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Recent benthic foraminiferal distribution in the Elbe Estuary (North Sea, Germany): a response to environmental stressors

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Abstract

For the past 200 years, estuarine environments experienced intense and rapid environmental degradations due to human interventions. In addition, Global Changes are modifying the estuarine physiography, leading to a re-structuration of marginal marine benthic communities. The aim of this study is to document, the modern assemblage composition and the species-environment relations of benthic foraminifera upstream the Elbe Estuary (southern North Sea) and to observe what has changed since the first survey in 1981. For this purpose, a surface sampling was carried out from 22 stations along the transitional area of the Elbe Estuary. Living (rose-Bengal stained) and dead foraminiferal assemblages were analysed as well as hydrological and sedimentological parameters (such as salinity, pH, grain-size, and organic matter). Living faunas are characterized by very low densities and largely dominated by *Ammonia* species. Dead assemblages are more diverse and dominated by *Ammonia aomoriensis*, *Haynesina germanica*, and *Criboelphidium selseyense*. Salinity and grain-size seem to be the major factors influencing foraminiferal distributions in the transitional area. Under the ongoing climate changes, future strategies will be taken to foster the application of benthic foraminifera as biomonitoring tool in the Elbe Estuary, via this baseline investigation.

Keywords

Foraminifera; benthic ecology; transitional environments; river; Elbe Estuary; North Sea.

1 Introduction

Transitional environments such as estuaries, coastal lagoons, and tidal marshes are fragile ecotones influenced by tidal, wave and fluvial processes. Over the last two centuries, these naturally stressed environments, including the Elbe Estuary (North Sea, Germany), experienced deleterious environmental degradations due to widespread anthropogenic influences (such as industry, shipping traffic, dredging, aquaculture, urban discharge, and agricultural runoff). Human activities further led to an intense decline in terms of faunal and floristic diversity and biomass (Diaz and Rosenberg, 2008). At the Elbe Estuary, low-lying transitional environments are further increasingly affected by the consequences of Global Warming and the associated rise in mean sea level (MSL), as the increased intrusion of saline waters (IPCC, 2019). Moreover, in shallow near-coastal areas, such as the tidally influenced part of the Elbe River, rising MSL has a strong impact on the range and velocity of the oscillating tidal

currents, as well as storm surges that preferentially occur at rising tides (Arns et al., 2015; Horsburgh and Wilson, 2007).

Benthic foraminifera (BF) are well adapted to their habitat, have short life spans, and their bio-mineralized tests have a high preservation potential in the sedimentary records. Thus, they are considered as reliable indicators to trace natural- and human-induced environmental changes for present-day and the geological past (e.g., Dolven et al., 2013; Frontalini et al., 2013; Nordberg et al., 2017; Polovodova Asteman et al., 2015). The distribution of BF in transitional and estuarine areas is the result of complex interactions between a large number of biotic and abiotic parameters (e.g., Armynot du Châtelet et al., 2016; Frontalini et al., 2014; Martins et al., 2015; Milker et al., 2015a). Natural stress caused by variations in salinity, sediment grain-size, organic load, and tidal exposure may interfere with anthropogenic stress factors, enhancing the high variability of these ecosystems (e.g., Alve, 1995; Camacho et al., 2015; Francescangeli et al., 2017; Hayward et al., 2004a). The foraminiferal communities are adapted to cope with natural changing environmental parameters and may show faunal characteristics (e.g., in composition, diversity and abundance of stress-tolerant taxa) similar to assemblages exposed to human-induced stress (Hess et al., 2020). Several studies investigated the recent ecological quality of transitional and adjacent marine environments. The majority of these studies showed the value of the foraminiferal tool in biomonitoring programs (e.g., Alve et al., 2016; Bouchet et al., 2012; El Kateb et al., 2020; Martins et al., 2020). They also showed that distinguishing human impact from natural stress can be difficult and remains controversial in transitional environments (Dauvin, 2007; Müller-Navarra et al., 2016). This particularly holds true for the direct and indirect impacts of Global Warming, which are expected to re-structure marginal marine foraminiferal communities in the near future (Müller-Navarra et al., 2017; Schmidt et al., 2015; Weinmann and Goldstein, 2016). Therefore, the continuation and resumption of baseline studies is required to constrain the yet unknown resilience of recent foraminiferal faunas, to assess the impact of Global Change on their distribution in near-coastal ecosystems, and to improve their application for monitoring future environmental changes in transitional areas (Schönfeld, 2018).

The present paper reports a baseline study of the recent diversity of BF, their assemblage composition and ecological interactions upstream the Elbe Estuary. Although an important estuarine area of Northern Europe, BF have not been studied after the pioneering work of Wang (1983). This study is based on a few samples only and provided the first distribution data on recent foraminifera in the estuary. Under the aspects of ongoing climate change with predicted decreasing riverine runoff and increasing sea level, the rise of global marine traffic, and recent shipping route management measures, the motivation of this study is to document which species presently occur in the Elbe Estuary and what has changed since the first survey in 1981.

1.1 Study area

The Elbe River is one of the largest rivers that drains into the Wadden Sea (southern North Sea region) and has a wide estuary. The Elbe River has a length of 1094 km and the fourth largest catchment area (148 268 km²) of Middle Europe (Carstens et al., 2004) (Figure 1). Between 1900 and 2016, the yearly mean of the Elbe River runoff varied between 379.54 and 1374.85 m³/s (701.71 m³/s on average) (Global Runoff Data Centre, GRDC). The Elbe Estuary (Lower Elbe) represents the tidally influenced part of the Elbe River (about 140 km in length). It begins at a weir at Geesthacht and ends at its seaward border at Cuxhaven (Carstens et al., 2004) (Figure 1B). The tidal part can be divided, based on salinity, into an upper limnic section (0.3 - 2.6 psu) and a lower brackish part which

corresponds to the transitional area. The lower Elbe is a well-mixed estuary, characterized by a mesotidal regime (mean tidal range of 2.97 m), highly variable water temperature (-0.3 - 24 °C) and oligo- to polyhaline conditions (1.2 - 22 psu) in combination with high turbidity (Carstens et al., 2004). The substrate of the riverbed is composed of medium to fine sands with clay pebbles, and patchy mud drapes on sand with ripples (Schönfeld et al., 2014). About half of the area of the transitional waters is represented by intertidal mudflats. In the estuary, the shallow subtidal areas reach a maximum depth of about 25 m (Figure 1C).

The Elbe River represents a frequently used shipping route to Hamburg ports and is called by 50 000 vessels per year. Dredging of the navigation channel is done frequently, resulting in a successive amplification of currents, wave action and tidal levels with the latter ranging from <3 m at the inlet to ~3.5 m at the ports of Hamburg (Kappenberg and Grabemann, 2001). Before the German reunification in 1989, the Elbe River was one of the most heavily polluted rivers in Europe (in terms of organic enrichment, nutrients or chemical contaminants) (Krysanova et al., 2006). Since then, the water quality has gradually improved (IKSE, 2019; Serna et al., 2010). However, the Elbe Estuary is still considered as a highly stressed transitional environment (Wetzel et al., 2012), as it further experienced many human-made modifications over the last centuries such as diking, land reclamation or navigation channel deepening (Boehlich and Strotmann, 2019).

2 Materials and methods

The sampling campaign was carried out, in collaboration with the Helmholtz-Zentrum Geesthacht (HZG), on board of the research vessel (RV) “Ludwig Prandtl”. In late July 2011, twenty-two surface samples were collected along a transect in the transitional waters of the Elbe Estuary, from the port of Glückstadt down to the river’s mouth near Cuxhaven (Figure 1C). A total of five samples (stations 4 to 8) were collected along a cross-shore transect to observe possible lateral variations of abiotic and biotic parameters. The sample set was accomplished by four surface samples taken on RV Alkor cruise (AL438) in late May 2014 (Schönfeld et al., 2014) (Figure 1C). All sampling stations of the Prandtl cruise were localised in the Elbe navigation channel, where on-board measurements of the water depth at each station were subsequently referred to the nearest tide-gauge record. From east to west, the considered gauges comprise: Stör-Sperrwerk, Brokdorf, Brunsbüttel Mole 1, Osteriff MPM, Otterndorf MPM, Cuxhaven Steubenhöft, and Mittelgrund. The tide-gauge data were provided by the Federal Waterways and Shipping Administration (WSV). Corresponding sediment-surface levels varied between -4.49 m and -18.79 m relative to NHN (Normalhöhennull datum, German Ordnance level) (Error! Reference source not found.).

