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Upward nitrate transport by phytoplankton in oceanic waters: balancing nutrient budgets in oligotrophic seas

In oceanic gyres, primary producers are numerically dominated by small (1-5 µm diameter) pro- and eukaryotic cells that primarily utilize recycled nutrients produced by rapid grazing turnover in a highly efficient microbial loop. Continuous losses of nitrogen to depth by sinking, either as single cells, aggregates or fecal pellets, are balanced by both nitrate inputs at the base of the euphotic zone and nitrogen-fixation. This input of N (new nitrogen) to balance export losses (the biological pump) is a fundamental aspect of nitrogen cycling and central to understanding carbon fluxes in the ocean. In the Pacific Ocean, detailed nitrogen budgets at the time-series station HOT require upward transport of nitrate from the nutricline (80-100 m) into the surface layer (~0-40 m) to balance productivity and export needs. However, concentration gradients are negligible and cannot support the fluxes. Physical processes can inject nitrate into the base of the euphotic zone, but the mechanisms for transporting this nitrate into the surface layer across many 10s of m in highly stratified systems are unknown. In these seas, vertical migration by the very largest 10^2-10^3 µm diameter) phytoplankton is common as a survival strategy to obtain nitrogen from sub-euphotic zone depths. This vertical migration is driven by buoyancy changes rather than by flagellated movement and can provide upward nitrogen transport as nitrate (mM concentrations) in the cells. However, the contribution of vertical migration to nitrate transport has been difficult to quantify over the required basin scales. In this study, we use towed optical systems and isotopic tracers to show that migrating diatom (*Rhizosolenia*) mats are widespread in the N. Pacific Ocean from 140°W to 175°E and together with other migrating phytoplankton (*Ethmodiscus*, *Halosphaera*, *Pyrocystis*, and solitary *Rhizosolenia*) can mediate time-averaged transport of N (235 µmol N m^{-2} d^{-1}) equivalent to eddy nitrate injections (242 µmol NO_3^- m^{-2} d^{-1}). This upward biotic transport can close nitrate budgets in the upper 250 m of the central Pacific Ocean and together with diazotrophy creates a surface zone where biological nutrient inputs rather than physical processes dominate the new N flux. In addition to these numerically rare

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large migrators, there is extensive evidence in the literature of ascending behavior in small phytoplankton that contributes to upward flux as well. Although passive downward movement has dominated models of phytoplankton flux, there is now sufficient evidence to require a rethinking of this paradigm. Quantifying these fluxes is a challenge for the future and requires a reexamination of individual phytoplankton sinking rates as well as methods for capturing and enumerating ascending phytoplankton in the sea.

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Introduction

Nitrogen in the euphotic zone of the open sea has long been recognized to partition into two distinct pools of availability (Dugdale & Goering 1967). New nitrogen represents introduction of N from outside the euphotic zone, either in the form of deep NO_3^- or nitrogen-fixation, while regenerated N results from consumption and remineralization of dissolved or particulate N (Dugdale & Goering 1967). While regenerated N dominates the total phytoplankton uptake, new N is critical to balance losses due to vertical fluxes and is linked to total system productivity (Eppley & Peterson 1979). This has been expressed as the *f* ratio where '*f*' = new/total N uptake and ranges from 0-1. On longer time scales, new N input must balance sedimentary losses or the system will experience net losses of nitrogen (Eppley & Peterson 1979). The surface waters of the open ocean are considered low 'f' ratio environments: N and P often occur at nM concentrations, and ammonium is the dominant form taken up by phytoplankton (Lipschultz et al. 1996; Raimbault et al. 2008; Wu et al. 2000). The *f* ratio increases in the light-limited lower depths of the euphotic zone due to the increased availability of nitrate at the nutricline, thus creating what has been recognized as a two-layered structure (Goldman 1988). This general pattern can be modified in regions of low iron input, where iron availability limits macronutrient consumption creating regions of high nutrient-low chlorophyll (HNLC) where low phytoplankton biomass persists despite elevated nutrient concentrations (de Baar et al. 2005). These HNLC zones tend to be in equatorial or high latitude regions (Boyd et al. 2007), leaving much of the central gyres in a macronutrient (N or P) limited state. Further complexity is introduced by eutrophic zone nitrification. This process introduces nitrate internally rather than from exogenous sources (Ward 2008), can support the sustained nanomolar nitrate concentrations ubiquitous in the gyres (Lipschultz et al. 2002) and substantially affects *f*-ratio calculation based on experimental $^{15}NO_3^-$ uptake (Clark et al. 2008). However, it is unclear whether it can provide the produce oxygen anomalies used as geochemical signatures (Jenkins & Goldman 1985) to calculate export loss-based new production estimates.

The nutritionally-dilute environment creates strong evolutionary pressures on phytoplankton to decrease cell size (increased surface:volume ratios) as well as for mixotrophy to supplement photosynthesis. In these strongly stratified environments, small prokaryotes are numerically dominant and often are specialists for exploiting either the light-rich, but nutrient limited, upper euphotic zone, or the region at the base of the euphotic zone where light becomes limiting and nutrients increase to µM concentrations (Malmstrom et al. 2010). In the Pacific Ocean, this transition zone is also associated with the boundary between shallow and deep phytoplankton communities of diatoms, dinoflagellates and other phytoplankton resolved by light microscopy (Venrick 1988; Venrick 1990). Within the phytoplankton community is also a rare, but ubiquitous, flora of giant phytoplankton (10^2-10^3 µm diameter) that avoids competition with the smaller phytoplankton by utilizing a vertical migration strategy (Villareal et al. 1993; Villareal & Lipschultz 1995; Villareal et al. 1999b). Buoyancy regulation rather than flagellated motility allows these taxa to migrate 50-100+ m on a multiple-day time scale, acquire nitrate in sub-euphotic zone nitrate pools, and then return to the surface for photosynthesis (Villareal & Lipschultz 1995; Villareal et al. 1996; Woods & Villareal 2008). Such use of sub-nutricline derived nitrate to support carbon fixation at the surface defines the process as new production.

This group of phytoplankton have unique characteristics that identify them as vertical migrators to great depth in the open sea. *Rhizosolenia* mats, the best-studied migrators, are associations of multiple species of the diatom genus *Rhizosolenia* that form intertwined aggregates (Fig. 1) from <1-30 cm in size (Villareal & Carpenter 1989; Villareal et al. 1996). First observed as "confervae" by Darwin (Darwin 1860) from the South Atlantic, they occur in the N. Atlantic, N. Pacific and Indian Oceans (Villareal & Carpenter 1989). The high biomass available in single *Rhizosolenia* mats has made them useful general models of vertical migration

in non-flagellated phytoplankton with the caveat that almost all the physiological and compositional data are from a limited region of the eastern central N. Pacific gyre. Initially described as possessing diazotrophic symbionts (Martinez et al. 1983), subsequent work found no evidence of diazotrophy (Villareal & Carpenter 1989). *Rhizosolenia* mats possess mM internal NO_3^- pools (Villareal et al. 1996), utilize NO_3^- via nitrate reductase (Joseph et al. 1997), take up NO_3^- in the dark (Richardson et al. 1996), have a $\delta^{15}N$ (3-4 per mil) similar to the deep NO_3^- pool(Villareal et al. 1993), ascend at up to 6.4 m h^{-1}, become negatively buoyant under nutrient-depletion (Villareal et al. 1996) and positively buoyant as they take up nitrate (Richardson et al. 1996), and are documented down to several hundred meters by direct ROV observations (Pilskaln et al. 2005). These characteristics indicate a life cycle vertical migration to deep nitrate pools similar to the non-motile dinoflagellate *Pyrocystis* (Ballek & Swift 1986), a migration notable for the greater distance (~100 m) than that found in numerous flagellated taxa that migrate in the coastal zone (Kamykowski et al. 1978). Mat consumption by the vertically migrating lantern fish *Ceratoscopelus warmingii* (Robison 1984) provides at least one pathway for this C to be sequestered in the deep sea although the fate of these diatom mats is perhaps the least understood aspect of their biology. Free-living *Rhizosolenia* and *Ethmodiscus* spp, the dinoflagellate *Pyrocystis* spp., and the prasinophyte *Halosphaera* spp. each possess some subset of characteristics such as internal nitrate pools and buoyancy control that suggest a similar life-history characteristic (Villareal & Lipschultz 1995). Phytoplankton migrators are clearly transporting N (and presumably P) upward, but the significance of the process in oceanic nutrient budgets was hard to assess due to the limited geographic range of observations and abundance estimates (Emerson & Hayward 1995; Johnson et al. 2010). Although this flora is endemic to all warm oceans, their large size and relatively low numbers (~10^0-10^2 m^{-3}) have made quantification uncommon as research efforts focused on the dominant nano and picoplankton that are 6-7 orders of magnitude more abundant.

Recent observations of isotopic anomalies in phytoplankton groups (Fawcett et al. 2011) and unresolved nutrient inputs (Ascani et al. 2013; Johnson et al. 2010) have focused attention on phytoplankton sinking and ascent, and the role this may be playing in connecting deep nutrient pools with surface productivity. Nutrient budgets are key to constraining the "biological pump", the active removal of CO_2 from the surface ocean to the deep sea by biological processes (DeVries et al. 2012). At a first approximation, use of upwelled nitrate leads to little net export of carbon (Lomas et al. 2013) since carbon dioxide is transported upward along with deep nitrate as it upwells due to advection or turbulence (Eppley & Peterson 1979). This occurs as a result of the stoichiometric remineralization of organic material below the euphotic zone that releases CO_2 proportional to the amount incorporated into the organic material at the surface. This CO_2 is then returned, in general, by the same processes that return nitrate to the euphotic zone. However, vertical migration and N transport by phytoplankton uncouples N and C transport. Unlike NO_3^- injection by physical mixing, there is no stoichiometric transport of DIC (dissolved inorganic carbon) associated with migrating phytoplankton; thus, this N use drives net drawdown of atmospheric CO_2^- from the euphotic zone. However, the importance of potential CO_2 removal is dependent on unanswered questions surrounding the fate of these phytoplankton. In an analogous fashion, nitrogen-fixation can support net carbon drawdown to depth since the N source (N_2 gas) is uncoupled from the deep CO_2 pool (Eppley & Peterson 1979).

