Research Article

The response of foraminifera to rapid sea-level rise from tidal restoration of Ni-les'tun marsh, Oregon, U.S.A

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ABSTRACT

Foraminifera preserved in saltmarshes are widely used to reconstruct relative sea-level change (RSL), and inferred from this, coseismic vertical coastal motions following an earthquake. However, how quickly foraminifera respond to rapid changes in RSL is poorly understood. Here, we present a six-year foraminiferal study of the tidal restoration of Ni-les'tun marsh and a comparison of modern and fossil assemblages. We installed eight stations on the marsh and sampled these stations for live foraminifera prior to and during the first six years after tidal restoration (2011–2017), and we extruded one short core at station 1 in 2016. At stations 1 to 7, tidal flat/low marsh assemblages, dominated by *Miliammina fusca,* colonized 10 months to 2.5 years after tidal restoration. At station 8, the first living mixed assemblage of foraminifera, dominated by *Haplophragmoides wilberti,* was found 2 years after tidal restoration. Our observations suggest that *M. fusca,* and to some extent *H. wilberti,* are opportunistic species (r-strategists), able to increase their standing crop rapidly after invading a new habitat (to up to ~3600 specimens per 10 cm^3 sediment volume). Potential causes for the delay in foraminifera colonization include their reproductive cycle and/or limited food availability due to the slow response of the vegetation community and soil development to tidal restoration. However, the similarity among assemblages and concentrations of agglutinated foraminifera between the fossil and modern sediments, indicate that post-depositional taphonomic processes have minimal influence when incorporated in the stratigraphic record. Although foraminifera have shown a delayed response to tidal restoration in the Ni-les'tun marsh, the similarities between the modern and fossil assemblages indicate that the delayed response of foraminifera to tidal restoration is undetectable in study areas with low sedimentation rates (in this case 3.3 mm/yr) after tidal restoration. In the case of high post-earthquake sedimentation rates, sampling a few cm higher rather than immediately above an earthquake contact could avoid uncertainties of coseismic vertical motions when foraminifera have a delayed colonization.

1. Introduction

Foraminifera are unicellular protists, living in deep marine to coastal environments (e.g., d'Orbigny, 1826; Sen Gupta, 2003; Murray, 2014). Their diversity, morphology, species composition, geochemistry and preservation potential has enabled foraminifera to be widely used to reconstruct paleoenvironmental conditions (e.g., Kucera et al., 2005; Lisiecki and Raymo, 2005; Jorissen et al., 2007; Ravelo and Hillaire-Marcel, 2007).

In intertidal environments, modern foraminifera have a strong relationship to elevation with respect to the tidal frame because of differing degrees of tidal inundation and related environmental conditions such as salinity, substrate, vegetation, and pH (e.g., Scott and Medioli, 1978; de Rijk and Troelstra, 1997; Horton and Edwards, 2006; Walker et al., 2020). Due to their strong relation to elevation, foraminifera have been used as indicators to reconstruct past relative sea-level (RSL) changes (e.g., Gehrels, 1994; Kemp et al., 2011; Walker et al., 2021). Similarly, intertidal foraminifera have been used to reconstruct earthquake-induced (coseismic) land-level changes along the U.S. Pacific Northwest coast (e.g., Guilbault et al., 1995; Nelson et al., 1996a;

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Hawkes et al., 2011; Milker et al., 2016) and elswehere (e.g., Hayward et al., 2016) where large earthquakes occur. During such great earthquakes coastal areas along the U.S. Pacific Northwest coast subside, which leads to sudden RSL rise and the subsequent burial of saltmarshes by lower intertidal sediment (e.g., Nelson et al., 1996b; Atwater and Hemphill-Haley, 1997).

The accuracy of RSL reconstructions depends on how quickly foraminifera respond to RSL changes, especially for rapid events such as the recolonization of buried saltmarshes after coseismic coastal subsidence. A delay in re-colonization of buried saltmarshes could lead to coseismic subsidence estimates that include contributions from postseismic land-level motions (Horton et al., 2017) and therefore induce an uncertainty in inferring earthquake magnitudes (Wang et al., 2013). To study the response of foraminifera to coseismic coastal subsidence, we conducted an experiment in the Ni-les'tun marsh of Bandon Marsh National Wildlife Refuge (BMNWR) where tide gates were removed in August 2011 to restore the tidal hydrology of the marsh (Fig. 1). The removal of tide gates simulated an instantaneous, rapid ~1 m RSL rise that is approximately equivalent to a Mw 8.1–8.8 earthquake along the U.S. Pacific Northwest coast (Wang et al., 2013). Horton et al. (2017) previously showed that foraminifera first recolonized the Ni'les-tun marsh no earlier than 11 months after tidal restoration. Here, we extend the foraminiferal observations spatially and temporally to analyze the recolonization of a range of intertidal environments over a period of six years after tidal restoration. We also investigated a sediment core from the marsh to understand the degree to which the present changes during restoration are analogs of changes in the fossil record. We used a multi-proxy approach combining microfossil, geochemical and sedimentological data to elucidate possible reasons for the delayed recolonization of the Ni-les'tun marsh by foraminifera. This study expands our knowledge of saltmarsh dynamics following tidal restoration and of the subsequent ecological responses by foraminifera.

2. Study area

Ni-les'tun marsh is situated on the north bank of the Coquille River estuary in southern Oregon, U.S. Pacific coast (Fig. 2). It consists of freshwater and intertidal marshes and encompasses a total area of 2.4 km^2 (Silver et al., 2015), and is part of the BMNWR. Since the late 1800s Ni-les'tun marsh was diked, ditched, and drained, and then used as pasture for domestic animals and for agriculture until 2009 (Beard, 2013; U.S. Fish and Wildlife Service, 2019). Gates installed at the heads of key tidal channels (Fig. 2C) prevented tides from entering most parts of the marsh, except for some low elevation areas that had a muted tidal influence (Brophy and van de Wetering, 2012; Brophy et al., 2014).

To restore the tidal hydrology of the marsh, tidal channels were excavated in 2009, and dike and tide gates were removed in August 2011 (Brophy and van de Wetering, 2012; Brophy et al., 2014; Brown et al., 2016; Fig. 2C). Subsequently, mean daily maximum tidal heights, calculated from water logger data in lower Fahys Creek (Fig. 2C), rose to heights comparable to those of the Coquille River (Brophy et al., 2014; Horton et al., 2017). Similarly, salinity, measured by conductivity-temperature data loggers (Fig. 2C), increased immediately after tidal restoration (Brophy et al., 2014; Horton et al., 2017), indicating that tidal hydrology had been restored within a month of dike breaching. Ni-les'tun marsh is now connected to the Coquille River via the Fahys, Redd and No Name Creeks (Fig. 2C), and is influenced by semidiurnal and mesotidal tides having a great diurnal range of 2.02 m (Mean Higher High Water, MHHW (2.15 m NAVD88) to Mean Lower Low Water, MLLW (0.13 m NAVD88)) in the Coquille river (tidal epoch 1983–2001; Fig. 2C) (Ewald, 2003). Eyewitnesses didn't report any extreme flooding of the Ni-les'tun marsh after tidal restoration until September 2017.

The climate in the Coquille River area is temperate with warm and dry summers and wet and cool autumns and winters (Peel et al., 2007). Mean monthly air temperatures, measured at the national weather station in Bandon (ID: GHCND:USC00350471; National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information, 2021; Fig. 2A) for the observational period (2011–2016) where highest in July and August, ranging between 16.9°C (July 2011) and 14.6°C (July 2012), and lowest in January and December, ranging between 4.0°C (December 2013) and 8.6°C (January 2015). Total monthly precipitation was lowest in July and August, ranging between 0 mm (July 2013) and 2.3 mm (August 2014) and highest from September to March, ranging between 530.6 mm (December 2015) and 176.8 mm (September 2013).

3. Material and methods

3.1. Sampling design

We installed eight sampling stations near pre-existing United States Geological Survey surface elevation tables and groundwater loggers that had elevational control (Fig. 2C and Table 1). We surveyed stations 1 to 4 to surface elevation tables and stations 5 to 8 to groundwater wells using Real-time Kinematic-GPS/GNSS and total station equipment (Brophy and van de Wetering, 2012; Fig. 2C).

