



Planktic foraminiferal production along an offshore–onshore transect in the south-eastern Bay of Biscay

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ABSTRACT

The distribution of planktic foraminifera from the continental slope onto the shelf of the south-eastern Bay of Biscay is discussed in relation to environmental factors. Samples were obtained between March and November, 2006–2008, along a bathymetric transect from 2000 to 145 m water depth, from 50 km off the shelf-break onto the outer shelf. Live specimens and empty tests (> 100 μm) were collected with vertical plankton tows from the sea surface to a maximum water depth of 700 m, and temperature, salinity, oxygen concentration, and fluorescence/chlorophyll-*a* concentration were recorded. Additional data on chlorophyll-*a* concentration and sea surface temperature were derived from satellite imagery (Aqua MODIS and SeaWiFS). Planktic foraminifera were most abundant in the upper 80 m of the water column at all locations, with decreasing numbers towards the coast in March, April, and June. In November, maximum numbers of live specimens occurred at the outer shelf location. In July, planktic foraminiferal standing stocks were low throughout the sampling area.

Chlorophyll-*a* concentration (i.e., food) and fresh water input were found to affect the abundance of planktic foraminifera along the transect; however we found no influence of water depth or proximity to the shelf.

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1. Introduction

Planktic foraminifera have been ubiquitous in the open oceans for about 100 million years. Planktic foraminifera are one of the most frequently applied microfossil groups in paleoceanography and the reconstruction of past environmental changes, due to their wide distribution and high sensitivity to sea surface parameters. Their calcareous tests record geochemical information about the ambient seawater such as temperature, salinity, and trophic state of surface waters. Many major open oceanic environments have been analysed for the seasonal and spatial distribution of modern planktic foraminifera, contributing to a

broad understanding of the ecology of planktic foraminifera (e.g., Bé, 1960, 1977; Bé and Tolderlund, 1971; Tolderlund and Bé, 1971; Bé and Hutson, 1977; Fairbanks and Wiebe, 1980; Fairbanks et al., 1982; Bé et al., 1985; Hemleben et al., 1989; Schiebel and Hemleben, 2005, and references therein).

It is generally assumed that planktic foraminifera do not inhabit shelf seas (e.g., Hemleben et al., 1989). Planktic foraminiferal (PF) tests are present in the sediments of marginal seas, though, and are believed to result from specimens that were transported by currents from their live habitats (Arnold and Parker, 1999). Only few studies have been published on planktic foraminifera from marginal environments by, for example, Saidova (1957, Sea Okhotsk), Lipps and Warne (1966, Sea Okhotsk), Parker (1973, Gulf of California), Wang et al. (1985, East China Sea), and Brunner and Biscaye (2003, Middle Atlantic Bight). Previous investigations on planktic foraminifera in the Bay of Biscay were carried out on sediment assemblages collected by grab sampling and gravity cores (Caralp, 1968; Pujol, 1980), and planktic foraminifera were analysed as part of the total zooplankton community (determined at a phylum level) collected with plankton tows (Albaina and Irigoien, 2007).

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We discuss the distribution of planktic foraminifera along a depth transect in the south-eastern Bay of Biscay, from the mesobathyal continental slope onto the outer shelf. Production of planktic foraminifera in the upper water column (0–700 m water depth) is discussed as a response to changing environmental conditions during a seasonal succession. The aim of this study is to contribute to a better mechanistic understanding of the spatial and seasonal distribution of planktic foraminifera in marginal marine environments. This project contributes to the French FORCLIM project, targeted at an improved understanding of planktic foraminifera as proxies of paleohydrology of the North Atlantic (Howa et al., 2007).

2. Oceanographic setting

The Bay of Biscay is a semi-enclosed basin in the transitional eastern North Atlantic (Fig. 1). The general circulation in the central area of the Bay of Biscay is characterised by weak cyclonic surface circulation (Koutsikopoulos and Le Cann, 1996), and cyclonic and anticyclonic eddies (Fig. 1; SWODDIES, Slope Water Oceanic Eddies; Pingree and Le Cann, 1992). Along the continental slope, currents are mainly oriented poleward (Pingree and Le Cann, 1990). The warm and salty Navidad Current penetrates the southern part of the Bay of Biscay from the Portuguese margin (warm water extension of the Iberian Poleward Current in the Bay of Biscay) particularly during winter (Pingree and Le Cann, 1990; Garcia-Soto et al., 2002; Le Cann and Serpette, this issue).

Below the surface mixed layer, eastern North Atlantic Central Water (ENACW) is present down to 600 m water depth. Between about 600 and 1300 m, Mediterranean Outflow Water (MOW) is characterised by relatively high salinity and low oxygen concentration (van Aken, 2000). Northeast Atlantic Deep Water (NEADW) occurs from 1300 to 3000 m water depth (e.g., Durrieu et al., 1999).

The SW French continental shelf is characterized by freshwater input from the Gironde and Adour rivers (Fig. 1). The Gironde has an average annual flux of $1100 \text{ m}^3 \text{ s}^{-1}$ with a seasonal maximum runoff of $\sim 5000 \text{ m}^3 \text{ s}^{-1}$ in February, $\sim 3250 \text{ m}^3 \text{ s}^{-1}$ in spring, and a minimum of $\sim 100 \text{ m}^3 \text{ s}^{-1}$ in summer (Schäfer et al., 2002). The Adour river has a mean discharge of $350 \text{ m}^3 \text{ s}^{-1}$ (Brunet and Astin, 1999). The Adour and other rivers draining the Pyrenees are expected to have a high seasonal variability in runoff (Coynel et al., 2005). Peak flow may exceed $1000 \text{ m}^3 \text{ s}^{-1}$ during few days in winter and spring (Gil and Sanchez, 2000). In general, the fresh water plumes of both Gironde and Adour rivers flow northwards along the coast, but winds may force plumes to the south (Froidefond et al., 1996, 2002; Puillat et al., 2004). Increased water discharge of the Gironde and Adour rivers may cause significant increase of nutrients triggering primary productivity in waters of the Bay of Biscay (Puillat et al., 2004; Kelly-Gerrey et al., 2006).

In the Bay of Biscay, thermal stratification occurs between May and mid September, resulting in a pycnocline at about 50 m depth, whereas the upper water column between January and the beginning of April is completely mixed (Puillat et al., 2004, and references therein). During mid September to December, progressive erosion of the thermocline is caused by wind-driven mixing of the surface ocean. Stratification as a result of river runoff and freshwater input peaks between March and June. In fall, stratification decreases because of decreased river discharge and increased wind-driven mixing (Puillat et al., 2004).

Chlorophyll-*a* concentration is highest in March, April, September, and October in the Bay of Biscay (Fernandez et al., 1991). During stratified periods, maximal chlorophyll-*a* concentration is recorded at the bottom of the euphotic zone near the pycnocline (Laborde et al., 1999). During winter, wind-driven mixing causes deepening of the seasonal pycnocline, and nutrient concentrations in surface waters increase progressively (Tréguer et al., 1979).