The samples were obtained by means of a 20 x 20 cm Van Veen grab and box corer (20 x 20 cm surface, cruise AL438 only) that collects sediment over a surface area of about 400 cm². At each station, the physicochemical parameters of the river water (i.e., temperature, salinity, dissolved oxygen (O₂) and oxygen saturation (AOU)) were measured directly on board using the flow-through FerryBox system (Petersen, 2014). Concurrent, discrete water samples were collected with the FerryBox to measure total alkalinity (TA) and dissolved inorganic carbon (DIC). These samples were collected in 300 ml biological oxygen demand (BOD) bottles, and directly preserved with saturated mercury chloride (HgCl₂). TA and DIC were measured with a VINDTA 3C (Versatile Instrument for the Determination of Total dissolved inorganic carbon and Alkalinity) at the Helmholtz-Zentrum Geesthacht (HZG). The data were calibrated with Dickson (Scripps Institution of Oceanography) certified reference materials (CRM batch #187). All calcite saturation state (Ω) and pH values were calculated from temperature, salinity, TA and DIC

data by using the CO2SYS program of Lewis and Wallace (1998) with the equilibrium constants of Mehrbach (1973), refit by Dickson (1987). The local in-situ water depth at time of sample collection was detected by the on board Acoustic Doppler Current Profiler (WorkHorse Broadband ADCP 1200kHz, Firmware Version 51.40).

On board of the RV Prandtl, the grab was opened and the sediment was deposited in a container in its genuine position. Two aliquots of surface sediment of 1 cm thickness were subsampled and stored in plastic graduated vials. The first aliquot was used for sedimentological analyses and the second for faunal investigations. Immediately after sampling, foraminiferal samples were treated with Rose Bengal dye (2 g of Rose Bengal in 1000 ml of 95% ethanol) to distinguish living (stained) from dead (unstained) specimens (Lutze and Altenbach, 1991; Walton, 1952). The samples were left in the mixture to optimize the staining for more than two weeks (Schönfeld et al., 2012).

2.1 Sedimentological and geochemical analyses

For grain-size analysis, all samples were treated with 10-30 % of hydrogen peroxide (H_2O_2) and with acetic acid (CH_3COOH) to remove organic remains and carbonate contents, respectively. The remaining sediment was wet-sieved through a 2000 μm screen to remove coarse particles. Samples were then suspended in water with addition of a 0.05 % solution of Tetra-Sodium Diphosphate Decahydrate ($Na_4P_2O_7 \times 10H_2O$) as a dispersing agent. Measures were carried out using a HELOS KF Magic Laser particle-size distribution analyser (for details see Bunzel et al., 2020). Sediment grain-size quantifications, including sand, mud and mean grain-size (M_{GS}) were performed using the software GRADISTAT version 8.0 (Blott and Pye, 2001), based on the procedure described by Folk and Ward (1957).

Organic matter (OM) contents were estimated by loss-on-ignition (LOI) (Ball, 1964). The LOI is calculated using the following equation (Equ. 1):

$$OM_{LOI} = \left(\frac{M_{T1} - M_{T2}}{M_{T1}} \right) \quad (Equ. 1)$$

where OM_{LOI} is an estimation of the percentage of organic matter from loss-on-ignition method; M_{T1} represents the mass of sample remaining after heating in a convection oven at 105 °C for 24 h; and M_{T2} is the sample mass remaining after incineration in a muffle furnace at 550 °C for 6 h.

2.2 Foraminiferal analysis

Wet samples (about 50 cm^3 volume) were gently sieved with tap water over a 63 μm and 500 μm mesh sieves, and both fractions were dried at 38°C. In coastal environments, separation methods are often necessary because of the low foraminiferal abundance related to a high sedimentation rate (Francescangeli et al., 2020; Schönfeld and Lübbers, 2020). Therefore, foraminiferal tests were concentrated by flotation with Sodium Polytungstate (SPT) at a density of 2.3 g/cm^3 (Parent et al., 2018). This non-toxic method provides an optimal foraminiferal recovery ($\geq 95\%$) and a minimal recovery of sediment particles ($\leq 20\%$) (Parent et al., 2018). The floatate and the deposited residue were then re-washed with tap water to prevent the formation of salt crystals and dried at 38°C. All specimens from the Rose Bengal stained (living) assemblage and about 200 specimens (where possible) from dead assemblages from the $>63 \mu m$ fraction were dry-picked and counted under a binocular microscope ZEISS-Stemi 508. Foraminifera were identified based on the literature from transitional areas in the region (e.g., Müller-Navarra et al., 2016) and online dataset (WoRMS-Editorial-Board, 2018). As foraminiferal morphotypes may include

different genotypes, molecular-based taxonomical studies were also considered for identification (e.g., Bird et al., 2020; Darling et al., 2016; Hayward et al., 2004b). The morphological identification of Elphididae was based on Darling et al. (2016). In particular, the well-known *Criboelphidium excavatum* was named as *Criboelphidium selseyense* corresponding to S5 genetic type of Darling et al. (2016). The identification of the different morphotypes of the genus *Ammonia*, was based on the criteria given by Richirt (2019), i.e., the suture elevation (flush-raised) and the pore diameter: *A. aomoriensis*, *A. aberdoveyensis* and *A. tepida* correspond to T6, T2 and T1 genetic type of Richirt et al. (2019), respectively. A transmitted light microscope (Keyence VHX-6000) was used to photograph living and dead specimens of *Ammonia*. For the dead assemblages, the density of potentially reworked taxa (reworked specimens/cm³), i.e., highly damaged specimens (due to post-mortem processes), and broken specimens, impossible to identify, were recorded as well.

2.3 Data analysis

For each sample, the relative abundance of BF, the faunal density (FD; specimens/cm³), the species richness (S) and diversity index (H'_{bc}) (Chao and Shen, 2003) were calculated.

Additionally, a non-metric multidimensional scaling (NMDS) was performed on the dead assemblages using abundance data including species >1% in at least three stations, rescaled to 100% after removing less abundant species. We used NMDS with two dimensions and Bray Curtis distance (Bray and Curtis, 1957) as similarity measure. The stress was minimized using a monotone regression (Sibson, 1972). The intend of the NMDS was to compare present-day foraminiferal distributions with past ones (Wang, 1983). For the comparison, some taxonomical assumptions were done. For instance, we considered that *Protelphidium germanicum* or *Protelphidium depressulum* in Wang (1983) correspond to *Haynesina germanica* and *Haynesina depressula*. As the *Ammonia* species identification by Wang (1983) was not transferable to modern concepts, specimens belonging to *Ammonia* were pooled for the NMDS analysis. The R software (version 3.6.3; R-Core Team, 2017) and R packages entropy (Hausser and Strimmer, 2014), and vegan (Oksanen et al., 2016) were used for diversity measures and NMDS analysis, respectively.

3 Results

3.1 Environmental parameters

River water salinity in the estuary showed a clear increase downstream of the Elbe mouth with values ranging between 1.8 and 25.5 psu in July 2019 (Figure 2A). The water temperature was quite constant along the river stream, with values from 21.8 to 22.9°C (Figure 2B). The pH ranged between 7.52 and 7.95, showing a gradual increase downstream (Figure 2C). Similar to salinity and pH, O₂ increased towards the river mouth (especially from stations 14 to 22) from 205.7 and to 248.1 µmol/L (Figure 2D). On the contrary, oxygen saturation (AOU) decreased from 53.2 to -13.6 µmol/L, indicating a supersaturation in the outer estuary. The calcite saturation state (Ω) gradually increased towards the river mouth, with values ranging between 0.55 and 3.36. Along the cross-shore transect, water parameters did not show lateral variations.

