DEPARTMENT OF MARINE SCIENCES

BENTHIC FORAMINIFERAL FAUNA AND HYDROGRAPHY IN THE SKAGERRAK (NORTH SEA)

A comparative analysis of 1992/93 and 2020 surveys

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Abstract

European shelf seas are important but vulnerable environments as they provide many important ecosystem services and at the same time warm faster than the nearby oceans. To better evaluate climate effects on the ecosystem, the instrumental record of the hydrography can be extended using sediment archives. The Skagerrak acts as a major depositional basin of the North Sea thus providing a high-resolution geological record available for paleoclimate- and environmental reconstruction. Previous studies have shown that the prevailing water masses in the Skagerrak basin can be traced by using recent benthic foraminiferal fauna.

The aim of the present study is to revisit the Hirtshals-Torungen transect between Denmark and Norway previously studied in 1992/93 (Bergsten et al., 1996) to investigate potential changes to the foraminiferal assemblages and hydrographic conditions. Fifteen surface sediment samples taken in 2020 were analyzed for living- (stained), dead-, and total benthic foraminiferal fauna. Hydrographical data from the 2020 survey was compared to data from the period 1950 – 2020, available at the International Council for the Exploration of the Sea (ICES) database.

My results show three distinct total fauna assemblages in 2020 and 1992/93 along the Hirtshals-Torungen transect. These include the *Elphidium excavatum assemblage* on the Danish slope with high turbidity induced by the STC and the NJC; the *Haplophragmoides bradyi assemblage* in the deep basin, with relatively stable hydrographical conditions affected by cascading inflows; and, finally, the *Cassidulina laevigata assemblage* in 2020 and the *Globobulimina turgida assemblage in 1992/93*, which dominate the Norwegian slope and the "transition zone" influenced by the cyclonic circulation of Atlantic water.

The hydrographic time series for 1950 - 2020 show an increase in temperature and salinity in the Skagerrak basin, accompanied by a decrease in oxygen concentration in both the surface and deep water. Despite the long-term warming trend, the hydrographical conditions at the moment of sampling in 1992/93 and 2020 showed similar conditions in terms of temperature and salinity, partly attributed to an exceptionally high influence of Atlantic inflow in the late 1980s. However, an extended period with no significant oxygen replenishment in the deep basin prior to the survey of 1992/93 could possibly explain the higher relative abundance of *Globobulimina turgida*, a foraminifer capable of denitrification, in 1992/93 as compared to 2020.

1 Introduction and study area

Marginal shelf seas provide important ecosystem services such as fisheries, recreation, shipping, wind farms (ICES, 2020) and stand for about one third of the marine primary production (de Haas et al., 2002, and ref therein). As such, shelf seas host large part of the global population and are therefore subjected to human-induced deterioration of the environment, e.g. eutrophication and pollution, as a product of agriculture and/or water waste discharge (Howarth et al., 1996). Shelf seas are also particularly vulnerable to climate change, as these shallow waters warm up faster than the nearby oceans, the adjacent landmasses, and the global climate (Dulvy et al., 2008). An increased (natural- or anthropogenic) nutrient input to these often-enclosed environments, lead to periods of increased primary production and potentially cause oxygen depletion in deep water and in stagnant water bodies.

The North Sea is one of the largest marginal seas in the world and inhabit a large population of marine species of fish, sea birds and mammals and is one of the world most important fishing grounds (EEA, 2008). The North Sea is potentially vulnerable to climate changes with associated changes to the hydrography. With its shallow basin (average 50 m), it is sensitive to shifts in salinity, temperature, and nutrient input. These factors are to a large extent controlled by the sources of incoming ocean water with its connection to the Atlantic Ocean, mainly through the Norwegian Sea in the north, but also the English Channel in the south and with brackish water input from the Baltic Sea. Two large ocean climate anomalies have been recorded in the North Atlantic region since the 1960s, with simultaneous major effects on the ecology of the North Sea (Edwards et al., 2002). In the late 1970s, the sea surface temperature and phytoplankton abundance in the North Sea showed simultaneous minimum values during what is known as the Great Salinity Anomaly (GSA) (Edwards et al., 2002). An increased influence of exceptionally low saline water in the North Atlantic coincided with a reduced inflow of warm, nutrient rich Atlantic water to the North Sea (Edwards et al., 2002). This was associated with a major impact on both phytoplankton community and fish stock in the North Sea, with both decreased abundance of warm temperate species and temporary introduction of sub-arctic zooplankton species (Edwards et al., 2002). The opposite trend was observed in the late 1980s and early 1990s, where the inflow of Atlantic water entered as the North Sea. The unusually warm, nutrient rich water entering the North Sea was associated with an ecological regime shift, expressed through an exceptionally high abundance of phytoplankton, and an introduction of an unprecedented number of oceanic species (Edwards et al., 2002).

The Skagerrak, with an average depth of 210 m, is the major depositional basin of the North Sea and represents a part of North Sea ecoregion (ICES, 2020). It is estimated that 70 % of the water entering the North Sea circulate through the Skagerrak before leaving the basin (Danielssen et al., 1996). Hence, geological deposits of the Skagerrak stand as a potential record of past hydrographical changes in the North Sea. Although being hydrographically well investigated (Albretsen et al., 2011; Aure & Dahl, 1994; Danielssen, 1996; Rodhe, 1996; Sætre et al., 2003), the Skagerrak exhibit complex hydrographical conditions and even more complex interactions of hydrographical changes with impacts on the local ecosystems. Delineating potential changes in the water masses over time is important as it allows to establish transport paths of natural and anthropogenic tracers in the region.

Foraminifera (amoeboid protist present in a high abundance in marine sediments) are sensitive to environmental changes and have a high preservation potential which make them ideal for paleoclimate- and environmental reconstruction. Foraminifera have played important role in proxy (environmental indicator) development, which is done by correlating present day physical and/or chemical conditions to specific data derived from foraminiferal assemblages, e.g., species composition, morphological features, or chemical composition of their shells (tests), (e.g., paleotemperature proxy (Barker et al., 2005); environmental indicators, (e.g., Alve, 1995; Polovodova Asteman & Nordberg, 2017)). In a study by Bergsten et al. (1996), the distribution of benthic foraminifera was studied along a transect taken across the Skagerrak between Hirtshals (Denmark) and Arendal (Norway) in response to different water masses dominating the area.

The aim of the present study is to revisit the stations of Bergsten et al. (1996) for contemporary foraminiferal assemblages and hydrographic parameters and to compare the results from the 1990s to the 2020. Additionally, by looking at the living (stained) assemblage, possible taphonomical effects (e.g., carbonate dissolution and transport) can be determined. By correlating the recent foraminiferal fauna with the dominant water masses and prevailing currents in Skagerrak, the observational record of hydrographical regimes in Skagerrak can extended beyond the 1950s by using the geological record.

1.1 Hydrography

The Skagerrak is part of the North Sea continental sea system, located between Sweden, Denmark, and Norway (Figure 1). Together with Kattegat it makes up a transition zone for exchange of Atlantic water through the North Sea and brackish water from the Baltic Sea (Gustafsson, 1997). With a mean depth of 210 m, in contrast to Kattegat (23 m) and the most of the North Sea (50 m), the Skagerrak reaches 710 m in its deepest part at the Norwegian Trench, along the Norwegian coast (Gustafsson, 1997). Closer to the Danish coast, the depth tapers off to less than 40 m (Gustafsson, 1997).

The current system in the Skagerrak is displayed in Figure 1. Flowing along the Danish west coast is the South Jutland Current (SJC) with a large contribution of river run-off from northwestern Europe. The SJC meets with Atlantic water coming from the northern North Sea going along the southern slope of the Norwegian Trench in form of the Southern Trench Current (STC) (Keld Conradsen et al., 1994). This deflects the water to the east to form the Northern Jutland Current (NJC) that flows eastward along the Danish coast (Figure 1). The low salinity (30-33 PSU) of the NJC, is due to the discharge of large rivers along the continent that also carries a lot of nutrients (Gustafsson, 1997). An outflow of brackish water from the Baltic Sea forms the Baltic Current (BC), meets with the NJC to make up the Norwegian Coastal Current (NCC), ultimately leaving the Skagerrak along the Norwegian west coast (Bergsten et al., 1996).

