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A chalkier ocean? Multi-decadal increases in North Atlantic coccolithophore populations

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Coccolithophores and the carbon cycle

Increasing atmospheric CO_2 concentrations are resulting in both warmer sea surface temperatures due to the greenhouse effect and increasingly carbon-rich surface waters. The ocean has absorbed roughly one third of anthropogenic carbon emissions (*1*), causing a shift in carbon chemistry equilibrium to more acidic conditions with lower calcium carbonate saturation states (ocean acidification). Organisms that produce calcium carbonate structures are thought to be particularly susceptible to these changes (*2-4*).

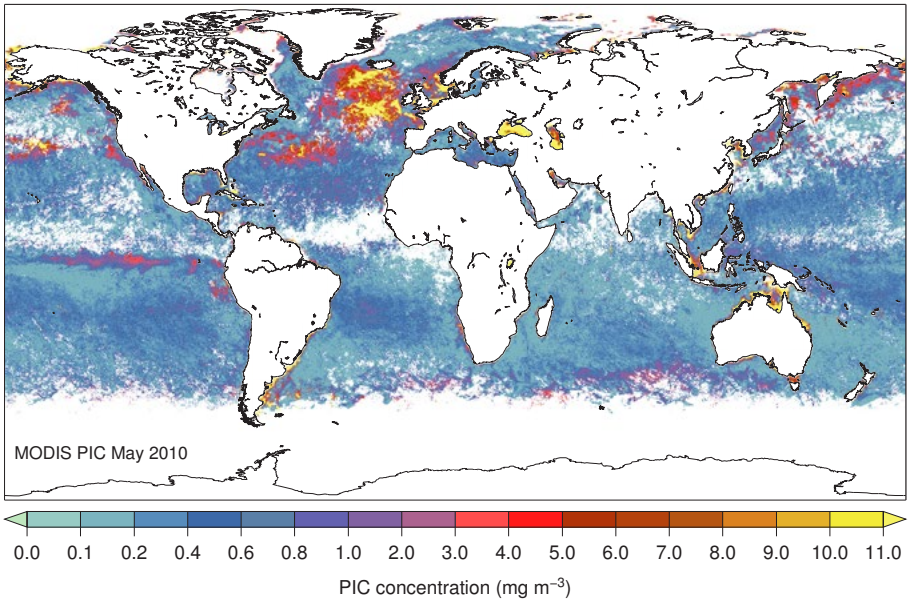

Figure 1. Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua satellite-derived particulate inorganic carbon (PIC) concentration (mg m^{-3}) averaged for the month of May 2010 highlights prominent coccolithophore blooms in the North Atlantic.

Coccolithophores are the most abundant type of calcifying unicellular micro-algae in the ocean, producing microscopic calcium carbonate plates called coccoliths (*5*). Low-pH conditions have been shown to disrupt the formation of coccoliths (calcification; e.g., (*6*)). Therefore, it is generally expected that a higher-CO_2 ocean will cause a reduction in calcification rates or a decrease in the abundance of these calcifiers. Such changes could have far-reaching consequences for marine ecosystems, as well as global carbon cycling and carbon export to the deep sea.

Coccolithophores use sunlight to synthesize both organic carbon through photosynthesis and particulate inorganic carbon (PIC) through calcification. Detrital coccolithophore shells form aggregates with organic material, enhancing carbon export to the deep sea (*7*). Coccolithophores also produce dimethyl sulfide (DMS), a climatically relevant trace gas that impacts cloud formation, ultimately influencing Earth's albedo (*8, 9*). At the ecosystem level, coccolithophores compete for nutrients with other phytoplankton and provide energy for the rest of the marine food web. Coccolithophores have a broad range of irradiance, temperature, and salinity tolerances

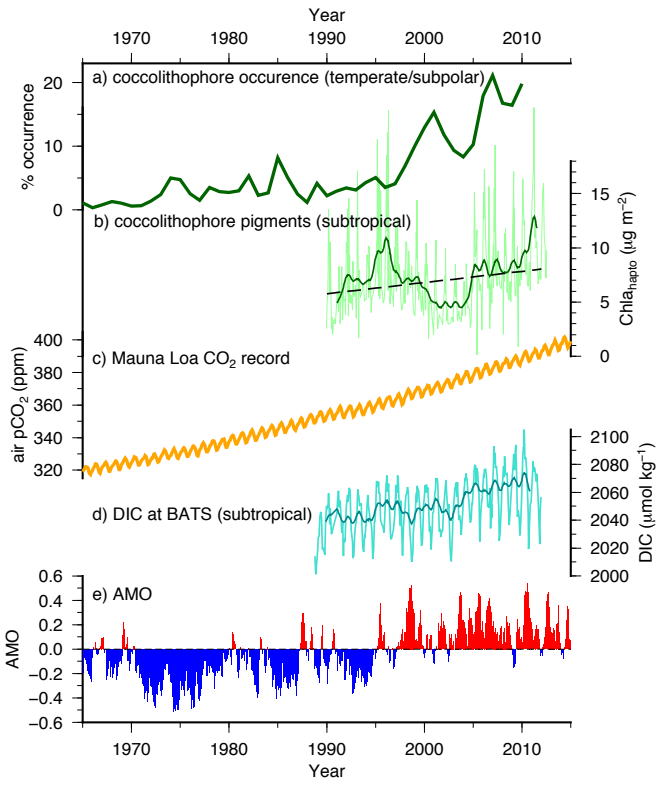

Figure 2. Time-series data from 1960 to 2015 on *(a)* CPR coccolithophore annual occurrence in the temperate/subpolar North Atlantic, *(b)* 140m depth-integrated chlorophyll *a* from coccolithophores (haptophytes) at BATS in the subtropical North Atlantic (µg m^{-2}) with a 2-year Gaussian filter (dark green) and a linear regression (dashed line), *(c)* global atmospheric CO_2 concentration from Mauna Loa (ppm), *(d)* dissolved inorganic carbon (DIC) at BATS (µmol kg^{-1}) with a 2-year Gaussian filter (darker turquoise), and *(e)* the Atlantic Multidecadal Oscillation (AMO) index.

(*10, 11*). Moreover, their relatively low nutrient requirements and slow growth rates offer a competitive advantage under projected global warming and ocean stratification (*5*). This plasticity and opportunistic behavior can be critical for persistence in a changing oceanic environment. Given the wide range of biogeochemical and ecological processes impacted by coccolithophores, it is important to assess how anthropogenic changes may affect coccolithophore growth and calcification.

Many laboratory studies have investigated the impact of future environmental conditions on coccolithophores by decreasing pH, increasing dissolved inorganic carbon, and increasing temperature to mimic end-of-century projections. However, these have often yielded conflicting results: Some show a decrease, while others show no change or even increased calcification (e.g., (*6, 12, 13*)). For example, laboratory simulations of contemporary oceanic changes (increasing CO_2 and decreasing pH) show that coccolithophores have the ability to modulate organic carbon production and calcification in response to variable amounts of dissolved inorganic carbon (DIC) but that low pH only affects these processes below a certain threshold (*14*). Another study indicated that coccolithophores could adapt to warming and high CO_2 levels over the course of a year, maintaining their relative particulate organic carbon (POC) and PIC production per cell (*15*). One of the limitations of all laboratory experiments is that only a handful of species (and strains) are studied, which is only a tiny fraction of the diversity present in the oceans. Given the challenges of extrapolating laboratory results to real world oceans, studying recent trends in natural populations may lead to important insights.

The North Atlantic is both a region with rapid accumulation of anthropogenic CO_2 (*1*) and an important coccolithophore habitat (Fig. 1), making this region a good starting point to search for *in situ* evidence of anthropogenic carbon effects on diverse coccolithophore populations. Two recent studies did precisely that: Rivero-Calle et al. (2015)(*16*) in the subpolar North Atlantic, and Krumhardt et al. (2016)(*17*) in the North Atlantic subtropical gyre. Using independent datasets, these two studies concluded that coccolithophores in the North Atlantic appear to be increasing in abundance and, contrary to the prevailing paradigm, responding positively to the extra carbon in the upper mixed layer.

Evidence from long-term *in situ* monitoring (two independent case studies)

Rivero-Calle et al. (2015) used data from the Continuous Plankton Recorder (CPR), a filtering device installed on ships of opportunity, to assess changes in coccolithophore populations from 1965 to 2010 in the subpolar North Atlantic. This highly productive, temperate region is dominated by large phytoplankton and characterized by strong seasonal changes in the mixed layer depth, nutrient upwelling, and gas exchange that lead to intense, well established spring phytoplankton blooms.

Because coccolithophore cells are smaller than the mesh size used by the CPR, they cannot be accurately quantified in the CPR data set. Some coccolithophore cells do, however, get caught in the mesh and their occurrence (i.e. probability of presence) can be calculated and serve as a proxy for coccolithophore abundance. Using recorded presence or absence of coccolithophores over this multidecadal time-series, the authors showed that coccolithophore occurrence in the subpolar North Atlantic

increased from being present in only 1% of samples to > 20% over the past five decades (Fig. 2).

To assess the importance of a wide range of diverse environmental drivers on changes in coccolithophore occurrence, Rivero-Calle and co-authors used random forest statistical models. Specifically, they examined more than 20 possible biological and physical predictors, including CO_2 concentrations, nutrients, sea surface temperature and the Atlantic Multidecadal Oscillation (AMO), as well as possible predators and competitors. Global and local CO_2 concentrations were shown to be the best predictors of coccolithophore occurrence. The AMO, which has been in a positive phase since the mid-1990s (Fig. 2) and is associated with anomalously warmer temperatures over the North Atlantic, was also a good predictor of coccolithophore occurrence, but not as strong of a predictor as CO_2.

The authors hypothesize that the synergistic effects of increasing anthropogenic CO_2, the recent positive phase of the AMO, and increasing global temperatures contributed to the observed increase in coccolithophore occurrence in the CPR samples from 1965 to 2010.

Complementing the Rivero-Calle et al. (2015) study, Krumhardt et al. (2016) used phytoplankton pigment concentration data from the long-running Bermuda Atlantic Time-series Study (BATS) and satellite-derived PIC data to assess recent changes in coccolithophore abundance in the subtropical North Atlantic. This region of the North Atlantic is characterized by Ekman convergence and downwelling, resulting in an oligotrophic environment. Despite relatively low productivity, subtropical gyres cover vast expanses of the global ocean and are thus important on a global scale.

In the North Atlantic subtropical gyre, researchers at BATS have performed phytoplankton pigment analyses since the late 1980s, as well as a suite of other oceanographic measurements (nutrients, temperature, salinity, etc.). This rich dataset provided insight into phytoplankton dynamics occurring at BATS over the past two decades. Coccolithophores contain a suite of pigments distinctive to haptophytes. Though there are many species of non-calcifying haptophytes in the ocean (*18*), the main contributors to the haptophyte community in oligotrophic gyres are coccolithophores (*19*). Using a constant haptophyte pigment to chlorophyll *a* ratio Krumhardt et al. (2016) quantified relative abundance of the coccolithophore chlorophyll *a* ($Chla_{hapto}$) over the BATS time-series. A simple linear regression revealed that coccolithophore pigments have increased in the upper euphotic zone by 37% from 1990 to 2012 (Figure 2). On the other hand, total chlorophyll *a* at BATS only increased slightly over this time period.

While satellite-derived chlorophyll *a* is used as a proxy for biomass and abundance of the entire phytoplankton community (*20*), satellite-derived PIC is formulated to specifically retrieve calcium carbonate from coccolithophore shells (*21, 22*). Therefore, satellite PIC can be used as a proxy for coccolithophore abundance. Although there has been virtually no change in total chlorophyll *a* over most of the North Atlantic subtropical gyre over the satellite era (1998-2014), predominantly positive trends were shown over this time period for PIC (*17*). This indicates that coccolithophore populations appear to be increasing over and above other phytoplankton species in the subtropical gyre.

Like Rivero-Calle et al., Krumhardt et al. explored possible environmental drivers of this increase in coccolithophore pigments at BATS and coccolithophore PIC throughout the gyre. They performed linear correlations between variability of hypothesized drivers and coccolithophore chlorophyll *a* concentrations

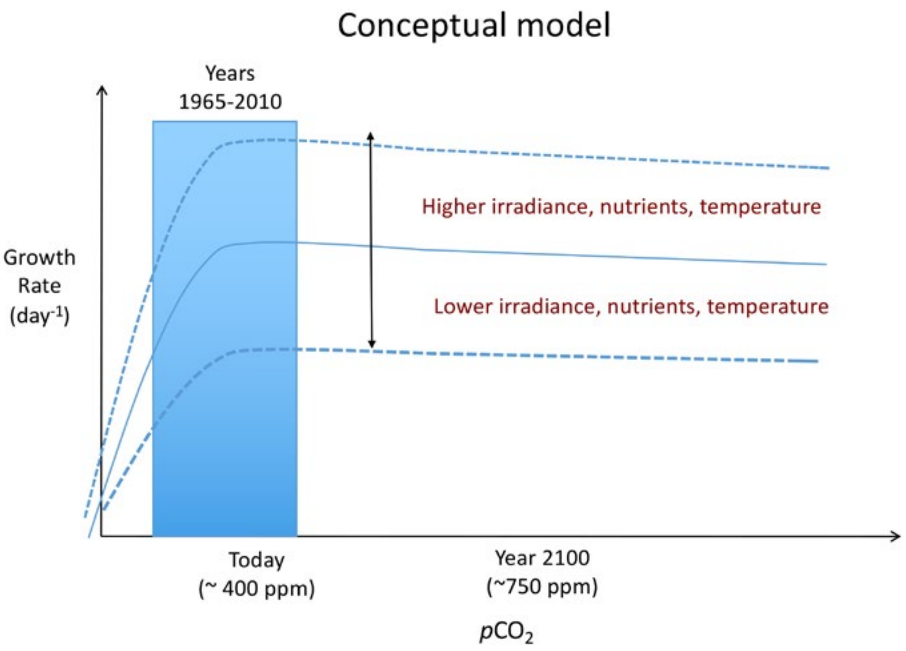

Figure 3. Conceptual model on coccolithophore growth rate (d^{-1}) as a function of pCO_2. This figure is adapted from data presented in Rivero-Calle et al. (2015).

at the BATS site. Increasing DIC, specifically the bicarbonate ion (HCO_3^-) fraction, showed a strong positive correlation with pigments from coccolithophores, explaining a significant fraction of the coccolithophore pigment variability. DIC in the upper mixed layer at BATS has been increasing steadily over the past several decades from absorption of anthropogenic CO_2 (Fig. 2; *23*) and coccolithophores may be responding to this. But how does extra carbon in the water explain the increases in coccolithophore populations?

