# Ecology

"The dynamic interaction of individual organisms and populations with the physical and biotic components of the marine environment is of central importance in understanding the manifold characteristics of oceanic ecosystems. This includes the productivity of the oceans, the factors governing the distribution and range of organisms in a geographic region, the abundance and fecundity of species, the pattern of energy flow through the marine ecosystem, and the analysis of fossil remains in reconstructing ancient environments and interpreting the history of the Earth. Planktonic Foraminifera are of special significance in the study of modern and ancient marine ecosystems owing to their widespread occurrence in modern oceans, with rather clearly defined faunal provinces for many species, and the fact that they produce calcitic shells that contribute substantially to the micro-fossil faunal record" (Hemleben et al. 1989).

Most of the about 50 extant planktic foraminifer morphospecies are ubiquitous in the global ocean (e.g., Bé 1977; Hemleben et al. 1989). Single genotypes of those morphotypes are more limited to ocean basins and regions (e.g., Darling and Wade 2008). Three modern morphospecies are endemic to the Pacific and Indian Oceans, i.e. *Globigerinella adamsi*, *Globoquadrina conglomerata*, and *Globorotaloides hexagonus*. In addition, certain morphotypes (e.g., *G. sacculifer* forma *immaturus*) are limited to the Pacific and Indian Oceans

(André et al. 2013). The pink variety of *Globigerinoides ruber* has been limited to the modern Atlantic Ocean, and became extinct in the Pacific and Indian Oceans following Marine Isotope Stage (MIS) 5.5 around 125 kyrs (Thompson et al. 1979). The global distributions of some ten small-sized, rare, and dissolution-susceptible species, including *Globorotalia cavernula*, *Gallitellia vivans*, and most tenuitellid species are not well constrained due to under-sampling with plankton tows (usually >100-µm mesh-size) and dissolution during sedimentation. Best documented are the distributions of the $\sim 35$ most abundant, large-sized, and dissolution-resistant species, from plankton tows and surface sediment samples. In this chapter, general ecological demands of planktic foraminifers, the effects on shell production, and spatial and temporal distribution patterns are discussed. Particular ecological demands at the species level are discussed with their classification in Chap. 2.

Subtropical and temperate waters harbor the most diverse planktic foraminifer assemblages (e.g., Bé and Tolderlund 1971; Schmidt et al. 2004a; cf. Peters et al. 2013). Patchy distribution patterns of planktic foraminifers on various temporal and spatial scales are caused by small-scale to meso-scale hydrographic features such as fronts and eddies (Boltovskoy 1971; Beckmann et al. 1987; Siccha et al. 2012).

Hydrology, availability of nutrients in surface waters, and primary production affect the production of planktic foraminifers. Average standing stocks of adult specimens (>100 μm) range from 10 to 100 specimens per cubic meter. Largest standing stocks of ∼190 individuals per liter are reported from Antarctic sea ice (Spindler and Dieckmann 1986), 1250 individuals (>63 μm) per cubic meter occurred in surface to subsurface waters off the ice edge in the Arctic summer (Carstens et al. 1997), and 720 individuals (>100 μm) per cubic meter in the temperate North Atlantic during spring (Schiebel and Hemleben 2000). Those large standing stocks result from high prey availability supporting the production of a wide range of opportunistic species. For example, standing stocks of opportunistic species like *G. bulloides*, *N. dutertrei*, and *N. pachyderma* are positively related to upwelling intensity and eutrophic conditions (e.g., Naidu and Malmgren 1996; Ivanova et al. 1999; Schiebel et al. 2004). In contrast, the largest overall standing stocks in tropical and subtropical waters occur rather marginal than central to major upwelling cells, caused by overall negative effects high primary production, chlorophyll concentration, and turbidity exert through light attenuation on symbiont-bearing species in central upwelling cells (Schiebel et al. 2004). However, the same morphospecies may react to overall similar ecological conditions (e.g., upwelling) in different ways, which may have various reasons. Ecological conditions may differ in detail. For example, the supply of prey may be different in quality and quantity at the spatial and temporal scale. In addition, certain morphospecies may be represented by different genotypes with different ecological adaptations. For example, *N. dutertrei* is positively related to increasing upwelling intensity (early bloom species) in the Arabian Sea (Kroon and Ganssen 1988), whereas it signifies post-upwelling conditions in the San Pedro Basin, NE Pacific (Sautter and Sancetta 1992). The wide (at least) bimodal temperature range and ecological coverage of *N. dutertrei* may indicate the presence of different genotypes (cf. Morard et al. 2015).

Average annual export production of planktic foraminifers is highest in mesotrophic waters in the temperate to subpolar ocean, caused by low average stratification of the surface water column, and frequent nutrient supply. Seasonally enhanced availability of prey during spring and fall fosters production of opportunistic species, and generalist species persist during more stratified and lower productive summer conditions (cf. Schiebel 2002; Žarić et al. 2005). Oligotrophic waters of the subtropical gyres host the lowest standing stocks due to lack of prey (e.g., Bé 1960). However, trophic conditions do not directly translate into standing stocks, and the distribution of planktic foraminifers results from a variety of factors in addition to hydrology and food (Schiebel 2002; Siccha et al. 2009).

Following the most obvious observations, sea surface temperature (SST, surface mixed layer temperature, well documented by discrete measurements and satellite imagery) may affect the distribution of species. The assumption is abundantly pursued in paleoceanography following the temperature effect on the $\delta^{18}O$ signal of planktic foraminifer tests. In turn, a direct affect of SST on the distribution of planktic foraminifer species could not yet be demonstrated, and various temperature-dependent parameters like the quality of prey (e.g., various algae) may be involved. In addition, most planktic foraminifer species are largely eurythermal (Fig. 7.1), and occur over a wide temperature range of 15–20 °C (up to 25 °C, Bé and Tolderlund 1971), with an optimum temperature range of ∼10 °C (Lombard et al. 2011). In addition to alimentation and temperature, salinity is a limiting factor to the distribution of planktic foraminifers. According to results from culture experiments, some species endure a wide salinity range of 20–45 PSU, and are most productive (reproduction rate >70 %) in waters of 33–38 PSU (e.g., Bijma et al. 1990b, 1992).

**Practical salinity units, PSU:** Salinity of water may be given in practical salinity units (PSU). PSU is used for practical reasons, for example, when deriving
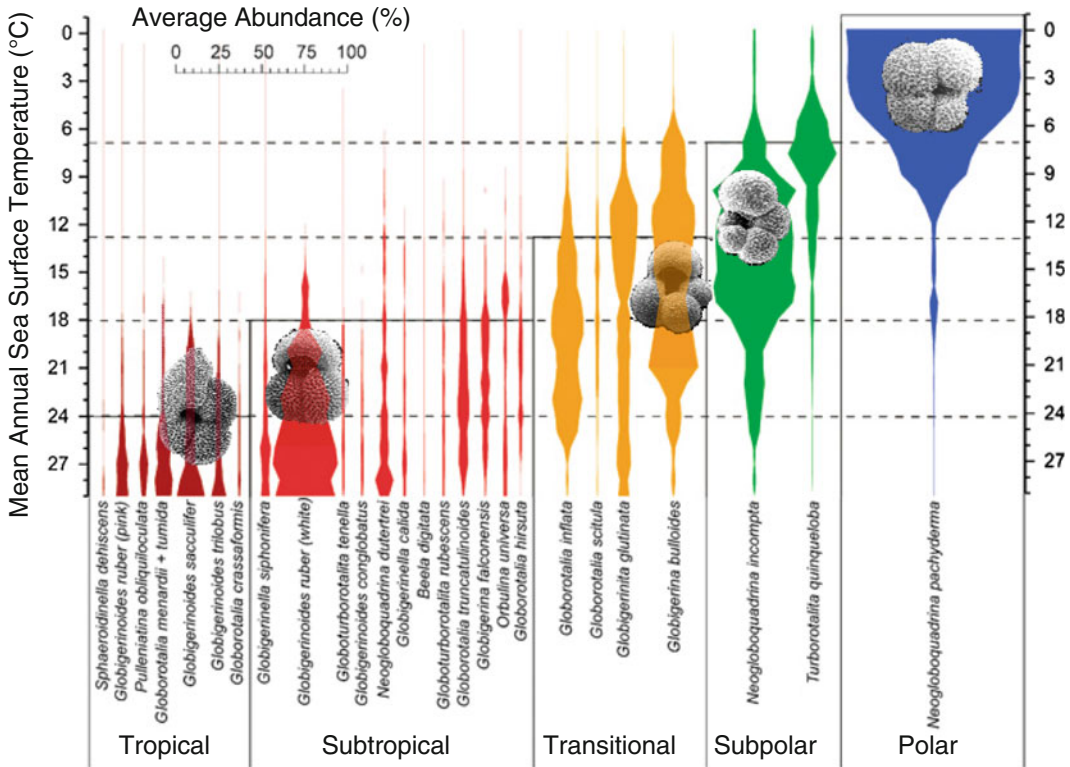
**Fig. 7.1** Temperature related distribution of planktic foraminifer species in surface-sediment data from the Atlantic Ocean (Kucera et al. 2005) averaged at one degree centigrade intervals. The relation of species and sea surface temperature (SST) largely resembles the distribution in other ocean basins (Bradshaw 1959; Bé and Tolderlund 1971; Bé 1977; Bé and Hutson 1977; Žarić et al. 2005). The proportions of the major species of the respective assemblages are displayed by colored bars. Subsurface-dwelling *Globorotalia* species merely coincide with the given SSTs, and are possibly affected by ecological parameters related to SST. Modified after Kucera (2007)