The organic matter (OM) of the sediment samples from the Prandtl 2019 cruise ranged from 0.2 to 9.4% (Figure 2E). Although OM did not show a clear pattern, the highest values were recorded upstream. The sediment grain-size was mostly muddy in the first three sampling stations (clay plus silt was 96.7% on average) (Figure 2F). Downstream, sediment grain-size became rapidly sandy (93.4% sand on average) (Figure 2G). The mean grain-

size (M_{GS}) ranged between 72.6 to 527 μm (Figure 2F). Along the cross-shore transect, sediment parameters showed lateral variations. In particular, the lowest OM contents were localized in the deep river channel (stations 5 to 7) associated to the coarsest sediment grain-size.

3.2 Living and dead benthic foraminiferal assemblages

Living BF were found from station 9 downstream in 2019. Stations 1 to 8 as well as stations 14 and 22 were devoid of living BF. The faunal density (FD) varied between 0.05 and 4.6 (specimens/cm³) (Figure 4A). The highest value was registered at station 20, although a clear downstream pattern was not visible. Species richness (S) ranged from 1 to 5, while diversity (H'_{bc}) ranged from 0 to 1.26 (Figure 4B-C), also lacking a trend along the transect. The living fauna was exclusively dominated by hyaline taxa. *Ammonia aomoriensis* and *A. tepida* were largely the most abundant species (59.6 and 22.0% on average, respectively; Figure 4D and 5). They were associated with *Criboelphidium selseyense* (13.8% on average) and *Haynesina germanica* (4.4% on average). Rare species (0.21% on average) included *Quinqueloculina seminula* and *Buliminella elegantissima*. The distribution and proportions of the individual living species did not show a particular trend along the Elbe Estuary.

Living BF were present, in low abundance, only in samples 774 and 775 from cruise AL438. *Haynesina germanica* and *A. aomoriensis* were the most abundant taxa (37.9 and 31.8% on average, respectively), associated with *C. selseyense*, *A. tepida* and *Criboelphidium williamsoni* (22.1, 4.0, and 2.7% on average, respectively).

Dead foraminifera were found at all stations, except of Stations 6 and 7, in 2019. The FD varied between 0.44 and 203.52 (specimens/cm³) (Figure 4A). The highest values were observed at stations 9-12 and 20-21. At the same stations, the highest densities (110 specimens/cm³) of reworked taxa were found. The densities of the dead assemblages were on average about 40 times greater than that of living species (0.89 and 36.67 specimens/cm³, respectively). Species richness (S) ranged from 4 to 15, while the diversity (H'_{bc}) ranges from 1.22 to 1.97 (Figure 4B-C). For S and H'_{bc} , a specific trend along the transect could not be recognised. The diversity of the dead assemblages was on average two times greater than that of living the living fauna (with 0.85 and 1.70, respectively). The dead assemblage was largely dominated by hyaline species (98.3% on average) with the occurrence of a few agglutinated and porcelaneous species (1.75 and 0.14% on average, respectively). *Haynesina germanica* and *A. aomoriensis* were the most abundant species (31.1 and 29.1% on average) followed by *E. selseyense* (18.23% on average) (Figure 4D). Minor species (relative abundance >5% in at least one sample) included *A. aberdoveyensis*, *A. tepida*, *C. williamsoni*, *H. depressula* and *Entzia macrescens* (6.2, 3.5, 2.8, 2.3, and 1.6% on average, respectively). The distribution of dead species did also not show a recognizable trend along the Elbe Estuary.

The dead assemblages from cruise AL438 were also dominated by *H. germanica* (28.4 %, on average), followed by *A. aomoriensis*, *C. selseyense* and *A. aberdoveyensis* (18.1, 14.4, and 11.1% on average, respectively). Minor species included *C. williamsoni*, *A. tepida* and *H. depressula* (9.1, 8.5, and 2.9% on average, respectively).

4 Discussion

4.1 Benthic foraminifera from the Elbe Estuary

In the Elbe Estuary, population densities of the living fauna and abundances of dead specimens are in the range of values (0-600 specimens/cm³) previously observed in similar coastal environments (e.g. Alve and Murray, 2001;

Armynot du Châtelet et al., 2018a; Dimiza et al., 2016; Mojtahid et al., 2016). In terms of species richness, a low number of species (0-26 species) for the living faunas and dead assemblages was likewise reported, for instance, in other estuaries along the transitional environments of the English Channel (for details see Armynot du Châtelet et al., 2018b). On the contrary, the overall number of species (gamma-diversity) is much lower compared to open marine settings. This is generally due to the fact that in transitional environments there is a highly annual, seasonal and daily variability of environmental parameters (such as salinity, temperature, and oxygen). The natural environmental instability in conjunction with anthropogenic-induced stress may often result in the decrease of the foraminiferal abundance and diversity in transitional environments (Armynot du Châtelet et al., 2004; Cearreta et al., 2000; Francescangeli et al., 2016; Frontalini and Coccioni, 2011).

Based on our results, the sediment composition constitutes a limiting factor for the distribution of BF in the Elbe Estuary (Figure 6). For both, living faunas and dead assemblages, the highest densities were found at M_{GS} of 100 – 200 μm , i.e., fine sands. By contrast, samples with $M_{GS} > 300 \mu m$ were barely devoid of BF (both living and dead). Sediment grain-size can be translated as a function of the hydrodynamic conditions, i.e., bedload sorting at maximum current strength, and thereby depicts a limiting factor when it exceeds its critical threshold (Murray, 2001). Accordingly, in the Canche Estuary (Northern France), a strong decrease of foraminiferal density from upper salt marsh areas to the river channel was observed, in correspondence to an increase of the grain-size (Armynot du Châtelet et al., 2009; Francescangeli et al., 2018). According to these studies, samples with high sand contents (>88%) were completely azoic. Likewise in the Loire Estuary (Western France), foraminifera were nearly absent in the sandy bottom of the navigation channel because of the physical disturbance by dredging (Mojtahid et al., 2016). In the Elbe Estuary, indeed, the highly frequent dredging of the navigation channel and the relative amplification of currents (Kappenberg and Grabemann, 2001) disturbs the natural depositional processes and hamper the recruitment and establishment of BF **biozoenos**. The mechanical action of waves and tidal currents has a significant effect on BF, namely the destruction of small and less resistant specimens, and the ensuing reduction of foraminiferal density and diversity (Francescangeli et al., 2018; Martins et al., 2016b). This is evident from the high number of reworked and broken specimens found in the investigated area. They also comprise species living in the navigation channel and not only those from the adjacent tidal flats.

The salinity may play an important role on the foraminiferal distributions along the Elbe Estuary as well. Living species occurred only from the station 9 downstream, where the salinity was ≥ 7.4 psu. This seems to be the lower salinity threshold that allows living BF to thrive in the brackish zone of the estuary. However, there is a quasi-periodic displacement of the salinity front upstream by up to ~20 km, monthly, because of episodic hydrological and meteorological events (Stanev et al., 2019). As such, higher salinities may transiently prevail at these sites. However, a daily monitoring of hydrological parameters across the transition zone is required to test this hypothesis. In the near Baltic Sea, BF required a minimum of 5 to 9 salinity units to survive (Frenzel, 1996). By contrast, in the navigation channel of the Guadiana Estuary at the border between Spain and Portugal, living BF were found even in oligohaline waters (0.5-5 psu) (Laut et al., 2016). This could mean that more than considering absolute values, one should take into account the amplitude of salinity variations (Lübbbers and Schönfeld, 2018). In addition, low salinities and strong fluctuations may induce to the development of small test sizes and test abnormalities as reported by Polovodova and Schönfeld (2008). Indeed, the dead BF assemblages from the Elbe Estuary were characterised by an elevated number of small specimens with the occurrence of some aberrant forms.

In conclusion, the low salinities and abrupt salinity changes might not be optimal for the proliferation of BF in the Elbe Estuary.

Another important aspect to consider is that the lower salinity threshold (<7.4 psu, where living foraminifera are absent) coincides to the lowest values of Ω , around the under-saturation limit ($\Omega < 1$). For calcifying organisms, these conditions are not optimal for test generation and reproduction. In a culturing experiment, it has been demonstrated that test growth in the entire population of *A. aomoriensis* could only take place at Ω values >1 and temperatures of 13°C and less (Haynert and Schönfeld, 2014). Under summer conditions (18 °C), however this species was able to grow even under-saturation at Ω of ca. 0.6 (Haynert and Schönfeld, 2014). Although this parameter may indisputably play a role for the successfully proliferation of shelled organisms, clear signs of dissolution have not been noticed on the tests of foraminifera from the Elbe Estuary.

