Nutrient dynamics in the deep blue sea

David M. Karl

For more than a century, oceanographers have studied the interactions between the photosynthetic production of organic matter and nutrient dynamics in the sea. This research has been field-oriented and transdisciplinary, occurring at the intersections of research in microbiology, physics, analytical chemistry, cell physiology and ecology. The global database derived from this collective effort established a sound scientific understanding of nutrient dynamics and the vital role of microorganisms, both autotrophic and heterotrophic, in the coupled organic-matter production and decomposition cycles in the sea. However, novel approaches used over the past two decades, including new designs for field experiments, repeat field observations and remote-sensing capabilities, together with updated methods of sample analysis, have led to a revolution in our thinking about the mechanisms and controls of nutrient dynamics in the deep blue sea. Contemporary paradigms bear only partial resemblance to the dogma of the past, and are likely to evolve further as new data and new ideas are presented for open discussion and debate.

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The surface waters of the open ocean, defined collectively as those deep water regions seaward of the continental shelves, have traditionally been viewed as low population density (biomass), low productivity, low nutrient environments. This conceptual characterization has been applied particularly to the vast subtropical gyres of the world ocean, which, together, represent nearly 40% of the Earth's surface (Fig. 1) [1]. Because these subtropical open-ocean ecosystems are the dominant BIOME (see Glossary) on our planet, the biogeochemical processes that they support have global consequences.

Presently, one-half of photosynthesis on Earth is marine [2], and most of this sea-based production occurs in open-ocean habitats. Largely for this reason, the deep blue sea has been dubbed the 'invisible rainforest' [3]. Like the rainforests on land, the open ocean is a key component of global productivity. In stark contrast however, the open ocean functions by fundamentally different production pathways with different eco-rules and controls.

We now recognize that the rates of organic matter production in the central ocean gyres of the North Atlantic and North Pacific Oceans are more than twice their historical values, although it is uncertain whether this is a failure of previous field methods to obtain accurate estimates or a result of a temporal variation in habitat productivity [4]. If the rates of organic matter production have actually increased over the past few decades, then antecedent changes must have occurred in the nutrient dynamics in these ecosystems.

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At first it might appear contradictory that high rates of organic matter production could be sustained in environments where the concentrations of essential major and minor nutrients are barely detectable. However, it is well established that productivity in the open sea is maintained not by high nutrient loading, as might be found in an agricultural setting, but by rapid nutrient recycling. The difference in relative nutrient loading leads to variations in gross and net production [5]; the latter represents the organic matter production in 'excess' of local, coupled needs for respiration and other vital cell functions and which, in the steady state, is available for export or 'harvest' from the system.

Ecosystems with high turnover rates, such as the oceanic subtropical gyres, support relatively low rates of net organic matter production and export despite rates of gross production that are an order of magnitude larger. Because open-ocean ecosystems are dominated by very small unicellular primary producers (0.6–10 μm in diameter) with rapid growth rates and coupled death rates, it is not uncommon for 90% or more of the nutrients required to sustain primary production to be locally remineralized within the microbial food web, usually through the dissolved organic matter pool [6–8]. As opposed to the particulate organic matter present in a typical terrestrial ecosystem that turns over once per decade [2],

Glossary

Aeolian: aeolian processes include the erosion, transport and deposition of material by wind.
Biogenic: material, processes or activities of living or once-living organisms.
Biome: an area on the earth's surface that has a particular set of characteristics.
Euphotic zone: the topmost layer of a lake or sea in which there is sufficient light for net primary production.
Isopycnal surfaces: surfaces of constant density.
Lithogenic: material, processes or activities relating to rocks.
Mesopelagic zone: depths of between 200 and 2000 m, below the euphotic zone, where there is insufficient light for net photosynthesis. In this region, there is net respiration and net nutrient remineralization.
Mesozooplankton: animal plankton, typically in the size range 0.2–2 mm in length.
Photoautotroph: an organism that obtains its energy from light and uses CO_2 as its sole carbon source.
Photoheterotroph: an organism that obtains its energy from light and uses organic compounds as its carbon source.
Syntrophic relationships: where the growth of one organism depends on the provision of growth factors or substrates by another organism growing in the vicinity.

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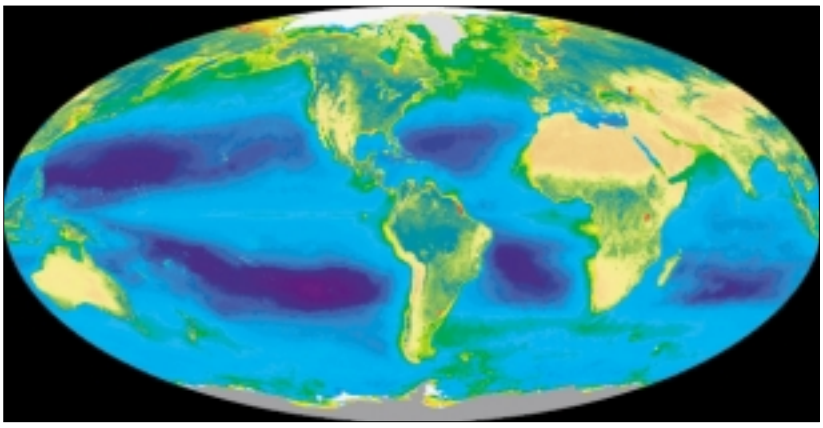


Fig. 1. Mean annual surface chlorophyll distributions as seen by the SeaWiFS ocean color satellite. The subtropical gyres correspond to deep blue regions that are indicative of the low chlorophyll (chlorophyll <0.1 mg m^{-3}), low nutrient oceanic habitats that dominate our planet. Imagery courtesy of NASA-Goddard Space Flight Center and the Orbital Sciences Corporation (Gene Feldman; http://seawifs.gsfc.nasa.gov/SEAWIFS.html).

organic matter in the deep blue sea is renewed every week. Consequently, the response time of planktonic ecosystems is rapid; slight shifts in nutrient dynamics, or in the physical processes that impact on them, can lead to major changes in the sequestration of CO_2 and other bioelements both in the short- and long term. Ultimately, the resupply of nutrients from outside the habitat will determine the extent to which an ecosystem can export organic matter without a gradual loss of biomass and concomitant decrease in future potential for organic matter production and export [9].