seawater salinity from data on electrical conductivity. The more descriptive 'per mil' (‰) unit of seawater salinity is usually very close to PSU. Salinity of seawater typically amounts to 35 g/kg.

In contrast to surface dwelling species, sub-surface dwelling species like most globorotalids (Fig. 7.1), are not exposed to sea surface conditions, and hence not affected by, for example, SST. The distribution pattern of subsurface dwellers is possibly limited by the flux of organic matter arriving at depth, as well as the distribution of subsurface water bodies (e.g., Weyl 1978; Deuser et al. 1981; Durazzi 1981; Hemleben et al. 1985; Healy-Williams 1983; Healy-Williams et al. 1985; Itou and Noriki 2002; Schiebel et al. 2002a, b; Peeters et al. 2004).

## 7.1 Distribution in the Global Ocean

### 7.1.1 Biogeographic Provinces

Modern planktic foraminifer assemblages are attributed to five major faunal provinces at the global scale (Figs. 7.1 and 7.2): Tropical, sub-tropical, temperate, subpolar, and polar (e.g.,
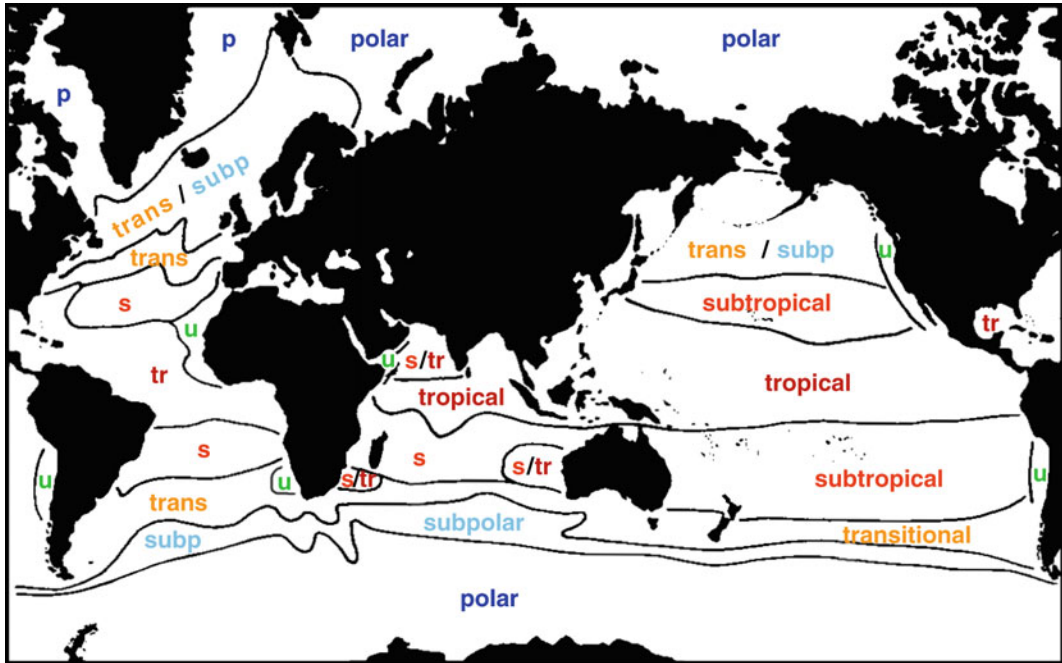
**Fig. 7.2** Foraminifer provinces according to data from plankton tows and sediment samples (Hemleben et al. 1989, and references therein). Latitudinal provinces are polar (p), subpolar (subp), transitional (trans), subtropical (s), and tropical (tr). A sixth province is characterized by upwelling (u) and eutrophic conditions. Provinces in the Indian Ocean are characterized by mixing of subtropical-to-tropical (s/tr) faunal elements, and transitional-to-subpolar (trans/subp) faunal elements in the North Pacific and Atlantic Ocean. Modified after Hemleben et al. (1989)

Bradshaw 1959; Bé 1959, 1977; Hemleben et al. 1989; Kucera 2007). Those faunal provinces roughly follow zonal and areal distribution patterns, displaying water temperature and salinity (Phleger 1960; Bé and Tolderlund 1971; Tolderlund and Bé 1971; Caron et al. 1987; Bijma et al. 1990b), radiation (symbiont-bearing species; Erez 1983; Erez and Luz 1983), turbidity of ambient water (Ortiz et al. 1995), the abundance of prey, and trophic demands of planktic foraminifers at a species level (e.g., Spindler et al. 1984; Schiebel et al. 2001). To a yet unknown extend, distribution and abundance of planktic foraminifers may also follow the distribution of predators (Berger 1971). A sixth province follows the major upwelling regions, and is almost exclusively defined by eutrophic conditions, the abundance of prey, and to some extent by turbidity. Upwelling conditions are characterized by a dominance of the symbionts-barren species *G. bulloides* (e.g., Thiede 1975). In general, the biogeography of foraminifers, and foraminifer provinces are characterized by the overall distribution of species, as well as the presence of indicator species like *G. bulloides*. Depending on the genotype, *G. bulloides* (Fig. 7.3) indicates enhanced production of algal prey at temperate to high latitudes during spring, or upwelling conditions at low to mid latitudes.

