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Nitrogen isotopic composition of planktonic foraminifera from the modern ocean and recent sediments

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Abstract

We investigated the controls on the $\delta^{15}N$ values of shell-bound organic matter of planktonic foraminifera (foraminifera-bound $\delta^{15}N$, or FB-$\delta^{15}N$). The bulk biomass $\delta^{15}N$ of live foraminifera collected from plankton tows at Sta. S in the Sargasso Sea is within ~1‰ of the FB-$\delta^{15}N$ of the same species picked from surface sediments from the low-latitude North Atlantic. The FB-$\delta^{15}N$ value in the surface sediments is strongly correlated with the $\delta^{15}N$ of thermocline nitrate, the dominant source of new N to the euphotic zone. The three euphotic-zone-dwelling, symbiotic, spinose species, *Globigerinoides ruber*, *Globigerinoides sacculifer*, and *Orbulina universa*, have a FB-$\delta^{15}N$ similar to or slightly higher than that of the nitrate supply to the euphotic zone, whereas the deeper-dwelling, non-spinose, and/or asymbiotic forms have higher $\delta^{15}N$. In the Cariaco Basin sediment trap samples, the FB-$\delta^{15}N$ of *O. universa* varies substantially (1.2‰ between the lowest and highest value), in some cases in step with $\delta^{15}N$ changes in the bulk sinking N, while the subeuphotic-zone-dwelling, asymbiotic, and/or non-spinose species are generally higher in FB-$\delta^{15}N$ and less variable through the time series. The higher and less temporally variable FB-$\delta^{15}N$ values of the deeper dwellers are consistent with their partial reliance on subsurface suspended particulate nitrogen, the $\delta^{15}N$ of which is elevated and relatively stable over time. As an alternative, possibly additional explanation for the lower FB-$\delta^{15}N$ of the euphotic-zone dwellers (despite their likely tendency to feed on high-$\delta^{15}N$ zooplankton), the dinoflagellate symbionts may reduce the $\delta^{15}N$ elevation of a foraminifera's biomass relative to its diet by reducing the efflux of low-$\delta^{15}N$ ammonium.

The N isotopes are a potentially powerful tool to study changes in the oceanic budget and cycling of fixed N. The dominant sources and sinks in the N budget as well as the processes involved in N cycling influence the $\delta^{15}N$ values of oceanic nitrate in distinct ways ($\delta^{15}N = [\{^{15}N:{}^{14}N_{sample}\}/\{^{15}N:{}^{14}N_{reference}\} - 1]$, where atmospheric N_2 is used as the reference). In suboxic zones of the ocean water column, denitrification preferentially removes ^{14}N-bearing nitrate, leaving the residual nitrate elevated in $\delta^{15}N$ (Brandes et al. 1998). The residual high-$\delta^{15}N$ nitrate is mixed throughout the global ocean, leading to a mean ocean nitrate $\delta^{15}N$ that is elevated relative to the N inputs to the ocean. Remineralization of newly fixed N with a $\delta^{15}N$ value of −2‰ to 0‰ (Carpenter et al. 1999) replaces the N lost by denitrification on a global scale. Because its $\delta^{15}N$ is lower than that of mean ocean nitrate, it lowers the $\delta^{15}N$ of nitrate in the shallow subsurface, or thermocline, of some regions (Wong et al. 2002; Knapp et al. 2005; Casciotti et al. 2008). The $\delta^{15}N$ of subsurface nitrate is incorporated into biomass produced in the surface ocean. As a result, in surface-ocean regions of complete nitrate consumption (most of the tropical, subtropical, and temperate open ocean), the $\delta^{15}N$ value of sinking N, if preserved in the sediment record, should record the $\delta^{15}N$ of subsurface nitrate, and thus provide indications of changes in N fixation and denitrification in the past. In regions of incomplete nitrate consumption in surface waters, such as the high latitudes and upwelling zones, the $\delta^{15}N$ value of the nitrate in the euphotic zone is increased by isotopic fractionation during partial nitrate assimilation. As a result, the $\delta^{15}N$ of surface nitrate and sinking N reflects (in addition to the $\delta^{15}N$ of nitrate supplied into the euphotic zone) the degree of nitrate utilization in these nutrient-rich regions (Altabet and Francois 1994), and thus it has been used to reconstruct past changes in polar ocean nutrient status (Francois et al. 1997).

However, bulk sedimentary organic N has major limitations as a proxy for past changes in the $\delta^{15}N$ of N export. Outside of sedimentary environments characterized by high organic matter preservation (e.g., upwelling regions and continental margins) (Altabet et al. 1999), bacterially driven degradation can significantly elevate the $\delta^{15}N$ of sedimentary N relative to the N sinking out of the surface ocean (Altabet and Francois 1994). Sedimentary organic N can also be contaminated by terrestrial input, especially in coastal regions and/or in settings where very little marine organic matter is preserved and buried (Schubert and Calvert 2001).

To avoid the artifacts associated with diagenetic alteration, a growing body of paleoceanographic work has focused on the organic matter internal to microfossils, with most work to date involving the siliceous frustules of diatoms (Robinson and Sigman 2008). The organic matter within diatom frustules appears to be native to the diatoms and protected from early bacterial diagenesis (Ingalls et al. 2003; Poulsen et al. 2003). However, due to the limited geographic distribution of diatoms in sediments, the use of

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diatom-bound organic matter is confined to high-latitude and upwelling regions, where diatom-bound $\delta^{15}N$ (DB-$\delta^{15}N$) has been used as a proxy to infer past changes in surface nutrient status. In addition to its geographic limitations, DB-$\delta^{15}N$ may be problematic in other ways. In particular, DB-$\delta^{15}N$ is elevated by ~4‰ relative to the expected $\delta^{15}N$ of diatom biomass and of the sinking flux (Robinson and Sigman 2008), and it may vary among diatom species inhabiting the same water column (Horn et al. 2011). This raises the concern that changes in the $\delta^{15}N$ relationship between diatom biomass and frustule-bound N could lead to down-core changes in DB-$\delta^{15}N$ that are independent of changes in surface-ocean nutrient status (Jacot Des Combes et al. 2008).

We have begun to develop the use of the organic N that is trapped within the walls of the calcium carbonate "shells" (i.e., tests) of planktonic foraminifera (foraminifera-bound $\delta^{15}N$, FB-$\delta^{15}N$) as a tool for studying past changes in the marine nitrogen cycle. Transmission and scanning electron microscopy show that an organic matrix is laid down between layers of calcite when foraminifera form or add chambers to their tests (Hemleben et al. 1988; Spero 1988). Previous studies of shell-bound organic matter in individual foraminifera species show minimal differences in amino acid composition among modern foraminifera, foraminifera from surface sediments (King and Hare 1972), and microfossils as old as 300 kyr (Robbins and Brew 1990), suggesting physical protection of the shell-bound N.

The $\delta^{15}N$ value of most planktonic foraminifera species from the surface sediments at several open-ocean sites was found to be very close to the $\delta^{15}N$ value of upper thermocline nitrate (Ren et al. 2009), which is the dominant source of N to the euphotic zone (Altabet 1988; Knapp et al. 2005). Hence, FB-$\delta^{15}N$ is a promising archive for paleoceanographic N isotope studies as a recorder for shallow subsurface nitrate $\delta^{15}N$ in the oligotrophic regions, and it is particularly valuable in places where diagenesis reduces our confidence in bulk sediment N isotope records.

FB-$\delta^{15}N$ in the sediments from the Caribbean Sea and South China Sea were found to be higher during the last ice age than the current interglacial at both locations. The implied elevation of thermocline nitrate $\delta^{15}N$ in both regions was interpreted as evidence for less ice-age N fixation (Ren et al. 2009, 2012). These findings, together with reconstructions of changes in water-column denitrification, provide perhaps the most direct evidence to date for the longstanding hypothesis of a feedback between denitrification and N fixation across the global ocean that stabilizes the size of the ocean N reservoir (Broecker 1982).

However, we currently lack sufficient knowledge regarding the physical and biological controls on FB-$\delta^{15}N$. One plausible view is that foraminifera obtain most of their N from some component of suspended particulate organic matter (POM), and they have a $\delta^{15}N$ ~3‰ higher than this N source because they preferentially excrete low-$\delta^{15}N$ ammonia, as appears to apply to other zooplankton (Checkley and Miller 1989). In this case, FB-$\delta^{15}N$ of the euphotic-zone-dwelling species may be similar to, or at least correlated with, the integrated $\delta^{15}N$ of the new N supply to the euphotic zone (Ren et al. 2009), which is dominated by nitrate from below and augmented by N fixation. In this view, the observation of higher FB-$\delta^{15}N$ in subeuphotic-zone-dwelling species than in euphotic-zone dwellers (Ren et al. 2009) may result from the observed increase in the $\delta^{15}N$ value of the suspended POM below the euphotic zone (Saino and Hattori 1980).