We took a total of 200 surface samples (1-cm-thick) for foraminiferal, and 120 surface samples for sedimentological, and geochemical analyses. Initial sampling started three days prior to tidal restoration in August 2011 and then samples were taken periodically (bi-weekly in the first month after tidal restoration and then monthly) during the first year of restoration. Another set of samples for foraminiferal investigations
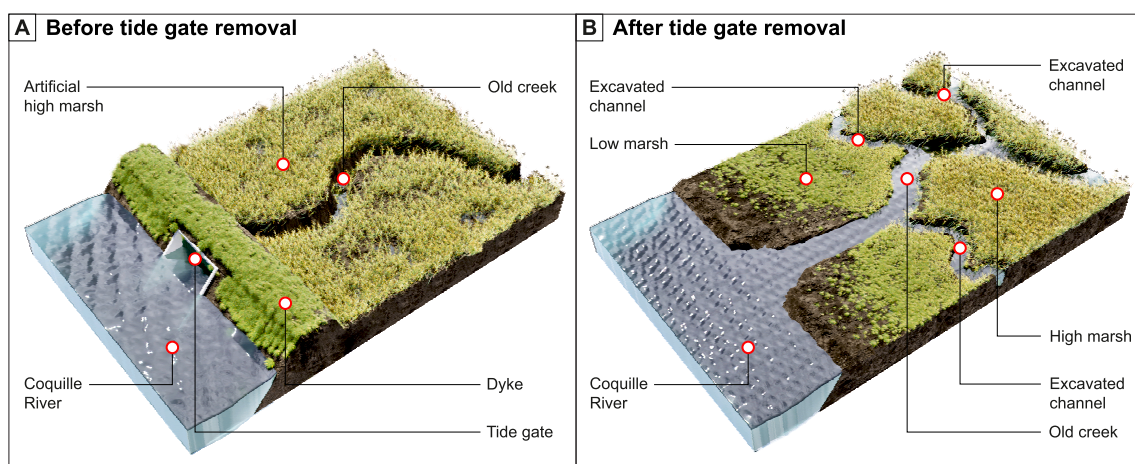

Fig. 1. A schematic illustrating the tidal restoration of the Ni-les'tun marsh.
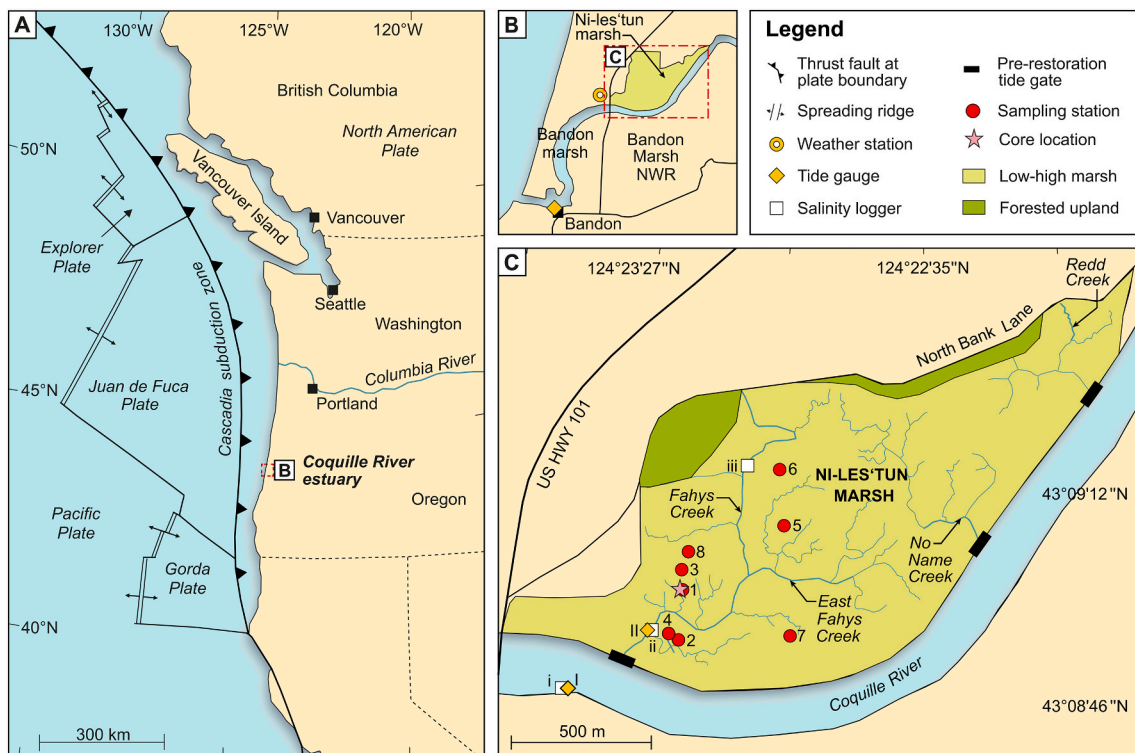
Fig. 2. A. Map of the Pacific coast of central North America showing major features of the Cascadia subduction zone and location of the study area in the Coquille River estuary. B. Bandon Marsh National Wildlife Refuge (BMNWR) with the Ni-les'tun marsh (restoration site) and Bandon marsh (control site) and location of the permanently installed Bandon tide gauge and weather station. C. Location of the investigated stations (red circles) and the short core (light red star) in the Ni-les'tun marsh (see also Table 1) and location of the temporarily tide gauges (installed in the Coquille River (I) and Lower Fahys Creek (II)), and salinity loggers installed in the Coquille River (i) and in the Fahys Creek (ii, iii). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Latitude, longitude, prerestoration elevation, and plant community changes at the investigated stations in the Ni-les'tun marsh (NAVD88 = North American vertical datum of 1988).

Ni-les'tun marsh (NM) stations	Latitude	Longitude	Elevation [m NAVD88]	Pre-restoration vegetation 2011	Post-restoration vegetation 2012	Post-restoration vegetation 2017
Station 1	43° 8.894′N	124° 23.270′W	1.45	*Juncus balticus, Agrostis stolonifera, Scirpus microcarpus, Distichlis spicata, Potentilla anserina*	*Carex lyngbyei, S. microcarpus, J. balticus*	*C. lyngbyei, Triglochim maritinum, S. microcarpus, D. spicata*
Station 2	43° 8.894′N	124° 23.301′W	1.50	*D. spicata, A. stolonifera*	*D. spicata*	*D. spicata*
Station 3	43° 9.027′N	124° 23.279′W	1.68	*P. anserina, J. balticus, A. stolonifera*	*Eleocharis palustris, D. spicata, A. stolonifera*	*E. palustris, Salicornia virginica*
Station 4	43° 8.882′N	124° 23.270′W	1.74	*D. spicata, A. stolonifera*	*D. spicata*	*D. spicata*
Station 5	43° 9.120′N	124° 22.997′W	1.84	*Lotus* spp., *Trifolium repens, Fescue arundinacea*	*Atriplex patula*	*Deschampsia cespitosa, Trifolium maritinum, S. microcarpus, D.spicata*
Station 6	43° 9.245′N	124° 23.019′W	1.98	*J. balticus, Lotus* spp., *P. anserina, Fescue* spp.	*A. pacifica, J. balticus*	*A. stolonifera, Argentina egedii, E. palustris*
Station 7	43° 8.890′N	124° 22.966′W	1.99	*Festuca arundinacea, Lotus* spp.	*A. stolonifera, F. arundinacea*	*A. stolonifera, A. patula, D. spicata*
Station 8	43° 9.065′N	124° 23.271′W	2.07	*P. anserina, A. stolonifera*	*A. pacifica, A. stolonifera, Fescue* spp.	*D. cespitosa, P. anserina, A. patula*

were taken every two to six months until September 2017. We did not take replicates or pseudoreplicates.

Vascular plants were described in August 2011, August 2012 and September 2017 following Eilers (1975) and Hawkes et al. (2010).

We also extruded one 19-cm-long core (inner diameter 10 cm) from station 1 in March 2016 to evaluate how changes in modern foraminiferal faunas during restoration compare with changes in the fossil record. Core stratigraphy was described using the methods of Nelson (2015).