Additional provinces are defined by particular ecological conditions, and mixing of different water bodies and faunas, particularly conspicuous in the Arabian Sea and northern Pacific Ocean (Fig. 7.2). Planktic foraminifer population dynamics in the Arabian Sea is affected by monsoon-induced effects in physical and biological properties of surface waters, and suboxic to anoxic conditions below the seasonal thermocline (e.g., Kroon 1988; Kroon and Ganssen 1988; Brock et al. 1992; Curry et al. 1992; Ivanova et al. 1999; Schiebel et al. 2004). The North Pacific is characterized by seasonal changes in
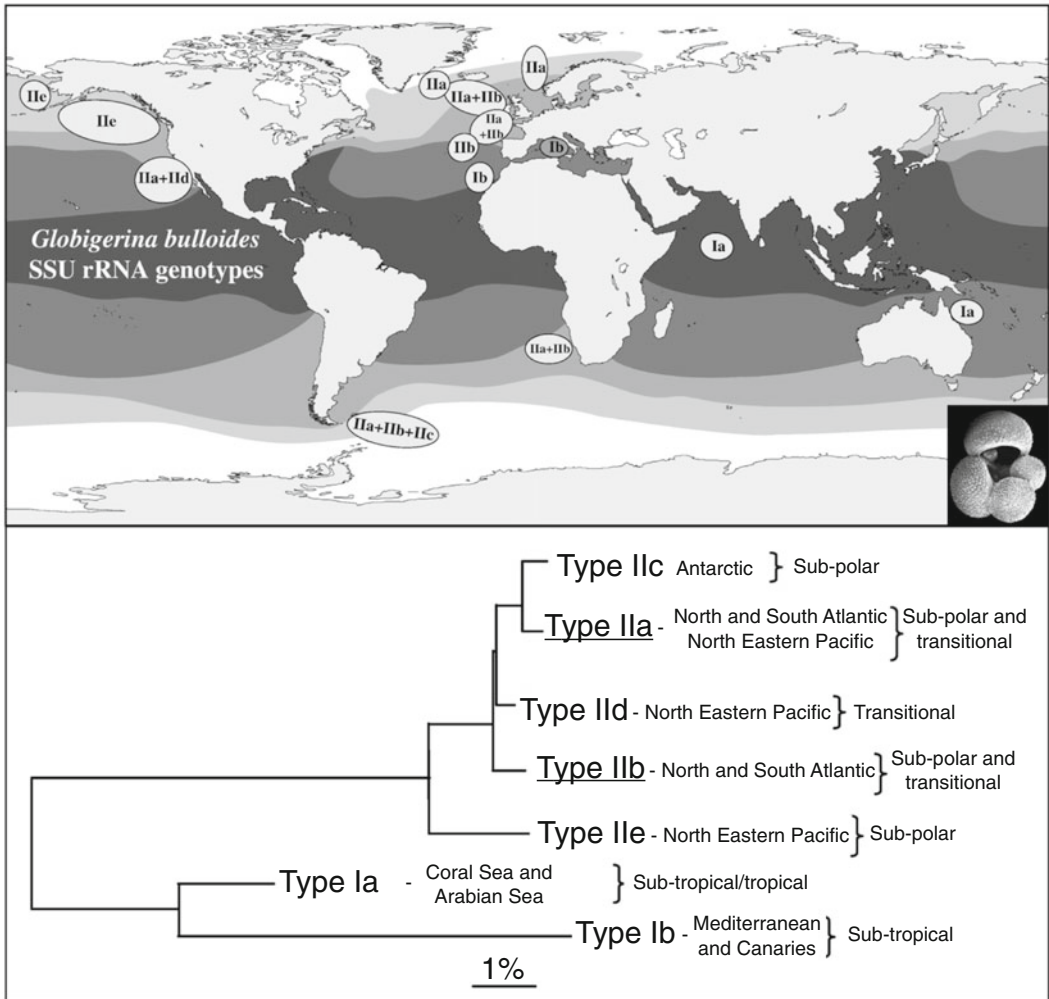
**Fig. 7.3** Biogeographic distribution (*upper panel*) and evolutionary relationships (*lower panel*) of SSU rRNA genotypes isolated for the morphospecies *G. bulloides*, superimposed on the map of five major planktic foraminifer faunal provinces according to Bé and Tolderlund (1971). Genotypes isolated by Darling et al. are shown in *light grey* (1999, 2000, 2003, 2007; Stewart 2000). Mediterranean Type Ib (shown in *dark grey*) from De Vargas et al. (1997). The tree is re-drawn from Darling et al. (2007), and is rooted on the *G. bulloides* Type I genotypes at the base of the *G. bulloides* clade in the phylogenetic tree of Darling et al. (2000; see also André et al. 2014). The bipolar genotypes are underlined. From Darling and Wade (2008)

the Kuroshio-Oyashio confluence, and mixing of tropical-to-subtropical and polar-to-subpolar faunal elements (e.g., Eguchi et al. 1999; Mohiuddin et al. 2002). Faunal mixing caused by hydrodynamic features (e.g., upwelling and currents), and regional shifts of faunal provinces occurs on various temporal scales such as, for example, seasonal to glacial-interglacial time-scales (e.g., Ivanova et al. 2003; Ishikawa and Oda 2007). In addition, changing planktic foraminifer assemblages, and 'warmer' faunal elements in the eastern Pacific Ocean off California since the 1970s presumably indicate a warming trend (Field et al. 2006).

## 7.1.2  Diversity

Diversity of modern planktic foraminifers on the global scale is highest within the oligotrophic subtropical gyres (Fig. 7.4), as a consequence of both biological and ecological effects (Ottens and Nederbragt 1992; Brayard et al. 2005; Žarić et al. 2005; Beaugrand et al. 2013). Slightly enhanced diversity in particular at the poleward boundaries of the subtropical gyres (Fig. 7.4) may result from hydrodynamic effects, i.e. expatriation and mixing of faunal elements by currents (cf. Berger 1970a; Weyl 1978; Ottens 1991; Ottens and Nederbragt 1992). Particular ecological conditions like very high productivity in upwelling areas, and the short productive season in polar latitudes cause decreased diversity in comparison to adjacent waters, and lower latitudes, respectively (e.g., Ottens and Nederbragt 1992). Secondary effects causing decreased diversity of sediment assemblages (i.e. data used in numerical models, from, e.g., Prell et al. 1999) are differential dissolution and winnowing (e.g., Dittert et al. 1999). Reflecting the sum of parameters affecting ecological niches, the global diversity pattern is positively related to, and may be best explained (following numerical models) by absolute temperature (Rutherford et al. 1999; Beaugrand et al. 2013).

The distribution of genotypes appears geographically more restricted than the distribution of morphotypes, as for example in *G. bulloides* (Darling and Wade 2008). Primary production and the availability of prey are assumed major driving forces for regional and vertical ecological partitioning, and diversity of planktic foraminifers (Seears et al. 2012). The association of symbiont-bearing planktic foraminifer species may affect ecological partitioning by limiting those species to euphotic waters (Seears et al. 2012). Symbiont-barren species may well be depth-parapatric, as shown for *H. pelagica* Type I (above 100 m), and *H. pelagica* Type IIa (below 100 m) from the same site (Weiner et al. 2012). Both Seears's et al. (2012) and Weiner's et al. (2012) conclusions are supported by extensive genetic analyses. Gene flow and

speciation are interpreted to follow ecological adaptation.

Species populate their typical depth habitat (e.g., Weiner et al. 2012) according to specific ecological demands, and may ascend and descend in the water column during ontogeny (Hemleben et al. 1989). For example, *Globorotalia truncatulinoides* spends most time of its life in subsurface and deep waters, and ascends to the sea surface during late winter/early spring to reproduce, for example, near the Azores Island and Bermuda (e.g., Durazzi 1981; Healy-Williams 1983; Healy-Williams et al. 1985; Hemleben et al. 1985; Mulitza et al. 1997; Schiebel et al. 2002a, b). The vertical separation of species is more evident in the tropics than in polar waters owing to a wider diversity of hydrographic and biotic variables from surface to depth at low latitudes compared to the more homogeneous water column at high latitudes on average (Schmidt et al. 2004a, b).