Nitrogen budgets of the upper water column that quantify nitrate and nitrogen-fixation inputs are therefore central to understanding the biogeochemical cycles of carbon in the euphotic zone and the remineralization region immediately below (often termed the twilight zone). Turbulent processes dominate transport across the nutricline and recent advances in profiling technology coupled with long-term deployments of floats have highlighted the role that mesoscale eddies play in supplying NO_3^- to the base of the euphotic zone (~100-150 m) (Ascani

et al. 2013; Johnson et al. 2010; McGillicuddy et al. 2007; McGillicuddy & Robinson 1997). At the long-term Hawai'i Ocean Time-series (HOT) station, annual nutrient budgets balance in the upper 250 m when eddy injection is included, indicating that the required nitrate fluxes to support primary production are met by nitrate remineralized from sinking material in the upper 250 m. However, NO_3^- concentrations rapidly decrease to nanomolar levels immediately above the nutricline (~80-100 m) (Johnson et al. 2010). There is no mechanism to move NO_3^- along this negligible diffusion gradient into the upper water column where most community production occurs and budgets require (Johnson et al. 2010). However, < 30 µm diameter eukaryotes cells are found with $\delta^{15}N$ signatures of 4-5 at 30-60 m in the Sargasso Sea, suggesting sub-euphotic zone nitrate is reaching these depths (40+ m above the nutricline) (Fawcett et al. 2011). Nitrate budgets using profiling floats and subsequent modeling have indicated that a biological transport of nitrate upward is the most likely mechanism for supply the upper euphotic zone (Ascani et al. 2013; Johnson et al. 2010)

Phytoplankton migrating across this gradient could provide a mechanism for transport via subsurface uptake and subsequent shallow excretion (Singler & Villareal 2005). In the eastern N. Pacific gyre, vertical migration is estimated to account for an average of 14% of new production with maximum values up to 59% (Singler & Villareal 2005; Villareal et al. 1999b). This transport has proven difficult to quantify on larger scales due to the challenges in enumerating and sampling these populations. The taxa involved, *Rhizosolenia*, *Pyrocystis*, *Halosphaera*, and *Ethmodiscus* spp. are sufficiently rare (~10^0-10^2 cells m^{-3}) that large water samples or nets are required to enumerate them. Migrating diatom aggregates (*Rhizosolenia* mats, up to 30 cm in size) are fragile, requiring enumeration and hand-collection by SCUBA divers (Alldredge & Silver 1982; Carpenter et al. 1977). Further complication arises from the observations that small mats (~1 cm) dominating the *Rhizosolenia* mat biomass are visible only with sophisticated *in-situ* optical sensors that overcome both contrast problems and depth limitations for SCUBA (Villareal et al. 1999b). Moreover, the recognition that in the open ocean cells < 5 µm in diameter dominate uptake and remineralization has shifted focus away from the largest size fractions towards the very smallest phytoplankton (Azam et al. 1983; Hagström et al. 1988; Karl et al. 2001; Li et al. 2011; Malone 1980; Maranon et al. 2001).

In this paper, we present a synthesis of both literature reports and direct observations to address the broader scope of vertical migration and nutrient transport in the open sea. For vertical migration to be relevant to oceanic nitrogen cycles, migrators must be widespread, episodically abundant at levels sufficient to support the required rates, and possess the chemical and isotopic signatures of deep nitrate pools. We present new data using *in-situ* optical systems complemented by isotopic and abundance data that spans much of the N. Pacific Ocean. Also presented is a synthesis which documents the widespread abundance of vertically migrating *Rhizosolenia* mats in the Pacific Ocean and their quantitative importance in transporting and releasing N as NO_3- within the upper 250 m.. We also compile published data on other migrating phytoplankton in the genera *Rhizosolenia*, *Ethmodiscus*, *Halosphaera*, and *Pyrocystis*, concluding that they constitute a ubiquitous and under-sampled aspect of nutrient cycling linked directly to the behavioral characteristics of the phytoplankton. Finally, we present literature evidence that ascending behavior in smaller phytoplankton is sufficiently widespread to require a systematic re-evaluation of the paradigm of predominant downward movement of phytoplankton in the ocean.

Methods and Materials

Six research cruises between 1993-2003 examined *Rhizosolenia* mat biology along longitudinal transects at ~28-31° N from California to Hawaii and Hawaii to west of Midway Island (Fig. 2). *Rhizosolenia* mats were hand-collected by SCUBA divers (0-~20 m) as part of a

multi-year effort to enumerate and characterize their biology. Briefly, divers collected mats in polymethylpentane plastic containers (250-500 ml volume), and returned them to the ship in a closed ice chest. Mat lysis (Martinez et al. 1983) was not observed. Mats were sorted into sinking and floating mats (Villareal et al. 1996), and then filtered onto precombusted GF/F filters followed by measurement of the concentration and isotopic composition of particulate organic N and C by continuous-flow isotope ratio mass spectrometry (CF-IRMS) (Montoya et al. 2002). Divers enumerated mats in the upper 20 m using a 1 m^2 frame equipped with a flow meter (Singler & Villareal 2005; Villareal et al. 1996). Integrated abundance used a trapezoidal integration to the maximum depth sampled (~20 m) and is reported as mats m^{-2}. In addition, abundance data were drawn from literature sources (Alldredge & Silver 1982; Martinez et al. 1983) extending the time frame to 26 years.

A towed optical system (Video Plankton Recorder) was used to quantify abundance in the upper 150 m [15]. To collect the 2003 VPR data set, we employed a recalibrated and tested VPR also used in our 1996 study (Pilskaln et al. 2005; Villareal et al. 1999b). The VPR package consisted of a CCD video camera synchronized at 30 frames sec^{-1} to a xenon strobe (600 nm), a video recorder and CTD, all mounted to a tow frame with a rear stabilizing fin (Davis et al. 1992). Collected videotape was in Hi-8/S-VHS video format. The intersection of the strobe light volume and the camera's field of view represented an elongate trapezoid shape with a 7 cm depth of field and an individual image volume of 0.12 liter. A non-reparable malfunction of the VPR-interfaced CTD on our 2003 cruise made structural adjustments necessary in order to complete the VPR surveys which involved mounting the VPR (minus its CTD) to the CTD rosette. The fin section and camera/strobe section of the VPR were separated and remounted to the CTD rosette in order to have the camera field of view extended out (~40 cm) from the rosette frame with an unobstructed view of the water column. Additionally the fin was positioned on the top of the rosette so that the camera view remained oriented into the flow as the CTD rosette was lowered and "towed" through the water column. Ship speed was maintained at 1 knot during CTD rosette/VPR tows in which the wire-in/out speed was maintained at 12 m min^{-1}. Four complete round-trips of the CTD rosette/VPR package between the surface and 150 m were completed at each station with a calculated water volume of 0.5 m^3 viewed per each 0-150 m leg and 4.0 m^3 per station tow-yo series. To provide synching of the CTD data and the VPR imagery for post-cruise analysis, a stopwatch was zeroed when the camera and strobe were turned on prior to deployment over the side. The stopwatch time was then recorded when the CTD rosette/VPR system began the first leg of the tow-yo series between the surface and 150 m and the time was recorded at the top and bottom of each 150 m leg.

VPR video from the tow-yo series completed at 10 stations and coincident with SCUBA-survey and sampling of *Rhizosolenia* mats in the upper 60 m, was examined post-cruise. The analogue imagery from these stations was digitized and sub-sampled every 0.2 s, which assured us that we were viewing new water volume, considering the image dimensions and the ship and wire-in/out speed. The VPR data presented is from 4 of ten 2003 stations. Significant issues with the other stations' VPR image quality (i.e., focus electronic interference problems) and/or video recorder failures rendered the VPR imagery from 6 of the 10 stations unreliable for mat quantification. IDL and ImageJ software were used to time-link CTD data to each image, to view the collected imagery and identify *Rhizosolenia* mats, and to compile mat counts. Mat identification was based on their distinctive morphology of intertwining diatom chains, forming aggregations approximately ~1 cm in size (Villareal et al. 1996), a size class rarely observed or enumerated by divers. Based on the depth occurrence of each identified *Rhizosolenia* mat, we determined the mat abundance within the depth intervals of 0-20 m, 20-50 m, 50-100 m and 100-150 m.

Results and Discussion

Abundance and depth distribution of Rhizosolenia mats

Rhizosolenia mats (Fig. 1) were observed by divers at every station sampled over the 19 year period spanning the cruises (Fig. 2). In general, maximum abundance occurred at the surface (up to ~12.5 mats m^{-3}) with decreasing abundance at depth (Fig. 3). However, mats were clearly visible at depth to the limit of visibility. While mats were visible at all stations in Fig. 2, abundance was quite variable and occasionally (4 of 96 stations) below detection limit of the sampling frame. (~1 mat in 30 m^3). For the 1989-2003 cruises cruises (the 2008 cruise was snorkel only with no abundance data collected), average integrated abundance was 4.1 ± 5.7 mats m^{-3} with a range of 0.03-27.5 mats m^{-2} excluding the 4 station where mats were below enumeration limits (Fig. 4). These values were combined with literature reports from this area in Fig. 4, generating an unprecedented 26 year summary of *Rhizosolenia* mat distribution and diver-estimated abundance.