Environmental controls on coccolithophore growth

A few studies have shown that, in contrast to most other phytoplankton, coccolithophore photosynthesis (specifically, the widespread coccolithophore species *Emiliania huxleyi*) can be carbon-limited at today's CO_2 levels (e.g., *14, 24*). This suggests that increases in surface DIC (e.g., due to the uptake of anthropogenic CO_2) may alleviate growth limitation of coccolithophores. By reducing the amount of energy spent on carbon concentrating mechanisms, coccolithophores may invest in other metabolic processes such as growth, PIC or POC production. This explains why a relatively small increase in DIC could increase coccolithophore competitive ability, especially in oligotrophic environments where phytoplankton are routinely in competition for scarce nutrients.

Rivero-Calle and co-authors compiled numerous published laboratory studies that assessed coccolithophore growth rates as a function of pCO_2. The compilation, which included several species and strains of coccolithophores, showed that there is a quasi-hyperbolic increase in coccolithophore growth rates as pCO_2 increases (Fig. 3). The range of local pCO_2 concentrations in the subpolar/temperate North Atlantic from 1965 to 2010 (~175 to 435 ppm) spanned the pCO_2 levels over which there is a substantial increase in published coccolithophore growth rates (Fig. 3). Growth rates tend to stabilize at ~500 ppm CO_2, indicating that coccolithophore populations may continue to respond positively to increasing CO_2 for the next few decades.

Other environmental factors (e.g., temperature, light, and available nutrients) may also impact and modulate coccolithophore growth rates, resulting in a net neutral or net negative impact in spite of increasing atmospheric (marine) CO_2 (DIC) concentrations (see conceptual model, Fig. 3). For example, severe nutrient limitation in the subtropics may cause coccolithophores to be outcompeted by smaller marine cyanobacteria. In the subpolar North Atlantic, nutrients are more plentiful than in the subtropics, but Earth system models have predicted that climatic warming in this region may result in increased water column stratification (*25*). Under these stratified low-nutrient conditions, smaller phytoplankton such as coccolithophores could become more prevalent at the expense of larger phytoplankton such as diatoms (*26, 27*). However, if nutrient concentrations decline to the point at which they become the limiting factor for growth, then coccolithophore populations will also be negatively affected. Furthermore, the associated drop in pH from CO_2 dissolving into the upper mixed layer can eventually be detrimental to coccolithophore growth and calcification. Specifically, pH values below 7.7 negatively affected the coccolithophore *Emiliania huxleyi* in laboratory experiments (*14*), though most oceanic regions will not show such a low pH any time in the near future. In short, anthropogenic CO_2 entering the ocean may allow coccolithophores a competitive edge in the near future in some regions such as the North Atlantic, but other compounding influences from anthropogenic climate change such as severe nutrient limitation or ocean acidification are also important to consider, particularly in the oligotrophic gyres.

Open questions and future directions

While recent work has provided new insight into the impact of several environmental factors (irradiance, nutrients, temperature, pH, DIC) on coccolithophores, many questions remain. Among these, the vertical distribution of coccolithophore communities, grazing rates, and viral infection on coccolithophores, and species-specific responses to environmental change are relatively unexplored areas of research. For instance, some studies have shown species-specific and even strain-specific variability in the response of coccolithophores to CO_2 (28, 29), but how various coccolithophore species respond to nutrient or light limitation is relatively unknown. Due to its cosmopolitan distribution and ability to grow relatively easily in the lab, *E. huxleyi*, has become the "lab rat" species. However, it may not be the most important calcite producer globally (*30*), nor the most representative of the coccolithophore group as a whole. As part of its peculiarities, *E. huxleyi* can both produce several layers of coccoliths and also exhibit a naked form without coccoliths, posing questions about the importance of non-calcified forms in the projected acidified oceans and about the role of calcification *per se* (*31*). Indeed, the fundamental question of why coccolithophores calcify is still unresolved and may vary between species (*5, 32*). In addition, while we recognize that some zooplankton groups graze on coccolithophores (coccoliths have been found in pelagic tintinnid ciliates

(*33*), as well as copepod guts and fecal pellets (*34-36*)), little is known about predation rates or specificity in natural populations. Finally, we know that viruses can also cause bloom termination and that *E. huxleyi* can induce coccolith detachment to avoid viral invasion (37); however, there are still many unknowns related to bloom dynamics. Until we understand what drives coccolithophore calcification and variations in growth and mortality rates, we will have an incomplete picture of the role that coccolithophores play in marine ecology and the carbon cycle.

Krumhardt et al (2016) and Rivero-Calle et al (2016) both arrive at a simple conclusion: Coccolithophore presence in the North Atlantic is increasing. The common denominators in this equation are increasing global CO_2 levels and increasing global surface temperatures. Therefore, even given regional oceanic variability in environmental drivers, we might expect to see similar trends in coccolithophore abundance in other regions. Given coccolithophores' positive response to increasing anthropogenic CO_2 and temperature, as well as general fitness under conditions that may be more prevalent in the future ocean, coccolithophores may become an even bigger player in the marine carbon cycle, which may have unexpected consequences.

Acknowledgments

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What controls the distribution of dissolved organic carbon in the surface ocean?

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Around 662 billion tons of organic carbon are dissolved in the ocean, making the pool one of Earth's major, exchangeable carbon reservoirs. Dissolved organic carbon (DOC) has many ecological functions. It can form complexes with metals (*1*); absorb UV and visible light, acting as a "sunscreen" for marine microorganisms and controlling primary production in the upper water column (*2*); it has antioxidant activity, reacting with free radicals in the media (*3*); but most importantly, it serves as substrate for the microbial loop and as a vehicle for carbon sequestration in the ocean. Therefore, DOC plays an important role in climate on geological time scales.

Because the amount of atmospheric CO_2 is of the same magnitude as the DOC pool, and is closely linked to it through exchange, variations in one of these reservoirs can affect the other, impacting the carbon cycle with consequences for climate. Significant net DOC remineralization would lead to an increase of atmospheric CO_2, enhancing greenhouse warming at the surface of the Earth. Net oxidation of only 1% of the seawater DOC pool within 1 year would be sufficient to generate a CO_2 flux of 7 PgC/yr, comparable to that produced annually by fossil fuel combustion (*4*). It has also been proposed that a large-scale oxidation of DOC may have prevented a dramatic global glaciation ('snowball earth') in the Neoproterozoic period (*5*).

Despite its importance, knowledge about DOC dynamics is relatively limited; in fact, it was considered highly inert until about three decades ago when a new analytical technique for measuring it via high-temperature catalytic oxidation stimulated new interest (*6*). The technique eventually provided more accurate DOC values, showing that it was more involved in the carbon cycle than previously thought and that its concentrations vary with depth, time, and location. Considering DOC distributions observed in the surface Atlantic Ocean (Fig. 1), we see values in the subtropical gyres of 65-70 μmol Kg^{-1}, the highest concentrations in the tropics (> 70 μmol Kg^{-1}), the lowest in the Southern Ocean (< 50 μmol Kg^{-1}), and moderate concentrations in the northern North Atlantic (55-60 μmol Kg^{-1}); this pattern is consistent in other ocean basins. So what controls this distribution and can we predict it? Even with improved analytical techniques, DOC is not a variable that can be measured easily at sea, and the sampling must

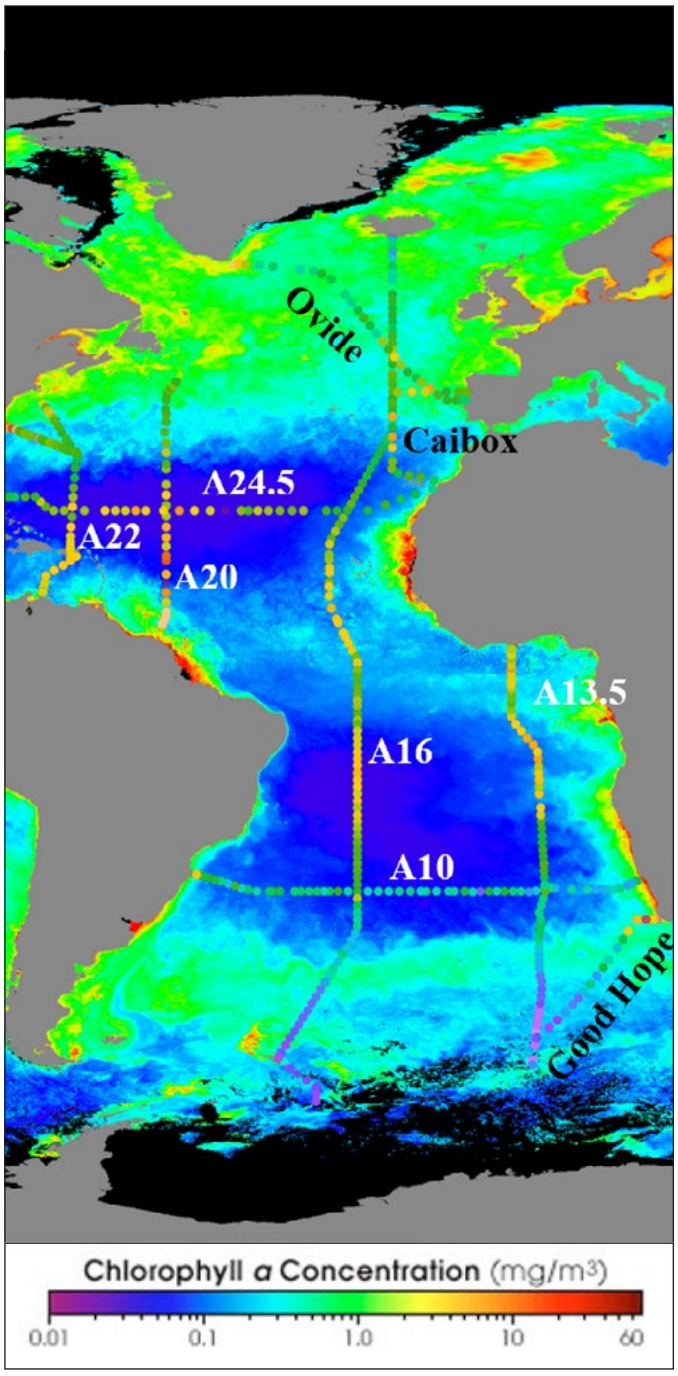

Figure 1. Dissolved organic carbon (DOC) concentrations (dots) over the average ocean chlorophyll concentration measured by SeaWiFS since launch (background, from NASA http://earthobservatory.nasa.gov/IOTD/view.php?id=4097). In white letters, cruise lines from the US Repeat Hydrography program (http://ushydro.ucsd.edu/) and in black letters, Spanish cruises. See figure 4 for DOC concentrations scale (in micromoles per kilogram).

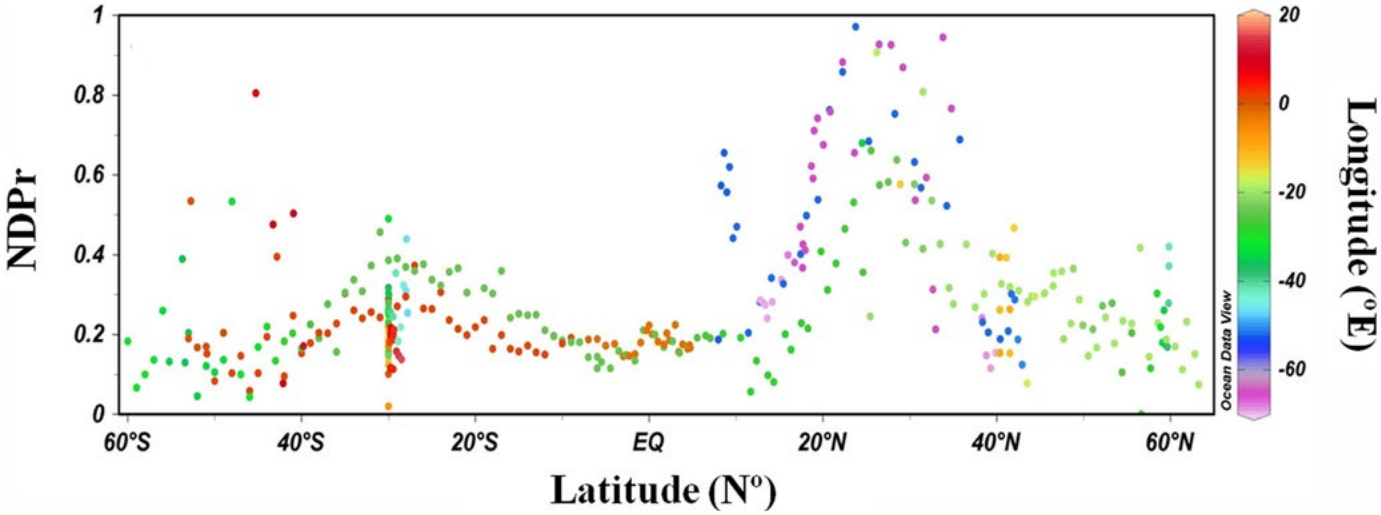

Figure 2. Meridional distribution of the calculated net DOC production as a fraction of NCP (NDPr), using data from the lines shown in Fig. 1, with the color bar depicting longitude. Figure was developed using (*18*) and modified from Romera-Castillo et al. (*19*).

be done carefully since it is easy to contaminate. Therefore, DOC data are typically fewer than those of other more readily determined variables such as nutrients and oxygen. If we could predict DOC from variables for which much greater global ocean coverage exists, we could fill the very large spatial and temporal gaps in the DOC fields.