## 7.2  Interannual and Seasonal Distribution

Interannual variability in the production of planktic foraminifers follows variations in seasonal hydrographic and ecological changes. Consequently, standing stocks in mid latitudes may vary by more than one order of magnitude at the species to assemblage level (e.g., Schiebel and Hemleben 2000). Interannual variability of planktic foraminifer assemblages has been assumed primarily caused by trophic conditions in the productive (euphotic) surface ocean (e.g., Schiebel 2002). Regional variability may be caused by shifting fronts between water bodies due to differences in climate zones and wind patterns. In contrast, species assemblages may be (qualitatively) similar when comparing corresponding seasons. Quantitative changes in production and flux of planktic foraminifer tests may be best recorded from different latitudes and ocean basins by sediment trap samples (e.g., Žarić et al. 2005) (see Chap. 10 Methods, Table 10.1 and Fig. 10.2).
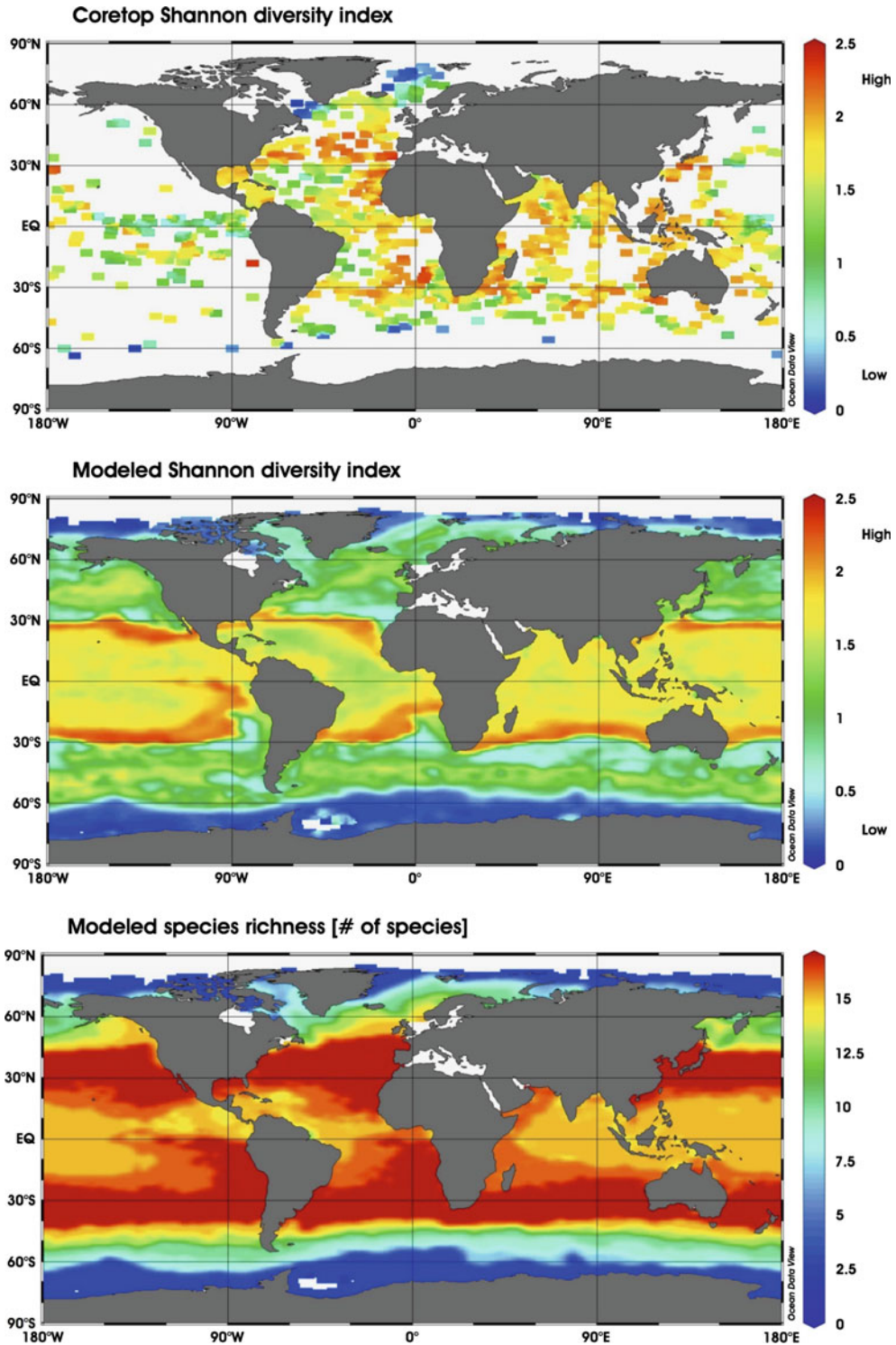
**Fig. 7.4** High planktic foraminifer diversity at the global scale occurs at the poleward margins of the subtropical gyres. Diversity is lowest in polar waters. *Upper panel*: Shannon diversity is best represented in coretop assemblages according to the data of Prell et al. (1999). *Middle panel*: Modeled Shannon-Wiener diversity (*H′*, see Chap. 10). *Lower panel*: Modeled species richness (# of species) calculated from the model. *White* and *pink G. ruber* combined. Higher values correspond to higher diversity. Note different scale bars. After Žarić et al. (2005)

The seasonal distribution pattern of planktic foraminifers is most pronounced at mid to high latitudes, displaying phytoplankton succession and food chain (e.g., Bé 1960, 1977; Schiebel and Hemleben 2005; Fraile et al. 2009). In polar oceans, single maximum planktic foraminifer production occurs during the short summer, when light and temperature conditions cause enhanced primary and secondary production (Fig. 7.5). The planktic foraminifer fauna of the polar ocean is dominated by two rather small species, *Neogloboquadrina pachyderma* and *Turborotalita quinqueloba*, with *G. bulloides*, *Globigerinita glutinata*, and *Globigerinita uvula* being the most common accessory species (Carstens et al. 1997; Volkmann 2000; Pados and Spielhagen 2014). *Neogloboquadrina pachyderma* survives even in brine channels (up to 82 PSU) within the annual Antarctic sea ice (not in the Arctic!), where it feeds on diatoms (Dieckmann et al. 1991; Spindler 1996). In mid latitudes, two seasons of enhanced production during spring and fall are caused by the interplay of increased mixing depth of surface waters, nutrient recycling, and light intensity. Spring production of planktic foraminifers in mid-latitudes was shown to considerably outnumber the autumn-production (Schiebel and Hemleben 2000; Schiebel et al. 2001). In low latitudes, light intensity and temperature are high throughout the year, seasonality is low, and productivity follows regional conditions like monsoonal activity and upwelling intensity (e.g., Kroon and Ganssen 1989; Ivanova et al. 1999; Conan and Brummer 2000; Schiebel et al. 2004).

Seasonality is expressed by the co-occurrence of planktic foraminifer species, which signify different zonal distributions and hydrographic conditions (Hemleben et al. 1989; Schiebel 2002; Schiebel and Hemleben 2005; Jonkers and Kučera 2015). Seasonal changes between monsoon-driven upwelling, surface ocean mixing versus stratification, and trophic conditions result in a mix of sedimentary test assemblages. Absolute changes in water temperature ($\Delta T$) and productivity ($\Delta P$) may hence be reconstructed from species assemblages, as well as stable isotopes ($\delta^{18}O$ and $\delta^{13}C$) and Mg/Ca ratios (e.g.,

Williams et al. 1979; Saher et al. 2009; Wit et al. 2010; Feldmeijer 2014), and Cd/Ca ratios of tests from different species (Ripperger et al. 2008). In addition to multi-species analyses, ontogenetic changes in the chemical compositions (stable isotopes and element ratios, see Chap. 10) may provide additional information for more refined reconstructions of hydrographic changes (e.g., Katz et al. 2010). Considering the complexity of both planktic foraminifer population dynamics and regional hydrology, modern analytical methods as LA-ICP-MS (see Sect. 10.7.1) provide detailed quantitative data to achieve a higher level of understanding of paleoceanographic processes (e.g., Eggins et al. 2003; Wit et al. 2010).

## 7.3 Trophic Effects

The relative preference for zooplankton and phytoplankton prey by spinose and non-spinose planktic foraminifers, respectively (see Chap. 4), affects the spatial and temporal distribution of species according to the quantity and variety (i.e. quality) of available food. Most symbiont-bearing species prefer lower latitudes and less turbid (i.e. less productive) waters, whereas symbiont-barren species occur at higher relative abundance at higher latitudes and more productive (i.e. more turbid) waters (e.g., Bé and Tolderlund 1971; Bé 1977; Ottens 1992; Ortiz et al. 1995; Schiebel and Hemleben 2000). At the global scale, relative abundance of spinose species is highest in the oligotrophic central water masses in the subtropical gyres, where copepods and other zooplankton predominate (Hemleben et al. 1989 and references therein; Barnard et al. 2004; Schiebel et al. 2004; Buitenhuis et al. 2013; Moriarty and O'Brien 2013). In contrast, non-spinose species are more abundant in eutrophic waters with high phytoplankton production, such as upwelling regions, with the exception of symbiont-barren spinose *G. bulloides*.

