An SEM image the penultimate chamber of a specimen of Globorotalia inflata with a heavy calcite crust that has obscured the original wall texture. This secondary calcification, normally close to the end of the foraminifer's life can drastically increase the shell weight. Note that the suture lines remain distinct.
9.

Synthesis and Outlook:

“Senses and Sensivity”
The research that composes this thesis has focused on the shells of planktonic foraminifera as proxies in palaeoceanographic research. Planktonic foraminifera are natural floating laboratories; their wide-ranging distribution and considerable abundance make them an ideal 'transporter' of palaeoceanographic information. Additionally as they are unwittingly carried along in the ocean currents they cannot avoid inhospitable conditions. This research has been funded by the European Project on Ocean Acidification (EPOCA) ultimately the aim has been to further understand the proxies that are in use testing features that may alter, affect or negate the impact of Ocean acidification in the geological record. Our results, for Termination III combined with known responses to Termination I, demonstrate that surface dwelling planktonic foraminifera are affected by changes in the carbonate chemistry, over glacial-interglacial transitions. As such planktonic foraminifera can be a good recorder of the bad, i.e. ocean acidification.

Synthesis and Outlook:

“Senses and Sensivity”
9.1.0 Synthesis

9.1.1 Research questions

In order to reconstruct glacial to interglacial changes in shell weight as a proxy for reduced calcification with ocean acidification to be the major cause, competing signals such as seasonality, depth habitat, bioturbation, dissolution and methodological error have to be removed from the record. Using core material representing Modern, Termination I and Termination III a set of key questions were determined that needed to be answered:

- What is the impact of methodological error upon shell weight studies?
- What is the influence of size?
- Is it possible to reconstruct specific environments, or Seasons?
- Is it possible to disentangle the, at times, competing (palaeo)environmental information of season, depth habitat, dissolution and expatriation?

9.1.2 Research Methodology

Proxies are inherently dependent upon the strength of their producibility, reproducibility (precision) and validity (accuracy). Potential bias in proxy measurements between laboratories and the resulting papers may ultimately lead to artefacts in the record. These artefacts can be introduced prior to sieving through chemical treatment (i.e. pre-cleaning, Chapter Three), through selection of size fraction (Chapter Five), in the measurements themselves or in the data processing (i.e. normalisation, Chapter Two). The preparatory chemicals may impact upon the geochemical and physiological characteristics of planktonic foraminifera [Bé and Anderson, 1976b; Fallet et al., 2009; Ganssen, 1981; Kahn, 1979; Nagtegaal et al., 2012; Savin and Douglas, 1973; Wierzbowski, 2007], however our results suggest otherwise. Using multiple samples from the North Atlantic and Gulf of Aden we concluded that, for a given selection of chemicals, no apparent effect occurs on trace metal and stable isotope geochemistry, faunal abundance or shell weight for hydrogen peroxide and sodium pyrophosphate.

In Chapter Two we discussed the shell weight proxy as a measure for either reduced calcification and/or dissolution. Recent papers have cast doubt on the reliability of sieving to accurately partition a sample into the stated mesh size [Beer et al., 2010a; Kroon and Darling, 1995], though we consider this to be in fact due to the micropalaeontologists view point. We propose that the treatment of foraminiferal size normalised weight (SNW) should be genus and/or species specific taking into account the
complexity of chamber size, shape and thickness. As shell weight studies utilise a standard uniform normalisation for all species to shell size this can be greatly affected by the shell. For example, the gross morphology, chamber arrangement and ornamentation which all greatly vary between species.

