dunne, 2011).

Models in which projected climate change alters the environmental drivers of NPP provide estimates of spatial changes and of the rate of change of NPP. For example, four global coupled climate—ocean biogeochemical Earth System Models (WGI AR5 Chapter 6) projected an increase in NPP at high latitudes as a result of alleviation of light and temperature limitation of NPP, particularly in the high-latitude biomes (Steinacher et al., 2010). However, this regional increase in NPP was more than offset by decreases in NPP at lower latitudes and at mid-latitudes due to the reduced input of macronutrients into the photic zone. The reduced mixed-layer depth and reduced rate of circulation may cause a decrease in the flux of macronutrients to the euphotic zone (Figure 6-2). These changes to oceanic conditions result in a reduction in global mean NPP by 2 to 13% by 2100 relative to 2000 under a high emission scenario (Polovina et al., 2011; SRES (Special Report on Emission Scenarios) A2, between RCP6.0 and RCP8.5). This is consistent with a more recent analysis based on 10 Earth System Models (Bopp et al., 2013), which project decreases in global NPP by 8.6 (\pm 7.9), 3.9 (\pm 5.7), 3.6 (\pm 5.7), and 2.0 (\pm 4.1) % in the 2090s relative to the 1990s, under the scenarios RCP8.5, RCP6.0, RCP4.5, and RCP2.6, respectively. However, the magnitude of projected changes varies widely between models (e.g., from 0 to 20% decrease in NPP globally under RCP 8.5). The various models show very large differences in NPP at regional scales (i.e., provinces, see Figure PP-1b).

Model projections had predicted a range of changes in global NPP from an increase (relative to preindustrial rates) of up to 8.1% under an intermediate scenario (SRES A1B, similar to RCP6.0; Sarmiento et al., 2004; Schmittner et al., 2008) to a decrease of 2-20% under the SRES A2 emission scenario (Steinacher et al., 2010). These projections did not consider the potential contribution of primary production derived from atmospheric nitrogen fixation in tropical and subtropical regions, favoured by increasing stratification and reduced nutrient inputs from mixing. This mechanism is potentially important, although such episodic increases in nitrogen fixation are not sustainable without the presence of excess phosphate (e.g., Moore et al., 2009; Boyd et al., 2010). This may lead to an underestimation of NPP (Mohr et al., 2010; Mulholland et al., 2012; Wilson et al., 2012), however, the extent of such underestimation is unknown (Luo et al., 2012).

Care must be taken when comparing global, provincial (e.g., low-latitude waters, e.g., Behrenfeld et al., 2006) and regional trends in NPP derived from observations, as some regions have additional local environmental influences such as enhanced density stratification of the upper ocean from melting sea ice. For example, a longer phytoplankton growing season, due to more sea ice—free days, may have increased NPP (based on a regionally validated time-series of satellite NPP) in Arctic waters (Arrigo and van Dijken, 2011) by an average of 8.1x10¹² g C yr⁻¹ between 1998 and 2009. Other regional trends in NPP are reported in Sections 30.5.1 to 30.5.6. In addition, although future model projections of global NPP from different models (Steinacher et al., 2010; Bopp et al., 2013) are comparable, regional projections from each of the models differ substantially. This raises concerns as to which aspect(s) of the different model NPP parameterizations are responsible for driving regional differences in NPP, and moreover, how accurate model projections are of global NPP.

From a global perspective, open ocean NPP will decrease moderately by 2100 under both low- (SRES B1 or RCP4.5) and high-emission scenarios (*medium confidence*; SRES A2 or RCPs 6.0, 8.5, Sections 6.3.4, 6.5.1), paralleled by an increase in NPP at high latitudes and a decrease in the tropics (*medium confidence*). However, there is *limited evidence* and *low agreement* on the direction, magnitude and differences of a change of NPP in various ocean regions and coastal waters projected by 2100 (*low confidence*).