3.2. Foraminiferal analyses

We analyzed 165 out of the 200 surface samples collected for foraminifera. Stations 5 to 8 contained no foraminifera in the earlier phase of tidal restoration and therefore were investigated at a lower temporal resolution until first foraminifera have been found. All samples were bulk stained with Rose Bengal (Walton, 1952) on the sampling day to help identify living specimens, stored in a buffered ethanol/ water solution (50:50), and refrigerated at 5°C for at least two weeks (Schönfeld

et al., 2012). Wet sample volume of each sample was measured. The short core from station 1 was sampled at 0.5 cm intervals for the first 5 cm. The volume of surface and fossil samples was standardized to 10 cm^3.

We wet-sieved all surface and core samples through 500 μm and 63 μm screens, and we used a wet-splitter (Scott and Hermelin, 1993) to split the fraction between 63 and 500 μm into eight equal aliquots (Horton, 1997; Horton and Edwards, 2006). Foraminifera were counted wet under a binocular microscope to prevent drying of the organic residue and destruction of organic-bounded agglutinated tests (de Rijk, 1995), and to facilitate the identification of modern stained foraminifera. Only tests with all but the last chamber clearly stained red were counted as living at the time of collection (Murray and Bowser, 2000). We counted at least 100 living foraminifera where possible (Kemp et al., 2020). We counted live foraminifera (e.g., Murray, 1971) rather than dead (e.g., Horton, 1999 to total (e.g., Scott and Medioli, 1980) assemblages. Murray (1971) stated that only foraminiferal life assemblages can be used to interpret environmental conditions. Nevertheless, only detailed observation of the life assemblage over a considerable period of time can be used to determine all aspects of a population (Buzas, 1968).

Taxa were identified according to the taxonomic descriptions in Andersen (1953) and Milker et al. (2015a). A taxonomic correction of *Haplophragmoides* species presented in Milker et al. (2015a, 2015b, 2016) and Horton et al. (2017) was necessary, following the descriptions and illustrations of *Haplophragmoides wilberti* and *Haplophragmoides manilaensis* in Andersen (1953). We concentrated on hard-shelled foraminifera since soft-shelled foraminifera are difficult to preserve in the fossil record (Kitazato et al., 2017).

We calculated the Shannon-Wiener diversity (Shannon, 1948) of the live populations. To compare the live populations at the restoration site six years after tidal restoration with the averaged live populations at the control site (Bandon marsh; Fig. 1B; Milker et al., 2015b), we used Correspondence Analysis (CA; Hirschfeld, 1935). Shannon-Wiener diversity and CA were calculated with PaST, version 4.03 (Hammer et al., 2001).

3.3. Grainsize and geochemical analyses

We analyzed 120 surface samples for grainsize and geochemistry (stable carbon isotopes (δ^{13}C) and C/N). For grainsize measurements, all samples were treated with hydrogen peroxide (20%) to oxidize organic matter (Robinson, 1927). Grainsize distribution was then determined with a Beckman Coulter Laser Diffraction Particle Size Analyzer. Sand, silt and clay contents are reported as differential volume (i.e., the percentage of total volume that each size class occupies) based on the Wentworth Phi Scale (Wentworth, 1922).

Bulk geochemical analyses of surface samples have frequently been used in coastal environments (e.g., Lamb et al., 2006; Kemp et al., 2010; Engelhart et al., 2013). Our geochemical samples were immediately refrigerated (~4°C) in darkness to prevent photo-oxidation of the organic components and to limit microbial activity (Khan et al., 2015). For analysis of stable carbon isotopes (δ^{13}C) and C/N ratios, approximately 1 cm^3 of wet bulk sediment was treated with 5% HCl for 18 h to remove inorganic carbon, rinsed with at least 1500 ml of deionized water, dried in an oven at 40°C overnight, and ground to a fine powder (Vane et al., 2013). The samples were measured in a Costech Elemental Analyzer coupled on-line to an Optima dual-inlet mass spectrometer. The ratios of C and N were calibrated through an acetanilide standard (formula $CH_3CONHC_6H_5$) because it contains C and N atoms in proportions broadly similar to that found in vegetation, soils and sediments. All C/N values are expressed on a weight ratio basis. The δ^{13}C values were calculated relative to the Vienna Pee Dee Belemnite (VPDB) scale using a within-run laboratory standard (cellulose, Sigma Chemical prod. no. C-6413) calibrated against NBS 19 and NBS 22 standards (compare with Vane et al. (2013)).

We used the non-parametric Mann-Kendall trend test (Mann, 1945) to analyze whether the temporal trends in the sedimentological and geochemical data are significant at the 95% confidence level. Calculations were made with PaST, version 4.03 (Hammer et al., 2001).

4. Results

4.1. Vegetation response to tidal restoration

Before tidal restoration, plant communities at station 1 consisted mainly of *Juncus balticus* and *Agrostis stolonifera*, reflecting minimal tidal influence with occasional brackish water inflow. The remaining stations were dominated by *Distichlis spicata* (station 2 and 4), *Potentilla anserina* (station 3 and 8), *Lotus* spp. (station 5), *J. balticus* (station 6) and *Festuca arundinacea* (station 7) (Table 1).

Stations 1 to 4 have an elevation of 1.45 to 1.74 m NAVD which is between mean tide level (MTL) and mean high water (MHW) (Table 1 and Fig. 3). At station 1 *Juncus balticus* and *Agrostis stolonifera* were replaced by *Carex lyngbyei*, *Scirpus microcarpus* and *J. balticus* in August 2012, and by *C. lyngbyei*, *Triglochin maritima*, *S. microcarpus* and *Distichlis spicata* in August 2017 (Table 1). Stations 2 and 4 were furthermore dominated by *D. spicata* in August 2012 and 2017. Station 3 consisted of *Potentilla anserina*, *J. balticus*, and *A. stolonifera* in August 2011, of *Eleocharis palustris*, *D. spicata* and *A. stolonifera* in August 2012, and of *E. palustris* and *Sarcocornia perennis* in August 2017.

Stations 5 to 7 have an elevation of 1.84 to 1.99 m NAVD and are situated between ~MHW and MHHW (Table 1). At stations 5–7, *Lotus* spp. was a common species besides *Trifolium repens* and *Fescua arundinacea* (Station 5) as well as *J. balticus* and *P. anserina* (Station 6) in August 2011 (Table 1). In August 2012, *Lotus* spp. was absent at Stations 5–7 and *Atriplex patula* colonized at Station 5, *P. anserina* and *J. balticus* at Station 6, and *A. stolonifera* and *F. arundinacea* at station 7. In August 2017, *Deschampsia cespitosa*, *T. maritima*, *S. microcarpus* and *D. spicata* were present at station 5, *A. stolonifera*, *P. anserina* and *E. palustris* at station 6, and *A. stolonifera*, *A. patula* as well as *D. spicata* at station 7.

Station 8 has an elevation of 2.07 m NAVD which is close to MHHW (Table 1). *P. anserina* and *A. stolonifera* were the dominant plants at station 8 in August 2011 and in August 2012 (Table 1). They were replaced by *D. cespitosa*, *P. anserina* and *A. patula* in August 2017.

4.2. Foraminifera response to tidal restoration

Live foraminifera were restricted to stations 1 and 3 before tidal restoration (August 2011). At these stations between 2 and 34 living specimens (per 10cm^3 sediment volume) were identified. These assemblages were dominated by *Miliammina fusca*, *Balticammina pseudomacrescens* and *Entzia macrescens* (Fig. 3).

At stations 1 to 4, a low number of living specimens (1–66 specimens per 10cm^3) were found during the first nine months after tidal restoration (Fig. 3). The first high numbers of live specimens (136–3594 per 10cm^3) were present ten months (June 2012) after flooding and were dominated by a monospecific live population of *M. fusca* (99–100%). *Miliammina fusca* continued to dominate stations 1 to 4 (>40%) until the end of the observation period in August 2017. Other species colonized these stations including calcareous species (1%–61%), which appeared 25 (September 2013) to 37 (September 2014) months after tidal restoration, and *Reophax* spp. (4–37%) which appeared 55 months (March 2016) after tidal restoration. Species diversity at station 1 was highest in the first nine months after restoration (1.35 ± 0.16) but decreased thereafter (0.13 ± 0.17) due to the dominance of *M. fusca* (Figs. 3 and 4). The species diversity at stations 2 to 4 increased 37 months after restoration (0.91 ± 0.33).

