

## RESEARCH ARTICLE

10.1002/2014PA002735

## Key Points:

- First global compilation and statistical synthesis of controls on  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$
- The  $\delta^{18}\text{O}$  primarily shows basin differences and  $\delta^{13}\text{C}$  primarily shows depth habitat
- The  $\delta^{13}\text{C}$  offsets between same-sized living and post-reproductive dead individuals

## Supporting Information:

- Readme
- Text S1, Figures S1–S28, and Tables S1–S5
- Data set S1
- Data set S2

## Correspondence to:

T. H. G. Ezard,  
t.ezard@soton.ac.uk

## Citation:

Ezard, T. H. G., K. M. Edgar, and P. M. Hull (2015), Environmental and biological controls on size-specific  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  in recent planktonic foraminifera, *Paleoceanography*, 30, 151–173, doi:10.1002/2014PA002735.

Received 9 OCT 2014

Accepted 12 JAN 2015

Accepted article online 15 JAN 2015

Published online 7 MAR 2015

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

# Environmental and biological controls on size-specific $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in recent planktonic foraminifera

Thomas H. G. Ezard<sup>1,2</sup>, Kirsty M. Edgar<sup>3</sup>, and Pincelli M. Hull<sup>4</sup>
<sup>1</sup>Centre for Biological Sciences, University of Southampton, Southampton, UK, <sup>2</sup>School of Ocean and Earth Sciences, National Oceanography Centre Southampton, University of Southampton, Southampton, UK, <sup>3</sup>School of Earth Sciences, University of Bristol, Bristol, UK, <sup>4</sup>Department of Geology & Geophysics, Yale University, New Haven, Connecticut, USA

**Abstract** As living organisms, planktonic foraminifera are not passive tracers of the environment. Their test geochemistry—arguably the single most important resource for paleoceanographic research—reflects the combined signal of environmental, biological, and preservational processes. For most species, comparisons of test stable isotopic composition within and among taxa provide the primary means for disentangling the relative influences of these different processes. Here we test the foundations of our paleoceanographic interpretations with the first quantitative comparison of the determinants of carbon and oxygen isotopic variation across multiple ocean basins, studies, and species by re-analyzing size-specific data collated from the literature. We find clear evidence of species-specific biological effects (i.e., vital effects), as the intercepts of size-specific carbon and oxygen isotopic compositions differ significantly among species. Trends in body size and isotopic composition, particularly in dinoflagellate bearing taxa, suggest that much of the size-dependent isotopic variation observed in death assemblages (i.e., core tops and sediments) relates to factors influencing the maximum size obtained by adults rather than ontogeny. The presence and type of photosymbiont hosted (dinoflagellate, chrysophyte, or none) were a major factor affecting species- and size-specific  $\delta^{18}\text{O}$  values. In contrast, size-related trends in  $\delta^{13}\text{C}$  values were driven by depth habitat (mixed layer, thermocline, subthermocline), symbiont ecology and whether the assemblage was alive or dead when sampled. On this broad geographic and oceanographic scale, ocean basin and biome had a significant effect on  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values. Our analysis and its model-averaged predictions provide a quantitative basis for interpreting size-specific isotopic variation in 22 species of modern macroperforate planktonic foraminifera. We conclude by highlighting existing data gaps and outstanding questions of the relative influence of environmental, preservational, and biological processes on variation in the test geochemistry of planktonic foraminifera.

## 1. Introduction

Planktonic foraminifera precipitate calcium carbonate tests. The stable isotopic compositions of these tests are influenced by the ambient environment including the isotopic composition of seawater, temperature, and carbonate ion concentrations [Spero *et al.*, 1997; Spero, 1998]. Because of this, the carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope values of foraminiferal tests are arguably the most important tool available for paleoceanographic reconstructions [Emiliani, 1954; Spero, 1998; Zeebe *et al.*, 2008; Pearson, 2012].

The use of foraminiferal isotopes for this purpose is, however, not without complications. Isotopic offsets between foraminifera and their environment can arise during test calcification because biology and ecology interact to modify an individual's external and internal microenvironment [Duplessy *et al.*, 1970; Shackleton *et al.*, 1973; Duplessy *et al.*, 1981b, 1981a; Jørgensen *et al.*, 1985; Spero *et al.*, 1997; Spero, 1998; Wolf-Gladrow *et al.*, 1999; Zeebe *et al.*, 2008]. In the fossil record, the geochemistry of foraminiferal tests can also reflect postmortem processes like dissolution and recrystallization [Lohmann, 1995; Pearson *et al.*, 2001; Sexton *et al.*, 2006] in addition to biology and ecology [Erez, 1978; Erez and Honjo, 1981; Friedrich *et al.*, 2012] or the environment and climate in which an individual lived [Emiliani, 1954; Spero, 1998; Birch *et al.*, 2013].

More than half a century of research dedicated to disentangling the determinants of isotopic composition in planktonic foraminifera has led to the great utility of foraminifera in paleoceanography [e.g., Emiliani, 1954; Emiliani, 1971; Savin and Douglas, 1973; Spero *et al.*, 1997; Wolf-Gladrow *et al.*, 1999; Pearson *et al.*, 2001; Zeebe *et al.*, 2008]. However, many outstanding issues remain in interpreting stable isotopic data, even in extant taxa. This is largely because we have detailed experimental data on just a few model species [e.g., Erez

and Luz, 1982; Jørgensen *et al.*, 1985; Spero *et al.*, 1997] and generally sparse (if any) calibration data for the rest. We also need to account for multiple covarying influences of preservation, oceanography, and biology [e.g., see discussions in Bornemann and Norris, 2007; Birch *et al.*, 2013].

Here we begin addressing this gap by synthesizing existing field data to test whether the empirical evidence supports the purported influence of key hypothesized drivers of isotopic variability in modern planktonic foraminifera. We focus on species-specific size-fractionated isotope curves and interspecific crossplot comparisons (i.e.,  $\delta^{13}\text{C}$  versus  $\delta^{18}\text{O}$ ; as in Pearson and Wade [2009], Friedrich *et al.* [2012], and Birch *et al.* [2013]) because they are one of the most effective means of constraining the effect of biological and preservational processes on foraminiferal calcite  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  composition [e.g., D'Hondt and Zachos, 1993; Pearson *et al.*, 1993; Norris, 1996].

More specifically, we examine the relative influences of environmental, biological, and preservational factors on the size- $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  trends in foraminiferal tests. Environmental influences include those factors that most paleoceanographic studies seek to infer, including temperature, salinity, and carbonate ion concentration [e.g., Urey, 1947; Epstein *et al.*, 1953; Spero *et al.*, 1997; Zeebe, 1999; Pearson, 2012]. Biological factors refer to all aspects of organismal physiology (e.g., biomineralization, kinetic effects, metabolism, respiration, photosymbiosis, and reproduction) and life history (e.g., diet, depth habitat, and seasonality) affecting the isotopic composition of foraminiferal calcite. These are commonly referred to as “vital effects” [Erez, 1978; Spero, 1998] and are, at times, used simply to describe some poorly constrained biological process(es) overprinting the primary environmental signal (as in Erez [1978]). Preservational factors including carbonate saturation state may drive postmortem alteration (e.g., dissolution, recrystallization, and cementation) of foraminiferal calcite [Lohmann, 1995; Pearson *et al.*, 2001; Wilson *et al.*, 2002; Sexton *et al.*, 2006].

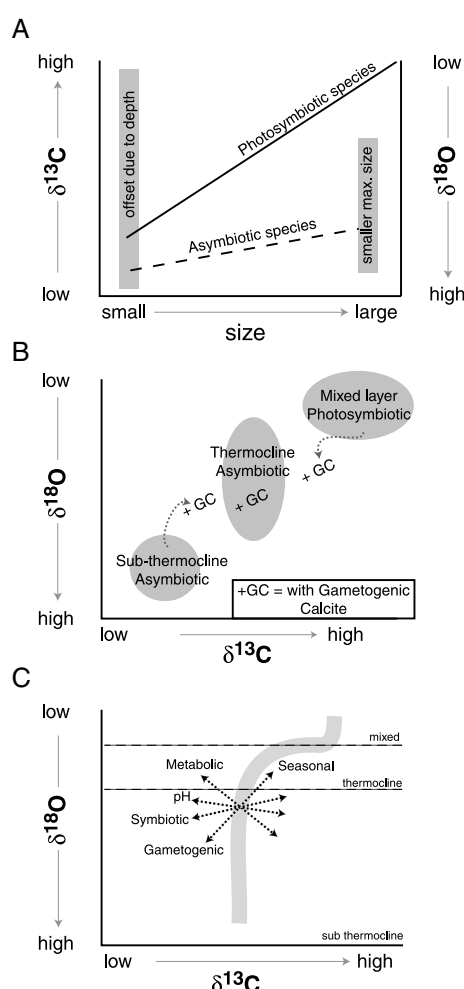
To date, modern calibration studies have typically been limited to testing environmental conditions in a single oceanographic location, on a subset of species and parameters [but see Schmidt and Mulitza, 2002]. Here we consider all available data to disentangle the relative influence of environment, biology, and preservation on species-specific trends in size-dependent  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  relationships. How much evidence is there for key biological characteristics (i.e., depth habitat and symbiont ecology) in size-specific isotopes? How important are environmental and preservational factors in influencing these relationships? We begin by reviewing the background of these existing sets of hypotheses.

## 2. Background

Crossplots of carbon and oxygen isotopes from multiple species are used to identify the symbiotic status (Figure 1a) and relative depth habitats (Figure 1b) of most modern and fossil planktonic foraminifera. This identification relies on the fact that shallow dwelling species typically have relatively low  $\delta^{18}\text{O}$  and high  $\delta^{13}\text{C}$  values as compared to deeper dwelling species (Figure 1b) [Ravelo and Fairbanks, 1992, 1995; Coxall *et al.*, 2007; Aze *et al.*, 2011; Birch *et al.*, 2013]. These interspecific isotopic relationships reflect the isotopic structure of the water column: generally, cooler nutrient-enriched deep waters have higher  $\delta^{18}\text{O}$  and lower  $\delta^{13}\text{C}$  values relative to warmer surface waters. Vertical gradients in the isotopic composition of seawater generally arise in  $\delta^{18}\text{O}$  due to thermal stratification (i.e., fractionation is temperature sensitive:  $\delta^{18}\text{O}_{\text{calcite}}$  is lower in warm, shallow waters and higher in cool deep waters) [e.g., Pearson, 2012] and in  $\delta^{13}\text{C}$  due to the isotopic composition of dissolved inorganic carbon (DIC;  $\delta^{13}\text{C}$  of DIC is high in shallow waters where  $^{12}\text{C}$  is bound up in algae and low in deep waters where it has been remineralized) [e.g., Spero *et al.*, 1991].

Correctly identifying foraminiferal depth habitat is paramount for paleoceanographic studies seeking to understand change at a given water depth. However, accurate depth habitat determinations are complicated by biological and preservational factors like species-specific offsets, seasonality, and differential dissolution susceptibility (Figure 1c), which can act to collapse or even invert the order of inferred depth habitat [Savin and Douglas, 1973; Shackleton *et al.*, 1973; Ravelo and Fairbanks, 1995; Pearson *et al.*, 2001; Sexton *et al.*, 2006; Birch *et al.*, 2013; John *et al.*, 2013]. In addition, many biological processes, like metabolic and photosynthetic rates, are directly affected by depth-dependent environmental conditions [Erez and Honjo, 1981; Spero and Williams, 1989; Norris, 1998; Zeebe *et al.*, 2008].

Two well-known biological effects influencing size-specific isotope composition in planktonic foraminiferal species include the formation of gametogenic calcite and the presence or absence of photosymbionts.



**Figure 1.** Theoretical schematic for the influence of ecology and biology on size-specific and intraspecific stable isotopes. (a) Size-related trends in  $\delta^{13}\text{C}$  for asymbiotic versus photosymbiotic species, (b) depth habitat effect on  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ , and (c) crossplot summary of dominant factors hypothesized to drive interspecific offsets. This figure is a schematic, which indicates general expectations and not actual data.

Planktonic foraminiferal species with photosynthetic algal symbionts are typically thought to have higher  $\delta^{13}\text{C}$  and lower  $\delta^{18}\text{O}$  values at any given body size than asymbiotic taxa due to shallower average depth habitats driven by the availability of photosynthetically active radiation (Figure 1a). In addition, species with dinoflagellate endosymbiotic algae typically have steeper size-specific  $\delta^{13}\text{C}$  curves, which are attributed to the increasing effect of algal preferential  $^{12}\text{C}$  uptake on the internal inorganic carbon pool with increasing symbiont density or activity through ontogeny [Spero and Deniro, 1987; Norris, 1996, 1998; Bijma et al., 1999; Wolf-Gladrow et al., 1999]. Steep size- $\delta^{13}\text{C}$  relationships are not a foolproof means of identifying photosymbiont bearing taxa: some asymbiotic taxa, including *Globigerina bulloides*, exhibit relatively large  $\delta^{13}\text{C}$  trends (for example, see trends in Spero and Lea [1996] and Birch et al. [2013]); some dinoflagellate-bearing taxa (e.g., *Orbulina universa* in Birch et al. [2013]) show substantial isotopic variation; and species with chrysophyte endosymbionts are difficult to identify on the basis of their  $\delta^{13}\text{C}$  values [Norris, 1998; Bornemann and Norris, 2007].

A third size-specific isotopic relationship attributed to biology is the tendency for  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  to positively covary at small foraminiferal body sizes (roughly  $<300\ \mu\text{m}$ ) [Berger et al., 1978; Norris, 1998; Spero, 1998]. This pattern is variously attributed to kinetic effects (e.g., calcification rate-dependent isotopic discrimination) and/or metabolic effects (e.g., decreasing influence of respired  $\text{CO}_2$  with increasing body size) [e.g., Berger

Immediately prior to reproduction (gametogenesis) and death [Be, 1980; Hemleben et al., 1989], many species of planktonic foraminifera sink through the water column and add an additional layer of calcite to their test called gametogenic calcite [Erez and Honjo, 1981; Hemleben et al., 1989; Lohmann, 1995; Schiebel and Hemleben, 2005]. The bias in large, postreproductive individuals toward lower  $\delta^{13}\text{C}$  and higher  $\delta^{18}\text{O}$  values is thus typically attributed to reproduction-associated calcite crust formation at depth [Duplessy et al., 1981a; Schweitzer and Lohmann, 1991; Lohmann, 1995; Norris, 1998]. Alternative hypotheses for lower  $\delta^{13}\text{C}$  and higher  $\delta^{18}\text{O}$  values in postreproductive individuals include the preferential dissolution of ontogenetic calcite [Hemleben et al., 1989; Wu and Berger, 1989; Caron et al., 1990; Lohmann, 1995] or the ingestion of symbionts before gametogenesis [Ni et al., 2007; Birch et al., 2013]. The amount of gametogenic calcite deposited varies both within and among species [Be and Ericson, 1963; Schweitzer and Lohmann, 1991; Hamilton et al., 2008], so its influence is typically considered primarily in thick-crust species like *Globorotalia tumida* or *Truncorotalia truncatulinoides* [Duplessy et al., 1981a; Schweitzer and Lohmann, 1991; Lohmann, 1995; Hamilton et al., 2008].

et al., 1978; McConnaughey, 1989; Norris, 1998; Birch et al., 2013]. Considered together, size-specific isotope trends are typically attributed to metabolic and/or kinetic effects, the presence/absence of photosymbionts, and the presence/absence of gametogenic calcite in small-, medium-, and large-bodied individuals, respectively [e.g., Duplessy et al., 1981a; Spero and Deniro, 1987; McConnaughey, 1989; Lohmann, 1995; Norris, 1998; Spero, 1998; Hamilton et al., 2008]. However, in the sedimentary record, additional factors can influence size-specific isotopic composition. For instance, postreproductive individuals compose a large portion of sedimentary assemblages [Berger, 1971; Schweitzer and Lohmann, 1991] and variation in maximum adult body size can be due to light availability, season, and temperature among others [Berger et al., 1978; Spero and Williams, 1988, 1989; Spero et al., 1991]. Calcite preservation is an additional important factor in sedimentary carbonates [Wu and Berger, 1989; Lohmann, 1995; Pearson et al., 2001; Sexton et al., 2006].