DOC is produced in the upper water column by phytoplankton (primary producers). Actually, half of the inorganic carbon that is fixed by phytoplankton is transformed to DOC. Heterotrophic microbes consume most of that DOC, but ~ 4% of global annual net primary production (~2 Pg C y^{-1}) (*7*) accumulates as DOC, much of which is exported to the mesopelagic via vertical mixing and convergence, thus contributing to the biological carbon pump.

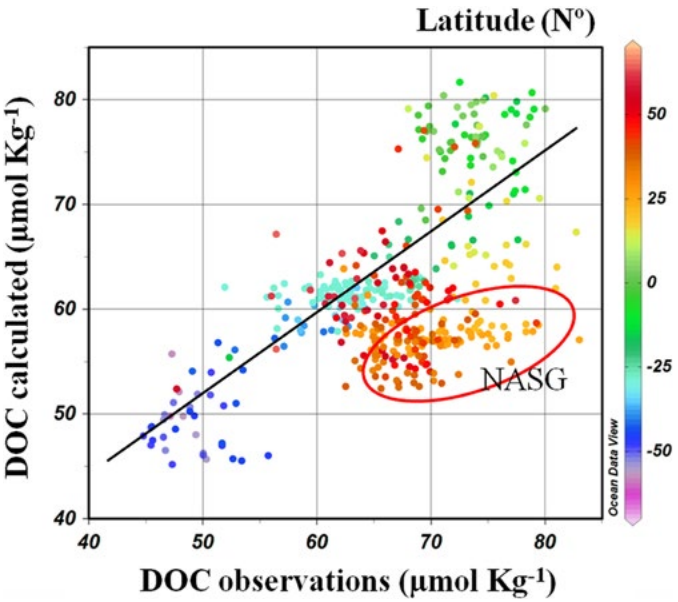

Figure 3. Relationship between surface DOC observations and DOC calculated from nitrate observations along the lines in Fig. 1. The *z* axis (color bar) indicates the latitude (°N). Figure was developed using (*18*) and modified from Romera-Castillo et al. (*19*).

New primary production, the foundation of a system's net community production (NCP), depends on new nutrients reaching the euphotic zone, which happens primarily via upwelling in divergence zones and winter vertical mixing. NCP is the balance of the carbon generated by primary producers minus that lost through heterotrophic respiration (prokaryotes and animals). It can be estimated either by a loss of reactants (CO_2 or nutrients) or a gain in products (suspended POC, DOC, and export production) (*8*).

In our work, we needed to establish the fraction of NCP that was present in dissolved form (i.e., the net DOC production ratio, or NDPr). For that, we simply estimated NCP from the nitrate (NO_3^-) that is consumed in the euphotic zone (ΔNO_3^-):

ΔNO_3^- = new NO_3^- (introduced from deeper layers) - remaining NO_3^- (at surface) (Eq. 1)

In the same way, we also calculated net accumulated DOC, or ΔDOC:

ΔDOC = DOC in euphotic zone – DOC introduced from deeper layers (Eq. 2)

The ratio between ΔDOC and ΔNO_3^- gave us the NDPr:

NDPr = ΔDOC/ΔNO_3^- (Eq. 3)

NDPr was calculated throughout the Atlantic Ocean using observations of DOC and NO_3^- from >15 international oceanographic cruises over the last decade,

including those occupied by the US Repeat Hydrography Program (Fig. 1). Values of NDPr mostly varied between 0.1 and 0.4 (Fig. 2), with the exception of the North Atlantic Subtropical Gyre (NASG), where NDPr values reach >0.8 at times. After sensitivity testing, we applied a NDPr value of 0.17 to the entire basin, which yielded the smallest error between calculated and observed DOC concentrations. Applying this NDPr value to ΔNO_3^- (i.e. NCP) obtained from cruise data, we estimate ΔDOC (Eq. 4), in which 6.6 is the molar conversion from N to C units:

$$\mathbf{\Delta DOC = \Delta NO_3^- * 6.6 * 0.17 = NCP * 0.17 \quad (Eq.\ 4)}$$

To obtain the calculated DOC concentration ($DOC_{calculated}$), we added the DOC concentration of underlying source waters (DOC_{source}) to ΔDOC (Eq. 5):

$$\mathbf{DOC_{calculated} = DOC_{source} + \Delta DOC \quad (Eq.\ 5)}$$

When comparing calculated vs. observed DOC (Fig. 3), we found significant agreement (R^2 = 0.64; p < 0.001; n=268) throughout the Atlantic, except in the western North Atlantic, where observed DOC > estimated DOC, especially in the southern sector. After this validation of our approach using nutrients and DOC observations, we applied the method to the more extensive NO_3^- distributions available in the World Atlas Ocean (WOA) climatology to develop a $DOC_{calculated}$ map for the entire Atlantic (Fig. 4a). The calculated values agree well with the observations, with a total error of 8.94%.

How much DOC is annually produced in the surface Atlantic Ocean? Total organic carbon export (considered equivalent to NCP) in the Atlantic has been estimated to be 4.15-4.3 Pg C y^{-1} (*9, 10*). Applying the 0.17 NDPr (equation 3) indicates that 0.70-0.75 Pg C y^{-1} accumulates in the Atlantic surface as DOC; as such, the Atlantic accounts for ~36% of the global net DOC production of ~2 Pg C y^{-1}.

In permanently stratified areas like the southern sectors of the NASG, our approach is invalid since there is little nutrient input from underlying depths. Also, the static view of our approach does not take into account advection that will modify the DOC distributions, nor does it account for eventual removal of accumulated and advected DOC by microbes. To account for these influences on distribu-

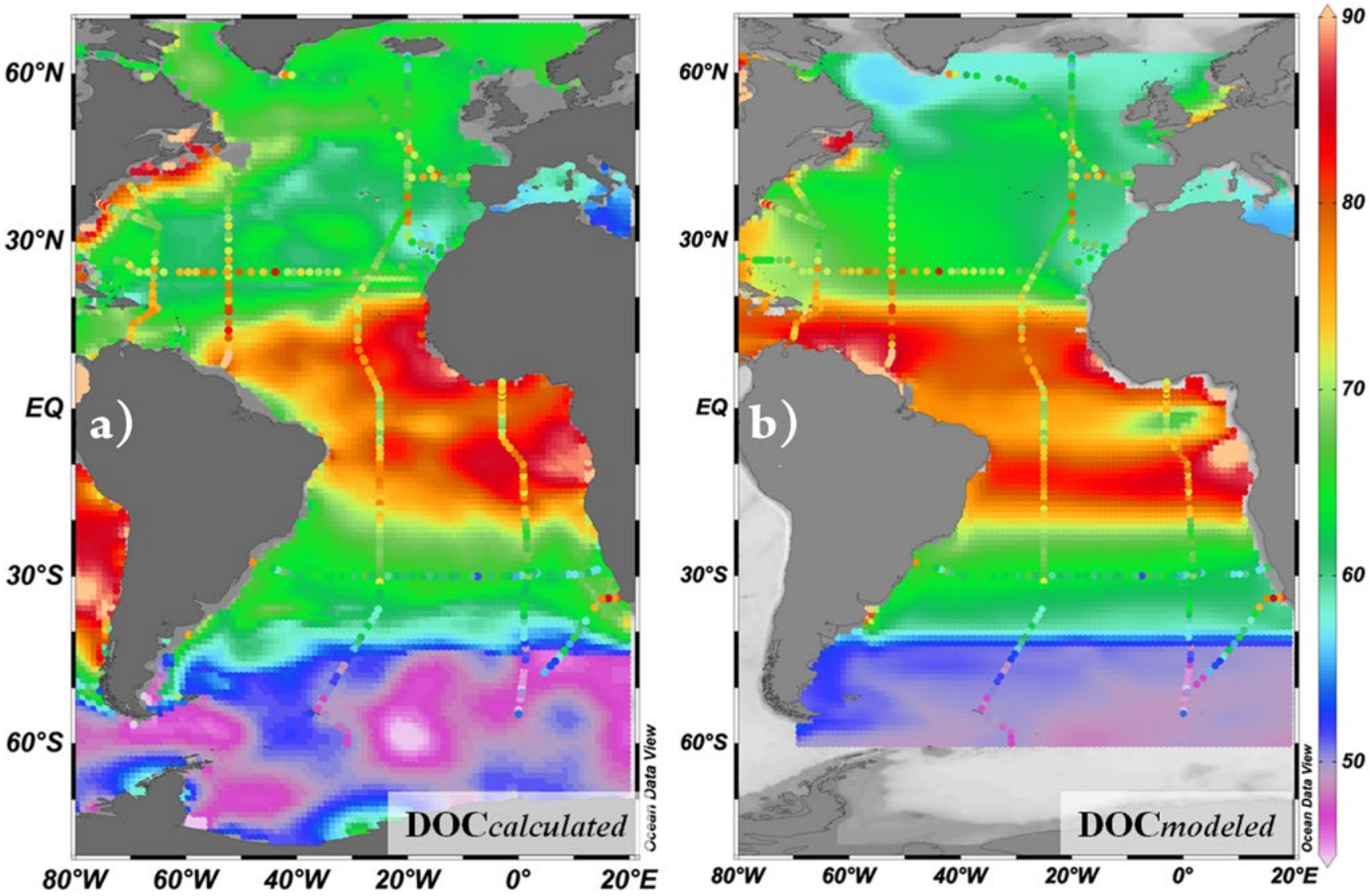

Figure 4. Dissolved organic carbon concentrations (micromoles per kilogram) in the surface Atlantic Ocean: **A**) Observed DOC (colored dots) underlain by calculated DOC (background); **B**) Observed DOC (colored dots) underlain by modeled DOC. Figure was developed using (*18*) and modified from Romera-Castillo et al. (*19*).

tions, we applied the ΔNO_3^- measurements to a steady-state ocean circulation model including terrestrial DOC inputs and DOC remineralization (Fig. 4b). In the model, zonal advection is evident through enrichment of DOC in the Caribbean Sea. Also, inputs of terrestrial DOC are observed near the outflow of the Amazon River. However, the model only slightly improved the match between observations and modeled DOC, with a total error of 8.71% vs. the 8.94% obtained before the model application.

The correspondence between observations and modeled values was good, considering that we are comparing observations of DOC from cruises during specific seasons with estimates based on more idealized nutrient climatology. The main mismatch is found in the western NASG, where observations can reach 13 μmol Kg^{-1} higher than calculated values. Local production and/or allochthonous inputs of either new nutrients or DOC must be considered. Local production of DOC could result from addition of nitrogen from sources beyond vertical mixing such as diazotrophic N_2 fixation, atmospheric deposition, and river runoff. Alternatively, DOC can be concentrated by evaporation, as is sea salt. However, none of these explain the high DOC values observed in the NASG. DOC flux estimated from dissolved organic nitrogen (DON) released by N_2 fixation (*11*) is too low to explain the extra DOC. Regarding the atmospheric deposition, aerosol optical depth data suggest higher deposition in the eastern than in the western North Atlantic (*11*), and no excess of DOC is observed there. According to salinity distributions from the World Ocean Atlas, advection of DOC from the closest major rivers (Amazon and Orinoco) does not extend far enough northward to explain the NASG anomaly. Salinity normalization of DOC does not erase the feature, indicating that evaporation is not the cause. Those elevated values of carbon are found during cruises from 2003 in the same area (*12*), so it appears to be a persistent feature. The anomaly also coincides with a DON maximum and a light stable isotope ($\delta^{15}N$) composition in the particulate organic carbon based on measurements recorded in 2004 (*13*). An explanation for these anomalies has not been confirmed.

Conclusions

New nutrients are the fundamental driver of net DOC accumulation in the surface Atlantic Ocean. As such, climate-driven changes in ocean dynamics, which will affect the supply of nutrients to the euphotic zone, will affect the DOC inventory. The effects of climate change on the nutrient supply to the upper water column are not well known, but they will depend on the opposing influences of thermal stratification and upwelling intensification. Some authors predict an intensification and spatial homogenization of coastal upwelling systems (*14, 15*). Such would increase the nutrient input to the euphotic zone and the net DOC production. In contrast, others have reported that ocean warming should intensify thermal stratification, reducing nutrient flux by vertical mixing in regions not affected by coastal upwelling systems (*16, 17*). Depending on which of these phenomena dominate, the nutrient supply will change, in turn changing the DOC budget and its distribution. Furthermore, the percentage of NCP accumulating as DOC (i.e. NDPr), found here to be ~17%, could change in response to a shift in the balance of autotrophs and heterotrophs. This multitude of influencing factors will undoubtedly impact the future course of the oceanic DOC budget.

Acknowledgments

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Marine mixotrophs exploit multiple resource pools to balance supply and demand

By Ben Ward, University of Bristol

> *"So, in the sea, there are certain objects concerning which one would be at a loss to determine whether they be animal or vegetable."*
>
> —Aristotle, The History of Animals

Our understanding of marine ecosystems is strongly influenced by the terrestrial macroscopic world we see around us. For example, the distinction between phytoplankton and zooplankton reflects the very familiar divide between plants and animals. Mixotrophs are organisms that blur this distinction by combining photosynthetic carbon fixation and the uptake of inorganic nutrients with the ingestion of living prey (*1*). In the macroscopic terrestrial realm, the obvious examples of mixotrophs are the carnivorous plants. These organisms are so well known because they confound the otherwise clear divide between autotrophic plants and heterotrophic animals - in terrestrial environments, mixotrophs are the exception rather than the rule. There appear to be numerous reasons for this dichotomy involving constraints on surface area to volume ratios, the energetic demands of predation, and access to essential nutrients and water. Without dwelling on these aspects of macroscopic terrestrial ecology, it appears that many of the most important constraints are relaxed in aquatic microbial communities. Plankton have no need for the fixed root structures that would prevent motility, and in the three-dimensional fluid environment, they are readily exposed to both inorganic nutrients and prey. In addition, their small size and high surface area to volume ratios increase the potential efficiency of light capture and nutrient uptake. As such, mixotrophy is a common and widely recognised phenomenon in marine ecosystems. It has been identified in a very broad range of planktonic taxa and is found throughout the eukaryotic tree of life. Despite its known prevalence, the potential impacts of mixotrophy on the global cycling of nutrients and carbon are far from clear. In this article, I discuss the ecological niche and biogeochemical role of mixotrophs in marine microbial communities, describing some recent advances and identifying future challenges.