These interpretations currently rely on several assumptions that have not been properly evaluated. It is not yet known whether the shell-bound N that we analyze in sediments has a $\delta^{15}N$ value that is similar to (or has a constant offset from) that of the bulk biomass of the foraminifera. Moreover, selection among possible N sources may complicate matters. Many euphotic-zone-dwelling foraminifera almost certainly discriminate in the forms of N they consume, perhaps preferentially consuming zooplankton as well as larger phytoplankton (Bé et al. 1977; Spindler et al. 1984). In contrast, the deeper-dwelling, nonspinose foraminifera species appear to feed more passively and thus less selectively. In culture, they feed on phytoplankton (Spindler et al. 1984); in the subeuphotic zone of the ocean, their diet may be composed largely of detrital organic matter (Bé et al. 1977; Spindler et al. 1984). Finally, while most euphotic-zone-dwelling foraminifera have algal symbionts, the deeper-dwelling foraminifera typically do not. In corals, symbionts play an important role in regulating the $\delta^{15}N$ relationships between coral tissues and their N sources (Hoegh-Guldberg et al. 2004), and perhaps also between coral tissues and the carbonate-associated organic matter that the corals produce (Muscatine et al. 2005). Thus, the influence of algal symbionts on FB-$\delta^{15}N$ deserves consideration, particularly with regard to understanding the FB-$\delta^{15}N$ difference observed between shallow- and deep-dwelling planktonic foraminifera species.

In this study, we report FB-$\delta^{15}N$ results for multiple species of planktonic foraminifera from zooplankton net tows from the Sargasso Sea, sediment traps from the Cariaco Basin, and surface sediments from several different open-ocean regions. This first preliminary study, which we expect to augment greatly in the coming years, nevertheless yields important initial insights into FB-$\delta^{15}N$ and its use as a paleoceanographic tool.

Methods

Sample collection—On 21 and 22 July 2008, foraminifera were collected using a 1-m^2, 200-μm-mesh plankton net over the upper 200 m from the Sargasso Sea near Hydrostation S (32.2°N, 64.5°W; Fig. 1). Samples were preserved in a 5–10% pH-buffered formalin solution and refrigerated until processing. A similar preservation protocol has been tested previously on phytoplankton cells, and has shown no N isotopic effect (Fawcett et al. 2011). Planktonic foraminifera individuals were then picked under a microscope. Specimens were picked and processed for foraminifera biomass $\delta^{15}N$ analyses within a week after sampling, and within a month for shell-bound $\delta^{15}N$ analyses. Bulk foraminifera biomass $\delta^{15}N$ was measured on *Globigerinoides ruber* (for pink-pigmented and white *G. ruber* separately), *Globigerinoides sacculifer*, *Orbulina*

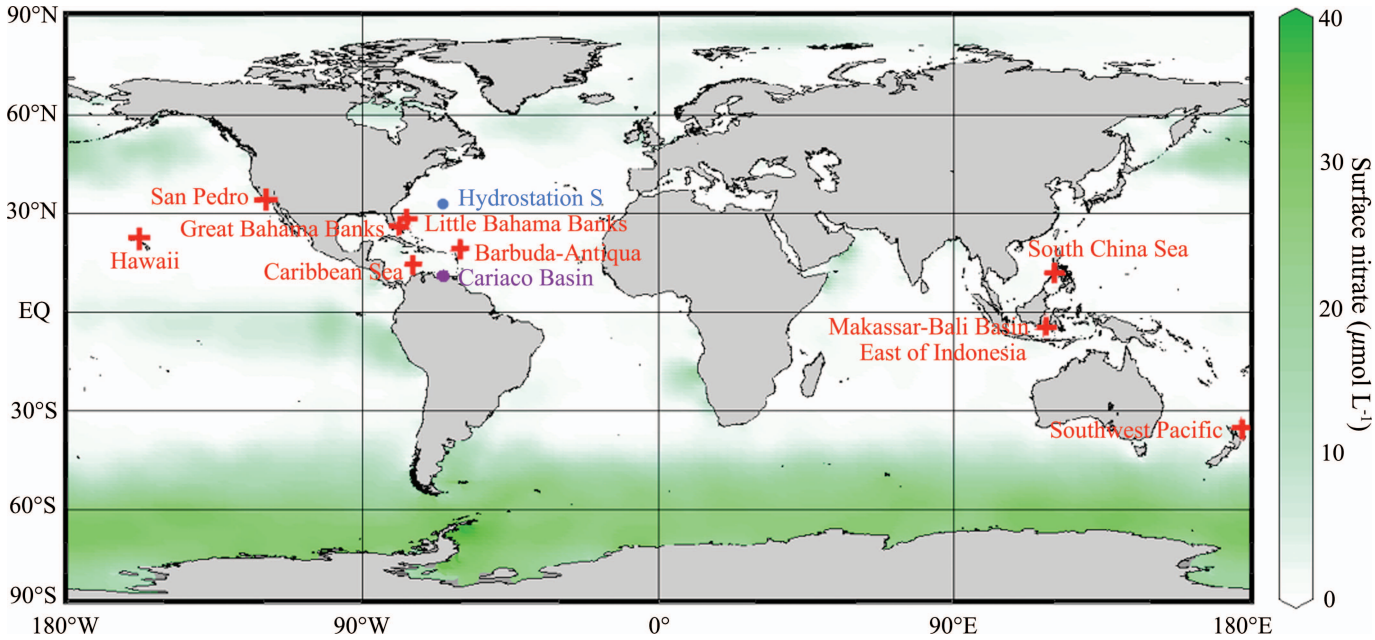

Fig. 1. Collection locations for the samples in this study. Surface sediment samples are shown with red crosses. Net tow samples from the upper ocean were collected at Hydrostation S (blue circle). Both sediment trap material and surface sediments were obtained from the Cariaco Basin (purple circle). Map shading shows the mean annual surface nitrate concentration from *World Ocean Atlas* 2005 (http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html).

universa, *Globigerinella aequilateralis*, *Globorotalia menardii*, *Hastigerina pelagica*, and *Globorotalia crassaformis*. Six foraminifera individuals from six individual tows were used in each analysis to yield an average δ^{15}N during the towing period. Shell-bound δ^{15}N was measured only for *G. ruber*; due to the large number of shells needed for an analysis (*see* below), it was necessary to combine the individuals from all six tows.

Foraminifera were picked from sinking material collected by a moored sediment trap at 275-m water depth in the Cariaco Basin (10.5°N, 64.7°W; Fig. 1) between March 1998 and October 1999. Each sample represents a 2-week collection period, with sediment trapping procedures outlined by Thunell et al. (2004). FB-δ^{15}N was measured on *G. ruber*, *G. sacculifer*, *O. universa*, *G. aequilateralis*, *G. menardii*, *Neogloboquadrina dutertrei*, *G. crassaformis*, and *Globigerina bulloides*, which were previously picked from a 1 : 16 split of each sample for the faunal study of Tedesco and Thunell (2003). Samples were binned when necessary to obtain adequate quantity of N for analysis (Fig. 2). FB-δ^{15}N measured from the sediment trap was compared with the FB-δ^{15}N of surface sediments collected nearby (*see* below).

Surface sediments were obtained from the San Pedro Basin in the eastern North Pacific (33.5°N, 118.0°W, 0–6 cm of multicore collected sediments, > 150-μm size fraction), near Hawaii (20.8°N, 157.3°W, 2578-m water depth, 0–1 cm in multicores, > 150-μm size fraction), and from the Cariaco Basin (10.7°N, 64.7°W, 366-m water depth, 1–1.5 cm in gravity core GC7-1, > 63-μm size fraction). FB-δ^{15}N was measured on *O. universa*, *N. dutertrei*, and *G. bulloides* at the San Pedro Basin, on *G. ruber* and *G. sacculifer* near Hawaii, and on *G. ruber*, *G. sacculifer*, *O. universa*, *G. aequilateralis*, *G. menardii*, *N. dutertrei*, and *G. bulloides* in the Cariaco Basin. We also made new measurements of FB-δ^{15}N for several species from locations for which we have previously published data, including the North Atlantic near Little Bahama Bank (26.0°N, 77.5–78.1°W, 1049–1067-m water depth, grouped box cores, 0–5 cm, > 500 μm), Great Bahama Bank (24.3–24.5°N, 79.2–79.4°W, 600–728-m water depth, grouped box cores, 0–5 cm; from 75- to 125-μm as well as > 500-μm size fractions), Barbuda Antiqua (17.5°N, 61.0°W, 4030-m water depth, 5–10 cm in gravity core EN18, > 250-μm size fraction), the Makassar-Bali Basin east of Indonesia (6.8°S, 117.0°E, 419-m water depth, 1–2 cm in multicore, > 150 μm), and the western South Pacific near New Zealand (36.4–37.4°S, 176.7–177.4°E, 663–2252-m depth, 0–1 cm in multicores, > 150 μm). Finally, we include previously measured FB-δ^{15}N at the near core-top sediments from Ocean Drilling Program Site 999A at the Caribbean Sea (12.8°N, 78.8°W, 2827-m water depth, 4–7cm, > 250 μm) (Ren et al. 2009), and Marion Dufresne Site 972142 in the South China Sea (12.7°N, 119.5°E, 1557-m water depth, 3–4 cm, > 250 μm) (Ren et al. 2012) to expand our global survey of FB-δ^{15}N. The locations and the annual mean surface nitrate concentration at these sites are shown in Fig. 1.