The multiple potential competing and confounding drivers on test  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values illustrate the challenge of reconstructing ambient environmental conditions from planktonic foraminifera. Our re-analysis of 22 previous studies on 22 modern planktonic foraminiferal species [Berger et al., 1978; Kahn, 1979; Kahn and Williams, 1981; Williams et al., 1981; Bouvier-Soumagnac and Duplessy, 1985; Oppo and Fairbanks, 1989; Schweitzer and Lohmann, 1991; Ravelo and Fairbanks, 1992; Donner and Wefer, 1994; Norris et al., 1994; Billups and Spero, 1995; Kroon and Darling, 1995; Ravelo and Fairbanks, 1995; Ortiz et al., 1996; Niebler et al., 1999; Elderfield et al., 2002; Hillaire-Marcel et al., 2004; Keigwin et al., 2005; Bornemann and Norris, 2007; Franco-Fraguas et al., 2011; Friedrich et al., 2012; Birch et al., 2013] synthesizes their results into the wider context, providing a quantitative evidence base as a foundation for future research.

### 3. Methods

#### 3.1. Stable Isotopic ( $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ) Size Compilation

We compiled measurements of sieve size-specific stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ) data for 22 extant macroperforate species [e.g., Hemleben et al., 1989; Aze et al., 2011], updating species names in our compilation (Table 1) following the scheme used by Aze et al. [2011]. In all cases, stable isotope measurements were made on multiple individuals. We included all size-specific isotopic data that we could find from the literature, for all modern macroperforate species, as long as three size classes of isotopic data were available. Species-specific justifications are given in supporting information. Note that we distinguish between *Globigerinoides ruber* pink and *G. ruber* white (summarized in Darling and Wade [2008]) and the left (sinistral) coiling *Neogloboquadrina pachyderma* and the right (dextral) coiling *Neogloboquadrina incompta* [Darling et al., 2000, 2004, 2006; Darling and Wade, 2008]. *Globigerinoides sacculifer* (with and without a sac-like final chamber) and *Globigerinoides trilobus* are all included in *G. sacculifer* [Hemleben et al., 1987; André et al., 2013].

We examined all modern species with sufficient data (i.e., 22 species), rather than just the handful of species most commonly used in paleoceanography because we aimed to quantify the evidence base underpinning species-specific isotope variability. This necessitated a comparative study across as many species as possible in order to test the effect of shared evolutionary history on observed vital effects with sufficient statistical power. In addition, we included multiple lineages to assess the general applicability of isotopic inferences from modern “workhorse” species to other lineages of foraminifera, as modern taxa are not present in deeper time. Our data compilation is uploaded as supporting information for transparency and to facilitate re-analysis and inspection.

We only considered studies with planktonic foraminiferal isotopes from field-based research that presented three or more sieve-size fractions in order to assess the factors effecting isotopic trends with body size. We deliberately excluded laboratory experiments from the present study as laboratory studies test a portion of the full range of natural environmental conditions and are only available for a small subset of modern foraminifera [Jørgensen et al., 1985; Spero and Lea, 1996; Spero et al., 1997; Bijma et al., 1999; Wolf-Gladrow et al., 1999]. From hereon, we refer to sieve-size fractions as “size fractions” or “size” and recognize that the numerical values do not represent the actual size of a given foraminifera, but rather the midpoint between sieve mesh sizes.

#### 3.2. Biological Categorization

Each species was classified according to four major characteristics: the presence or absence of spines (i.e., spinosity), type of photosymbiont (i.e., none, chrysophyte, or dinoflagellate), depth habitat (i.e., mixed layer,

**Table 1.** Species Tested and Their Biological Categories<sup>a</sup>

Species	Spinose	Symbionts	Depth Habitat	Biome
<i>Globigerina bulloides</i>	1	None <sup>b</sup>	ML <sup>b,e,f,g,h</sup>	PT <sup>b,c,q,r,s</sup>
<i>Globigerinella calida</i>	1	None	T <sup>b,g,i,j</sup>	TS <sup>b</sup>
<i>Globigerinoides conglobatus</i>	1	Dinoflagellates <sup>b</sup>	ML <sup>b,g,i,k</sup>	TS <sup>k,o,t</sup>
<i>Globorotaloides hexagonus</i>	1	None	ST <sup>e,i,k,m</sup>	TS <sup>c,q,r,s</sup>
<i>Globoconella inflata</i>	0	Chrysophytes	T <sup>i,k,n</sup>	PT <sup>b,k,o,t</sup>
<i>Globigerinoides ruber pink</i>	1	Dinoflagellates <sup>b</sup>	ML <sup>b,d,g,l,o</sup>	TS <sup>c,o,t</sup>
<i>Globigerinoides ruber white</i>	1	Dinoflagellates <sup>b,c</sup>	ML <sup>b,d,g,l,o</sup>	TS <sup>c,o,t</sup>
<i>Globoturborotalita rubescens</i>	1	None	ML <sup>b,d,k</sup>	TS <sup>c,k,w</sup>
<i>Globigerinoides sacculifer</i>	1	Dinoflagellates <sup>b</sup>	ML <sup>b,d,g,l</sup>	TS <sup>c,o,t</sup>
<i>Globigerinella siphonifera</i>	1	Chrysophytes <sup>b</sup>	ML <sup>b,f,k,l,n,p</sup>	TS <sup>c,k,q</sup>
<i>Globorotalia tumida</i>	0	None <sup>d</sup>	ST <sup>f,i,k,n</sup>	TS <sup>c,k</sup>
<i>Globorotalia unguata</i>	0	None <sup>d</sup>	T	TS <sup>b</sup>
<i>Hirsutella hirsuta</i>	0	None <sup>b</sup>	ST <sup>i,k,n</sup>	TS <sup>b,k,o</sup>
<i>Hirsutella scitula</i>	0	None <sup>d</sup>	ST <sup>b,k,l,n</sup>	PT <sup>c,k,q,t</sup>
<i>Menardella menardii</i>	0	Chrysophytes <sup>b</sup>	T <sup>f,k,l,n</sup>	TS <sup>k,o,t</sup>
<i>Neogloboquadrina dutertrei</i>	0	Chrysophytes <sup>b</sup>	T <sup>b,g,l</sup>	TS <sup>k,o</sup>
<i>Neogloboquadrina incompta</i>	0	None <sup>b</sup>	T <sup>k,n</sup>	PT <sup>o</sup>
<i>Neogloboquadrina pachyderma</i>	0	None <sup>b</sup>	T <sup>k,n</sup>	PT <sup>k,o,r,s,w</sup>
<i>Orbulina universa</i>	1	Dinoflagellates <sup>b</sup>	ML <sup>b,g,k,l,n</sup>	TS <sup>c,k,o,t</sup>
<i>Pulleniatina obliquiloculata</i>	0	Chrysophytes <sup>b</sup>	T <sup>i,k,l,n</sup>	TS <sup>d,o,t</sup>
<i>Truncorotalia crassaformis</i>	0	None <sup>b</sup>	ST <sup>i,k,l</sup>	TS <sup>k</sup>
<i>Truncorotalia truncatulinoides</i>	0	None <sup>b</sup>	ST <sup>b,e,i,k,l,n</sup>	PT <sup>c,k,o,q,t</sup>

<sup>a</sup>PT indicates species with biome classified as polar/transitional; TS indicates tropical/subtropical. The ML dominant depth habitat is mixed layer, with T for thermocline and ST for subthermocline.

<sup>b</sup>Hemleben et al. [1989].

<sup>c</sup>Bé and Hutson [1977].

<sup>d</sup>Bé [1977].

<sup>e</sup>Fairbanks and Wiebe [1980].

<sup>f</sup>Fairbanks et al., 1982.

<sup>g</sup>Bé et al. [1985].

<sup>h</sup>Friedrich et al. [2012].

<sup>i</sup>Berger [1969].

<sup>j</sup>Niebler et al. [1999].

<sup>k</sup>Bé and Tolderlund [1971].

<sup>l</sup>Ravelo and Fairbanks [1992].

<sup>m</sup>Ortiz et al. [1996].

<sup>n</sup>Kucera [2007].

<sup>o</sup>Darling and Wade [2008].

<sup>p</sup>Huber et al. [1997].

<sup>q</sup>Birch et al. [2013].

<sup>r</sup>Spero and Lea [1996].

<sup>s</sup>Schiebel and Hemleben [2005].

<sup>t</sup>Parker [1960].

<sup>u</sup>Ivanova et al. [2003].

<sup>v</sup>Aze et al. [2011].

<sup>w</sup>Triantaphyllou et al. [2010].

thermocline, and subthermocline), and primary biogeographic habitat (i.e., biome) (Table 2). These four ecological categories are well-documented characteristics of modern planktonic foraminifera [Hemleben et al., 1989; Schiebel and Hemleben, 2005; Kucera, 2007] and have known effects on the stable isotopic composition of individuals [Pearson, 2012].

More than a third of modern planktonic foraminifera species host photosymbiotic algae within their cytoplasm [Bé and Hutson, 1977; Gastrich, 1987; Hemleben et al., 1989; Spero, 1998]. Species hosting photosymbionts typically inhabit relatively oligotrophic waters [Hemleben et al., 1989], with either dinoflagellate or chrysophyte symbiotic algae supporting test growth, survivorship, and reproduction [Bé et al., 1982; Faber et al., 1989; Hemleben et al., 1989]. Of the five species known to host chrysophytes in our analysis (Table 1), only *Globigerinella siphonifera* is thought to have obligate—rather than facultative—chrysophyte endosymbiotic algae [Faber et al., 1988, 1989; Hemleben et al., 1989; Huber et al., 1997; Bijma et al., 1998]. Given the difficulty distinguishing between obligate and facultative photosymbiosis in



**Table 2.** Biological, Environmental, and Preservational Explanatory Variables Tested<sup>a</sup>

Variable	Type	Levels
Spinose	Binary	Presence/absence of spines
Biome	Binary	Tropical/subtropical versus polar/transitional
Basin	Four-way categorical	Atlantic (including Caribbean, Southern, and Weddell; see text), Chukchi, Indian, Pacific
Symbionts	Three-way categorical	None, chrysophytes, dinoflagellates
Live/dead assemblage	Binary	Plankton nets/tows versus sediment material
Water depth	Continuous	Depth from where the sample was taken, either meters below sea level (live assemblages) or sediment-water interface (death assemblages)
Depth habitat	Three-way categorical	Mixed, thermocline, or subthermocline

<sup>a</sup>See supporting information for more details.

foraminifera [Hemleben *et al.*, 1989], and the possibility that this distinction does not exist (i.e., all species are obligate [see Gastrich, 1987; H. Spero, personal communication, 2014]), we simply group species according to the type of symbiotic algae that they host: dinoflagellate, chrysophyte, or none (as summarized by Bé and Hutson [1977], Hemleben *et al.* [1989], Bijma *et al.* [1998], and Spero [1998]).

We used modern observations (SCUBA, plankton tows, and depth stratified plankton tows) to categorize species according to three depth ecologies: mixed layer, thermocline, and subthermocline (Table 2). We avoided stable isotopically inferred depth-habitat rankings (as summarized by Aze *et al.* [2011] among others) to avoid circularity in our analyses. Among the studies that collected depth stratified information in extant individuals [Berger, 1969; Bé and Tolderlund, 1971; Fairbanks and Wiebe, 1980; Fairbanks *et al.*, 1982], the depth of species often varied across their range, by season, or between cruises. We therefore categorize species by dominant depth habitat (Table 2 after Berger [1969], Bé and Tolderlund [1971], Bé and Hutson [1977], Fairbanks *et al.* [1980, 1982], Bé *et al.* [1985], Hemleben *et al.* [1989], Ravelo and Fairbanks [1992], Ortiz *et al.* [1996], Huber *et al.* [1997], Niebler *et al.* [1999], Kucera [2007], Darling and Wade [2008], and Friedrich *et al.* [2012]).

The biogeography of extant planktonic foraminiferal species has been well known in plankton tows and core top sediments since the 1960s [Parker, 1960; Bé and Tolderlund, 1971; Bé, 1977]. Authors typically divide species distributions into five main faunal provinces [Bé and Tolderlund, 1971; Darling and Wade, 2008]: polar, subpolar, transitional, subtropical, and tropical. As with depth habitat, many morphological species span several provinces [Kucera, 2007; Darling and Wade, 2008] and we used maximum species abundance to identify three primary faunal provinces: polar, tropical/subtropical, and transitional/upwelling (including subpolar, transitional, and upwelling species) [Schiebel and Hemleben, 2005; Kucera, 2007]. After this process, only *N. pachyderma* was classified as “polar” so we consider biome a binary trait: “tropical/subtropical” or “transitional-polar” (Table 2 after Parker [1960], Bé and Tolderlund [1971], Bé and Hutson [1977], Hemleben *et al.* [1989], Spero and Lea [1996], Ivanova *et al.* [2003], Schiebel and Hemleben [2005], Darling and Wade [2008], Triantaphyllou *et al.* [2010], Aze *et al.* [2011], and Birch *et al.* [2013]).

### 3.3. The Database

The database, excluding outliers, features 1358 oxygen and 1147 carbon stable isotope measurements from all the major ocean basins. The data, uploaded as supporting information, include isotopic measurements from recently living individuals (from plankton tows) and long-dead individuals (predominantly from core top samples, including some sediment traps). Fifteen of the 22 species have carbon and oxygen data from both life (plankton nets) and death (traps and cores) assemblages. The influence of this factor (life/death) on  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values was tested as a binary explanatory character. The influence of sampling depth, for the plankton tow, sediment trap, or core top, on stable isotopic values was examined as continuous explanatory variables after some preliminary analyses.

Data availability varied substantially among species. For instance, we had from 4 (*G. unguolata*) to 120 (*G. sacculifer*)  $\delta^{18}\text{O}$  measurements per species (see supporting information and Figure 4 for details). Spatial coverage was similarly skewed: the majority of data come from the Atlantic Ocean, with particularly sparse

**Table 3.** Number of Size-Specific Stable Isotope Records in Our Compilation by Ocean Basin<sup>a</sup>

Basin	Oxygen	Carbon
Atlantic	972	767
Caribbean	25	25
Chukchi	110	110
Indian	156	154
Pacific	77	73
Southern	17	17
Weddell	3	3

<sup>a</sup>A scarcity of size-dependent oxygen and carbon stable isotope records in the Pacific Ocean, Southern Ocean, and Caribbean Sea is readily apparent. For geographic distribution, see Figure 2.

records from the Caribbean Sea, Pacific Ocean, Southern Ocean, and Weddell Sea (Table 3). Many sample sites are relatively close to land and in regions influenced by seasonal upwelling (Figure 2). The only species sampled in the Caribbean Sea was *G. sacculifer* and the only species sampled in the Southern Ocean species was *N. pachyderma*. Since our goal here is a comparison among species and basins, the sparsely sampled Caribbean Sea and Southern Ocean basins were amalgamated with the Atlantic

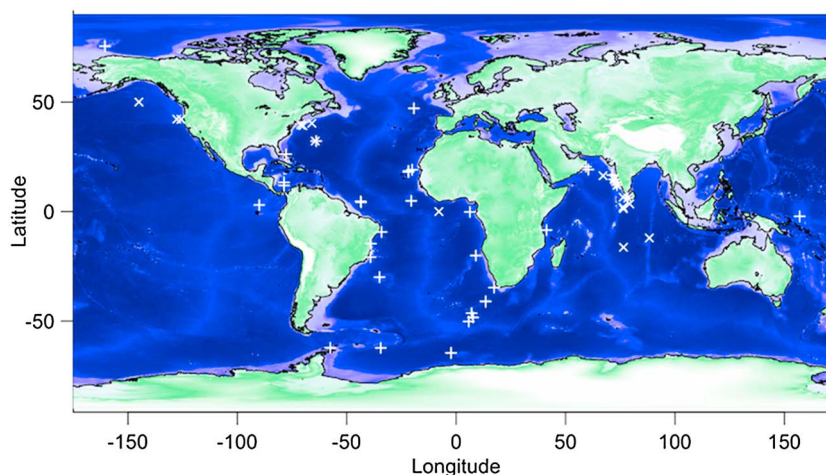
Ocean for the purpose of analyses. "Ocean" basin was therefore considered as a four-way categorical variable contrasting the Atlantic, Pacific, Indian, and Arctic Oceans.