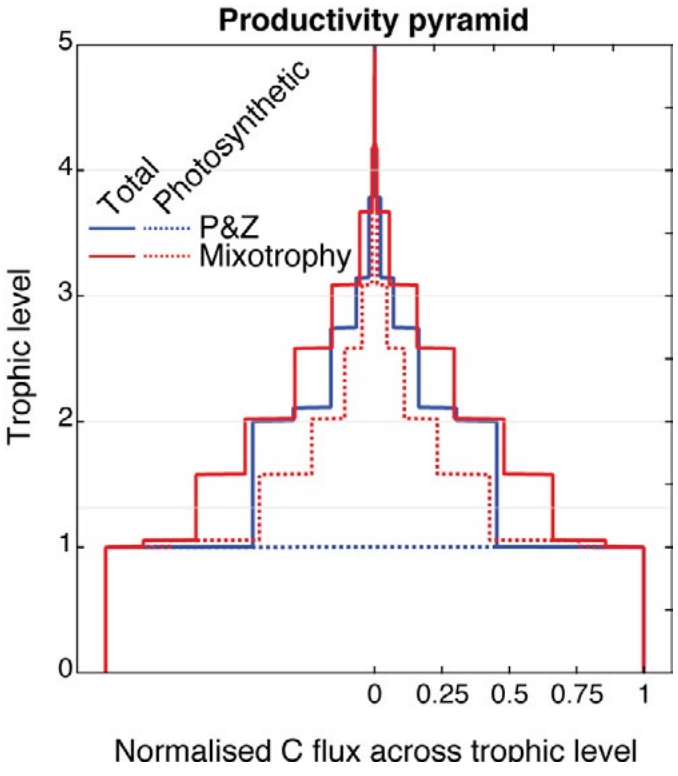

Figure 1. Ecological pyramids (solid lines) represent the total carbon flux at each trophic level (normalised to total primary production) within two configurations of a global food web model (*12*). More biomass is transferred up the food chain in the mixotrophic model because the mixotrophic model allows photosynthesis (dotted lines) above the first trophic level. Figure adapted from Ref. (*12*).

A ubiquitous and important strategy

Mixotrophy appears to be a very broadly distributed trait, appearing in all marine biomes from the shelf seas (*2*) to the oligotrophic gyres (*3*), and from the tropics (*4*) to the polar oceans (*5*). Within these environments, mixotrophy is often a highly successful strategy. For example, in the subtropical Atlantic, mixotrophic plankton make up >80% of the pigmented biomass, and are also responsible for 40-95% of grazing on bacteria (*3, 4*). Similar abundances and impacts have also been observed in coastal regions (*2, 6*).

How does the observed prevalence of mixotrophy affect the biogeochemical and ecological function of marine communities? To understand the potential answers to this question, it is helpful to review the constraints associated with the assumption of a strict dichotomy between autotrophic phytoplankton and heterotrophic zooplankton. Within this paradigm, primary production is restricted to the base of the food web, tightly coupled to the supply of limiting nutrients. Furthermore, the vertical export of carbon is limited by the supply of exogenous (or "new")

nutrients (*7*), since any local regeneration of nutrients from organic matter is also associated with the local remineralisation of dissolved inorganic carbon. Energy and biomass are passed up the food web, but the transfer across trophic levels is highly inefficient (*8*) (Fig. 1) because the energetic demands of strictly heterotrophic consumers can only be met by catabolic respiration.

In the mixotrophic paradigm, several of these constraints are relaxed. Primary production is no longer exclusively dependent on the supply of inorganic nutrients because mixotrophs can support photosynthesis with nutrients derived from their prey. This mechanism takes advantage of the size-structured nature of marine communities (*9*), with larger organisms avoiding competitive exclusion by eating their smaller and more efficient competitors (*10-12*). In addition, the energetic demands of mixotrophic consumers can be offset by phototrophy, leading to increased efficiency of carbon transfer through the food web (Fig. 1). These two mechanisms dictate that mixotrophic ecosystems can fix and export more carbon for the same supply of limiting nutrient, relative to an ecosystem strictly divided between autotrophic phytoplankton and heterotrophic zooplankton (*12*).

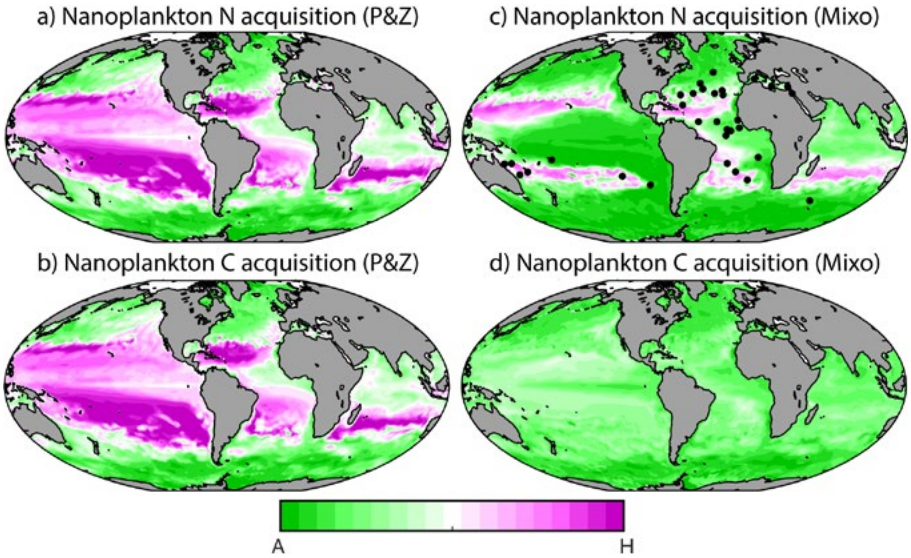

Figure 2. Depth-integrated balance of autotrophic and heterotrophic acquisition of N and C by nanoplankton (2 - 20 µm) in a global marine ecosystem model (*12*). The left-hand panels correspond to a model with mutually exclusive phytoplankton and zooplankton. The right-hand panels correspond to a model with only mixotrophic plankton. Black dots in panel c indicate sites where *in situ* nutrient addition experiments have identified (at least occasional) limitation by that nutrient element (*26*). Figure adapted from Ref. (*12*).

The trophic flexibility associated with mixotrophy appears likely to have a profound effect on marine ecosystem function at the global scale. Fig. 2 contrasts the simulated fluxes of carbon and nitrogen through the intermediate nanoplankton (2 - 20 µm diameter) size class of a global ecosystem model (*12*). The left-hand maps show the balance of autotrophic and heterotrophic resource acquisition in a model with mutually exclusive phytoplankton and zooplankton. At low latitudes and especially in the oligotrophic subtropical gyres, the inorganic nitrogen supply is acquired almost exclusively by the smallest and most competitive phytoplankton (not shown). This leaves an inadequate supply for larger and less competitive phytoplankton, and as such, the larger size classes are dominated by zooplankton (as indicated by the purple shading in Fig. 2a, b). In the more productive polar oceans and upwelling zones, grazing pressure prevents the smaller phytoplankton from exhausting the inorganic nitrogen supply, leaving enough for the larger phytoplankton to thrive in these regions (as indicated by the green shading).

The right-hand maps in Fig. 2 show the balance of autotrophic and heterotrophic resource acquisition in the intermediate size-class of an otherwise identical model containing only mixotrophic plankton. As in the model with mutually exclusive phytoplankton and zooplankton, the inorganic nitrogen supply in the oligotrophic gyres is exhausted by the smallest phytoplankton (see the purple shading in Fig. 2c). However, Fig. 2d indicates that this is not enough to stop photosynthetic carbon fixation among the mixotrophic nanoplankton. The nitrogen acquired from prey is enough to support considerable photosynthesis in a size class for which phototrophy would otherwise be impossible. For the same supply of inorganic nutrients, this additional supply of organic carbon serves to enhance the transfer of energy and biomass through the microbial food web, increasing community carbon:nutrient ratios and leading to as much as a three-fold increase in mean organism size and a 35% increase in vertical carbon flux (*12*).

Trophic diversity and ecosystem function

Marine mixotrophs are broadly distributed across the eukaryotic tree of life (*13*). The ability to combine photosynthesis with the digestion of prey has been identified in ciliates, cryptophytes, dinoflagellates, foraminifera, radiolarians, and coccolithophores (*14*). Perhaps the only

major group with no identified examples of mixotrophy are the diatoms, which have silica cell walls that may hinder ingestion of prey. While some mixotroph species are conceptually more like plants (that eat), others are more like animals (that photosynthesise). A number of conceptual models have been developed to account for this observed diversity. One scheme (*15*) identified three primarily autotrophic groups that use prey for carbon, nitrogen or trace compounds, and two primarily heterotrophic groups that use photosynthesis to delay starvation or to increase metabolic efficiency. More recently, an alternative classification (*16, 17*) identified three key groups on a spectrum between strict phototrophy and strict phagotrophy. According to this classification, primarily autotrophic mixotrophs can synthesise and fully regulate their own chloroplasts, whereas more heterotrophic forms must rely on chloroplasts stolen from their prey. Among this latter group, the more specialised species exploit only a limited number of prey species, but can manage and retain stolen chloroplasts for relatively long periods. In contrast, generalist mixotrophs target a much wider range of prey, but any stolen chloroplasts will degrade within a matter of hours or days (*18*).

This diversity of trophic strategies is clearly more than most biogeochemical modellers would be prepared to incorporate into their global models. Nonetheless, many of the conceptual groups identified above are associated with the ability of mixotrophs to rectify the often-imbalanced supply of essential resources in marine ecosystems (*19*). This is clearly relevant to the coupling of elemental cycles in the ocean, and it appears likely that the relative abundance of different trophic strategies can impact the biogeochemical function of marine communities (*1, 20*). For example, recent work suggests that a differential temperature sensitivity of autotrophic and heterotrophic processes can push mixotrophic species towards a more heterotrophic metabolism with increasing temperatures (*21*). An important goal is therefore to accurately quantify and account for the global-scale effects of mixotrophy on the transfer of energy and biomass through the marine food web and the export of carbon into the deep ocean. We also need to assess how these effects might be sensitive to changing environmental conditions in the past, present, and future.

These processes are not resolved in most contemporary models of the marine ecosystem, which are often based on the representation of a limited number of discrete plankton functional types (*22*). In terms of resolving mixotrophy, it is not the case that these models have overlooked the one mixotrophic group. Instead, it may be more accurate to say that the groups already included have been falsely divided between two artificially distinct categories. As such, modelling mixotrophy in marine ecosystems is not just a case of increasing complexity by adding an additional mixotrophic component. Instead, progress can be made by understanding the position, connectivity, and influence of mixotrophic and non-mixotrophic organisms within the food web as an emergent property of their environment, ecology, and known eco-physiological traits. This is not a simple task, but progress might be made by identifying the fundamental traits that underpin the observed diversity of functional groups. To this end, a recurring theme in mixotroph ecology is that plankton exist on a spectrum between strict autotrophy and strict heterotrophy (*14, 23, 24*). Competition along this spectrum is typically framed in terms of the costs and benefits of different modes of nutrition. Accurate quantification of these costs and benefits should allow for a much clearer understanding of the trade-offs between different mixotrophic strategies (*25*), and how they are selected in different environments. In the future, a combination of culture experiments, targeted field studies, and mathematical models should help to achieve this goal, such that this important ecological mechanism can be reliably and parsimoniously incorporated into global models of marine ecosystem function.

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Nutrient distributions reveal the fate of sinking organic particles in the ocean

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The ocean's "biological pump" regulates the atmosphere-ocean partitioning of carbon dioxide (CO_2), and has likely contributed to significant climatic changes over Earth's history (*1*, *2*). It comprises two processes, separated vertically in the water column: (i) production of organic carbon and export from the surface euphotic zone (0-100m), mostly as sinking particles; and (ii) microbial remineralization of organic carbon to CO_2 in deeper waters, where it cannot exchange with the atmosphere. The depth of particulate organic carbon (POC) remineralization controls the longevity of carbon storage in the ocean (*3*), and strongly influences the atmospheric CO_2 concentration (*4*). CO_2 released in the mesopelagic zone (100-1000m) is returned to the atmosphere on annual to decadal timescales, whereas POC remineralization in the deep ocean (>1000m) sequesters carbon for centuries or longer (*5*). A common metric for the efficiency of the biological pump is thus the fraction of sinking POC that reaches the deep ocean before remineralization (*6*), referred to as the particle transfer efficiency, or T_{eff}.