Similar to other estuaries, benthic foraminiferal communities from the Elbe Estuary constitute of low-diverse assemblages, dominated by few stress-tolerant taxa. They include typical species of macro- and meso-tidal transitional zones from Atlantic areas (e.g. Francescangeli et al., 2020; Leorri et al., 2008). The living assemblages in the Elbe estuary are largely dominated by *A. aomoriensis* and *A. tepida* (together >80%, on average). In transitional areas, these are common taxa able to live from intertidal to subtidal environments. While *A. tepida* seems to be ubiquitous, *A. aomoriensis* was mostly found in northern Europe and along China and Japan coasts (Bird et al., 2020; Hayward et al., 2004b; Saad and Wade, 2016a; Schweizer et al., 2011). This disjoint distribution of *A. aomoriensis* was attributed to human-assisted dispersal (Pawlowski and Holzmann, 2008). Although both species have similar ecological preferences, *A. aomoriensis* seems to prefer more brackish conditions (Bird et al., 2020). In the dead assemblages, the *Ammonia* species are associated with *H. germanica* and *C. selseyense*. Although these taxa are widespread in transitional environments (from intertidal to subtidal), *H. germanica* tends to dominate in the upper part of the intertidal gradient (low marshes and tidal flats) (e.g. Armynot du Châtelet, 2018; Francescangeli et al., 2017), while *C. excavatum* (here *C. selseyense*) prefers the lowest part of the intertidal gradient (tidal flat and tidal channels) (Debenay and Guillou, 2002; Müller-Navarra et al., 2016). In laboratory experiments, it has been recently demonstrated that *C. excavatum* is able to cope better with lower salinities as compared to *H. germanica* and *A. tepida* (Lintner et al., 2020a; Lintner et al., 2020b). In the navigation channel of the Elbe River, the *Ammonia* species are always dominant along the salinity gradient and its distribution seems not to be related to any other environmental parameter. *Haynesina germanica* and *C. selseyense* on the other side better thrive in the adjacent tidal flats and pioneer zone of the salt marsh areas, being barely absent in the living fauna of the navigation channel. However, the low number of living specimens, does not support the computation of any statistically-significant ecological model.

4.2 Living versus dead assemblages

In the Elbe Estuary, the density and diversity of the dead assemblages were, on average, forty and two times greater than that of the living population. Such strong differences between the abundances and species inventory of dead assemblages and the corresponding living faunas were often reported (e.g. Armynot du Châtelet et al., 2011; Milker et al., 2015a). In open marine environments, it has been demonstrated how predation, transport, post-deposition and early diagenetic processes may be the responsible for these discrepancies (e.g., Alves Martins et al., 2019; Di Bella et al., 2017; Duros et al., 2012). In coastal and transitional environments, the same processes are involved but sediment dynamics, triggered by tide and waves, may amplify them by introducing huge dissimilarities

between living populations and dead assemblages (Armynot du Châtelet, 2018; Martins et al., 2016a). As
aforementioned, in the navigation channel of the Elbe Estuary, sediment dynamics (such as transport and re-
sedimentation) associated to human actions are particularly intense and this may be an important factor driving
such differences. These processes may lead to a higher number of dominating species in the dead assemblages
than in the living counterpart with ambiguous ecological significance (Armynot du Châtelet, 2018; Martins et al.,
2016a). In terms of species composition, in fact, in the navigation channel of Elbe Estuary, the living fauna is
Ammonia-dominated, while the dead fauna is mainly composed of species living in the nearby salt marsh and tidal
flat areas. For instance, *A. aberdoveyensis* was found only in the dead fauna. This species has been reported in the
upper part of the intertidal areas and salt marshes (Bird et al., 2020). However, the respective genotype T2A has
not yet been recorded in the North Sea outside the United Kingdom shores. A few specimens of *A. aberdoveyensis*
were occasionally found at the vegetation boundary of the salt marsh off Schobüll, Schleswig-Holstein (Schönfeld,
pers. observ.). Therefore, the species is seemingly very rare in the German Bight.

However, sediment dynamics may not be the only factor to induce these discrepancies. Like other microorganisms,
such as dinoflagellates (Fitt et al., 2000) or diatoms (Wang et al., 2015), the density and diversity of BF can vary
seasonally in response of the fluctuations of biotic and abiotic variables (such as temperature, food supply, salinity)
(Milker et al., 2015b; Murray and Alve, 2000; Wilson and Dawe, 2006). Temporal variations in foraminiferal
faunas have been observed in different environments from transitional to the deep sea (Fontanier et al., 2003;
Gustafsson and Nordberg, 2000; Kawahata et al., 2002). For instance, agglutinated species represented more than
80% of the total individuals in the lower Guadiana Estuary (South-eastern Portugal) during winter, when fluvial
discharge peaked (Camacho et al., 2015). In the same area, calcareous species became more dominant and
expanded into upper estuarine zones during summer, when normal marine conditions prevailed. In light of this,
one may not exclude that during the sampling period, the environmental conditions favoured the extensive
occurrence of living *A. aomoriensis* and *A. tepida*, although the reasoning is uncertain and needs further
investigations.

To conclude, the living fauna is a snapshot of local ecological conditions at the time of sampling, whereas the dead
assemblage represents a time-averaged association, modified by taphonomic processes, involving wide-ranging
ecological interactions, and their potential transport and re-deposition (Hawkes et al., 2010; Murray and Alve,
2000). It is evident that for environmental studies, including environmental biomonitoring or impact assessment,
the use of the living faunas is mandatory. Dead assemblages can be used in other contexts. For example, they may
be useful for sea-level reconstructions (e.g., Edwards et al., 2004; Horton et al., 1999; Scott and Medioli, 1980),
because they are less affected by seasonal fluctuations and more similar to fossil assemblages from sediment cores
(Berkeley et al., 2009). Living faunas and dead assemblages provide different environmental signals, and should
be used separately to correctly investigate the relation between the biota and abiotic parameters. In baseline studies,
it is therefore important to analyse both, living and dead faunas in order to have an extended overview of the
environmental characteristics. If paleo-environmental reconstructions are intended, one should select the area
where the differences between the living and dead assemblages are as low as possible (Armynot du Châtelet, 2018;
Martins et al., 2016a). As matter of fact, the navigation channel may not be the best place to collect sediment cores
for paleo-environmental studies in the Elbe Estuary.

4.3 A visit to the 1980s

In April 1981, a surface sampling was carried out in the navigation channel of the Elbe Estuary from Glückstadt to Helgoland (outer estuary; Wang, 1983; Wang and Murray, 1983). In 1981, the living faunas were largely dominated by *C. excavatum* (>90%), while *C. excavatum*, *A. beccarii* and *Protelphidium germanicum* (here *H. germanica*) were the most abundant species in the dead assemblages (Figure 7A). As such, the differences to our results are profound. In the living assemblages, *C. excavatum* (here *C. selseyense*) is replaced by the two aforementioned *Ammonia* species, predominantly by *A. aomoriensis*. One may argue that this discrepancy could be due to seasonal effects because our sampling was done in late July (Prandtl cruise). However, it is very unlikely to have such a faunal turnover of the dominant species (e.g., Alve and Murray, 2001; Francescangeli, 2017; Saad and Wade, 2016b). In addition, this hypothesis is corroborated by the fact that on May 2014 (Alkor cruise), *A. aomoriensis* was already the most abundant species together with *H. germanica*. A possible explanation could be the appearance of *A. aomoriensis* in the Wadden Sea at the end of 1990s (Pawlowski and Holzmann, 2008). In the Kiel Fjord, data from the year 2000 suggest that the new immigrant *A. aomoriensis* successfully settled in because the species was adapting easily to brackish conditions (Schweizer et al., 2011). Although *C. selseyense* and *A. aomoriensis* probably share the same ecological niche, the latter has a more opportunistic behaviour (Nikulina et al., 2008). This taxon, originally described from Asia, was probably transported in ballast tank water by shipping (Pawlowski and Holzmann, 2008) and successfully colonised brackish environments close to waterfronts. Human-induced introduction of alien species is a serious problem, and it also concerns foraminifera. For instance, the invasion of the “Japanese” species *Trochammina hadai* initially took place in west coast of North America (McGann et al., 2012; McGann and Sloan, 1996; McGann et al., 2000). More recently, the species invaded Brazil and occupied the ecological niche of *C. excavatum* (Eichler et al., 2018).