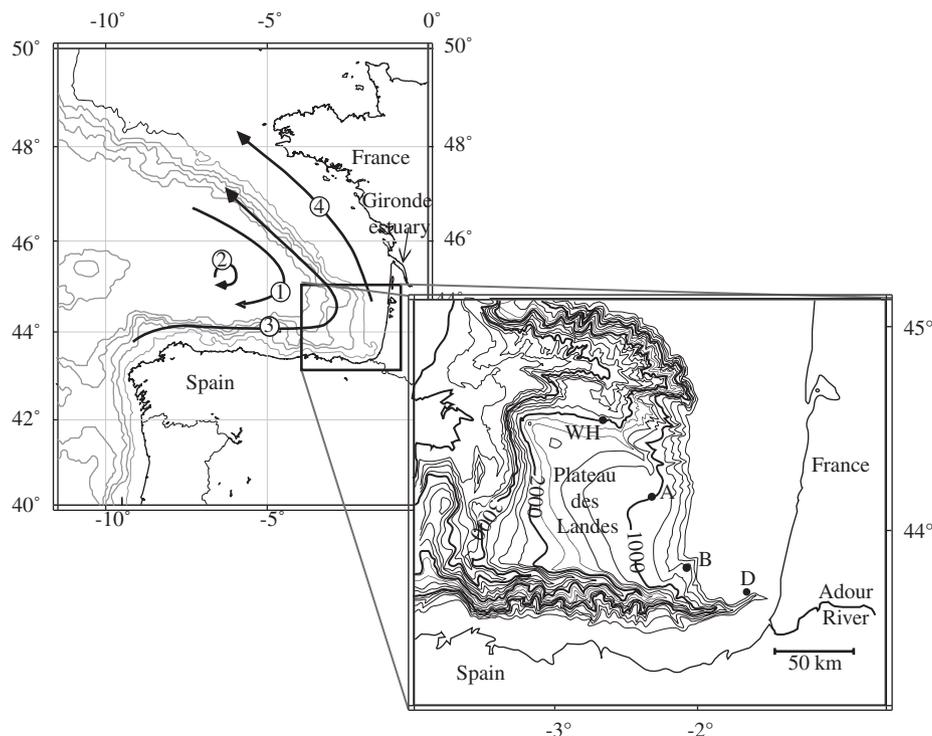


Fig. 1. Sampling Stations WH, A, B, and D (black dots) at the Plateau des Landes, slope and outer shelf at the southern Bay of Biscay. Overview shows the general hydrology (Koutsikopoulos and Le Cann, 1996): (1) general oceanic circulation, (2) eddies, (3) Navidad Current, warm water extension of the Iberian Poleward Current in the Bay of Biscay (Pingree and Le Cann, 1990; Garcia-Soto et al., 2002), and (4) shelf residual circulation.

3. Ecological setting and plankton succession

The Bay of Biscay belongs to the Northeast Atlantic Shelf Provinces, and is affected by seasonal variability (Longhurst, 1998). In winter, waters are rich in nutrients, but light limitation leads to low plankton productivity (Obata et al., 1996). In spring, high nutrient concentrations and increasing light levels facilitate new phytoplankton production (Tréguer et al., 1979). In early summer, thermal stratification of the upper water column causes low nutrient concentration, and local new production occurs along hydrographic fronts (Wollast and Chou, 2001; Lunven et al., 2005). In fall, increased mixing and nutrient entrainment into surface waters cause another period of increased plankton production (Marquis et al., 2007). Consequently, phytoplankton assemblages in the Bay of Biscay change on a seasonal scale (Tréguer et al., 1979; Lampert, 2001).

Prymnesiophytes (mainly coccolithophores) are often the dominant group of phytoplankton in the Bay of Biscay (Beaufort and Heussner, 1999; Wollast and Chou, 2001). Coccolithophores are present throughout the year and exhibit a seasonal succession (Beaufort and Heussner, 1999; Lampert, 2001). In summer, minor upwelling events (Froidefond et al., 1996) lead to large coccolithophore blooms (Holligan et al., 1983; Fernandez et al., 1991; Beaufort and Heussner, 1999). In comparison to coccoliths, the abundance of diatoms, dinoflagellates, and silicoflagellates exhibits strong seasonal variation. Diatoms are most abundant during the spring phytoplankton bloom (Lampert, 2001; Wollast and Chou, 2001) with significant secondary peaks during winter (Beaufort and Heussner, 1999). Diatoms may profit from riverine freshwater input into the Bay of Biscay (Fernandez et al., 1991). In fall, sporadic but intense dinoflagellate blooms are described by Lavender et al. (2004). Maximum silicoflagellate numbers were observed between January and May, i.e., winter and spring (Beaufort and Heussner, 1999).

4. Materials and methods

In order to investigate the planktic foraminiferal distribution in the south-eastern Bay of Biscay, four sites were sampled along a transect from 145 to 2000 m water depth, from the shelf-break to the Plateau des Landes (Fig. 1). Samples were obtained during five cruises with the R/V Côte de la Manche in June 2006, April and November 2007, and March and July 2008 (Table 1).

During cruises PECH 1, PECH 3, and PECH 6, WP2 plankton nets (Research Equipment, KC Denmark A/S) with an opening of 0.255 m² were used for sampling. On the third and fourth sampling campaigns (PECH 4 and PECH 5), a Hydrobios MultiNet[®] type MIDI (0.25 m² opening) equipped with five nets was used. All hauls were carried out with 100 µm nets. Samples were collected from the same water depth intervals on all five cruises down to

100 m depth at 20-m sampling intervals (0–20–40–60–80–100 m), and 700 m at 100 and 200 m intervals (100–200–300–500–700 m) depending on total water depth. Sampling was carried out at 0.2–0.3 ms⁻¹ haul velocity with the different towing systems. Sampled volumes of water were calculated from data recorded with a digital flow meter attached to the plankton nets. Simultaneously, temperature and salinity were recorded with a Sea-bird's 911plus CTD, attached to a rosette water sampler SBE32 equipped with oxygen and fluorescence sensors. Chlorophyll-*a* was analysed from distinct water depths to calibrate fluorescence data. In November 2007 (PECH 4), temperature, salinity, and fluorescence were recorded with sensors attached to the Hydrobios multinet at Stations B and D.

To show the temporal development of sea surface temperature (SST) and chlorophyll-*a* concentration at the sampling area between January 2006 and August 2008, SeaWiFS and Aqua MODIS imagery (<http://oceancolor.gsfc.nasa.gov>) was analysed (Fig. 2). Eight day means of SST from Aqua MODIS images and chlorophyll-*a* concentration from SeaWiFS images were processed for a 1° × 1° area at Station WH (Fig. 2). Chlorophyll-*a* data were not available from SeaWiFS for January 2008 to March 2008, and data from Aqua MODIS were analysed from this time interval.

Plankton samples were stained on board with Rose Bengal (1.0 mg l⁻¹ ethanol) in order to discriminate living foraminifera from dead specimens (Lutze and Altenbach, 1991) and soaked in 95% alcohol for preservation. Stained tests were assumed cytoplasm-bearing and living at the time of sampling. Unstained tests were assumed empty during the time of sampling and referred to as dead specimens. In the laboratory, samples were wet sieved into size classes of 100–150 µm and > 150 µm. All planktic foraminiferal tests were picked from the wet samples and counted.

5. Environmental conditions during sampling

Different hydrographic situations with respect to surface water stratification were encountered during sampling. In summer, surface waters were well stratified, displayed by large temperature differences in the upper 100 m of the water column (Fig. 3). Maximum stratification of the upper water column was developed in June and July with maximum surface water temperatures around 21 °C, and a ~7–9.5 °C decrease in temperature in the upper 100 m (Fig. 3, Appendix A). Pycnocline depth was ~50 m at Station WH shoaling to ~30 m at Station D (Appendix A). In March, April, and November sea surface temperatures ranged around 13–14 °C, with less than ~2 °C temperature decrease in the upper 100 m (Fig. 3). In March, surface waters were completely mixed at the hemipelagic Stations WH and A (Fig. 1, Appendix A).

Decreased surface water salinities were observed at all stations, and most pronounced at Stations D and B closest to the

Table 1

Location of net tows during the five PECH sampling campaigns at Station WH, A, B, and D, in the Plateau des Landes area, south-eastern Bay of Biscay.