N isotope methods—The protocol for measuring FB-δ^{15}N (Ren et al. 2009) includes (1) chemical treatment of the foraminifera shells to remove external N contamination, followed by acid dissolution of the cleaned shells, (2) conversion of organic N released into solution to nitrate by persulfate oxidation (Nydahl 1978; Knapp et al. 2005), (3) measurement of nitrate concentration by chemiluminescence

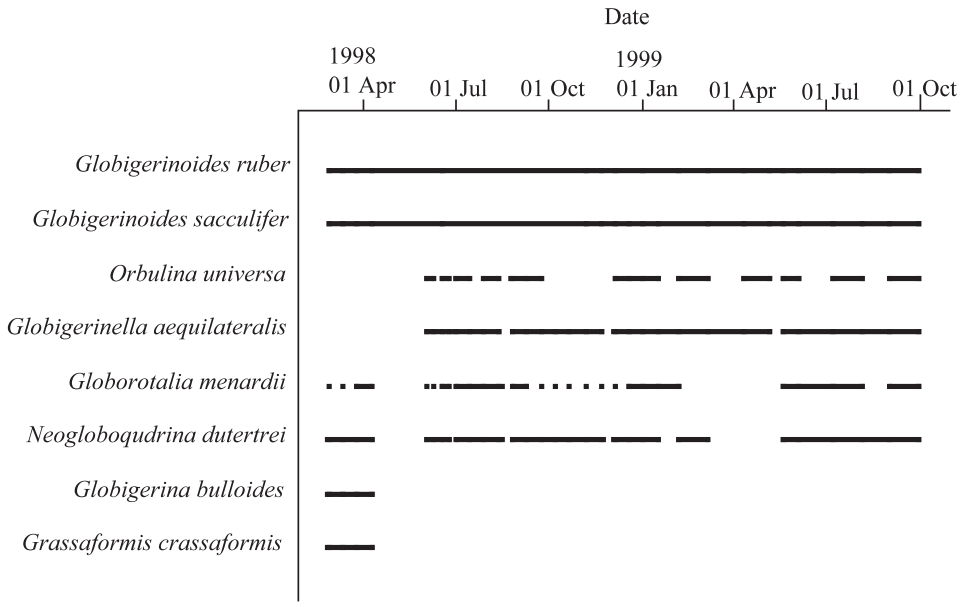

Fig. 2. Temporal distribution of the specimens of each foraminifera species picked from the sediment trap at 275 m in the Cariaco Basin. Each sediment trap sample was collected continuously for 2 weeks, but in order to obtain adequate N for FB-δ^{15}N analysis, foraminifera samples from some adjacent intervals were combined. The lengths of the continuous lines correspond to the lengths of the time periods over which the samples were grouped and analyzed.

(Braman and Hendrix 1989), and (4) bacterial conversion of nitrate to nitrous oxide (Sigman et al. 2001), with measurement of the δ^{15}N of the nitrous oxide by gas chromatography–isotope ratio mass spectrometry using a modified Thermo GasBench II and DeltaPlus (Casciotti et al. 2002). For measuring foraminifera biomass δ^{15}N, we replaced step 1 with several gentle rinses with deionized water, to remove attached detrital material and the buffered formalin.

As the first step in cleaning the samples prior to FB-δ^{15}N analysis, 2 to 5 mg of foraminifera tests per sample were gently crushed, treated with 5 min of ultrasonication in 2% sodium hexametaphosphate (pH 8), and then rinsed twice with deionized water. For sediment samples, we conducted a reductive cleaning using sodium bicarbonate–buffered dithionite-citrate reagent as a precaution to avoid any organic contamination associated with metal oxides (Mehra and Jackson 1958); we have no evidence to date that this step is needed. All samples were then treated with a potassium persulfate/sodium hydroxide solution and autoclaved for 55 min on a slow vent setting (Nydahl 1978; Knapp et al. 2005). The persulfate cleaning was previously compared with bleach cleaning and yielded no difference in nitrogen content or isotopic composition (Ren et al. 2012). We applied the persulfate cleaning in this study because it is likely to be a harsher treatment and also requires less time. The remaining amount, 1 to 3 mg of cleaned foraminifera tests, was subsequently completely dissolved in 6 mol L^{-1} hydrochloric acid, releasing organic matter for analysis.

Repeated isotopic measurements as well as cleaning replicates were made when possible. Standard deviations (1σ) for biomass δ^{15}N and FB-δ^{15}N cleaning replicates were generally better than 0.2‰ 1SD.

Results

Foraminifera biomass and shell-bound δ^{15}N in the Sargasso Sea—The δ^{15}N of the foraminifera biomass collected from the upper 200 m of the Sargasso Sea falls between 2‰ and 4‰, with the exception of *H. pelagica*, which is at least 2‰ higher than the rest of the species (Fig. 3). Among the species studied, the δ^{15}N values of *G. ruber* and *G. sacculifer* biomass are most similar to the δ^{15}N of the shallow thermocline (200–250 m) nitrate in the Sargasso Sea (2.6‰; Knapp et al. 2005). All species except *H. pelagica* have a δ^{15}N that is significantly lower than the δ^{15}N of the deep nitrate (5.2‰; Knapp et al. 2005), and similar to that of the POM sinking out of the euphotic zone (with a measured annual average δ^{15}N of 3.7‰ at 150 m; Altabet 1989). The shell-bound δ^{15}N of the surface plankton tows was only measured on *G. ruber*; it was about 1‰ higher than its biomass δ^{15}N. More analyses on the shell-bound δ^{15}N will be needed to evaluate the significance of this shell-bound-to-biomass difference. The foraminifera biomass δ^{15}N of most of the measured species is similar to (within 0.5‰ of) the average shell-bound δ^{15}N measured in surface sediments from the North Atlantic sites near Barbuda Antiqua, Great Bahama Bank, Little Bahama Bank, and/or the open Caribbean Sea (Fig. 3).

FB-δ^{15}N in sediment traps and surface sediments in the Cariaco Basin—Over the period for which we have FB-δ^{15}N data, the flux-weighted mean δ^{15}N of the bulk sinking POM is 4.5‰ and 3.7‰ for the 275-m and 1200-m sediment traps in the Cariaco Basin, respectively (Fig. 4, gray solid and dashed lines). The bulk POM δ^{15}N of the shallower trap is most similar to the δ^{15}N of the nitrate at the depth of nitrate concentration maximum during the