Similar to our previous VPR data sets [12,23], the 2003 VPR imagery revealed an abundance of *Rhizosolenia* mats that were ≤1 cm in size. These small-sized mats are under-counted in diver surveys [12, 23]. Our observations along a transect line from 168-177° W found mats were distributed to at least 150 m (Fig. 5). The vertical distribution had no consistent pattern with some stations (Sta. 7) showing a surface maximum, while other stations (Sta. 5) had a maximum at depth. In all cases, abundance did not drop to zero at the deepest strata. Integrated values (Table 1) ranged from 188-17,062 mats m^{-2}. The single replicated samples (Sta. 12) showed good agreement between profiles with the two samples within 2% of the mean. When VPR and diver counts were compared, divers consistently under-estimated mat abundance. The 0-150 m integrated VPR counts were up 6-2,843 times higher than the diver-based 0-20 m integrated counts (Table 1). VPR-based integrated abundance varied nearly 200-fold from 80-17,062 mats m^{-2} with 90% below diver accessible depths and had no relationship (r^2=0.08) to diver-based abundance in the 0-20 m range (Table 1). The 2003 counts were up to 100-fold higher than VPR-based abundance data collected 2,000 km to the east in 1996 (Villareal et al. 1999b).

Nitrogen isotope values

Mat $\delta^{15}N$ was uniformly elevated across the basin (Fig. 6, 7) and averaged 2.91±0.28 (95% C.I., n=181) when combined with historical data (Villareal et al. 1993; Villareal et al. 1999b; Villareal et al. 1996). Ascending mats were significantly (p=0.05) depleted in ^{15}N relative to sinking mats (Fig. 6, Table 2), consistent with the impact of isotopic fraction during nitrate uptake and reduction when nitrate is available in excess (Granger et al. 2004). 60% of the observed values were in the 2-6 per mil range and enriched in ^{15}N relative to the suspended particulate material at the surface (Fig. 7). The $\delta^{15}N$ of the ambient NO_3^- pool in 2002 at 200-400 m ranged from 5.29-6.73 per mil consistent with historical observations (Fig. 7). Inclusion of additional data from Station ALOHA(Casciotti et al. 2008) highlighted the lighter isotopic values of NO_3^- in the nutricline expected as the result of the remineralization of diazotrophically derived N. The similarity to the *Rhizosolenia* mat $\delta^{15}N$ is clear and strongly suggests that mats are generally migrating to the 150-200 m depth range. Mats in both years contained mM internal NO_3^- pools and were actively excreting NO_3^- (Singler & Villareal 2005). While we could not measure the isotopic composition of this excreted N, kinetic considerations suggest the resulting mat would be enriched in $^{15}NO_3^-$ and lead to the observed ascending/descending $\delta^{15}N$ mat differences. During 2002-2003, C:N ratios in sinking mats were significantly higher than in ascending mats across the entire longitudinal gradient (Table 2), a marker resulting from unbalanced uptake of N and C and consistently tied to a vertical migration strategy (Villareal et al. 1996).

These data provide a clear picture of *Rhizosolenia* mat abundance across the Pacific Ocean as well as within their vertical migration range. The latitudinal distribution extends from ~24° to ~35° N with additional observations near Oahu, Hawai'i (Cowen & Holloway 1996), the coastal California current, and equatorial Pacific (Alldredge & Silver 1982). Mats were observed over 50° of longitude (~1/2 the width of the Pacific Ocean) and were abundant at the western terminus of the cruise set. We found no further records in the Pacific Ocean west of this point, but the broad distribution in the Indian Ocean (Carpenter et al. 1977; Wallich 1858; Wallich 1860), North and South Atlantic Ocean (Caron et al. 1982; Carpenter et al. 1977; Darwin 1860), equatorial Atlantic Ocean (Bauerfeind 1987) and north and south Central Pacific Ocean (Alldredge & Silver 1982) supports a reasonable expectation that their distribution extends across the entire Pacific Ocean (Villareal & Carpenter 1989). Abundance is lower in the Sargasso Sea (Carpenter et al. 1977), although they are still present. Our 2003 VPR observations confirm the earlier report that small *Rhizosolenia* mats dominate both numerically (Villareal et al. 1999b),[23] and in particulate Si contribution (Shipe et al. 1999). These small mats are virtually invisible to divers due to the low contrast of small mats, and the depth limitations imposed on blue-water SCUBA techniques (~20 m) preclude diver enumerations at depths (Villareal et al. 1999b),[23]. We conclude that the pattern of numerically dominant small mats extending to depth is the prevailing distribution of *Rhizosolenia* mats and that the mats are both widespread and abundant in the Pacific Ocean.

Rhizosolenia mat $\delta^{15}N$ values show a pattern dominated by values typical of sub-euphotic zone nitrate. Prior to this study, only a handful of values were published raising the possibility that these were not representative of larger scales. However, our current data set spans nearly ½ the Pacific Ocean and clearly shows high $\delta^{15}N$ NO_3^- pools as an N source. Vertical migration is a consistent feature of their biology and occurs across the entire distributional range. A re-assessment of the quantitative importance of mat N transport is required and is particularly timely given the urgent need to identify mechanisms capable of closing euphotic zone nitrate budgets (Ascani et al. 2013; Johnson et al. 2010). In the next section, we will consider the implications for nutrient cycling and the role of ascending motion in general in phytoplankton.

Significance to oceanic nutrient cycles

The upward nitrate flux problem derives from budgeting analysis that concludes that nitrate introduced at the base of the euphotic zone must be transported upward many 10s of meters to zones of net community production and export (Ascani et al. 2013; Johnson et al. 2010). In order to assess the potential role of *Rhizosolenia* mats in the Pacific, and by inference, other migrating phytoplankton, we evaluated this using our new data and previously published models. Nitrogen transport rates are calculated from abundance data coupled to a turnover model that includes parameters for photosynthetic rates, sinking to depth, nutrient acquisition, ascent and doubling (Richardson et al. 1998; Villareal et al. 1996). Briefly, photosynthesis at the surface permits nitrate assimilation from internal pools. Negative buoyancy increases as the mats undergo progressive N limitation and sink to depth (Villareal et al. 1996). Nitrate assimilation occurs at depth and in the absence of light, leading to buoyancy reversals and ascent to the surface (Richardson et al. 1996). At the surface, the pattern repeats with some fraction of the nitrate being lost via excretion (Singler & Villareal 2005). Protist parasitism has been noted and probably results in nitrate release as well (Villareal & Carpenter 1989). This is shown conceptually in Fig 8.

The nitrogen transport rates calculated from the VPR abundance ranged from 6-444 µmol N m^{-2} d^{-1} (Table 1) with an average daily rate of 172 µmol m^{-2} d^{-1}. However, our abundance data are not uniformly distributed across the year. *Rhizosolenia* mat observations are biased towards

June-October due to weather constraints on diving operations. We have only limited reports from April/May (Alldredge & Silver 1982; Villareal & Carpenter 1989) and no quantitative estimates for the balance of the year. Therefore, using a conservative 6 month distribution window to reflect this, we calculate an annual flux based on abundance at each of our stations (range = 1.1-79.9 mmol N m^{-2} y^{-1}). The upper value is directly comparable to the eddy injection N (88 mmol N m^{-2} y^{-1}) calculated to balance the N budget in the upper 250 m (Johnson et al. 2010). These calculations suggest that nitrogen transport via *Rhizosolenia* mats scales on an event basis that is comparable to eddy injection of nitrate to the euphotic zone, while recognizing that upward transport is not sustained at that level. This calculation is a conservative underestimate since anecdotal observations indicate mats are present year round in the eastern Pacific (Alldredge & Silver 1982).

Finding the proper spatial and temporal scales for comparison is a challenge. Eddy injection (a physical process) and *Rhizosolenia* mat dynamics (a biological process) likely operate, and are certainly recorded, on different time scales. For example, the nutrient budgets were assembled for the Hawai'i Ocean Time-Series region at Station ALOHA at 22° 45'N, a latitude that has high trade winds much of the year that inhibit diving operations. *Rhizosolenia* mat data were collected several hundred kilometers to the north (~28-30°) where wind conditions permit divers to routinely enter the water. Eddy turbulent kinetic energy and numbers of eddies in the mat collection areas are low (Chelton et al. 2011) relative to Station ALHOA. We have no site where both long-term N budgets and *Rhizosolenia* mat abundance are available. In addition, *Rhizosolenia* mats are not unique in their migration strategy, and comprehensive consideration of phytoplankton upward nitrate transport requires inclusion of other migrating phytoplankton taxa. A brief review is presented here to provide the required perspective and background to justify inclusion of these taxa in the subsequent calculations.

Other vertically migrating phytoplankton taxa: life history and abundance

The literature on other migrating, non-flagellated phytoplankton in the open sea is dispersed and the natural history of this group poorly represented in the literature of the past several decades. There are several taxa that must be represented and spanning a broad taxonomic range: *Pyrocystis*, *Halosphaera*, *Ethmodiscus*, and free living *Rhizosolenia*.