So, like the rainforests on land, the deep blue sea is a fragile ecosystem sustained in the short term by the rapid turnover of nutrients and in the longer term by the continued supply of nutrients from external sources. Under conditions of non-steady-state or pulsed nutrient delivery, the system can respond by short-term accumulations of biomass, episodic export, or both. In this regard, the ecological scale used for this time–space integral assessment of nutrients is critical.

A key consideration to emphasize is that ecosystems run on energy, not just on the flux of nutrient elements, and behind each cycle of mass is the transduction of bioenergy and production of heat. Ultimately, this bioenergy is derived from absorption of sunlight or biological oxidation of reduced inorganic and organic compounds, which, except in rare instances, are also dependent upon solar energy [10]. Although flows of matter are cyclic in nature, the flow of energy is unidirectional and must be continuously supplied to sustain nutrient cycling in the deep blue sea. Unfortunately, few quantitative studies of marine ecological energetics, especially for planktonic communities, are available [11]. Global environmental forces, including human-induced climate change, could potentially disrupt the flow of energy or nutrient-delivery processes, leading to fundamental changes in the diversity and function of the open-ocean marine food webs. To predict the biogeochemical consequences of climate-induced habitat changes, we need a comprehensive understanding of nutrient dynamics, as well as a hierarchy of models that can link the complex nutrient–organism interactions accurately with the dynamics of physical forcing on multiple time and space scales. Because the models are data driven [12], they will evolve as new knowledge of open-ocean ecosystems is obtained. Although there has been substantial progress in recent years, leading to the revision of several paradigms, we still lack a universal theory of nutrient dynamics in the sea and we continue to field-test legitimate competing hypotheses in our efforts to gain a comprehensive understanding of the key processes involved.

This paper will focus on the relationships between nutrient dynamics and primary production, and between surface ocean production and export processes; that is, the controls on the various open-ocean biological carbon pumps [13]. It will also briefly review where we currently stand, and speculate on where we might be heading.

Current and shifting paradigms of nutrient dynamics and export production

The production of organic matter in the sea – as on land – is sustained by a continuous supply of usable energy and life's essential building blocks, including essential major elements such as C, N and P; essential minor elements such as Fe and Zn; and, for many marine organisms, essential trace organics such as B-complex vitamins. The minimum threshold concentration needed to support organic matter production is different for each essential nutrient. These nutrient requirements also vary considerably among different species, and at different phases of development or growth for a given species; the 'average' composition of a photosynthetic microbial cell in the open ocean is ~1.10^9 C:1.7×10^8 N:1.10^7 P: 2.2×10^4 Fe:1 vit-B_{12}, on a molar basis. According to the Law of the Minimum [14], organic matter production is controlled by the nutrient that is available in the lowest concentration relative to the needs for growth. Consequently, it is not necessarily the nutrient in highest demand (typically C) or the one present in lowest concentration in the environment (typically trace organics) that controls the total rate of production by the ecosystem, but rather a dynamic balance between nutrient supply and nutrient demand.

The two current paradigms of greatest importance to nutrient dynamics in the open ocean are: (1) the nitrate-dependent 'new production' concept [15] and its subsequent extension to include a consideration of coupled particulate matter export from the system [9]; and (2) the 'C-N-P fixed stoichiometry of marine organic matter' concept [16]. Together with the frequently cited assumption of a steady-state ocean, these biogeochemical 'rules' have guided the design and implementation of field programs and have constrained our data interpretation and biogeochemical modeling efforts [17]. Ongoing time-series investigations in the subtropical open-ocean