9.1.3 The influence of size

Size fractions separate out sizes that may represent different ecological and/or ontogenetic stages precluding direct comparisons. The literature is inconsistent with different research groups providing contradictory answers using conventional oxygen ($\delta^{18}$O) and carbon ($\delta^{13}$C) stable isotope analysis [Elderfield et al., 2002]. Offsets between size fractions could reflect changes in metabolism during ontogeny, i.e. physiological

Figure 9-1. Schematic representation of the Summer stratification versus Winter mixing on the influence of the signal recorded. With stratification small sized foraminifera will experience a considerably different set of temperatures than larger sized foraminifera.
changes, or could also reflect changes in the depth habitat of foraminifera, i.e. environmental changes. Our results, presented in *Chapter Four* suggest that these contradictions in the literature can be best explained as representing real changes in the upper water column, or environmental shifts (i.e. season or depth habitat) for non-symbiotic species (Figure 9.1). For symbiotic species, considering the change in volume associated with growth changes in the standing stock of photosynthetic symbionts may lead to an overprinting in later ontogenetic stages.

Our observations, in *Chapter Five*, show that despite differences in size, and potential ecological habitat shell weight of the shallow dwelling *Globigerina bulloides* and the intermediate dwelling *Globorotalia inflata* follows the changes in atmospheric carbon dioxide. However, for the deeper dwelling, *Globorotalia truncatulinoides* (dextral) no discernible change occurs which could be interpreted to be either an adaption to lower carbonate ion concentration at depth, limited exposure or biogeography changes.

### 9.1.4 Reconstructing specific seasons

In *Chapter Six* we show that it is possible to reconstruct seasonality using the oxygen isotope (δ¹⁸O) composition of individual shells of *Globigerinoides ruber* and *G. bulloides*, two species with distinctly different seasonal preferences, from deep-sea sediments off Somalia. Combining the δ¹⁸O measurements of individual specimens of both species to obtain temperature ranges with Mg/Ca based mean calcification temperatures allows us to reconstruct temperature extrema (Figure 9.2). Our results show that the extreme seasonal temperature contrasts in the tropics are caused by the West-Asian monsoon system. During the past 20 kyrs the seasonal temperature range has fluctuated from its present value of 15°C to mean values of 13°C and 11°C for the Holocene and LGM, respectively. The data for the LGM suggest that the maximum temperature was lower, whilst minimum temperature remained approximately constant. The rather minor variability in lowest summer temperatures during the LGM suggests roughly constant summer monsoon intensity, and lowered productivity during reduced upwelling. At the start of the Holocene the SW-monsoon was even weaker than during the last glacial, while the NW-monsoon operated already in its Holocene mode.

### 9.1.5 Detangling specific effects

Associated morphological (decreasing test thickness) and geochemical (depletion of δ¹³C) changes are predicted from culture studies testing the susceptibility of planktonic foraminifera to changes in the carbonate ion concentration. However, in situ and sedimentological observations indicate that this sensitivity to increasing CO₂ may be complicated by changes associated with other biotic (i.e. competition) and abiotic (i.e.
Figure 9-2. Global warming is predicted to shift the climatic system so that more extreme warm events are recorded, reconstructions of seasonality are therefore required. (a) Seasonal temperature changes due to global warming means that hot weather events will become the norm with more extreme events. (b-c) Reconstructions based upon individual specimen oxygen isotope values allow for these extreme events, cold or hot, to be determined (Chapter Six).