Despite these caveats, the data compilation includes life and death assemblages that are representative of the major lineages of recent planktonic foraminifera, low to high latitude ecosystems, the major ocean basins, and the full range of planktonic foraminiferal ecologies across a range of sampling depths. As such, it provides a means for testing the determinants of size-specific stable isotopic composition in planktonic foraminiferal calcite.

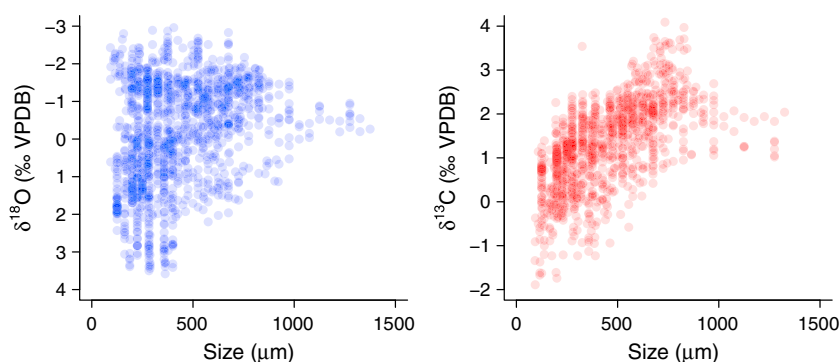
Plotted together, the full data set emphasizes a few fundamental patterns (Figure 3). Small planktonic foraminifera individuals are found throughout the world's oceans, but the largest body sizes only dominate assemblages in the warmer tropical/subtropical biome [Schmidt *et al.*, 2004, 2006; Al-Sabouni *et al.*, 2007]. The relatively narrow environmental range of the largest individuals is reflected in their narrow  $\delta^{18}\text{O}$  range (roughly  $-2$  to  $1\text{‰}$  in the  $>800\text{ }\mu\text{m}$  fraction) as compared to the smallest body sizes (roughly  $-3$  to  $4\text{‰}$  in the  $<500\text{ }\mu\text{m}$  fraction) (Figure 3). In contrast to the scattered cone of  $\delta^{18}\text{O}$  values,  $\delta^{13}\text{C}$  values exhibit a positive, saturating relationship with body size: there is an initial increase in  $\delta^{13}\text{C}$  values with body size that eventually plateaus in the largest individuals. We sought to explain the substantial variation in both carbon and oxygen through nonlinear mixed effect models incorporating environmental, preservational, and biological drivers (Table 1).

### 3.4. Model Formulation

We used a statistical modeling approach to derive minimum adequate models (MAMs) and model-averaged predictions of species and size-specific stable carbon and oxygen isotopic trends. Based on existing knowledge of the relationship between isotopic composition and body size (i.e., an increasing linear and



**Figure 2.** Distribution of available species and size specific stable isotopic measurements for Holocene to Recent planktonic foraminifera used in this study. Core tops and sediment traps (plus) and net tows (cross) plotted against a global bathymetric map extracted from the NOAA server at a resolution of 10 min using the marmap R package (version 0.8).



**Figure 3.** Multispecies compilation size-specific oxygen and carbon isotope values. Size refers throughout to the average sieve size in microns ( $\mu\text{m}$ ) for a given measurement. The number of individuals per measurement ranges from a few in the largest size fractions to hundreds in the smallest.

concave-down, nonlinear relationship with size [Berger *et al.*, 1978; e.g., Vincent and Berger, 1981; Birch *et al.*, 2013]) and initial data visualization (Figures 3 and 4), we fitted nonlinear models of the form

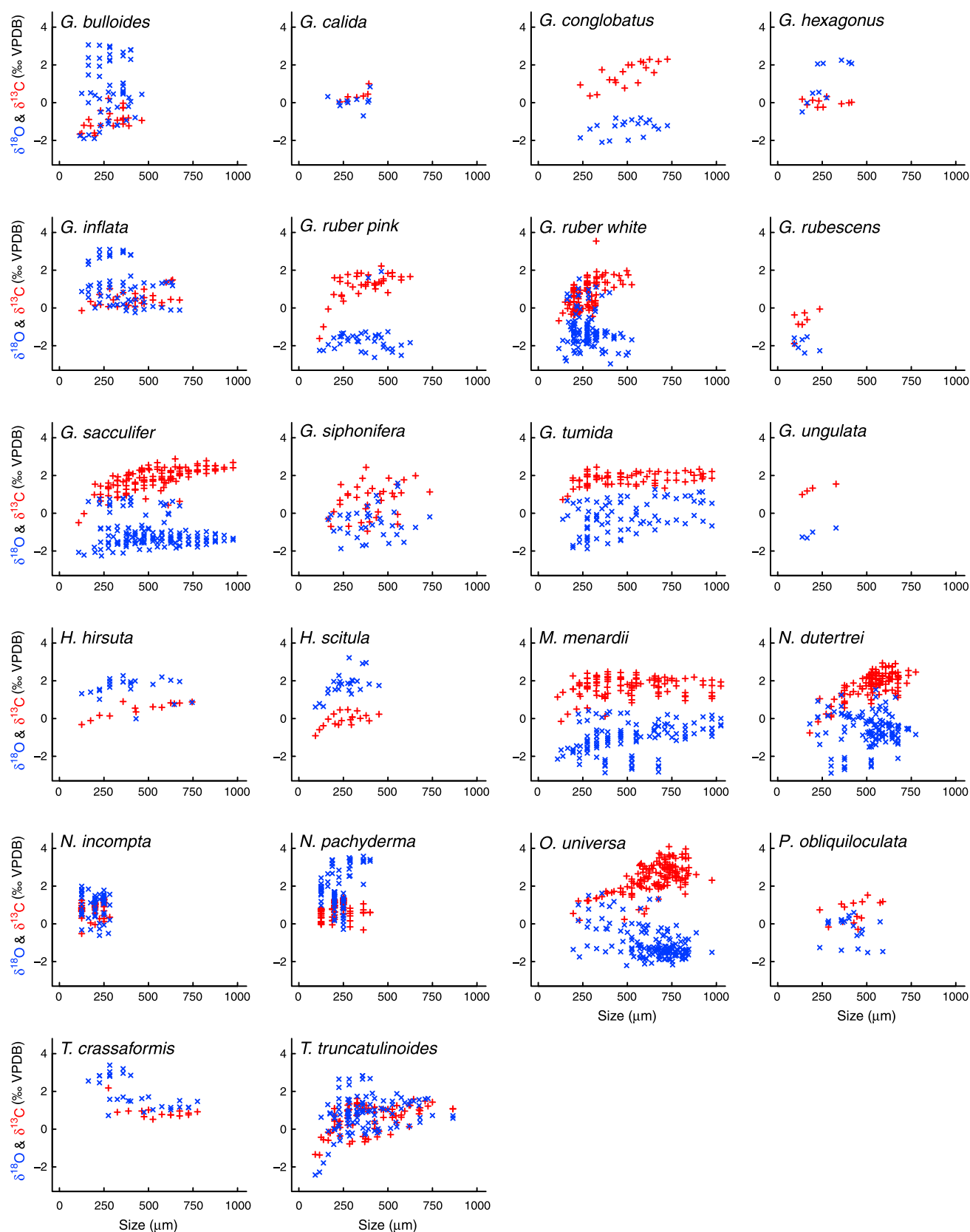
$$y_i = a_i + b_i x + c_i x^2 + \varepsilon_i \quad i = 1, 2, \dots, 22. \quad (1)$$

where  $y$  is the isotope of interest (carbon or oxygen) and  $x$  is size;  $a$ ,  $b$ , and  $c$  are regression parameters that describe the size-dependent change in isotopic composition:  $a$  is the intercept,  $b$  describes the linear increase, and  $c$  the nonlinear (concave down) component of the relationship;  $\varepsilon_i$  is the residual error. Note that we do not force the linear term to increase rather than decrease, nor did we force the nonlinear term to be concave down rather than concave up. Instead, we determined the most likely values of these terms statistically. The subscript  $i$  is the species-specific component, which allowed us to test if—and, if so, quantify how—regression parameters varied across the 22 species analyzed. Each biological, ecological, and preservational factor identified (Table 1) was assumed initially to influence each regression parameter (i.e.,  $a$ ,  $b$ , and  $c$ ), with the potential for multiple explanatory factors to influence each parameter. We fitted models using various functions in the nlme [Pinheiro and Bates, 2000] and minpack.lm libraries in the R environment (version 3.0.2 [R Core Team, 2014]). The supporting information contains the data compilation, the annotated computer scripts for model fitting, and the diagnostic plots as justification for our analytical decisions.

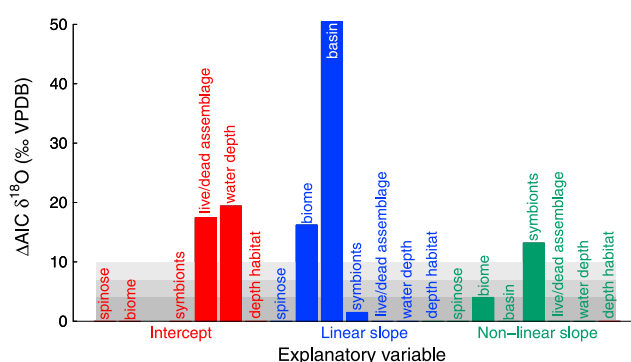
All models contain fixed and random effects. Fixed effects are explanatory covariates that influence the mean value of the response variable (i.e., here the environmental, preservational, or biological factors assumed to affect all species); random effects explain the residual variation around those mean trends that cannot be explained by the general fixed effects and therefore is assumed to correspond to (here) differential species-specific responses. Random effects are relevant here because the data are not independent: isotope values within the same species are likely more similar to each other than to isotope values from other species. We aimed to test for species-specific intercepts (parameter  $a$ ) and linear and nonlinear slopes (parameters  $b$  and  $c$ ) as random effects to determine whether a species (or group of species) differed from the mean trend as modeled by the fixed effects (i.e., environment, biology, and preservation). However, we found that there are insufficient data to adequately test for species-specific size dependence in  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values (for full discussion, see supporting information). With the data at hand, we were only able to evaluate species-specific intercepts (i.e., differences in parameter  $a$  among species), which were justified from the model diagnostics (see supporting information).

The raw species-specific data (Figure 4) revealed a great deal of variation in size-specific carbon and oxygen isotope values within and among species. For example, species like *Orbulina universa* appear to have constrained relationships between size and  $\delta^{13}\text{C}$ , whereas *Globigerinella siphonifera* is more variable. We directly accounted for this difference in variation among species (i.e., heteroscedasticity) and an observed non-independence of model residuals (see supporting information), by extending our basic model formulation to incorporate species-specific variances and autocorrelated errors with size fractions. We could not test for differences among equipment calibrations in different research laboratories.





**Figure 4.** Compilation of size-specific oxygen and carbon isotopes plotted by species. δ<sup>18</sup>O data are in blue cross and δ<sup>13</sup>C in red plus symbols.



**Figure 5.** Variation in  $\delta^{18}\text{O}$  explained by environmental, biological and preservational variables (Table 2), split into contributions to the intercepts (red), linear slopes (blue), and nonlinear (concave) term (green). The bar heights are the difference in Akaike Information Criterion ( $\Delta\text{AIC}$ ) between the minimum adequate model (MAM) with and without the focal variable listed: a larger bar indicates that a particular explanatory variable is more influential than a shorter bar. The horizontal grey shaded areas are the criteria of Burnham and Anderson [2002, p. 71] to delineate models: bars within the dark grey region denote a  $\Delta\text{AIC}$  of up to 4 (i.e., model outputs with and without variable are very similar); bars within the grey region denote a  $\Delta\text{AIC}$  of 4–7 (“considerably less” support); the light grey zone is a  $\Delta\text{AIC}$  of 7–10; bars in the white zone beyond the light grey suggest that the model’s support is “essentially none,” i.e., the focal term explains substantial variation. Variables listed without bars are not included in the MAM. The label for basin in the intercept term is missing because it did not converge on a solution when that term was removed from the MAM.

not converge on a solution. The AIC provides a compromise between variance explained and parameters used. Our MAMs for oxygen and carbon (see supporting information) have both the lowest AIC and the fewest parameters.

We found numerous candidate models, which show similar performance in their ability to explain size-specific carbon and oxygen isotope compositions [Burnham and Anderson, 2002, p. 71]. We therefore present model-averaged predictions across all models, weighting by relative likelihood as inferred by the Akaike weights. Akaike weights can be interpreted as the probability that a given model is the “correct” model of those fitted. The model with the lowest AIC has the highest weight. For a more detailed discussion of the statistical models, see the supporting information.

## 4. Results

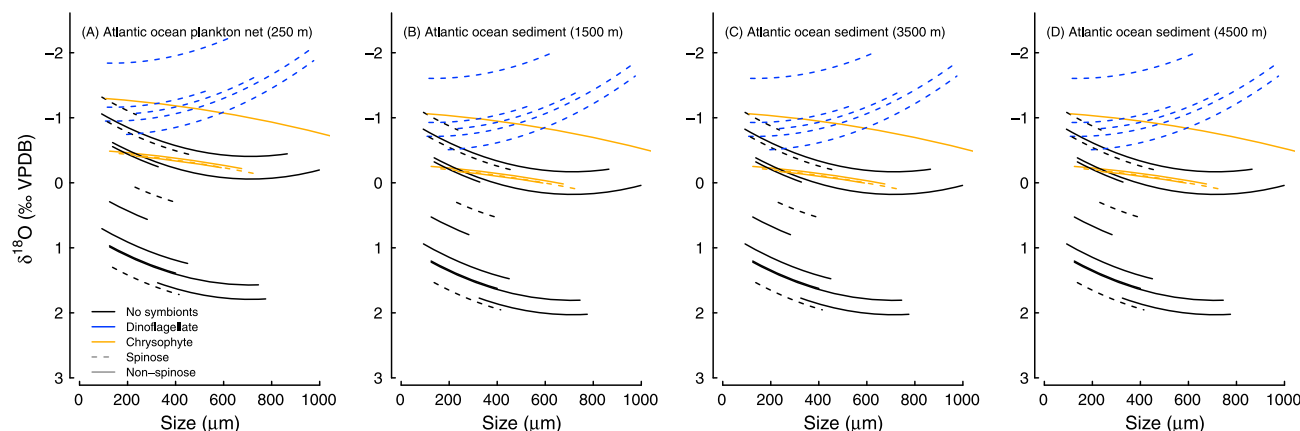
### 4.1. Species-Specific Effects on Size-Specific $\delta^{18}\text{O}$

Including species-specific intercepts as a random effect improved model fits significantly over models that excluded them, as did autocorrelated residual structures with size and species-specific size-variance relationships (see diagnostic plots in the supporting information). Autocorrelated residual structures with size-specific variance were included because we found that successive size-specific measurements of  $\delta^{18}\text{O}$  were more similar than expected by strictly random (white) noise. Similarly, species-specific variance was included by incorporating the different amounts of expressed variation, and therefore residuals, within each of the species in the fitted models (Figure 4). The most influential components of the minimum adequate model (MAM) on changes in  $\delta^{18}\text{O}$  values are ocean basin (impacting the intercept and linear slope) followed by sampling depth, live/dead assemblages, biome, and the presence and type of symbionts (Figure 5). We find no evidence that depth habitat explains a significant amount of the variation in  $\delta^{18}\text{O}$ .