The seafloor topography of the Skagerrak basin coupled with the inflow of both Atlantic water and Baltic Sea water creates a deep reaching cyclonic circulation within the Skagerrak where the surface water is renewed continuously (Rodhe, 1996). The long-term hydrographical variations within the basin show a significant difference below and above 300 m. This distinction is due to the sill depth of the Skagerrak basin being 270 m, where above this level the water is exchanged continuously, reflecting the seasonal and annual variations. In the deepest part of the basin, below 400-500 m, however, the water can stay stagnant for periods of several years (Van Weering et al., 1987, and ref therein). During the stagnant periods, and increased temperature (by diffusion) and decreased oxygen and density (salinity) are observed (Aure & Dahl, 1994). The stagnant periods are eventually interrupted by cascade-like inflows of water (Rodhe, 1996). These cascading flows have been described by Ljøen and Svansson (1972) where three events of bottom water exchange were identified for the period 1950-1969. The central North Sea water is cooled during winter and stays homogenous from top to bottom in terms of salinity and temperature throughout the year. During exceptionally cold winters, the density of the North Sea water becomes greater than the Skagerrak bottom water, which enables a cascading flow to North Sea water to enter the deepest parts of the Skagerrak basin. The flow enters along the Danish slope and reaches the Norwegian slope approximately one month later through lateral mixing. The bottom water exchanges between 1950-1969 were reflected in the hydrography by a decrease in both temperature and salinity (~3.5°C and 34.5-35 PSU) (Ljøen & Svansson, 1972).

Three major water masses have been defined within the Skagerrak basin with different residence times: The Skagerrak Coastal Water (0-30 m; 4.5-10°C; 25-32 PSU) with a short residence time, The Skagerrak Intermediate Water (30-150 m; 4.5-10°C; 32-35 PSU) with a residence time of approx. three months, and the Atlantic Water (>150-200 m; 5.5-8.5°C; >35 PSU) with a ~2 year turnover time (Polovodova Asteman et al. 2017, and ref therein).

The occurrences of water exchange within the Skagerrak are mostly affected by large atmospheric forcing, with the overall exchange being intensified during periods of positive North Atlantic Oscillation (NAO) index (Winther & Johannessen, 2006). The NAO index is given by the pressure difference between Azores (high pressure) and Iceland (low pressure) and measures the strength of westerly winds. A positive NAO index (i.e., large pressure difference) is correlated stronger westerlies and warmer winters with an increased precipitation in the northern Europe, as well as in increased inflow of Atlantic water into the North Sea. The increased inflow is further correlated to the outflow of the NCC (Winther & Johannessen, 2006). A negative NAO index (small pressure difference) is instead related to cold and dry winters in northern Europe.

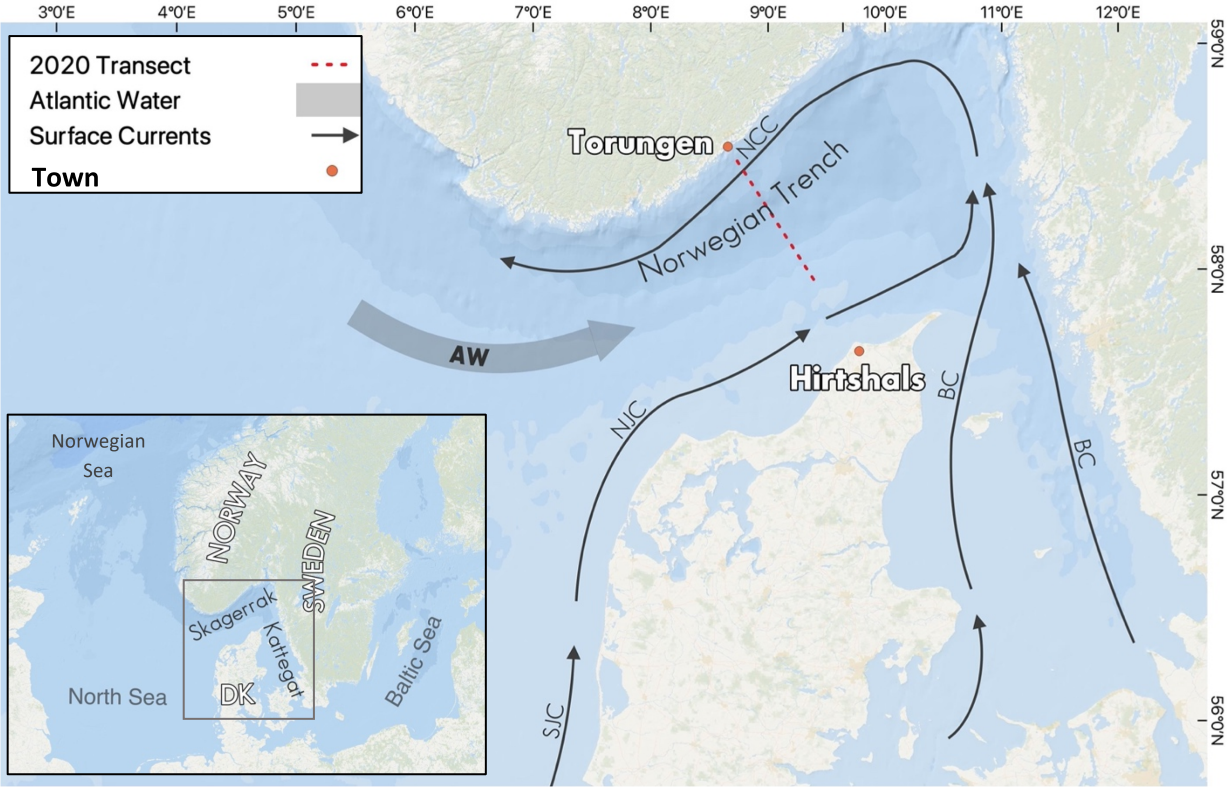


Figure 1. The major current system in Skagerrak (arrows) and the Hirtshals-Torungen transect (dashed red line). The abbreviations are as follows: DK-Denmark; SJC- South Jutland Current; NJC – North Jutland Current; BC – Baltic Current; NCC – Norwegian Coastal Current; AW – Atlantic bottom water. The relative depth of the basin is reflected by the blue color with the deepest blue indicating the Norwegian Trench along the Norwegian coast. The red dashed line indicated geographical extent of CTD measurements and sediment samples during 2020 survey.

1.2 Sediments

The Skagerrak acts as a major depositional basin for the entire North Sea as it receives sediments not only from the North Sea, but also the North Atlantic, the Baltic, and the Scandinavian mainland (van Weering et al., 1993). The sedimentation rate varies between the slopes and the deep part of the basin where the northern- and southern slopes receives 20 mm y^{-1}, while the deepest part of the Norwegian trench have a sedimentation rate of 8-14 mm y^{-1} (Van Weering et al., 1987). The highest accumulation rate occur the northeastern Skagerrak and have been estimated to a range of different rates, 4.4 mm y^{-1} (van Weering et al., 1987) but also as high as 110 mm $^{-1}$ (Bøe et al., 1996).

The relatively high current strength and variability along the Danish coast result with higher sand content, with textures going from silty sands in the shallower areas of southern Skagerrak (35-100 m), going into silty clays along the slopes and clays at the deeper parts of the basin (Van Weering et al., 1987, Rodhe & Holt, 1996). Although organic material from primary producers reach the Skagerrak basin, the accumulated sediments portion is mainly attributed to the inorganic portion provided by the NJC, as the bulk of the organic matter becomes degraded (van Weering et al., 1993). The total organic content (TOC) is relatively stable (2.1-2.3 wt. %) at depths below 250 m, and lower at the Danish slope (1.1 %) (Alve & Murray, 1995). The TOC in Skagerrak show an increasing trend over the past 4500 years within a range of 1.2-2.5 % (Polovodova Asteman et al., 2017).

1.3 Previous studies on foraminiferal assemblages

Previous studies of the recent benthic foraminifera in the Skagerrak basin include studies e.g. Höglund (1947), Corliss & Van Weering (1993), Alve & Murray (1995), Bergsten et al. (1996), and Conradsen et al. (1994). The studies vary in methodology, with different sediment depths (top 0-3 cm or 0-10 cm) and using sieves of varying mesh size (63-150 µm). Furthermore, some studies distinguish between living (stained) and dead (non-stained) fauna (e.g., Corliss & Van Weering, 1993; Klitgaard-Kristensen et al, 2002) whereas others only consider the total fauna (living + dead) (e.g., Bergsten et al. 1996).