The NMDS shows significant dissimilarities between the dead assemblages from 1981 and 2019 (and 2014), although they were dominated by the same species (Figure 7B). As BF are strictly linked to the surrounding environmental conditions, it is evident that something has changed in the Elbe Estuary during the last forty years. Following the original description of Wang and Murray (1983) “foraminiferal assemblages in estuarine sediments may consist of: (1) indigenous (living + dead) forms living mainly on tidal flats and marshes; (2) reworked, or relict forms derived from the erosion of penecontemporaneous or older sediments; and (3) open marine forms transported in by tidal currents either as bedload or in suspension within the water column (exotic specimens)”, foraminiferal assemblages in the navigation channel are the results of a mixing of these three components. In the Elbe Estuary, the same authors found that about 22-24% of the total assemblage was composed by exotic species, brought in the suspension load. On the contrary, our results show that the percentage of exotic species (such as *Asterigerina mamilla*, *Egerelloides scabra*, and *Reussolina laevis*) is negligible (on average <1 %). This may suggest that there was a change in the hydrodynamic conditions. Over the past forty years, the deepening of the navigation channel to accommodate the development of maritime traffic led to the speeding of the tidal currents (Boehlich and Strotmann, 2019). The boosting of the sediment dynamics probably not only prevented the development of a sustaining living BF as discussed above, but even inhibited the settlement of suspended species coming from the outer estuary. The present dead foraminiferal assemblages are mainly composed by bedload transported specimens from the surrounding intertidal areas. This hypothesis is supported by the fact that the distribution of dead individuals, in terms of foraminiferal densities, is very similar to that of reworked specimens. Therefore, they are subjected to the same physical process.

4.4 Expected future environmental changes

Although there was an overall improvement of the water quality over the last decades, the nutrient load of the Elbe Estuary is still too high by about one third of ecologically acceptable values, despite the recent implementation of enforced water management measures (e.g., the ban of fertilizer and slurry spreading close to sluice systems and improvements of waste water treatment) (IKSE, 2019; Serna et al., 2010). Moreover, the nitrogen load is imbalanced versus phosphorous (31:1) as compared to the Redfield ratio (16:1). The high nitrate availability would rather promote the growth of bacterial biofilms than feeding diatoms, which are an essential food source for marginal marine foraminifera (e.g., Austin et al., 2005).

At the estuary, active salt marsh patches represent the transitional zone between the marine/fluvial and terrestrial realms, significantly contributing to the wave-energy attenuation in the estuarine environment during storm surges (e.g., Feagin et al., 2009). However, the landward propagation of these coastal wetlands, as a function of sea-level rise (SLR), is prevented by massive dikes in the hinterland, leading to an increased erosion rate at their seaward margins (Kirwan and Megonigal, 2013; Mariotti and Fagherazzi, 2010). As a result, a loss of these wetlands will likely lead to higher-energy conditions in the river channel during storm surges under projected future SLR scenarios.

Sea level rise, higher spring tides and storm surge water levels, and dredging of the navigation channel will further increase sediment erosion and re-deposition. The extensive slack-water mud drapes will diminish, which are a food source for grazing foraminifera. It is conceivable that only those species will be successfully coping with the changes, which may use different food sources and are highly mobile changing microhabitats, also in vertical direction. *Ammonia* species have these capabilities indeed (e.g., Langer et al., 1989). We therefore speculate that the population density of living benthic foraminifera will decrease in the Elbe Estuary, and that the dominance of *A. aomoriensis*, together with *A. tepida*, will further increase in the coming decade.

5 Conclusions

Living and dead foraminiferal communities along the navigation channel of the Elbe Estuary are composed by low abundant and poorly diversified assemblages. Low salinities and rapid salinity changes, coupled to the high-frequency dredging of the navigation channel, confines the proliferation of benthic foraminifera in the estuary. This has been different 40 years ago. Sediment dynamics, strengthened by human-related interventions, induce big discrepancies between living fauna and dead assemblages in terms of densities, diversities and species composition. The living fauna is largely dominated by *A. aomoriensis*, an invasive species, that probably appeared in the Wadden Sea around the year 2000. In the dead fauna, *A. aomoriensis* is associated to *H. germanica* and *C. selseyense*. These taxa were probably bedload transported from the surrounding marsh and tidal flat areas. This study evidences the importance of baseline investigations to plan further environmental monitoring of ongoing climate and human-related changes in the Elbe Estuary, based on benthic foraminifera.

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Data availability

All data reported in this manuscript will be archived in the PANGAEA Open Access library (www.pangaea.de).

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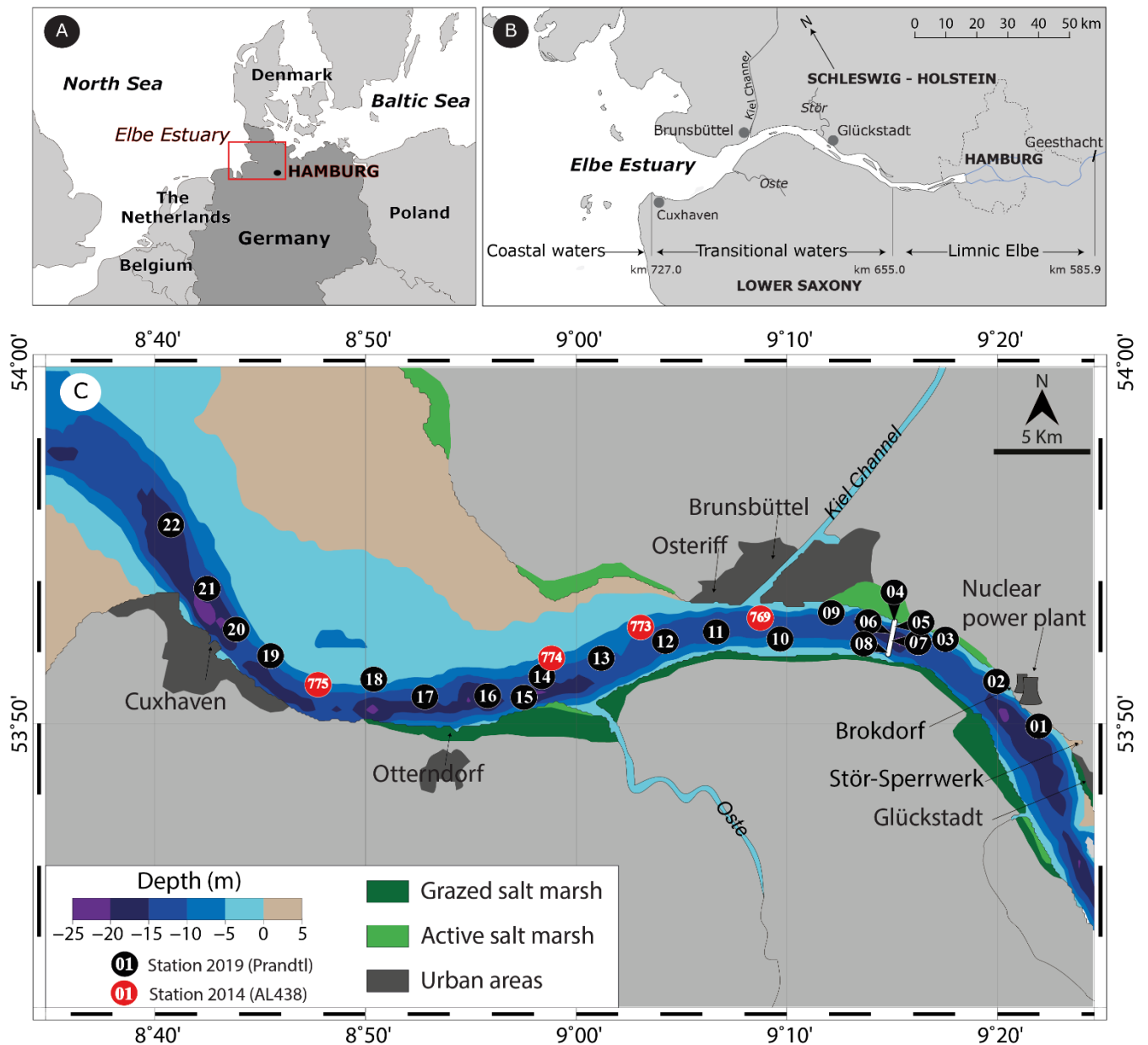


Figure 1. A) Location of the Elbe Estuary in Europe; B) Categories of surface water bodies in the Elbe Estuary (modified from Carstens et al. 2004); C) Bathymetry of the Elbe Estuary and location of the sampling stations from RVs Prandtl 2019 and Alkor (AL438) 2014 cruises (Schönfeld et al., 2014). Positions of the tidal-gauges are indicated as well. Geographical coordinates are referred to World Geodetic System 1984 (WGS-84).