Differential reaction of planktic foraminifer species to changing ecological conditions causes species successions, which are characteristic of
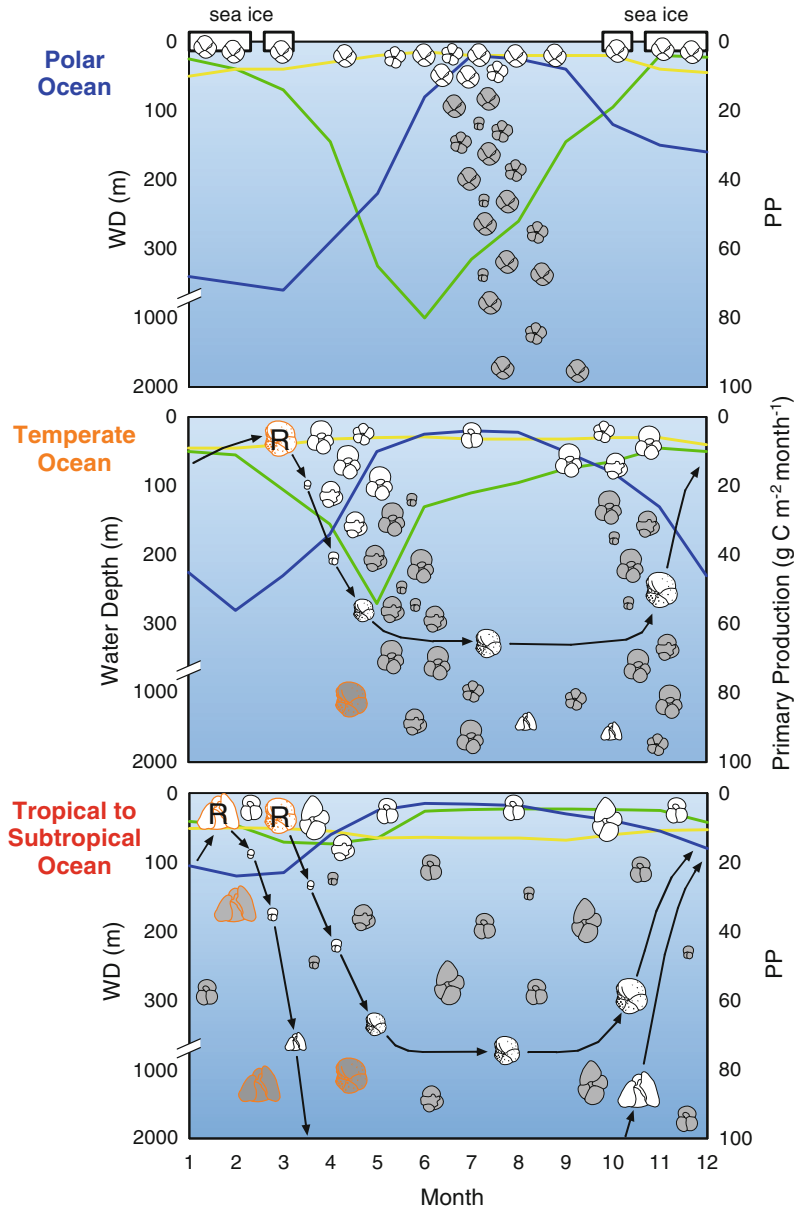
**Fig. 7.5** Schematic view of seasonality, depth habitat (living specimens shown by *white* tests), and sedimentation of empty planktic foraminifer tests (*grey*), compiled from plankton-tow and sediment-trap samples (see Table 10.1, Fig. 10.2). Ecological parameters after Longhurst (1998). Mixed layer water depth (y-axis to the left, *blue line*) and photic depth (1 % isolume, *yellow line*), and integrated primary production (PP, *green line*, y-axis to the right). Biological production depends on the availability of nutrients, mixed layer depth, and light level. Seasonal succession of species according to their ecological demands (e.g., food) is exemplified by *Neogloboquadrina pachyderma* for the polar ocean (*upper panel*), and by *Globigerinita glutinata* and *Globigerina bulloides* for the temperate ocean (*middle panel*).

During winter, *N. pachyderma* lives in the lower layers of the Antarctic (not Arctic) sea ice. *Turborotalita quinqueloba* is present in the polar ocean during summer and in the temperate ocean during seasons of low water temperature. Mass flux of empty tests follows periods of major biological production. Intermediate and deep-dwelling planktic foraminifer species ascend to the sea surface to reproduce (*black* 'R'), and empty tests settle to the seafloor after reproduction. In the tropical to subtropical ocean (*lower panel*), intermediate and deep-dwelling species inhabit deeper waters than at mid-latitudes. In the tropical to subtropical ocean, production of planktic foraminifers is more balanced than at higher latitudes. From Schiebel and Hemleben (2005)
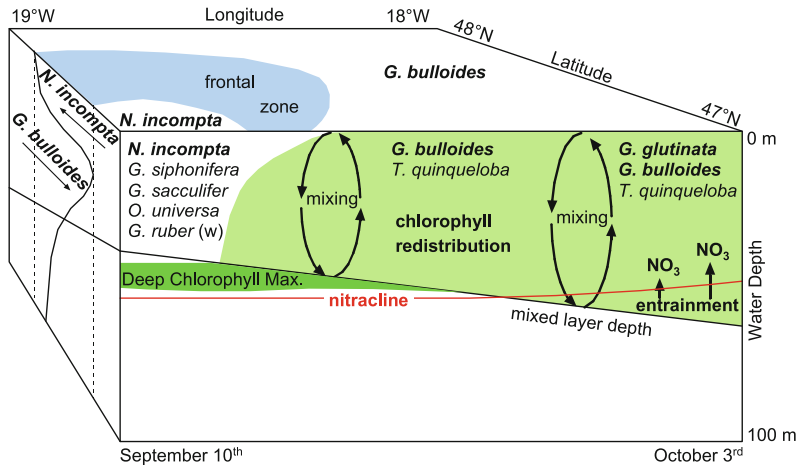
**Fig. 7.6** Schematic view of hydrographic, trophic, and faunal development in the eastern North Atlantic around 47 °N, 20 °W (BIOTRANS), between 10 September and 3 October 1996. A first change in the planktic foraminifer assemblage resulted from mixing and chlorophyll redistribution in the upper 100 m of the water column. A second change due to increased mixing depth and entrainment of nutrients from below the nutricline (incl. nutricline) followed by new phytoplankton production. As a result of chlorophyll redistribution, mainly *G. bulloides* increased in numbers. Subsequent to nutrient entrainment, *G. glutinata* proliferated (*front panel*). Depths distributions of *N. incompta* and *G. bulloides* are within the frontal area are interlocked (*side panel*). Redrawn from Schiebel et al. (2001)

different ecosystems (e.g., Deuser et al. 1981; Kroon and Ganssen 1989; Schiebel et al. 2001). At the regional and seasonal scale, the quantity and quality of food is predominantly important for the distribution of shallow- and subsurface-dwelling planktic foraminifers (Fig. 7.6). Within several days, planktic foraminifers have been shown to respond to the redistribution of chlorophyll and entrainment of nutrients by enhanced growth rates and increasing numbers of large individuals (Schiebel et al. 1995). When surface water mixing increases and the thermocline shifts to depth, for example, caused by enhanced wind stress (e.g., Schiebel et al. 1995) or induced by eddies (Kupferman et al. 1986; Beckmann et al. 1987; Fallet et al. 2011; Steinhardt et al. 2014), chlorophyll may be redistributed from the deep chlorophyll maximum and nutrients may be entrained into surface waters (Fig. 7.6). As a first consequence, the faunal portion of opportunistic species increases (e.g., *G. bulloides*). *Globigerina bulloides* is the most common morphospecies in the temperate ocean (Fig. 7.1), and has been the first planktic foraminifer species, which has been identified as indicator of trophic conditions by Thiede (1975). Subsequently, planktic foraminifer species that prefer 'fresh' prey (e.g., *Globigerinita glutinata*) proliferate, caused by entrainment of nutrients into the mixed layer and new phytoplankton (e.g., diatoms) production (Schiebel et al. 2001, 2004).

After food sources are exhausted, opportunistic species and species specialized on particular food sources decline in numbers, and a 'background fauna' displays the average regional hydrology and biogeographic zone (Schiebel and Hemleben 2000). Consequently, opportunistic species are not characteristic of distinct depth habitats and absolute temperatures but of the quantity and quality of prey, which should be considered when interpreting the isotopic composition of their tests.