Station	WH	A	B	D
Latitude	44°33'N	44°10'N	43°50'N	43°42'N
Longitude	2°45'W	2°20'W	2°03'W	1°34'W
Water depth (m)	2000	1000	550	145
Distance from coast (km)	115	79	52	12
Distance from shelf break (km)	50	23	2	–1
PECH 1	22/06/2006	23/06/2006	24/06/2006	25/06/2006
PECH 3	15/04/2007	16/04/2007	16/04/2007	17/04/2007
PECH 4	25–28/11/2007	28/11/2007	29/11/2007	29/11/2007
PECH 5	2/03/2008	2/03/2008	3/03/2008	3/03/2008
PECH 6	8/07/2008	9/07/2008	10/07/2008	11/07/2008

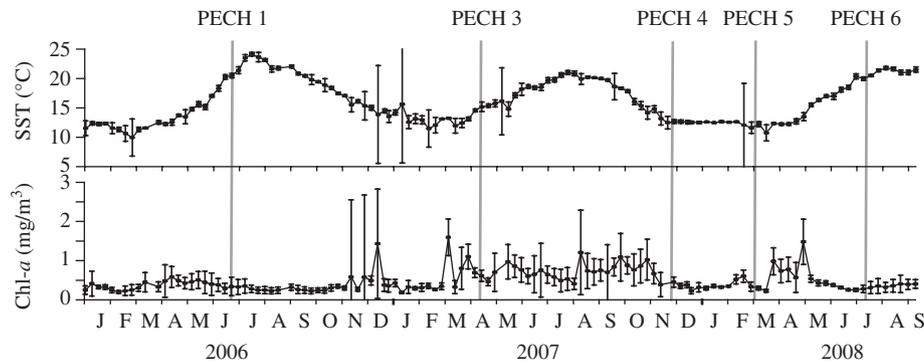


Fig. 2. Sea surface temperature (SST) and chlorophyll-*a* processed from SeaWiFS images of the Bay of Biscay from January 2006 to September 2008. Data represent averages of a 1° square area at Station WH (44–45°N, 2–3°W).

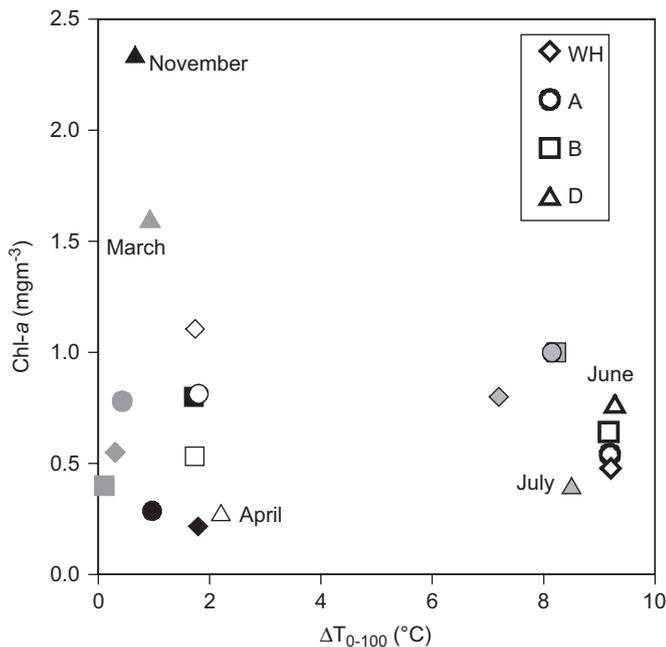


Fig. 3. Temperature difference between the water surface and 100 m water depth (ΔT_{0-100}) as a measure of stratification of the upper water column, with strong stratification at large ΔT_{0-100} and a well mixed water column at small ΔT_{0-100} .

coast (Fig. 1). At Station D, surface water salinity was decreased by at least 0.5–1 PSU during all sampled seasons, and was as low as 29.8 PSU in April 2007 (Appendix A). At 100 to ~500 m water depth, salinity was less variable than in surface waters. Increased salinity and decreased oxygen concentration occurred below 500 m water depth (Appendix A).

Chlorophyll-*a* concentration was highest around the pycnocline, between 20 and 60 m depth in April, June, and July (up to $\sim 1 \text{ mg m}^{-3}$) (Appendix A). In November and March, maximum chlorophyll-*a* concentration was observed between the sea surface and 15 m water depth at Station D close to the shelf-break (up to $\sim 1.7 \text{ mg m}^{-3}$). Lowest chlorophyll-*a* concentration in surface waters occurred during November ($< 0.3 \text{ mg m}^{-3}$) at the hemipelagic Stations WH and A (Fig. 3). High mesoscale variability of chlorophyll-*a* concentration during times of generally high local chlorophyll-*a* concentration (Appendix A) is displayed by large standard deviation of the chlorophyll-*a* data deduced from satellite imagery (Fig. 2). Regional and interannual variability of chlorophyll-*a* concentration and distinct seasonal changes in SST at the southern Bay of Biscay are encompassed by our sampling intervals, though the most extreme conditions were possibly not captured (Fig. 2).

6. Distribution of planktic foraminiferal standing stocks and empty tests

6.1. Distribution of cytoplasm-bearing tests

In general, standing stocks decreased from the open marine site towards the shelf, and from early spring to summer (Figs. 4 and 5). Living PF ($> 100 \mu\text{m}$) were most frequent in the upper 60–80 m of the water column at all four sampling locations and during all sampling periods (Fig. 4).

In April 2007, standing stocks decreased from the hemipelagic Station WH (545 specimens m^{-3}) towards the shelf-break (Station D, 82 specimens m^{-3}) (Fig. 5 and Appendix B). Living specimens were frequent down to 300 m depth at all three deep-water Stations WH, A, and B. Maximum numbers of 205 specimens m^{-3} occurred in the upper 20 m at Station WH. In June 2006, PF were less frequent in surface waters than in April 2007, and living specimens were abundant between 80 and 500 m depth (Fig. 4). Total numbers of living PF decreased following the same gradient from the deep-water Station WH (190 specimens m^{-3}) towards shelf-break Station D (30 specimens m^{-3}) (Fig. 5). In July, standing stocks were very low at all four sampling locations (2–16 specimens m^{-3}) (Appendix B). In November 2007, PF were most abundant in the upper 100 m, and only few living specimens occurred below 100 m depth ($< 9\%$ of the total standing stock). Total FP numbers were low at Station WH and B (< 23 specimens m^{-3}), and as high as 183 specimens m^{-3} at Station D (Figs. 4 and 5).

6.2. Distribution of cytoplasm-bearing tests in relationship to environmental parameters

In general, the abundance of living PF in surface waters was related to chlorophyll-*a* concentration and sea surface salinity (Fig. 4). On a regional scale, highest abundance of living PF at offshore Station WH in April, at Station A in March and at onshore Station D in November (Fig. 4), was positively related to surface water chlorophyll-*a* concentration (Fig. 8). During March, April, and June, maximum PF abundance occurred at water depths of maximum chlorophyll-*a* concentration (Fig. 4). At times and locations of strongly decreased sea surface salinity (< 35 PSU, i.e., more than 0.5 PSU lower than at subsurface waters), PF numbers were low despite high chlorophyll-*a* concentration at pycnocline depth (Fig. 4). Exceptionally low numbers of living PF at 20–40 m at Station B (Fig. 4, March) coincided with large numbers of jellyfish. Low abundance of living PF at Station WH in November coincided with high densities of salps in the upper 100 m of the water column.