Conradsen et al. (1994) used data from several studies to assess distribution of the total foraminiferal faunas (>150 µm) in the Skagerrak and Kattegat area. Most of the samples were collected at shallower depths with only 18 out of 177 samples being taken below 200 m water depth and no samples at all from deeper than 560 m (Conradsen et al, 1994). Studies of the living (stained) fauna in Skagerrak have been done by Corliss & van Weering (1994) only considering calcareous species >150 µm, and by Alve and Murray (1995,1996?) considering both calcareous and agglutinated species >63 µm.

Finally, Bergsten et al. (1996) studied distribution of recent benthic foraminifera (total fauna >125 µm) in 1992/93 along a transect across the Skagerrak between Hirtshals (Denmark) and Arendal (Norway) in response to the different water masses dominating the area. The study delineated four major groups (A, B, C and D) of species, which are described below.

- Group A dominated the deep basin associated with Atlantic water (> 400 m: OS03, OS02, OS01, and OS15: Fig. 2) and included many species that did not occur as abundantly in the remaining groups. These species formed the *Haplophragmoides bradyi* assemblage, with species *H. bradyi, Ammoglobigerina globigeriniformis, Pullenia bulloides, Glomospira charoides, Pullenia subcarinata, Trochammina pusilla, and Brizalina skagerrakensis* (as *Bolivina skagerrakensis:* Bergsten et al., 1996).
- Group B dominated the Norwegian slope (stations OS6, OS5 OS4, and 9201: Fig. 2), influenced by outflowing water, consisted of species common within the other groups (e.g., within Group C). The group B also contained species significant to only that group e.g., *Uvigerina celtica* (as *Uvigerina peregrina:* Bergsten et al., 1996)*, Bulimina marginata, Trifarina angulosa, Liebusella goësi, Melonis barleeanum* and *Hyalinea balthica.*
- Group C dominated the Danish slope of the Norwegian Trench (stations 9202, 9205, and OS16: Fig. 2), characterized by water from the northwest and west North Sea and the Atlantic Ocean, and contained the significant species *Stainforthia fusiformis, Cribrostomoides jeffreysi,* and *Gavelinopsis praegeri.*
- Group D displayed a low-diversity fauna characterized by species *Elphidium excavatum, Elphidium magellanicum* and *Ammonia beccari.* Group D included samples taken in the shallow, sandy area off Denmark (stations 9202 and 9203, Figure 2), dominated by the NJC with water from the southern North Sea. Many of the species within this group were reported

to be in a worn state, suggesting a redeposition of a large part of the fauna, which was attributed to internal transport of sand within the area (Bergsten et al., 1996).

The agglutinated foraminifera were most abundant at the deepest stations OS1 and OS15 (up to 78 %) and stayed below 50 % at the remaining stations. The deepest stations also had the lowest absolute abundance 30-80 ind. g^{-1}, while abundance at the remaining stations showed a range of 80–200 ind.g^{-1}.

2 Methods

2.1 Sediment sampling

In October 2020, on board of *R/V Skagerak*, a total of 15 surface sediment samples were collected at eight stations together with hydrographical data along a transect stretching across the Skagerrak basin (Figure 2). To enable a comparison of the faunal assemblage of 2020 to that of 1992/93, the stations were strategically placed close to the stations presented in Bergsten et al (1996). Due to the continuous repair and shortening, the wire on the sampling winch has become approximately 600 m long, which made it impossible to sample the deepest part of Skagerrak, below 603 m water depth. Hence, the deepest station OS1 from the 1992/93 survey could not be revisited during this expedition (Fig. 2).

All sediment samples were collected with a Gemini corer, allowing to retrieve intact surface sediments, and simultaneously taking replicates at each station to overcome issues with patchiness of fauna. At each station, the uppermost 0 - 3 cm of sediment were transferred into wide-neck PVC bottles, stained with Rose Bengal - ethanol solution according to Schönfeld et al. (2013) and stored at 5 °C. The sediment sampling was planned to be done in 3 replicates per station but due to rough weather, most of the stations were completed in two replicates (Table 2). In the laboratory, the sediment surface was marked on the bottle to estimate the sediment volume prior to sieving. After that the samples were sieved through 1 mm, 125 µm and 63 µm screen, using sodium pyrophosphate to separate sediment aggregates where necessary. The residual fractions were collected on filter paper and were dried at 50 °C overnight. Some samples were split using a dry splitter due to high sand content.

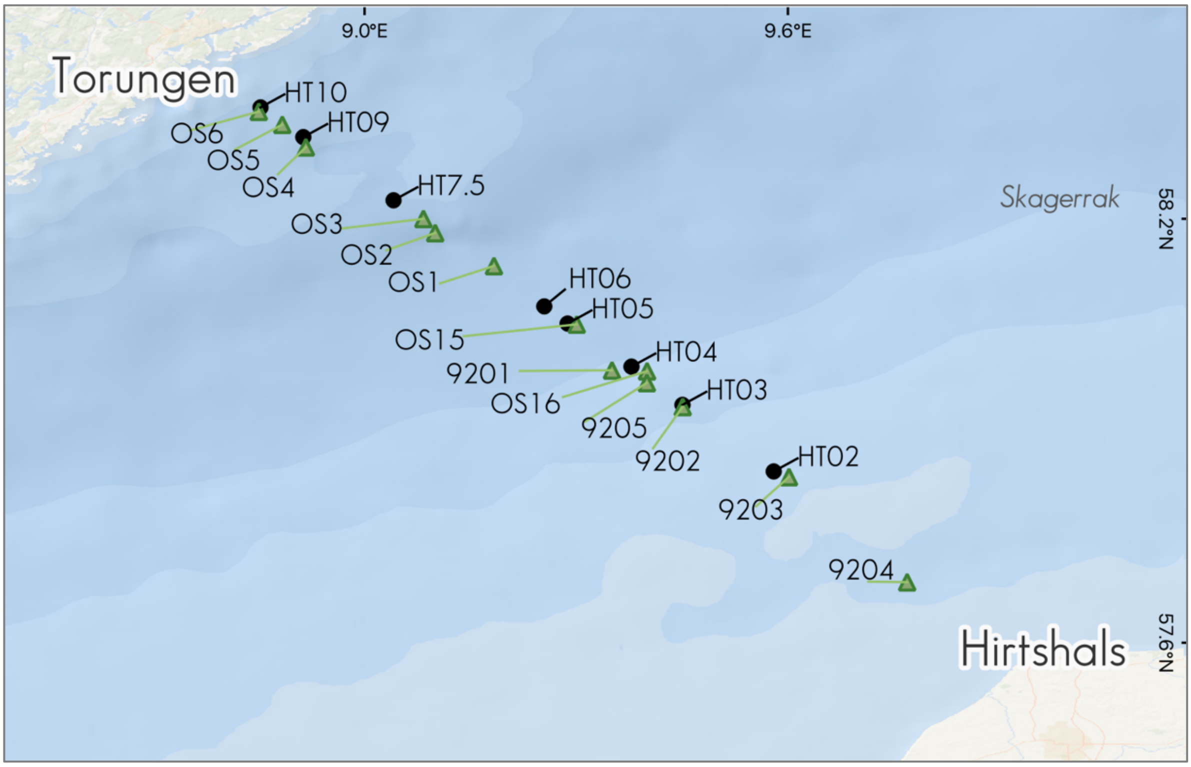


Figure 2. Stations along the transect between Hirtshals and Torungen showing stations from both surveys done in 1992/93 by Bergsten et al (1996) and in 2020 (this study). The stations from the

current study (black circles) have been strategically placed close to stations sampled in the study by Bergsten et al 1996 (green triangles).

2.2 Hydrographic measurements and data

During the sampling campaign in 2020, hydrographical data was collected using an Idronaut Ocean Seven 316 Plus CTD (Idronaut, 2020). Both up- and down cast were recorded but presented herein is only the downcast data. The measured parameters included pressure [dbar], temperature [°C], salinity [PSU], dissolved oxygen [ppm], pH and turbidity [FTU]. Other collected parameters not used in this thesis were conductivity [mS/cm], Eh [mV], dissolved oxygen [%]. The raw data was plotted using Ocean Data View (Schlitzer, 2021) and was interpolated using DIVA-gridding.