At stations 5 to 7, first notable numbers of living foraminifera (41–251 specimens per 10cm^3) were found 16 (December 2012), 18 (February 2013), and 31 (March 2014) months after tidal restoration, respectively (Fig. 3). The live populations were again monospecific by
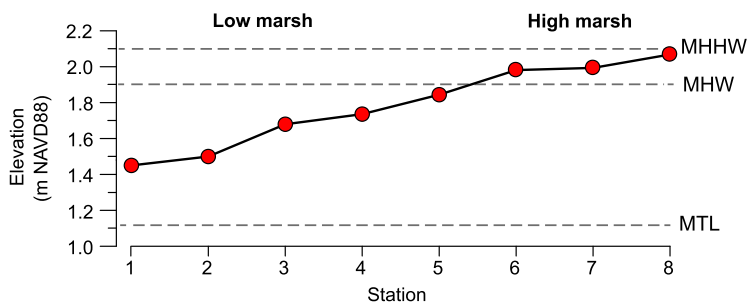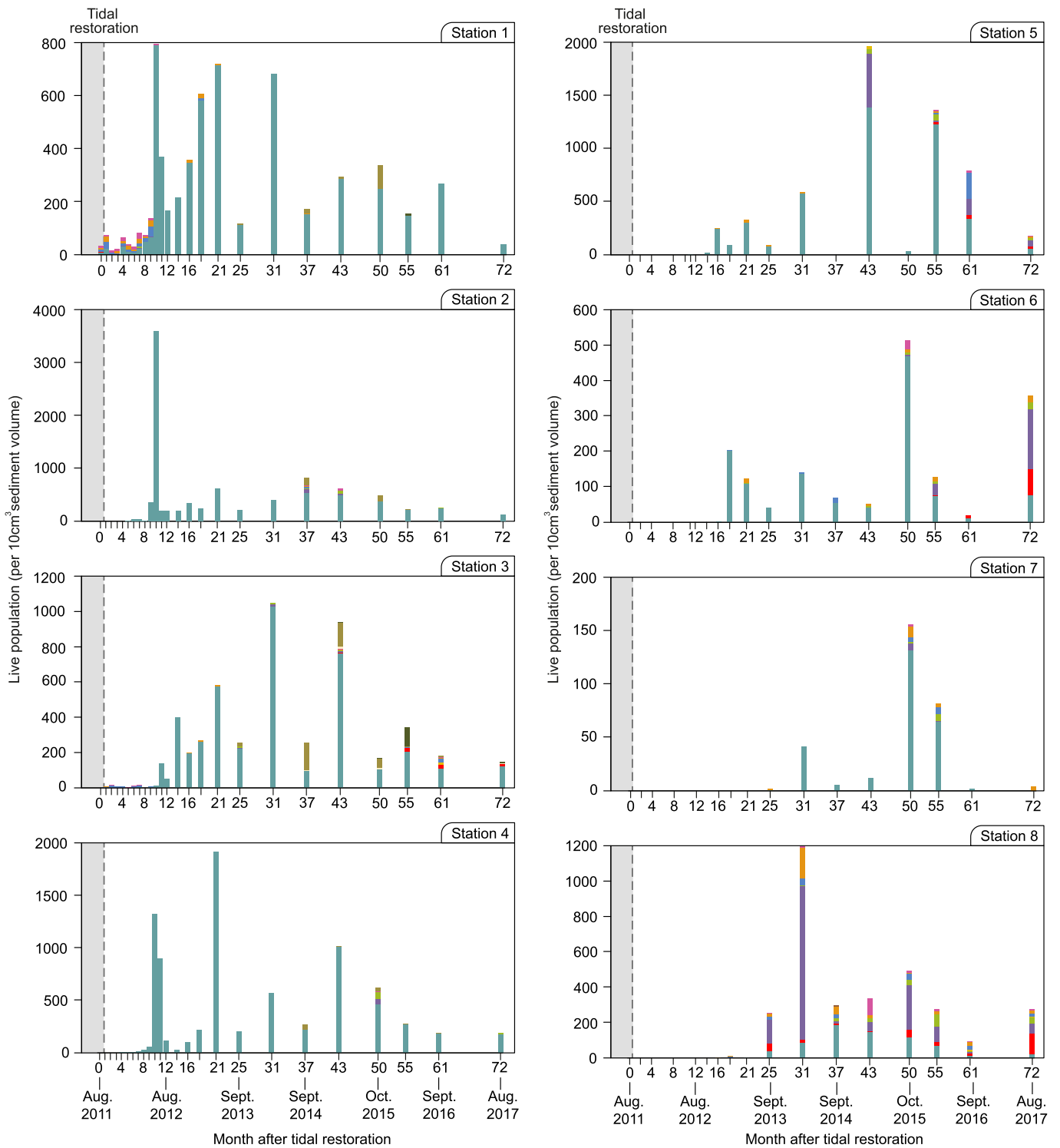
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Fig. 3. Live foraminifera (per 10cm^3 sediment volume) in the Ni-les'tun marsh before and during 72 months after tidal restoration (please note that stations 5 to 8 were counted on a lower temporal resolution because they contained no foraminifera during the earlier phase of tidal restoration), and station prerestoration elevations with tidal datums (mean tide level (MTL), mean high water (MHW) and mean higher high water (MHHW)) measured at the Bandon tide gauge (Fig. 2B). Note that due to sediment accretion the surface of the Ni-les'tun marsh rose by an average of 4.9 cm (Brown et al., 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
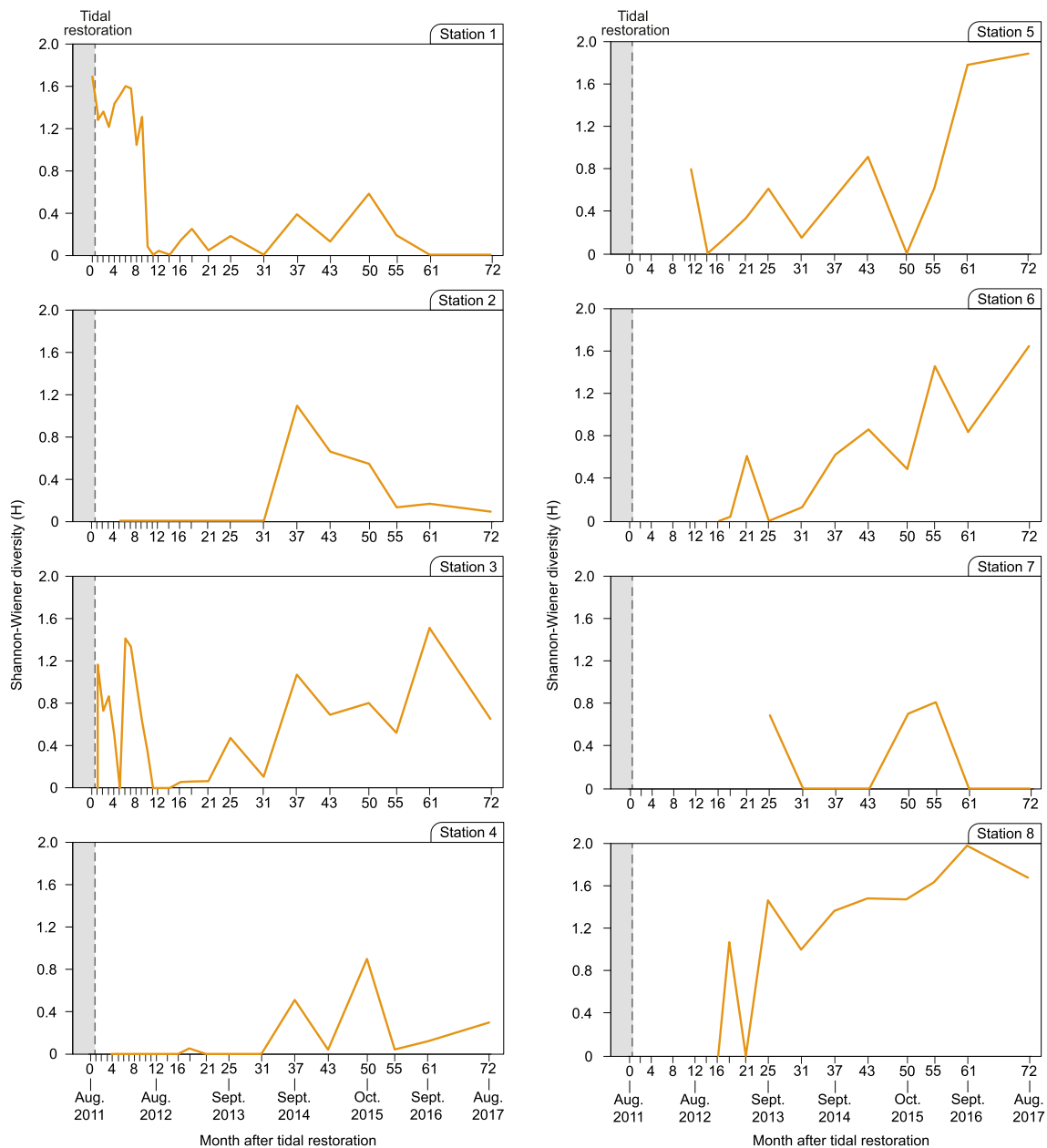

Fig. 4. Shannon-Wiener diversity in the Ni-les'tun marsh before and during 72 months after tidal restoration.