Pyrocystis species are positively buoyant warm water, non-motile dinoflagellates with a dominant cyst-like non-motile stage typically 10^7 μm^3 (Rivkin et al. 1984b). They undergo a "once in a lifetime" migration to the nutricline (Rivkin et al. 1984b) and are considered members of the shade flora (Sournia 1982). Reproduction occurs by release of a brief reproductive stage from a cyst-like vegetative form (Swift & Durbin 1971). Bilobate reproductive stages release immature vegetative stages that swell up to near full size in ~10 min (Swift & Durbin 1971), become positively buoyant within 13 h and indistinguishable from the cyst-like form after 15 h (Swift et al. 1976b). Thecate, dinoflagellate stages appear as swarmers in some species (Meunier & Swift 1977; Swift & Durbin 1971). Buoyancy reversals in the cyst form occur when negatively-buoyant nutrient-depleted stages descending to the nutricline are resupplied with NO_3^- and become positively buoyant, consistent with acquiring NO_3^- at depth (Ballek & Swift 1986). Non-motile stage cells take up NO_3^- and NH_4^+ at almost equal rates in the light and dark (Bhovichitra & Swift 1977) and field-collected cells at the surface contain up to 8 mM internal nitrate pools (Villareal & Lipschultz 1995). Growth rates in culture range up to 0.2 div day^{-1} (Bhovichitra & Swift 1977), with doubling times of 4-14 (*P. fusiformis*) and 10-22 days (*P. noctiluca*) in field populations (Swift et al. 1976a). Abundance is reported up to 200 cells m^{-3} in the Atlantic Ocean (Rivkin et al. 1984a; Swift et al. 1976a) and 40-50 cells m^{-3} in the Pacific Ocean (Sukhanova 1973; Sukhanova & Rudyakov 1973). Photosynthetic and light acclimation curves from field populations showed a time-averaging of the light field such that C fixation at

the surface supported a near-constant doubling rate throughout the euphotic zone (Rivkin et al. 1984a).

Halosphaera is a genus of positively buoyant non-motile phycomate prasinophytes noted throughout the oceans (poles to tropics) from the earliest days of oceanography (Agassiz 1906; Schmitz 1878; Sverdrup et al. 1942). It is listed as a member of the shade flora (Sournia 1982). Reproduction occurs by swarmer formation with up to 50,000 flagellated swarmers released from a phycoma (Parke & den Hartog-Adams 1965). Individual swarmers can vegetatively reproduce, and then after 14-21 days start to increase in size at 5-10 µm d^{-1} to reach a species-specific diameter of several hundred microns. At this time, the cytoplasm undergoes numerous divisions to form flagellated swarmers (Parke & den Hartog-Adams 1965). Size and photosynthetic rates (3-~6 ng C $cell^{-1}$ h^{-1}) are similar to *Pyrocystis* (Rivkin & Lessard 1986). Growth rates are poorly known; reproduction is linked to lunar rhythms in the North Sea and adjacent waters. Internal nitrate pools up to 100 mM have been documented (Villareal & Lipschultz 1995), and deep populations with seasonal descent and ascent are noted in the Mediterranean Sea (Wiebe et al. 1974). Abundance ranges from ~10^{-3} cells m^{-3} (Wiebe et al. 1974) to 340 cells L^{-1} (Gran 1933). *Halosphaera* is representative of a number of species that reproduce by phycoma and swarmer formation, including members of the genus *Pterosperma*. Typical concentrations reported for the Mediterranean are 1-3 L^{-1}; *Pterosperma* is reported at ~40 cells L^{-1} in HNLC areas of the Pacific Ocean (Gomez et al. 2007). In the text calculation on N-transport, we have assumed an abundance of 200 cells m^{-3} (0.2 cells L^{-1}) as a conservative mid range value of the 9 order of magnitude abundance range for this group.

Ethmodiscus spp. are solitary centric diatoms and are the largest known with a diameter of > 2,000 µm in the Pacific Ocean; cells are somewhat smaller in the Atlantic Ocean (Villareal & Carpenter 1994; Villareal et al. 1999a). Internal nitrate concentrations from surface-collected samples reached 27 mM in the Sargasso Sea (Villareal & Carpenter 1994). Cells become increasing negatively buoyant as internal NO_3^- pools are depleted with positively buoyant cells having significantly higher internal nitrate concentrations than sinking cells (Villareal & Lipschultz 1995). Nitrate reductase activity, C doubling and Si uptake rates can support doubling times of 45-75 h in large Pacific cells (Villareal et al. 1999a); cell cycle analysis suggests division rates of 0.4-0.7 div d^{-1} in smaller Atlantic cells(Lin & Carpenter 1995). Abundance ranges from 0.03-4.7 cells m^{-3} in the Atlantic and 0.02-6 cells m^{-3} in the central Pacific gyre (Belyayeva 1968; Belyayeva 1970; Villareal et al. 2007). Maximum reported abundance is 27.3 cells m^{-3} in equatorial waters off Chile (Belyayeva 1972) and increases westward into the open Pacific Ocean with the highest values near the equator (Belyayeva 1970). Ascent rates reach 4.9 m hr^{-1} (Moore & Villareal 1996b) and like *Pyrocystis* and *Rhizosolenia*, appears to result from active ionic regulation of inorganic (Woods & Villareal 2008) and organic compounds required for osmoregulation (Boyd & Gradmann 2002). Living cells have been collected in downward facing sediment traps at 5400 m (Villareal 1993) indicating living cells with positive buoyancy at great depth.

Several of the *Rhizosolenia* species that are found in mats also exist as free-living diatom chains. These species exhibit similar characteristics to mat-forming spp. Internal nitrate pools are present at up to 26 mM (Moore & Villareal 1996a). Individual species (non-aggregated) ascend at up to 6.9 m h^{-1}, depending on species and are also listed as members of the shade flora (Sournia 1982). Growth rates for buoyant species are known from laboratory (0.37-0.78 div d^{-1}) [79] and field (1.0 div d^{-1}) (Yoder et al. 1994) studies. Other characteristics are similar to *Rhizosolenia* mats (Moore & Villareal 1996a). Little abundance information is available. *R. castracanei* is reported at up to 10^3 cells L^{-1} from the Bay of Naples (Marino & Modigh 1981) and 50 cells m^{-3} in Sargasso Sea warm core rings (TAV and T. J. Smayda, unpublished data). *R. debyana* reached 10^6 cells L^{-1} in the Gulf of California in bloom conditions (Garate-Lizarraga et al. 2003); similar

abundance was likely in the equatorial Pacific "Line in the Sea" front accumulation (Yoder et al. 1994).

Significance of migrating phytoplankton to the North Pacific nitrogen budget

In this final step of the calculation, we incorporated these additional migrating taxa into the model. In order to compare the spatially limited input of a mesoscale eddy with the broader distribution patterns of phytoplankton, we combined conservative abundance data and growth rate estimates for *Halosphaera*, *Ethmodiscus*, *Pyrocystis* and solitary *Rhizosolenia* spp. (Table 2) and calculated their combined contributions to NO_3^- flux to be 62.5 µmol N m^{-2} d^{-1}. Using profiler-derived estimates of eddy NO_3^- injection from the Pacific Ocean (Johnson et al. 2010) , we considered the nitrate input via eddy injection over the entire time frame of measurement (145 mmol NO_3^- m^{-2} over 600 days), and computed an average daily eddy injection rate of 242 µmol NO_3^- m^{-2} d^{-1}. Nitrate transport of *Rhizosolenia* mats (2002/2003 data) combined with other taxa equals 235 µmol N m^{-2} d^{-1}. This nearly equals the average daily eddy injection of nitrate (242 µmol NO_3^- m^{-2} d^{-1}). Our previous VPR estimates of mats (Villareal et al. 1999b) is lower, and reduces the upward transport to 179 µmol N m^{-2} d^{-1} if we include those abundance estimates. However, within the uncertainties of both calculations, this is remarkably good agreement. On a time scale of weeks to months, migrating phytoplankton can transport sufficient N from deep euphotic zone pools to the upper euphotic zone to significantly impact nutrient budgets. Upward biological transport of nitrate is quantitatively important to the biogeochemistry of surface waters in the N. Pacific gyre. Other mechanisms may exist, but migration alone appears to be sufficient to dominate the required upward transport.

Acquisition of imported N by other phytoplankton requires release of internal nitrate pools or remineralization by grazers. *Rhizosolenia* mats directly release nitrate. Using excretion rates (Singler & Villareal 2005) for NO_3^- (2 cruise range: 22.8-23.7 nmol N µg chl^{-1} h^{-1}) and published N:Chl ratios (1.7 µmol N: µg chl a) (Villareal et al. 1996), we calculate N-specific release of ~1.3% h^{-1} or up to 31% d^{-1}. Release rates vary with Fe status, buoyancy status and location along the E-W gradient (Singler & Villareal 2005); however, it is clear that over time scales of days to weeks, *Rhizosolenia* mats (and by inference, other high nitrate cells) will release NO_3^-. Grazers on this size class are poorly known. Hyperiid amphipods are associated with mats, as well as parasitic dinoflagellates and ciliates (Caron et al. 1982; Villareal & Carpenter 1989; Villareal et al. 1996). Nitrate is probably released during feeding by myctophids as well (Robison 1984). Energy dissipation via reduction of oxidized N and subsequent release provides additional pathways to the environment in nitrate-using cells (Lomas et al. 2000). Such release by both *Rhizosolenia* and other ascending, high NO_3^- cells provides the needed mechanism for transporting NO_3^- to the required depths for net community production (Johnson et al. 2010), balancing isotope budgets (Altabet 1989), and providing sources for the observed difference in the $\delta^{15}N$ of NO_3^- in small pro- and eukaryotes (Fawcett et al. 2011).