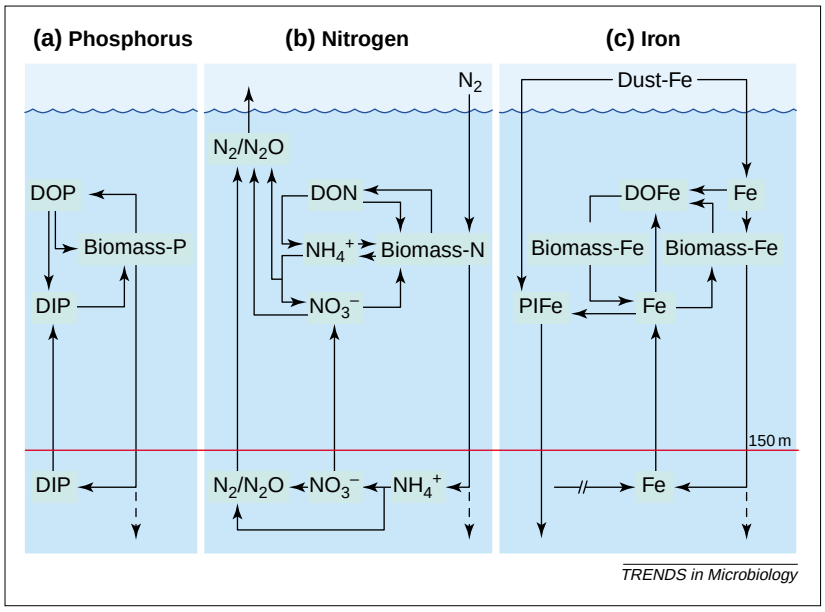


Fig. 2. Schematic representations of three different nutrient delivery and cycling pathways. (a) Phosphorus. Delivery of dissolved inorganic P (DIP) from the mesopelagic zone (>150 m) by eddy diffusion processes. In the surface ocean, P cycles between DIP and dissolved organic (DOP) forms through the activities of living organisms (biomass-P). In this schematic model, there is a balance between the export of P and the delivery from below. (b) Nitrogen. Delivery of dissolved inorganic N in the form of nitrate (NO_3^-) from the mesopelagic zone and export of biomass-N from surface waters, as for P; the similarities end here. As opposed to P, N has a very complex redox cycle both in surface and in deep waters where it can be both oxidized and reduced by selected groups of microorganisms. N_2 fixation can also provide an additional source of new N to the system, which balances losses from denitrification. (c) Iron. Delivery of Fe from both above (aeolian input) and below the euphotic zone is shown along with the complex interactions of dissolved Fe with organic ligands to form various dissolved organic Fe (DOFe) complexes. These are important for establishing Fe solubility and Fe bioavailability. Much of the Fe that is delivered as dust remains as insoluble particulate inorganic (lithogenic) Fe (PIFe), and some of the dissolved Fe can be scavenged onto inorganic or organic particles with eventual removal from the system. The export flux of Fe generally exceeds the delivery from below, so the ecosystem relies on a continued supply of bioavailable Fe from aeolian delivery.

gyres are now beginning to challenge the general validity of these concepts, replacing them with several new and still-emerging ecosystem paradigms [4,18,19].

There are multiple potential pathways for the supply of major nutrients to the productive surface layers of the open ocean (Fig. 2), and the relative importance of each pathway varies depending upon the nutrient in question [20]. For example, nitrate and phosphate are both delivered to the surface ocean via eddy diffusive processes or by seasonal deep-mixing entrainment of nutrients from the MESOPELAGIC ZONE (200–2000 m). The deep, subsurface reservoir of inorganic nutrients is continuously renewed by net release from, and oxidation of, exported particulate and dissolved organic matter. Because there is a long-term balance of C, N and P delivery and export by this process, the so-called constant Redfield ratio biological pump, the bi-directional reflux of nutrient elements in fixed stoichiometric ratios does not permit the net removal of CO_2 from the upper water column because the import and export of carbon are in balance [13,17]. Other nutrient delivery export processes must therefore be responsible for net carbon sequestration in the deep blue sea.

In selected habitats, horizontal advection and mixing along ISOPYCNAL SURFACES could supply nitrate, phosphate and possibly other essential nutrients provided there is a favorable concentration gradient. However, this mechanism is not considered to be too important in the open sea because the horizontal gradients of rate-limiting nutrients are relatively weak [21–23]. Another potential source for selected nutrients is the delivery by atmospheric dry and wet deposition. Fe, for example, is primarily derived from the wet deposition of dust originating from remote continental sources (Fig. 2). The AEOLIAN supply of Fe to the open ocean is seasonally phased, interannually variable and climate sensitive [17,24,25], and does not necessarily vary in phase with other potential nutrient supply mechanisms. This creates a situation where the delivery of N and P is decoupled from the supply of Fe. In contrast to most other nutrient elements, Fe distributions in the sea are affected not only by biological uptake, export and remineralization (typical nutrient-like behavior), but also by chemical interaction with a variety of organic ligands, including siderophores, and by scavenging onto living and non-living particulate matter, including colloids (Fig. 2) [26].

The aeolian supply of Fe to the sea surface can lead to large blooms of diatoms that eventually exhaust the next limiting nutrient, aggregate and sink rapidly out of the water column. This event-driven diatom sedimentation pump can remove fresh organic matter efficiently from the upper ocean to the deep sea, thereby sequestering carbon for relatively long time-scales (centuries) even if the organic matter is removed in Redfield ratio stoichiometry. The large, bloom-forming diatoms are also typically enriched in Fe relative to other phytoplankton cells [27], and this can have significant ecological consequences for Fe resupply because the organic matter removed in these pulsed sedimentation events escapes mesopelagic zone remineralization.

In the case of N, there are other potential microbiological sources and sinks that must also be evaluated in the ecosystem balance, including the import of fixed N by the reduction of dissolved N_2 gas via bacterial fixation, and the loss of fixed N by the formation of N_2 via bacterial denitrification of nitrate (Fig. 2). The long-term balance between these two processes will influence the N:P stoichiometry of the subsurface nutrient pool as well as the N-status of the surface-dwelling communities [28,29], leading to various ecological consequences (discussed later). Ironically, the reduction of NO_3^- to N_2/N_2O (denitrification) also requires active nitrification ($NH_4^+ \rightarrow NO_3^-$) to provide the oxidized substrate because most, if not all, of the exported N is in the most reduced form (NH_4^+ and organic N). Mesopelagic zone nitrification could therefore be the key process in the nutrient dynamics of the deep sea.

Finally, the migrating plant and animal pump is a process whereby mobile organisms effect a translocation of nutrients, either in a net upward or net downward direction, in conjunction with their periodic

vertical migrations. The role of MESOZOOPLANKTON in this process has been studied in detail at two open-ocean locations [30,31]. Although mesozooplankton migrations are generally considered to result in net downward fluxes of C and N, it is possible that periodic vertical migrations could result in a net upward flux of other essential nutrients. For example, when zooplankton consume food with a high N:P ratio, P is selectively retained by the organism as it is needed for balanced growth [32]. It is even conceivable that additional P can be assimilated during mesopelagic zone metabolism of the P-depleted foodstuffs consumed in near-surface waters. If so, then mesozooplankton might actually be exchanging surface N for deep-water P during their daily migration to depth, and this would help to promote and sustain N_2 fixation in near-surface waters. This hypothesis remains to be tested.