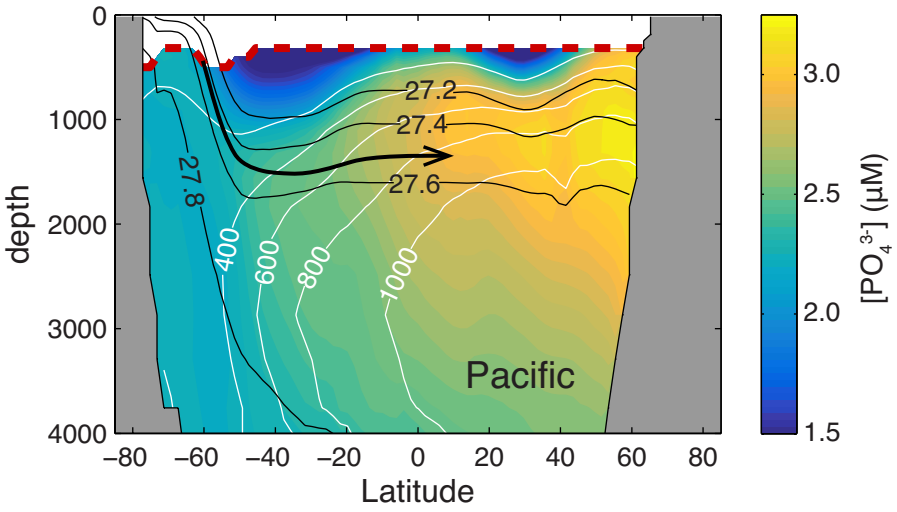

Figure 1. Zonal-mean section of $[PO_4^{3-}]$ in the Pacific Ocean. Particle remineralization is diagnosed from the accumulation rate of PO_4^{3-} over time, following water masses (black arrow) as they spread along isopycnals (black contours) in an ocean circulation model. White contours represent the transport time (in years) since passing the upper boundary at 300m or the base of the wintertime mixed layer, whichever is deeper (red dashed line). Conceptually, the remineralization rate is given by the ratio of $[PO_4^{3-}]$ to the transport time gradients along an isopycnal.

Currently, the factors that govern particle remineralization depth are poorly understood and crudely represented in climate models, compared to the lavish treatment of POC production by autotrophic communities in the surface (*7*). This compromises our ability to predict the biological pump's response to anthropogenic warming, and its potential feedback on atmospheric CO_2 (*8*). Over the last decade, a number of studies have identified a promising path towards closing this gap. If systematic spatial variations in T_{eff} can be identified throughout the modern ocean, we might discern their underlying environmental or ecological causes (*9*, *10*). However, direct observations from sediment traps are too sparse to constrain time-mean particle fluxes through the mesopelagic zone at the global scale, and no consensus pattern of T_{eff} has emerged from these analyses.

Particle flux reconstruction

Instead of relying on sparse particle flux observations, a recent study took an alternative approach, leveraging the geochemical signatures that are left behind when particles remineralize (*11*). Products of remineralization include inorganic nutrients like phosphate (PO_4^{3-}), whose global distributions are well characterized by hundreds of thousands of shipboard observations (*12*).

In shallow subsurface waters, nutrient accumulation reflects the remineralization of both organic particles and dissolved organic matter, which is advected and entrained from the euphotic zone. Dissolved organic phosphorous (DOP) decomposes rapidly, and is almost completely absent by depths of ~300m in the stratified low latitude ocean (*13*), and below the wintertime mixed layer in high latitudes (*14*). Deeper in the water column, particulate organic phosphorous (POP) remineralization is the only process that generates PO_4^{3-} within water masses as they flow along isopycnal surfaces (Fig. 1). Rates of POP remineralization can therefore be diagnosed from the accumulation rate of PO_4^{3-} along transport pathways in an ocean circulation model. This calculation requires a very faithful representation of the large-scale circulation,

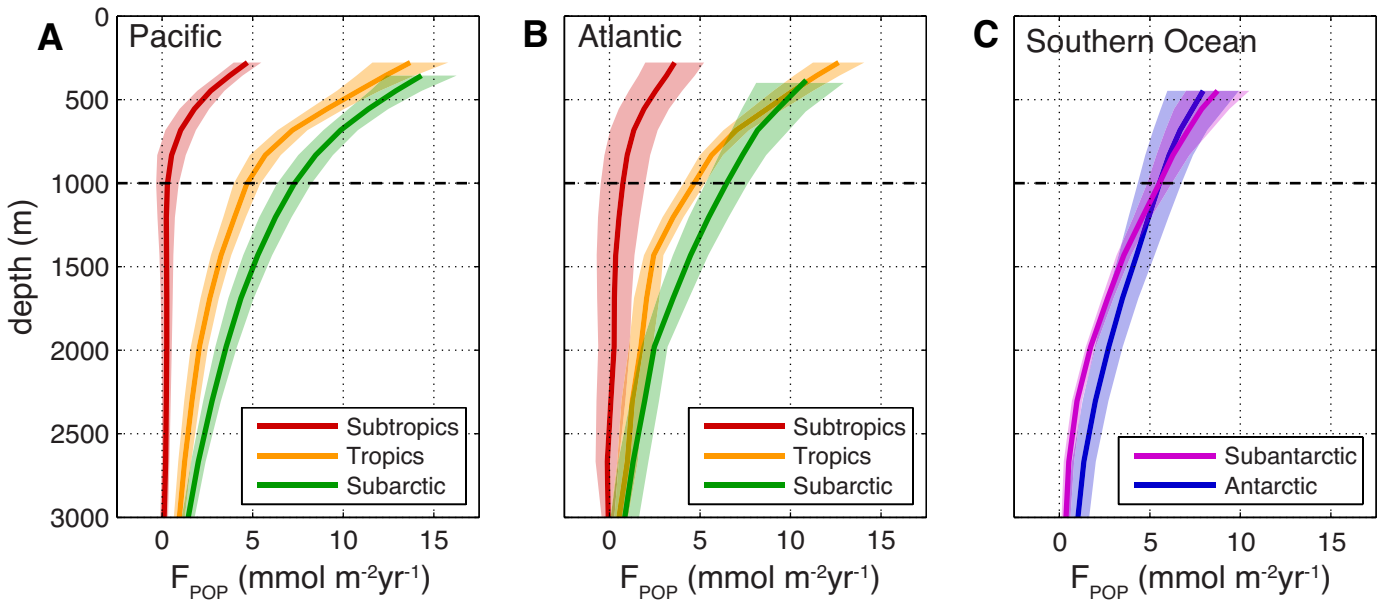

Figure 2. Reconstructed profiles of F_{POP} in the (*A*) Pacific, (*B*) Atlantic and (*C*) Southern Oceans. Shaded envelopes represent uncertainty in regional mean fluxes (1 S.D.), quantified using a Monte Carlo method to sample the uncertainty in observed [PO_4^{3-}] and model circulation.

as provided by the Ocean Circulation Inverse Model (OCIM), whose flow fields are optimized to match observed water mass tracer distributions (*15*).

Assuming that organic matter burial in sediments is negligible, the integrated POP remineralization beneath a given depth horizon is equal to the flux of POP (F_{POP}) through that horizon, allowing complete reconstruction of flux profiles from ~300m to the deep ocean. Averaging these fluxes over large ocean regions serves to extract the large-scale signal from small-scale noise (Fig. 2). Regional-mean F_{POP} profiles show striking differences in shape and magnitude between subarctic, tropical, and subtropical regions, which are remarkably consistent between the Pacific and Atlantic Oceans (Fig 2a,b). F_{POP} near 300m is similar in subarctic and tropical zones, but attenuates faster through the mesopelagic in the tropics, reaching values of ~5mmol $m^{-2}\,yr^{-1}$ at 1000m, compared to ~7mmol $m^{-2}\,yr^{-1}$ in subarctic oceans. Subtropical F_{POP} attenuates even faster, and is indistinguishable from zero throughout most of the water column. In the Southern Ocean, F_{POP} is ~5mmol $m^{-2}\,yr^{-1}$ at 1000m in both the Antarctic and subantarctic regions, but the subantarctic flux profile attenuates slightly faster (Fig. 2c).

Patterns of transfer efficiency and underlying mechanisms

While these reconstructions place a robust constraint on POP fluxes to the deep ocean, they do not constrain rates of POP export at the base of the euphotic zone (z_{eu}) that are needed to estimate the particle transfer efficiency (T_{eff}). Remote sensing approaches are widely used to estimate large-scale organic carbon export, which can be converted to POP using an empirical relationship for particulate P:C ratios (*16*). However, multiple algorithms have been proposed to estimate net primary production and convert it to export, yielding widely different regional-mean rates (*11*). One way to pare down this variability is to weight each algorithm based on its ability to reproduce tracer-based export estimates in each ocean region (*17*, *18*). This yields an "ensemble" estimate for the areal-mean POP export rate in each region, and an uncertainty range that reflects both observational error and the variability between satellite algorithms (Fig. 3a).

Combining the ensemble estimates of POP export with reconstructed F_{POP} at 1000m reveals a systematic pattern of transfer efficiency from z_{eu} to the deep ocean (Fig. 3a). The subtropics exhibit the lowest T_{eff} of ~5%, significantly lower than expected from the canonical Martin Curve relationship (*19*), which is often considered to represent an "average" particle flux profile. In the tropics and the subantarctic zone of the Southern Ocean, T_{eff} clusters close to the Martin Curve prediction of ~15%. The subarctic and Antarctic regions (i.e. high latitudes) are the most efficient at delivering the surface export flux to depth with T_{eff}>25%, although these values are also associated with the largest uncertainty (Fig. 3a).

What controls the strong latitudinal variation of transfer efficiency? Particle flux attenuation is determined by the sinking speed and bacterial decomposition

rate of particles: fast sinking and slow decomposition both result in greater delivery of organic matter to the deep ocean. Decomposition rates increase as a function of temperature in laboratory incubation studies (*20*), controlled by the temperature-dependence of bacterial metabolism. In a recent compilation of Neutrally Buoyant Sediment Trap (NBST) observations, particle flux attenuation was strongly correlated with upper ocean temperature between 100-500m (*21*), consistent with this effect. An almost identical temperature relationship explains ~80% of the variance in reconstructed regional T_{eff} estimates (Fig. 3b).

An equally compelling argument can be made for particle sinking speeds controlling the pattern of T_{eff}. According to the current paradigm of marine food webs (*22*), communities dominated by small phytoplankton export small particles that sink slowly, relative to the large aggregates and fecal pellets produced when large plankton dominate. The fraction of photosynthetic biomass contributed by tiny picoplankton (F_{pico}) varies from <30% in subarctic regions to >55% in oligotrophic subtropical regions (*23*), and explains ~86% of the variance in reconstructed T_{eff} (Fig. 3c). F_{pico} also predicts flux attenuation in NBST profiles as skillfully as upper-ocean temperature (R^2 = 0.81 and 0.82 respectively), but was not considered previously (*21*). Due to the spatial covariation of these factors in the ocean, statistical analysis alone is insufficient to determine the relative contributions of temperature and particle size to latitudinal variations in transfer efficiency.

Conclusions and future directions

Reconstructing deep-ocean particle fluxes has left us with a clearer understanding of the biological pump in the contemporary ocean and its climate sensitivity. Deep remineralization in high latitude regions results in efficient long-term carbon storage, whereas carbon exported in subtropical regions is recirculated to the atmosphere on short timescales (*11*). Atmospheric CO_2 is likely more sensitive to increased high latitude nutrient utilization during glacial periods than previously recognized, whereas the expansion of subtropical gyres in a warming climate might result in a less efficient biological pump.

One caveat is that the new results highlighted here constrain POP transfer efficiency, not POC, and the two might be decoupled by preferential decomposition of one element relative to the other. The close agreement of these results with Neutrally Buoyant Sediment Trap observations (which measure POC) is encouraging, and suggests that the reconstructed pattern of T_{eff} is applicable to carbon. More widespread deployment of NBSTs, which circumvent the sampling biases of older sediment trap systems (*24*), would help confirm or refute this conclusion. A second limitation is that the wide degree of uncertainty in high latitude export rates (Fig. 3a) obscures estimates of T_{eff} in these regions. New tracer-based methods to integrate export across the seasonal cycle (*25*) will hopefully close this gap and enable more careful groundtruthing of satellite predictions.

Two plausible mechanisms –particle size and temperature – have been identified to explain large latitudinal

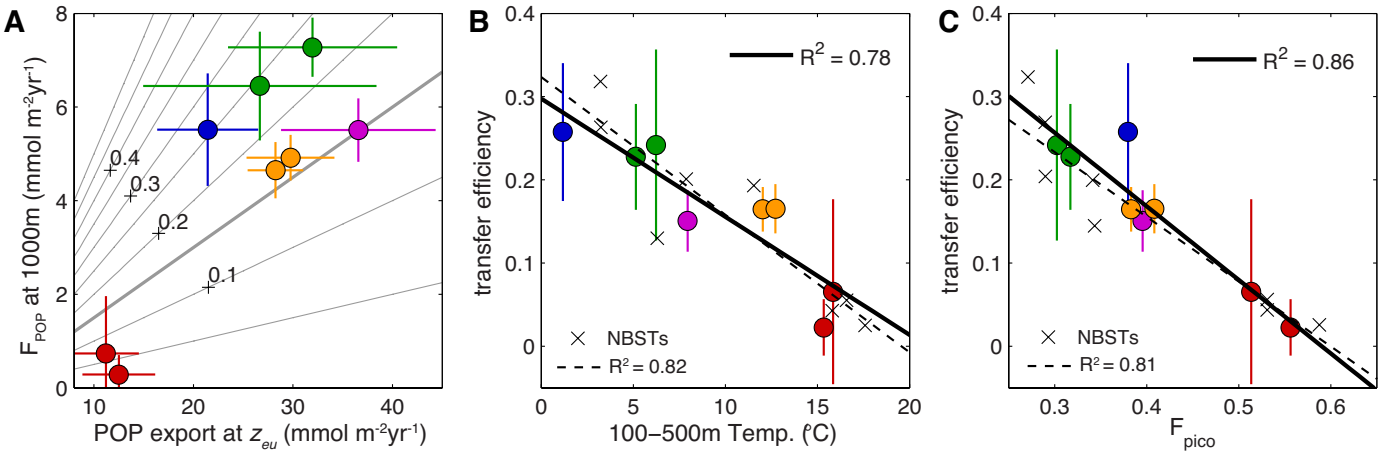

Figure 3. **A**. POP export versus flux at 1000m for each region, color-coded as in Fig. 2. Light grey contours show the fraction of the export flux that reaches 1000m, i.e. the transfer efficiency; thick contour represents the prediction of the Martin Curve relationship, assuming z_{eu}=100m. **B**. Relationship between average 100-500m temperature and transfer efficiency for the regional reconstructions (colored dots and solid line), and from Neutrally Buoyant Sediment Trap (NBST) flux profiles (crosses and dashed line). **C**. Same as **B**, but correlating transfer efficiency against abundance of picoplankton (F_{pico}).

variations in transfer efficiency, and new observational systems hold the potential to disentangle their effects. Underwater Visual Profilers (UVP) can now accurately resolve the size distribution of particles in mesopelagic waters (*26*). Although UVPs provide only instantaneous snapshots (quite literally) of the particle spectrum rather than time-mean properties, large compilations of these data will help establish the spatial pattern of particle size and its relationship to microbial community structure. In parallel, ongoing development of the RESPIRE particle incubator will allow for in-situ measurement of POC respiration (*27*), and better establish its temperature sensitivity.