The uncertainty in the vertically migrating flora abundance is not trivial; *Halosphaera* abundance records span 9 orders of magnitude and this uncertainty profoundly affects the calculations. While *Halosphaera* may be extreme, it highlights the difficulties in enumerating a frequently rare and largely ignored component of the marine phytoplankton. Moreover, there are significant gaps in our knowledge of the biology of these taxa, their life cycles and migration timing that create uncertainties in how to apply this information.

Conclusions

Upward transport by phytoplankton is a quantitatively significant mechanism for transporting nutrients to the oceanic euphotic zone across broad regions of the open sea. There are multiple taxa involved and all oligotrophic seas possess several of them. In these large cells,

NO_3^- excretion is probably the inevitable consequence of the mM to nM concentration gradients across the cell surface (Ter Steege et al. 1999). Although the congruence between the required N flux for budgets and the contribution from migrating flora is surprisingly good, the deeper significance of our finding is in the combined role that biology and physics play in moving essential nutrients in both directions between deep pools and the surface. NO_3^- importation by the vertically migrating flora is but one component of active material rearrangement by the biota. Zooplankton diel vertical migration transports material out of the euphotic zone for remineralization and is a significant loss to the euphotic zone (Steinberg et al. 2000; Steinberg et al. 2002; Steinberg et al. 2008). It can represent 10-50% of the C and N flux out of the euphotic zone (Bollens et al. 2011) and up to 82% of the P flux (Hannides et al. 2009). When combined with phytoplankton vertical migration, the picture that emerges is of biological transport, both upward and downward, superimposed on both physically driven and biologically mediated new nitrogen inputs. Nitrogen-fixation coupled with NO_3^- release by the vertically migrating flora creates a zone of biological nutrient sources near the surface distinct from a deeper zone dominated by physical processes. In the Pacific Ocean, surface and deep phytoplankton communities persist over 1000's of km with a separation at the transition from nutrient- to light-limitation (~100 m) (Venrick 1982; Venrick 1999). A pattern emerges of a hydrographically structured two (or more)-layered euphotic zone with differing phytoplankton communities and biological/physical inputs of new nitrogen. Turbulent diffusion and eddy injection of NO_3^- dominates at the base of the euphotic zone; biological processes move N towards the surface and together with nitrogen-fixation provide the community production required to close new N nutrient budgets.

Ascending behavior in non-flagellated phytoplankton is not limited to giant cells in the ocean. Positive buoyancy is the result of lift (cell sap density) exceeding ballast (silicate frustule in diatoms, cell wall in others)(Woods & Villareal 2008) and theoretical considerations have suggested that there is a minimal cell size that can support positive buoyancy (Villareal 1988). However, there is persistent evidence of positive buoyancy in smaller (10s vs 100s µm diameter) spring bloom diatoms (Acuña et al. 2010; Jenkinson 1986; Lännergren 1979), Antarctic diatoms (Hardy 1935), deep chlorophyll maximum diatoms (Waite & Nodder 2001) and post-auxospore diatoms (Smayda & Boleyn 1966; Waite & Harrison 1992). Cells as small as 200 μm^3 (equivalent spherical diameter= ~8 µm) could be capable of positive buoyancy (Waite et al. 1997). These observations are scattered, but consistent with laboratory data that in sinking rate experiments, some fraction of healthy cultures are generally positively buoyant (Bienfang 1981). Stoke's velocities of this size range of phytoplankton are < 1-2 m d^{-1} (Smayda 1970); however, aggregation and chain formation could increase the effective size and the Stoke's velocity. Clearly, there are numerous aspects of this phenomenon that are unresolved, but the core observation that ascending behavior occurs in a variety of non-flagellated phytoplankton cannot be ignored.

The abundant but scattered data that document ascending behavior in a diversity of both small and large cells are contrary to standard concepts of passive phytoplankton settling in the ocean, but is consistent with evolutionary adaptation to a physical partitioning of light and nutrient resources (Ganf & Oliver 1982; Smetacek 1985). We have considered only the largest vertical migrators, but persistent reports of small, ascending phytoplankton coupled with the long-noted potential of flagellated forms to vertically migrate in the open sea (Nielsen 1939) opens entirely new linkages between events in the deep euphotic zone (Brown et al. 2008; McGillicuddy et al. 2007) and the response of surface communities. The ascent of some fraction of the biomass is a mechanism rarely considered in models of nutrient cycling in the open sea but should not be ignored. Quantifying these upward fluxes is a challenge for existing instrumentation and will likely require new approaches.

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Table 1 (on next page)

N flux across the nutricline calculated from video plankton recorder (VPR) and diver-based observations made during 2003.

Table 1. N flux across the nutricline calculated from video plankton recorder (VPR) and diver-based observations made during 2003. Flux calculations assumed 0.19 and 2.5 µmol N mat^{-1} (Villareal et al. 1999b) for small and large mats, respectively, and a specific rate increase of 0.14 d^{-1} (Richardson et al. 1998) Diver and VPR estimates are added due to the non-overlapping nature of the abundance estimates. These estimates are supplemented with contributions to upward nitrate flux from other (non-*Rhizosolenia* mat) migrating phytoplankton. Doubling time reflects the time required to migrate to depth, acquire nutrients, return to the surface and divide and is based on direct measurement or best available information.

Rhizosolenia mats

Integrated mats (mats m^{-2})	Sta. 5	Sta. 6	Sta. 7	Sta. 12a	Sta. 12b
Divers (0-20 m)	26	3	3	6	6.4
VPR (0-20 m)	188	38	3938	38	300
VPR (0-150 m)	2,475	188	6,562	17,062	16,612
VPR:Diver (0-20)	7	13	1313	6	47
N flux (µmol N m^{-2} d^{-1})					
Diver-based N flux	8.9	1	1	2	2
VPR-based N flux	64	5	170	442	430
TOTAL (Diver+VPR)	73	6	171	444	432

Other Migrating Phytoplankton

Taxon	Abundance 0-100 m (cells m^{-3})	N doubling time rate (d^{-1})	nmol N $cell^{-1}$	N flux µmol N d^{-1}
Ethmodiscus spp.	1	0.09	29	3.2
Halosphaera spp.	200	0.1	1.5	33.2
Pyrocystis spp.	200	0.06	0.8	17.0
Rhizosolenia spp.	50	0.14	1.6	9.2
TOTAL				62.5

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Table 2(on next page)

Compositional values of *Rhizosolenia* mats from 2002-2003. These data span from apprpoximately 145° W to 178° E.

Table 2. Compositional values of *Rhizosolenia* mats from 2002-2003. These data span from apprpoximately 145° W to 178° E.

Year	2002			2003		
	$\delta^{15}N$	$\delta^{13}C$	C:N	$\delta^{15}N$	$\delta^{13}C$	C:N
Mat Buoyancy						
ascending	1.38±0.6 (30)	-30.41±0.45 (30)	8.0±0.5 (51)	2.5±0.4 (95)	-30.71±.30 (92)	6.9±1.6 (92)
sinking	3.6±0.8 (5)	-30.41±0.22 (5)	12.3±1.8 (18)	3.5±0.5 (34)	-30.80±.80 (34)	12.3±0.8 (34)

Figure 1

Fig. 1. *Rhizosolenia* mats

Fig. 1. *Rhizosolenia* mats A. Orientation view of *Rhizosolenia* mats *in-situ*. Numerous mats are evident; the largest is approximately 6 cm in diameter. Station 13, 5 July 2002, 30.438 N 145.450 W B. Individual *Rhizosolenia* mat approximately 3 cm in size. Station 13, 5 July 2002, 30.438 N 145.450 W C. micrograph of individual mat *Rhizosolenia* chains. The large diameter chain is ~100 µm in diameter. Brown regions are the nuclear mass and protoplasm of individual chains. Some cell lysis is evident due to the pressure of the cover slip. Sta. 13 7 Sept. 1992 31.38 N 149.89 W.