References

- Arrigo, K.R. and G.L. van Dijken, 2011: Secular trends in Arctic Ocean net primary production. *Journal of Geophysical Research*, **116(C9)**, C09011, doi:10.1029/2011JC007151.
- Beaulieu, C., S.A. Henson, J.L. Sarmiento, J.P. Dunne, S.C. Doney, R.R. Rykaczewski, and L. Bopp, 2013: Factors challenging our ability to detect long-term trends in ocean chlorophyll. *Biogeosciences*, **10(4)**, 2711-2724.
- Behrenfeld, M.J., R.T. O'Malley, D.A. Siegel, C.R. McClain, J.L. Sarmiento, G.C. Feldman, A.J. Milligan, P.G. Falkowski, R.M. Letelier, and E.S. Boss, 2006: Climate-driven trends in contemporary ocean productivity. *Nature*, 444(7120), 752-755.
- Bopp, L., L. Resplandy, J.C. Orr, S.C. Doney, J.P. Dunne, M. Gehlen, P. Halloran, C. Heinze, T. Ilyina, R. Séférian, J. Tijiputra, and M. Vichi, 2013: Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences*, **10**, 6225-6245.
- Boyce, D.G., M.R. Lewis, and B. Worm, 2010: Global phytoplankton decline over the past century. Nature, 466(7306), 591-596.
- Boyd, P.W. and S.C. Doney, 2002: Modelling regional responses by marine pelagic ecosystems to global climate change. *Geophysical Research Letters*, 29(16), 53-1–53-4, doi:10.1029/2001GL014130.
- Boyd, P.W., R. Strzepek, F.X. Fu, and D.A. Hutchins, 2010: Environmental control of open-ocean phytoplankton groups: now and in the future. *Limnology and Oceanography*, 55(3), 1353-1376.
- Chavez, F.P., P.G. Strutton, C.E. Friederich, R.A. Feely, G.C. Feldman, D.C. Foley, and M.J. McPhaden, 1999: Biological and chemical response of the equatorial Pacific Ocean to the 1997-98 El Niño. Science, 286(5447), 2126-2131.

- Chavez, F.P., M. Messié, and J.T. Pennington, 2011: Marine primary production in relation to climate variability and change. Annual Review of Marine Science, 3(1), 227-260.
- Field, C.B., M.J. Behrenfeld, J.T. Randerson, and P. Falkowski, 1998: Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, 281(5374), 237-240.

Hamme, R.C., P.W. Webley, W.R. Crawford, F.A. Whitney, M.D. DeGrandpre, S.R. Emerson, C.C. Eriksen, K.E. Giesbrecht, J.F.R. Gower, M.T. Kavanaugh, M.A. Peña, C.L. Sabine, S.D. Batten, L.A. Coogan, D.S. Grundle, and D. Lockwood, 2010: Volcanic ash fuels anomalous plankton bloom in subarctic northeast Pacific. *Geophysical Research Letters*, **37**(19), L19604, doi:10.1029/2010GL044629.