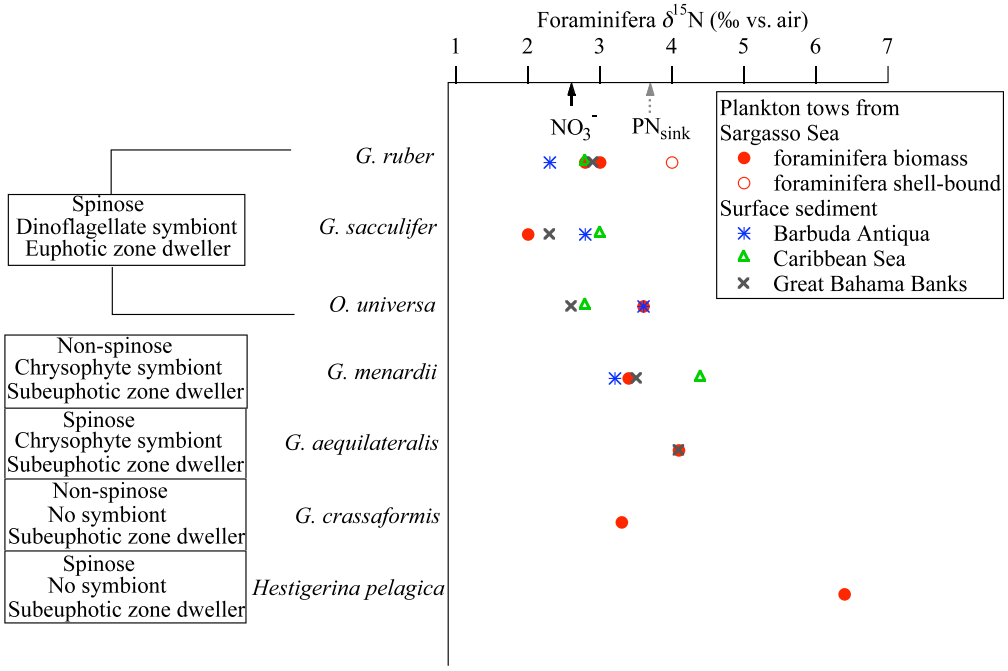

Fig. 3. δ^{15}N of the foraminifera biomass (red filled circles) and foraminifera shell-bound organic matter (red open circles) from the net tow materials from Sta. S, Sargasso Sea, in comparison with FB-δ^{15}N measured in the surface sediments from the western tropical and subtropical North Atlantic sites near Barbuda Antiqua (blue asterisks), Great Bahama Bank (black crosses), and in the Caribbean Sea (green triangles). The lower- and higher-biomass δ^{15}N analyses of *G. ruber* are for the white and pink form, respectively. For the water column near Sta. S, we also show the δ^{15}N of nitrate in the shallow thermocline (at 200 m, solid black arrow) (Knapp et al. 2005), and the δ^{15}N of the sinking particulate nitrogen (PN_{sink}) (at 150 m, gray dashed arrow) (Altabet 1988).

years of these collections (4–4.5‰ at 125–150 m) (Thunell et al. 2004). The δ^{15}N of bulk sinking POM exhibits seasonal variation, especially in the shallow trap, with lower δ^{15}N typically occurring in winter and from late spring to early summer (Fig. 4).

Among the foraminifera species for which we have substantial time-series data, *O. universa*, *G. menardii*, and *G. dutertrei* all show significant temporal variation. Some of the variation appears to be correlated with changes in the δ^{15}N of the bulk sinking POM, at least in 1998 (Fig. 4). The flux-weighted mean FB-δ^{15}N values for these three species, as well as for *G. aequilateralis*, do not appear to be easily biased towards a particular season, because either their FB-δ^{15}N or their abundance is not very seasonally variable, although the time-series FB-δ^{15}N of *O. universa* has stronger variation. Due to sample size limitations, we performed only one analysis for each of the other four species, *G. ruber*, *G. sacculifer*, *G. crassaformis*, and *G. bulloides*. Judging from the relatively uniform abundance of *G. ruber* and *G. sacculifer* throughout the sampling period, and since the fossils were binned from all of the individual collections, we suspect that our measured FB-δ^{15}N for the two species resembles the annual mean (Fig. 2). However, the other two species, *G. bulloides* and *G. crassaformis*, were taken from only two successive collections in the spring upwelling season of 2002 (Fig. 2). Thus, their measured FB-δ^{15}N may not be representative of the annual mean.

The FB-δ^{15}N values of most species in the surface sediments in the Cariaco Basin are within ~0.5‰ of the FB-δ^{15}N from the sediment trap (Fig. 4), with the sediment FB-δ^{15}N being slightly higher than the sediment trap FB-δ^{15}N (Fig. 5). *G. bulloides* is an exception in our analysis, with the surface sediment FB-δ^{15}N being ~1.5‰ higher in the sediments than in our sediment trap collection (Figs. 4, 5). We suspect that the sediment trap–based FB-δ^{15}N of *G. bulloides*, most of the specimens for which came from a single trap collection in late spring of 2002, is an underestimate of its annual mean FB-δ^{15}N. This is supported by the observation of relatively low δ^{15}N of both the bulk sinking POM and the FB-δ^{15}N of other planktonic foraminifera during this time (Fig. 4). During the intense spring upwelling period, nutrient-rich thermocline water is brought up to the euphotic zone, briefly lowering the δ^{15}N of euphotic zone POM (Thunell et al. 2004).

The δ^{15}N differences among these eight examined species in Cariaco sediment traps and surface sediments generally agree with our findings from the plankton tow and surface sediment data from other regions. The two euphotic-zone-dwelling, symbiotic, and spinose species, *G. ruber* and *G. sacculifer*, have the lowest δ^{15}N among all species, and are closest to the bulk sinking POM δ^{15}N in the shallowest trap, and to the δ^{15}N of thermocline nitrate (Fig. 4). The subeuphotic-zone-dwelling, asymbiotic, and/or non-spinose species are slightly higher in their FB-δ^{15}N, with *G. aequilateralis* being the highest.

FB-δ^{15}N in surface or near-core-top sediments—We compared the surface sediment FB-δ^{15}N data with δ^{15}N

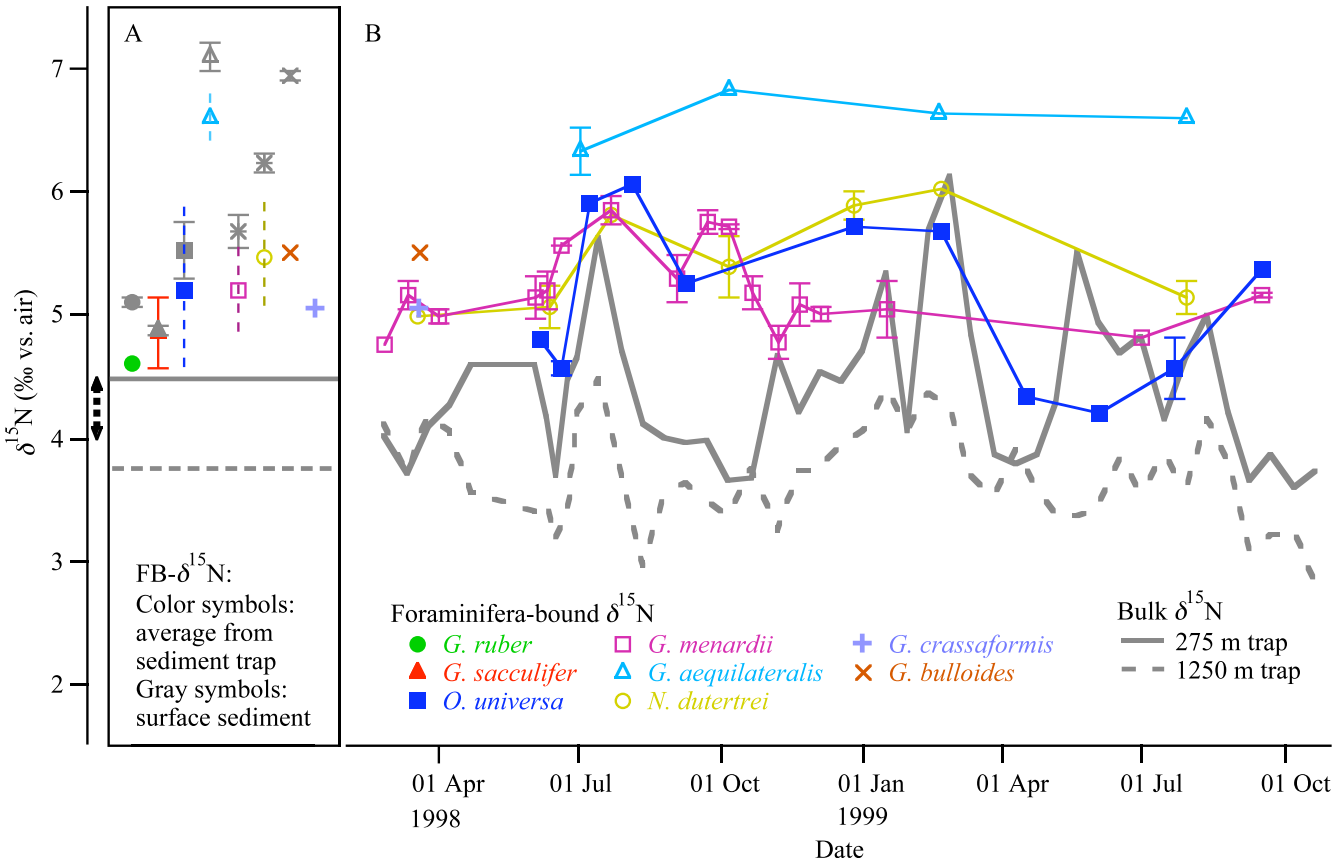

Fig. 4. (A) Flux-weighted mean FB-δ^{15}N (color symbols), and bulk sinking δ^{15}N from sediment traps at two depths (solid line: 275 m; dashed line: 1200 m), in comparison with FB-δ^{15}N measured from the surface sediments (gray symbols) in the Cariaco Basin. (B) Time-series of FB-δ^{15}N (connected symbols) and the δ^{15}N of bulk sinking POM (lines) in the sediment trap samples from February 1998 to October 1999. Solid error bars on both panels indicate standard deviations for cleaning replicates. Dashed error bars indicate standard deviations describing the δ^{15}N variation over the studied period. The black dashed line with arrows on the y-axis indicates the range of observed nitrate δ^{15}N at the depth of nitrate maximum (125–150 m) in November 1997 (Thunell et al. 2004).