The CTD-data from the Hirtshals-Torungen transect spanning the period 1950-2020 was downloaded from International Council for the Exploration of the Sea (ICES) database. Low-resolution CTD-data was used, as the high-resolution data contained fewer stations and few measured parameters, often only including temperature, salinity, and pressure. The low-resolution data contained the temperature, salinity, and dissolved oxygen. For these parameters, a summer (May-Aug) mean of the year 1992 along the transect was calculated to represent the conditions of the 1992/93 survey. Additionally, a monthly mean over the period 1950-2020 was calculated for the surface water (50-100 m), bottom water (>600 m), using the statistical software R (2021). Furthermore, a five-year running mean for the whole basin (all depths) for the period 1950-2020, is represented by a moving-average trendline produced in Excel.

2.3 Foraminiferal analysis

In order to compare my results to a previous foraminiferal survey across the transect done during the summers of 1992 and 1993 (Bergsten et al., 1996), this study is based only on a coarser sediment fraction >125 µm. Approximately 300 individuals, for both dead (non-stained, empty tests) and, where possible, living (stained) foraminifera, were counted and identified to the lowest possible taxonomic level. As agglutinated *Rhabdammina* spp. only occurred as fragments, they were noted when present but were excluded from further analysis. Individuals, which were considered transported (judging by abnormally rough test texture, milky appearance or missing more than 50 % of the test) were counted separately but were excluded from any other analyses, following Bergsten et al. (1996).

Bergsten et al. (1996) presented their data only on total fauna from the uppermost 0-6 or 0-8 cm. This was done because living (stained) benthic foraminifera were observed to occur in the Skagerrak sediments down to 9-10 cm core depth (Nordberg, personal communication, 2021). In contrast, this study is based on the most surficial (0-3 cm) sediments and includes living-, dead-, and total faunas. To compare my data with data from Bergsten et al. (1996), all data from the 1990s (available only as hard copies) was digitized and the data for the uppermost 3 samples (0-1 cm, 1-2 cm, and 2-3 cm) were summed to represent the topmost sediment layer (0-3 cm). Some of the data stored as the hard copies in the archive, turned out to be incomplete. For example, at station OS05 foraminifera were counted within the intervals 0-1 and 2-3 cm, meaning the data for the core interval 1-2 cm were missing, most likely due to that interval not being analyzed. Therefore, for the purpose of this thesis, an assumption had to be made, that these results should be sufficient to compare with the results of 2020.

The same data analysis was performed on four data sets, including three data sets from the 2020 survey considering total-, living- and, dead faunas, and one being total fauna from 1992/93. Following Bergsten et al. (1996), taxa with a relative abundance of >2 % in at least 5 samples or >5 % in at least one replicate were used for an R-mode principal component analysis (PCA). Additionally, the same constraints were used for a CABFAC-analysis. The R-mode PCA analysis asserts correlations between variables (species), in contrast to Q-mode PCA that is based on correlation between cases (samples) (Hirama et al., 2010). As the original data from 1992/93 was received as one replicate from each station, the selection of taxa is based on the relative abundance at each station, not within each replicate. The PCA-analysis was conducted on the correlation matrix of the log-ratio transformed relative abundance (%) data from each replicate by using software PAST v.4 (Hammer et al., 2001). A CABFAC-analysis was performed on the species relative abundance grouped by station. The number of factors taken into consideration for the CABFAC-analysis was factors that explain at least 5 % of the data. Factor scores above 1.5 (or below -1.5) are considered major contributors and are selected to distinguish the different assemblages.

3 Results

From the eight stations along the Hirtshals-Torungen transect (Figure 2) a total of 15 samples were collected including two replicates per station (**Table 1**). An exception represented station HT05 where sampling difficulties occurred due to stormy weather and therefore only one replicate was retrieved. The deepest recorded station was HT06 at 603 m water depth in the deep basin and the shallowest station HT02 was at 67 m, approximately 35 km off the coast of Denmark.

During sediment sieving, a high content of sand-sized (> 63µm) sediment fraction was noticed by visual inspection as the replicates from stations HT02 and HT03 contained significantly larger amounts of sand compared to the remaining samples. Station HT10 also contained a considerable amount of sand, but not at much as HT02 and HT03. As the samples were stained with Rose-Bengal (preventing freeze-drying) the sand content was not measured quantitatively in this study. However, the sand content of Bergsten et al. (1996) is listed in Table 1. Other sample notes and visual inspections not considered here are listed in the Appendix.

3.1 Hydrography

3.1.1 2020 Survey

In October of 2020, the temperature within the Skagerrak basin ranged between 6.4 and 14.9 °C, and together with a salinity range of 24.5-35.3 PSU, formed a pycnocline at 50-80 m water depth. Close to the Danish coast (stations HT02), the higher temperature and the low salinity at the surface reflect the NJC flowing into the Skagerrak basin, also reflected in the highest turbidity of 3.3 FTU seen along the slope towards the Danish coast. The turbidity stayed below 1 FTU within a major of the remaining part of the basin. On the Norwegian coast, a less saline water mass (<32 PSU) above ~30 m water depth likely reflects the NCC flowing out of the basin (stations HT10 through HT05, **Error! Reference source not found.**). Theses currents together make up the Skagerrak Coastal Water. Below that and down to pycnocline depth salinity increases to 32-35 PSU reflecting Skagerrak Intermediate Water, surfacing in the middle of the transect (HT04 and HT03). Below the pycnocline depth, salinity stayed consistently >35 PSU indicating a major influence of Atlantic Water or the so-called Skagerrak Basin Water. The entire basin at all depths remained well oxygenated with a dissolved oxygen content range of 4.7-7.1 ml l^{-1}. A lower oxygen content was observed within the bottom waters below 450 m, as well as along the slopes of the basin closer to the Danish and Norwegian coasts (Fig. 3). The pH follows the distribution of dissolved oxygen (pH range: 8.1-8.3), with lower values detected in areas of lower oxygen concentrations.

Table 1. Overview of sediment samples and stations from surveys undertaken in 2020 (this study) and in 1992/93 (Bergsten et al, 1996).

Station		Coordinates		Sand content (% >63 µm)	Water depth		Replicates
2020	1992/93	2020	1992/93	1992/93	2020	1992/93	2020
	9204		N 57°41'9/E 9046'8	67.7		58	
HT02	9203	N 57°50'6/E 9°34'8	N 57°50'5/E 9036'5	65.2	67	70	2
HT03	9202	N 57°56'2/E 9°27'0	N 57°56'2/E 9°27'3	61.5	192	177	2
	9205		N 57°58'4/E 9°24'0	19.0		294	
HT04	OS16	N 57°59'5/E 9°22'7	N 57°59'4/E 9°24'1	5.2	374	350	2
	9201		N 57°59'8/E 9°21'2	2.7		450	
HT05	OS15	N 58°3'1/ E9°17'3	N 58°03'2/E 9°18'2	0.8	543	525	1
HT06		N 58°04'6/E 9°15'3			603		2
	OS01		N 58°08'0/E 9°11'0	0.6		637	
	OS02		N 58°11'1/E 9°06'0	3.9		525	
HT7.5	OS03	N 58°13'6/E 9°02'5	N 58°12'0/E 9°05'0	0.6	441	411	2
HT09	OS04	N 58°18'9/E 8°54'8	N 58°18'5/E 8°55'0	0.4	302	325	2
	OS05		N 58°20'0/E 8°53'0	2.3		252	
HT10	OS06	N 58°21'5/E 8°51'2	N 58°21'6/E 8°51'0	49.9	188	177	2