An even more remarkable open-ocean process is the vertical migration of primary producers, including diatoms and N_2-fixing cyanobacteria [33–35]. It has been hypothesized that both nitrate (diatoms) and phosphate (N_2 fixers) can be transported across physical mixing barriers by the vertical migrations of these microorganisms. These active migrations can also be supplemented by the passive upward flux of low bulk density (lipid-rich) organic matter produced at depth via selective decomposition of exported particulate organic matter [36]. This latter passive upward flux would select for P owing to the known P-enrichment of lipids. As well as serving to decouple the N and P cycles, these selective movements of plants and nutrients could help to sustain organic matter production and export during the most stratified periods of the year. It is presently unknown how frequent, how widespread or how important these processes are for the total nutrient balance in the deep blue sea.

N_2 fixation: controls by P and Fe

The N-starved oceanic gyres should provide an ideal habitat for the proliferation of N_2-fixing microorganisms that would supply bioavailable N and shift the ecosystem balance towards limitation by a non-nitrogenous essential nutrient. N_2-fixing microorganisms, when present, can have a profound impact on nutrient dynamics, including organic matter stoichiometry and the potential for net sequestration of CO_2.

Marine N_2-fixing organisms are exclusively prokaryotic (including representatives from both domains, Bacteria and Archaea) but beyond that single characteristic they show a remarkable morphological diversity ranging from relatively large (mm in length), filamentous forms such as *Trichodesmium*, to unicells (3–5 μm diameter), to ecto- and endosymbiotic associations with a variety of unicellular and multicellular eukaryotic hosts [37]. A low N:P ratio in the dissolved nutrient pool in the surface ocean is generally a necessary but, by itself, insufficient condition for the natural selection of N_2-fixing microorganisms. Fe, for example, is also required for nitrogenase (the enzyme responsible for N_2 reduction) activity. Because Fe is extremely insoluble in oxygenated seawater, the bioavailability of Fe is controlled by the presence of a variety of organic ligands that enhance Fe solubility (Fig. 2) [38,39]. This leads to questions concerning the proximate control(s) of ecosystem N_2-fixation rates, including Fe, P or other growth factors. These key ecophysiological controls on new and export production are not included in our current biogeochemical paradigms or ecosystem models.

If organic matter production and export in a given ecosystem are not controlled by the input of new N in the form of nitrate, but rather by the combination of nitrate delivery plus local N_2 fixation as implied above, or by another essential nutrient altogether (P, Fe or B-complex vitamins), then the frequently employed field assessment of new (nitrate) versus regeneration (ammonium) production using ^{15}N-tagged exogenous substrates requires major reevaluation. Additional conceptual complications might also arise if Fe is found to control new production in the open sea because its local source – dust deposited on the sea surface – is tied back to the continents, whereas the local sink is via settling of BIOGENIC and LITHOGENIC particles (Fig. 2). In reality, contemporary open-ocean ecosystems are probably poised at or near the point where multiple essential nutrients, simultaneously or alternately, limit organic matter production and export. The time frame used for these biogeochemical assessments is critical because of well-documented pulsed delivery of selected nutrients, differential elemental residence times and, for certain nutrients and certain organisms, the capacity for uptake and storage beyond the immediate needs for growth.

Subtle shifts in community structure, for example the selection for N_2-fixing microorganisms that themselves might be coupled to aperiodic Fe-deposition events, can fundamentally change the production rates, processing mechanisms and ultimate fates of carbon and associated bioelements (Fig. 3). If Fe and fixed N are co-limiting, as might occur in subtropical gyres, the addition of excess Fe should select for either free-living N_2-fixing microorganisms or diatoms containing endosymbiotic N_2-fixing cyanobacteria (diazotrophic diatoms), or both (Fig. 3) [13]. The N_2-fixing bloom would continue until the Fe pulse, or the concentration of bioavailable P, vitamins or some other essential nutrient, limits further growth. The B-complex vitamins, especially vitamin B_{12} (cyanocobalamin), could be a special case because they are not usually essential nutrients for prokaryotes, which can synthesize them *de novo*, but are essential for most eukaryotes, including diatoms (Fig. 4). Vitamin bioavailability could be the switch that determines whether diazotrophic diatoms or free-living N_2-fixing microorganisms emerge following a pulsed addition of Fe (Figs 3 and 4). However, for open-ocean ecosystems to be sustained over the long