measurements of subsurface nitrate, bulk sinking POM, as well as surface suspended POM from the locations where these data are available (Table 1). Subsurface and thermocline nitrate δ^{15}N values were generally taken from the depth range that the nitrate δ^{15}N and concentration data imply to represent the dominant source for annually integrated nitrate supply, and averaged over multiple years or different analyses whenever possible. The δ^{15}N of the sinking POM was taken from the shallowest sediment traps deployed at these sites, in order to best approximate the δ^{15}N of the POM sinking out of the euphotic zone (although shallow traps also suffer greater uncertainties associated with the removal of "swimmers"). The details of these data are given in the notes of Table 1.

We observe a strong correlation between FB-δ^{15}N and shallow thermocline nitrate δ^{15}N (Fig. 6; Table 1). The three euphotic-zone-dwelling, symbiotic, and spinose species, *G. ruber*, *G. sacculifer*, and *O. universa*, have a FB-δ^{15}N very similar to nitrate δ^{15}N. The greatest discrepancy is observed in the Cariaco Basin (Fig. 6), where the three species appear to be ~1‰ higher than the subsurface nitrate δ^{15}N. The FB-δ^{15}N values of the other species—*G. aequilateralis*, *G. menardii*, *N. dutertrei*, *Globorotalia truncatulinoides*, and *G. bulloides*—which are generally subeuphotic-zone dwellers, asymbiotic, and/or non-spinose, are generally higher than the measured thermocline nitrate δ^{15}N by 1‰ to 2‰. Nevertheless, the spatial variation in the FB-δ^{15}N of these species is also strongly correlated with the observed differences in nitrate δ^{15}N among the sampled regions (Fig. 6).

Discussion

The δ^{15}N relationship between foraminifera biomass and shell-bound N—The δ^{15}N of foraminifera biomass for the five symbiotic species (*G. ruber, G. sacculifer, O. universa, G. menardii, G. aequilateralis*) is close to their FB-δ^{15}N values measured in western subtropical and tropical North Atlantic surface sediments (Fig. 3). There is the obvious assumption in this comparison that the sedimentary foraminifera were deposited under conditions that are similar to those of today. The age of the Caribbean Sea sediment sample is 4.2 ka according to Schmidt et al. (2004), based on ^{14}C dating and δ^{18}O correlation, and the surface sediments near Barbuda Antiqua are late Holocene in age based on foraminifera and nannofossil abundance data calibrated with oxygen isotope records (Reid et al. 1996). The surface sediments near Great Bahama Bank and

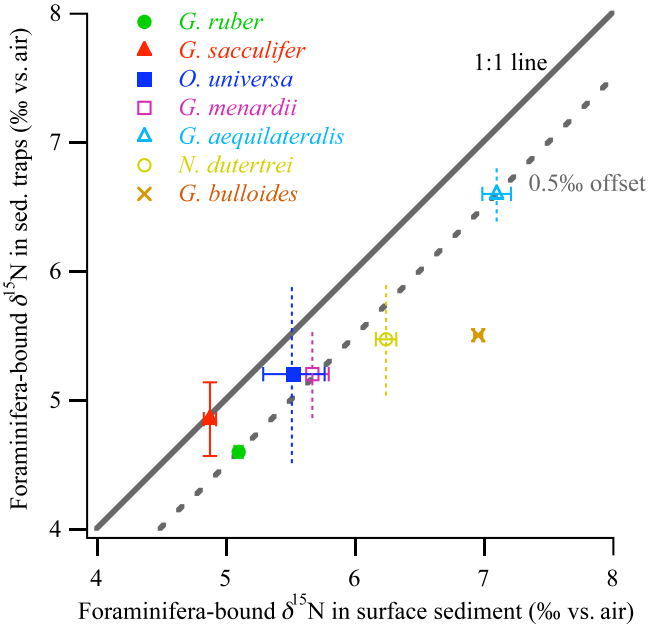

Fig. 5. FB-δ^{15}N in sediment trap collections and nearby core-top sediments in the Cariaco Basin. Error bars are as for Fig. 4. The *G. bulloides* sediment trap FB-δ^{15}N reflects only a single springtime month (*see* text).

Little Bahama Bank are not dated. In any case, the lack of a clear systematic difference between the surface-ocean foraminifera biomass and sedimentary microfossil measurements is at least suggestive that foraminifera biomass and shell-bound N have a similar δ^{15}N, and that the N isotope dynamics of the western Atlantic have not changed greatly over the Holocene.

The similarity between foraminifera biomass and shell-bound N is consistent with one available study on corals, which shows that their carbonate-associated organic N is similar in δ^{15}N to the coral tissue in symbiotic corals (Muscatine et al. 2005). However, in asymbiotic corals, Muscatine et al. (2005) observed that the carbonate-associated δ^{15}N is ~4‰ greater than the tissue. Because the two asymbiotic foraminifera species in this study (*G. crassaformis* and *H. pelagica*) were not sufficiently abundant in our sediment samples, we were not able to address their shell-bound-to-biomass difference by comparing biomass δ^{15}N from the net tows with FB-δ^{15}N in the sediments.

The biomass of *H. pelagica* is significantly higher in δ^{15}N than that for the other six species studied. As we explain below, foraminifera species lacking symbionts (such as *H. pelagica*) are likely to have a larger foraminifera biomass-to-diet δ^{15}N difference than the species with symbionts, such as *G. ruber*, *G. sacculifer*, and *O. universa*. This may contribute to the higher δ^{15}N values in *H. pelagica*. Furthermore, *H. pelagica* is predominantly, if not exclusively, carnivorous, whereas other asymbiotic, non-spinose forms appear to have a stronger preference for phytoplankton (Bé et al. 1977; Anderson et al. 1979); thus, its high δ^{15}N may also reflect its high mean trophic level (Minagawa and Wada 1984).

Direct measurement on shell-bound δ^{15}N of net tow materials was only made on *G. ruber*. The shell-bound δ^{15}N of *G. ruber* from the net tows is 1‰ higher than that of its biomass and similarly higher than its FB-δ^{15}N in western tropical North Atlantic surface sediments (Fig. 3). While this is a significant difference, the similarity between net tow foraminifera biomass δ^{15}N and sediment FB-δ^{15}N for most species causes us to question whether this difference will prove robust over multiple samplings. Nevertheless, it is worth considering the processes that may cause such a difference.

One interesting possibility involves the internal N distribution between the foraminifera and the symbiotic dinoflagellates. Symbionts can represent a significant fraction of the foraminifera biomass (Spero and Parker 1985). In scleractinian corals, the δ^{15}N of dinoflagellate symbionts is often lower than that of the host tissue, as expected if the symbionts consume the ammonium generated from the metabolism of the coral host (Hoegh-Guldberg et al. 2004; Swart et al. 2005). If the same dynamic applies to symbiont-bearing foraminifera, the foraminifera biomass δ^{15}N from the net tows would be lowered by the inclusion of the symbiont biomass, whereas the shell-bound N may derive from the host foraminifera tissue, with its slightly higher δ^{15}N. It has been observed for some foraminifera species (e.g., *G. sacculifer*) that most of the symbionts are digested prior to final calcification and gamete release (Bé et al. 1983). Thus, the foraminifera (plus symbiont) biomass δ^{15}N measured from a net tow might be more similar to the "final" FB-δ^{15}N found in the sediments than to the shell-bound δ^{15}N from a shallow net tow. Our preliminary comparisons for *G. ruber* fit this prediction.