Small specimens (100–150 μm) were most abundant ($> 50\%$ of the total fauna $> 100 \mu\text{m}$) at the three deep-water Stations WH, A,

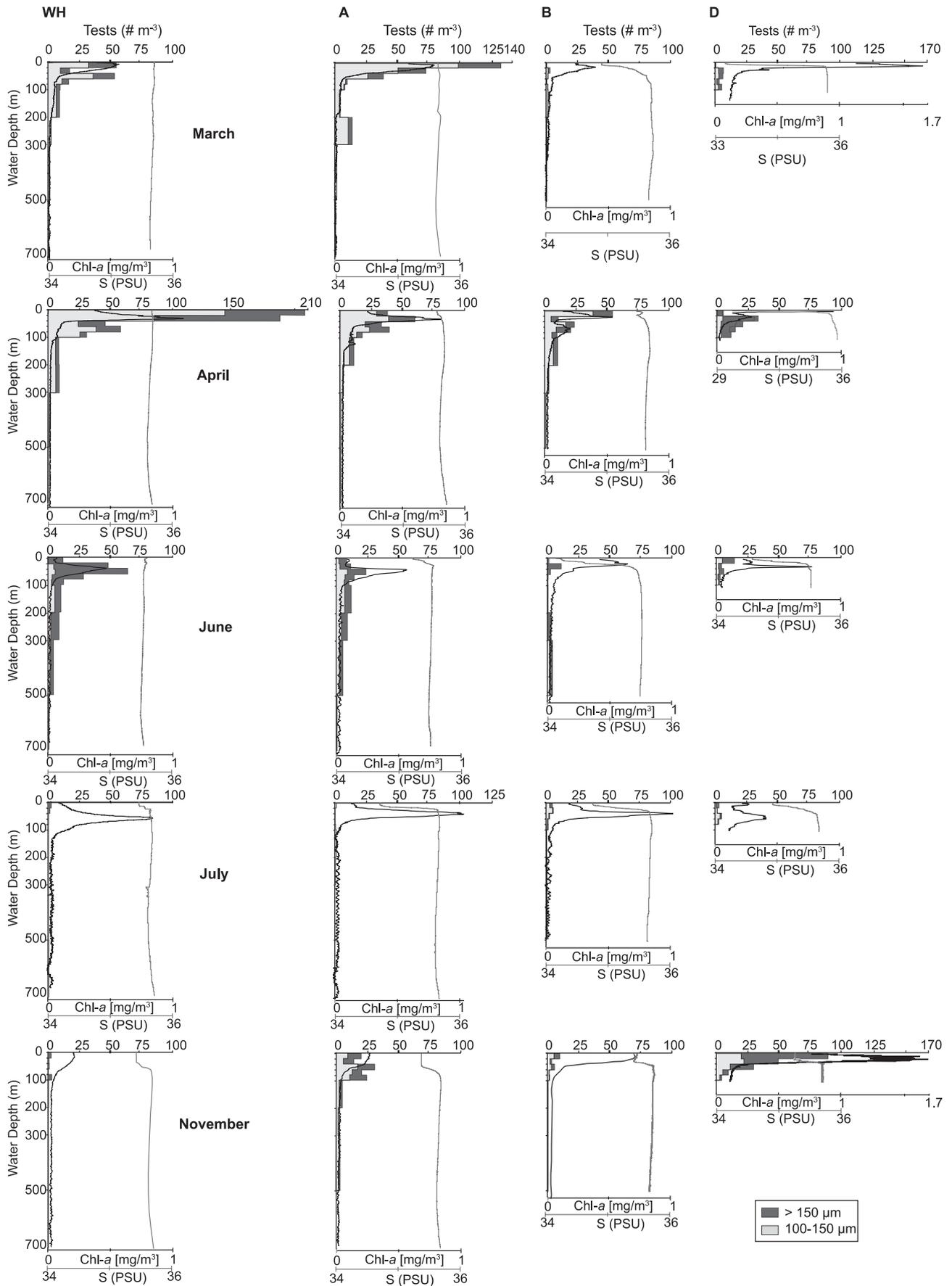


Fig. 4. Number of stained (cytoplasm bearing, living) planktic foraminifera per cubic meter of sampled sea water (dark grey: size fraction > 150 μm; light grey: size fraction 100–150 μm), in comparison to chlorophyll-a concentration (mg m⁻³, black line) and salinity (PSU, grey line) at Stations WH, A, B, and D, from March to November.

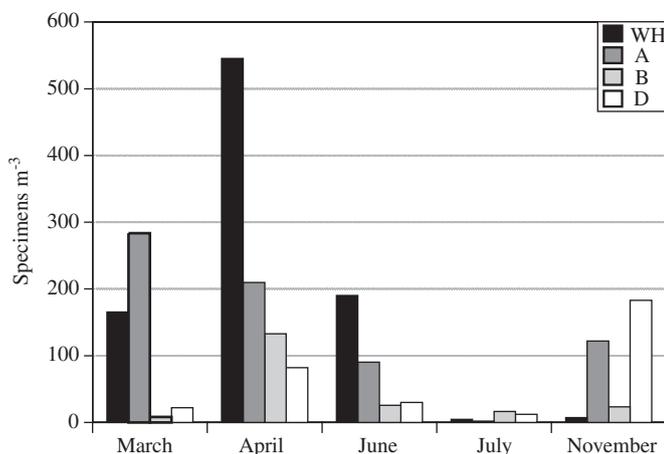


Fig. 5. Standing stocks of living planktic foraminifera per cubic meter of seawater at Stations WH, A, B, and D, from March to November.

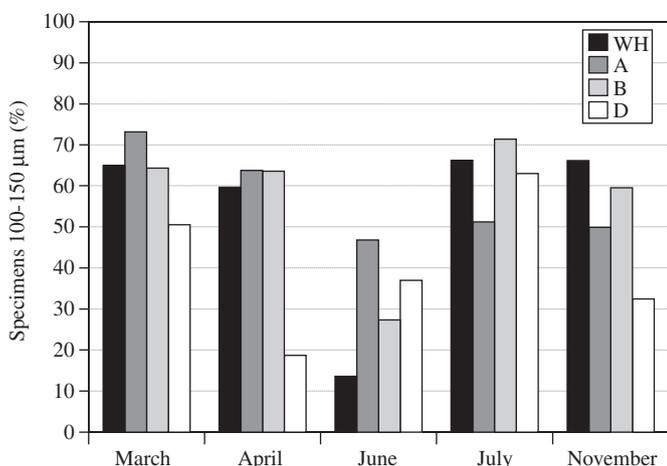


Fig. 6. Percentage of living PF of the 100–150 μm size fraction at Stations WH, A, B, and D, from March to November.

and B during March, April, July, and November (Fig. 6). In June, small specimens (100–150 μm) were overall much less frequent than during the other sampled months with a minimum of 13% of the total fauna >100 μm at Station WH. In general, small specimens were least abundant at shelf-break Station D, with a minimum of 18% in April.

6.3. Distribution of empty tests

Maximum numbers of empty tests were recorded in April at all sampled stations (Fig. 7 and Appendix B). However, empty test concentrations were two to five times lower than the number of live individuals in April, and as much as 28 times lower in June at Station WH. The empty test assemblage was mainly composed of small specimens (100–150 μm), in contrast to the living fauna (Figs. 4 and 7). At Station D, in April, an exceptional ~45% of the assemblage of empty tests belonged to the small size fraction. Empty planktic foraminiferal tests were found throughout the sampled water column from surface waters to 700 m depth without any depth preference. Highest numbers of empty tests occurred during April at depth of highest abundance of living PF or just below (Figs. 4 and 7). Empty test concentrations decreased toward the coast, following the distribution of the living fauna.

7. Discussion

The distribution of planktic foraminifera along the depth transect from deep-water Station WH to Station D at the shelf-break (Fig. 1), in the following is discussed as a result of seasonal and regional changes in ecologic conditions. The effect of water depth and proximity to the shelf on the abundance of planktic foraminifera is evaluated in comparison to the distribution of planktic foraminifera in the open oceans of similar latitude and environmental prerequisite. Finally, implications of changes in the abundance of planktic foraminifera along an offshore–onshore gradient on the paleoceanographic interpretation of fossil assemblages are given.