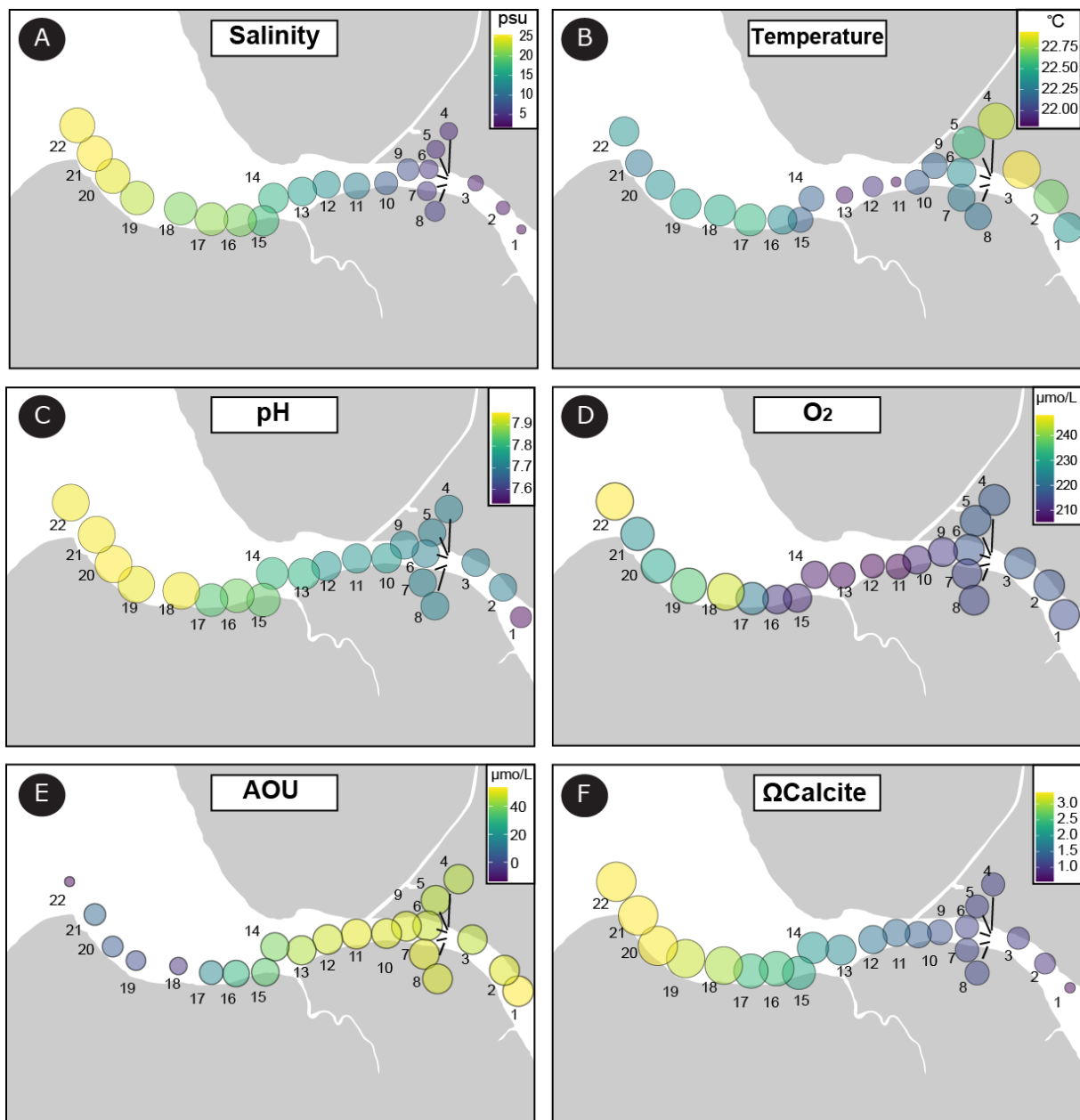


Figure 2. Water parameters for the 22 sampling stations in the Elbe Estuary: salinity, temperature, pH, dissolved oxygen (O₂), oxygen saturation or apparent oxygen utilisation (AOU) and calcite saturation state (Ω).

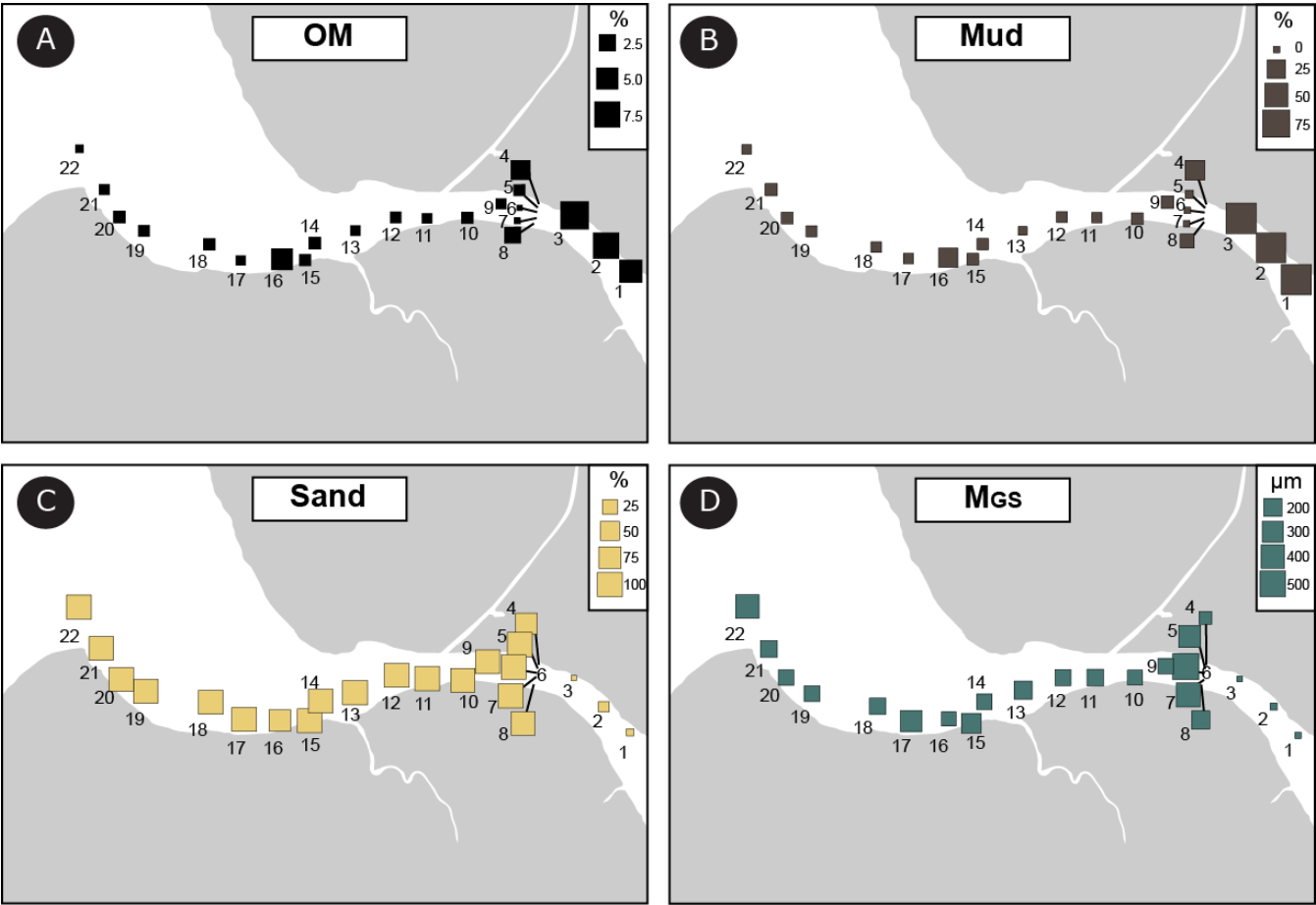


Figure 3. Sediment parameters for the 22 sampling stations in the Elbe Estuary: organic matter (OM), mud, sand and mean grain-size (Mgs),