M. fusca (99%) and this species dominated until the end of the observational period (>40%). Between months 49 (September 2015) and 61 (September 2016), species such as *B. pseudomacrescens* (9–30%, stations 5 and 7), *Haplophragmoides wilberti* (18–24%, stations 5 and 6) and *Trochammina inflata* (5–40%, stations 5 and 6), increased in relative abundance. At stations 5 and 6, species diversity increased during the months after tidal restoration reaching a maximum of 1.5 and 1.3, respectively, at 72 months (August 2017) (Fig. 4). There was no pattern in species diversity at station 7.

At station 8, the first live population of foraminifera (272 specimens per 10cm^3) was found 25 months (September 2013) after tidal

restoration (Fig. 3). It was a mixed assemblage, dominated by agglutinated species *H. wilberti* (51%), *T. inflata* (16%) and *M. fusca* (14%). The live populations remained mixed until the end of the observational period with the introduction of other agglutinated species (e.g., *Haplophragmoides manilaensis*, *Trochamminita irregularis*, *B. pseudomacrescens*, and *E. macrescens*). Species diversity increased after 16 months of tidal restoration reaching a maximum of 2.00 at 61 months (September 2016) after tidal restoration (Fig. 4).

The dead assemblages are comparable to the observed live populations, however, the dead assemblage species occurred generally in higher total numbers at most stations with 61 to 792 dead compared to

23 to 338 live specimens (per 10cm³) averaged over each station (Fig. S1). Major differences between live populations and dead assemblages include low numbers of dead specimens at station 2 (1–35 specimens per 10cm³) and station 4 (0–9 specimens per 10 cm³) where live specimens were absent during the first nine months after restoration. They also include unusual high numbers of 2427 specimens of dead *H. wilberti* compared to only three live specimens per 10cm³ at Station 1 seven months after tidal restoration.

4.3. Grainsize and geochemical response to tidal restoration

At all stations, grainsize distributions showed a general increase in silt and clay and a general decrease in sand content in the first year after tidal restoration, with a higher variability and less pronounced change at station 5 to 8 (Fig. 5). Significant temporal trends ($p < 0.05$; Table S2) were observed at station 1 (58.5% increase in silt, 10.5% increase in clay

and 68.2% decrease in sand) and at station 4 (16.5% increase in clay, 20.7% increase in silt and 32.5% decrease in sand) following tidal restoration. The grainsize at stations 6 and 7 show a significant temporal increase in silt of 38.8% and 25.4%, increase in clay of 9.8% and 10.1%, and decrease in sand of 48.7% and 35.4%. Stations 5 has a significant increase in clay of 10.7% and a significant decrease in sand of 37.3% before tidal restoration to one year after tidal restoration.

At stations 1 to 8 the C/N ratios remained relatively constant through time, which was supported by the by the Mann-Kendall trend test results with p values >0.05. An exception is the short-term decrease to 7.7–10.4 at stations 2, 4, 6 and 7 in early September 2011 and the strong increase to 32.6 and 30.9 at stations 2 and 6 in late September 2011 (Fig. 6).

There was a short-term increase in δ^{13}C to −20.7‰ −−24.4‰ at almost all stations, except stations 2 and 5, in early September 2011, followed by a decrease to −23.2‰ and −30.3‰ in late September 2011. The values then remained constant one year after tidal restoration at
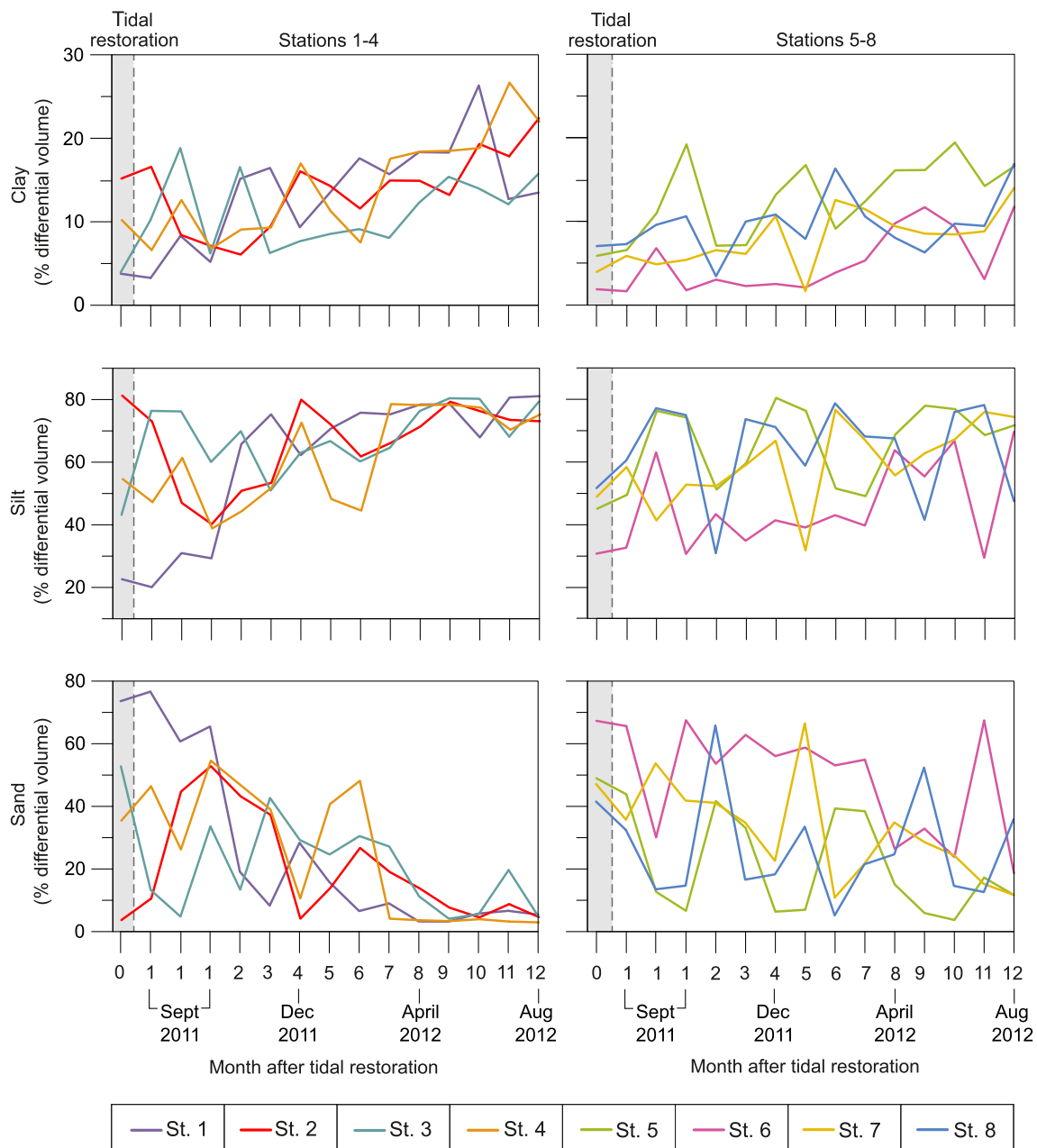