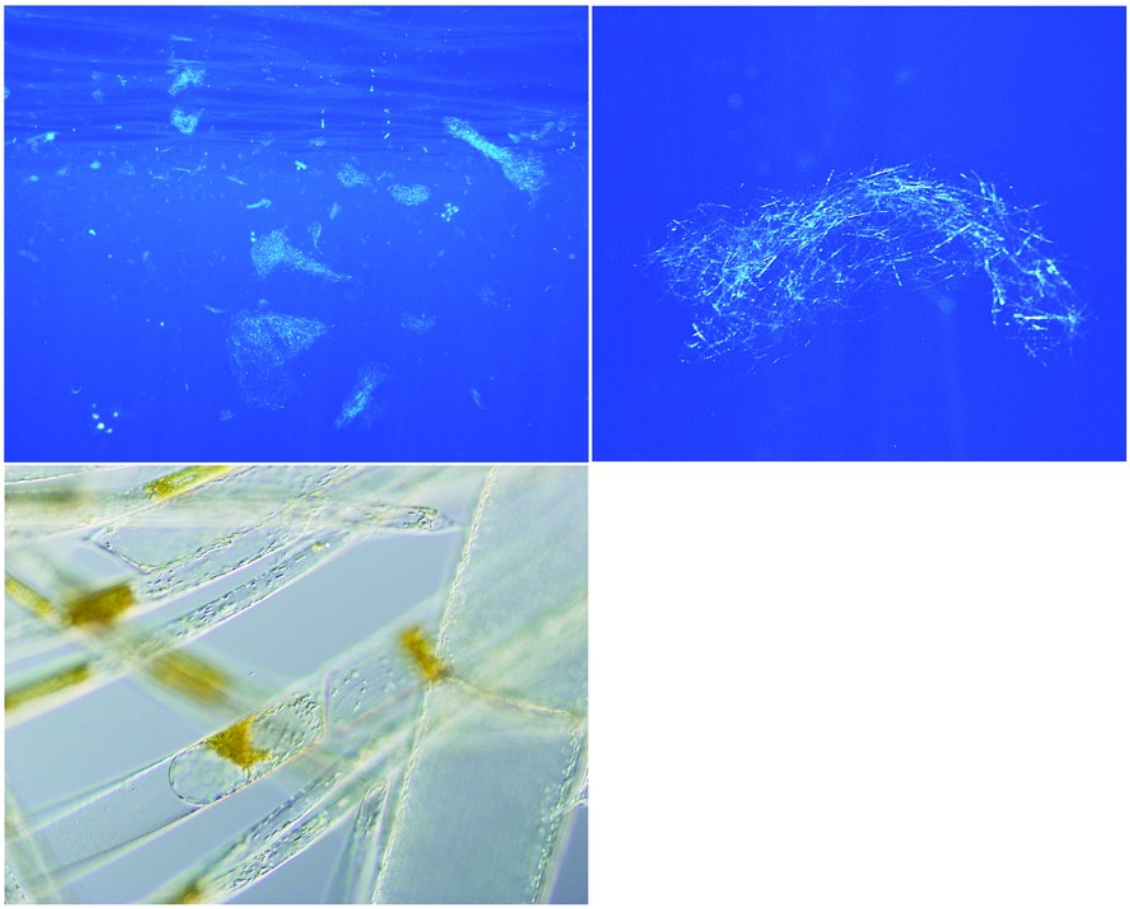

Figure 2

Cruise track map of sampling locations.

Fig. 2: Cruise track map of sampling locations. Cruises RNBT17WT (Mar/April 1989), W9208C (Aug. 1992), PacMat (May/June. 1993), RoMP95 (Jun./Aug. 1995), RoMP96 (Jun./Aug. 1996), RoMP2002 (Jun. 2002), RoMP2003 (Aug./Sept. 2003), POOB2008 (Jul. 2008).

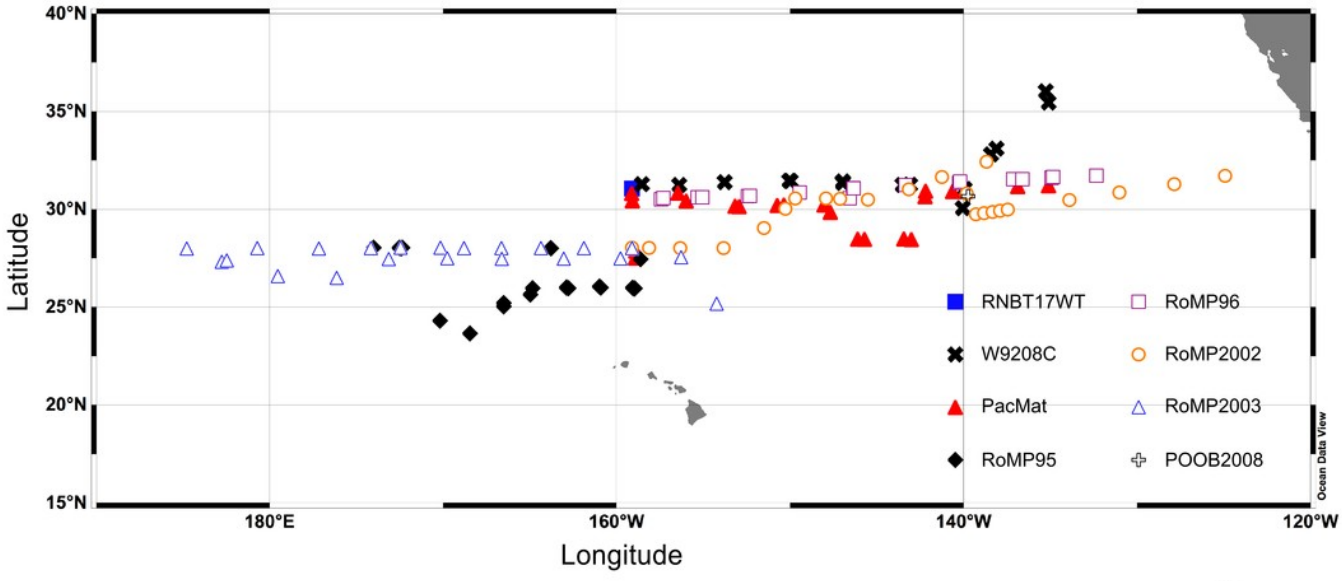

Figure 3

Vertical distribution and abundance of *Rhizosolenia* mats observed by divers.

Fig. 3 Vertical distribution and abundance of *Rhizosolenia* mats observed by divers. Abundance was estimated visually using a metered frame. The 1982 data are from Alldredge and Silver (Alldredge & Cox 1982) . The remaining data (67 stations) are from cruises summarized in Fig. 2. For purposes of plotting, a zero abundance at a depth was recorded as 0.01 mats m^{-3}. Integrated mat abundance used actual values collected.

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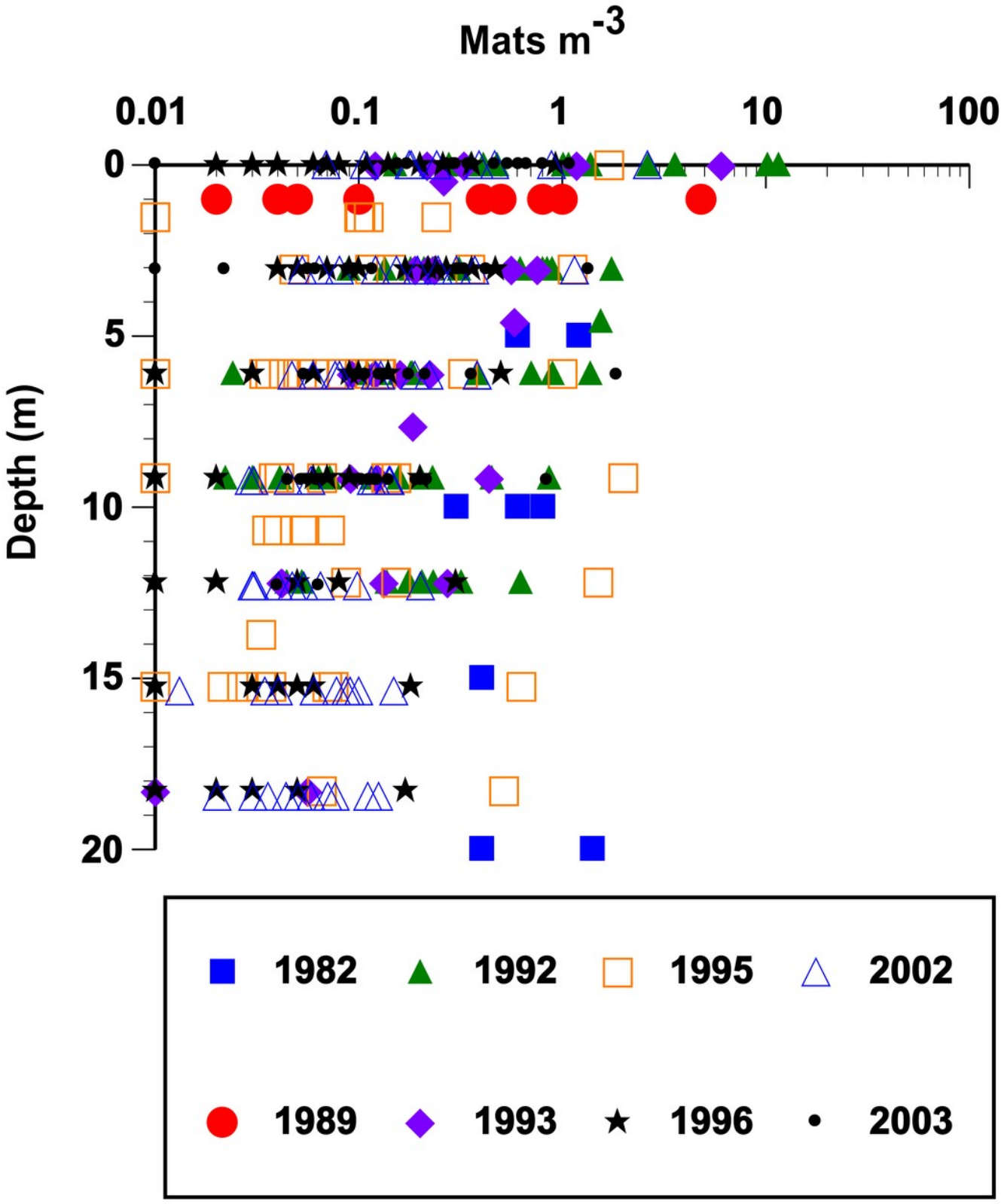

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Figure 4

Rhizosolenia mat integrated abundance

Fig. 4. *Rhizosolenia* mat integrated abundance. Diver-collected abundance in the upper 60 m. Data are from 6 cruises spanning 1992-2003 and literature sources (Alldredge & Silver 1982 ; Martinez et al. 1983) . Total number of stations, n=96. Filled squares indicate stations where mats were observed but not quantified. The A is Sta. ALOHA of the Hawai'i Ocean Time-Series (HOT).