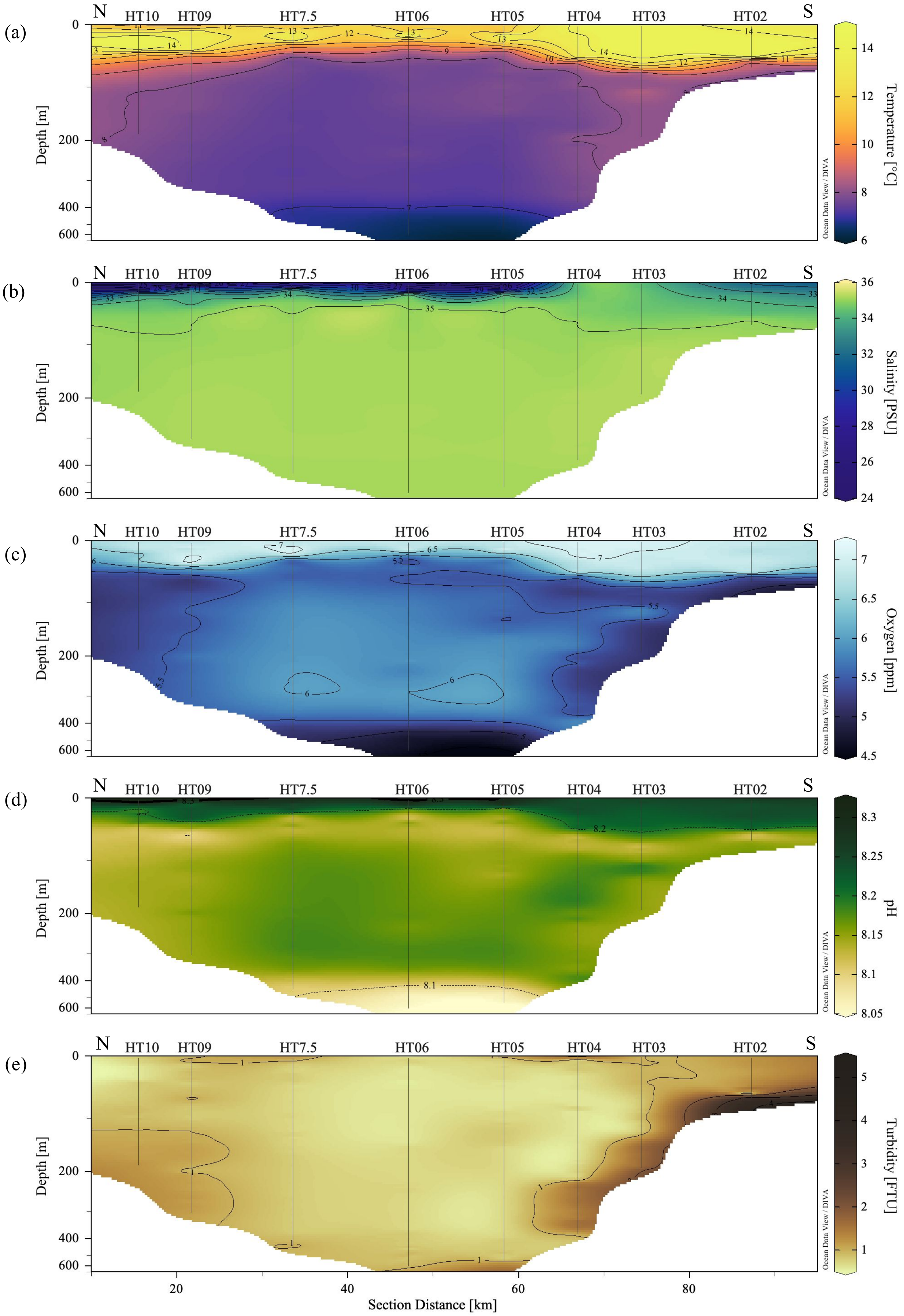

(a)
N
HT10
HT09
HT7.5
HT06
HT05
HT04
HT03
HT02
S
Depth [m]
0
200
400
600
Temperature [°C]
14
12
10
8
6
Ocean Data View / DIVA
(b)
Salinity [PSU]
36
34
32
30
28
26
24
(c)
Oxygen [ppm]
7
6.5
6
5.5
5
4.5
(d)
pH
8.3
8.25
8.2
8.15
8.1
8.05
(e)
Turbidity [FTU]
5
4
3
2
1
20
40
60
80
Section Distance [km]

Figure 3. Hydrography transects (October 2020) of the distribution of temperature (a), salinity (b), oxygen content (c), pH (d) and turbidity (e) between Hirtshals (right-hand side) and Torungen (left-hand side). Note the expansion of the top part along the y-axis (ODV built-in function). Each parameter has a scatter plot to better visualize the vertical variation of each parameter (bottom right corner).

3.1.2 1992 Survey

During the summer of 1992 (May - Aug), the temperature and salinity in the Skagerrak basin ranged between 5.9-18.6 °C and 18.0-35.3 PSU with a pycnocline 20-30 m water depth (Figure 4). Below the pycnocline, the salinity stayed consistently > 35 PSU. The entire basin was well oxygenated with an oxygen range of 4.4 – 8.2 ml l^{-1}. The lower oxygen content is observed along the Danish slope and at water depths below 400 m.

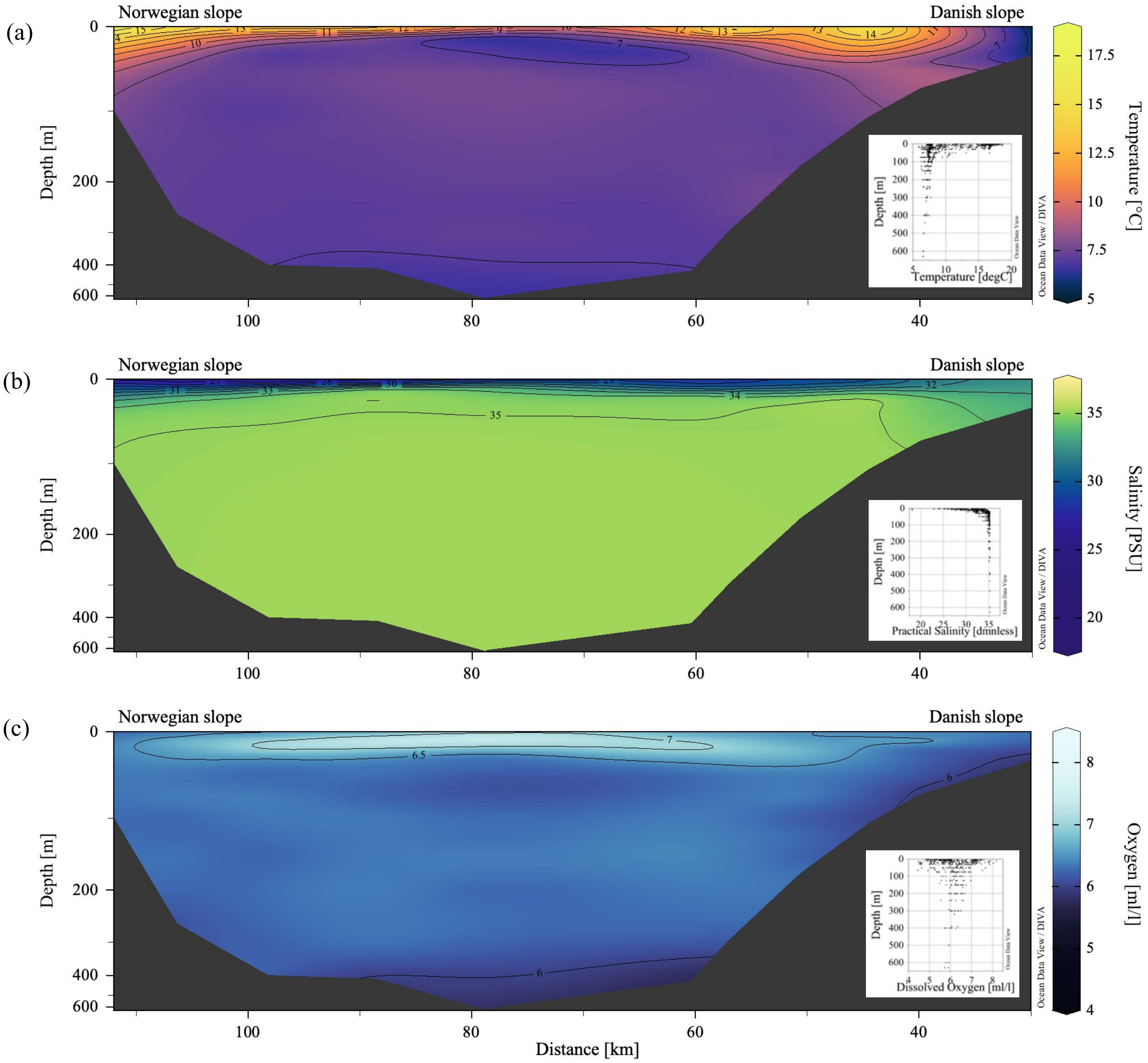


Figure 4. Hydrography transects (May-Aug 1992) of the distribution of temperature (a), salinity (b), and oxygen content (c) between Hirtshals (right-hand side) and Torungen (left-hand side). Note the expansion of the top part along the y-axis (ODV built-in function). Each parameter has a scatter plot to better visualize the vertical variation of each parameter (bottom right corner).