Temperature, salinity) factors. Complicating this further is the potential for pre- and post-burial processes to obscure valuable information. Presented in Chapter Seven is a coupled geochemical-morphological analysis utilising an approach that allows for accurate oxygen and carbon isotopic measurements from specimens >5μg in weight along a core top depth transect in the North Atlantic. Contradictory to prior analysis in some species shell mass appears to increase with depth in some species. Sedimentation rates suggest that exposure time to corrosive water masses, rather than water depth in itself may play an important role. Differential dissolution between populations of ‘lighter’ and ‘heavier’ tests, a bi-product of physiological and ecophenotypical processes, may also affect the average test mass. Correction factors that assume that dissolution is unidirectional may lead to over estimation [Barker et al., 2004; Rosenthal and Lohmann, 2002].
In *Chapter Eight* elaborating upon the work of *Wit et al.* [2013] and *Ganssen and Kroon* [2000] we applied the single specimen oxygen isotope method to a North-South transect core top for *G. inflata*. As unlike *G. bulloides*, *G. inflata* shell weight shows no correlation with latitude despite changes in both carbonate ion concentration, with higher latitudes having lower concentrations than lower latitudes, and changes in seasonality. Our observations between 65 and 40°N are in line with calcification in warmer waters at lower latitudes. However, between 40 and 25°N a second population with enriched $^{18}$O values, out of equilibrium with the upper 500m regardless of season, appear. *Wit et al.* [2013] considered that the bimodality is related to an increase in bioturbated specimens. Whereas, whilst we acknowledge that bioturbation could potentially be a likely cause, we suggest that given that latitude that this bimodality occurs a more plausible explanation is for an influx of individuals expatriated from colder waters. In any case, these specimens would then be out of equilibrium with the ambient environment.

### 9.2.0 Outlook

#### 9.2.1 Sensitivity of Shell weight

The sensitivity of shell weight to atmospheric carbon dioxide, and/or equivalent carbon chemistry perturbations, in the natural environment as opposed to laboratory studies is dependent upon (i) the initial starting conditions, (ii) the rate of change in concentrations and (iii) concurrent changes (i.e. temperature). In order to calculate the sensitivity of shell weight to atmospheric carbon dioxide ($pCO_2$) the data for the last glacial maximum from core NEAP8K was utilised [Barker and Elderfield, 2002]. The transition from MIS 2 to 1 was chosen as an independent age model (i.e. $^{14}$C-dating) and climatic records are available for this time period. First interpolation was used to generate an equally spaced record of both shell weight of *G. bulloides* (300-355μm) and $pCO_2$, which represent 0.5kyr per sample, using a linear integration method (Figure 9.3A). In order to remove potentially erroneous data points a Gaussian smoothing method with a filter width of 7 samples was utilised, the calculation is as follows where the sample (ti) and weighting (w) via:

$$\frac{(w_1t_i + w_2t_{i-1} + w_3t_{i-1} +......)}{\sum w} \quad [\text{Eq. 9.1}]$$

The upper and lower two data points were removed as this method ultimately gives a tail/head affect and the data generated is potentially inaccurate (Figure 9.3B). The first derivative of both the CO$_2$ concentration and shell weight was taken using a three box moving window, and converted into per kilo-year (kyr). Prior to the LGM the correla-
Figure 9-3. Shell weight change during the Last Glacial Maximum. (a) Interpolation was used to generate an equally spaced record of both shell weight of G. bulloides (300-355 μm) and CO$_2$ that represent 0.5 kyr per sample, using a linear interpolation method (b) removal of potentially erroneous data points using a Gaussian smoothing method with a filter width of 7 samples (c) the correlation between ΔpCO$_2$ and Δshell mass (d) climatic events during the allotted time period. Data from Barker and Elderfield [2002].

- **Figure 9-3A**: Atmospheric Carbon dioxide (pCO$_2$) and Shell weight (μg) over time.
- **Figure 9-3B**: δ$^{18}$O H$_2$O (SMOW, ‰) changes over time.
- **Figure 9-3C**: δ$^{18}$O H$_2$O (SMOW, ‰) changes over time, with a linear trend line (y = -0.0399x + 0.0968) and R$^2$ = 0.2732.
- **Figure 9-3D**: δ$^{18}$O H$_2$O (SMOW, ‰) changes over time, with a linear trend line (y = -0.0478x + 0.2536) and R$^2$ = 0.4363.
Figure 9-4 Change in shell weight during Termination III. Composite shell weight record of (a) G. bulloides and (b) G. inflata. As per Figure 9.3 calculated (c) change in shell weight against change in pCO$_2$ (blue, G. bulloides and red, G. inflata). (d) Climatic events during the allotted time period.
The correlation between Δ$pCO_2$ and Δshell mass was observed to be weak (Figure 9.3C), potentially due to the D/O warming and cooling events (Figure 9.3D) or the mechanics of a glacial world (i.e., shift in the position of the Gulf Stream, North Atlantic Intermediate Water and Gulf Stream) suppressing the variability. Therefore in order to deal with this only 1.5-25kya was selected for calculation of the shell mass sensitivity given that this period represents a continuous change in a single direction (Figure 9.3C; blue circles). The same analysis was performed upon the calculated composite shell weight record for Termination III (Chapter Five) (Figure 9.4). The response and sensitivity of shell weight to rates of change in atmospheric carbon dioxide would be expected to change depending on initial starting conditions. However, it would appear that other parameters may alter this (Figure 9.5), as we see a reduction in shell weight during periods of decreasing atmospheric carbon dioxide concentrations when shell weight should increase.