In general, the production of planktic foraminifera is closely linked to the availability of food, i.e., phytoplankton (mainly diatoms) and small zooplankton (e.g., Anderson et al., 1979; Hemleben et al., 1989; Schiebel and Hemleben, 2005, and references therein). Changes in primary production cause seasonal and mesoscale variability of planktic foraminifer standing stocks (e.g., Tolderlund and Bé, 1971; Deuser, 1986; Thunell and Honjo, 1987; Kincaid et al., 2000; Schiebel and Hemleben, 2000; Mohiuddin et al., 2002; Lončarić et al., 2007). At open marine environments of mid-latitudes, the production of planktic foraminifera is strongly affected by seasonality (e.g., Ottens, 1992; Obata et al., 1996; Longhurst, 1998; Schiebel and Hemleben, 2000). In the south-eastern Bay of Biscay, seasonal production of planktic foraminifera is similar to the open eastern North Atlantic (Schiebel and Hemleben, 2000).

Most planktic foraminifera dwell at water depths above and close to the deep chlorophyll-*a* maximum, i.e., the upper 80 m of the water column (Fairbanks and Wiebe, 1980; Hemleben et al., 1989; Ortiz et al., 1995; Schiebel and Hemleben, 2005). Cytoplasm-bearing individuals below 80 m depth are surface-dwellers that are part of the settling fauna although they still contain cytoplasm (Schiebel et al., 1995), or subsurface-dwelling species (Vincent and Berger, 1981).

7.1. Regional differences in the distribution of living planktic foraminifera

In the south-eastern Bay of Biscay, standing stocks decreased from deep-water Station WH towards shelf Station D during spring and early summer (Fig. 5). Planktic foraminifera were most abundant at the offshore end of transect where chlorophyll-*a* concentration was highest (Fig. 8a). Decreasing standing stocks of planktic foraminifera towards the coast are described also for other ocean margins of similar latitude (Lidz, 1966; Gibson, 1989). However, standing stocks were low (Appendix B: in April, average number at 0–100 m of 230 specimens m⁻³ at Station WH) compared to the pelagic North Atlantic (Schiebel and Hemleben, 2000; 720 specimens m⁻³). Albaina and Irigoien (2007) report a maximum of 846 specimens m⁻³ during spring 2004, indicating that maximum abundance of planktic foraminifera was possibly not sampled in April 2007 (Appendix B: max at 0–100 m of 526 specimens m⁻³ at Station WH), and confirming high spatial and temporal variability of PF abundance at the southern Bay of Biscay (Fig. 4).

7.2. Seasonal changes in plankton production and abundance of living planktic foraminifera

In the Bay of Biscay, diatoms and coccolithophores are major contributors to phytoplankton mass production in spring (e.g., Labry et al., 2004). Compared to spring, plankton production during summer is low, and less marked and more dispersed in fall (e.g., Longhurst, 1998; Ceballos and Alvarés-Marqués, 2006). As a consequence, three different seasonal conditions of planktic foraminiferal production can be distinguished in the south-eastern Bay of

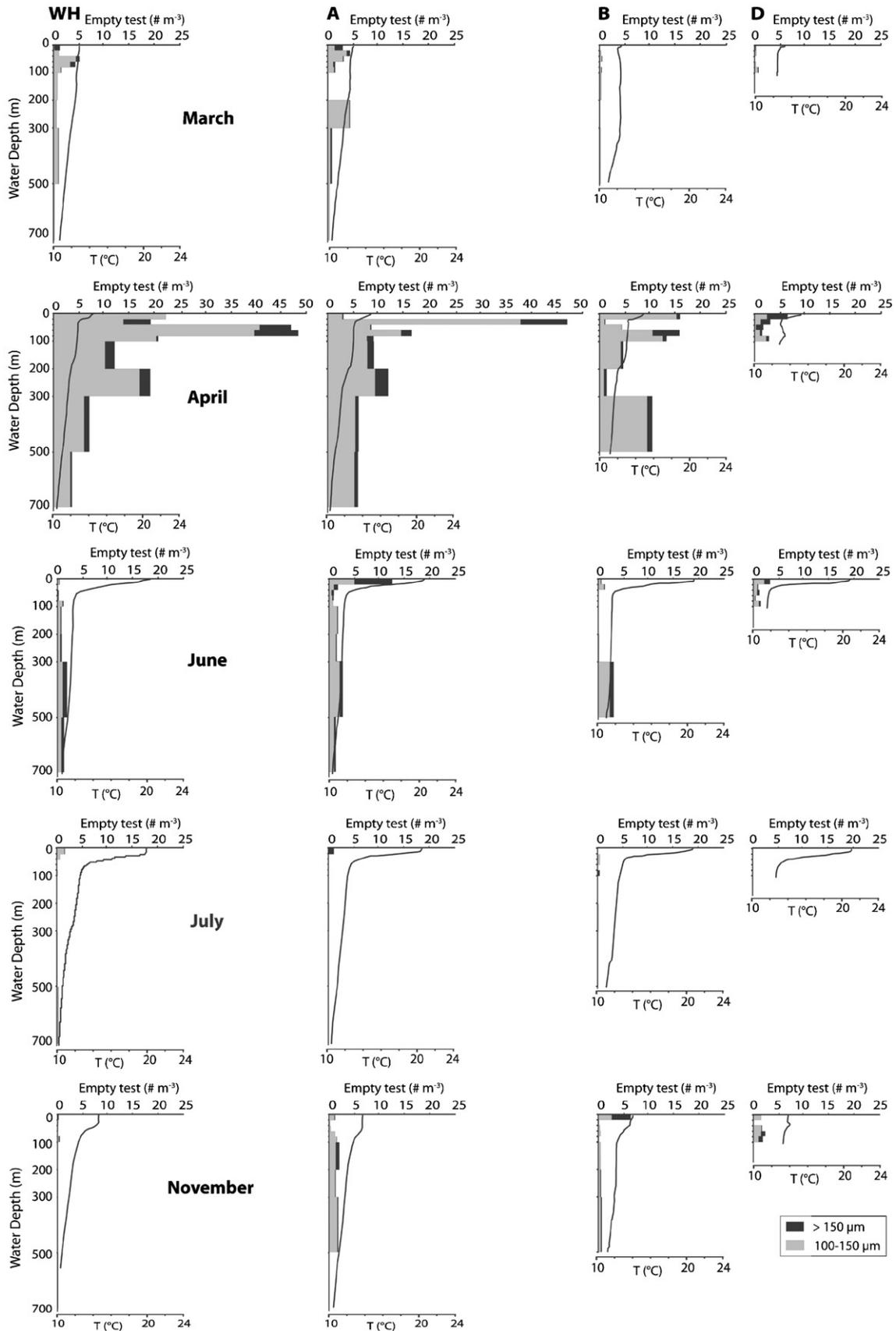


Fig. 7. Number of empty (dead) planktic foraminiferal tests per cubic meter of sampled sea water (black: size fraction > 150 μm; grey: size fraction 100–150 μm) at Stations WH, A, B, and D, from March to November. Temperature (°C) is shown by the black line.