3.1.3 1950-2020

The hydrographic variations in the period between 1950 through 2020 along the Hirtshals-Torungen transect are shown in **Error! Reference source not found.**. The figure shows the monthly mean values between 50-100 m (red lines) and bottom waters >600 m (blue lines), and an annual mean of all depths combined 0 to >600 m (black lines). Also shown are linear trends in dashed lines. Worth noting is the lack of oxygen data in both the upper layer and deep layer for 1960 - 1980 and from 2010 towards present day. The years 1992 and 2020 are marked with grey rectangles to enable easier comparison of parameters.

As seen in Figure 5 (a), the temperature shows a greater variation in the surface layer (red line) compared to the deep layer (blue line). A general decrease of ~0.5 °C occurred from 1950 until 1988, after which the temperature has increased towards 2020 by ~1.5 °C (black line). Both the upper layer and the deep layer show a general increase of about 1°C throughout the period 1950-2020 (red and blue dashed lines).

The salinity within the basin shows a general increase between the 1950s until 1991 (black line) after which it temporary decreases and in 2020 reaches the same salinity as in the early 1990s (Fig. 5b). The top layer shows no significant long-term change (red line). The deep layer shows an increase from 35.10 to 35.15 PSU through the whole period (blue dashed line).

The dissolved oxygen within the basin shows a general decreasing trend in the period 1950 - 2020 (Fig. 5c, black line). The same decreasing trend is seen in both the surface and bottom water oxygen (red and blue lines), with the lowest oxygen concentration in the bottom water seen in 1990, followed by a rapid increase in 1991.

When comparing the annual mean of 1992 and 2020 (black line, all depths combined), the conditions are similar. In 1992 the annual means were 8.6°C, 33.9 PSU and 6.2 ml/l compared to 8.9°C, 34.0 PSU and 6.1 ml/l in 2020 for temperature, salinity, and dissolved oxygen respectively.

A rapid decrease in temperatures in the deep layer below the sill (approx. 270 m) occurred in thirteen times (1954, 1963, 1966, 1970, 1980, 1982, 1994, 1996, 2001, 2005, 2011, 2013 and 2018) over the period 1950-2020, occurring every 5 years on average. A simultaneous drop in salinity in the deep layer occurred for the years 1970, 1980, 1996, and 2001 (Fig. 5b). The oxygen concentration shows a rapid increase approximately fourteen times in the period 1980-2008 (1982, 1984, 1986, 1991, 1993, 1994, 1996, and every year from 1999 though 2005), occurring once every two years on average. A simultaneous rapid change is seen for all three parameters exclusively in 1996 and 2001.

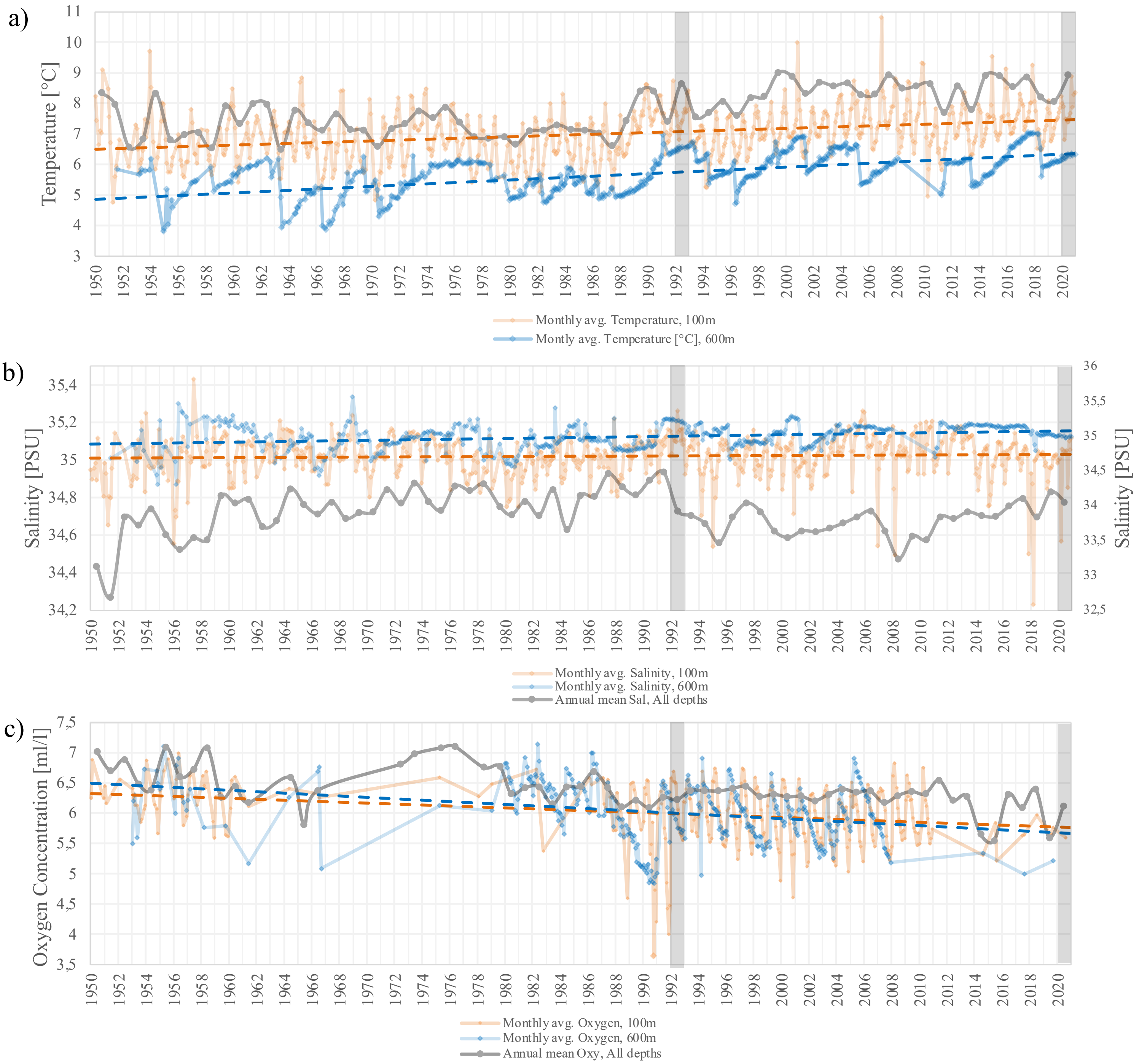


Figure 5. Monthly mean (a) temperature, (b) salinity, and (c) dissolved oxygen for the surface water (50-100 m, red), bottom water (> 600 m, blue) with corresponding linear trendlines (red and blue dashed). A moving average of the preceding five years at all depths is also shown (black). Missing data in the dissolved oxygen-record (2009-2013, 2015-2016, 2018, and 2020). The practical salinity has a separate axis for the 5 yr moving average (black) on the right-hand side.

3.2 Foraminiferal data

3.2.1 2020 Survey

From the 15 sediment samples collected in 2020, the majority contained enough empty tests to easily reach 300 dead individuals (Table 2). In contrast, more than half of the analyzed samples had an apparent low abundance of stained foraminifera. This resulted in these samples not reaching a total of

300 living individuals (Table 2). A total of 124 species were identified, with an additional of 22 being assigned to genus level. Out of these two groups, 53 turned out to be agglutinated and 93 being calcareous species (Table A1). Individuals considered transported ranged between 0 and 30 % in the non-stained fauna, with the highest abundance seen at station HT10 (30 %), in proximity to the Norwegian coast, and stations HT02 (7 %) and HT03 (6 %), close to the Danish coast. The data on transported individuals were excluded from further analysis.

Table 2. Counted foraminiferal individuals from each core top.

Core	Counted Dead	Counted living
HT02A	349	97
HT02B	284	134
HT03A	307	136
HT03B	346	44
HT04A	290	337
HT04B	319	327
HT05A	389	332
HT06A	297	149
HT06B	335	316
HT7.5A	429	328
HT7.5B	329	324
HT09A	345	65
HT09B	323	323
HT10A	320	166
HT10B	375	270
Total	5037	3348

The absolute abundance of the total fauna in 2020 showed a range of 15 – 309 ind. cm^{-3} and the non-stained ranged between 12 and 299 ind. cm^{-3}, both datasets showing higher abundances along the slopes compared to the deeper basin (Figure 6). The living (stained) fauna ranged from 1 to 18 ind. cm^{-3}, with the highest values seen in the deep basin at station HT04.