Offsets exist between temporally similar, but spatially different, shell weight records [Barker and Elderfield, 2002; Moy et al., 2009] (Figure 9.6), which could be due to human error (Chapter Two), size fraction effects (Chapter’s Four and Five), or due to differences in the mechanism and cause for shell generation. This final point is intriguing as it is not yet known why planktonic foraminifera secrete such elaborate shells, although throughout the Cenozoic similar shapes have evolved repeatedly.

**Figure 9-5 (above and opposite page). Shell weight change in response to changes in carbon dioxide concentration for both the LGM and TIII.** Hypothetical (a) linear and (b) exponential scenarios for shell weight in response to change in pCO$_2$ and Carbon dioxide concentration. The actual data points of G. bulloides (300-355μm) for (c) Termination I [Barker and Elderfield, 2002] following Figure 9.3 and for (d) Termination I [Barker and Elderfield, 2002] and Termination III (Chapter Five).
suggesting that there exists some adaption to their pelagic lifestyle [Cifelli, 1969; Scott, 1974a].

9.2.2 Shell weight as a proxy for seawater density?

“The further delineation of morphological variation and comparison of such trends with as many environmental variables as possible is required. Such variables should include temperature, salinity, water depth and density. Much more study is required on the possible morphological responses to resistance to sinking of planktonic foraminifera. In this connection, studies in particular are required of the relationship between test morphology and the density of water. Morphological variables examined
Planktonic foraminifera evolved from benthic ancestors on two separate occasions. Due to their planktonic occurrence in the upper ocean, planktonic foraminifera, must somehow have developed a way to regulate their buoyancy in sea water of different densities, and hence as a function of sea water temperature and salinity. Certainly the reoccurrence of similar forms throughout the Cenozoic indicates a degree of functional morphology within test construction. This adaption to a planktonic lifestyle requires the facilitation of a number of specialized modifications.
Chapter Nine

(A) Globigerinoides trilobus

- $y = 0.6597e^{0.0079x}$, $R^2 = 0.9713$
- $y = 1.2079e^{0.0067x}$, $R^2 = 0.9573$
- $y = 1.4367e^{0.0064x}$, $R^2 = 0.9285$

(B) Globigerinoides ruber

- $y = 0.0544x - 7.6508$, $R^2 = 0.9832$
- $y = 0.1081x - 19.818$, $R^2 = 0.9907$
- $y = 0.0762x - 10.654$, $R^2 = 0.9262$

Shell weight (µg) vs. Shell size (µm)
to counteract changes in seawater density through the development of simple and efficient mechanism to modify their overall buoyancy (i.e. through adaptations in shell morphology, number of chambers, pore density or wall thickness) in order to remain buoyant at different densities. Whilst, the competitive advantage bestowed upon planktonic foraminifera through the formation of a relatively dense mineralized skeletons either intra- or extra-cellularly is unknown it undoubtly and unavoidably increases the sinking rate. These organisms must therefore actively keep themselves buoyant within the water column.