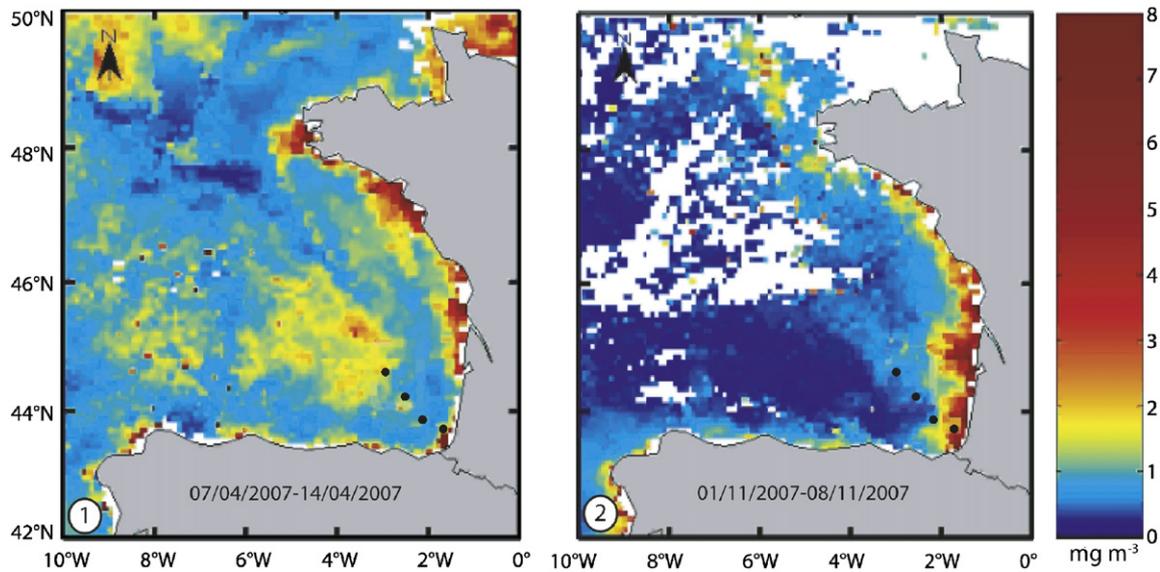


Fig. 8. Chlorophyll-*a* (mg m^{-3}) in the Bay of Biscay, from SeaWiFS images (<http://oceancolor.gsfc.nasa.gov>): (a) April 2007, before PECH 3 (Table 1), showing high phytoplankton production in the central part of the Bay of Biscay. (b) November 2007, before PECH 4, showing enhanced phytoplankton production along the coast of the south-eastern Bay of Biscay, in comparison to April, and low phytoplankton production in the central Bay of Biscay. Sampling locations are indicated by black dots (Fig. 1).

Biscay: (1) high production during spring, (2) low production during summer, and (3) sporadic production during fall (Figs. 4 and 5).

Highest PF production occurred during spring (Fig. 4; March and April) at times of high phytoplankton production, surface water mixing, and entrainment of nutrients into open marine surface waters (Schiebel et al., 1995; Obata et al., 1996; Schiebel and Hemleben, 2000; Lampert, 2001; Marquis et al., 2007). In summer (Fig. 4; June and July), limited PF production occurred at times of strong surface water stratification and nutrient limitation in surface waters (Appendix A) (Tréguer et al., 1979; Schiebel et al., 2001). Consequently, standing stocks of planktic foraminifera decreased from spring to summer (Fig. 5). In June, small sized (100–150 μm) living PF were much less abundant than during the other sampling periods at the offshore Stations WH, A, and B (Fig. 6), indicating a mature population and reduced new production (Schiebel et al., 1997; Schiebel and Hemleben, 2000). In July, standing stocks were too low throughout the sampling area (Figs. 4 and 5) to facilitate interpretation of regional differences. In late November, low PF abundance at offshore Station WH (Fig. 5) contrasts with increased plankton production typical of mid-latitudes during fall (Schiebel et al., 2001; Marquis et al., 2007). However, phytoplankton production in the Bay of Biscay during fall is dominated by dinoflagellates, and described as intense but sporadic and unsystematic (Labry et al., 2004; Lavender et al., 2004), and may hence result in patchy and regionally low abundances of planktic foraminifera.

7.3. Surface water salinity and standing stocks of planktic foraminifera

In general, hydrography affects the temporal and spatial distribution of planktic foraminifera on a medium to large scale in the open oceans (e.g., subtropical gyres: Weyl, 1978; eddies: Kupferman et al., 1987) and marginal environments (e.g., river plumes: Ufkes et al., 1998; Middle Atlantic Bight: Brunner and Biscaye, 2003). Mesoscale variability of environmental conditions and hydrography is a recurring phenomenon also in the southern Bay of Biscay (Figs. 3 and 8; Pingree and Le Cann, 1992), and may affect the distribution of planktic foraminifera sampled along transect during all seasons (Figs. 1 and 4).

Low-salinity river-plumes either trigger or inhibit the production and abundance of planktic foraminifera depending on the parameters that co-vary with salinity (Ufkes et al., 1998). In particular, Station D near the shelf-break (Fig. 1) is located in reach of the Adour river plume, and low salinities indicate the presence of fresh water dilution during all sampled seasons (Fig. 4 and Appendix A). Regionally enhanced phytoplankton and PF production at Station D in November could be attributed to freshwater and nutrient input from the Adour river (Puillat et al., 2004; Kelly-Gerreyn et al., 2006) and subsequent mixing of surface waters (Tréguer et al., 1979). In November 2007, high chlorophyll-*a* concentration occurred along the French coast of the Bay of Biscay, including Station D (Fig. 8b), and instigated PF production. In contrast, in March, April, and July, low standing stocks of planktic foraminifera (Appendix B) were found in the upper 20 m of the water column at low salinity (Fig. 4) and low chlorophyll-*a* concentration (Fig. 8a). Below the low-salinity layer, the planktic foraminiferal standing stocks reached higher values, a scenario that has also been observed at the Congo river plume (Ufkes et al., 1998) and in the Caribbean at the Amazon–Orinoco river plume (Schmuker and Schiebel, 2002). Although planktic foraminifera have a high tolerance to salinity changes (e.g., Bijma et al., 1990; Ortiz et al., 1995) and are possibly not directly affected by low salinity (Fernandez et al., 1991; Ufkes et al., 1998), the exceptional low salinity (<30 PSU) observed in April at Station D may inhibit production of planktic foraminifera.

7.4. Distribution of empty tests and implication on fossil assemblages

The distribution of empty tests in general displays the distribution of the standing stocks (Figs. 4 and 7). Empty tests were most abundant during April, during peak production of living planktic foraminifera. Low numbers of empty tests during March may indicate a developing fauna at the beginning of seasonal mass production of planktic foraminifera, at a given average individual life-time of one month of most surface dwelling species (e.g., Schiebel and Hemleben, 2005). Low numbers of empty tests during June, July, and November reflect low standing stocks (Fig. 7).

Predominance of small tests (100–150 μm) at the offshore Stations WH, A, and B (Figs. 1 and 7), is characteristic of undisturbed planktic foraminiferal faunas, with high numbers of small specimens and an exponential decrease of specimens towards larger size classes (Schiebel and Hemleben, 2000). At

onshore Station D, small empty tests were less frequent than at the offshore locations (Figs. 6 and 7), which may indicate a disturbed fauna lacking most of its juvenile and neanic individuals (Schiebel and Hemleben, 2000). During times of maximum empty test production in April, small tests are three times more frequent