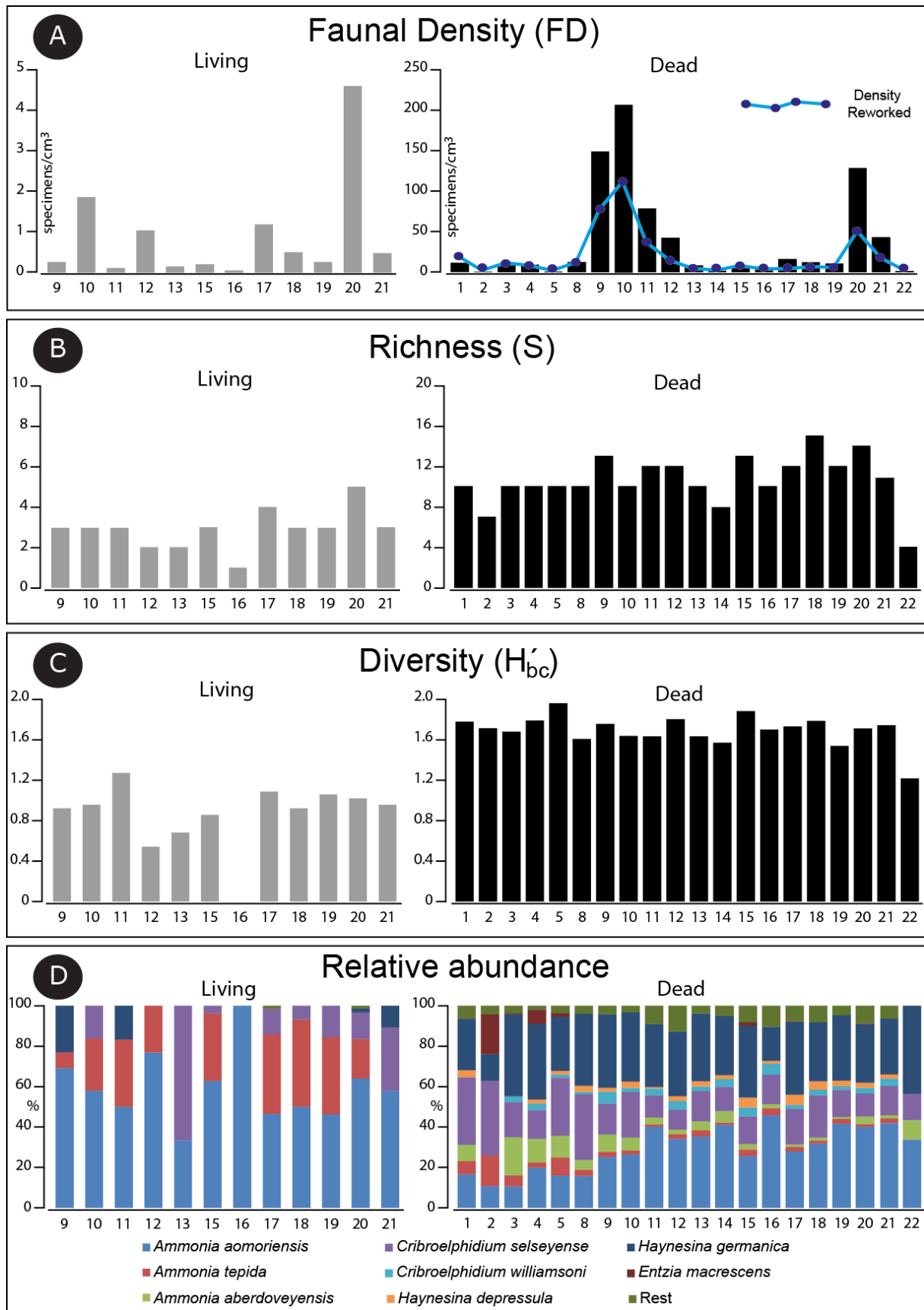


Figure 4. Characteristics of living and dead foraminiferal assemblages in the Elbe Estuary: A) Faunal density (FD, specimens/cm³); B) Species richness (S); C) Diversity (H'_{bc}), and D) Relative abundance of the most dominant species.

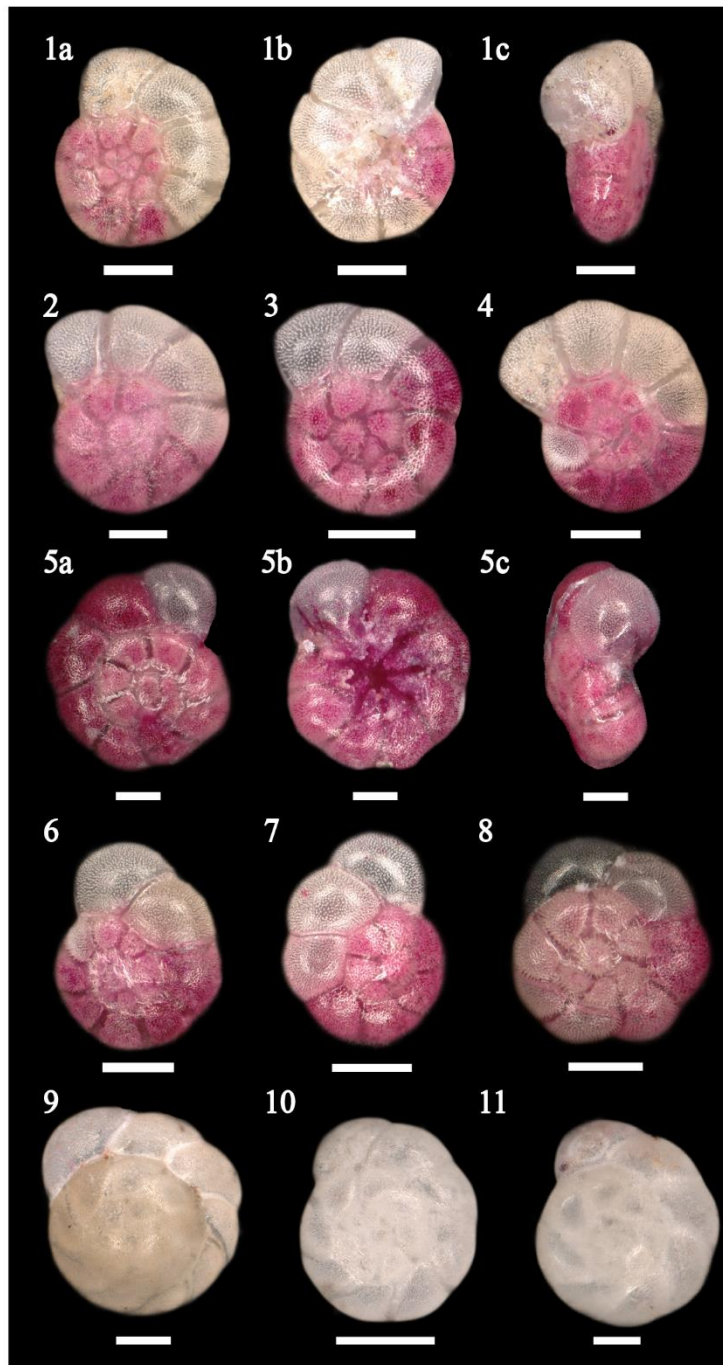


Figure 5. Transmitted light images (Keyence VHX-6000) of different of *Ammonia* species in the Elbe Estuary: 1a-b-c) Dorsal, ventral and lateral view of *Ammonia aomoriensis* (T6); 2-4) *Ammonia aomoriesis*; 5a-b-c) Dorsal, ventral and lateral view of *Ammonia tepida* (T1); 5-8) *Ammonia tepida*; 9-11 *Ammonia aberdoveyensis* (T2). Morphotypes T1, T2 and T6 after Richirt et al. (2019).