Relationship of FB-δ^{15}N to other nitrogen pools—Planktonic foraminifera are heterotrophic zooplankton, obtaining N mostly from some fraction of the POM in ocean waters. Foraminifera diets appear to be diverse and complex, with many of the paleoceanographically important species being omnivorous, as documented by field and laboratory observations of their feeding behavior (Bé et al. 1977; Anderson et al. 1979; Spindler et al. 1984). Planktonic foraminifera are observed to prey mostly upon zooplankton (dominated by copepods, but also including tintinids, radiolaria, and other zooplankton in the same or higher size class), as well as eukaryotic phytoplankton (apparently mainly diatoms, where they are available) (Anderson et al. 1979; Spindler et al. 1984). The importance of bacteria in the diet of some benthic foraminifera (Muller and Lee 1969) raises the possibility that the planktonic foraminifera species may also feed on the cyanobacteria and heterotrophic bacteria living in the surface ocean. For the symbiotic corals, the symbiont–coral system may obtain dissolved inorganic N (typically ammonium) from the surrounding waters, in addition to N from the prey (Muscatine et al. 1979). However, the concentration of inorganic N (especially ammonium) is typically $\geq$ 10-fold higher on reefs than in the open oligotrophic surface ocean (Muscatine et al. 1979; Lipschultz 2001). Furthermore, symbionts associated with foraminifera often exhibit very high volume-normalized rates of primary production

Table 1. FB-δ^{15}N in the surface or near-core-top sediments, δ^{15}N of subsurface nitrate, bulk suspended POM in the euphotic zone, and bulk sinking POM below the euphotic zone, from various open-ocean sites with low-nutrient surface waters.

	Great Bahama Bank	South China Sea	Hawaii	Indonesia	San Pedro	New Zealand	Cariaco Basin
Globigerinoides ruber (‰)	2.9	4.9	4.8	5.1	NA	7.2	4.6
Globigerinoides sacculifer	2.3	5.1	5.1	4.6	NA	NA	4.8
Orbulina universa	2.6	4.9	NA	NA	8.4	7.3	5.2
Globigerinella aequilateralis	4.1	7.4	NA	6.9	NA	8.6	6.6
Globorotalia menardii	3.5	6.1	NA	7.1	NA	NA	5.2
Neogloboquadrina dutertrei	3.8	5.2	NA	6.8	10.2	NA	5.5
Globorotalia truncatulinoides	NA	NA	NA	NA	NA	9.4	NA
Globigerina bulloides	NA	NA	NA	NA	11.6	NA	5.5
Subsurface nitrate*	2.6	4.7	4.5	5	8.3	7	4.3
Sinking POM†	3.7	3.3	3–3.5	NA	8.4	NA	4.4
Suspended POM in the euphotic zone‡	−1–0	2–4	0.5–1.5	NA	NA	NA	NA

NA, not available.
* Refer to Fig. 6 figure caption.
† δ^{15}N values of the sinking POM were measured from sediment traps at 150 m in the Sargasso Sea (Altabet 1989), below 600 m in the South China Sea (Gaye et al. 2009), between 150 and 500 m near ALOHA Sta. (Casciotti et al. 2008), at 500–550 m in the San Pedro Basin (Altabet et al. 1999; Collins et al. 2011), and at 275 m in the Cariaco Basin (Thunell et al. 2004).
‡ δ^{15}N values of the suspended POM within the euphotic zone were measured by Altabet (1989) in the Sargasso Sea, by Saino and Hattori (1987), as well as Yang (unpubl.) in the South China Sea, and by Casciotti et al. (2008) at the ALOHA Sta.

relative to the surrounding water (Caron et al. 1995). This means that foraminifera are acquiring N faster than phytoplankton through some process, and their active feeding, followed by translocation of N waste to their symbionts, is the obvious explanation.

The δ^{15}N of heterotrophic zooplankton is 2–3‰ higher than their food source, due to preferential excretion of ^{14}N-rich ammonia (Checkley and Miller 1989). We thus expect FB-δ^{15}N to be correlated with the δ^{15}N of their food source, although the δ^{15}N offset from their diet may be different between symbiotic and asymbiotic species (*see* next section). Because studies on specific plankton groups and particulate N pools are few, we are limited to comparing FB-δ^{15}N with the available δ^{15}N data on subsurface nitrate and bulk suspended and sinking POM (Table 1; Fig. 6).

Comparison between foraminifera and suspended POM $\delta^{15}N$—Across diverse regions (e.g., the subtropical North Atlantic, the South China Sea, and near Hawaii), the FB-δ^{15}N of the euphotic-zone dwellers is higher than the bulk suspended POM in the euphotic zone by approximately 2–3‰. This observation is at least superficially consistent with the argument that planktonic foraminifera obtain N mostly from the suspended POM pool and have δ^{15}N values that are 2–3‰ higher than their diet (Ren et al. 2009). However, bulk suspended POM includes various unicellular forms (e.g., phytoplankton, bacteria, and protozoan grazers) and organic detritus, and planktonic foraminifera probably distinguish among these pools in their feeding. A recent study in the summertime Sargasso Sea found that the cyanobacteria *Prochlorococcus* and *Synechococcus* have a δ^{15}N value similar to or slightly lower than bulk POM (−1‰ to ~ 0‰), while eukaryotic phytoplankton δ^{15}N is more variable but typically higher than bulk POM δ^{15}N and prokaryote δ^{15}N, by > 3‰ (Fawcett et al. 2011). It is also known that the δ^{15}N of smaller zooplankton in the euphotic zone (i.e., in the 250–1000-μm fraction) centers around 2–3‰ in the Sargasso Sea (Montoya et al. 2002). Since eukaryotic phytoplankton and smaller zooplankton are likely to be the main source of N to planktonic foraminifera, it appears that the three euphotic-zone-dwelling, symbiotic, and spinose species, *G. ruber*, *G. sacculifer*, and *O. universa*, have δ^{15}N values that are not very different from their food source. Below the euphotic zone, the δ^{15}N of suspended POM increases sharply with depth (Altabet 1988), which correlates strongly with the decrease in POM concentration with depth, and likely results from isotopic fractionation during organic matter breakdown. This may partly explain the higher δ^{15}N for the subeuphotic dwellers, which we will discuss in more detail in the next section.

Comparison between foraminifera and sinking POM $\delta^{15}N$—At steady state, N export out of the euphotic zone must be balanced by the sum of the sources of new nitrogen to the euphotic zone (Eppley and Peterson 1979), such that the δ^{15}N of the sinking flux should also converge on the flux-weighted mean δ^{15}N of the new N sources (Altabet 1988, 1989). However, confirmation of this supposition is

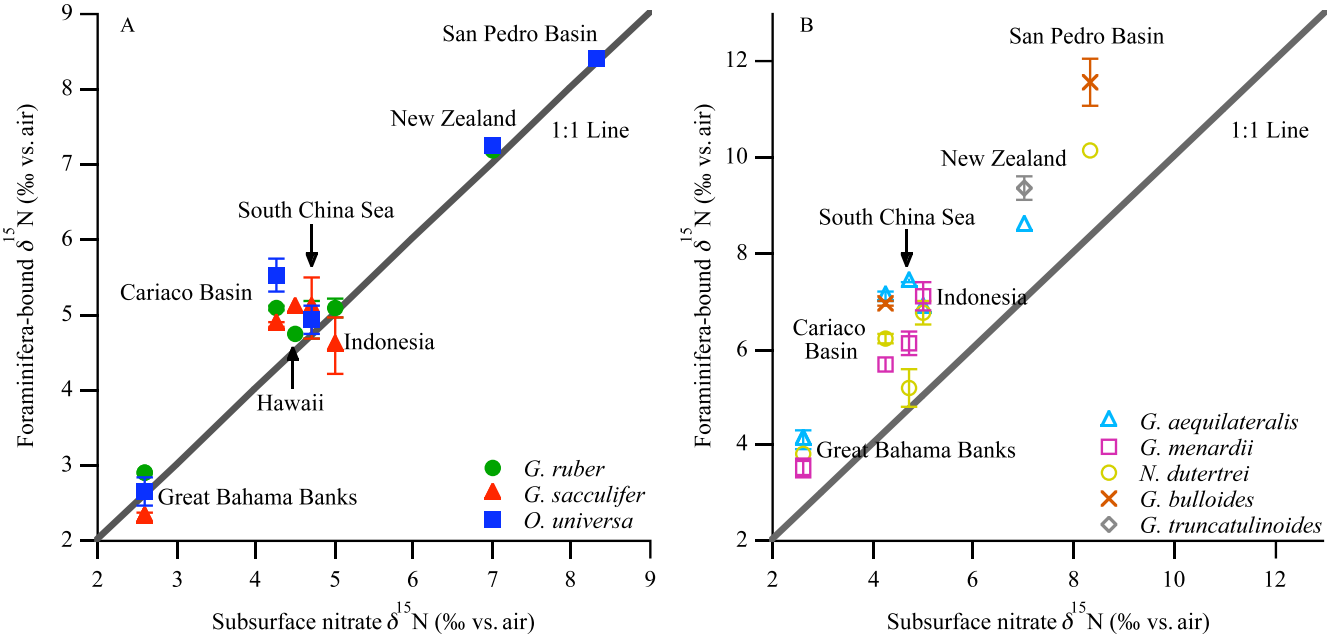

Fig. 6. Comparison between the measured or estimated shallow subsurface (i.e., thermocline) nitrate δ^{15}N and FB-δ^{15}N of (A) the euphotic-zone-dwelling, symbiotic, spinose species and (B) the subeuphotic-zone-dwelling, asymbiotic, and/or non-spinose species. The error bars for FB-δ^{15}N indicate standard deviations based on cleaning replicates. Subsurface nitrate δ^{15}N values used for comparison were measured at 200 m at the Bermuda Atlantic Time-series Study (BATS) site (Knapp et al. 2005), integrated from 80 to 150 m at the South China Sea (Wong et al. 2002), averaged from 100 to 150 m near the Hawaii Islands (Knapp et al. 2011), at 100 m in the Makassar-Bali Basin (R. Robinson unpubl.), 200–300 m in the San Pedro Basin (Liu and Kaplan 1989; M. Prokopenko unpubl.), Subantarctic Mode Water as measured in the Subantarctic Zone south of Australia (DiFiore et al. 2006), and 125–150 m in the Cariaco Basin (Thunell et al. 2004).