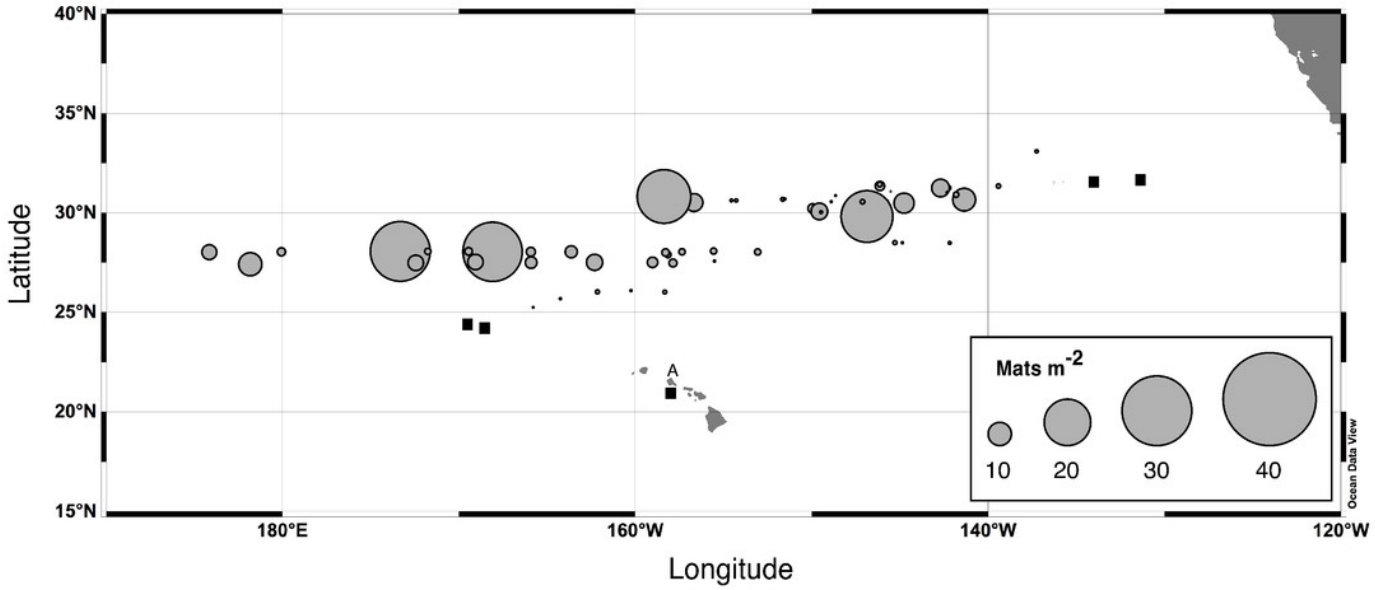

Figure 5

Vertical distribution of *Rhizosolenia* mats observed by the video plankton recorder. Data are from Aug./Sept. 2003.

Fig. 5. Vertical distribution of *Rhizosolenia* mats observed by the video plankton recorder. Data are from Aug./Sept. 2003. Station positions are given in the figure.

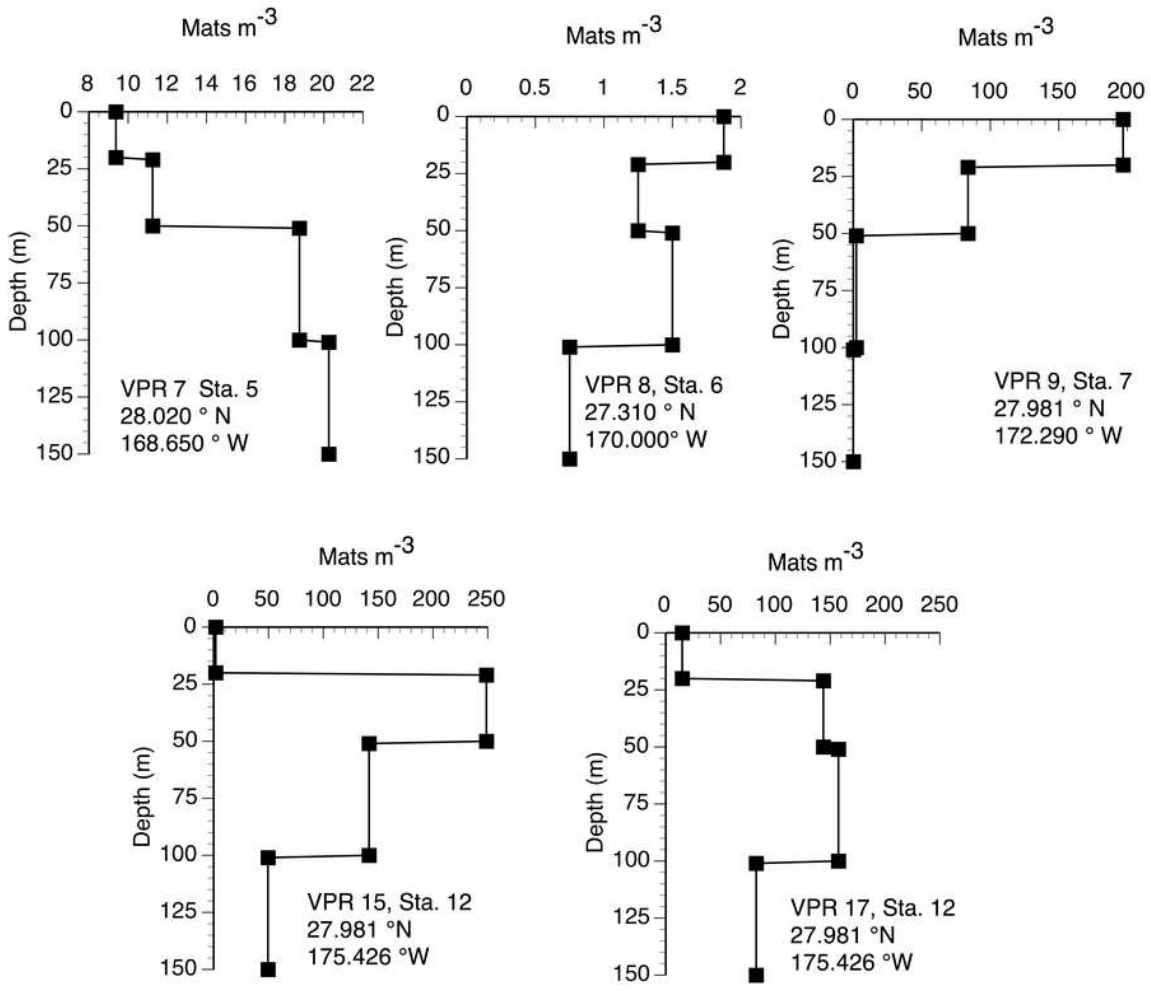

Figure 6

Histogram of *Rhizosolenia* mat δ^{15}N. (n=170).

Fig. 6. Histogram of *Rhizosolenia* mat δ^{15}N. (n=170). Bins are 2 per mil with the lower value included in the bin and the higher value representing the upper limit. Ascending mats were statistically lighter (2.17±0.32 per mil, n=125) than descending mats (3.53±0.39 per mil, n=45). Error bars are 95% confidence intervals. Samples were collected at regular intervals on RoMP2002 and RoMP2003 (Fig. 2)

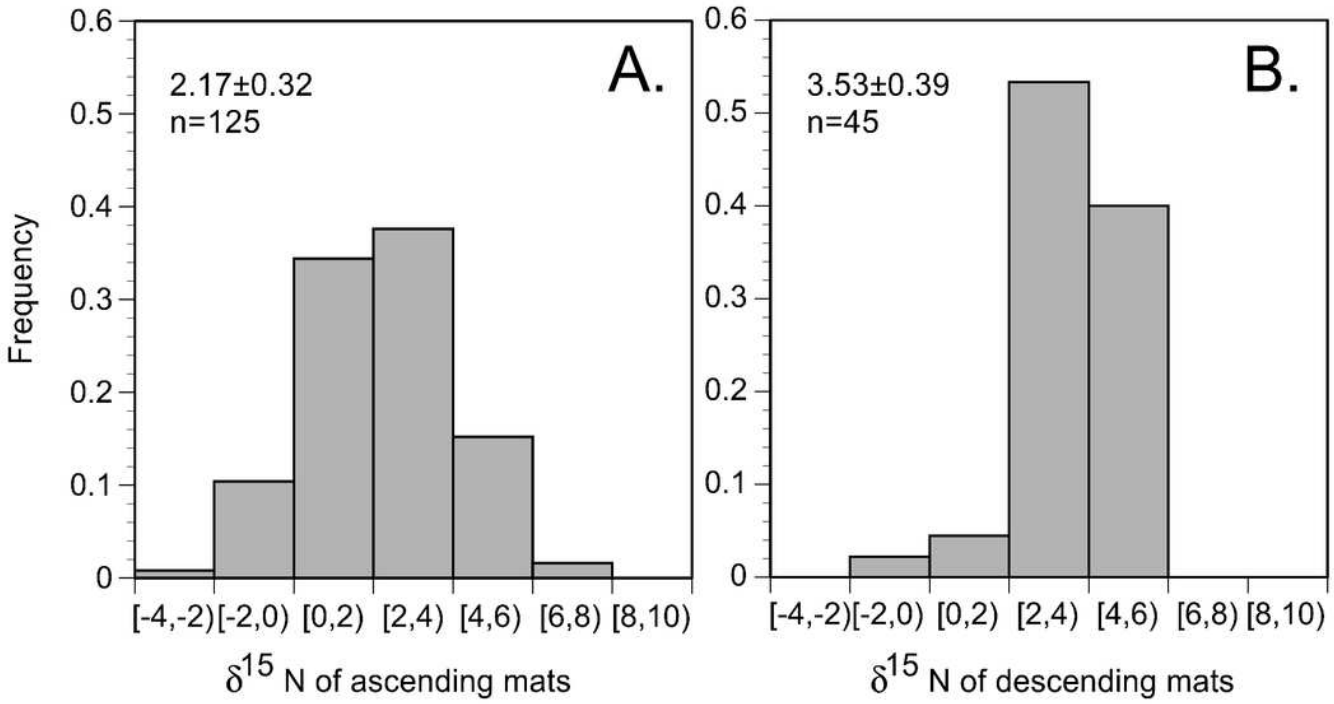

Figure 7

Particulate $\delta^{15}N$ and nitrate $\delta^{15}N$ of the sampled areas in the Pacific Ocean