The relative abundance of agglutinated individuals within the total fauna ranged between 3 and 56 %, with the highest abundance within the deepest basin (HT05 and HT06) (Figure 6). The distribution of non-stained agglutinated tests follows a similar pattern to that of the total fauna, whereas the abundance of stained agglutinated tests increases steadily going from the Norwegian slope (HT10) to the Danish slope HT02) (Figure 7).

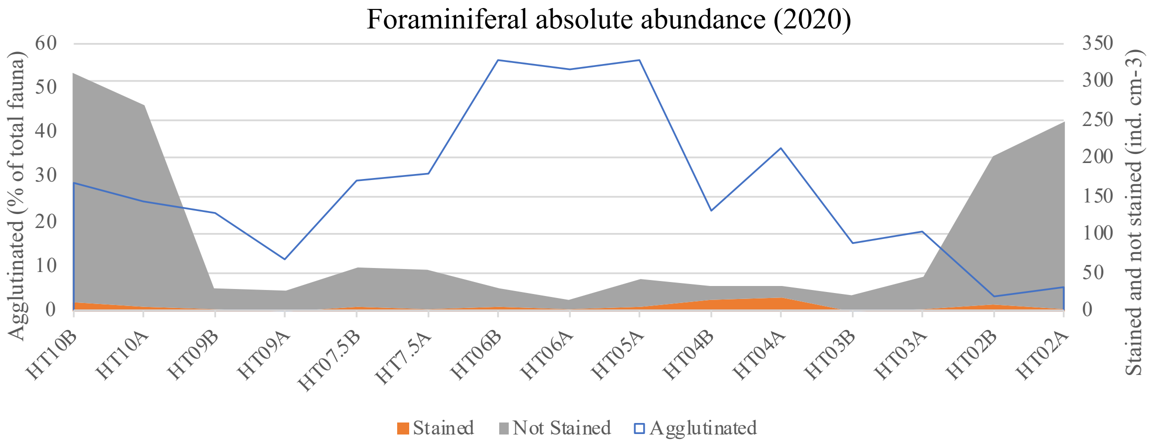


Figure 6. Foraminiferal absolute abundance (ind. ml^{-3}) for each station (including replicates) collected along the Hirtshals-Torungen transect in 2020. The stained (orange) and not stained (grey) absolute abundances are stacked to show the absolute abundance of the total fauna (grey and orange). The relative abundance of agglutinated test (blue line) is plotted with a separate y axis to the left.

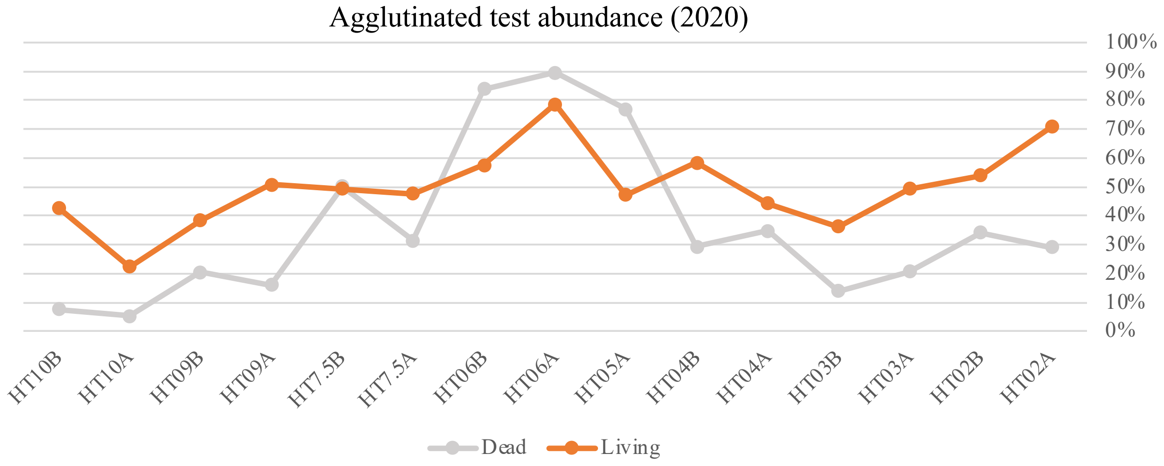


Figure 7. Relative abundance of agglutinated tests in stained and non-stained fauna at each station (including replicates) collected along the Hirtshals-Torungen transect in 2020.

3.2.1.1 Total fauna

Presented in the four following sections, including this one, are the species that were present at >2 % in five samples or >5 % in at least one sample within each data set and thus selected for further statistical analysis. A total of 25 species remained for further analysis within the total fauna of 2020 (Table 3).

The dominant species (>10 %) are *Brizalina skagerrakensis, Bulimina marginata, Cassidulina laevigata, Eggereloides medius, E. scaber, Elphidium excavatum, Gavelinopsis praegeri, Haplophragmoides bradyi, Hyalinea balthica, Melonis barleeanum, Reophax fusiformis, R. rostrata,* and *Uvigerina celtica*. Accessory species (5-10 %) are *Ammonia spp., Cibicides lobatulus, Cribrostomoides kosterensis, C. subglobosum, E. albiumbilicatum, E. magellanicum, Globobulimina turgida, Glomospira charoides, Liebusella goësi juv., Planorbulina mediterranensis, Psammosphaera fusca,* and *Saccammina sphaerica*. None of the rare species (>2 %) were present in at least five samples and were thus excluded from further analysis. Unidentified agglutinated species are present at 0 – 13.6 %.

Table 3. Total fauna 2020: selected species present at >5 % (accessory species marked yellow and dominant species marked green) in at least one sample or >2 % (rare species marked red) in five samples (%). Station order is from the Norwegian slope (HT10) to the Danish slope (HT02). A and B

represent replicate samples.

	HT10		HT09		HT7.5		HT06		HT05	HT04		HT03		HT02	
	A	B	A	B	A	B	A	B	A	A	B	A	B	A	B
Agglutinated other	1,4	4,1	1,2	1,1	0,9	2,6	0,4	0,8	0,1	-	1,5	2,2	1,0	5,3	13,6
Ammonia spp.	-	-	-	-	-	-	-	-	-	-	-	4,9	3,2	7,7	9,8
Brizalina skagerrakensis	4,1	3,5	17,9	10,5	19,9	11,4	0,9	2,0	1,5	6,2	4,8	1,3	1,2	-	0,7
Bulimina marginata	13,7	11,1	14,0	13,5	10,6	5,1	0,9	1,1	2,3	11,9	10,8	0,2	0,5	2,3	1,3
Cassidulina laevigata	29,2	22,3	15,9	18,6	13,9	14,7	2,2	8,2	3,5	16,7	13,5	11,0	11,8	0,6	0,7
Cibicides lobatulus	0,6	-	0,2	-	0,1	-	0,7	-	0,1	-	1,1	4,4	7,1	2,1	3,6
Cribrostomoides kosterensis	-	-	-	-	-	-	-	-	0,1	-	2,5	5,1	7,4	-	1,3
Cribrostomoides subglobosum	-	0,2	0,2	1,9	6,3	2,9	1,3	2,8	5,1	2,9	2,5	-	-	-	-
Eggereloides medius	2,9	4,5	16,7	18,2	16,8	17,2	33,4	23,3	14,5	8,1	7,5	7,1	2,7	5,3	6,9
Eggereloides scaber	-	0,8	0,2	2,0	-	2,2	-	2,2	4,8	-	0,2	-	-	16,8	5,6
Elphidium albiumbilicatum	-	-	0,2	-	-	-	-	-	-	-	0,2	-	6,6	-	3,1
Elphidium excavatum	1,0	2,6	2,4	1,3	-	-	-	0,8	-	-	0,5	21,0	16,7	35,7	29,7
Elphidium magellanicum	-	-	-	-	-	-	-	-	-	0,2	-	3,5	5,7	-	1,3
Gavelinopsis praegeri	-	-	-	-	-	-	-	-	-	0,2	0,5	10,2	7,9	0,2	1,8
Globobulimina turgida	1,8	2,7	8,7	5,5	0,3	0,3	0,7	0,2	0,6	3,8	4,9	-	0,5	0,2	-
Glomospira charoides	-	-	0,7	-	0,4	1,7	8,5	6,1	0,7	-	-	-	-	-	-
Haplophragmoides bradyi	0,4	2,0	0,7	1,1	7,3	10,8	23,5	12,6	12,7	4,1	2,6	-	-	-	-
Hyalinea balthica	15,5	11,0	7,7	10,8	3,9	4,2	0,7	1,4	3,5	8,6	7,8	-	1,0	-	0,7
Liebusella goësi juv.	-	0,3	-	2,4	-	0,6	-	-	1,3	3,7	7,5	-	-	-	-
Melonis barleeanum	1,6	2,9	4,6	1,3	1,2	3,6	-	3,1	13,1	1,0	0,5	-	-	-	-
Planorbulina mediterranensis	-	-	-	-	-	-	-	-	-	0,2	-	7,1	8,4	0,2	0,7
Psammosphaera fusca	-	-	-	-	-	2,2	0,4	2,2	5,1	0,2	0,2	-	-	2,6	2,9
Reophax fusiformis	-	2,0	0,2	-	-	-	-	0,5	0,1	1,7	10,8	9,1	0,2	4,0	1,8
Reophax rostrata	1,0	0,9	-	-	-	-	-	-	-	10,8	0,3	-	-	-	-
Saccammina sphaerica	-	-	-	-	1,2	2,2	9,4	7,9	5,9	-	-	-	-	-	-
Uvigerina celtica	9,8	10,2	0,2	3,0	3,3	3,1	1,8	0,8	3,9	1,6	1,1	-	0,2	-	-