complicated by changes in the δ^{15}N of the sinking flux through the water column. Studies from various regions, including the Cariaco Basin (Fig. 4), have shown a lower mean δ^{15}N for sinking particles caught in deep sediment traps than in shallower ones (Saino and Hattori 1987; Altabet et al. 1991; Thunell et al. 2004). It has been proposed that selective removal of compounds enriched in ^{15}N (Altabet et al. 1991) or repackaging of sinking particles in the interior of the ocean (Conte et al. 2001) may explain the observed changes in the δ^{15}N of sinking POM, but the actual cause of this decrease is unclear. Because of this apparent change in sinking δ^{15}N with depth, measurement of sinking POM δ^{15}N may not always represent the δ^{15}N of the integrated N supply to the euphotic zone.

In contrast to the observed decrease in the δ^{15}N of bulk sinking POM in Cariaco Basin, our measured FB-δ^{15}N from the sediment trap capturing sinking foraminifera is very similar to the specimens collected in the surface sediments (Fig. 5). The slightly lower FB-δ^{15}N of some species in the sediment trap samples than in the sediment may derive from interannual or longer timescale variation in the N isotope dynamics of the Cariaco Basin, which is certainly possible given the dynamic nature of the basin on even decadal and centennial timescales (Zhang and Millero 1993). Alternatively, the difference may involve an early diagenetic change in the FB-δ^{15}N. However, the N content of the foraminifera is similar between the sediment trap samples and surface sediments, suggesting minimal loss of shell-bound organic N (data not shown). FB-δ^{15}N measurement in traps over a longer time interval will be needed to confirm the robustness of the similarity between sinking and sedimentary foraminifera. Details aside, our initial results from the Cariaco Basin suggest that the FB-δ^{15}N signals produced in the surface ocean are well preserved during export through the water column and burial in the sediment.

Despite uncertainties associated with the δ^{15}N of sinking POM, comparison between FB-δ^{15}N and sinking POM also shows the similarity one would expect (Table 1). For example, in the San Pedro Basin, where the subsurface nitrate δ^{15}N is elevated relative to the deep ocean as a result of transport of subsurface nitrate from the water-column denitrification zone in the eastern tropical North Pacific oxygen minimum zone (Altabet et al. 1999), the δ^{15}N of the planktonic foraminifera and the sinking POM are both higher than elsewhere (*G. ruber* FB-δ^{15}N and sediment trap POM δ^{15}N are both around 8.4‰).

In the Cariaco Basin, the δ^{15}N of the sinking POM, especially in the shallow trap, shows seasonal variation in which the minimum δ^{15}N occurs during winter and late spring (Thunell et al. 2004). Among the species sampled from multiple time intervals, the euphotic-zone-dweller *O. universa* shows greatest variation and strongest correlation with changes in the sinking POM δ^{15}N, while the δ^{15}N values of the other subeuphotic-zone dwelling, and/or non-spinose species *G. aequilateralis*, *G. menardii*, and *G. dutertrei* vary less through the studied period. Many of the planktonic foraminifera species exhibit a lunar or

semilunar reproductive cycle, such that an individual foraminifera would spend on average a couple of weeks to a month in the upper water column prior to sinking to the seabed (Hemleben et al. 1988). Thus, the lack of seasonal variation in the subeuphotic-zone-dwelling and non-spinose species cannot be explained by generation timescales. We propose that it results from the δ^{15}N of their food source varying less over time. Below the euphotic zone, planktonic foraminifera probably derive their N largely from the decaying organic matter, which is likely to have a longer residence time and less seasonal isotopic variation than the POM within the euphotic zone, and its δ^{15}N is elevated by bacterial degradation (Altabet 1988). This is supported by the observations that non-spinose foraminifera prey relatively passively on phytoplankton or dead zooplankton debris in cultures (Spindler et al. 1984); below the euphotic zone, phytoplankton are generally scarce, and organic detritus is their most likely food source.

Comparison between sedimentary FB-δ^{15}N and shallow subsurface nitrate δ^{15}N—FB-δ^{15}N strongly correlates with the measured shallow thermocline nitrate δ^{15}N (Fig. 6; Table 1), with the three euphotic-zone-dwelling, symbiotic, and spinose species, *G. ruber*, *G. sacculifer*, and *O. universa*, being closest to the subsurface nitrate δ^{15}N (generally within $\pm$ 0.4‰). The largest deviation is in the Cariaco Basin, where the three species appear to be $\sim$ 1‰ higher in δ^{15}N than the subsurface nitrate δ^{15}N. One plausible explanation is that the δ^{15}N of the euphotic zone net N supply may be greater than the δ^{15}N of the shallow thermocline nitrate, because of coastal upwelling and lateral advection across the basin. Alternatively, as raised already herein, it is possible that the difference is driven by interannual or longer-term changes in the δ^{15}N of the nitrate supply in the basin (i.e., the δ^{15}N of the nitrate supply during the time of our study is 0.5–1.0‰ lower than the long-term average).

We have previously argued that FB-δ^{15}N is correlated with the δ^{15}N of the total new N sources to the euphotic zone (Ren et al. 2009). If so, the correlation between FB-δ^{15}N and thermocline nitrate δ^{15}N would imply a similar, likely minor, contribution from N fixation to the total new N in all these regions. This is consistent with previously published isotopic balance of the N pools in the Sargasso Sea and near Hawaii (Altabet 1988; Knapp et al. 2005; Casciotti et al. 2008). Alternatively, these data could suggest that the planktonic foraminifera are consuming a N pool that is dominantly supported by nitrate supply from below, such that FB-δ^{15}N is more reflective of the δ^{15}N of the nitrate supply and less sensitive to changes in the direct N input from N fixation. Eukaryotic biomass in the Sargasso Sea is typically higher in δ^{15}N near the nitracline and deep chlorophyll maximum, becoming lower in the mixed layer (Fawcett et al. 2011). These authors inferred that the eukaryotes are utilizing "new" nitrate mixed up from below. Since eukaryotes appear to contribute more N than prokaryotes to planktonic foraminifera, FB-δ^{15}N may be less sensitive than bulk POM to direct additions of low δ^{15}N from newly fixed N to the euphotic zone. In any case, these data suggest that the FB-δ^{15}N of euphotic-zone-dwelling forms is a good recorder of the δ^{15}N of the thermocline nitrate supply.

The role of symbionts in interspecies isotopic differences—Subeuphotic-zone-dwelling, asymbiotic, and/or non-spinose species tend to have a higher δ^{15}N than the shallow subsurface nitrate (Fig. 6B) and than euphotic-zone-dwelling, spinose, symbiotic species (Fig. 6A). The spinose forms have been argued to specialize in zooplankton predation, while the non-spinose forms appear to rely more on herbivory (Bé et al. 1977; Spindler et al. 1984). The difference in diet would be expected to render the non-spinose forms lower in FB-δ^{15}N, in the opposite sense of the observations. However, as described previously herein, one possible compensating factor is the characteristic increase in the δ^{15}N of suspended POM with depth below the euphotic zone (Altabet 1988). If the deeper-dwelling species obtain a larger proportion of their N from these subeuphotic-zone particles, they should indeed have a higher δ^{15}N than the euphotic-zone dwellers (Fig. 7) (Mintenbeck et al. 2007).