- Henson, S.A., J.L. Sarmiento, J.P. Dunne, L. Bopp, I. Lima, S.C. Doney, J. John, and C. Beaulieu, 2010: Detection of anthropogenic climate change in satellite records of ocean chlorophyll and productivity. *Biogeosciences*, 7(2), 621-640.
- Longhurst, A.R., 1998: Ecological Geography of the Sea. Academic Press, San Diego, CA, USA, 560 pp.
- Luo, Y.-W., S.C. Doney, L.A. Anderson, M. Benavides, I. Berman-Frank, A. Bode, S. Bonnet, K.H. Boström, D. Böttjer, D.G. Capone, E.J. Carpenter, Y.L. Chen, M.J. Church, J.E. Dore, L.I. Falcón, A. Fernández, R.A. Foster, K. Furuya, F. Gómez, K. Gundersen, A.M. Hynes, D.M. Karl, S. Kitajima, R.J. Langlois, J. LaRoche, R.M. Letelier, E. Marañón, D.J. McGillicuddy Jr., P.H. Moisander, C.M. Moore, B. Mouriño-Carballido, M.R. Mulholland, J.A. Needoba, K.M. Orcutt, A.J. Poulton, E. Rahav, P. Raimbault, A.P. Rees, L. Riemann, T. Shiozaki, A. Subramaniam, T. Tyrrell, K.A. Turk-Kubo, M. Varela, T.A. Villareal, E.A. Webb, A.E. White, J. Wu, and J.P. Zehr, 2012: Database of diazotrophs in global ocean: abundances, biomass and nitrogen fixation rates. *Earth System Science Data*, *4*, 47-73, doi:10.5194/essd-4-47-2012.
- Mohr, W., T. Großkopf, D.W.R. Wallace, and J. LaRoche, 2010: Methodological underestimation of oceanic nitrogen fixation rates. PLoS ONE, 5(9), e12583, doi:10.1371/journal.pone.0012583.
- Moore, C.M., M.M. Mills, E.P. Achterberg, R.J. Geider, J. LaRoche, M.I. Lucas, E.L. McDonagh, X. Pan, A.J. Poulton, M.J.A. Rijkenberg, D.J. Suggett, S.J. Ussher, and E.M.S. Woodward, 2009: Large-scale distribution of Atlantic nitrogen fixation controlled by iron availability. *Nature Geoscience*, **2(12)**, 867-871.
- Mulholland, M.R., P.W. Bernhardt, J.L. Blanco-Garcia, A. Mannino, K. Hyde, E. Mondragon, K. Turk, P.H. Moisander, and J.P. Zehr, 2012: Rates of dinitrogen fixation and the abundance of diazotrophs in North American coastal waters between Cape Hatteras and Georges Bank. *Limnology and Oceanography*, 57(4), 1067-1083.
- Polovina, J.J., J.P. Dunne, P.A. Woodworth, and E.A. Howell, 2011: Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES Journal of Marine Science*, **68(6)**, 986-995.
- Rykaczewski, R.R. and J.P. Dunne, 2011: A measured look at ocean chlorophyll trends. Nature, 472(7342), E5-E6, doi:10.1038/nature09952.
- Saba, V.S., M.A.M. Friedrichs, M.-E. Carr, D. Antoine, R.A. Armstrong, I. Asanuma, O. Aumont, N.R. Bates, M.J. Behrenfeld, V. Bennington, L. Bopp, J. Bruggeman, E.T. Buitenhuis, M.J. Church, A.M. Ciotti, S.C. Doney, M. Dowell, J. Dunne, S. Dutkiewicz, W. Gregg, N. Hoepffner, K.J.W. Hyde, J. Ishizaka, T. Kameda, D.M. Karl, I. Lima, M.W. Lomas, J. Marra, G.A. McKinley, F. Mélin, J.K. Moore, A. Morel, J. O'Reilly, B. Salihoglu, M. Scardi, T.J. Smyth, S.L. Tang, J. Tjiputra, J. Uitz, M. Vichi, K. Waters, T.K. Westberry, and A. Yool, 2010: Challenges of modeling depth-integrated marine primary productivity over multiple decades: a case study at BATS and HOT. *Global Biogeochemical Cycles*, 24, GB3020, doi:10.1029/2009GB003655.
- Saba, V.S., M.A.M. Friedrichs, D. Antoine, R.A. Armstrong, I. Asanuma, M.J. Behrenfeld, A.M. Ciotti, M. Dowell, N. Hoepffner, K.J.W. Hyde, J. Ishizaka, T. Kameda, J. Marra, F. Mélin, A. Morel, J. O'Reilly, M. Scardi, W.O. Smith Jr., T.J. Smyth, S. Tang, J. Uitz, K. Waters, and T.K. Westberry, 2011: An evaluation of ocean color model estimates of marine primary productivity in coastal and pelagic regions across the globe. *Biogeosciences*, 8(2), 489-503.
- Sarmiento, J.L., R. Slater, R. Barber, L. Bopp, S.C. Doney, A.C. Hirst, J. Kleypas, R. Matear, U. Mikolajewicz, P. Monfray, V. Soldatov, S.A. Spall, and R. Stouffer, 2004: Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles*, 18(3), GB3003, doi:10.1029/2003GB002134.

Schmittner, A., A. Oschlies, H.D. Matthews, and E.D. Galbraith, 2008: Future changes in climate, ocean circulation, ecosystems, and biogeochemical cycling simulated for a business-as-usual CO2 emission scenario until year 4000 AD. *Global Biogeochemical Cycles*, 22(1), GB1013, doi:10.1029/2007GB002953.

Steinacher, M., F. Joos, T.L. Frölicher, L. Bopp, P. Cadule, V. Cocco, S.C. Doney, M. Gehlen, K. Lindsay, J.K. Moore, B. Schneider, and J. Segschneider, 2010: Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences*, 7(3), 979-1005.

Westberry, T., M.J. Behrenfeld, D.A Siegel, and E. Boss, 2008: Carbon-based primary productivity modeling with vertically resolved photoacclimation. *Global Biogeochemical Cycles*, 22(2), GB2024, doi:10.1029/2007GB003078.

Wilson, S.T., D. Böttjer, M.J. Church, and D.M. Karl, 2012: Comparative assessment of nitrogen fixation methodologies, conducted in the oligotrophic North Pacific Ocean. Applied and Environmental Microbiology, 78(18), 6516-6523.

This cross-chapter box should be cited as:

Boyd, P.W., S. Sundby, and H.-O. Pörtner, 2014: Cross-chapter box on net primary production in the ocean. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 133-136.