Two additional models, with different parameter combinations, fell within two AIC values of the minimum adequate model, suggesting they also had “substantial” support [Burnham and Anderson, 2002, p. 71]. The Akaike weight of the minimum adequate model alone is 0.37, indicating just under a 40% probability that this is the “correct” model of those fitted. The three models sum to almost 0.8. The model-averaged predictions

We fitted models that estimated the influence of both fixed and random effects simultaneously. Initially, the full models for both carbon and for oxygen contained all of the seven biological, ecological, and preservational fixed effects (Table 2) fitted to each of  $a$ ,  $b$ , and  $c$ ; random species-specific intercepts; species-specific variances; and autocorrelated errors. We then reduced initial model complexity by backward model simplification [Crawley, 2002].

We assess the explanatory power of the candidate environmental, preservational, and biological variables from their contribution to the minimum adequate model (MAM). The MAM was obtained by backward model simplification from the full model using the Akaike Information Criterion (AIC) and likelihood ratio tests [Pinheiro and Bates, 2000; Crawley, 2002]. Here we define the MAM by the lowest AIC score. Testing the global set of models was not possible because numerous combinations do



**Figure 6.** (a–d) Model-averaged species-specific predictions of body size against  $\delta^{18}\text{O}$ . All predictions are made assuming a common ocean basin (Atlantic), biome (tropical/subtropical), sample type (core top), and water depth (3500 m) for the purposes of comparison. We exclude *N. incompta* from this plot because of its restricted biogeographic range. Dinoflagellate-bearing species are drawn in blue, chrysophyte-bearing species in orange, and asymbiotic species in black. Spinose species indicated by dashed lines and non-spinose species with solid lines.

(Figure 6) and coefficients (Table 4) are weighted by the probability of each model and therefore depend heavily on these three models. After controlling for geography and sampling depth, the impact of the three classes of symbionts is clear in the model-averaged predictions (Figure 6): species without symbionts have nonlinear, positive  $\delta^{18}\text{O}$  to body size relationships; species with chrysophyte symbionts have linear, slightly positive size dependence in  $\delta^{18}\text{O}$ ; and species with dinoflagellate symbionts have nonlinear, negative size-dependent  $\delta^{18}\text{O}$  compositions.

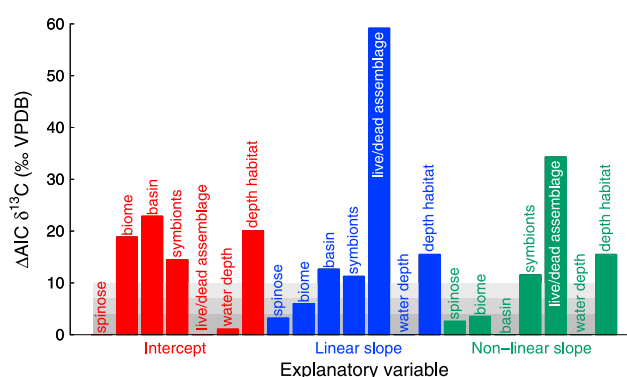
#### 4.2. Species-Specific Effects on Size-Specific $\delta^{13}\text{C}$

Size-specific carbon isotope trends are more complicated than for oxygen (Figure 7). There is still a crucial role of species-specific random intercepts, differential isotopic variation among species, and autocorrelated errors. As for  $\delta^{18}\text{O}$  values, ocean basin (intercept, linear slope) and symbiont type (all parameters) are major determinants of size-specific  $\delta^{13}\text{C}$  values. Unlike for  $\delta^{18}\text{O}$  values, depth habitat (all parameters) has a substantial influence on the observed variation in size-specific  $\delta^{13}\text{C}$  values. Model-averaged coefficients are given in Table 5; the major explanatory driver of size-dependent  $\delta^{13}\text{C}$  is the difference between live and dead assemblages (Figures 7 and 8). The summed Akaike weights for the five models with “substantial”

**Table 4.** Model-Averaged Coefficients for the  $\delta^{18}\text{O}$  Models<sup>a</sup>

	Intercept <i>a</i>	Linear Slope <i>b</i>	Nonlinear (Concave) Term <i>c</i> ( $\times 10^{-3}$ )
Intercept	−0.758 (0.385)	0.006 (0.002)	−0.007 (0.002)
Spinosity: true	0.054 (0.05)	0 (0)	0 (0)
Biome: tropical/subtropical	−0.201 (0.187)	−0.006 (0.002)	0.007 (0.002)
Basin: Chukchi Sea	1.225 (0.339)	−0.012 (0.002)	0 (0)
Basin: Indian Ocean	−0.977 (0.131)	0 (0)	0 (0)
Basin: Pacific Ocean	−0.94 (0.216)	0 (0.001)	0 (0)
Symbionts: dinoflagellates	−0.001 (0.011)	0 (0.001)	−0.002 (0.001)
Symbionts: none	0 (0.009)	0.002 (0.001)	−0.002 (0.001)
Live/dead assemblage	−0.234 (0.059)	0 (0)	0 (0)
Water depth	0 (0)	0 (0)	0 (0)
Depth habitat: subthermocline	1.34 (0.432)	0 (0)	0 (0)
Depth habitat: thermocline	0.731 (0.389)	0 (0)	0 (0)

<sup>a</sup>To read this table, note that the intercept includes 0 for continuous effects (water depth) and the first level for categorical variables (i.e., non-spinose, polar/transitional biome, Atlantic Ocean, chrysophyte symbionts, dead assemblages, and mixed layer species). The effect of moving from one of those categories to another is obtained by adding the coefficient, or by adding the coefficient\*variable for the continuous variable. Each column added together thereafter gives the parameter value (*a*, *b*, *c*), which you then multiply by size to get predicted size. Therefore, for example, shifting from a chrysophyte-bearing species to an asymbiotic one results in a positive increase in the linear slope parameters, i.e., a steeper linear slope. For species specific intercept adjustments, see Table S2.



**Figure 7.** Variation in  $\delta^{13}\text{C}$  explained by environmental, biological, and preservational variables (Table 2), split into contributions to the intercepts (red), linear slopes (blue), and nonlinear (concave) term (green). The bar heights are the difference in Akaike Information Criterion ( $\Delta\text{AIC}$ ) between the minimum adequate model (MAM) with and without the focal variable listed: a larger bar indicates that a particular explanatory variable is more influential than a shorter bar. The horizontal grey shaded areas are the criteria of Burnham and Anderson [2002, p. 71] to delineate models: bars within the dark grey region denote a  $\Delta\text{AIC}$  of up to 4 (very similar); bars within the grey region denote a  $\Delta\text{AIC}$  of 4–7 (“considerably less” support); the light grey zone is a  $\Delta\text{AIC}$  of 7–10; bars in the white zone beyond the light grey suggest that the model’s support is “essentially none,” i.e., the focal term explains substantial variation.

support is 0.75; the model weight of the MAM is 0.23 indicating less confidence that the model is “correct” than for the analogous  $\delta^{18}\text{O}$  analysis. This low confidence in the single “best” model emphasizes the importance of a model-averaging approach that avoids choosing a single model as “correct.”

### 4.3. Model-Averaged Predictions of Size-Specific $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$

Model-averaged predictions for  $\delta^{18}\text{O}$  trends with body size reveal two main patterns in an Atlantic comparison of life (Figure 6a) and death assemblages (Figures 6b–6d) across increasing core top water depths (Figures 6b–6d). Life and death assemblages, regardless of sampling depth, show the same patterns within and among symbiont groups in  $\delta^{18}\text{O}$  (described in section 4.1). Dinoflagellate bearers are distinguished by more negative  $\delta^{18}\text{O}$  values than all other taxa, except *G. siphonifera*, particularly at larger sizes.

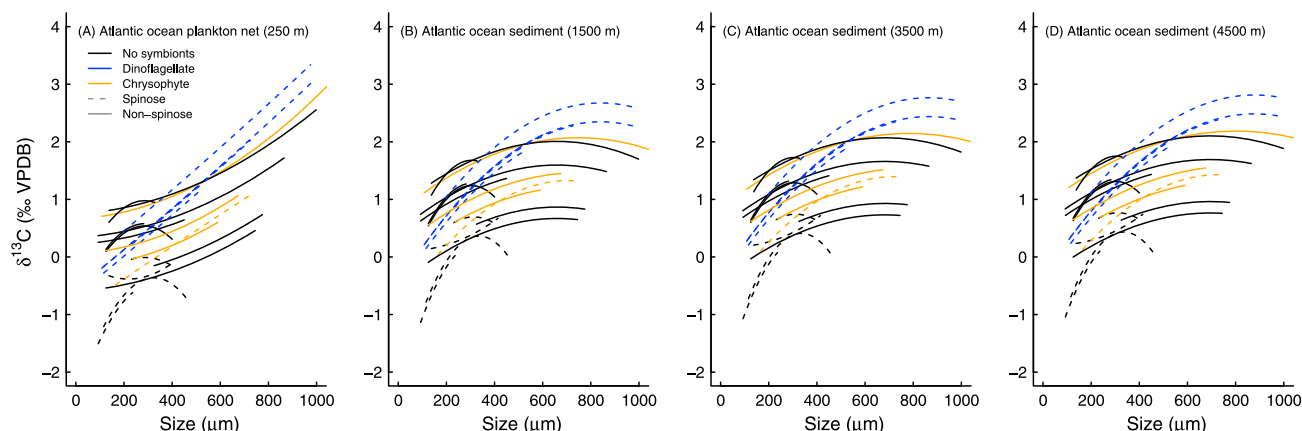
In contrast, model-averaged predictions for  $\delta^{13}\text{C}$  trends with body size highlight clear differences between life (Figure 8a) and death (Figures 8b–8d) assemblages. The larger living taxa have a positive, concave-up relationship between body size and  $\delta^{13}\text{C}$ . Dinoflagellate bearing taxa have the steepest relationship between body size and  $\delta^{13}\text{C}$ , but absolute values generally overlap with other symbiont ecologies at all body sizes (Figure 8a). In death assemblages,  $\delta^{13}\text{C}$  values are nonlinear, initially increasing but then plateauing to an approximately zero trend at the largest body sizes (Figures 8b–8d). As with  $\delta^{18}\text{O}$ , we find little effect of increasing bottom water depth on  $\delta^{13}\text{C}$  trends, as might be expected with increasing diagenetic alteration of foraminiferal tests (Figures 8b–8d).

Model-averaged predictions of reconstructed  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values are presented in crossplots in Figure 9 for two scenarios (core top 1500 m and plankton net 250 m) in the Atlantic and Indian Oceans. Two main results are apparent. First, the Indian Ocean predictions yield lower  $\delta^{18}\text{O}$  values than their Atlantic counterparts (Figure 9, top versus bottom rows), but the relative order of taxa by symbiont type is consistent.

**Table 5.** Model-Averaged Coefficients for the  $\delta^{13}\text{C}$  Models<sup>a</sup>

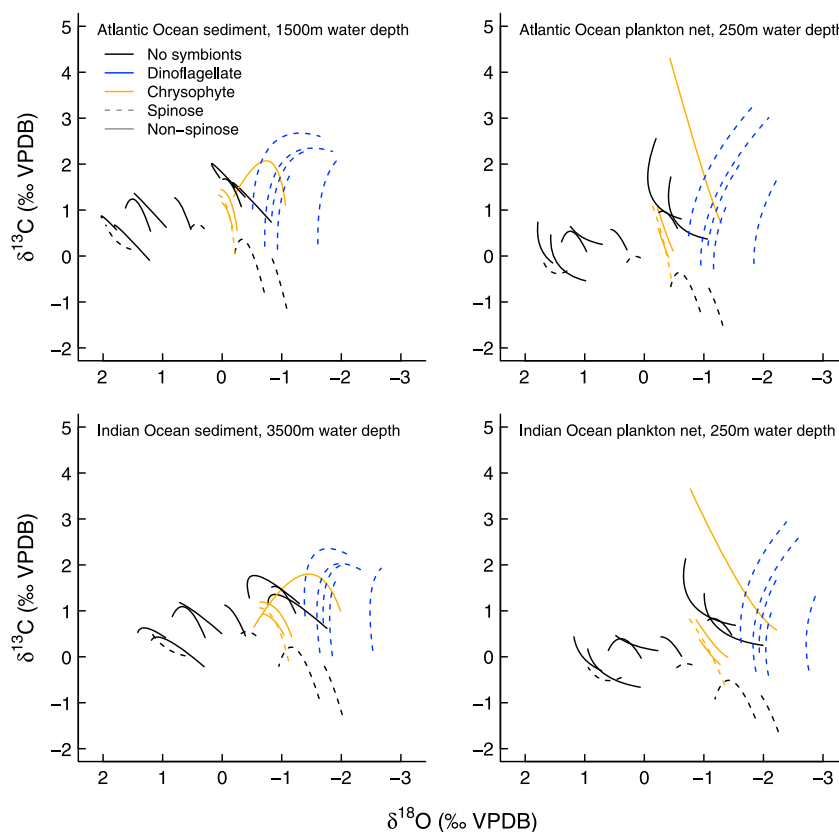
	Intercept	Linear Slope	Nonlinear (Concave) Term
Intercept	−2.458 (0.562)	0.013 (0.003)	−0.014 (0.005)
Spinosity: true	0 (0)	−0.004 (0.002)	0.007 (0.003)
Biome: tropical/subtropical	1.306 (0.263)	−0.003 (0.001)	0.003 (0.001)
Basin: Chukchi Sea	1.55 (0.335)	−0.005 (0.002)	0.004 (0.005)
Basin: Indian Ocean	−0.117 (0.097)	0 (0)	0 (0)
Basin: Pacific Ocean	0.119 (0.17)	0 (0.001)	0 (0)
Symbionts: dinoflagellates	0.672 (0.557)	0 (0.003)	0 (0.004)
Symbionts: none	−1.149 (0.293)	0.01 (0.001)	−0.019 (0.001)
Live/dead assemblage	−0.054 (0.087)	−0.003 (0.001)	0.004 (0.001)
Water depth	0 (0)	0 (0)	0 (0)
Depth habitat: subthermocline	2.401 (0.475)	−0.016 (0.003)	0.028 (0.005)
Depth habitat: thermocline	1.537 (0.474)	−0.007 (0.003)	0.009 (0.005)

<sup>a</sup>For description, see Table 4. For species specific intercept adjustments, see Table S4.



**Figure 8.** (a–d) Model-averaged species-specific predictions of body size against  $\delta^{13}\text{C}$ . All predictions are made assuming a common ocean basin (Atlantic), biome (tropical/subtropical), sample type (core top), and water depth (3500 m) for the purposes of comparison. We exclude *N. incompta* from this plot because of its restricted biogeographic range. Dinoflagellate-bearing species are drawn in blue, chrysophyte-bearing species in orange, and asymbiotic species in black. Spinose species indicated by dashed lines and non-spinose species with solid lines.

Dinoflagellate-bearing taxa typically have the lowest  $\delta^{18}\text{O}$  values in the assemblage, perhaps due to precipitation in warm, well-lit surface waters, followed by chrysophyte bearers, and then asymbiotic taxa with the highest  $\delta^{18}\text{O}$  values. Second, the curvature of the species trajectories reflects the nonlinear dependence of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values with size. The deeper prediction (1500 m, core top) has the shallowest within species slopes of  $\delta^{13}\text{C}$  to  $\delta^{18}\text{O}$  values. Species-specific curves are given in the supporting information.



**Figure 9.** Species-specific model-averaged cross plot predictions highlight the influence of ocean basin, water depth, and sampling method on size- $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  trends. Dinoflagellate-bearing species are drawn in blue, chrysophyte-bearing species in orange, and asymbiotic species in black. Spinose species indicated by dashed lines and non-spinose species with solid lines. We exclude *N. incompta* from this plot because of the restricted range of existing samples.