Distribution and ecological demands of intermediate- and deep-dwelling species like *Globorotalia scitula*, *Globorotalia hirsuta*, and *G. truncatulinoides*, are not as well known as those of shallow-dwelling species. Deep-dwelling

species reproduce much less often (possibly as little as once per year) than shallow-dwelling species (every fortnight to once per month; Fig. 7.7). The intermediate to deep habitat is ecologically more uniform than the surface habitat, and fine scale changes in the deep planktic foraminifer distribution have not yet been sufficiently quantified. Due to their slow reaction on changing ecologic conditions, deep-living species can be used as tracers of intermediate to deep water-masses (e.g., Berger 1970b). For example, *G. truncatulinoides* probably enters the Caribbean Sea with the Subtropical Underwater through the Anegada Passage in water depths between 100 and 300 m (Schmuker and Schiebel 2002). *Globorotalia truncatulinoides* and *Globorotalia menardii* are transported within ambient water bodies by currents (e.g., Gulf Stream) over long distances (Weyl 1978), and the isotopic signature of tests is applied to the reconstruction of major current patterns, as well as life-modes of deep-living species (Mulitza et al. 1997; Spencer-Cervato and Thierstein 1997; Cléroux et al. 2007, 2009; Feldmeijer 2014).

## 7.4 Vertical Distribution in the Water Column

The vertical distribution (Figs. 7.6 and 7.7) of planktic foraminifers is affected by the distribution of prey in the same way as the horizontal, regional to global pattern (e.g., Bé 1960; Schiebel et al. 2001; Seears et al. 2012). Highest standing stocks of planktic foraminifers on the vertical scale are associated with the deep chlorophyll maximum usually sited around the seasonal thermocline and pycnocline in the upper 100 m of the water column (e.g., Fairbanks and Wiebe 1980; Schiebel et al. 2001; Field 2004). A comprehensive statistical analysis of the variable depth habitat of individual species in response to environmental and biological factors is exemplified for the subtropical NE Atlantic by Rebotim et al. (2016). Understanding the vertical distribution, i.e. depth habitat of planktic foraminifers in the water column is of crucial importance for reliable reconstruction of, for example, temperature and

primary productivity in paleoceanography (e.g., Phleger 1945; Wang 2000). The depth habitat of species has been directly determined from vertical plankton tows and the use of opening-closing nets (e.g., Bé 1962; Fairbanks et al. 1982; Hemleben et al. 1989; Schiebel et al. 1995), and indirectly from data on stable oxygen isotopes and Mg/Ca ratios of test calcite as temperature proxy, and hence relative measure of stratification and water depth at a regional scale (Fairbanks et al. 1980, 1982; Kohfeld et al. 1996; Mulitza et al. 1997; Field 2004; Cléroux et al. 2007, 2009; Hathorne et al. 2009; Groeneveld and Chiessi 2011).

Vertical distribution of planktic foraminifers in the water column is presumably affected by various biogenic effects such as (i) the need of sunlight of the symbiont-bearing, and independence from light by symbiont-barren species (e.g., Bé 1960; Vincent and Berger 1981; Seears et al. 2012; Weiner et al. 2012), (ii) ontogenetic vertical migration and reproduction at certain water depths (e.g., Hemleben et al. 1989; Bijma et al. 1990a; Schiebel et al. 1997), and (iii) the distribution and quality of prey (e.g., Schiebel et al. 2001). In addition, abiogenic environmental effects have been reported as affecting the depth distribution among which are surface water mixing and transportation of specimens caused by gales (Schiebel et al. 1995; Brunner and Biscaye 1997), and fresh water lenses impeding the ascent of individuals to surface waters (Deuser et al. 1988; Carstens and Wefer 1992; Carstens et al. 1997; Ufkes et al. 1998; Schmuker and Schiebel 2002).

Continent-derived matter affects the vertical distribution patterns of planktic foraminifers in hemipelagic regions along continental margins differently than in the pelagic ocean. Shelf seas are largely barren of living planktic foraminifers (e.g., Sousa et al. 2014), except where individuals have been transported onto the shelf by currents (cf. Bandy 1956; Berger 1970b). Test-size cohorts of species increasingly lack small (i.e. pre-adult) tests with decreasing water depth when approaching the continent (Retailleau et al. 2011). The lack of small test, and fragmentation of assemblages in comparison to deep marine test-size cohorts (e.g., Peeters et al. 1999; Schiebel and Hemleben 2000) is interpreted to be
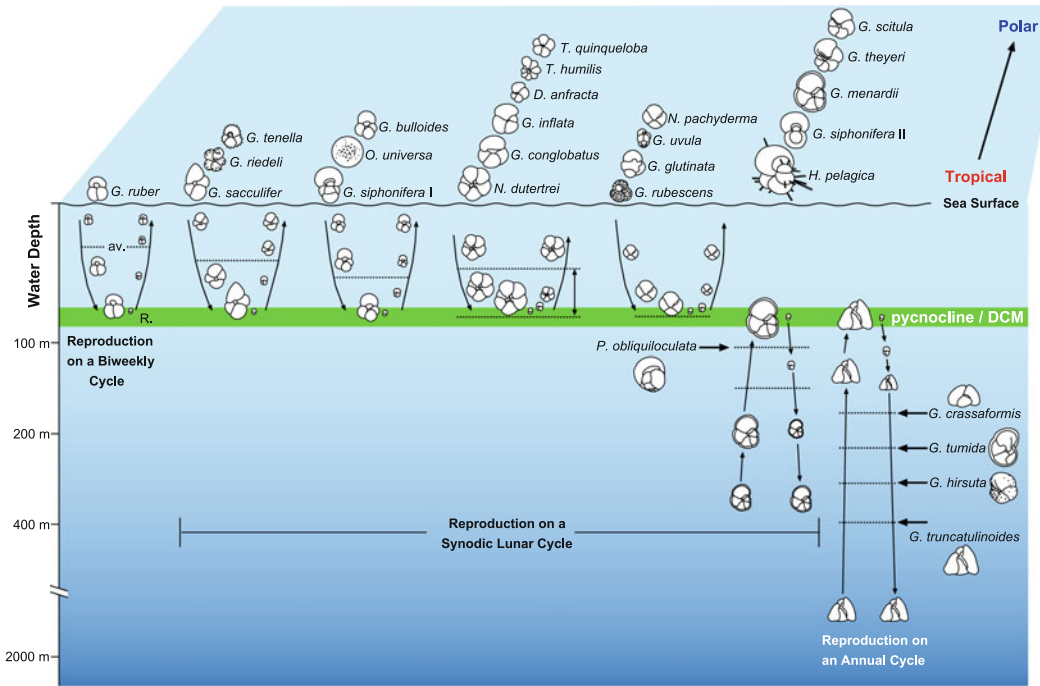
**Fig. 7.7** Idealized scheme of planktic foraminifer depths habitats and life cycle in the pelagic ocean. The average water depth inhabited by planktic foraminifers (av., *stippled horizontal lines*) varies at the species level. Different foraminifer species inhabit average water depths ranging from the upper 10 m to 400 m, and *G. truncatulinoides* dwells in extreme depths down to 2000 m. Dwelling depths result from ecologic conditions and biologic prerequisites, and affect relative depths of different species rather than absolute water depths. For example, the average dwelling depth of *G. ruber* (*white*, sensu lato, s.l.) usually ranges above the pycnocline; depending on hydrographical conditions, the depth-distribution of any *G. ruber*-type may be within reach of the pycnocline. Symbiont-bearing species depend on light and live in the euphotic zone of the ocean. Symbiont-barren species may settle in deep waters below the euphotic zone. Planktic foraminifers reproduce (R.) at species-specific depth relative to the pycnocline (i.e. seawater density), and distinct temperature and salinity conditions. Enhanced availability of prey at the deep chlorophyll maximum (DCM, associated with the pycnocline) provides trophic conditions, which support the survival of juveniles. In the *upper panel*, species are arranged according to their relative latitudinal position. *Globigerinoides ruber* is known to reproduce twice per month. *Globigerina bulloides*, *G. sacculifer*, *N. pachyderma*, *T. quinqueloba*, *H. pelagica,* and other shallow-dwelling species reproduce on a synodic lunar cycle. An annual reproduction cycle is assumed for *G. truncatulinoides*, and may be similar in other deep-dwelling species. After Schiebel and Hemleben (2005)

an indication of changing ecological conditions. River discharge from the continent affects surface salinity and trophic conditions in neritic and hemipelagic waters, which may not provide the ecological needs of planktic foraminifers (Retailleau et al. 2009). Those planktic foraminifers individuals expatriated to hemipelagic waters may still grow in size but may not reproduce. The depth-distribution of species may differ from that in pelagic waters. Subsurface dwelling *G. scitula* (Itou et al. 2001, NW Pacific; see also Schiebel et al. 2002a, NE Atlantic; see also Oberhänsli et al. 1992) were found to dwell in surface waters in the hemipelagic SE Bay of Biscay (Retailleau et al. 2011), and to the NE off the Congo River mouth (R. Schiebel, unpublished data). In addition to other offshore-onshore effects, tidal currents and local upwelling over the shelf-break and submarine canyon heads are discussed as sites of enhanced primary production, and to foster the production of opportunistic planktic foraminifer species like *G. bulloides*

(Brunner and Biscaye 2003; Machain-Castillo et al. 2008; Retailleau et al. 2012).