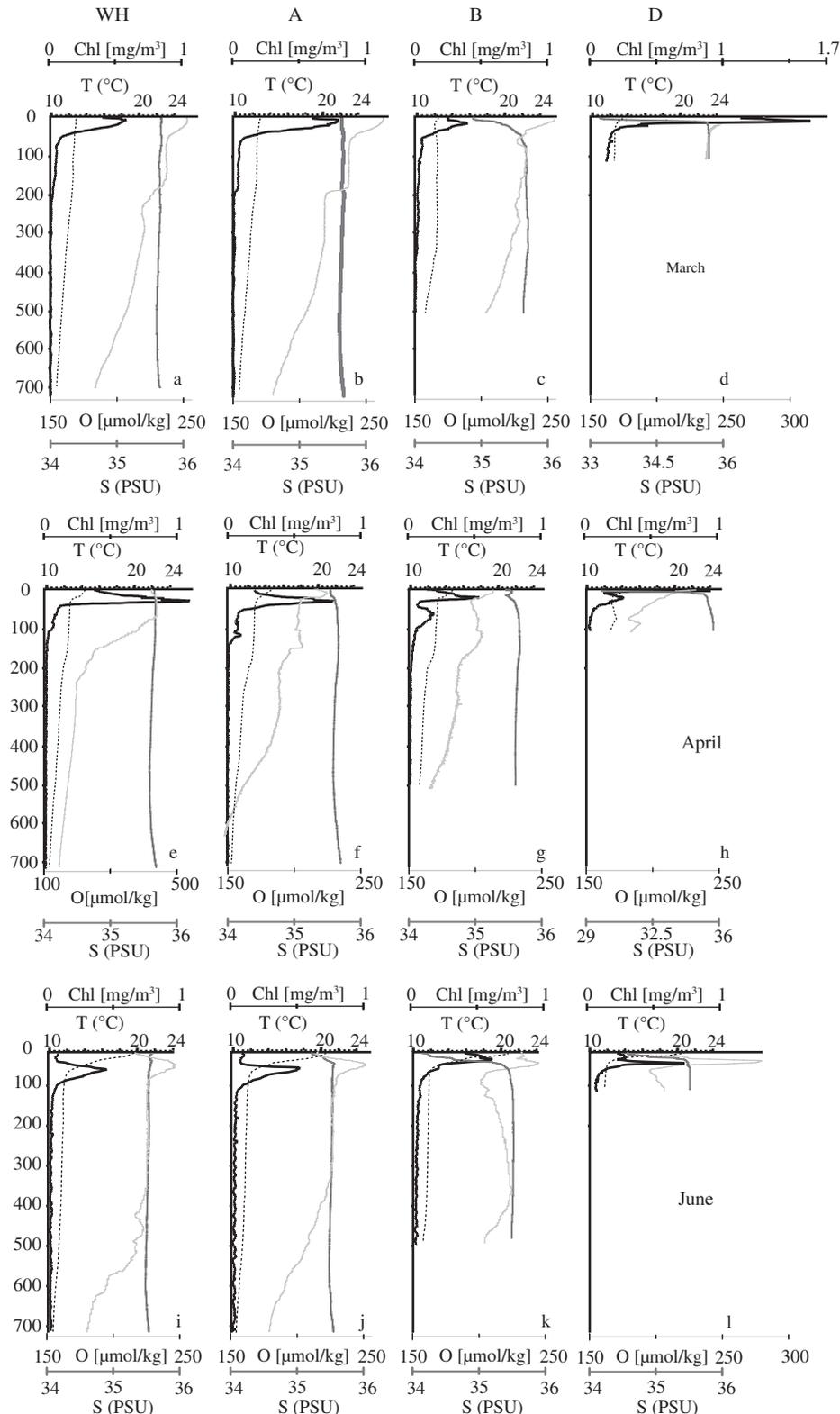


Fig. A1. Temperature ($^{\circ}\text{C}$, stippled line), salinity (PSU, bold grey line), oxygen ($\mu\text{mol kg}^{-1}$, thin grey line), and chlorophyll-*a* (mg m^{-3} , black line), between the sea surface and 700 m water depth at Stations WH, A, B, and D, during March, April, June, July, and November. Please note different scales for dissolved oxygen at Station WH in April, and for salinity at Station D in April and March.

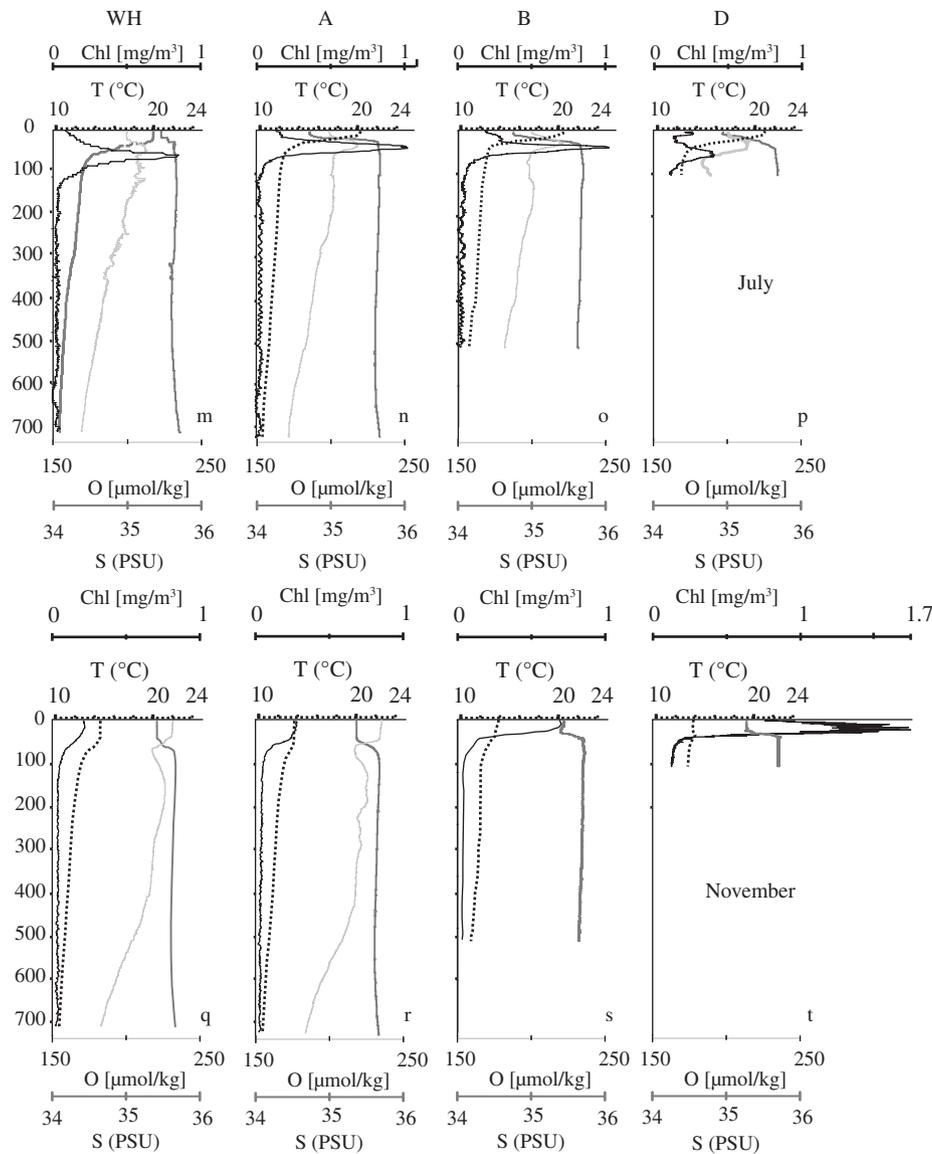


Fig. A1. (Continued)

at offshore Stations WH, A, and B (~60%) than at onshore Station D (~20%, Fig. 7). Fossil assemblages at onshore locations near the shelf-break would hence be expected to contain significantly less small sized tests than assemblages further offshore. However, additional data would be needed to confirm the size distribution of sediment assemblages of planktic foraminifera along water depth transects from the open ocean onto the shelf.