## 5. Discussion

We compiled all available size-specific stable isotope data for modern macroperforate planktonic foraminifera and statistically investigated the controls on test  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values across species, space, life history, ontogeny, and death. In summary, our key results are

1. A strong ocean basin effect on both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values (Figures 5, 7, and 9);
2. A clear symbiont effect on size-specific test  $\delta^{18}\text{O}$  values (Figures 6 and 9);
3. A significant species-specific effect on  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  intercepts (parameter  $a$ , the basal species offsets; see Tables S2 and S4);
4. An important death assemblage effect modifying apparent  $\delta^{13}\text{C}$  to body size relationships and interpretations (Figures 5, 7, and 8);
5. A depth habitat effect on all  $\delta^{13}\text{C}$  parameters (Figure 7) but not on  $\delta^{18}\text{O}$  parameters (Figure 5); and
6. The identification of key sampling gaps in the modern calibration set of life and death assemblages (Figure 2).

The relationships and models presented here are, insofar as is currently possible, an unbiased reflection of the available data across multiple ocean basins on the key drivers of size-dependent changes in planktonic foraminiferal test oxygen and carbon isotopic composition (see the supporting information for fuller discussion and additional figures). While the model-averaged predictions (Tables 4 and 5) can be used as a predictive tool, we caution against unfettered interpretations because of the inequalities and skew in the available data used to build the models (Figure 3 and Table 3). Our model-averaged results and coefficients should be considered as a set of falsifiable hypotheses, which are rooted in empirical observation and robust statistical methodology, but that are highly dependent upon existing empirical observations. The goal should be to test, reject, and revise these results through targeted field collections and experiments in the future. We structure our discussion around seven emergent questions for ongoing research.

### 5.1. Is Isotopic Variance Driven Primarily by Species-Specific Differences (i.e., Species-Specific Vital Effects) or by General Environmental, Preservational, and Biological Processes?

There is a significant impact of both. All reported models included a species-specific intercept term as a random effect (Tables S2 and S4), as well as several other environmental, preservational, and biological influences (Figures 5 and 7). Species-specific differences in intercepts could reflect underlying biological offsets between taxa [e.g., Erez and Honjo, 1981; Spero and Deniro, 1987; Wolf-Gladrow *et al.*, 1999; Hesse *et al.*, 2014], like different basal metabolic, photosynthetic, and/or calcification rates or other untested environmental and preservational drivers, like seasonality or preservation potential [Berger, 1970; Deuser *et al.*, 1981; Curry *et al.*, 1983; Deuser, 1987; Lohmann, 1995]. It is generally expected that closely related species will be more similar in terms of their biology and ecology, due to their shared evolutionary history, than to more distantly related species [Felsenstein, 1985; Harvey and Pagel, 1991; Freckleton *et al.*, 2002]. Thus, we might expect a significant effect of evolutionary relatedness on the isotopic size-dependency trends in foraminiferal tests that could be used to supplant the “random” species-specific effect. Shared evolutionary history could thus “crack open” the black box of “vital effects” [Spero *et al.*, 1991; Wolf-Gladrow *et al.*, 1999; Zeebe *et al.*, 2008]. Unfortunately, with data only available for 22 species, we had insufficient statistical power to fully test for a role of shared evolutionary history [Pagel, 1999]. The preliminary analyses we could perform suggested a very weak, albeit intriguing, effect of evolutionary history on species-specific intercepts, with much weaker effects on  $\delta^{18}\text{O}$  than  $\delta^{13}\text{C}$  (Figure S28 in the supporting information).

### 5.2. Can the Presence of Dinoflagellate and Chrysophyte Photosymbionts be Reliably Inferred From Stable Isotopes?

Yes, with caution. In deep time, the recognition of photosymbiosis relies exclusively on foraminiferal carbon and oxygen isotopes [e.g., Pearson *et al.*, 1993; D'Hondt *et al.*, 1994; Norris, 1998]. Norris [1996] proposed four criteria to identify photosymbiont-bearers in the fossil record: photosymbiont-bearing taxa have (i) the most negative  $\delta^{18}\text{O}$  values in the assemblage, (ii) minimal size-related changes in test  $\delta^{18}\text{O}$  due to persistent shallower depth habitat throughout ontogeny, (iii) more positive  $\delta^{13}\text{C}$  values at all body sizes (again due to shallow depth habitat), and (iv) steeper size- $\delta^{13}\text{C}$  relationships. These criteria are, perhaps, best suited for identifying dinoflagellate bearers, with chrysophyte bearers only weakly (if at all) meeting the criteria [Bornemann and Norris, 2007]. For dinoflagellate-bearing taxa, our results support the cautious use of criteria i

and iv, as these taxa generally have the most negative  $\delta^{18}\text{O}$  values (Figures 7 and 9; particularly true for the largest body sizes) and steepest size- $\delta^{13}\text{C}$  relationships (Figure 8; particularly true for the smallest body sizes). Criteria ii and iii are not supported as useful indicators of photosymbiosis. Asymbiotic and chrysophyte-bearing taxa show less size-dependent  $\delta^{18}\text{O}$  change than dinoflagellate bearers (Figure 6) violating criterion ii. We fail to find consistent, size-independent  $\delta^{13}\text{C}$  offsets among the three symbiont groups, violating criterion iii (Figure 6). For paleoceanographic identification of dinoflagellate bearing taxa, we suggest the combined use of criteria i and iv.

In contrast to the dinoflagellate bearers, chrysophyte-bearing species are hard to distinguish on the basis of their  $\delta^{13}\text{C}$  values. Chrysophyte bearers are significantly distinct from asymbiotic species in  $\delta^{13}\text{C}$  on all three parameters (equation (1)), but the effect size is so small that it is unlikely to be detected in noisy, empirical, fossil data. Four of the five chrysophyte-hosting species analyzed are thought to be only facultative hosts whereas all five species of dinoflagellate bearing species are obligate photosymbiotic. This difference, compounded by differences in the algal size, density, and location, may affect the carbon subsidy provided by the symbionts to the host during normal chamber formation. In other words, chrysophyte symbionts in planktonic foraminifera may be nearly “invisible” in carbonate  $\delta^{13}\text{C}$  because chrysophytes have a lower photosynthetic uptake and thus reduced carbon isotopic fractionation relative to their dinoflagellate counterparts [Bijma *et al.*, 1998].

Our analysis suggests, for the first time, that all three groups (dinoflagellate, chrysophyte, and asymbiotic) can be distinguished on the basis of their oxygen isotope values (see characteristic convex  $\delta^{18}\text{O}$  curve across ontogeny in Figure 6 and discussion of slopes below). This is surprising, particularly given the relatively weak symbiont influence on  $\delta^{13}\text{C}$  values as compared to depth habitat and environmental parameters. Indeed, the presence and type of symbiont is the only biological or ecological factor tested that explains a significant proportion of the variance in oxygen isotope to body size relationship: note the bar heights in Figure 5 and the negative slopes for chrysophyte-bearing species versus neutral (live assemblages) or positive (dead assemblages) slopes for dinoflagellate species in Figure 6. This size-specific oxygen metric for the identification of planktonic foraminifera hosting chrysophyte symbionts is promising but would benefit from further, explicit sampling in the recent and Neogene fossil record.

### 5.3. Can Oceanographic and Ecological Inferences From a Single Site be Applied Globally?

No, particularly not for  $\delta^{13}\text{C}$ . Note the impact of basin and biome on  $\delta^{18}\text{O}$ , including the missing biome that did not converge (Figures 5 and 7). The stable isotopic composition of seawater is known to vary regionally and by ocean basin [Zachos *et al.*, 1994; Rohling and Cooke, 1999; LeGrande and Schmidt, 2006; Pearson, 2012]. Test isotopic composition is further influenced by local environmental conditions such as the temperature, salinity, and carbonate saturation state of the water from which it precipitates [e.g., Spero *et al.*, 1997; Zeebe, 1999; Hesse *et al.*, 2014]. If the location effect was due solely to seawater composition (e.g., isotopes and carbonate saturation), then it should only impact the intercept term,  $a$ , of the size-isotope relationships (Figures 5 and 7, red bars). For both carbon and oxygen, ocean basin had a significant effect on the linear slope of the relationship (Figures 5 and 7, blue bars), implying that reconstructed size-specific isotopic gradients are, in part, site specific. Multiple mechanisms could underlie site-specific  $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$  body size relationships including temperature-dependent metabolic and growth rates [Lombard *et al.*, 2009; Regaudie-De-Gioux and Duarte, 2012; Hesse *et al.*, 2014], carbonate ion effects [Spero *et al.*, 1997; Bijma *et al.*, 1999; Zeebe, 1999], and life history (e.g., seasonality and depth ontogeny) [Sautter and Thunell, 1991; Eguchi *et al.*, 2003; Fallet *et al.*, 2010].

Environment has long been considered to be the primary determinant of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values [e.g., Emiliani, 1954; Hays *et al.*, 1976; Billups and Spero, 1995], as it modifies the external (e.g., seawater composition, temperature, and carbonate saturation) and internal (e.g., respiration and photosynthesis) drivers of carbonate isotopic composition [Wolf-Gladrow *et al.*, 1999; Hesse *et al.*, 2014]. Our results underline the importance of considering environment when using size-specific isotopic relationships in fossil foraminifera, as the slope of this relationship, even in well-preserved samples, can vary.

### 5.4. Does the Difference in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ Values Among Species Reflect Their Relative Depth Habitat?

From the current compilation, the evidence is mixed. In our analyses, depth habitat failed to account for significant variation in  $\delta^{18}\text{O}$  (Figure 5) but influenced all parameters for size trends in  $\delta^{13}\text{C}$  (Figure 7). The lack

of evidence for a depth habitat influence in  $\delta^{18}\text{O}$  may arise because the horizontal geographical variation overwhelms the vertical signal, or may reflect an underlying limitation of isotopically defined depth habitats.

Sixty years ago, Cesare Emiliani first inferred differing depth habitat preferences of planktonic foraminifera using the average  $\delta^{18}\text{O}$  composition of species and assuming isotopic equilibrium with the surrounding waters [Emiliani, 1954]. Then, as now, stable isotopic measurements provided a convenient means for identifying a single “average” depth habitat for each species, an inference critical for determining depth-specific temperatures and water column stratification [Hemleben *et al.*, 1989; Mulitza *et al.*, 1997, 2003]. In reality, planktonic foraminiferal populations live across a broad range of water depths that vary between locations, with ontogeny, and with water column structure, among others [Duplessy *et al.*, 1981a; Ravelo and Fairbanks, 1992; Niebler *et al.*, 1999; Cl  roux *et al.*, 2013]. Many species have highly dynamic populations, with large differences in population abundance and adult body size across seasons and years [Deuser *et al.*, 1981; Eguchi *et al.*, 2003; Mohtadi *et al.*, 2009]. In our study, as in all strictly paleoceanographic calibrations, seasonal signals are unaccounted for but could isotopically overwhelm the effect of depth habitat. In short, our failure to find a significant depth habitat may arise because oxygen isotopes are less informative of depth habitat than has long been hypothesized (a criticism first raised by Shackleton *et al.* [1973]). The alternatives are (1) that our data are simply insufficient to test the effectiveness of  $\delta^{18}\text{O}$  values for assessing foraminiferal relative vertical position in the water column or (2) that by subdividing depth habitat into three general categories, mixed layer, thermocline, and subthermocline, we obfuscated fine, continuous, vertical differences in depth habitats recorded in  $\delta^{18}\text{O}$ . More data are required to assess the role of depth habitat on species’ size-specific  $\delta^{18}\text{O}$  through paired tow, sediment trap, and core top studies.

### 5.5. Is There a Diagenetic Effect on Test $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ Values?

Probably not in the core top samples we examined. Our model-averaged predictions indicate that the overall pattern of test size- $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values and the depth ordering of species are consistent across the range of tested water depths (1500–4500 m; Figures 6 and 8). In particular,  $\delta^{18}\text{O}$ -size gradients in dinoflagellate-bearing species are steeper (particularly at small sample sizes) than those of chrysophyte-bearing species, regardless of water depth (Figure 6). However, our results and inferences are notably restricted to relatively well preserved core top sediments and not the more extensively altered specimens typically found in sediment cores. Furthermore, our focus is on a comparison among ocean basins and between living and recently dead assemblages, rather than the effects of dissolution below the lysocline or in sediments.

As carbonate preservation varies strongly with water depth and geography due to variations in carbonate saturation state and sedimentary conditions [e.g., Archer, 1996; Ridgwell, 2007], and both have a significant effect on  $\delta^{18}\text{O}$  trends (Figures 5, 6, and 9), we briefly consider how depth-dependent isotopic changes might be attributed to diagenetic factors. Postmortem dissolution of planktonic foraminiferal tests in the water column and at the seafloor should lead to progressively higher  $\delta^{18}\text{O}$  and lower  $\delta^{13}\text{C}$  absolute values with increasing water depth [Savin and Douglas, 1973; Berger and Killingley, 1977; Bonneau *et al.*, 1980; Wu and Berger, 1989], with smaller and/or thinner-walled taxa being more susceptible than larger ones [Berger and Piper, 1972; Berger *et al.*, 1982; Wu and Berger, 1989; H  nisch and Hemming, 2004]. In contrast, replacement of planktonic foraminiferal calcite by inorganic calcite precipitated in situ at the seafloor (recrystallization) will result in overall higher  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values with the most pronounced impact on  $\delta^{18}\text{O}$  values [e.g., Schrag *et al.*, 1995; Pearson *et al.*, 2001]. We might also expect that the surface-dwelling, symbiont-bearing taxa show a more pronounced change with increased bottom water depth than the deeper-dwelling, thicker-walled taxa such as *G. tumida* or *P. obliquiloculata*. Although we do observe a significant effect of water depth on  $\delta^{18}\text{O}$  intercepts (parameter *a*; Figure 5), the effect is primarily driven by differences in the water depth of living, recently dead, and long-dead assemblages (i.e., there is a noticeable difference between Figures 6a and 6b–6d but not among Figures 6b–6d). Thus, we fail to readily observe expected diagenetic effects and, as such, we cannot easily explain the patterns observed in the dataset by differences in the degree of dissolution or recrystallization at the seafloor.

### 5.6. Does the Different Composition of Life and Death Assemblages Change the Underlying Drivers or Foraminiferal Stable Isotopic Trends?

Most likely. Here we find that the contrast between living and dead assemblages is the most important factor influencing the relationship between body size and  $\delta^{13}\text{C}$  (i.e., parameters *b* and *c*; Figure 7) and one of two

factors affecting basal  $\delta^{18}\text{O}$  values (parameter  $a$ ; Figure 5). We suspect that the importance of life versus death assemblages arises because ontogenetic factors like growth rate, symbiont density, and the addition of gametogenic calcite structure size-isotope relationships in living assemblages. In contrast, other factors structure size-isotope relationships in death assemblages, namely those that effect the ultimate adult body size attained by individuals. We dub this difference in isotopic composition, and the factors influencing them, between life and death assemblages the “Spero life-death effect” (SLDE).

In living assemblages of foraminifera sampled by nets or tows, the vast majority of individuals are small ( $<125\ \mu\text{m}$ ) [Emiliani, 1971; Ravelo and Fairbanks, 1995], and variation in size correlates to ontogenetic stage. In other words, small individuals are small because they are young and large individuals are large because they are old. The opposite is true in sedimentary death assemblages, where the majority of planktonic foraminifera are large ( $>125\ \mu\text{m}$ ) [Berger, 1971; Bé et al., 1985]. In these fossil assemblages, much of the observed size variation occurs in postgametogenic individuals. Medium to smaller individuals are small because they were small adults at the time they reproduced. Large individuals are large because they were large adults when they reproduced [e.g., Berger, 1971].