## 7.5 Diurnal Vertical Migration

Diurnal changes in depth habitat have been suspected of various planktic foraminifer species (e.g., Boltovskoy 1973, and references therein; Bé 1960; Bé and Hamlin 1967; Berger 1969; Holmes 1982). Rhumbler (1911) already presumed higher abundances of planktic foraminifers in day tows than in night tows (see also Bradshaw 1959; Bé 1960). However, systematic diurnal changes in dwelling depth could not yet be deduced from assemblage data. Depth-related distribution patterns have been attributed to heterogeneity, i.e. patchiness, which is best explained by differences in the spatial rather than temporal variability (cf. Boltovskoy 1971; Siccha et al. 2012).

Diurnal changes in dwelling depth are difficult to prove because any (sub-) diurnal migration pattern could be overlain and masked by other periodic changes such as depths changes of individuals over a reproduction cycle (e.g., Schiebel et al. 1997), local episodic events like storms (Schiebel et al. 1995), and transportation of planktic foraminifers within surface water masses by currents (Kupferman et al. 1986; Schiebel and Hemleben 2000). In addition, relations between grazers and prey, as well as parameters, which affect the absolute abundance of species during reproduction, both of which potentially affecting the depth distribution of species, so far remain unanswered.

Planktic foraminifers may be capable of limited active vertical migration by changing the quantity of lipids in their cytoplasm, and through activity of fibrillar bodies (see Chap. 3), to a yet unknown degree (Hansen 1975; Anderson and Bé 1976a, b). Individuals are presumed to migrate up and down the water column to occupy species-specific depth habitats predominantly for reproduction and alimentation at a synodic lunar cycle (i.e. two to four weeks on average, see Sect. 5.2), they can possibly not undertake active vertical diurnal migration over tens of meters like

other zooplankton and phytoplankton (cf. Boltovskoy 1973; Riley 1976; Holmes 1982; Ralston et al. 2007).

Evidence of systematic though passive diurnal change in the depth habitat of planktic foraminifers is provided by analyses of floating sediment traps (Siccha et al. 2012). The kilometer-scale and sub-diurnal variability of planktic foraminifer distribution in the surface water column in the central Bay of Biscay was sampled in spring 2009, using drifting sediment traps deployed at 200 m depth for three consecutive intervals between April 7 and 19, 2009. The hydrodynamic bias and its effects on the sampling efficiency, trap track, and sample composition (incl. species-specific size distributions) were carefully checked for sampling artefacts, and autocorrelation of the planktic foraminifer flux at distances <2 km could not be attributed to the temporal domain. Significant negative autocorrelation of the distribution of the total live foraminifer assemblage, as well as of living *G. scitula*, was detected for intervals of 2 km and 6 h, following the temporal signal of the internal tide in the Bay of Biscay. *Globorotalia scitula* is particularly well suited to detect depth changes in this study, because its average depth-habitat between 100 and 300 m (e.g., Erez and Honjo 1981; Ortiz et al. 1995) is bracketing the deployment depth of the sediment traps. Accordingly, the distribution of *G. scitula* indicates passive (non-selective for size!) diurnal displacement of assemblages by internal tidal waves rather than active individual depths migration (Siccha et al. 2012).

## 7.6 Test Size

Planktic foraminifer test size provides information on (paleo-) ecological conditions of the ocean (Figs. 7.8 and 7.9). Test-size analyses have been pursued since the early works of Ericson (1959) and Hecht (1976), following the ideas of Bergmann's (1847) rule relating body size to temperature, and hence ecogeography. Whereas ecological effects on body size are obvious (e.g., Bergmann 1847), the multiple factors that may affect foraminifer test size are difficult to
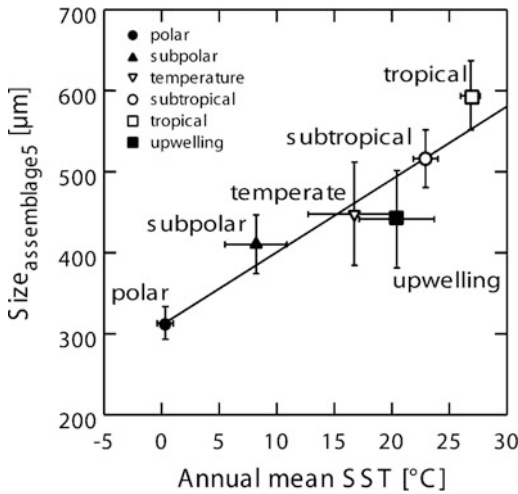
**Fig. 7.8** Average test size (μm) of the largest 5 % of specimens from samples (Size$_{assemblage5}$) per biogeographic area, plotted against annual average sea surface temperature (SST, data from Levitus et al. 1994). Error bars give the 95 %-confidence intervals. Linear regression, r = 0.938, *p* = 0.006). From Schmidt et al. (2004a).



**Fig. 7.9** Relationship of sea surface temperature (data from Levitus et al. 1994), maximum test size, and maximum (max.) relative abundance of single taxa (r$^2$ = 0.928, *p* = 0.001) in surface sediments (data from Prell et al. 1999). Note that *G. inflata* and *G. bulloides* have two optima both in size and abundance, possibly displaying varying ecological demands of different genotypes at the regional scale (cf. Darling and Wade 2008; Morard et al. 2011; André et al. 2014). *N. pachyderma* (sinistral coiled test) is signified by (*s*), and dextral *N. pachyderma* (i.e. *N. incompta*) by (*d*). From Schmidt et al. (2004a)

disentangle (Schmidt et al. 2006, and references therein). Over long time-intervals, evolutionary effects should be considered. The test size of species may increase over evolutionary time following Cope's rule (Stanley 1973; Schmidt et al. 2006). Mixing of fossil assemblages may result in test-size changes, which cannot be explained by evolution and ecological effects alone. When interpreting fossil assemblages, taphonomic effects including differential sedimentation and preservation of tests need to be taken into account (see Chap. 8). Fortunately, planktic foraminifers occur in large standing stocks and usually at sufficient numbers of ubiquitous species in above-CCD sediments over the past 100 million years, and serve as model organisms (among others) in deciphering relationships of body size, environment, and evolution (Schmidt et al. 2004b).

The modern ocean hosts some of the largest planktic foraminifers of all times (Schmidt et al. 2004b), resulting in high modern calcite flux and burial rates of foraminifer CaCO$_3$ (Schiebel 2002). Climate warming since the 1970s is assumed to still enhance planktic foraminifer calcite production (Field et al. 2006). Largest
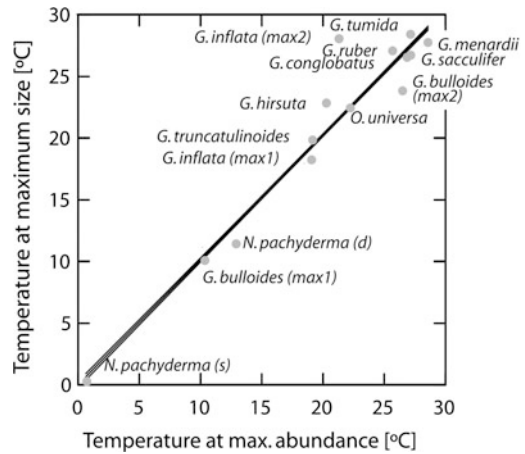
assemblage test-size in the modern ocean occurs at tropical and subtropical latitudes, and smallest test assemblages characterize high-latitude waters (Fig. 7.8). Given that most planktic foraminifer species occur over wide temperature and salinity ranges, and associated environmental parameters (Bé and Tolderlund 1971; Hemleben et al. 1987; Lombard et al. 2009, 2011), the positive correlation of maximum average test size and abundance with surface water temperature at the global scale is possibly significant (Fig. 7.9).