8. Conclusion

The distribution of living planktic foraminifera along a bathymetric transect in the south-eastern Bay of Biscay reveals the production of planktic foraminifera in the shallow waters of a mid-latitude marginal environment. The distribution of empty tests reflects the seasonality of planktic foraminifera production. In spring, the abundance of living planktic foraminifera decreased from the hemipelagic ocean (2000 m water depth) towards the shelf (<200 m depth), in response to the availability of food, displayed by chlorophyll-*a* concentration in surface waters. Towards the coast, freshwater discharge from rivers caused

decreased salinity in surface waters, which coincides with decreased chlorophyll-*a* concentration and decreased standing stocks of planktic foraminifera during spring and early summer. In late November, high standing stocks of planktic foraminifera occurred together with high chlorophyll-*a* concentration in surface waters near the coast. Our results indicate that the abundance of planktic foraminifera along the offshore–onshore transect in the southern Bay of Biscay, is mainly driven by the availability of food, and can be strongly affected by freshwater/nutrient input from rivers and mixing of the surface ocean.

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Table B1Numbers of planktic foraminiferal tests (# m⁻³) filled with cytoplasm (living) and empty tests (dead) at the sampling sites (Fig. 1) during March, April, June, July, and November.

	WH				A				B				D			
	Living		Dead		Living		Dead		Living		Dead		Living		Dead	
	> 150 µm	100–150 µm														
<i>March 2008</i>																
0–20	21.22	33.89	1.11	0.22	32.88	99.13	1.38	1.75	0.14	0.00	0.00	0.00	0.15	0.23	0.15	0.08
20–40	8.00	9.00	0.00	1.11	23.17	51.50	0.67	3.83	1.69	1.38	0.00	0.23	3.70	3.10	0.10	0.20
40–60	18.14	35.43	0.71	4.43	12.60	26.10	0.30	3.10	0.18	1.27	0.09	0.36	2.69	3.54	0.00	0.00
60–80	5.09	10.91	1.00	3.36	1.67	8.44	0.56	1.11	0.21	0.29	0.00	0.07	1.67	1.17	0.00	0.17
80–100	2.50	6.75	0.13	1.50	1.14	7.14	0.43	1.29	0.33	0.87	0.13	0.27	2.67	3.07	0.13	0.60
100–200	1.59	6.73	0.03	0.73	1.03	3.47	0.00	0.12	0.20	1.12	0.07	0.19				
200–300	0.45	2.35	0.12	0.50	2.84	10.31	0.34	4.22	0.11	0.06	0.00	0.05				
300–500	0.32	0.92	0.20	0.91	0.50	1.07	0.28	0.61	0.05	0.29	0.01	0.13				
500–700	0.05	0.16	0.01	0.14	0.11	0.26	0.11	0.37								
<i>April 2007</i>																
0–20	62.98	141.41	0	22.28	10.06	28.97	0.18	2.83	15.87	38.1	0.75	15.31	4.48	0.56	4.48	2.43
20–40	102.44	84.3	5.07	14.14	22.31	38.69	9.77	37.37	5.77	4.86	0.15	1.06	27.21	4.66	1.79	1.25
40–60	22.75	23	6.54	40.43	14.39	19.8	0.57	8.15	6.63	16.6	0.21	4.15	16.51	3.44	1.61	0.23
60–80	19.34	39.39	9.41	39.39	17.16	23.31	2.05	14.8	11.82	9.03	5.42	10.43	11.2	3.04	0.47	1.17
80–100	5.84	24.9	0.62	20.45	5.64	13.07	1.41	7.71	4.11	5.55	1.07	12.89	7.26	3.63	0.73	2.18
100–200	2.71	5.55	1.69	10.36	4.9	7.16	1.3	7.9	3.77	6.69	0.79	4.06				
200–300	3.19	5.91	1.95	17.15	1.15	1.97	2.41	9.63	0.2	2.89	0.62	0.99				
300–500	0.55	0.59	1.4	5.65	0.23	0.34	0.64	5.86	0.21	0.66	1.39	9.26				
500–700	0.13	0.2	0.43	3.36	0.14	0.26	0.8	5.65								
<i>June 2006</i>																
0–20	11.54	0.31	0.08	0.31	5.79	2.04	7.63	4.97	0.72	0.31	0.1	0.62	9.83	4.75	1.3	2.27
20–40	43.69	4.62	0	0	7.69	3.34	0.89	0.82	9.46	1.49	0.12	1.24	2.35	1.61	0.2	0.8
40–60	59.8	5.7	0.21	0	13.61	9.48	0.46	0.38	2.34	0.06	0	0.06	3.81	1.99	0.5	0.77
60–80	25.22	3.23	0.1	0.1	6.62	7.21	0.23	0.53	0.41	0.06	0.06	0.12	1.78	1.06	0.13	0.34
80–100	9.7	2.73	0.28	0.92	3.09	6.56	0	0.71	0.13	0.19	0	0.06	1.06	1.63	0.31	1.13
100–200	4.82	5.39	0.18	0.56	4.49	6.85	0.16	1.55	0.38	0.04	0	0.09				
200–300	6.49	2.21	0.31	0.49	4.18	4.23	0.2	1.21	1.07	1.77	0.11	0.17				
300–500	2.41	1.66	0.91	0.99	2.29	2.53	0.64	2.02	4.2	3.12	0.75	2.38				
500–700	0.46	0	0.61	0.7	0.26	0.01	0.32	0.87								
<i>July 2008</i>																
0–20	1.14	1.14	0.14	1.71	0.53	0.27	0.53	0.00	1.77	2.83	0.00	0.00	2.20	0.73	0.00	0.00
20–40	0.00	1.14	0.00	0.57	0.00	0.00	0.00	0.00	0.75	4.86	0.00	0.37	0.06	1.34	0.00	0.00
40–60	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.53	1.94	0.00	0.35	1.33	3.65	0.00	0.00
60–80	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.47	0.79	0.00	0.00	0.90	1.92	0.00	0.00
80–100	0.00	0.08	0.00	0.08	0.00	0.26	0.00	0.00	0.66	0.66	0.33	0.00	0.00	0.00	0.00	0.00
100–200	0.14	0.00	0.00	0.00	0.43	0.36	0.00	0.00	0.05	0.10	0.00	0.00				
200–300	0.03	0.08	0.00	0.00	0.07	0.14	0.00	0.05	0.20	0.24	0.00	0.16				
300–500	0.03	0.08	0.01	0.02	0.00	0.00	0.00	0.00	0.24	0.24	0.02	0.07				
500–700	0.17	0.17	0.08	0.17	0.00	0.05	0.00	0.00								
<i>November 2007</i>																
0–20	0.34	2.18	0.23	0	12.1	8.1	0.3	0.8	4	5.17	3.83	2.67	71.43	19.29	0	1.43
20–40	0.62	0	0	0.31	8.33	5.72	0	0.11	1.71	2.14	0	0.14	27.13	22	0	0
40–60	0.24	0.63	0	0.16	15.02	16.78	0	0.19	1.75	3.75	0	0.25	18.89	11.11	0.22	1.44
60–80	0	0	0	0	7.79	12.89	0	1.02	0.6	0.8	0	0.4	4.25	4.75	0.88	1.38
80–100	1.17	1.8	0.11	0.11	13.69	10.89	0.16	1.32	0.88	1	0	0.13	1.82	2.09	0.91	0.91
100–200	0.06	0.11	0.06	0.06	2.81	2.22	0.86	1.16	0.15	0.33	0.04	0.37				
200–300	0.02	0	0	0.11	0.45	1.81	0.14	1.02	0.18	0.32	0.16	0.34				
300–500	0.01	0.05	0	0.12	0.89	2.44	0.27	1.62	0.16	0.37	0.22	0.44				
500–700	0.02	0.07	0.02	0.22												

Test numbers are given for two test size fractions, 100–150 µm and > 150 µm.

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Appendix A

See Fig. A1.

Appendix B

See Table B1.

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