Despite known differences in the composition of life and death assemblages, size-related stable isotopic trends in fossils are often extrapolated to living populations using ontogenetic hypotheses such as developmental shifts in the relative importance of metabolic effects versus photosymbionts, ontogenetic depth habitat variation, and the addition of gametogenic calcite [e.g., Schweitzer and Lohmann, 1991; Norris, 1998; Birch et al., 2013]. The importance of life versus death assemblages to predicting size-specific isotopic composition (Figures 5 and 7) supports the consideration of other mechanisms for size-specific trends in death assemblages.

The size-related  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  trends in dinoflagellate bearing species (Figures 6 and 7) follow the pattern predicted by Spero and others [Spero and Williams, 1988; Spero and Lea, 1993] for isotopic variation among same-stage adults. By varying the amount of incident photosynthetically active radiation in lab cultures, Spero and Williams [1988] found they could alter both the maximum test size attained and the extent of  $^{13}\text{C}$  enrichment in the dinoflagellate-bearing species *Orbulina universa*. From this, they reasoned that, in death assemblages in nature, the largest adults should have high  $\delta^{13}\text{C}$  and low  $\delta^{18}\text{O}$  values due to growing in high irradiance and relatively warm surface oceans as compared to the smaller, individuals with low  $\delta^{13}\text{C}$  and high  $\delta^{18}\text{O}$  values growing closer to the thermocline [Spero and Williams, 1988]. Other work has also shown that variation in adult body size is driven by conditions experienced over the lifespan of the individuals [Caron et al., 1987a, 1987b; Lombard et al., 2009], that adult size relates to symbiont presence and activity [Caron et al., 1981; Bé et al., 1982; Spero and Lea, 1993], and that similar relationships between irradiance, body size, and isotopic composition occur in other taxa (e.g., *Globigerinoides sacculifer* and *Globigerina bulloides* in Spero [1992], Spero and Lea [1993], and Bemis et al. [1998]). These mechanisms, as detailed by Spero and others, are not ontogenetic mechanisms and the patterns observed cannot be attributed to the addition of gametogenic calcite alone. Rather, we consider the factors explored by Spero and others among those that affect the size and isotopic composition of same stage adults—that is, they are the mechanisms behind Spero life-death effects.

Spero life-death effects have already been shown to account for size-specific variation in  $\delta^{13}\text{C}$  in downcore assemblages (e.g., *G. sacculifer* as demonstrated in Spero et al. [2003]), with critical implications for paleoceanographic reconstructions. In our data, the Spero life-death effect is particularly evident in dinoflagellate-bearing taxa, which exhibit a positive  $\delta^{13}\text{C}$  to body size (Figure 8) and negative  $\delta^{18}\text{O}$  to body size (Figure 6) relationship. For example, compare the saturation in  $\delta^{13}\text{C}$  with increasing body size in death assemblages (Figures 8b–8d) to the apparently unbounded increase in living assemblages (Figure 8a).

The Spero effect directly contrasts with the ontogenetic hypothesis for trends in stable isotope composition with body size, which predicts—among other things—that the largest adults should have relatively high  $\delta^{18}\text{O}$  values due to reproduction (and the addition of gametogenic calcite) at depth. Ontogenetic hypotheses implicitly attribute the variation in body size, even in death assemblages, to differences in life history stage, i.e., the age of the individual foraminifera. Were the patterns in our data principally explained by ontogeny, we should be able to observe two distinct body size- $\delta^{13}\text{C}$ , and  $\delta^{18}\text{O}$  relationships: (i) a positive relationship at small body sizes due to metabolic and kinetic effects and (ii) a positive relationship between each of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  and the largest body sizes due to increasing symbiont density/activity and deeper habitat

preference in the water column. Regardless of symbiont type, we do not observe either of these relationships in oxygen (Figure 6) and only the former in carbon (Figure 8).

The importance of Spero life-death effects does not supplant all ontogenetic mechanisms, rather it emphasizes an additional set of factors to consider, particularly in individuals greater than roughly 200  $\mu\text{m}$ . For instance, *Schweitzer and Lohmann* [1991] found a mix of pregametogenic and postgametogenic individuals when examining *M. menardii* and *G. tumida* less than  $\sim 300 \mu\text{m}$ . In addition, juvenile foraminifera are common in the smaller size classes ( $< 125 \mu\text{m}$ ), but these are rarely measured for isotopic composition due to the difficulty of accurately identifying species and obtaining sufficient material for analysis (as discussed in *Friedrich et al.* [2012]).

The Spero life-death effect highlights an important issue for investigations of seasonality and interannual variation. In most paleoceanographic studies [e.g., *Killingley et al.*, 1981; *Koutavas et al.*, 2006; *Ganssen et al.*, 2011; *Khider et al.*, 2011; *Sadekov et al.*, 2013], long-term dynamics in seasonality and/or interannual variation is considered by examining isotopic variation through time within a narrow size, or weight, class of dead individuals. However, if variation in adult body size is primarily driven by environmental conditions, such studies exclude the very individuals that record the dynamics the authors seek to infer.

There are several means for identifying the relative importance and drivers of Spero life-death effects and ontogenetic mechanisms in future studies. These include comparing the size-specific isotopic trends in depth-stratified plankton tows and sediment traps, the use of single chamber laser ablation techniques (as in *Houston et al.* [1999]), the separation and independent analysis of postgametogenic (for SLDE) and pregametogenic (for ontogeny) individuals using shell weights (as in *Schweitzer and Lohmann* [1991]), and the careful consideration of temporal averaging across seasons, years and centuries (for examples of refined seasonal approaches, see *Fallet et al.* [2010]).

### 5.7. Are There Clear Targets and Gaps in the Existing Data Set That Would Allow Us to Refine Stable Isotopic Interpretations?

Yes. Although all the major ocean basins are represented, sampling is highly biased to death assemblages from shelf and upwelling environments in the Atlantic and Indian Oceans (Figure 2 and Table 3), leaving open ocean gyres alarmingly undersampled. In addition, there are relatively few studies that directly compare size-specific isotopic trends in tow data with sediment traps and core tops (important direct comparisons include *Williams et al.* [1981], *Bouvier-Soumagnac and Duplessy* [1985], and *Ravelo and Fairbanks* [1992]). With limited paired life and death assemblage data, the importance of depth habitat occupancy (i.e., vertical niche partitioning) and preservational factors as they influence size-specific isotopic trends is largely untested. It is unclear from the existing net tow literature whether species subdivide the water column as often inferred from stable isotopic data. Similarly, a more direct study of environmental effects including temperature, carbonate saturation, salinity, and nutrients is needed. With the current data compilation, we had the statistical power to test for coarse environmental effects through biome, basin, water depth, and depth habitat (Table 1).

For many species, there is a paucity of data (e.g., *G. rubescens*, *G. unguolata*, and *P. obliquiloculata*; Figure 4) or a high degree of scatter (e.g., *G. bulloides*, *N. incompta*, and *N. pachyderma*; Figure 4), further limiting our ability to make general inferences. The available size-specific isotopic data are predominantly from core top sediments (supporting information), but our understanding of the various controls on isotopic fractionation in calcite is developed primarily through ontogenetic studies of live individuals in culture and target species in nets. This biases our interpretation of death assemblages toward ontogenetic hypotheses rather than Spero life-death effects. In order to document and evaluate both ontogenetic and Spero life-death effects, size-specific calibrations across an expanded size range (as per *Friedrich et al.* [2012] and *Birch et al.* [2013]) of paired living and death assemblages from open ocean gyres and underrepresented ocean basins are needed. In contrast, understanding the evolution of species-specific vital effects requires additional sampling of unrepresented species in the Atlantic, to provide a sufficiently dense record in a single basin (Table 3).

Our supporting information includes the data compilation and annotated computer code to recreate the models fitted and discussed here. We hope that this resource encourages future studies to integrate new data into the wider context provided here, so that our predictions can be re-evaluated as additional data become available.



## 6. Conclusions

Modern planktonic foraminifera provide a ready means for generating, testing, and benchmarking theories used to infer paleoclimatic and paleoecologic change. Past studies have typically focused on the generation of new data for a few species or regions. Here we compiled all available existing data, synthesized existing knowledge using integrated statistical modeling, and examined the evidence base that underpins our understanding of isotope geochemistry in this important study system. Our results suggest that size-dependent  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  trends are mediated predominantly by differences among oceanic regions (basin and biome), the presence and type of symbionts, and for  $\delta^{13}\text{C}$ , depth habitat, sample water depth and whether the assemblage was alive or dead. We find compelling evidence, dubbed here the Spero life-death effect, for the dominance and importance of death assemblage factors in shaping size-dependent stable isotopic curves in fossil assemblages. Species-specific factors have a significant effect on the basal  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of taxa. Rather surprisingly, symbiont ecology is more important than depth habitat in explaining  $\delta^{18}\text{O}$  values.  $\delta^{18}\text{O}$ -size trends may represent a new tool for identifying the presence of chrysophyte-bearing taxa in the fossil record. Depth habitat is at least as important on  $\delta^{13}\text{C}$  values than symbiont ecology, which also contradicts typical expectations.

## Acknowledgments

We thank Leanne Elder, who compiled the data in Table 1, and all authors who made their data available—our data compilation, computer code, and justification for statistical decisions are available in the supporting information. We also thank Anieke Brombacher, Gavin Foster, Michael Hennehan, Paul Pearson, Richard Smith, Howie Spero, Paul Wilson, and two anonymous reviewers for insightful discussions and/or comments on earlier versions of the manuscript that improved our work. Financial support was provided by a NERC Advanced Research Fellowship NE/J018163/1 to T.H.G.E. and Leverhulme Early Career Fellowship ECF-2013-608 to K.M.E.

## References

- Al-Sabouni, N., M. Kucera, and D. N. Schmidt (2007), Vertical niche separation control of diversity and size disparity in planktonic foraminifera, *Mar. Micropaleontol.*, 63(1–2), 75–90, doi:10.1016/j.marmicro.2006.11.002.
- André, A., A. Weiner, F. Quillevère, R. Aurahs, R. Morard, C. J. Douady, T. de Garidel-Thoron, G. Escarguel, C. de Vargas, and M. Kucera (2013), The cryptic and the apparent reversed: Lack of genetic differentiation within the morphologically diverse plexus of the planktonic foraminifer *Globigerinoides sacculifer*, *Paleobiology*, 39(1), 21–39, doi:10.5061/Dryad.Rb06j.
- Archer, D. (1996), A data-driven model of the global calcite lysocline, *Global Biogeochem. Cycles*, 10(3), 511–526, doi:10.1029/96GB01521.
- Aze, T., T. H. G. Ezard, A. Purvis, H. K. Coxall, D. R. M. Stewart, B. S. Wade, and P. N. Pearson (2011), A phylogeny of Cenozoic macroperforate planktonic foraminifera from fossil data, *Biol. Rev.*, 86(4), 900–927, doi:10.1111/j.1469-185X.2011.00178.x.
- Bé, A. W. H. (1977), An ecological, zoogeographic and taxonomic review of recent planktonic foraminifera, in *Oceanic Micropaleontology*, edited by A. T. S. Ramsay, pp. 1–100, Academic Press, London.
- Be, A. W. H. (1980), Gametogenic calcification in a spinose planktonic foraminifer, *Globigerinoides sacculifer* (Brady), *Mar. Micropaleontol.*, 5(3), 283–310, doi:10.1016/0377-8398(80)90014-6.
- Be, A. W. H., and D. B. Ericson (1963), Aspects of calcification in planktonic foraminifera (Sarcodina), *Ann. N. Y. Acad. Sci.*, 109(1), 65–81, doi:10.1111/J.1749-6632.1963.Tb13462.X.
- Bé, A. W. H., and W. H. Hutson (1977), Ecology of planktonic foraminifera and biogeographic patterns of life and fossil assemblages in the Indian Ocean, *Micropaleontology*, 23(4), 369–414.
- Bé, A. W. H., and D. S. Tolderlund (1971), Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans, in *Micropaleontology of Marine Bottom Sediments*, edited by B. M. Funnell and W. K. Riedel, pp. 105–149, Cambridge Univ. Press, Cambridge, U. K.
- Bé, A. W. H., H. J. Spero, and O. R. Anderson (1982), Effects of symbiont elimination and reinfection on the life processes of the planktonic foraminifer *Globigerinoides sacculifer*, *Mar. Biol.*, 70(1), 73–86, doi:10.1007/BF00397298.
- Bé, A. W. H., J. K. B. Bishop, M. S. Sverdrlove, and W. D. Gardner (1985), Standing stock, vertical distribution and flux of planktonic foraminifera in the Panama Basin, *Mar. Micropaleontol.*, 9(4), 307–333, doi:10.1016/0377-8398(85)90002-7.
- Bemis, B. E., H. J. Spero, J. Bijma, and D. W. Lea (1998), Reevaluation of the oxygen isotopic composition of planktonic foraminifera: Experimental results and revised paleotemperature equations, *Paleoceanography*, 13(2), 150–160, doi:10.1029/98PA00070.
- Berger, W. H. (1969), Ecologic patterns of living planktonic foraminifera, *Deep-Sea Res.*, 16(1), 1–24, doi:10.1016/0011-7471(69)90047-3.
- Berger, W. H. (1970), Planktonic foraminifera: Selective solution and lysocline, *Mar. Geol.*, 8(2), 111–138, doi:10.1016/0025-3227(70)90001-0.
- Berger, W. H. (1971), Sedimentation of planktonic foraminifera, *Mar. Geol.*, 11(5), 325–358, doi:10.1016/0025-3227(71)90035-1.
- Berger, W. H., and J. S. Killingley (1977), Glacial-Holocene transition in deep-sea carbonates: Selective dissolution and stable isotope signal, *Science*, 197(4303), 563–566, doi:10.1126/Science.197.4303.563.
- Berger, W. H., and D. J. W. Piper (1972), Planktonic foraminifera: Differential settling, dissolution, and redeposition, *Limnol. Oceanogr.*, 17(2), 275–287.
- Berger, W. H., J. S. Killingley, and E. Vincent (1978), Stable isotopes in deep-sea carbonates: Box Core ERDC-92, West Equatorial Pacific, *Oceanol. Acta*, 1(2), 203–216.
- Berger, W. H., M.-C. Bonneau, and F. L. Parker (1982), Foraminifera on the deep-sea floor: Lysocline and the dissolution rate, *Mar. Geol.*, 5(2), 249–258.
- Bijma, J., C. Hemleben, B. T. Huber, H. Erlenkeuser, and D. Kroon (1998), Experimental determination of the ontogenetic stable isotope variability in two morphotypes of *Globigerinella siphonifera* (d'Orbigny), *Mar. Micropaleontol.*, 35(3–4), 141–160, doi:10.1016/S0377-8398(98)00017-6.
- Bijma, J., H. J. Spero, and D. W. Lea (1999), Reassessing foraminiferal stable isotope geochemistry: Impact of the oceanic carbonate system (experimental results), in *Use of Proxies in Paleoceanography: Examples From the South Atlantic*, edited by G. Fischer and G. Wefer, pp. 489–512, Springer, Berlin.
- Billups, K., and H. J. Spero (1995), Relationship between shell size, thickness and stable isotopes in individual planktonic foraminifera from two equatorial Atlantic cores, *J. Foraminiferal Res.*, 25(1), 24–37, doi:10.2113/gsjfr.25.1.24.
- Birch, H. S., H. K. Coxall, P. N. Pearson, D. Kroon, and M. O'Regan (2013), Planktonic foraminifera stable isotopes and water column structure: Disentangling ecological signals, *Mar. Micropaleontol.*, 101, 127–145, doi:10.1016/j.marmicro.2013.02.002.
- Bonneau, M. C., C. Vergnaudgrazzini, and W. H. Berger (1980), Stable isotope fractionation and differential dissolution in Recent planktonic foraminifera from Pacific box-cores, *Oceanol. Acta*, 3(3), 377–382.