The variation within water masses occurs over temporal timescales on orders of magnitude slower - e.g. seasonally, centennial, or millennial - than the life of planktonic organisms which inhabit them e.g. days, weeks, months, and in some exceptions years. Therefore, planktonic foraminifera make ideal recorders of water mass properties. Environmental impacts that interrupt a species’ optima, or inconvenience it in a way that may lead to a competitive disadvantage are considered to produce an overall assemblage change, rather than a physiological change. However, this is rather dependent on both the attendant environmental impact and function of both the calcification process and structures [Raven et al., 2005], for example shells have been thought to be the result of the need for: removal of metabolic poisoning by $Ca^{2+}$ protection; removal of excess CO$_2$ in photosynthesis; rigidity within test; support for feeding structures (i.e. rhizopodia; pseudopodia; or mucus webs). If the shell within planktonic foraminifera is in some way connected to buoyancy regulation it could explain their evolution and near-global dispersal [Caron and Homewood, 1983; Hart, 1980; 1999; Hart and Bailey, 1979; Hart et al., 2002; ]. The apparent modern hampered diversity [Stainforth et al., 1975], and recognisation of discreet morphological provinces [Kennett,
Chapter Nine

**A**

Annual average Seawater density

\[ y = -2.6628x + 75.009 \]

\[ R^2 = 0.4666 \]

**B**

Station 5 Net 5 (1986)

(i) (ii) (iii) (iv) (v) (vi) (vii) (viii) (ix) (x)

500 µm

**C**

Annual average Seawater density
Senses and Sensitivity

1976] coupled with cryptic speciation as exposed by genetic variability [André et al., 2012; Aurahs et al., 2009; Bijma et al., 1998; Darling et al., 2007; Darling et al., 2006b; de Vargas et al., 2002; de Vargas et al., 1999; de Vargas et al., 2001; Huber et al., 1997; Kucera and Darling, 2002; Kuroyanagi et al., 2008; Morard et al., 2011; Morard et al., 2009; Ujiié et al., 2012; Ujiié et al., 2010] supports the idea that water masses have played an important part in the associated polytheism in planktonic foraminifera.

The ~40 extant species of planktonic foraminifera occur in a range of environments and a variety of depths which they inhabit. Planktonic Foraminifera can be broadly split into spine bearing and non-spine bearing shell morphologies, associated, but not an absolute, is the use of these spines as refuges for photosynthetic algae during the day. Symbionts follow a diurnal movement inhabiting vacuoles in the shell during night where respiration of photosynthetically fixed inorganic carbon occurs. This association with symbionts greatly influences shell growth and longevity [Bé et al., 1982; Caron et al., 1981; Spero, 1998; Spero and Lea, 1993]. The requirement that symbiotic bearing planktonic foraminifera need to be reinfected with photosynthetic algae (i.e. dinoflagellates, chrysophytes) [Hemleben and Spindler, 1983] limits the depth habitat to the photic zone [Spero, 1998]. Current micropalaeontological inferences envision a fixed depth habitat for planktonic foraminifera, refining this view with more specific depths will allow for a greater understanding of the ecological niches that planktonic foraminifera fill. Given that a number of species are well constrained in their depth habitat to the photic zone because of their photosymbiotic algae, one can thus be confident that palaeo-reconstructions based upon their fossil shells reflects conditions of the ancient ocean’s photic zone.

In order to remain buoyant planktonic foraminifera must regulate their overall density to that of its specific depth habitat in the water column, or to descend towards a specific density level for reproduction. The groundless mechanism generally assumed to control buoyancy is adjustment by lipid production. This mechanism does not provide a ballast mechanism for sinking [Marszalek, 1973] to greater depths for reproduction at the end of the life cycle, which is accompanied by shell transformation [Erez, 1991; Furbish and Arnold, 1997; Takahashi and Bé, 1984] required for reaching deeper water masses. We hypothesize that the cal-