Fig. 5. Grainsize distribution (expressed as a percent of differential volume of sand, silt and clay) at the Ni-les'tun marsh stations prior to tidal restoration and during the first year of tidal restoration.
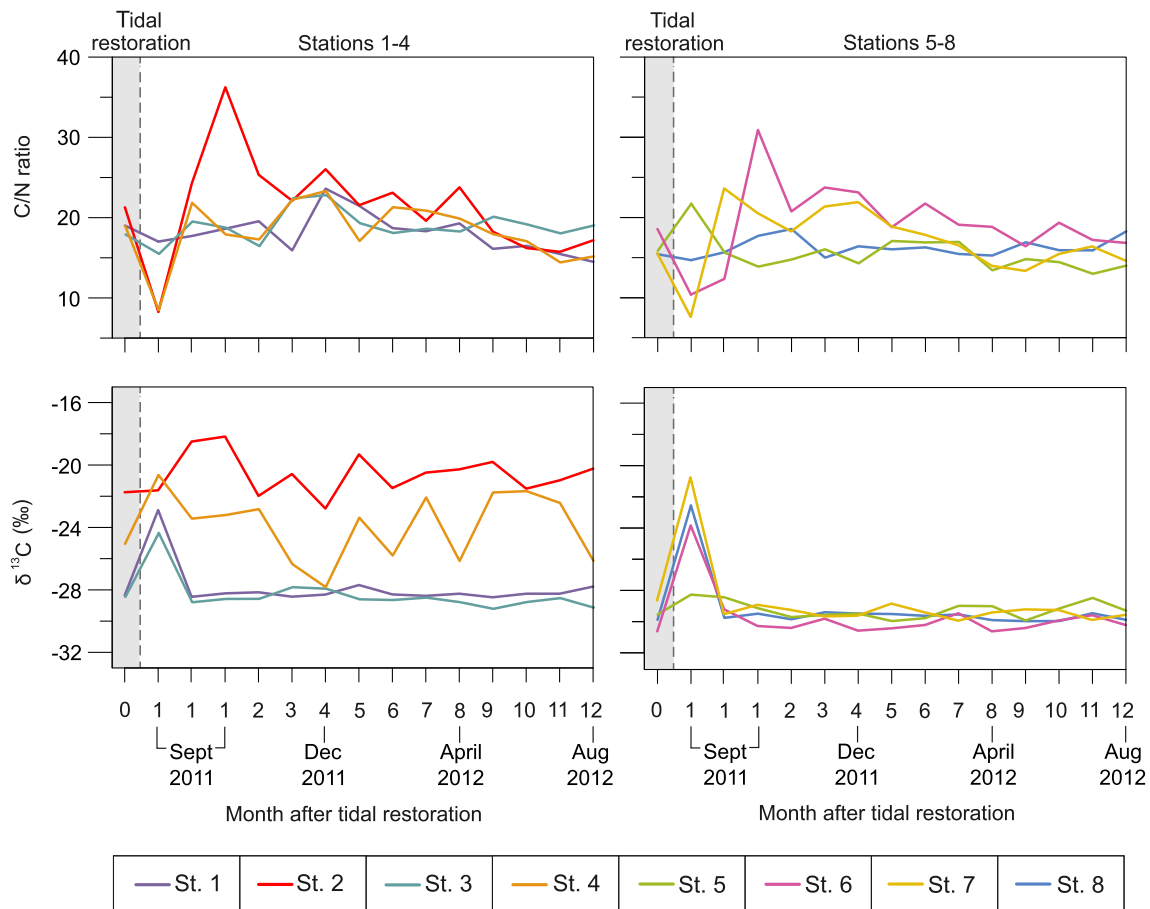
Fig. 6. C/N and δ¹³C values measured at the Ni-les'tun marsh stations prior to and during the first year after tidal restoration.

stations 1, 3 and 5–8. Stations 2 and 4 show fluctuating δ¹³C values between −28.4‰ and −18.2‰ and between −27.9‰ and −20.7‰ during the one year after tidal restoration. The Mann-Kendall trend test suggests significant temporal changes in δ¹³C at stations 3 and 7 (Table S2). They are, however, at very low amplitude (Fig. 6).

4.4. Fossil foraminifera in the short core

Core 1 taken at station 1 (Fig. 2C) is composed of a peaty mud (19–10 cm depth), overlain by a peat (10–1.5 cm depth) with a gradational lower contact (Fig. 7). Abruptly overlying the peat with a sharp contact (< 1 mm) is a 1.5-cm-thick mud, which we interpret as a postrestoration deposit. The total number of foraminifera in the prerestoration peat increases with decreasing depth, from 2 to 290 specimens
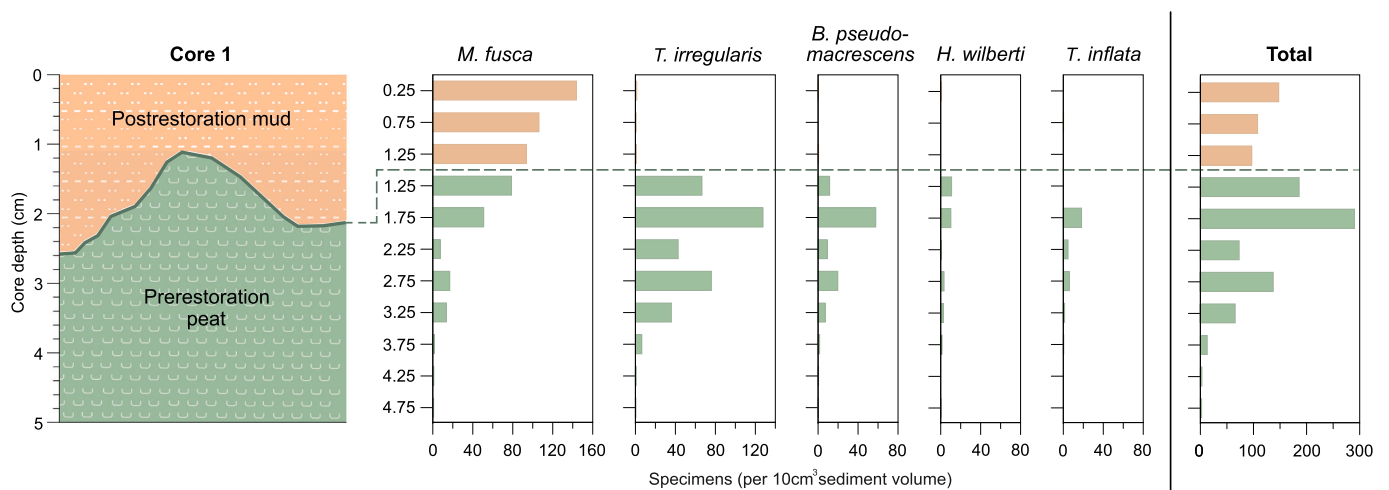

Fig. 7. Lithology of core 1 taken at station 1 (see Fig. 2C) with the dominant fossil species and total foraminifera (per 10cm³ sediment volume) in the upper 5 cm of the core. The green line marks the contact of the prerestoration peat to the postrestoration mud. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(per 10 cm^3). In the postrestoration mud, the total number of foraminifera range from 97, directly above the peat-mud contact, to 147 specimens (per 10 cm^3) one cm above the contact. The foraminiferal assemblage of the prerestoration peat, between 5 and 1.5 cm, is dominated by *T. irregularis* (1–128 specimens per 10cm^3) along with low abundances of *B. pseudomacrescens* and *M. fusca*. Immediately beneath the postrestoration mud, *M. fusca* increases in abundance (51 specimens per 10cm^3). The postrestoration mud is dominated by *M. fusca* (94–144 specimens per 10cm^3).

5. Discussion

5.1. Delayed response of foraminifera to tidal restoration

Tidal restoration of the Ni-les'tun marsh in 2011 had an immediate hydrologic effect (Brophy et al., 2014; Brown et al., 2016; Horton et al., 2017). Daily maximum tidal heights measured in the Ni-les'tun marsh rose by ~1 m and were almost comparable to that measured in the Coquille River one month after tidal restoration (Horton et al., 2017). Data from groundwater wells, installed in the Ni-les'tun marsh, showed that tides propagated freely throughout the marsh (Brophy et al., 2014) and that salinity increased to a level similar to that of the river within days after tidal restoration (Brophy et al., 2014; Horton et al., 2017).