- Bornemann, A., and R. D. Norris (2007), Size-related stable isotope changes in Late Cretaceous planktic foraminifera: Implications for paleoecology and photosymbiosis, *Mar. Micropaleontol.*, 65(1-2), 32–42, doi:10.1016/J.Marmicro.2007.05.005.
- Bouvier-Soumagnac, Y., and J. C. Duplessy (1985), Carbon and oxygen isotopic composition of planktonic foraminifera from laboratory culture, plankton tows and Recent sediment: Implications for the reconstruction of paleoclimatic conditions and of the global carbon cycle, *J. Foraminiferal Res.*, 15(4), 302–320.
- Burnham, K. P., and D. R. Anderson (2002), *Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach*, Springer, New York.
- Caron, D. A., A. W. H. Bé, and O. R. Anderson (1981), Effects of variations in light intensity on life processes of the planktonic foraminifer *Globigerinoides sacculifer* in laboratory culture, *J. Mar. Biol. Assoc. U.K.*, 62, 435–451.
- Caron, D. A., W. W. Faber, and A. W. H. Be (1987a), Growth of the spinose planktonic foraminifer *Orbulina universa* in laboratory culture and the effect of temperature on life processes, *J. Mar. Biol. Assoc. U.K.*, 67(2), 343–358.
- Caron, D. A., W. W. Faber, and A. W. H. Be (1987b), Effects of temperature and salinity on the growth and survival of the planktonic foraminifer *Globigerinoides sacculifer*, *J. Mar. Biol. Assoc. U.K.*, 67(2), 323–341.
- Caron, D. A., O. R. Anderson, J. L. Lindsey, W. W. Faber, and E. L. Lim (1990), Effects of gametogenesis on test structure and dissolution of some spinose planktonic foraminifera and implications for test preservation, *Mar. Micropaleontol.*, 16(1-2), 93–116, doi:10.1016/0377-8398(90)90031-G.
- Cléroux, C., P. deMenocal, J. Arbuszewski, and B. Linsley (2013), Reconstructing the upper water column thermal structure in the Atlantic Ocean, *Paleoceanography*, 28, 503–516, doi:10.1002/Palo.20050.
- Coxall, H. K., P. A. Wilson, P. N. Pearson, and P. E. Sexton (2007), Iterative evolution of digitate planktonic foraminifera, *Paleobiology*, 33(4), 495–516, doi:10.1666/06034.1.
- Crawley, M. (2002), *Statistical Computing: An Introduction to Data Analysis Using S-Plus*, Wiley, Chichester, U. K.
- Curry, W. B., R. C. Thunell, and S. Honjo (1983), Seasonal changes in the isotopic composition of planktonic foraminifera collected in Panama Basin sediment traps, *Earth Planet. Sci. Lett.*, 64(1), 33–43, doi:10.1016/0012-821x(83)90050-X.
- Darling, K. F., and C. A. Wade (2008), The genetic diversity of planktic foraminifera and the global distribution of ribosomal RNA genotypes, *Mar. Micropaleontol.*, 67(3-4), 216–238, doi:10.1016/j.marmicro.2008.01.009.
- Darling, K. F., C. M. Wade, I. A. Stewart, D. Kroon, R. Dingle, and A. J. L. Brown (2000), Molecular evidence for genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers, *Nature*, 405(6782), 43–47, doi:10.1038/35011002.
- Darling, K. F., M. Kucera, C. J. Pudsey, and C. M. Wade (2004), Molecular evidence links cryptic diversification in polar planktonic protists to quaternary climate dynamics, *Proc. Natl. Acad. Sci. U.S.A.*, 101(20), 7657–7662, doi:10.1073/pnas.0402401101.
- Darling, K. F., M. Kucera, D. Kroon, and C. M. Wade (2006), A resolution for the coiling direction paradox in *Neogloboquadrina pachyderma*, *Paleoceanography*, 21, PA2011, doi:10.1029/2005PA001189.
- Deuser, W. G. (1987), Seasonal variations in isotopic composition and deep-water fluxes of the tests of perennially abundant planktonic foraminifera of the Sargasso Sea: Results from sediment-trap collections and their paleoceanographic significance, *J. Foraminiferal Res.*, 17(1), 14–27.
- Deuser, W. G., E. H. Ross, C. Hemleben, and M. Spindler (1981), Seasonal changes in species composition, numbers, mass, size, and isotopic composition of planktonic foraminifera settling into the deep Sargasso Sea, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 33(1-3), 103–127, doi:10.1016/0031-0182(81)90034-1.
- D'Hondt, S., and J. C. Zachos (1993), On stable isotopic variation and earliest Paleocene planktonic-foraminifera, *Paleoceanography*, 8(4), 527–547, doi:10.1029/93PA00952.
- D'Hondt, S., J. C. Zachos, and G. Schultz (1994), Stable isotopic signals and photosymbiosis in Late Paleocene planktic foraminifera, *Paleobiology*, 20(3), 391–406.
- Donner, B., and G. Wefer (1994), Flux and stable isotope composition of *Neogloboquadrina pachyderma* and other planktonic foraminifers in the Southern-Ocean (Atlantic Sector), *Deep Sea Res., Part I*, 41(11-12), 1733–1743, doi:10.1016/0967-0637(94)90070-1.
- Duplessy, J. C., C. Lalou, and A. C. Vinot (1970), Differential isotopic fractionation in benthic foraminifera and paleotemperatures reassessed, *Science*, 168(3928), 250–251, doi:10.1126/Science.168.3928.250.
- Duplessy, J. C., P. L. Blanc, and A. W. H. Be (1981a), Oxygen-18 enrichment of planktonic foraminifera due to gametogenic calcification below the euphotic zone, *Science*, 213(4513), 1247–1250.
- Duplessy, J. C., A. W. H. Be, and P. L. Blanc (1981b), Oxygen and carbon isotopic composition and biogeographic distribution of planktonic foraminifera in the Indian Ocean, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 33(1-3), 9–46, doi:10.1016/0031-0182(81)90031-6.
- Eguchi, N. O., H. Ujiie, H. Kawahata, and A. Taira (2003), Seasonal variations in planktonic foraminifera at three sediment traps in the subarctic, transition and subtropical zones of the central North Pacific Ocean, *Mar. Micropaleontol.*, 48(1-2), 149–163, doi:10.1016/S0377-8398(03)00020-3.
- Elderfield, H., M. Vautravers, and M. Cooper (2002), The relationship between shell size and Mg/Ca, Sr/Ca,  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  of species of planktonic foraminifera, *Geochim. Geophys. Geosyst.*, 3(8), 1022, doi:10.1029/2001GC000194.
- Emiliani, C. (1954), Depth habitats of some species of pelagic foraminifera as indicated by oxygen isotope ratios, *Am. J. Sci.*, 252, 149–158.
- Emiliani, C. (1971), Depth habitats of growth stages of pelagic foraminifera, *Science*, 173(4002), 1122–1124, doi:10.1126/Science.173.4002.1122.
- Epstein, S., R. Buchsbaum, H. A. Lowenstam, and H. C. Urey (1953), Revised carbonate-water isotopic temperature scale, *Geol. Soc. Am. Bull.*, 64(11), 1315–1325, doi:10.1130/0016-7606(1953)64[1315:Rcits]2.0.Co;2.
- Erez, J. (1978), Vital effect on stable-isotope composition seen in foraminifera and coral skeletons, *Nature*, 273(5659), 199–202, doi:10.1038/273199a0.
- Erez, J., and S. Honjo (1981), Comparison of isotopic composition of planktonic foraminifera in plankton tows, sediment traps and sediments, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 33(1-3), 129–156, doi:10.1016/0031-0182(81)90035-3.
- Erez, J., and B. Luz (1982), Temperature control of oxygen-isotope fractionation of cultured planktonic foraminifera, *Nature*, 297(5863), 220–222, doi:10.1038/297220a0.
- Faber, W. W., O. R. Anderson, J. L. Lindsey, and D. A. Caron (1988), Algal-foraminiferal symbiosis in the planktonic foraminifer *Globigerinella aequilateralis*. I. Occurrence and stability of two mutually exclusive chrysophyte endosymbionts and their ultrastructure, *J. Foraminiferal Res.*, 18(4), 334–343.
- Faber, W. W., O. R. Anderson, and D. A. Caron (1989), Algal-foraminiferal symbiosis in the planktonic foraminifer *Globigerinella aequilateralis*. II. Effects of two symbiont species on foraminiferal growth and longevity, *J. Foraminiferal Res.*, 19(3), 185–193.
- Fairbanks, R. G., and P. H. Wiebe (1980), Foraminifera and chlorophyll maximum: Vertical distribution, seasonal succession, and paleoceanographic significance, *Science*, 209(4464), 1524–1526, doi:10.1126/science.209.4464.1524.
- Fairbanks, R. G., P. H. Wiebe, and A. W. H. Be (1980), Vertical distribution and isotopic composition of living planktonic foraminifera in the western North Atlantic, *Science*, 207(4426), 61–63, doi:10.1126/science.207.4426.61.

- Fairbanks, R. G., M. Sverdrup, R. Free, P. H. Wiebe, and A. W. H. Be (1982), Vertical distribution and isotopic fractionation of living planktonic foraminifera from the Panama Basin, *Nature*, 298(5877), 841–844, doi:10.1038/298841a0.
- Fallet, U., G. J. Brummer, J. Zinke, S. Vogels, and H. Ridderinkhof (2010), Contrasting seasonal fluxes of planktonic foraminifera and impacts on paleothermometry in the Mozambique Channel upstream of the Agulhas Current, *Paleoceanography*, 25, PA4223, doi:10.1029/2010PA001942.
- Felsenstein, J. (1985), Phylogenies and the comparative method, *Am. Nat.*, 125(1), 1–15, doi:10.1086/284325.
- Franco-Fraguas, P., K. Badaraco Costa, and F. A. de Lima Toldeo (2011), Relationship between isotopic composition ( $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ) and planktonic foraminifera test size in core tops from the Brazilian continental margin, *Brazilian J. Oceanogr.*, 59, 327–338.
- Freckleton, R. P., P. H. Harvey, and M. Pagel (2002), Phylogenetic analysis and comparative data: A test and review of evidence, *Am. Nat.*, 160(6), 712–726, doi:10.1086/343873.
- Friedrich, O., R. Schiebel, P. A. Wilson, S. Weldeab, C. J. Beer, M. J. Cooper, and J. Fiebig (2012), Influence of test size, water depth, and ecology on Mg/Ca, Sr/Ca, delta O-18 and delta C-13 in nine modern species of planktic foraminifers, *Earth Planet. Sci. Lett.*, 319, 133–145, doi:10.1016/j.epsl.2011.12.002.
- Ganssen, G. M., F. J. C. Peeters, B. Metcalfe, P. Anand, S. J. A. Jung, D. Kroon, and G. J. A. Brummer (2011), Quantifying sea surface temperature ranges of the Arabian Sea for the past 20 000 years, *Clim. Past*, 7(4), 1337–1349, doi:10.5194/Cp-7-1337-2011.
- Gastrich, M. D. (1987), Ultrastructure of a new intracellular symbiotic alga found within planktonic-foraminifera, *J. Phycol.*, 23(4), 623–632.
- Hamilton, C. P., H. J. Spero, J. Bijma, and D. W. Lea (2008), Geochemical investigation of gametogenic calcite addition in the planktonic foraminifera *Orbulina universa*, *Mar. Micropaleontol.*, 68(3–4), 256–267, doi:10.1016/j.marmicro.2008.04.003.
- Harvey, P. H., and M. Pagel (1991), *The Comparative Method in Evolutionary Biology*, Oxford Univ. Press, Oxford, U. K.
- Hays, J. D., J. Imbrie, and N. J. Shackleton (1976), Variations in Earth's orbit: Pacemaker of the Ice Ages, *Science*, 194(4270), 1121–1132, doi:10.1126/science.194.4270.1121.
- Hemleben, C., M. Spindler, I. Breiteringer, and R. Ott (1987), Morphological and physiological responses of *Globigerinoides sacculifer* (Brady) under varying laboratory conditions, *Mar. Micropaleontol.*, 12(4), 305–324, doi:10.1016/0377-8398(87)90025-9.
- Hemleben, C., M. Spindler, and O. R. Anderson (1989), *Modern Planktonic Foraminifera*, pp. 363, Springer, New York.
- Hesse, T., D. Wolf-Gladrow, G. Lohmann, J. Bijma, A. Mackensen, and R. E. Zeebe (2014), Modelling  $\delta^{13}\text{C}$  in benthic foraminifera: Insights from model sensitivity experiments, *Mar. Micropaleontol.*, 112, 50–61, doi:10.1016/j.marmicro.2014.08.001.
- Hillaire-Marcel, C., A. de Vernal, L. Polyak, and D. Darby (2004), Size-dependent isotopic composition of planktic foraminifers from Chukchi Sea vs. NW Atlantic sediments - Implications for the Holocene paleoceanography of the western Arctic, *Quat. Sci. Rev.*, 23(3–4), 245–260, doi:10.1016/j.quascirev.2003.08.006.
- Hönsch, B., and N. G. Hemming (2004), Ground-truthing the boron isotope-paleo-pH proxy in planktonic foraminifera shells: Partial dissolution and shell size effects, *Paleoceanography*, 19, PA4010, doi:10.1029/2004PA001026.
- Houston, R. M., B. T. Huber, and H. J. Spero (1999), Size-related isotopic trends in some Maastrichtian planktic foraminifera: Methodological comparisons, intraspecific variability, and evidence for photosymbiosis, *Mar. Micropaleontol.*, 36(4), 169–188, doi:10.1016/S0377-8398(99)00007-9.
- Huber, B. T., J. Bijma, and K. Darling (1997), Cryptic speciation in the living planktonic foraminifer *Globigerinella siphonifera* (d'Orbigny), *Paleobiology*, 23(1), 33–62.
- Ivanova, E., R. Schiebel, A. D. Singh, G. Schmiedl, H. S. Niebler, and C. Hemleben (2003), Primary production in the Arabian Sea during the last 135 000 years, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 197(1–2), 61–82, doi:10.1016/S0031-0182(03)00386-9.
- John, E. H., P. N. Pearson, H. K. Coxall, H. Birch, B. S. Wade, and G. L. Foster (2013), Warm ocean processes and carbon cycling in the Eocene, *Philos. Trans. R. Soc. London Ser. A*, 371(2001), doi:10.1098/Rsta.2013.0099.
- Jørgensen, B. B., J. Erez, N. P. Revsbech, and Y. Cohen (1985), Symbiotic photosynthesis in a planktonic foraminiferan, *Globigerinoides sacculifer* (Brady), studied with microelectrodes, *Limnol. Oceanogr.*, 30(6), 1253–1267.
- Kahn, M. I. (1979), Non-equilibrium oxygen and carbon isotopic fractionation in tests of living planktonic foraminifera, *Oceanol. Acta*, 2, 195–208.
- Kahn, M. I., and D. F. Williams (1981), Oxygen and carbon isotopic composition of living planktonic foraminifera from the northeast Pacific Ocean, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 33(1–3), 47–69, doi:10.1016/0031-0182(81)90032-8.
- Keigwin, L., M. Bice, and N. Coplen (2005), Seasonality and stable isotopes in planktonic foraminifera off Cape Cod, Massachusetts, *Paleoceanography*, 20, PA4011, doi:10.1029/2005PA001150.
- Khider, D., L. D. Stott, J. Emile-Geay, R. Thunell, and D. E. Hammond (2011), Assessing El Niño Southern Oscillation variability during the past millennium, *Paleoceanography*, 26, PA3222, doi:10.1029/2011PA002139.
- Killingley, J. S., R. F. Johnson, and W. H. Berger (1981), Oxygen and carbon isotopes of individual shells of planktonic foraminifera from Ontong Java Plateau, Equatorial Pacific, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 33(1–3), 193–204, doi:10.1016/0031-0182(81)90038-9.
- Koutavas, A., P. B. Demenocal, G. C. Olive, and J. Lynch-Stieglitz (2006), Mid-Holocene El Niño-Southern Oscillation (ENSO) attenuation revealed by individual foraminifera in eastern tropical Pacific sediments, *Geology*, 34(12), 993–996, doi:10.1130/G22810a.1.
- Kroon, D., and K. Darling (1995), Size and upwelling control of the stable isotope composition of *Neoglobobulimina dutertrei* (d'Orbigny), *Globigerinoides ruber* (d'Orbigny) and *Globigerina bulloides* d'Orbigny: Examples from the Panama Basin and Arabian Sea, *J. Foraminiferal Res.*, 25(1), 39–52, doi:10.2113/gsjfr.25.1.39.
- Kucera, M. (2007), Planktonic foraminifera as tracers of past oceanic environments, in *Proxies in Late Cenozoic Paleoceanography*, edited by C. Hillaire-Marcel and A. de Vernal, Elsevier, Oxford.
- LeGrande, A. N., and G. A. Schmidt (2006), Global gridded data set of the oxygen isotopic composition in seawater, *Geophys. Res. Lett.*, 33, L12604, doi:10.1029/2006GL026011.
- Lohmann, G. P. (1995), A model for variation in the chemistry of planktonic foraminifera due to secondary calcification and selective dissolution, *Paleoceanography*, 10(3), 445–457, doi:10.1029/95PA00059.
- Lombard, F., L. Labeyrie, E. Michel, H. J. Spero, and D. W. Lea (2009), Modelling the temperature dependent growth rates of planktic foraminifera, *Mar. Micropaleontol.*, 70(1–2), 1–7, doi:10.1016/j.marmicro.2008.09.004.
- McConnaughey, T. (1989), C-13 and O-18 isotopic disequilibrium in biological carbonates 2. In vitro simulation of kinetic isotope effects, *Geochim Cosmochim. Acta*, 53(1), 163–171, doi:10.1016/0016-7037(89)90283-4.
- Mohtadi, M., S. Steinke, J. Groeneveld, H. G. Fink, T. Rixen, D. Hebbeln, B. Donner, and B. Herunadi (2009), Low-latitude control on seasonal and interannual changes in planktonic foraminiferal flux and shell geochemistry off south Java: A sediment trap study, *Paleoceanography*, 24, PA1201, doi:10.1029/2008PA001636.
- Mulitza, S., A. Durkoop, W. Hale, G. Wefer, and H. S. Niebler (1997), Planktonic foraminifera as recorders of past surface-water stratification, *Geology*, 25(4), 335–338, doi:10.1130/0091-7613(1997)025<0335:Pfarop>2.3.Co;2.