Fig. 7. Particulate $\delta^{15}N$ and nitrate $\delta^{15}N$ of the sampled areas in the Pacific Ocean. Suspended particulate data (open symbols) are from the 2002 cruise, pooled from Sta. 1 (22.197 °N 157.960 ° W), 5 (28.008 °N 158.019 °W), 7 (28.000 °N 153.736 °W) and 10 (30.504 °N 149.615 °W). *Rhizosolenia* mat ^{15}N is averaged (box and whiskers) over all cruises (± 95% C.I.). Open symbols are suspended particulate material $\delta^{15}N$, large solid symbols are dissolved NO_3^- $\delta^{15}N$, small filled squares are the dissolved NO_3^- concentration (2003 stations). Red "X" are from Casciotti et al. (2008) at Station ALOHA. Black "X" are from the 2002 stations.

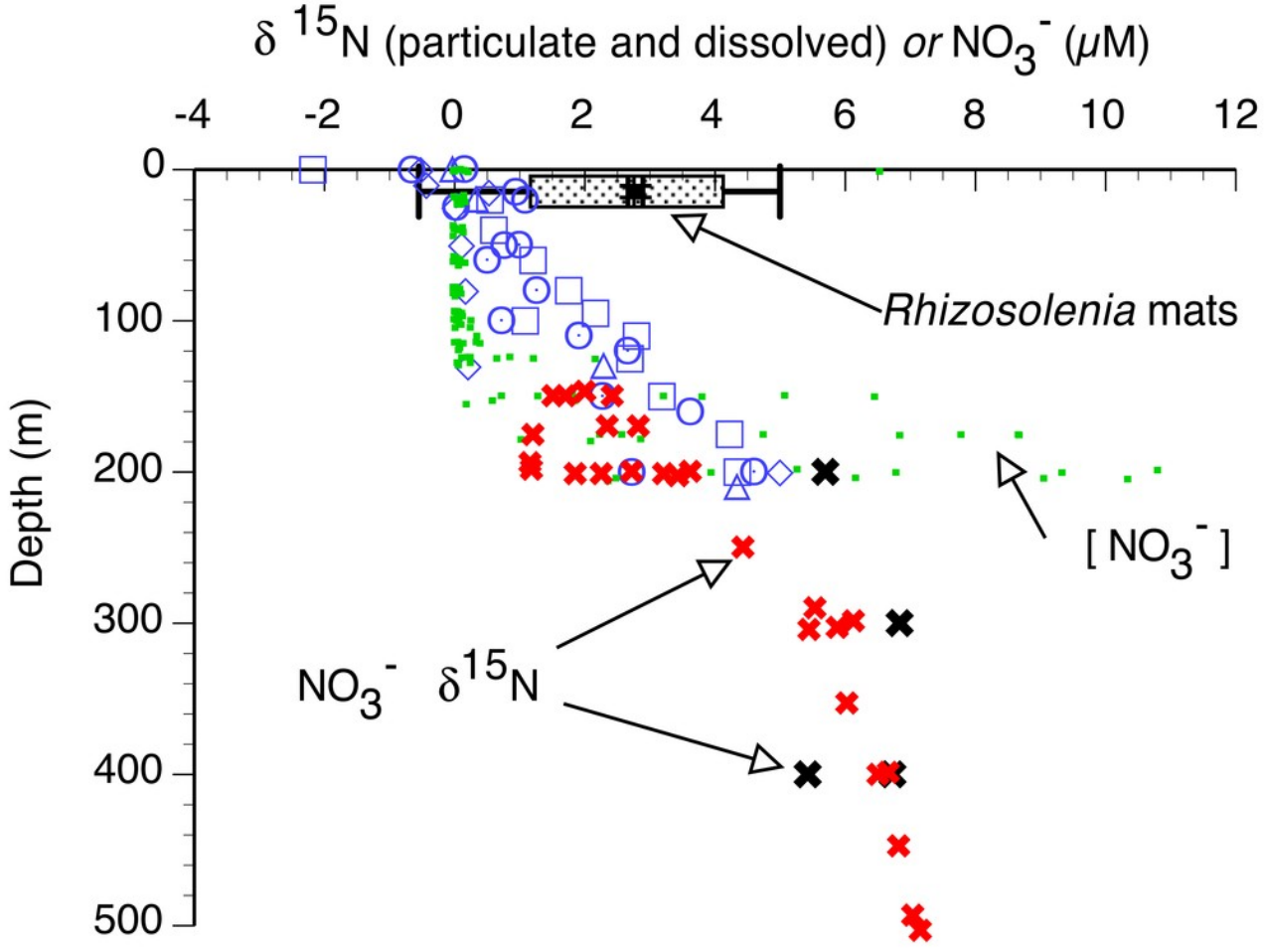

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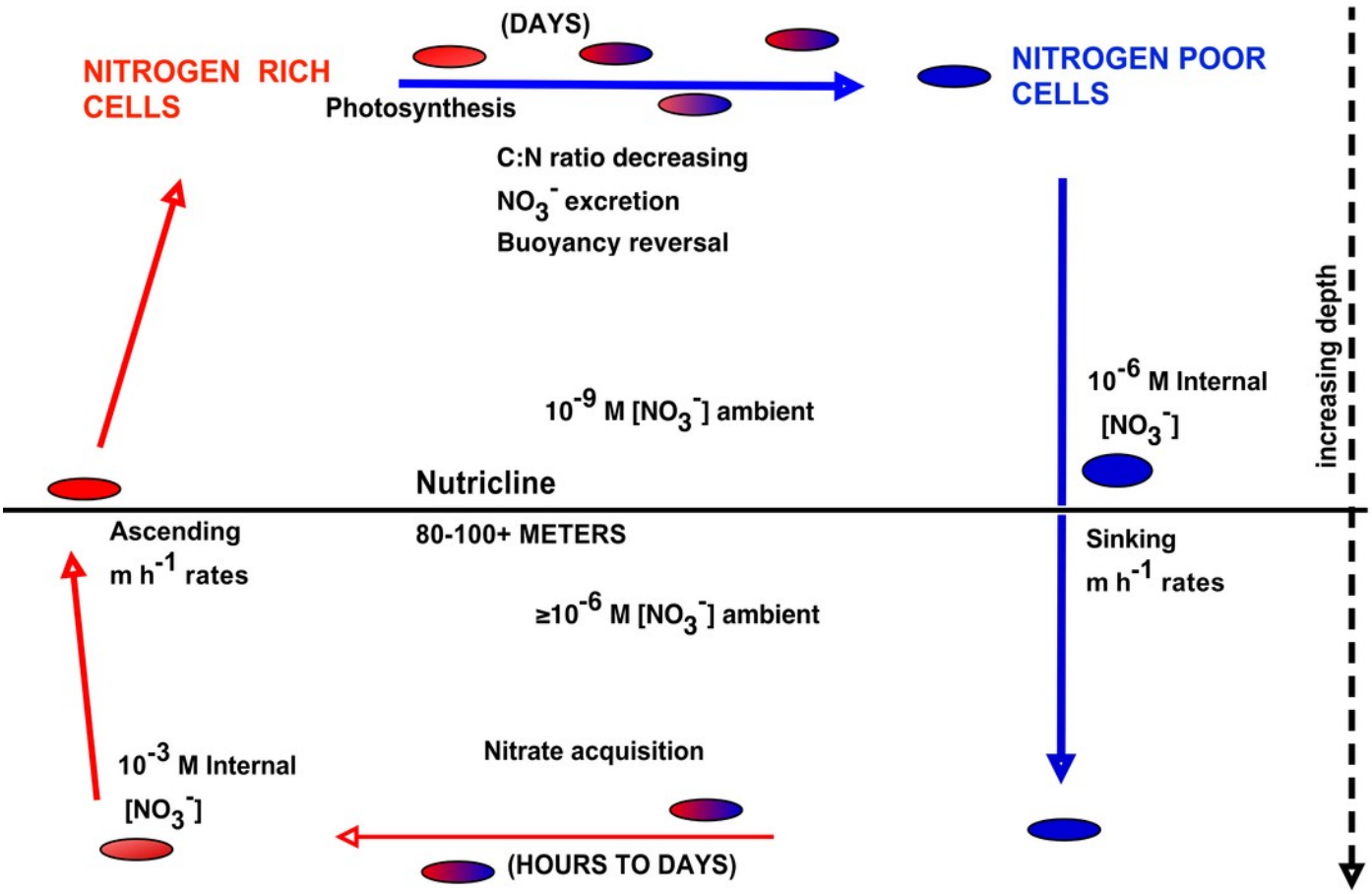
Figure 8

Conceptual model of vertical migration in *Rhizosolenia* mats and other giant phytoplankton.

Fig. 8. Conceptual model of vertical migration in *Rhizosolenia* mats and other giant phytoplankton. In this simplified representation, depth intervals are given in only general terms to allow for significant life history variation in the various taxa.



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