Over the next few years, the upcoming EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) campaign stands to revolutionize our understanding of the fate of organic carbon (28). These insights will allow for a more balanced treatment of the "dark side" of the biological pump in global climate models, compared to euphotic zone processes, improving our predictions of biological carbon sequestration in a warming ocean.

Acknowledgments

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Upcoming OCB Events

2016	
December 1	OCB Activity Proposals due December 1, 2016
2017	
June 26-29	2017 OCB Summer Workshop: June 26-29, 2017 (Woods Hole, MA) – registration will open in Spring 2017

New Addition to the OCB Project Office

The Ocean Carbon & Biogeochemistry (OCB) Project Office welcomes **new OCB Communications Officer Mairead (Mai) Maheigan**. She started her position with OCB on 11/7/16. Mai has research experience in coral ecology, marine biology, and wildlife conservation. She has held leadership positions in the field of communication for several organizations, including the Farallones Marine Sanctuary Association and more recently, the Coral Reef Alliance. She brings a wealth of experience and expertise in strategic communications and science writing and will be an excellent addition to the OCB team.

Welcome new OCB Ocean Time-series Committee members:

OCB welcomes new OTC members **Matt Church** (Univ. Montana), **Stephanie Henson** (National Oceanography Centre), **Naomi Levine** (Univ. Southern California), **David "Roo" Nicholson** (Woods Hole Oceanographic Inst.), **Oscar Schofield** (Rutgers Univ.), **Heidi Sosik** (Woods Hole Oceanographic Inst.), and **Angel White** (Oregon State Univ.). OTC members Richard Lampitt (National Oceanography Centre) and Michael DeGrandpre (Univ. Montana) will serve a second term. We thank outgoing OTC members Susanne Neuer (Arizona State Univ., chair), Craig Carlson (Univ. California, Santa Barbara, former chair), John Dunne (NOAA/GFDL), Mary Jane Perry (Univ. Maine), Paul Quay (Univ. Washington), and Ricardo Letelier (Oregon State Univ.) for their service.

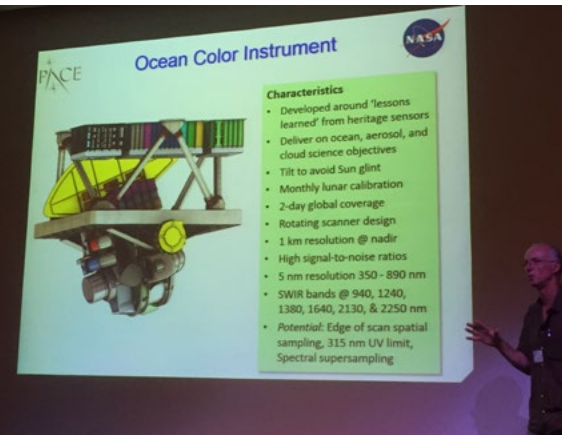
In other news, OTC members and time-series scientists recently published an e-Letter in *Science* in response to a recent *Science* paper by Hunter-Cevera *et al.* on the Martha's Vineyard Coastal Observatory.

Meeting Reports

A Report from the 2016 OCB Summer Workshop July 25-28, 2016 (Woods Hole, MA)

The 11th annual Ocean Carbon & Biogeochemistry summer workshop, sponsored by NSF and NASA, convened 186 participants from July 25-28, 2016 at the Woods Hole Oceanographic Institution in Woods Hole, MA. This year's summer workshop featured the following six plenary sessions:

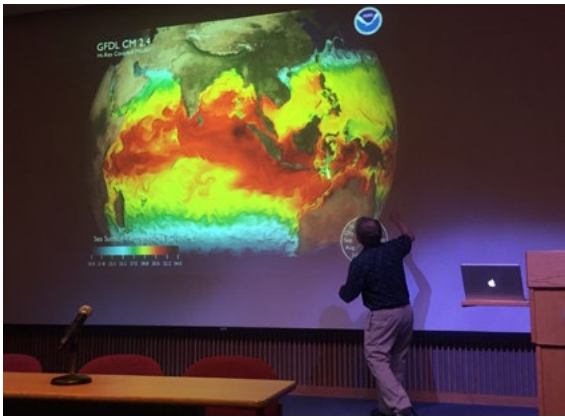
Plenary 1. EXport Processes in the Ocean from RemoTe Sensing (EXPORTS)
Plenary 2. The biology of carbon export – New processes and approaches
Plenary 3. Recent advances in quantifying ocean carbon uptake
Plenary 4. Quantifying ocean carbon, oxygen, and nutrient cycles
Plenary 5. The Indian Ocean – Monsoon-driven biogeochemical processes
Plenary 6. Marine ecosystem thresholds and regime shifts



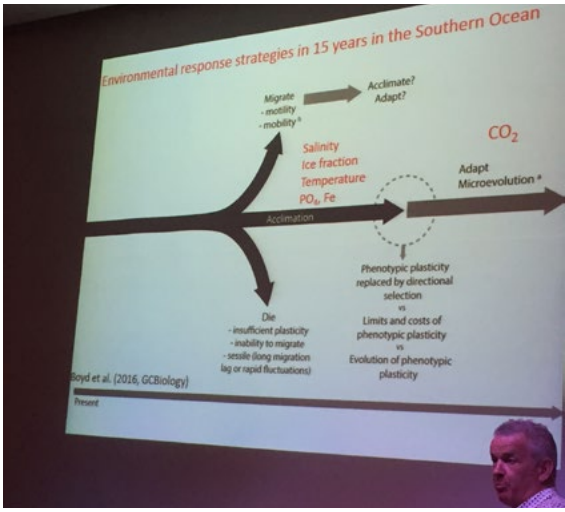
Day 1 kicked off with a presentation on the projected instrumentation and scientific capabilities of the NASA Plankton, Aerosol, Cloud, and ocean Ecosystems (PACE) Mission, which segued into the first plenary session on the proposed NASA EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) field campaign. Speakers in this session provided an overview of both the EXPORTS Science Plan and the Implementation Plan. The session also featured three scientific overview talks on the EXPORTS science questions, the first of which highlighted the influence of ecosystem characteristics such as plankton community structure on organic matter export from the euphotic zone. The second talk focused on key processes in the mesopelagic zone that affect vertical transfer of organic matter to depth. The third talk focused on how data generated by EXPORTS will reduce uncertainties in current and future estimates of export, including an overview of current modeling capabilities for different export pathways. The second plenary session of Day 1 was convened by organizers of a recent NSF workshop and white paper on novel biological processes and pathways regulating organic matter export and degradation. Speakers in this session explored potential contributions of mixotrophs, marine microgels, and episodic events (e.g., jelly falls) to biological pump function, and provided an overview of our current observational capacity to quantify carbon export and monitor changes in the biological pump over a range of temporal and spatial scales. The plenary session closed with a community-sharing presentation describing the Carbon Flux Explorer, an autonomous float that can quantify and photograph particulate carbon fluxes. After the plenary sessions, graduate students provided short presentations about their research interests and then all participants convened for a welcome reception and poster session.

Day 2 opened with agency updates from NSF, NASA, and NOAA representatives. Speakers in plenary session 3 then described data- and model-based approaches for studying internal variability (interannual to decadal) and anthropogenic change in ocean carbon uptake, and explored the role of physical processes (e.g., subduction, mesoscale and submesoscale processes, etc.) in modulating ocean carbon uptake. A presentation on the Coupled Model Intercomparison Project (CMIP) provided an overview of CMIP5 simulations of the ocean carbon cycle and how well these simulations reproduce anthropogenic CO_2 uptake and natural variability in ocean CO_2 associated with the biological pump. To provide a broader range of spatial and temporal perspectives, the session included talks on land-ocean exchanges of dissolved carbon across coastal, estuarine, wetland, and riverine systems and differences in ocean carbon storage during the last ice age, as constrained by paleo-proxies of ocean ventilation and deep-sea oxygen concentrations. This session concluded with a community-sharing presentation on *Carbon Hot Spot*, a nascent process study to characterize biophysical interactions and quantify ocean carbon uptake in Western Boundary Current regions such as the Kuroshio Extension. During the afternoon of day 2, speakers in plenary session 4 provided an overview of the Southern Ocean Carbon and Climate Observations and Modeling (SOCCOM) project and newly emerging seasonally resolved ocean carbon data sets from biogeochemical sensor-equipped Argo floats, which are providing unprecedented constraints on wintertime air-sea CO_2 dynamics in the Southern Ocean. The session concluded with a presentation on the rationale and plan for a global biogeochemical observing network based on Argo floats equipped with biogeochemical sensors to more effectively monitor changing ocean conditions. Immediately following the plenary session, communication professionals from COMPASS led interactive communication training workshops to help participants share their science across a broad range of audiences using various tools, outlets, and communication strategies. Participants reconvened in the evening hours for the inaugural OCB ocean film festival, featuring recent documentaries on the Palmer LTER in Antarctica and the CARIACO time-series.

After a morning poster session on day 3, participants enjoyed a presentation and Q&A session on the 2015 UN Climate Conference in Paris. Then speakers in plenary session 5 delivered a series of talks on the complex physical oceanographic and climatic drivers that influence biogeochemistry and biological processes in the Indian Ocean, where scientists are amidst planning for the second International Indian Ocean Expedition (IIOE2). The session opened with an overview presentation on key physical oceanographic features and observing resources in the Indian Ocean. Speakers then addressed links between physics, climate, and biogeochemical processes such as dissolved organic carbon (DOC) distribution and dynamics, iron limitation, trace metal cycling and measurements from GEOTRACES, nitrogen fixation, and oxygen



deficiency in different parts of the basin and associated effects on biology. The final presentation of the session focused on seasonally variable Indian Ocean boundary currents and their impacts on local ecology and biogeochemistry. Day 3 wrapped up with a presentation by the new US SOLAS (Surface Ocean Lower Atmosphere Study) representative to initiate discussion and brainstorm ideas to facilitate scientific exchanges and new collaborations on topical areas of interest to both OCB and SOLAS.



The final day of the workshop opened with a presentation on the proposed NASA field campaign Arctic-COLORS. The Arctic-COLORS science plan is undergoing revisions, so authors were seeking input from the OCB community. The final plenary session of the workshop, plenary 6, featured a series of talks on marine ecosystem thresholds and regime shifts. In this session, speakers explored phytoplankton response to natural climate variability and anthropogenic climate change (phenology, biogeography, community composition, etc.), implications of climate-driven changes in bloom phenology for higher trophic levels, ecological changes and associated shifts in benthic communities of the Pacific Arctic, and the development of tools such as early warning systems to identify and predict nonlinear shifts in ocean ecosystems. A separate 1.5-day meeting on Arctic-COLORS immediately following the OCB workshop provided an opportunity for more in-depth discussions and opportunities to gather feedback.

For more information, including links to plenary talks and webcast footage, please visit the workshop website or contact Heather Benway.

OCB Ocean Carbon & Biogeochemistry

GEOTRACES

Biogeochemical Cycling of Trace Elements Within the Ocean: A Synthesis Workshop

Over 100 scientists from 12 nations met at the Lamont-Doherty Earth Observatory in Palisades New York, USA, on 1 – 4 August 2016 for a synthesis workshop on the Biogeochemical Cycling of Trace Elements within the Ocean. The workshop focused on setting priorities for utilizing GEOTRACES trace element and isotope (TEI) data sets to advance scientific objectives at the interface of marine biogeochemistry and ecology, and was jointly sponsored by the GEOTRACES and OCB Programs. Workshop activities were organized around three scientific themes:

1. Biological uptake and trace element bioavailability,
2. Abiotic cycling and scavenging, including particulate and dissolved speciation, and
3. Export, recycling and regeneration

Following a series of plenary talks designed to stimulate discussion on these topics, participants spent the remainder of the workshop in smaller group discussions to identify knowledge gaps and develop ideas for synthesis activities and products that combine GEOTRACES TEI data with other biogeochemical and biological data sets. Tentative activities and products include:

- estimating bioavailability of iron (Fe)
- testing hypothesis for Fe and light co-limitation in the deep chlorophyll maxima;
- exploring Redfieldian concepts using GEOTRACES data and ocean models;
- calculating community trace metal demand vs. supply;
- developing a synthesis paper on existing methods and current state of knowledge on ligand composition and cycling;
- comparing radionuclide-based tracer methods for estimating downward flux of carbon, nutrients and trace metals;
- combining TEI distributions with AOU and preformed TEI concentrations to differentiate biotic (e.g., respiration) and abiotic (e.g., scavenging, physical transport) removal processes;
- estimating elemental scavenging using partition coefficients (K_d);
- combining particulate TEI and beam transmission data to develop algorithms for particle distributions that affect TEI scavenging; and
- developing synthesis paper on TEIs in nepheloid layers.

To learn more about and/or contribute to these activities, please contact Heather Benway (OCB) or Bob Anderson (LDEO). For more information, visit the workshop website or view the plenary presentations.