\[ \text{Figure 9-9 (opposite page). The relationship between seawater density and shell weight of planktonic foraminifera. (a) Seawater density versus shell weight of field collected specimens [Aldridge et al., 2012; van Leverink, unpublished; Metcalfe unpublished] of (b) G. bulloides for the North Atlantic. (c) The annual average seawater density (kg/m}^2\text{) for the sea surface, plotted using the Ocean Data View programme. For methodology see supplementary information.} \]
Figure 9-10. Single specimen oxygen isotope values of a species of planktonic foraminifera from a plankton tow in the North Atlantic Ocean showing how the oxygen isotope composition tracks the change in the hydrography. Single specimen oxygen isotope values of G. inflata (triangles) versus calculated seawater (red squares) and equilibrium (blue circles) oxygen isotope values. Inset is the oxygen isotope values versus sieve size for 0-50 meters tow interval.
cite shell provides the ballast necessary for species to reach deeper water levels or to stay buoyant at a fixed depth level at different densities (e.g. along a latitudinal transect waters become colder towards higher latitudes and as such surface ocean density increases). Modifications to the shell or cell therefore should be clearly measurable and detectable since it has been shown that a given depth in the water column, and hence at the same sea water density, both small and larger specimens are found together. Larger specimens appear thicker walled compared to smaller ones, obviously to compensate for the larger volume (Figure 9.8). This can only be possible if the foraminifera can change their overall buoyancy characteristics such that the overall weight of the organism precisely corresponds to the weight of the mass of ambient seawater that is displaced by the organism as predicted by Archimedes’ Law.

Planktonic foraminifera may modify their shell characteristics in order to reach desired depth levels in the ocean; to remain buoyant in the photic zone, obtain food (e.g. at the depth of the Deep Chlorophyll Maximum) or to reach depth levels for reproduction at the end of their life cycle. To do so a planktonic foraminifer cell may change its’ shell mass, size, volume, wall thickness, modify the number and/or size of pores, add or modify ornamentation (peripheral keel, pustules etc.), or may change the mass of the cytoplasmic tissue by changing its volume or composition, as sometimes is observed within other type of plankton, such as diatoms. Available evidence thus far, stems from studies in which only one or two of these parameters were quantified. For example Bé [1968] and Bé et al. [1973] showed that the shell porosity of the species Orbulina universa in the Indian Ocean increases with increasing temperature (and hence with decreasing sea water density). Furthermore, the apertures of subtropical to tropical species are considerably larger than colder water species giving a larger amount of open area [Bé, 1968]. At higher, sub-polar to polar latitudes, Simstich et al. [2003] showed that, using oxygen isotope measurements on fossil specimens, the reconstructed depth habitat of the species Tenuitella quinqueloba and Neogloboquadrina pachyderma (sinistral) appears to closely follows the isopycnals [surfaces/lines of equal density]. Orr [1969] established a relationship between the thickness of the penultimate chamber and water depth for Globigerinoides ruber in the Gulf of Mexico, a result of increasing secondary encrustment due to a inhabiting a greater water depth. Planktonic foraminifera are thus expected to alter their overall specific mass, through increasing their wall thickness, adding ornamentation, increasing their ‘cytoplasmatic lift effect’, and/or decreasing their volume and pore density [(and/or pore size), to neutralize the effect of higher seawater density (see Figure 9.9).

9.2.3 Single specimen stable isotopes

Reconstructions, of palaeoceanographic parameters (i.e. tempera-
Chapter Nine

Frequency

(Temperature) Cold Hot

assuming a normal distribution

Flux SF(T)

Topt Tm Tr

Winter

Topt Tm Tr

Summer

F(T) W(T)

2σF 2σW

Flux SF(T)

Topt Tm Tr

Winter

Topt Tm Tr

Summer

Flux SF(T)