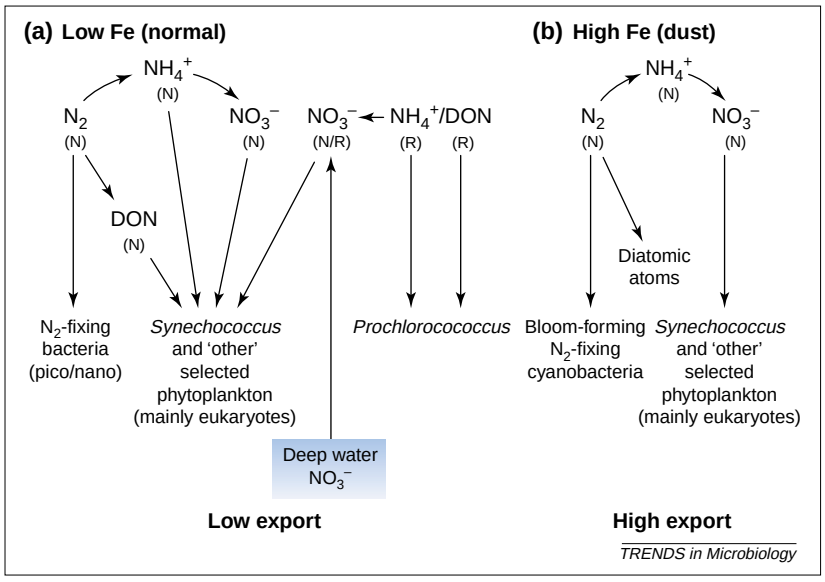


Fig. 3. Revised conceptual view of new (N) versus regenerated (R) N based on observations from the Hawaii Ocean Time-series (HOT) program in the North Pacific subtropical gyre. (a) Shows the normal, low Fe condition that is observed most of the year. N_2-fixing pico- and nanoplankton incorporate new N_2, part of which cycles locally through new ammonium (NH_4^+) to new nitrate (NO_3^-); new dissolved organic nitrogen (DON) is also produced during this process. All of these substrate pools are used for photosynthesis by the various groups of photoautotrophs. The other source of new N to the system is deep water NO_3^-, which also fuels a local regeneration cycle through NH_4^+ and DON back to NO_3^-. Consequently it would be difficult to distinguish between new and regenerated nutrient pools by the contentional use of ^{15}N-tagged tracers. This normal, low Fe condition supports low rates of net production, low rates of new production and low export. (b) During and following aperiodic dust deposition events there is a selection for larger, faster-growing, bloom-forming N_2-fixing organisms including the diatomic (diazotrophic) diatoms that harbor endosymbiotic N_2-fixing cyanobacteria. The microbial community processes in these Fe-pulsed systems are generally superimposed on the background state, and lead to high export production of recently synthesized, N_2-supported organic matter.

term, there must be an inter-species vitamin exchange that permits the continued survival and persistence of eukaryotic algae in the sea. Whether the prokaryotic N_2-fixing cyanobacteria living endosymbiotically with open-ocean diatoms provide vitamins to the host is unknown, but in all likelihood they probably do. If true, this would provide the rapidly growing diazotrophic diatoms with a distinct growth advantage over either asymbiotic diatoms or the generally slower-growing bloom-forming N_2-fixers, such as *Trichodesmium*.

Habitat variability and climate change: impacts on nutrient dynamics

Nutrient dynamics in the sea are inextricably linked to variations in physical processes, including climate. However, there is no universally applicable ecological theory that predicts the response of open-ocean ecosystems to habitat variability. Transient changes in the carrying capacity of an ecosystem, usually expressed as chlorophyll or total particulate organic matter concentrations, are usually associated with changes in nutrient supply. We now recognize that either enhanced nutrient delivery from turbulent mixing or enhanced stratification can lead to increases in ecosystem carrying capacity, productivity and export, with significantly different consequences for nutrient cycling [20]. Because open-ocean microbial assemblages are metabolically active with a potential for relatively high specific growth, they are poised to respond quickly and effectively to environmental perturbations ranging from stochastic event-scale phenomena with time constants of hours to days (e.g. storms and dust-deposition events), and to evolve over decadal and longer time-scales to climate-driven habitat change (e.g. variations in ocean circulation and stratification).

An important feature of climax community theory is the constancy of an ecosystem under stable climate conditions but, as a corollary, an anticipated change in community structure and dynamics following habitat perturbation including climate variations [40]. It has been suggested that the North Pacific subtropical gyre, once considered to be an ecosystem in a climax community successional stage, has undergone significant and unexpected changes over the past few decades in both population structure and mechanisms of nutrient cycling [4,18,41,42]. These changes are ultimately controlled by nutrient dynamics and, in particular, to changes in the supply rates and supply pathways of the production-rate-limiting nutrients.

Based largely on field data collected at the Hawaii Ocean Time-series (HOT) Station ALOHA (22°45′N, 158°W) over the past 13 years, it appears that the North Pacific subtropical gyre supports a larger standing stock of smaller PHOTOAUTOTROPHIC microorganisms today than it did 30 years ago [4]. The previous dominance of eukaryotic algae appears to have given way to a novel, diverse assemblage of prokaryotic phototrophs [43] and perhaps even a selection for novel PHOTOHETEROTROPHS [44–46]. It is presently unknown, and might never be known, whether these microorganisms have always been present and have simply escaped prior detection, or whether they are new inhabitants of these open-ocean ecosystems. The selection for, and retention of, these novel microorganisms and the existence of complex SYNTROPHIC RELATIONSHIPS, including unconventional nutrient sources and sinks, could be the rule in the deep blue sea.

The inability to balance N export in the subtropical North Pacific Ocean based on suspected sources led to a systematic analysis of the potential role of less-well-studied pulsed nutrient delivery by alternative physical and biological mechanisms, including breaking internal waves, mesoscale cyclonic eddies and N_2 fixation [22,34,47,48]. Because the dominant export pulse in summer coincided with periods of enhanced water column stratification, there was a suspicion that N_2 fixation might be a significant source for new N despite conventional wisdom to the contrary. Now, after more than a decade of observation and experimentation, the quantitative role of N_2 fixation seems to be well established.