Although tidal inundation had been rapidly restored, our long-term observations indicate a delay in the recolonization of live foraminifera of 10 to 31 months after tidal restoration. At the lower elevation stations (stations 1–4) between MTL and MHW, foraminifera responded 10 to 14 months after tidal restoration (Fig. 3). The live populations were dominated by *M. fusca* with minor contributions from calcareous species (e.g., *Haynesina* sp., *Quinqueloculina* sp.) and *Reophax* spp. This assemblage is indicative of a tidal flat to low marsh environment, where it was found in the Bandon marsh in 2011 and 2012 (Milker et al., 2015b; Figs. 2B and S3) and other saltmarshes along the Oregon coast (e.g., Hawkes et al., 2010; Engelhart et al., 2013; Milker et al., 2015a). At stations with higher elevations near or above MHW (stations 5–7), the first notable numbers of live foraminifera were further delayed, appearing 16 to 31 months after tidal restoration. These stations were also dominated by *M. fusca* during the first 43 months, after which *H. wilberti, B. pseudomacrescens,* and *T. inflata* appeared. This mixed agglutinated assemblage is indicative of middle to high marsh environments (e.g., Hawkes et al., 2010; Engelhart et al., 2013; Milker et al., 2015a). At station 8, which has the highest elevation near MHHW, the first live populations were found 25 months after tidal restoration. The composition of the live populations (e.g., *H. wilberti, T. inflata* and *M. fusca*) is comparable to middle to high marsh assemblages in the Bandon marsh observed in 2011 and 2012 (Milker et al., 2015b; Figs. 2B and S3) and elsewhere along the Oregon coast (e.g., Hawkes et al., 2010; Engelhart et al., 2013; Milker et al., 2015a), but the live populations varied through time suggesting that it was unstable in the six years after tidal restoration.

Studies of recolonization of saltmarsh foraminifera following a disturbance or restoration show a similar delayed response (Sherman and Coull, 1980; Cearreta et al., 2013; Hayward et al., 2015; Masselink et al., 2017). Fritz (2001) observed a virtual absence of foraminifera in the restored Kunz marsh, Sough Slough estuary (Oregon) two to three years after tidal restoration. In the Avon River, New Zealand, Hayward et al. (2015) generally observed a slow change in the foraminiferal assemblages two years after coseismic subsidence during the Canterbury earthquake in 2011, although there were short-term increases of *E. macrescens,* and colonization of formerly barren higher-elevation stations by *Trochamminita salsa*. In the Avon estuary (UK), Masselink et al. (2017) found that foraminifera were delayed by two years after tidal restoration and higher foraminiferal concentrations were only present five years after tidal restoration. Cearreta et al. (2013) observed low to moderate numbers of foraminifera ~6 to 10 years after restoration of a saltmarsh in the Bay of Biscay (Spain). Gerwing et al. (2017)

observed no short-term (5 months) effect on invertebrates in macrotidal mudflats as a result of the opening of spillway gates in the Petitcodiac River in New Brunswick (Canada).

The recolonization of Ni-les'tun marsh was dominated by *M. fusca*, and at station 8 by *H. wilberti*. This suggests that *M. fusca* and possibly *H. wilberti* are opportunistic species (r-strategist), able to reproduce rapidly after invading a new habitat or in response to environmental changes, as also inferred by Murray (2014). Supporting these inferences, nearly monospecific assemblages of *M. fusca* were observed from Lake Onoke in New Zealand where conditions regularly change from a brackish lake to a tidally influenced shallow-subtidal environment due to a temporarily installed barrier (Hayward et al., 2011; Hayward, 2014), reflecting this species' good adaption to changing environmental conditions.

5.2. Possible causes for the delayed response

Alve and Goldstein (2010) reported that foraminifera can be transported as propagules (juvenile stages) and survive in the sediment until conditions are suitable for growth and reproduction. At Ni-les'tun marsh, we assume propagules would have been immediately transported following tidal restoration. For example, at nearby Bandon Marsh, the low and high marsh assemblages are dominated by high numbers of *M. fusca, E. macrescens* and *T. inflata* (Milker et al., 2015b; Fig. S2). Despite the probable presence of propagules, we suggest that conditions were unsuitable for their growth during the first months after tidal restoration. Weinmann and Goldstein (2017) observed a relatively low abundance of specimens in a low marsh in Georgia but found a high number of propagules in a culture experiment with simulated conditions which supports our hypothesis.

Possible causes for delayed colonization include the foraminiferal reproductive cycle, lack of food availability and/or delayed environmental change at Ni-les'tun marsh. Horton et al. (2017) attributed the delayed response by foraminifera to restoration of Ni-les'tun marsh to their reproductive cycle. Notable total live numbers of foraminifera were first present in June 2012 (ten months after restoration), then their numbers generally declined and finally increased during the spring seasons of the following years (Fig. S3). Subsequently, we also found higher abundances during fall seasons. Our observations suggest that foraminifera mainly reproduce when air temperatures were > 10–13°C (measured at the national weather station in Bandon (ID: GHCND: USC00350471) in the spring and fall, but probably not when temperatures were higher and/or under dry conditions in the summer and when temperatures were much colder in winter (Fig. S3). It should, however, be noted that in the later phase of tidal restoration (September 2013 to August 2017), the sampling resolution was lower (every half year) so that small-scale temporal reproduction events are possibly not detected. Laboratory experiments similarly show slower reproduction rates for intertidal and subtidal species at low temperatures (e.g., Bradshaw, 1957; Kitazato and Matsushita, 1996; Saraswat et al., 2011; Weinmann and Goldstein, 2016). Field observations in temperate saltmarshes suggest that the largest living standing crops occur in summer (Parker and Athearn, 1959; Scott and Medioli, 1980; Horton and Murray, 2007) but also in spring and fall (Reiter, 1959; Saad and Wade, 2017). Other field studies suggest that some intertidal species have one major annual reproduction but that others have multiple reproduction periods in different seasons (e.g., Boltovskoy, 1964; Buzas, 1969; Walker, 1976; Murray, 1983; Diz et al., 2009).

It has also been reported that growth rates of foraminifera are related to higher concentrations of one of their main food sources, phytoplankton (e.g., Myers, 1942, 1943; Swallow, 2000; Schönfeld and Numberger, 2007). Phytoplankton, such as diatoms, are main primary producers in temperate intertidal settings, and so are food sources for foraminifera, along with bacteria, detritus or dissolved organic matter (Pascal et al., 2008). Diatom abundance is unlikely to be a limiting factor in foraminiferal reproduction in the Ni-les'tun marsh because Horton

et al. (2017) observed a rapid re-colonization of diatoms at three stations at the restoration site. However, saltmarsh species often prefer green or brown algae and bacteria (Alve and Murray, 1999; Armynot du Châtelet et al., 2009; Murray, 2014; Frail-Gauthier et al., 2019; Haynert et al., 2020). It has been shown that young soils of restored marshes are often depleted in (macro)organic matter, organic carbon, and nitrogen (Langis et al., 1991; Havens et al., 1995; Craft, 2000) and have low denitrification rates compared to the older soils of natural marshes (Thompson et al., 1995), indicating lower nitrogen recycling rates and lower primary production. For example, Brophy et al. (2014) reported that the organic carbon content in the reference (Bandon) marsh soils was on average twice as high as in the Ni-les'tun marsh, which could have limited the food availability for foraminifera in the Ni-les'tun marsh.

Our geochemistry data suggest little change in soil geochemistry during the first year after tidal restoration, with the exception of short-term changes two weeks after tidal restoration where δ^{13}C versus C/N values show an enhanced marine influence at most stations (Fig. 8), and of fluctuating δ^{13}C values at stations 2 and 4 during the first twelve months after tidal restoration suggesting a variable influence of marine and terrestrial DOC. A year after tidal restoration, station 2 was influenced by sea grasses and marine macroalgae, but other stations remained under the influence of freshwater macroalgae and DOC. This inference is supported by a high abundance of freshwater diatoms at station 8 during the first year after tidal restoration (Horton et al., 2017). Our grainsize data also indicate less distinct but variable trends at the higher elevation stations (stations 5–8) compared to the lower elevation stations (stations 1–4) where silt and clay contents increased and sand content decreased during the first year after tidal restoration.

Although we observed a distinct change in plant communities at most stations (Table 1), Brown et al. (2016) reported a lower species richness and percent plant cover compared to the pre-restoration Bandon marsh. They concluded that plant communities were continuing to change in the Ni-les'tun marsh four years after tidal restoration. If some foraminiferal species also feed on decaying plant material, for example as observed for *E. macrescens, B. pseudomacrescens* or *T. inflata* (Alve and Murray, 1999; Armynot du Châtelet et al., 2009), the delayed response of foraminifera to tidal restoration could partly be related to the slow process of plant community evolution in Ni-les'tun marsh.