Relative to the three euphotic-dwelling, spinose, and symbiont-bearing species (*G. ruber*, *G. sacculifer*, and *O. universa*), the three species *G. bulloides*, *H. pelagica*, and *G. aequilateralis* appear to have a higher FB-δ^{15}N, despite the fact that they are also spinose, and *G. bulloides* also tends to live in the shallow mixed layer (Hemleben et al. 1988). We note that these spinose species as well as all non-spinose species are either asymbiotic or have symbiotic chrysophytes instead of dinoflagellates (Hemleben et al. 1988), suggesting some role of symbionts in regulating the relationship between FB-δ^{15}N and the δ^{15}N of various N pools in the surface ocean.

We suggest that the effect of the dinoflagellate symbionts is as follows. Foraminifera (and zooplankton in general) feed on organic matter with a near-Redfieldian component of N. Most of this organic matter is respired. This leaves foraminifera with excess N, most of which they would excrete to the environment if they did not have symbionts (e.g., as observed in copepods). Indeed, the ability of foraminifera to acquire N from feeding, and their resulting inherent excess of N, is likely one of the drivers of the host–symbiont relationship (Jorgensen et al. 1985). In this context, perhaps the most important role of the symbionts from the perspective of the N isotopes is to partially transform foraminifera into primary producers (Caron et al. 1995), reducing their ammonium excretion into the environment. The excretion of low-δ^{15}N ammonium is what drives zooplankton (and animals in general) to be higher in δ^{15}N than their food source (Checkley and Miller 1989). Thus, the lack of large-scale ammonium excretion may cause symbiont-bearing foraminifera to have a δ^{15}N that is only minimally higher than their food source (Fig. 7). Consistent with this hypothesis, Uhle et al. (1997) noted from cultures that (dinoflagellate symbiont–bearing) *O. universa* biomass δ^{15}N was only 1.1‰ elevated relative to their food source, whereas (symbiont-free) *G. bulloides* was 3.0‰ higher. They explained this difference as resulting from an additional low-δ^{15}N N source from the symbionts; we hypothesize that it results from less

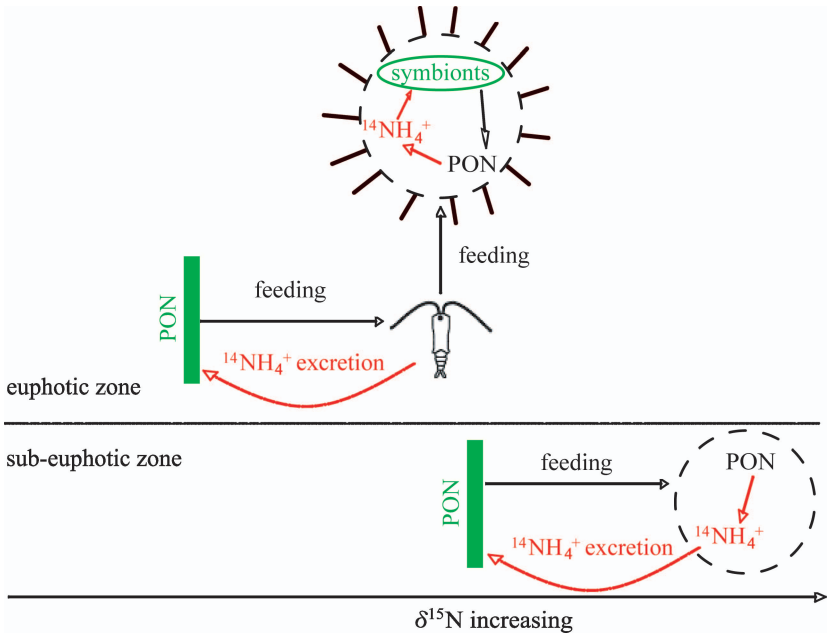

Fig. 7. Diagram of our tentative explanation for the causes of FB-δ^{15}N differences between the euphotic-zone-dwelling, symbiotic, spinose species (upper) and the subeuphotic-zone-dwelling, asymbiotic, and/or non-spinose species (lower). The higher δ^{15}N of the subeuphotic-zone-dwelling, asymbiotic species may be caused by their consumption of suspended POM from below the euphotic zone, the δ^{15}N of which is elevated due to isotopic fractionation during organic matter breakdown. A lack of excretion of ammonium (which has a low δ^{15}N, red arrow), resulting from assimilation of this regenerated N by the dinoflagellate symbionts, may also contribute to the lower δ^{15}N of the symbiotic foraminifera species, despite their probable consumption of zooplankton, which have a relatively high δ^{15}N because of their own ammonium excretion. This symbiosis-driven internal N recycling can also explain the apparent isotopic similarity between symbiotic foraminifera and their diet.

ammonium excretion by *O. universa*. Consistent with this, there is the observation from corals that the zooxanthellae are often lower in δ^{15}N than the coral tissue, suggesting that the zooxanthellae are using the low-δ^{15}N ammonium released by metabolism from the coral host (Hoegh-Guldberg et al. 2004; Swart et al. 2005).

We should also reiterate an additional potential effect mentioned earlier, again involving the symbionts but in a different way. In asymbiotic corals, it has been suggested that the carbonate-associated δ^{15}N is ~4‰ greater than the tissue, whereas this elevation in carbonate-associated δ^{15}N does not pertain to symbiotic corals (Muscatine et al. 2005). If this applies to foraminifera, it may explain part or all of the FB-δ^{15}N elevation of asymbiotic relative to symbiotic forms. This possibility, which we consider remote, can nevertheless be investigated using either net tow collections or foraminifera culturing.

Broader implications—The data reported here represent our first efforts to characterize and understand the controls on the δ^{15}N of planktonic foraminifera shell-bound organic matter. While much more work is required, the results so far support the use of FB-δ^{15}N as a paleoceanographic proxy for the δ^{15}N of the nitrate being supplied to the nutrient-poor tropical and subtropical surface ocean. A clear δ^{15}N distinction exists between spinose, symbiotic, euphotic-zone-dwelling forms and non-spinose, asymbiotic forms that tend to dwell deeper in the water column; the latter group is higher in δ^{15}N than both the euphotic-zone dwellers and the δ^{15}N of the nitrate supply. The available sediment trap data also suggest that the δ^{15}N of some of the non-spinose forms may vary less seasonally. All of these findings are consistent with the non-spinose forms grazing at least in part on the higher-δ^{15}N suspended organic matter found below the euphotic zone. However, other factors, in particular, the effects of algal symbiosis in the euphotic-zone dwellers may also be important. These mechanistic questions aside, both the spinose euphotic-zone dwellers and the non-spinose forms appear to have paleoceanographic value, although this conclusion is contingent on future results confirming that the FB-δ^{15}N–subsurface nitrate δ^{15}N offset is conserved for any given non-spinose species.

We suspect that the differences among foraminifera may tell us about changes in upper-ocean N cycling, including depth gradients in POM. To expand on this, preferential ^{14}N recycling should work to lower the δ^{15}N of euphotic zone POM and its components relative to the nitrate supply (Altabet 1988), and recycling may also lower the δ^{15}N of POM in the shallow mixed layer relative to the POM in the deeper euphotic zone (Altabet 1989). The rate of recycling relative to that of nitrate input from below may thus alter the δ^{15}N relationship of a given foraminifera species to the nitrate supply, and may change the δ^{15}N relationships among different foraminifera species. For example, some foraminifera species may be more strongly tied to phytoplankton relying on recycled N, while others may graze phytoplankton that are at least partly reliant on nitrate mixed up from below. If so, an increasing N recycling intensity in surface waters

should cause the FB-δ^{15}N of these foraminifera species to diverge. As a second example, the depth distribution of N fixation in the water column may affect the vertical structure of POM δ^{15}N in the euphotic zone, which may then manifest itself in the δ^{15}N relationships among foraminifera species with different depth preferences.

In the down-core study at Ocean Drilling Program Site 999 in the Caribbean Sea, FB-δ^{15}N was found to be similar among the three euphotic dwellers *G. ruber*, *G. sacculifer*, and *O. universa* during the late Holocene, consistent with the lack of depth gradient in the bulk suspended POM δ^{15}N in the present-day subtropical North Atlantic. However, during the last ice age, the three species had coherently different δ^{15}N, with *G. ruber* being the lowest, and *O. universa* the highest. Since *G. ruber* is the shallowest dweller of the three, and *O. universa* is the deepest, these data suggest a vertical gradient in the δ^{15}N of POM and/or its components during the last ice age (Ren et al. 2009). Understanding such down-core changes will require an improved understanding not only of the N metabolism within foraminifera but also of the N isotope dynamics of the various forms of POM that are involved in the upper-ocean N cycle. While many questions remain to be answered, the results of this study provide first indications that foraminifera-bound δ^{15}N can be used to reconstruct not only the δ^{15}N of the nitrate supply but also other aspects of open-ocean N cycling in the past.

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