The field evidence supporting the existence of significant N_2-based new production includes observations of the putative N_2-fixing microorganisms [49,50]; direct measurements of N_2-fixation rates using $^{15}N_2$ tracer techniques [51]; mass balance estimation of N/P and ^{15}N in suspended and exported particulate matter [48,51]; increased microbial

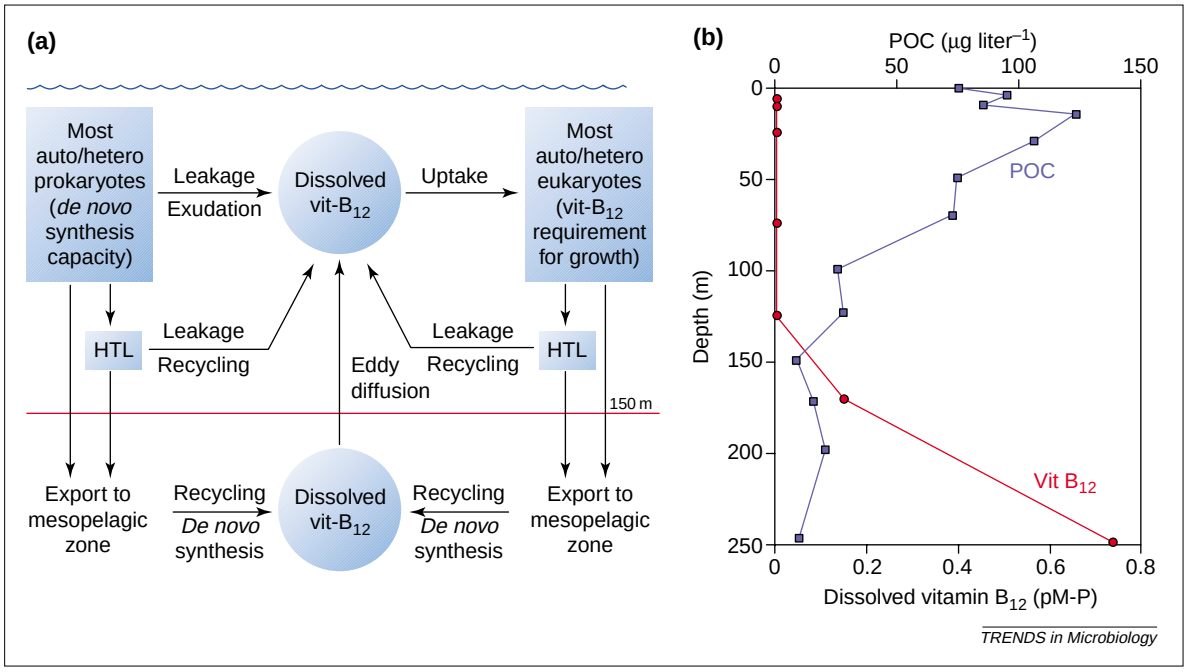


Fig. 4. The vitamin B_{12} cycle in the North Pacific subtropical gyre. (a) Shows the hypothesized interactions between the production of vitamin B_{12} by autotrophic and heterotrophic prokaryotes and the coupled transfer to surface ocean eukaryotic plankton via the dissolved vitamin B_{12} pool. Export of particulate vitamin B_{12} to the mesopelagic zone by all components of the food web, and subsequent remineralization at depth, drives a deep to surface ocean diffusion of this key nutrient. There might also be limited *de novo* synthesis at depth by the growth of mesopelagic prokaryotes. (b) Shows a 'typical' depth distribution of dissolved vitamin B_{12} concentration showing a 'nutrient-like' profile with net uptake in surface waters and net regeneration at depth. Also shown is the distribution of particulate organic carbon (POC) as a measure of biomass for this same location. Abbreviation: HTL, higher trophic levels, including mesozooplankton and fish. Data in (b) taken from [62].

assemblage affinities of P [52]; accumulations of C- and N-enriched, P-depleted dissolved organic matter [53]; and a decade-long, systematic loss of P from the upper water column [36]. These features are all consistent with the hypothesized shift from N to P control of ecosystem processes.

In environments like the western North Atlantic, where the atmospheric delivery of Fe and the presence of Fe-binding ligands exceed the ecosystem demand, N_2 fixation proceeds unabated until ambient phosphate is drawn down below nanomolar concentrations [54–56]. At Station ALOHA, near-surface phosphate concentrations are generally 10- to 100-times greater than this threshold (Fig. 5), implying either bioavailable Fe limitation or co-limitation by Fe/P (for N_2-fixing microorganisms), Si (for diazotrophic diatoms), vitamins (for eukaryotic subpopulations) or other essential nutrient control. This apparent 'surplus' of bioavailable P at Station ALOHA is fully consumed in the short term (days to weeks) during aperiodic blooms of photoautotrophs and, in the long term (years to decades), there appears to be a continuous net removal of bioavailable P, at least during extended periods of enhanced N_2 fixation [4]. As the supply of bioavailable P dwindles [36], there should be a selection for alternative 'P-capture' mechanisms, including novel enzymes that can mobilize the more recalcitrant, semi-labile organic phosphorus residues like C-P-bonded phosphonates, and a further shift in the cell size and activity spectra to smaller, slower-growing microorganisms. There will also be collateral impacts on the top-down grazing control of microbial populations and, therefore, on the nutrient cycling rates [32], further exacerbating P limitation. Even the effectiveness of viral infection and lysis might be impacted by P limitation [57] and this could, in turn, impact on microbial selection pressures. Without an adequate resupply of P and other nutrients, these stressed open-ocean ecosystems will lose biomass, biodiversity and their ecophysiological response capability to habitat variability and climate change.

A key negative feedback to enhanced N_2 fixation and export of high N:P organic matter is the eventual build-up of a mesopelagic nutrient reservoir that is also enriched in N scaled to P, relative to cellular needs (Fig. 6). As these regenerated nutrients slowly feedback