Community Announcements

Recent News

- NASA seeking panelists and external reviewers for ROSES 2016 A.28 Interdisciplinary Research in Earth Science (IDS) Program
- 2017 International Ocean Colour Science meeting - Call for Breakout Workshops
- Join the 2nd International Indian Ocean Expedition (IIOE-2) email list
- New Intergovernmental Oceanographic Commission (IOC) UNESCO working group Global Ocean Oxygen Network (GO2NE)
- Updated NSF Policies & Procedures Guide

Outreach and Policy

- New children's book about the 2015 US GEOTRACES expedition to the North Pole
- Follow UN Climate Change Conference 2016 (COP22) (Twitter: @COP22)
- Ocean Carbon and Biogeochemistry Program (2015). Temporal and Spatial Perspectives on the Fate of Anthropogenic Carbon: A Carbon Cycle Slide Deck for Broad Audiences with explanatory notes. Contributors: S. Khatiwala, T. DeVries, J. Cook, G. McKinley, C. Carlson, H. Benway. doi:10.1575/1912/7670

Publications and Scientific Planning

- Global Ocean Observing System seeks experts for advisory panel - Nominations due December 15
- Call for Nominations: Review of SOCCR-2
- Call for authors and technical inputs for the Fourth National Climate Assessment
- Public Input Period Now Open for the Next 10-year Federal Ocean Research Plan
- Seeking lead authors and review editors for first special report of IPCC 6th Assessment Report by December 6
- Final white paper *Towards a transformative understanding of the biology of the ocean's biological pump: Priorities for future research* now available
- EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) Implementation Plan finalized
- Final report on *The Rationale, Design and Implementation Plan for Biogeochemical-Argo*
- OCB time-series scientists publish e-Letter in *Science* on The Importance of Monitoring Earth's Largest Ecosystem
- News from partner programs:
  - NACP Fall Newsletter
  - SCOR Newsletter #33
  - IOCCP Conveyor #36
  - Fixed point Open Ocean Observatory network (FixO3) Newsletter
  - US CLIVAR October newsgram

Scientific Data Products and Activities

- Surface Ocean CO_2 Atlas (SOCAT) v4 release
- A multi-decade record of high-quality *f*CO2 data in version 3 of the Surface Ocean CO2 Atlas (SOCAT)
- Submit your data for the next GEOTRACES Intermediate Data Product, IDP2017 by December 1
- Report from the IOCCP-JAMSTEC 2015 Inter-comparison of inorganic nutrients CRMs measurements
- SenseOCEAN project
- Global Carbon Budget 2016
- Biogeochemical Argo website

Important Ocean Acidification Links

- NOAA Ocean Acidification Program
- Interagency Working Group on Ocean Acidification (IWG-OA)
- Ocean Acidification International Coordination Centre (OA-ICC) news stream
- NOAA Ocean Acidification Data Stewardship Project (OADS)

Ocean acidification communication and outreach resources

- Ocean Acidification - Changing Waters On The Oregon Coast
- The Calcification Challenge: Experience Ocean Acidification from a Coral Reef's Point of View
- OCB Ocean Acidification FAQs
- 20 Facts about Ocean Acidification
- OCB Ocean Acidification lab/outreach kit
- C-MORE Ocean Acidification Teacher's Kit
- Understanding Ocean Acidification Portal (NOAA's Channel Islands National Marine Sanctuary)

ASLO e-lecture series on ocean acidification:

The OCB Project Office has assisted with a topical series of ASLO e-Lectures on ocean acidification:

- Baumann, H. 2016. Combined effects of ocean acidification, warming, and hypoxia on marine organisms. *Limnology and Oceanography* e-Lectures 6:1-43.
- Feely, Richard A. and Doney, Scott. 2011. Ocean Acidification: The Other CO2 Problem. ASLO Web Lectures, doi: 10.4319/lol.2011.rfeely_sdoney.5.
- Jiang, Li-Qing, Arzayus, Krisa M., Gattuso, Jean-Pierre, Garcia, Hernam E., Chandler, Cynthia, Kozyr, Alex, Yang, Yan, Thomas, Rob, Beck, Brian and Spears, Tobias. 2016. How to Document - Ocean Acidification Data. Limnology and Oceanography e-Lectures, doi: 10.1002/loe2.10004.
- Paytan, Adina and Hönisch, Bärbel. 2016. Ocean Acidification - A Paleo Perspective. Limnology and Oceanography e-Lectures, doi: 10.1002/loe2.10003

Other Ocean Acidification News

- Ocean Acidification International Coordination Centre (OA-ICC) data compilation on the biological response to ocean acidification
- New ocean acidification pilot project in Africa: *OceAn pH Research Integration and Collaboration in Africa – ApHRICA*
- OA-ICC Training Course on Ocean Acidification (September 5-10, 2016, Ensenada, Mexico)

Inter-laboratory Comparison of Seawater CO_2 Measurements

A second inter-laboratory comparison of seawater CO_2 measurements is planned for the second quarter of 2017. We encourage all laboratories to participate, whether they participated in 2013 or not. Anonymity of laboratory results is assured. The costs for participation are expected to be about US $400. Please contact ebockmon@ucsd.edu to express interest so we can plan appropriately.

The test samples will be prepared in Andrew Dickson's laboratory at the Scripps Institution of Oceanography and will comprise four 500 mL bottles of two different seawaters (each in duplicate). Alkalinity and total carbon of these seawaters will be modified from natural seawater so as to create suitable test samples. The samples will also be analyzed at Scripps to provide reference values for the comparison. Please see doi:10.1016/j.marchem.2015.02.002 for results from the 2013 inter-laboratory comparison.

Education

IMBER ClimECO5: *Towards more resilient oceans: Predicting and projecting future changes in the ocean and their impacts on human societies*

OCB-sponsored participants of IMBER ClimECO5 from left to right: Paul Suprenand (Mote Marine Laboratory), Arnault Le Bris (Gulf of Maine Research Inst.), Jonathan Reum (Univ. Washington), Ellen Willis-Norton (Univ. Calif., Santa Cruz), Mark Morales (Univ. Calif., Santa Cruz), Tayler Clarke (Univ. Washington), Danny Kaufman (Virginia Inst. Marine Science), and Kathy Mills (Gulf of Maine Research Inst.).

Tayler Clarke completed her MSc at the University of Costa Rica in 2013. Her master's thesis focused on the spatial distribution and reproduction of shark and ray bycatch in shrimp trawl fisheries. Currently, she is a second year PhD student in William Cheung's lab at the Institute for the Oceans and Fisheries, University of British Columbia. Tayler continues to study shrimp trawl fisheries in her dissertation, this time focusing on climate change impacts. She hopes to work with Costa Rican universities and the national fishery management institute to integrate her PhD thesis into current fisheries management initiatives.

"I loved participating in the IMBER summer school because it gave me the opportunity to interact with so many motivated graduate students and early career researchers. The classes and workshops exposed us to interesting new tools and ideas. The best part was being able to collaborate on a research project with the instructors' guidance. Lisa and the instructors created a very positive, exciting environment that stimulated learning and collaborations. I am very grateful for the opportunity to have participated in IMBER summer school 2016!"

Daniel Kaufman is a PhD student in marine science at the Virginia Institute of Marine Science, College of William and Mary. He received his BS in physics from the University of Maryland, College Park. His current research examines phytoplankton dynamics and climate-induced impacts in the Ross Sea, Antarctica, using gliders and biogeochemical modeling. He also contributes to an investigation of effects of an-

thropogenic watershed use on the Chesapeake Bay using the Regional Ocean Modeling System.

"The atmosphere in the course was both really positive and energizing throughout. The highlight for me was meeting, exchanging ideas, and having fun with participants from such a wide variety of academic and personal backgrounds. The practical exercises and group project gave me a chance to gain valuable practice with new modeling approaches under the supervision of topic experts. Lectures during ClimEco5 introduced me to new ideas and expanded on ideas with which I had previously only passing familiarity, and this all made it a wonderful learning experience over a broad range of topics."

Arnault Le Bris was a postdoctoral research associate at the Gulf of Maine Research Institute (GMRI) when he attended the ClimEco5 summer school. Since then, Arnault has started a new research scientist position at the Centre for Fisheries Ecosystems Research at The Marine Institute of Memorial University of Newfoundland, Canada. During his postdoctoral research at GMRI, Arnault worked on understanding and forecasting the impacts of climate change and fishing on New England lobster fisheries. In his research, Arnault has paid special attention to the mechanisms underlying the responses in lobster life history traits to climate change.

"The ClimEco5 summer school delivered a unique interdisciplinary approach to address the issues that oceans, and the human societies depending on oceans, are facing. I was impressed by the diversity and quality of the lectures, which married perfectly with the diversity of the participants. I especially appreciated that all lecturers stayed the entire course, which allowed for deeper interactions between participants and lecturers, and contributed to numerous fun movements that we shared..."

Kathy Mills is an associate research scientist at the Gulf of Maine Research Institute in Portland, Maine. She is a quantitative fisheries ecologist, and her work focuses on understanding how environmental variability and climate change affect fish populations, fisheries, and fishing communities. Her recent work focuses on climate vulnerability assessment and adaptation approaches in marine fisheries.

"IMBER's ClimECO5 summer school was a great opportunity to gain an overview of tools and approaches that can be used to understand the ecological, social, and coupled social-ecological impacts of climate change on marine ecosystems. It was exciting to dig into these topics with lecturers who are international leaders in this field. It was also invigorating to meet so many students and early career scientists from across the world who are working on similar questions using a wide range of interesting approaches."

Mark Morales received his BS in Environmental Systems: Ecology, Behavior and Evolution at University of California San Diego. During his BS, Mark was involved with various research groups at the Scripps Institution of Oceanography where he studied coastal biological oceanography, Antarctic ecology and fisheries science. As a recipient of the NSF GRFP, Mark is now a 2nd year PhD student in Ecology and Evolutionary Biology at the University of California Santa Cruz. For his PhD, Mark is interested in teasing apart the relationships between interannual environmental variability and recruitment success of central California rockfish species. Mark is using state-of-the-art statistical and mathematical frameworks such as species distribution models, ocean circulation models, nutrient-phytoplankton-zooplankton models and individual-based movement and bioenergetics models to address his questions.

"The level of participant and instructor engagement during IMBER ClimEco5 exceeded my expectations. The amount of scientific and cultural diversity housed within the summer school was the most fascinating part to me. I have acquired many new collaborators, and more importantly friendships that will last throughout my career and beyond. The quality of instruction was terrific and I went home armed with many new tools under my belt that will surely allow me to tackle some of the most pressing questions in marine science. IMBER ClimEco5 is hands down the best event that I have attended as an early career scientist. Without the kind financial support from OCB, none of this would have been possible."

Ellen Willis-Norton is a PhD student in Ecology and Evolutionary Biology at the University of California, Santa Cruz. Her research seeks to understand how the California Current Ecosystem will respond to climate change. She is currently

working with colleagues at NOAA to publish a climate vulnerability assessment for 65 commercially important west coast fisheries. The assessment will be used as a starting point for her research examining how west coast fish species' habitat will shift with climate change and whether certain management tools can increase their resilience to a changing climate.

"The ClimEco5 summer school was truly an interdisciplinary experience led by renowned lecturers. The in-depth lectures allowed me to develop my species distribution modeling skills and experiment with new model approaches. Additionally, I learned about qualitative and agent-based modeling tools that I had never been exposed to before. The summer school also provided invaluable networking opportunities; I now am collaborating with PhD students and Post-Docs from around the world. I hope to maintain the relationships I made at the summer school throughout my career!"

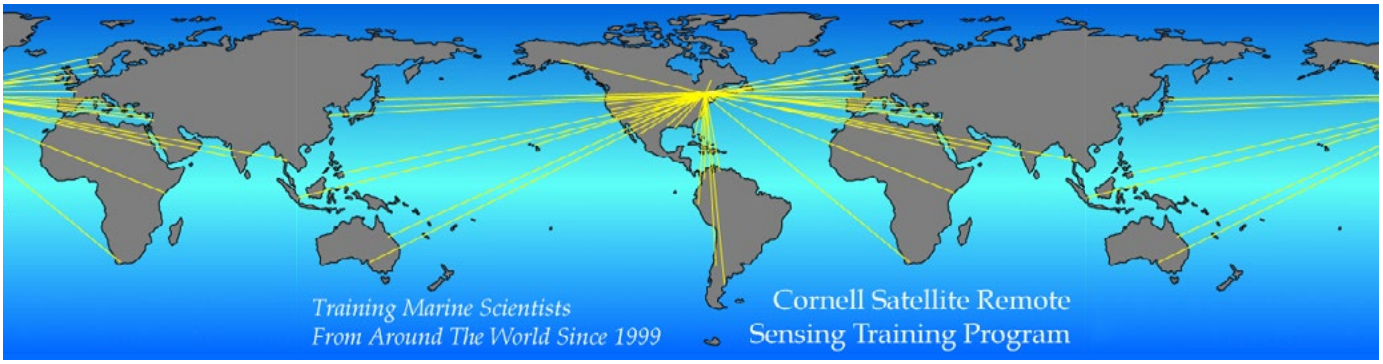
Third IOCCG Summer Lecture Series 2016
Frontiers in Ocean Optics and Ocean Colour Science
July 18-30, 2016 (Villefranche-sur-Mer, France)

Mike Sayers is a 2nd year PhD student at Michigan Tech University and a research scientist at the Michigan Tech Research Institute (MTRI), where his research has been focused on the use of bio-optical remote sensing methods to assess water quality changes in the Laurentian Great Lakes. Prior to his position at Michigan Tech, he received his BS and MS in remote sensing from Central Michigan University. His current interest is in the development and application of airborne and satellite hyperspectral inversion models for assessing primary production dynamics, harmful algal bloom occurrences, and benthic cover change.

"The 2016 IOCCG Summer Lecture Series in Villefranche-sur-Mer, France was a truly fantastic experience and incredibly valuable for my career in research. Some of the most distinguished researchers in the field delivered lectures that covered the entire range from fundamentals to state-of-the-art, leading-edge research, and went the extra distance to make sure we understood the concepts. I have already been able to apply some of the things I learned during the class to my research, which has given me fresh perspective moving forward. It was a pleasure to have been able to spend two weeks with my group of classmates; they are all wonderful people with diverse backgrounds and skills, and made the time very enlightening and enjoyable. I highly recommend this course to anyone studying ocean optics and ocean color remote sensing."