5.3. Comparison of modern and fossil assemblages and their implications for reconstruction of relative sea-level changes

Coastal areas along the U.S. Pacific Northwest instantaneous subsided during great earthquakes after which intertidal mud gradually accumulates over the buried saltmarsh peat or soil (e.g., Nelson et al., 1996b; Atwater and Hemphill-Haley, 1997). Post-depositional taphonomic processes may result in a decline in foraminiferal abundances in both the peats and muds. If these taphonomic processes are biased towards individual species, this may result in disparities between modern surface assemblages and their fossil counterparts (Berkeley et al., 2007; Chen et al., 2020). However, the foraminiferal assemblages in the modern and fossil samples from Ni-les'tun marsh were similar. For example, the post-restoration core 1 sediment is dominated by *M. fusca* with 97 to 99% of the total assemblage, which matches 96% at station 1 ten months after tidal restoration until the end of the observational period.

The similarities between the modern and fossil assemblages suggest that the delayed response of foraminifera is undetectable in study areas with low sedimentation rates (Hemphill-Haley, 1995; Leonard et al., 2004), such as Ni-les'tun marsh. The short core suggests a sedimentation rate of postrestoration sediment of 3.3 mm/yr for the first 4.5 years after tidal restoration, which includes sediment compaction. These estimates are similar to rates based on feldspar marker horizons in the Bandon and Ni-les'tun marshes, of ~1 to 4 mm/yr from 2009 to 2012 (Brown et al., 2016; and references therein) and in the range of average high marsh accretion rates of 0.8 ± 0.2 to 4.1 ± 0.2 mm/yr reported for Oregon tidal wetlands (Peck et al., 2020).

We further found total foraminiferal concentrations in the post-restoration sediment of core 1 comparable to live populations plus dead assemblages at station 1 in March 2016, which suggests that early diagenetic processes, such as bacterial degradation of organic cements of agglutinated species (de Rijk and Troelstra, 1999; Goldstein and Watkins, 1999; Murray and Alve, 1999; Chen et al., 2020) have little influence in the Ni-les'tun marsh. However, calcareous species were present in the surface samples but could not be found in the post-restoration core sediment. The absence of calcareous species in the post-restoration core sediment is probably a consequence of early diagenetic dissolution of calcareous tests, which is a well-known process in many organic salt marshes along the Oregon coast (Jennings and Nelson, 1992; Hawkes et al., 2010; Engelhart et al., 2013; Milker et al., 2015a, 2015b). The early diagentic dissolution of calcareous tests have implications for coseismic subsidence estimates because *M. fusca* is the most dominant indicator of both low marsh and tidal flat in sediment cores (e. g., Milker et al., 2016).

The post-restoration sedimentation rate in Ni-les'tun marsh is, however, orders of magnitude lower than rates following >1 to 2 m of coseismic subsidence during the greatest (>M9) earthquakes in other areas. For example, Jennings et al. (1995) found <2 foraminifera/cm^3 in tidal mud rapidly deposited following the greatest earthquake of the twentieth century in Chile in 1960. Further, Milker et al. (2016) observed mixed assemblages due to mixing of postseismic mud into preseismic peat deposits across different earthquake contacts in three sediment cores from the South Slough estuary (Oregon) that influence coseismic subsidence estimates. Likewise, Hawkes et al. (2010, 2011)
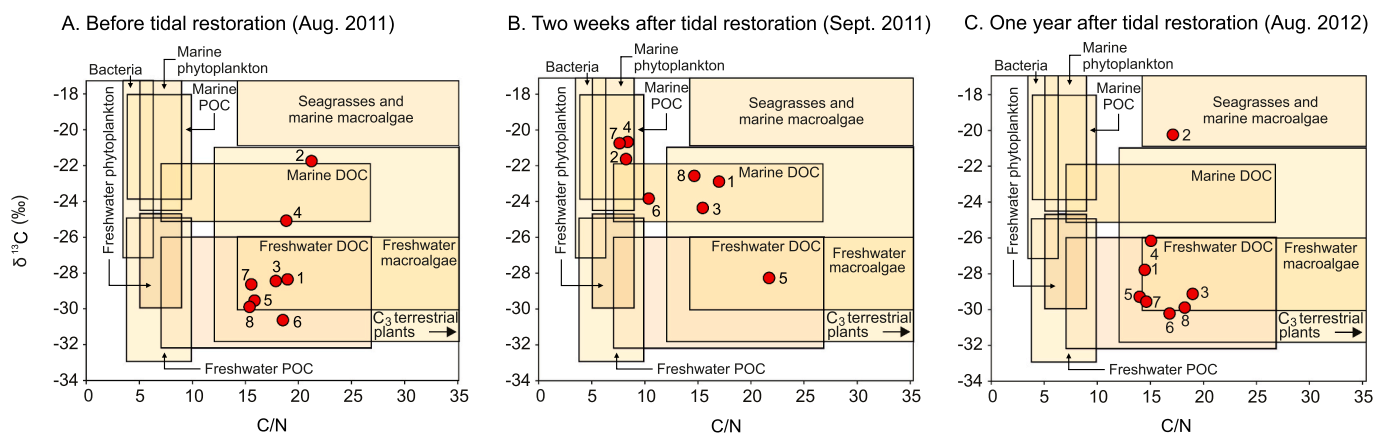

Fig. 8. δ^{13}C ratios and C/N values measured prior to (A), two weeks after (B), and one year after (C) tidal restoration compared to ranges of δ^{13}C ratios and C/N values from different sources of organic material found in intertidal environments (figure modified from Lamb et al. (2006) and Khan et al. (2015)).

used samples several centimeters above coseismically subsided salt-marsh soils at different sites in Oregon to calculate coseismic subsidence in order to avoid problems of lacking analogue (e.g., allochthonous) assemblages.

We therefore suggest that for such earthquake events where (1) postseismic sedimentation rates are very high, (2) samples contain low abundances, and likely unrepresentative assemblages, and (3) where foraminifera show a delayed colonization, sampling a few cm higher rather than immediately above a subsidence contact is necessary in order to capture the post-earthquake environment.

6. Conclusions

Our six-year observation of the Ni-les'tun marsh after tidal restoration indicates a distinct increase in total live foraminiferal numbers at the shallower stations no earlier than ten months after tidal restoration. At higher-elevation stations, notable numbers of live foraminifera were first present 16 to 31 months after tidal restoration. We found high numbers and a strong dominance of *M. fusca* at almost all stations, except for the highest station 8 where *H. wilberti* first colonized in high numbers. This suggests that *M. fusca* and *H. wilberti* are opportunistic species (r-strategists), able to increase rapidly from low concentrations after invading a new habitat.

We observed notable total live numbers of foraminifera mainly during spring and fall, suggesting that foraminifera mainly reproduced during periods of warmer air temperatures in the spring (and fall) rather than during high temperatures in the summer or low temperatures in winter. Other potential causes for the delayed response include limited food availability (1) due to slow saltmarsh soils development following tidal restoration, as shown by our grainsize and geochemistry data during the first year after tidal restoration, and (2) to low density plant communities if species feed on decaying plant material.

The agglutinated foraminiferal assemblages and concentrations in the modern and core samples from Ni-les'tun marsh were similar, which suggests that early diagenetic processes (i.e., bacterial degradation of organic cements of agglutinated species) have little influence in the Ni-les'tun marsh. However, calcareous species, observed in the surface samples, have not been found in the postrestoration core samples which points to dissolution of calcareous tests after burial. The similarities between the modern and fossil assemblages suggest that the delayed response of foraminifera is undetectable in study areas with low sedimentation rates as observed in the core with 3.3 mm/yr for the first 4.5 years after tidal restoration. However, in the case of high postseismic sedimentation rates, sampling a few cm higher rather than immediately above a subsidence contact could avoid uncertainties of coseismic subsidence estimates when having low abundances, unrepresentative assemblages, or a delayed foraminiferal colonization.

Data availability

All modern and fossil foraminiferal counts can be found in supplementary data S5 and S6, and grainsize and geochemical data in Supplementary data S7. The data are also available at https://doi.pangaea.de/10.1594/PANGAEA.941067.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.margeo.2022.106757. The census counts, grainsize and geochemical data can also be found at https://doi.pangaea.de/10.1594/PANGAEA.941067.

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