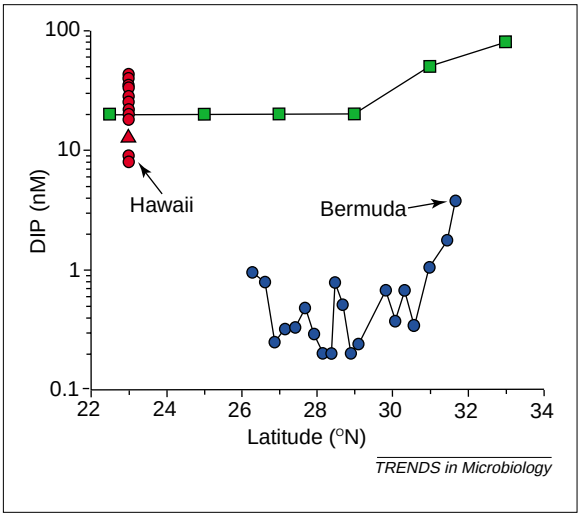


Fig. 5. Comparison of dissolved inorganic phosphorus (DIP) concentrations for the North Atlantic (blue circles) and North Pacific (green squares) regions showing significant offsets in the DIP inventories, especially for the subtropical regions. The red circles show the range of DIP concentrations observed at Station ALOHA for the period 1991–1997 and the red triangle is the value measured in Nov 1998. The severely P-depleted North Atlantic Ocean is hypothesized to be a consequence of the higher aeolian flux of Fe in this basin compared with the North Pacific [54]. Fe deposition can control N_2 fixation, which, in turn, controls the ambient P concentrations. This Fe-N_2 fixation-P syntrophy has numerous ecological consequences, as described in the text. Reproduced, with permission, from [54] ©2000 American Association for the Advancement of Science. http://www.scienceonline.org

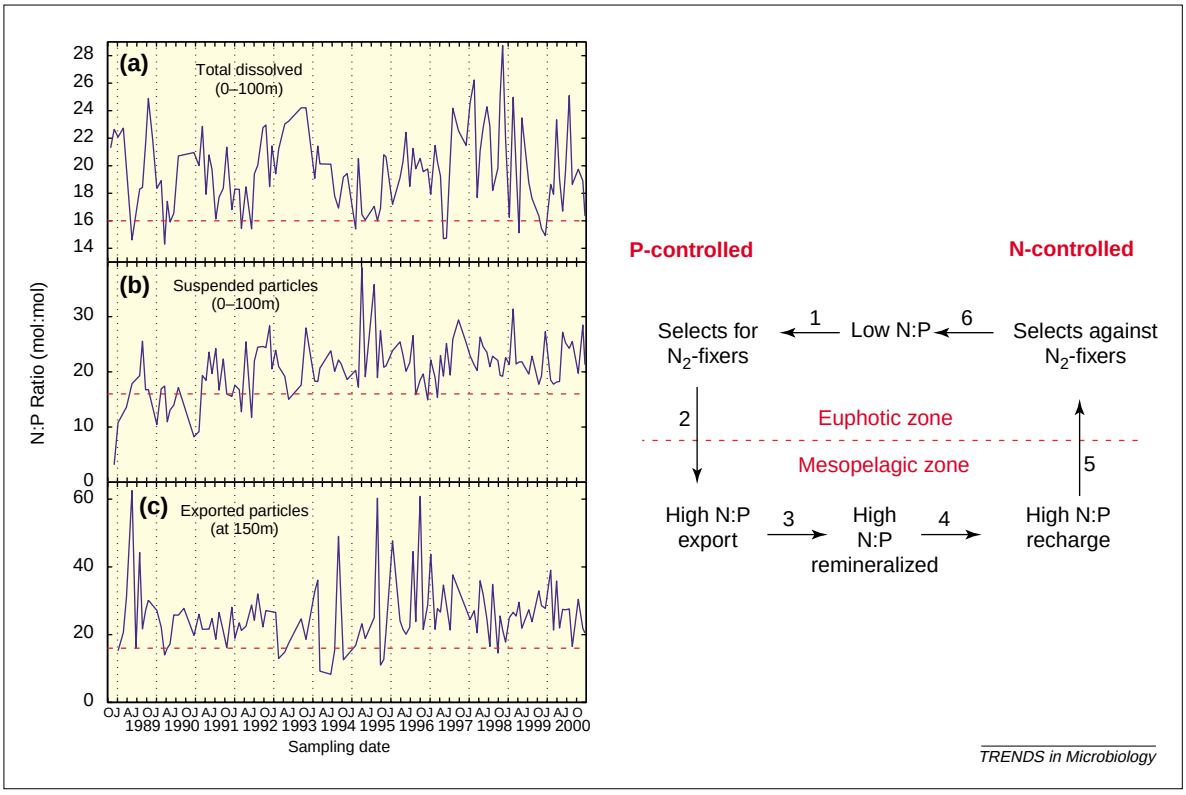


Fig. 6. The hypothesized N_2-fixation cycle at Station ALOHA begins with a low (<16:1) near-surface water N:P ratio in the dissolved nutrient pool. This selects for N_2-fixing microorganisms (1), resulting in a shift towards P-control, with numerous ecological consequences, including the production and export of organic matter with high (>16:1) N:P ratios (2). The remineralization of this exported material in the upper mesopelagic zone (3) over decadal time scales leads to a nutrient reservoir with an equally high N:P ratio as the entire pool turns over (3 and 4). This high N:P ratio nutrient pool feeds back into the surface waters by eddy diffusion and mixing (5) and selects against N_2-fixing microorganisms, forcing the system back to N-control. Selective losses of N, relative to P, by the combined processes of denitrification and differential export (6) leads to a low N:P ratio of bioavailable nutrients and the cycle starts over again. The data on the left are 3-pt running mean observations of the N:P molar ratios in total dissolved [inorganic plus organic; (a)] and total suspended particulate matter (b) in the upper 0–100 m, and (c) in exported particulate matter at the 150 m reference depth at Station ALOHA. These data display nutrient dynamics that are consistent with the hypothesized N_2-fixation cycle.

into the EUPHOTIC ZONE, they should select against N_2-fixing microorganisms and lead to another shift in community structure, ecological stoichiometry, grazing and export under the newly established nutrient regime. This alternation between N limitation and P (or P/Fe) limitation in the North Pacific subtropical gyre would be predicted to occur on an ~20–40 year cycle based on the estimated residence time of nutrients in the upper mesopelagic zone reservoir.