Topt Tm Tr

Winter

Topt Tm Tr

Summer

Flux SF(T)
Figure 9-11. Theoretical model for the temperature recorded at a site as a product of the temperature at the site and the species temperature tolerance. The Mix [1987] model in which (a) the temperature range of a species $F(T)$ versus the temperature range at a given site $W(T)$, assuming a normal distribution generates (b) the recorded temperature of a species. Based upon this model species will represent (c) Winter, (d) average and (e) Summer based upon the overlap (red section) between the species optima and the temperature distribution at a given location.
Chapter Nine

aeoceanographic researchers likely represents a composite signal of calcification at increasingly deeper depths (Figure 9.10). Sedimentary $\delta^{18}O$ values, of species that precipitate a secondary-gametogenetic crust, are therefore dependent, as per Mix [1987] upon: the vertical temperature gradient, amount and depth of gametogenetic calcification [Bé, 1980; Bé and Anderson, 1976a; Hamilton et al., 2008], potential ‘dissolution’ of early ontogenetic structures [Hemleben et al., 1979], and the susceptibility or resistance of secondary structures to post mortem dissolution [Caron et al., 1990](Chapter Seven).

If we consider that the magnitude of offset between small-early ontogenetic- and large-later ontogenetic stages- (Chapter Four) is dependent upon the vertical temperature gradient and that the sediment preservation is intrinsically linked to resistance or robustness of the test (Chapter Seven) for certain species palaeoceanographic conclusions are currently limited. Furthermore, consideration must be given toward the time of year that we are recording (Chapter Eight).

9.2.3.2 Seasonality

Numerous studies have clearly demonstrated the major control upon abundance of planktonic foraminifera and therefore productivity is seasonality [Deuser et al., 1986; Ganssen and Sarnthein, 1983; Reynolds and Thunell, 1985; Sautter and Thunell, 1989; Sautter and Thunell, 1991a; Sautter and Thunell, 1991b; Thunell and Honjo, 1987; Tolderlund and Bé, 1971; Wolfteich, 1994]. This is likely linked to the seasonal variation in the proliferation or attenuation of ecologically beneficial constraint as a function of the water hydrography, i.e. upwelling of nutrient rich water brought about by the strength of the Monsoon. Early researchers, utilising plankton tows, documented the seasonal succession of foraminiferal species reflecting the seasonal variation in the temperature and salinity and therefore nutrient properties of the water column [Bé, 1977; Bé and Tolderlund, 1971; Tolderlund and Bé, 1971]. Mix [1987] proposed that the mean isotopic composition, or the temperature recorded, is weighted toward the season that overlaps the species temperature tolerance (Figure 9.11a-b). This overlap will likely change through time. Whilst Figure 9.11c-e is theoretical, if we consider Termination III then the monthly

Figure 9-12 (opposite page) Contraction and expansion of the seasonal optimum and its influence of species abundance and oxygen isotope values. (a) Single specimen oxygen isotope values of G. bulloides (300-355μm) from core T90-9p over Termination III, dashed line is mean, solid line is mean corrected for the ice volume effect using [Bintanja and van de Wal, 2008]. (b) Abundance of G. bulloides. (c) Relative monthly insolation for 45°N, lighter (orange-reds) colours represent more insolation than darker (blues-purple) colours. (d) Difference between the temperature at the location and the species optima, based upon Figure 9.11.
G. bulloides (300-355 μm)

δ¹⁸O Oxygen Isotopes VPDB (‰)

Likelihood of occurrence

Low Temperatures

High Temperatures

Mean

Mean (ice volume corrected)

Theoretical species optima

Cold

Average

Hot
insolation (Figure 9.12c) would have led to the contraction or expansion (Figure 9.12b) of the relatively warm and cold periods and their synonymous faunas. Reconstructions at ~230kya likely do not represent the same season as at 220kya. This places a limitation not only upon the reconstruction of ‘Annual sea surface temperature’ to areas with low seasonality, i.e. low latitudes, but also to multi-proxy reconstructions where species that may co-exist in the present did not do so in the past. In order to better understand our proxies we should invest in a better understanding into the season, depth habitat, calcification and biology of our proxy carriers: planktonic foraminifera.