The latitudinal distribution pattern of planktic foraminifers is disrupted by currents and hydrographic fronts (Fig. 7.10a), including regional hydrographic features such as upwelling cells (e.g., Schiebel et al. 2001; Schmidt et al. 2004a, b). Hydrographic fronts presumably negatively affect test size, in addition to an overall negative affect on planktic foraminifer diversity (Ottens and Nederbragt 1992). Upwelled waters are colder than surrounding surface waters, comprise more macronutrients, and hence produce more food for
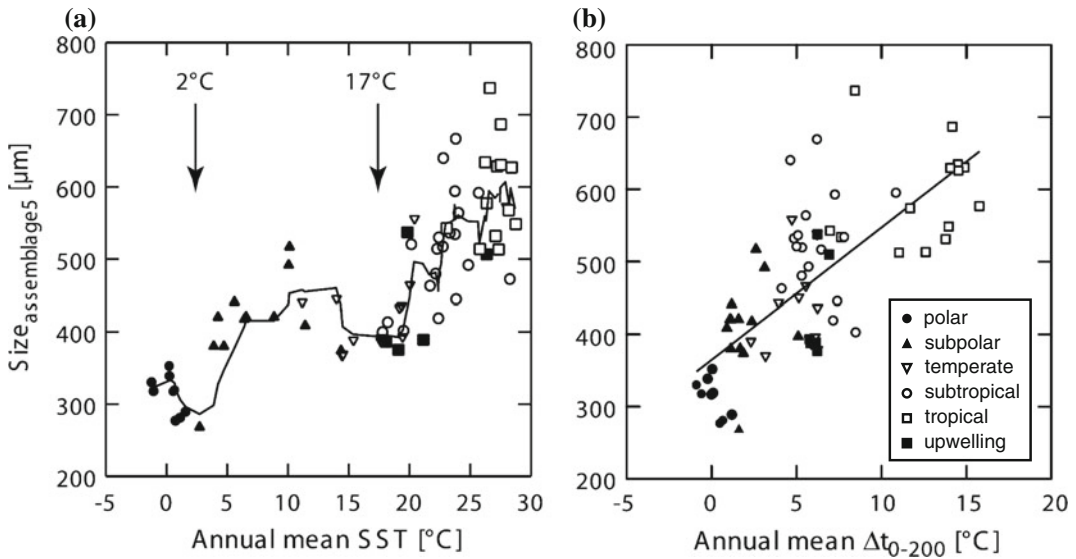
**Fig. 7.10** Average test size (μm) of the largest 5 % of specimens ($Size_{assemblage5}$) from Holocene sediment samples plotted against (*a*) mean annual sea surface temperature (SST [°C]). The areas of minimum size (*arrows*) at 2 °C and 17 °C correspond to the polar and the subtropical fronts, respectively. (*b*) Surface water stratification, given as the difference between mean annual SST and temperature at 200 m water depth ($\Delta T_{0-200}$). Small and large assemblage test sizes occur at weak (e.g., upwelling) and strong (e.g., central subtropical gyres) annual mean surface water stratification, respectively. Accordingly, planktic foraminifer test size indicates regional surface ocean stratification, and consequently of trophic conditions. The *black line* represents the five-point moving average in panel (*a*) and the regression line in panel (*b*). The legend relates to both panels (*a*) and (*b*). Temperature data from Levitus et al. (1994). Modified after Schmidt et al. (2004a)

planktic foraminifers. Due to enhanced biological productivity, upwelled waters are more turbid than lower productive waters, which favors small-sized symbiont-barren opportunists like *G. bulloides*, whereas larger symbiont-bearing generalist species like *G. sacculifer* are disadvantaged and hence less frequent, which results in an overall decreased test size and diversity. In contrast, low productivity in well-stratified surface waters, for example, in the subtropical gyres favors large-sized symbiont-bearing species (Figs. 7.8, 7.9 and 7.10b). Whereas primary production and the availability of freshly produced food (see Sect. 4.1) in surface waters affect the size of surface dwelling planktic foraminifer species and assemblages, subsurface dwelling species are affected by the flux of more or less degraded organic matter arriving at depth (e.g., Itou et al. 2001). Subsurface dwelling foraminifers, including predominantly globorotalid species, produce rather large-sized tests (at rather low water temperature), which might in part be caused by their longer life cycle in comparison to shallow-dwelling species, as well as by their generalist (K-selected) behavior.

The effect of ecology on test size is applied as a proxy of a variety of physical and chemical marine parameters as well as alimentation at the regional scale, and over the recent geological past. The largest sized tests of *G. ruber* in the eastern Mediterranean during the Holocene occurred during the formation of Sapropel S1, and far from optimum ecological conditions (Mojtahid et al. 2015). Decreased surface water salinity during S1 apparently caused a descent of the symbiont-bearing *G. ruber* to deeper waters (Deuser et al. 1988; Schmuker and Schiebel 2002; Rohling et al. 2004). Less favorable light-conditions and hence decreased symbiont activity at depth, in combination with decreased salinity, may have caused the production of smaller tests (Hemleben et al. 1989, and

references therein). The opposite reaction, i.e. the production of larger tests may be explained by delayed reproduction and prolonged maturity, resulting in longer individual growth and larger tests (Mojtahid et al. 2015).

The life of adult planktic foraminifer individuals is most often terminated by reproduction (see Chap. 5), after which the empty tests settle to depth through the water column, and, if not dissolved, form part of the sedimentary assemblage. Accordingly, sediment assemblages are biased towards the largest test-size attained by any species. In addition to individuals that have completed their life cycle by reproduction, smaller prematurely deceased individuals contribute to the sediment assemblages. Taking into account the usually log-normal size-distribution of planktic foraminifer species assemblages (Peeters et al. 1999; Schiebel and Hemleben 2000; Schmidt et al. 2006, and references therein), about half of the adult individuals are lost between the smaller size-class and the next larger size-class. Premature death may be caused by horizontal or vertical expatriation by currents (Berger 1970b; Vincent and Berger 1981; Schiebel et al. 1995) to waters, which provide suboptimal ecological conditions, for example, concerning the quality and quantity of food (cf. Schiebel et al. 2001), light attenuation (Bé et al. 1982, only in symbiont-bearing species), and salinity (cf. Bijma et al. 1994). Consequently, only specimens, which have completed their ontogenetic development (see Chap. 6) count towards the 'maximum size' proxy in paleo-ecological analyses (Schmidt 2002). In contrast, growth rate, survival rate and premature mortality, and the ratio of pre-adult tests of a certain species in sediment assemblages could serve as measure of expatriation and ecological change during the life of a planktic foraminifer.

## 7.7 Summary and Concluding Remarks

Ecological parameters affect production and distribution of planktic foraminifers (e.g., test calcite and biomass) at the species and assemblage level. Consequently, foraminifer tests are indicators of modern and past environmental change and carbon turnover. Unfortunately, the understanding of planktic foraminifer ecology remains fragmentary although first ideas date back to the late 19th and early 20th century (Murray 1897; Rhumbler 1911), and first targeted programs have been conducted from the 1950s (e.g., Bradshaw 1959; Bé 1960). The understanding is fragmentary by nature, since plankton tow samples of living specimens, and sediment trap samples of the test flux represent only temporal and local snap-shots of the population dynamics, Continuous Plankton Recorder (CPR) hauls only include a narrow depth-layer of the ocean. Laboratory cultures facilitate continuous observation over short intervals of time, but cannot entirely simulate ecological conditions of the natural habitat of planktic foraminifers, which embraces at least the upper 50 m of the water column, and includes a natural composition of prey, which may not be provided artificially. In addition, climate constantly changes at the regional to global scale, including ecological conditions at their entity. Consequently, a combination of the above given approaches needs to be pursued to better understand the production of planktic foraminifers. More complete monitoring programs, and reinforced concerted efforts of the international community of data producers (i.e., sampling, culturing, and modeling) should lead to a better understanding of foraminifers as qualitative and quantitative proxies of the changing climate and ocean.

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