This conceptual model of temporal alternation between N and P control of production and export processes provides a reconciliation of the paradigms that were developed in the 1960s to explain the fixed Redfield ratio, N-controlled ecosystem processes of that era, with the new paradigms that are necessary to accommodate contemporary observations in a sea of change [18]. The extent to which greenhouse gas-induced warming and other changes to the surface ocean will affect the abilities to switch between these two ecosystem states is currently unknown, but it seems almost certain that the dimensions of the subtropical gyres will expand and with that the oceans as a whole will become more stratified and more nutrient depleted.

Epilogue

With recently obtained open-ocean time-series datasets in hand we now have a revised, but still incomplete, view of nutrient dynamics in the deep blue sea; this article must be considered a review of work in progress. An apparent feature of these prokaryote- (*Prochlorococcus* and *Synechococcus*) dominated open-ocean ecosystems is a reliance on the growth of larger eukaryotic phototrophs for particulate organic matter export, usually following aperiodic physical and chemical perturbations. Both enhanced turbulence and enhanced stratification can accelerate nutrient export, but by fundamentally different biogeochemical pathways and with variable ecological consequences. Selection for N_2-fixing microorganisms and the aperiodic blooming of diatoms, some containing endosymbiotic N_2-fixing cyanobacteria, are two key processes that are poorly understood. Because P is the staff of life [58], we need to understand the P delivery and export processes completely, as well as controls on local recycling. A comprehensive chemical characterization of the relatively large dissolved organic phosphorus (DOP) pool would be a coveted biogeochemical contribution [59]. In any case, we must remain vigilant about the sea around us as we enter the Anthropocene era [60], the period of significant human impact on global nutrient cycles, because it is

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almost certain that we have already changed pre-industrial oceanic processes.

The role of the deep blue sea as a net sink for CO_2 depends on the balance between the export of carbon and the rate of dissolved inorganic carbon resupply from outside the system. We now recognize that a variety of essential nutrients can influence this balance, and dramatically alter the carbon sequestration potential of the sea. For example, a deficit of an essential non-carbon-containing nutrient might trigger the accumulation of dissolved organic carbon in certain subtropical marine ecosystems [53]. In a previous letter to this journal [61], I cited several limitations of the 'new versus regenerated production' paradigm as currently applied to open-ocean ecosystems. My comments concluded with a call for a new conceptual paradigm for the study of nutrient dynamics in the sea, one that fully accommodated N_2 fixation and Fe deposition. I reiterate that plea and now add Fe-N-P decoupling, the production and export of particulate and dissolved organic matter with variable C-N-P stoichiometry, diazotrophic diatoms, vitamin syntrophy and climate variability as additional considerations.

The conceptual view of a sparse but well-structured climax community in oceanic gyres that was in vogue in the 1970s has been replaced by a revised paradigm of a metabolically diverse microbial soup that is able to respond quickly to habitat variability and climate change [4,43–46,50]. The dynamic response of these diverse microbial assemblages to the pulsed delivery of nutrients, from both above and below the sea surface, produces a time-varying intersection of processes that can only be resolved and understood through complementary programs of high-frequency long-term ocean observations, hypothesis-testing field experimentation and comprehensive ecosystem model-data comparisons of the mean and physically perturbed ecosystem conditions. This challenge must be met if we are to provide our legislative decision-makers and society as a whole with meaningful input on the probable future state of the sea.

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Exploitation of the endoplasmic reticulum by bacterial pathogens

Craig R. Roy

The endoplasmic reticulum (ER) has unique properties that are exploited by microbial pathogens. Exotoxins secreted by bacteria take advantage of the host transport pathways that deliver proteins from the Golgi to the ER. Transport to the ER is necessary for the unfolding and translocation of these toxins into the cytosol where their host targets reside. Intracellular pathogens subvert host vesicle transport to create ER-like vacuoles that support their intracellular replication. Investigations on how bacterial pathogens can use the ER during host infection are providing important details on transport pathways involving this specialized organelle.

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One feature that all bacterial pathogens have in common is their ability to establish a niche within a eukaryotic host that will support replication. In many instances, bacterial pathogens colonize sites within the host that are normally sterile, a feat that often requires evasion of immune defense mechanisms. Another key component of a bacterial pathogen's lifestyle is transmission to an uninfected host upon completion of their replicative cycle. The bacterial virulence determinants mediating each of these tasks often function by interacting with or mimicking eukaryotic proteins [1]. Thus, like most microbiologists who are investigating bacterial pathogenesis at the molecular level, these organisms have had to learn eukaryotic cell biology out of necessity. However, bacteria have been around much longer than humans, and with age comes wisdom. It should therefore come as no surprise that bacteria can teach us a great deal about how our own cells function. This review will focus on bacterial subversion of the endoplasmic reticulum (ER). Recent studies on bacterial toxins that are transported to the ER and intracellular pathogens that replicate within this privileged niche are providing details on the basic cellular processes that require ER functions.

The cell biology of the ER

In eukaryotic cells, most proteins that are secreted or transported inside vesicles to other cellular organelles are synthesized at the ER [2]. Membrane and soluble proteins containing an amino-terminal signal sequence are translocated co-translationally into the ER through the Sec61 translocon (Fig. 1a) [3]. During translocation, coordinated asparagine-linked glycosylation and oligosaccharide-trimming reactions facilitate protein folding and allow recognition of misfolded proteins [4]. This ensures that translocated proteins are folded properly before they are sorted and delivered to other cellular locations. There are numerous chaperone proteins residing in the ER that interact physically with translocated substrates to help mediate proper folding (Fig. 1b) [5]. These include lectins such as calnexin and calreticulin;

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