Zhehai Shang earned his BS from the College of Chemistry at Beijing Normal University and is currently a graduate student at the University of Massachusetts Boston's School for the Environment, working with Dr. Zhongping Lee. Zhehai's research is focused on simulating light distribution in water under different environmental conditions.

"*The IOCCG summer lecture series provided a great opportunity to meet other scientists working in my field. Through my interactions with other participants, I learned a lot in my own area of research, as well as other related fields. The course included a series of lectures on fundamental theory and more specialized topics, as well as hands-on laboratory work. The lectures on basic theory were challenging, but when combined with lab experiences, the instructors were able to effectively convey important concepts. The topical lectures provided an opportunity to learn about interesting research findings and approaches, which will continue to inspire my research in the future. I am grateful to have had this opportunity and I thank all of the organizers, teachers, sponsors, and others who made this course possible.*"



OCB-sponsored participants of the Cornell Satellite Remote Sensing Course

Emily Bockmon studies carbonate chemistry in the ocean, focusing on best practices for measurement and calibration of instrumentation. In 2014, she completed her PhD at Scripps Institution of Oceanography where she is currently she is working as a researcher. Next year, Emily will begin as an Assistant Professor of Chemical Oceanography at California Polytechnic State University, San Luis Obispo. She is excited to focus on the Central Californian coastal upwelling environment and the local biogeochemistry and ocean acidification.

"For me, this class really was a crash course introducing me to the world of satellite measurements and data. I am very grateful to Bruce and the TAs for their patience and facilitation of the course, as well as my amazing peers who were willing to offer trouble-shooting help and great conversation. I appreciated how much hands-on work we did, diving into various datasets and possibilities for processing them. I walked away with practical knowledge and practice in collecting and using satellite data, which is exactly what I was hoping for. I feel as though I have been exposed to a new world of data, beyond the bench chemistry I am familiar with, and I am looking forward to pairing these measurements in the future."

Phil Bresnahan received his PhD from Scripps Institution of Oceanography in 2015. Working in Professor Todd Martz's lab, he developed *in situ* sensors to study the marine inorganic carbon system. His two main efforts involved designing a microfluidic total dissolved inorganic carbon analyzer for Argo floats and applying SeaFET/SeapHOx sensor technology in coastal ecosystems. Bresnahan is now an Environmental Scientist at the San Francisco Estuary Institute, a non-profit research organization focused on issues of mutual scientific and management-related importance in San Francisco Bay. At SFEI, he leads the efforts to characterize SF Bay's biogeochemical variability utilizing moored sensors.

"I couldn't speak more highly of the Cornell Satellite Remote Sensing Course. Every aspect (well, except for the cold showers—hopefully Cornell has fixed that by now!) exceeded my expectations. Bruce Monger's teaching style was thoughtful and effective and he was a great organizer; his passion for education and remote sensing reflectance was inspiring. While my core expertise is in situ sensor development and application, I fully realize the necessity of combining multiple tools and analytical approaches. I'm excited to see what doors the course opens for me! PS: I'm processing Landsat8/OLI data using my newly acquired skills as I write this. Thanks, OCB and Bruce, for a great opportunity!"

Dylan Catlett is a 2nd year PhD student in marine science at the University of California, Santa Barbara, and is advised primarily by Dave Siegel. Currently, his research interests lie in linking optical, chemotaxonomic, and molecular indices of phytoplankton community structure and diversity. Prior to beginning his graduate degree, he studied biology and chemistry at the University of North Carolina, Chapel Hill, where he also conducted research on the molecular responses of diatoms to iron and light limitation.

"The Satellite Remote Sensing course at Cornell was phenomenal. The course was extremely hands-on and application-oriented, making it an excellent and practical introduction to ocean color remote sensing and programming with Python. By the end of the course, I was able to comfortably obtain, process, and analyze satellite ocean color data. I returned to work after the course with much improved programming skills, which has already benefited my research immensely. The class was one of the most well organized I have ever experienced, and the instructor did a wonderful job creating a productive and fun learning environment. The diverse backgrounds of my fellow students led to interesting discussions, both in and outside of class, and further contributed to the educational experience. Finally, Ithaca was a joy to explore on days off. I would highly recommend this course to anyone with an interest in using ocean color remote sensing products in their research."

Jack Pan is a third-year PhD student working with Dr. Maria Vernet and Dr. Greg Mitchell at the Scripps Institution of Oceanography (SIO). He obtained his BS in Earth & Environmental Sciences at the University of California, Irvine, and MS in Marine Biology at SIO. Prior to enrolling at SIO, Jack worked on numerous projects at the Jet Propulsion Laboratory focusing on integrating oceanographic studies with applied sciences. In order to achieve a better understanding of the rapidly changing polar ecology and biogeochemistry, he is interested in utilizing optics-focused techniques to assimilate field measurements, remote sensing, and numerical models.

"*I have gained a tremendous amount of knowledge during the Cornell Satellite Remote Sensing course in summer 2016. During this class, I learned to process and effectively utilize satellite data for my research; materials from every lecture and lab session were almost instantly helpful to my work. The course instructor, Dr. Bruce Monger, is a very kind and patient individual. He explained the material very clearly and made sure every student was doing well; and moreover, he fostered a very friendly learning environment for students to fully engage in the material and help each other to excel. Personally, I am still in contact with many of my classmates, and even formed academic collaborations with some of them. This is one of the best classes that I have ever taken, and I would highly recommend it to anyone; but more importantly, I would like to sincerely thank OCB for giving me the opportunity to attend this class.*"

Melishia Santiago is a third year PhD student in the Graduate School of Geography at Clark University. Her work focuses on the study of Arctic marine environments and the combination of *in situ* measurements and satellite remote sensing. She investigates chromophoric dissolved

organic matter (CDOM) distribution and sea ice extent in the Bering, Chukchi, and western Beaufort seas. More generally, Melishia is interested in the biogeochemical impacts in the water column as sea ice declines in the western Arctic Ocean.

"All the skills and knowledge that I learned in the Cornell Satellite Remote Sensing course were really invaluable. The instructor and TAs were passionate about the subject. Thus, I was able to understand ocean color remote sensing concepts and apply them to my own research. It was truly a life changing experience!"

Priya Sharma is currently a doctoral candidate at University of Pennsylvania studying "Spatiotemporal dynamics of phytoplankton biomass from ocean color remote sensing and ensemble climate model simulations." Her research interests include assessing the evolution of phytoplankton group sizes and their functional types, ocean biological pump and response of ocean biology to various ENSO states. **She completed her** Master's degree at the University of South Pacific and also worked for the Pacific Center of Environment and Sustainable Development doing oceanographic research on tropical cyclones and exploring links between climate change and social science (e.g., traditional knowledge).

"Having the amazing opportunity to attend the 2016 Cornell Satellite Remote Sensing Course has deepened my knowledge of remote sensing and optical properties. The most exciting experience for me was the processing of various levels of geophysical satellite products to obtain spatial information. This course struck an equitable balance of theoretical and hands-on practical lessons. Importantly, **the data analysis tools and techniques** *that were taught were well aligned with my PhD thesis objectives, including empirical orthogonal function (EOF) analysis. I was also form collaborations with other participants of the course. Bruce is a very affable and approachable person, which made my experience during the Cornell course a very gratifying one."*

Inia M. Soto Ramos is currently a CONCORDE (Consortium in Coastal River-Dominated Ecosystems) postdoctoral researcher in the Division of Marine Science, University of Southern Mississippi at Stennis Space Center. She earned her BS in biology and education at the University of Puerto Rico, Mayaguez. She completed her MS and PhD degrees in biological oceanography at the University of South Florida. Her research interests include ocean color satellite remote sensing of coastal ecosystems, with emphasis on phytoplankton blooms and coastal ecosystems. Her current research is focused on coupling ocean color satellite imagery and high-resolution circulation models to understand the three-dimensionality of the Mississippi River Plume and the bio-optical surface response.

"The Cornell Satellite Remote Sensing Course was an outstanding experience! Dr. Bruce Monger is an exceptional professor and the course was applicable to any level of experience. Dr. Monger went the extra mile to make sure that everyone could adjust the learning experience to their own research. In my case, I have been working with satellite imagery for a few years; however I was not up to date on the technology and found myself with outdated skills. This course helped me get back on track and update my knowledge, especially my programming skills. Now, I feel much more confident with my skills and have since set up my personal computer system to integrate everything I learned during the course. I have been using the Python codes we learned during the class to process NASA's satellite imagery for two harmful algal bloom manuscripts (in progress) and for several other projects within my group. I have no words to truly express my gratitude to Dr. Monger, the enthusiastic and motivated TAs, Cornell University, and OCB for making this opportunity a reality for me and the other 8 talented early career scientists!"

After pursuing a BSc in Earth System Sciences at McGill University and a MSc in Earth and Ocean Sciences at the University of Victoria**, Jan-Erik Tesdal** began working toward a PhD in Earth and Environment Sciences at Columbia University. His broad undergraduate training emphasized a holistic view of the Earth System. Continuing in this spirit, his MSc research project focused on one of the iconic examples of how the biosphere can interact with the climate system: the CLAW hypothesis. For his PhD work, Jan-Erik narrowed his focus slightly to biological oceanography. He is especially intrigued by the interaction of the marine ecosystems with the physical environment. His current research centers on assessing the impact of melting Arctic Sea ice and freshwater flux on phytoplankton productivity and carbon export in the North Atlantic.

"The Cornell Satellite Remote Sensing course was a great experience for me. Learning the material and working through problem sets in a group setting was fun and exciting. The instructor and his TAs were very amiable and helpful, and the method-oriented teaching was ideal to help me learn the skills necessary for working with satellite data. It was especially useful to learn about the processing of satellite imagery through the conjunction of Python programming and SeaDAS. In addition to the great deal that I learned, I am very grateful for the opportunity afforded by this course to build new relationships from around the world. I can't imagine how my current research would suffer had I not taken this course."

Calendar

Please note that we maintain an up-to-date calendar on the OCB website.

2016	
November 7-18	UN Climate Change Conference 2016 (COP22) (Marrakech, Morocco)
November 14	International Conference on Marine Environment of the Red Sea (ICMERS 2016) (Thuwal, Saudi Arabia)
December 6-8	2nd International Marine Science Communication conference & high-level training workshop (Bruges and Ostend, Belgium)
December 12-16	Fall AGU Meeting (San Francisco, CA)

2017	
January 8-14	7th Annual Workshop on Genomics (Ceský Krumlov, Czech Republic)
January 9-11	Third Xiamen Symposium on Marine Environmental Sciences (XMAS 3) (Xiamen, China)
January 9-13	8th Biennial Conference of International Biogeography Society (Tucson, AZ)
January 18-19	Workshop on Environmental Concentrations, Cycling & Modelling of Technology Critical Elements (Rehovot, Israel)
January 22-27	AGU Chapman Conference on Extreme Climate Event Impacts on Aquatic Biogeochemical Cycles and Fluxes (San Juan, Puerto Rico)
February 26-March 3	2017 ASLO Aquatic Sciences Meeting (Honolulu, HI)
March 6-11	International Symposium on Drivers of Dynamics of Small Pelagic Fish Resources (Victoria, BC)
March 27-30	2017 Joint NACP and AmeriFlux Principal Investigators Meeting (PIM) (Bethesda, MD)
May 9-13	PAGES 5th Open Science Meeting (Zaragoza, Spain) (Special GEOTRACES session *Trace elements and their isotopes as geochemical proxies of past ocean conditions*)
May 15-18	2017 International Ocean Colour Science Meeting (Lisbon, Portugal)
May 21-26	14th International Symposium on the Interactions between Sediments and Water (Taormina, Italy)
May 22-25	International Conference on High Latitude Dust 2017 (Reykjavik, Iceland)
May 30-June 2	North Pacific Marine Science Organization (PICES) and the International Council for the Exploration of the Seas (ICES) 3rd Early Career Scientist Conference (Busan, Korea)
May 31-June 2	3rd Blue Planet Symposium (College Park, MD)
June 11-15	Ecosystem Studies of Subarctic and Arctic Seas (ESSAS) 3rd International Open Science Meeting (Tromsø, Norway)
June 26-29	2017 Ocean Carbon & Biogeochemistry (OCB) Workshop (Woods Hole, MA)
July 3-6	AMEMR (Advances in Marine Ecosystem Modeling Research) Conference (Plymouth, UK)
July 22-23	Gordon Research Seminar (New London, NH)
July 23-28	Gordon Research Conference in Chemical Oceanography (New London, NH)
August 13-18	Goldschmidt 2017 (Paris, France)
August 20-23	3rd International Workshop on Trait-Based Approaches to Ocean Life (Solstrand, Bergen, Norway)

2017	
August 21-25	10th International Carbon Dioxide Conference (Interlaken, Switzerland)
October 2-5	IMBER IMBIZO V: Marine biosphere research for a sustainable ocean: Linking ecosystems, future states and resource management (Woods Hole, MA)

FUNDING OPPORTUNITIES

For more information, please visit OCB's funding opportunities web page.

NSF

- Full list of upcoming NSF proposal deadlines
- NSF Research Coordination Networks (RCN)
- NSF Oceanographic Facilities and Equipment Support
- **November 15, 2016:** NSF Dynamics of Coupled Natural and Human Systems (CNH) proposal deadline
- **February 15:** NSF Chemical Oceanography, and Biological Oceanography and Physical Oceanography and Marine Geology & Geophysics proposal deadlines (NSF Dear Colleague Letter on North Atlantic-Arctic science)

NASA

- NASA ROSES 2016 solicitation
- **January 5 2017:** NASA ROSES-16 Amendment 44: A.7 Carbon Monitoring System NOI deadline
- **February 24:** NASA ROSES-16 Amendment 44: A.7 Carbon Monitoring System proposal deadline

NOAA

- NOAA Climate Program Office
- NOAA Ocean Acidification Program

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