- Mulitza, S., D. Boltovskoy, B. Donner, H. Meggers, A. Paul, and G. Wefer (2003), Temperature: Delta O-18 relationships of planktonic foraminifera collected from surface waters, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 202(1-2), 143–152, doi:10.1016/S0031-0182(03)00633-3.
- Ni, Y. Y., G. L. Foster, T. Bailey, T. Elliott, D. N. Schmidt, P. Pearson, B. Haley, and C. Coath (2007), A core top assessment of proxies for the ocean carbonate system in surface-dwelling foraminifera, *Paleoceanography*, 22, PA3212, doi:10.1029/2006PA001337.
- Niebler, H.-S., H.-W. Hubberten, and R. Gersonde (1999), Oxygen isotope values of planktic foraminifera: A tool for the reconstruction of surface water stratification, in *Uses of Proxies in Paleoceanography: Examples From the South Atlantic*, edited by G. Fischer and G. Wefer, pp. 165–189, Springer, Berlin.
- Norris, R. D. (1996), Symbiosis as an evolutionary innovation in the radiation of Paleocene planktic foraminifera, *Paleobiology*, 22(4), 461–480.
- Norris, R. D. (1998), Recognition and macroevolutionary significance of photosymbiosis in molluscs, corals, and foraminifera, in *Isotope Paleobiology and Paleocology*, vol. 4, pp. 68–100, Paleontol. Soc., Lawrence, Kans.
- Norris, R. D., R. M. Corfield, and J. E. Cartledge (1994), Evolutionary ecology of *Globorotalia* (*Globoconella*) (planktic foraminifera), *Mar. Micropaleontol.*, 23, 121–145.
- Oppo, D. W., and R. G. Fairbanks (1989), Carbon isotope composition of tropical surface water during the past 22,000 years, *Paleoceanography*, 4(4), 333–351, doi:10.1029/PA004i004p00333.
- Ortiz, J. D., A. C. Mix, W. Rugh, J. M. Watkins, and R. W. Collier (1996), Deep-dwelling planktonic foraminifera of the northeastern Pacific Ocean reveal environmental control of oxygen and carbon isotopic disequilibria, *Geochim. Cosmochim. Acta*, 60(22), 4509–4523, doi:10.1016/S0016-7037(96)00256-6.
- Pagel, M. (1999), Inferring the historical patterns of biological evolution, *Nature*, 401(6756), 877–884, doi:10.1038/44766.
- Parker, F. L. (1960), Living planktonic foraminifera from the Equatorial and Southeast Pacific, *Sci. Rep. Tohoku Uni., Second Series (Geology)*, 4, 71–82.
- Pearson, P. N. (2012), Oxygen isotopes in foraminifera: Overview and historical review, in *Reconstructing Earth's Deep-Time Climate—The State of the Art in 2012*, Paleontological Society Short Course, edited by L. C. Ivany and B. T. Huber, *Paleontol. Soc. Pap. Spec. Publ.*, 18, 1–38.
- Pearson, P. N., and B. S. Wade (2009), Taxonomy and stable isotope paleoecology of well-preserved planktonic foraminifera from the uppermost Oligocene of Trinidad, *J. Foraminiferal Res.*, 39(3), 191–217.
- Pearson, P. N., N. J. Shackleton, and M. A. Hall (1993), Stable isotope paleoecology of Middle Eocene planktonic foraminifera and multispecies isotope stratigraphy, DSDP Site 523, South Atlantic, *J. Foraminiferal Res.*, 23(2), 123–140.
- Pearson, P. N., P. W. Ditchfield, J. Singano, K. G. Harcourt-Brown, C. J. Nicholas, R. K. Olsson, N. J. Shackleton, and M. A. Hall (2001), Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs, *Nature*, 413(6855), 481–487, doi:10.1038/35097000.
- Pinheiro, J. C., and D. M. Bates (2000), *Mixed Effects Models in S and S-PLUS*, Springer, New York.
- Ravelo, A. C., and R. G. Fairbanks (1992), Oxygen isotopic composition of multiple species of planktonic foraminifera: Records of the modern photic zone temperature gradient, *Paleoceanography*, 7(6), 815–831, doi:10.1029/92PA02092.
- Ravelo, A. C., and R. G. Fairbanks (1995), Carbon isotopic fractionation in multiple species of planktonic foraminifera from core-tops in the tropical Atlantic, *J. Foraminiferal Res.*, 25(1), 53–74.
- R Core Team (2014), R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available at <http://www.R-project.org/>]
- Regaudie-De-Gioux, A., and C. M. Duarte (2012), Temperature dependence of planktonic metabolism in the ocean, *Global Biogeochem. Cycles*, 26, GB1015, doi:10.1029/2010GB003907.
- Ridgwell, A. (2007), Interpreting transient carbonate compensation depth changes by marine sediment core modeling, *Paleoceanography*, 22, PA4102, doi:10.1029/2006PA001372.
- Rohling, E. J., and S. Cooke (1999), Stable oxygen and carbon isotope ratios in foraminiferal carbonate, in *Modern Foraminifera*, edited by B. K. Sen Gupta, pp. 239–258, Kluwer Acad, Dordrecht, Netherlands.
- Sadekov, A. Y., R. Ganeshram, L. Pichevin, R. Berdin, E. McClymont, H. Elderfield, and A. W. Tudhope (2013), Palaeoclimate reconstructions reveal a strong link between El Nino-Southern Oscillation and Tropical Pacific mean state, *Nat. Commun.*, 4, doi:10.1038/Ncomms3692.
- Sautter, L. R., and R. C. Thunell (1991), Planktonic foraminiferal response to upwelling and seasonal hydrographic conditions: Sediment trap results from San Pedro Basin, Southern California Bight, *J. Foraminiferal Res.*, 21(4), 347–363.
- Savin, S. M., and R. G. Douglas (1973), Stable isotope and magnesium geochemistry of recent planktonic foraminifera from South-Pacific, *Geol. Soc. Am. Bull.*, 84(7), 2327–2342, doi:10.1130/0016-7606(1973)84<2327:Siango>2.0.CO;2.
- Schiebel, R., and C. Hemleben (2005), Modern planktic foraminifera, *Paläontologische Zeitschrift*, 79(1), 135–148.
- Schmidt, D. N., S. Renaud, J. Bollmann, R. Schiebel, and H. R. Thierstein (2004), Size distribution of Holocene planktic foraminifer assemblages: Biogeography, ecology and adaptation, *Mar. Micropaleontol.*, 50(3–4), 319–338, doi:10.1016/S0377-8398(03)00098-7.
- Schmidt, D. N., D. Lazarus, J. R. Young, and M. Kucera (2006), Biogeography and evolution of body size in marine plankton, *Earth Sci. Rev.*, 78(3–4), 239–266, doi:10.1016/j.earscirev.2006.05.004.
- Schmidt, G. A., and S. Mulitza (2002), Global calibration of ecological models for planktic foraminifera from coretop carbonate oxygen-18, *Mar. Micropaleontol.*, 44(3–4), 125–140, doi:10.1016/S0377-8398(01)00041-X.
- Schrag, D. P., D. J. Depaolo, and F. M. Richter (1995), Reconstructing past sea surface temperatures: Correcting for diagenesis of bulk marine carbonate, *Geochim. Cosmochim. Acta*, 59(11), 2265–2278, doi:10.1016/0016-7037(95)00105-9.
- Schweitzer, P. N., and G. P. Lohmann (1991), Ontogeny and habitat of modern menardiiform planktonic-foraminifera, *J. Foraminiferal Res.*, 21(4), 332–346.
- Sexton, P. F., P. A. Wilson, and P. N. Pearson (2006), Microstructural and geochemical perspectives on planktic foraminiferal preservation: "Glassy" versus "frosty", *Geochim. Geophys. Geosyst.*, 7, Q12P19, doi:10.1029/2006GC001291.
- Shackleton, N. J., J. D. H. Wiseman, and H. A. Buckley (1973), Nonequilibrium isotopic fractionation between seawater and planktonic foraminiferal tests, *Nature*, 242(5394), 177–179, doi:10.1038/242177a0.
- Spero, H. J. (1992), Do planktic foraminifera accurately record shifts in the carbon isotopic composition of seawater sigma-CO<sub>2</sub>, *Mar. Micropaleontol.*, 19(4), 275–285, doi:10.1016/0377-8398(92)90033-G.
- Spero, H. J. (1998), Life history and stable isotope geochemistry of planktonic foraminifera, in *Isotope Paleobiology and Paleocology*, *Paleontological Society Short Course*, edited by R. D. Norris and R. M. Corfield, *Paleontol. Soc. Pap. Spec. Publ.*, 4, 7–36.
- Spero, H. J., and M. J. Deniro (1987), The influence of symbiont photosynthesis on the delta O-18 and delta C-13 values of planktonic foraminiferal shell calcite, *Symbiosis*, 4(1–3), 213–228.
- Spero, H. J., and D. W. Lea (1993), Intraspecific stable isotope variability in the planktic foraminifera *Globigerinoides sacculifer*: Results from laboratory experiments, *Mar. Micropaleontol.*, 22(3), 221–234, doi:10.1016/0377-8398(93)90045-Y.



- Spero, H. J., and D. W. Lea (1996), Experimental determination of stable isotope variability in *Globigerina bulloides*: Implications for paleoceanographic reconstructions, *Mar. Micropaleontol.*, 28(3-4), 231–246, doi:10.1016/0377-8398(96)00003-5.
- Spero, H. J., and D. F. Williams (1988), Extracting environmental information from planktonic foraminiferal delta C-13 data, *Nature*, 335(6192), 717–719, doi:10.1038/335717a0.
- Spero, H. J., and D. F. Williams (1989), Opening the carbon isotope “vital effect” black box. I. Seasonal temperatures in the euphotic zone, *Paleoceanography*, 4(6), 593–601, doi:10.1029/PA004i006p00593.
- Spero, H. J., I. Lerche, and D. F. Williams (1991), Opening the carbon isotope “vital effect” black box. II. Quantitative model for interpreting foraminiferal carbon isotope data, *Paleoceanography*, 6(6), 639–655, doi:10.1029/91PA02022.
- Spero, H. J., J. Bijma, D. W. Lea, and B. E. Bemis (1997), Effect of seawater carbonate concentration on foraminiferal carbon and oxygen isotopes, *Nature*, 390(6659), 497–500, doi:10.1038/37333.
- Spero, H. J., K. M. Mielke, E. M. Kalve, D. W. Lea, and D. K. Pak (2003), Multispecies approach to reconstructing eastern equatorial Pacific thermocline hydrography during the past 360 kyr, *Paleoceanography*, 18(1), 1022, doi:10.1029/2002PA000814.
- Triantaphyllou, M. V., A. Antonarakou, M. Dimiza, and C. Anagnostou (2010), Calcareous nannofossil and planktonic foraminiferal distributional patterns during deposition of sapropels S6, S5 and S1 in the Libyan Sea (Eastern Mediterranean), *Geo-Mar. Lett.*, 30(1), 1–13, doi:10.1007/S00367-009-0145-7.
- Urey, H. C. (1947), The thermodynamic properties of isotopic substances, *J. Chem. Soc. (May)*, 562–581, doi:10.1039/Jr9470000562.
- Vincent, E., and W. H. Berger (1981), Planktonic foraminifera and their use in paleoceanography, in *The Oceanic Lithosphere*, edited by C. Emiliani, pp. 1025–1119, John Wiley, New York.
- Williams, D. F., A. W. H. Be, and R. G. Fairbanks (1981), Seasonal stable isotopic variations in living planktonic foraminifera from Bermuda plankton tows, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 33(1-3), 71–102, doi:10.1016/0031-0182(81)90033-X.
- Wilson, P. A., R. D. Norris, and M. J. Cooper (2002), Testing the Cretaceous greenhouse hypothesis using glassy foraminiferal calcite from the core of the Turonian tropics on Demerara Rise, *Geology*, 30(7), 607–610, doi:10.1130/0091-7613(2002)030<0607:TTCGHU>2.0.CO;2.
- Wolf-Gladrow, D. A., J. Bijma, and R. E. Zeebe (1999), Model simulation of the carbonate chemistry in the microenvironment of symbiont bearing foraminifera, *Mar. Chem.*, 64(3), 181–198, doi:10.1016/S0304-4203(98)00074-7.
- Wu, G. P., and W. H. Berger (1989), Planktonic foraminifera: Differential dissolution and the Quaternary stable isotope record in the West Equatorial Pacific, *Paleoceanography*, 4(2), 181–198, doi:10.1029/PA004i002p00181.
- Zachos, J. C., L. D. Stott, and K. C. Lohmann (1994), Evolution of early Cenozoic marine temperatures, *Paleoceanography*, 9(2), 353–387, doi:10.1029/93PA03266.
- Zeebe, R. E. (1999), An explanation of the effect of seawater carbonate concentration on foraminiferal oxygen isotopes, *Geochim. Cosmochim. Acta*, 63(13-14), 2001–2007, doi:10.1016/S0016-7037(99)00091-5.
- Zeebe, R. E., J. Bijma, B. Hönisch, A. Sanyal, H. J. Spero, and D. A. Wolf-Gladrow (2008), Vital effects and beyond: a modelling perspective on developing palaeoceanographical proxy relationships in foraminifera, in *Biogeochemical Controls on Palaeoceanographic Environmental Proxies*, edited by W. E. N. Austin and R. H. James, *Geol. Soc. London Spec. Publ.*, 45–58.