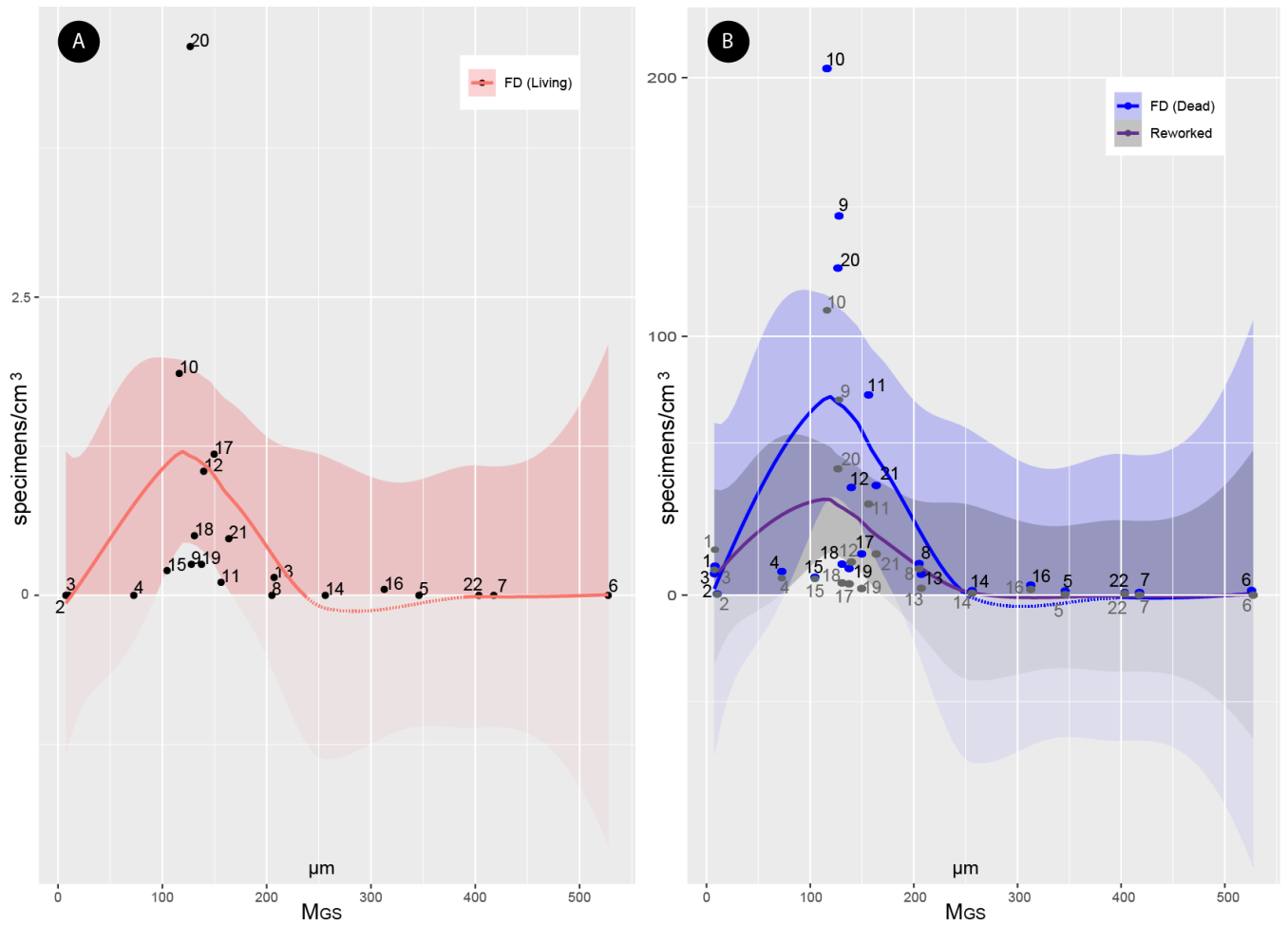


Figure 6. Relation between the mean grainsize (M_{GS} μm) and faunal density (FD, specimens/ cm^3) for living (A), dead and reworked (B) individuals. The lines represent the predict models from a local polynomial regression fitting by means LOESS (locally estimated scatter plot smoothing). Coloured areas represent the level of confidence (95%) of the relative loess curves.

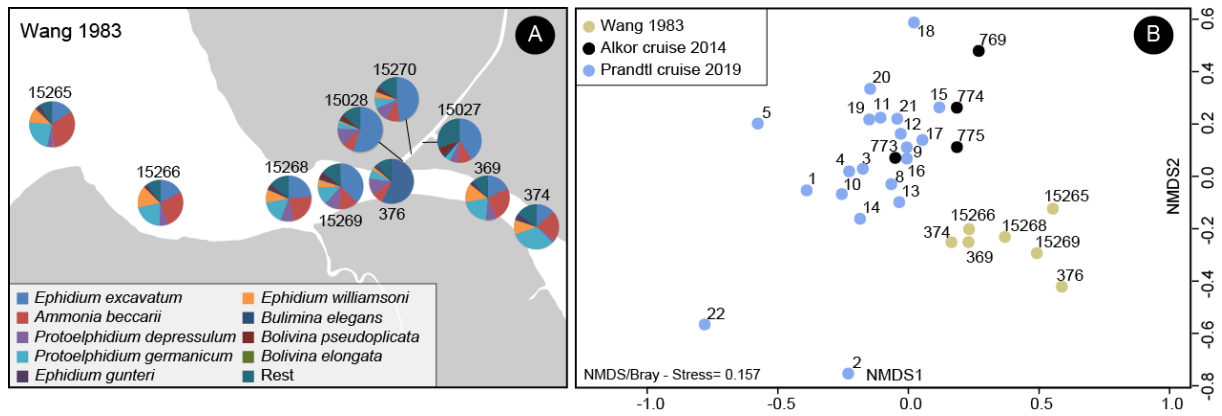


Figure 7. A) Distribution of the dead assemblages in the Elbe Estuary from Wang 1983; B) NMDS based on foraminiferal relative abundances from Wang (1983) (yellow circles), the current study (Alkor cruise 2014=black circles, Prandtl cruise 2019=blue circles).

Table 1. Geographical coordinates (WGS-84) and on-board measured water depth (m) for the 22 sampling stations in the Elbe Estuary, as well as the current tide levels observed at gauges located in the vicinity of the sampling stations, and the resulting sediment-surface levels (SSL) (m above NHN).

Stations	East-X	North-Y	SSL [m above NHN]
1	9° 21' 35.452"	53° 49' 56.489"	-7.5
2	9° 19' 44.367"	53° 51' 5.53"	-9.02
3	9° 17' 41.1"	53° 52' 10.182"	-8.71
4	9° 15' 12.438"	53° 52' 45.599"	-4.49
5	9° 15' 8.654"	53° 52' 41.084"	-15.87
6	9° 15' 33.503"	53° 52' 33.503"	-18.79
7	9° 14' 59.92"	53° 52' 23.038"	-17.7
8	9° 14' 47.461"	53° 52' 8.256"	-6.6
9	9° 12' 13.967"	53° 52' 32.38"	-6.22
10	9° 9' 34.178"	53° 52' 26.148"	-6.56
11	9° 6' 44.863"	53° 52' 28.859"	-10.91
12	9° 4' 18.137"	53° 52' 0.325"	-9.17
13	9° 1' 35.356"	53° 51' 21.298"	-15.1
14	8° 57' 54.183"	53° 50' 39.581"	-9.04
15	8° 56' 4.444"	53° 50' 25.469"	-9.51
16	8° 52' 59.138"	53° 50' 11.332"	-12.62
17	8° 50' 30.976"	53° 50' 49.114"	-4.74
18	8° 47' 56.893"	53° 50' 58.222"	-5.34
19	8° 45' 31.503"	53° 51' 29.074"	-6.12
20	8° 43' 53.385"	53° 52' 19.506"	-12.25
21	8° 42' 25.142"	53° 53' 37.619"	-16.41
22	8° 40' 57.633"	53° 55' 13.235"	-16.87