3.2.1.2 Living fauna

A total of 29 species remained for further analysis within the living fauna of 2020 (**Table 4**). The dominant species (>10 %) within the living fauna are *Ammonia* spp., *B. marginata, C. laevigata, E. medius, E. scaber, G. charoides, H. bradyi, H. balthica, L. goësi* juv., *M. barleeanum, R. fusiformis,* and *R. rostrata*. Accessory species (5-10 %) are *B. skagerrakensis, C. neoteretis, C. lobatulus, C. subglobosum, E. excavatum, G. praegeri, G. turgida, L. goësi, N. turgida, P. mediterranensis, P. bowmanni, P. fusca, P. bulloides, Q. seminula, T. bocki, Trochammina rotaliformis*, and *U. celtica*. The only rare species included is *Pyrgo williamsoni*. Unidentified agglutinated species are present at 0 - 8.5 %.

Table 4. Living fauna 2020: selected species present at >5 % (yellow, including >10 % in green) in at least one sample or >2 % (red) in five samples in living (stained) fauna 2020 (%). Station order is

from the Norwegian slope (HT10) to the Danish slope (HT02). A and B represent replicate samples.

	HT10		HT09		HT7.5		HT06		HT05	HT04		HT03		HT02	
	A	B	A	B	A	B	A	B	A	A	B	A	B	A	B
Agglutinated other	1,8	8,3	-	1,0	-	-	-	-	0,3	-	2,1	-	-	8,5	-
Ammonia spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	8,5	19,4
Brizalina skagerrakensis	6,0	5,2	-	5,4	-	1,0	-	3,0	0,9	3,3	0,3	4,4	4,5	-	0,7
Bulimina marginata	7,8	2,4	27,7	9,6	13,1	4,2	1,4	1,3	0,9	17,5	14,8	0,7	-	0,9	-
Cassidulina laevigata	31,3	19,0	4,6	17,6	25,3	20,3	3,4	11,9	4,5	11,6	3,9	20,6	25,0	-	0,7
Cassidulina neoteretis	-	-	6,2	-	-	-	-	-	-	-	-	-	-	-	-
Cibicides lobatulus	0,6	-	-	-	-	-	-	-	-	-	0,3	4,4	6,8	-	0,7
Cribrostomoides subglobosum	-	0,3	-	3,8	14,0	4,6	4,1	4,6	8,5	1,8	4,8	-	-	-	-
Eggereloides medius	3,6	8,0	41,5	23,3	18,6	13,1	40,5	13,2	5,7	8,9	8,2	21,3	25,0	8,5	20,1
Eggereloides scaber	-	1,7	1,5	1,6	-	0,7	-	4,6	2,4	-	0,3	-	-	23,6	14,2
Elphidium excavatum	-	-	-	-	-	-	-	0,7	-	-	-	8,1	-	6,6	-
Gavelinopsis praegeri	-	-	-	-	-	-	-	-	-	-	-	6,6	4,5	-	1,5
Globobulimina turgida	4,2	4,2	-	7,3	-	-	-	-	1,2	5,6	5,2	-	4,5	0,9	-
Glomospira charoides	-	-	-	-	0,3	2,9	12,2	5,9	0,9	-	-	-	-	-	-
Haplophragmoides bradyi	1,2	3,8	-	1,3	7,6	13,1	14,9	10,2	14,5	1,2	2,7	-	-	-	-
Hyalinea balthica	9,6	5,5	4,6	12,8	1,2	2,0	0,7	2,6	3,9	8,9	10,3	-	-	-	1,5
Liebusella goësi	1,8	2,8	6,2	0,3	5,2	2,0	-	-	0,6	5,9	1,5	-	-	-	-
Liebusella goësi juv.	-	0,7	-	3,8	-	1,3	-	-	2,7	6,8	14,8	-	-	-	-
Melonis barleeanum	4,2	5,2	-	1,3	-	5,6	-	4,6	23,3	0,9	0,9	-	-	-	-
Nonionella turgida	-	-	-	-	-	-	-	-	-	-	-	-	-	5,7	8,2
Planorbulina mediterranensis	-	-	-	-	-	-	-	-	-	-	-	2,2	9,1	-	-
Psammosphaera bowmanni	-	-	-	-	-	-	-	-	-	-	-	-	-	7,5	-
Psammosphaera fusca	-	-	-	-	-	3,3	-	-	-	-	-	-	-	8,5	8,2
Pullenia bulloides	-	-	3,1	-	4,3	4,9	4,7	8,3	1,8	0,3	-	-	-	-	-
Pyrgo williamsoni	-	1,0	-	0,3	0,3	-	2,0	1,7	0,9	2,1	0,6	-	2,3	3,8	3,0
Quinquerloculina seminula	-	-	-	0,3	-	1,0	-	-	-	-	-	-	2,3	1,9	7,5
Reophax fusiformis	-	3,8	-	-	-	-	-	-	-	-	17,3	24,3	2,3	12,3	4,5
Reophax rostrata	3,0	2,1	-	-	-	-	-	-	-	19,3	0,3	-	-	-	-
Textularia bocki	2,4	-	-	-	-	-	-	-	-	-	-	3,7	6,8	0,9	-
Trochammina rotaliformis	-	-	-	-	-	-	1,4	5,6	1,8	-	-	-	-	-	-
Uvigerina celtica	9,0	7,6	-	6,1	6,4	6,2	2,7	1,3	7,3	2,4	1,8	-	2,3	-	-

3.2.1.3 Dead fauna

A total of 22 species remained for further analysis within the dead fauna of 2020 (**Table 5**). The dominant species (>10 %) are *B. skagerrakensis, B. marginata, C. laevigata, E. medius, E. scaber, E. excavatum, G. praegeri, G. turgida, H. bradyi, H. balthica, S. sphaerica*, and *U. celtica.* Accessory species (>5 %) are *Ammonia spp*., *C. lobatulus, C. kosterensis, E. albiumbilicatum, E. magellanicum, G. charoides, M. barleeanum, P. mediterranensis, P. fusca,* and *T. bocki*. None of the rare species (>2 %) were present in at least five samples and were thus excluded from further analysis. Unidentified agglutinated species are present at 0 – 19.4 %.

Table 5. Dead fauna 2020: selected species present >5 % (yellow, including >10 % in green) in at least one sample or >2 % (red) in five samples in dead (not stained) fauna 2020 (%). Station order is from the Norwegian slope (HT10) to the Danish slope (HT02). A and B represent replicate samples.

	HT10		HT09		HT7.5		HT06		HT05	HT04		HT03		HT02	
	A	B	A	B	A	B	A	B	A	A	B	A	B	A	B
Agglutinated other	1,2	0,8	1,4	1,2	1,6	5,0	0,7	1,5	-	-	0,9	3,2	1,1	4,4	19,4
Ammonia spp.	-	-	-	-	-	-	-	-	-	-	-	6,9	3,6	7,4	5,7
Brizalina skagerrakensis	3,1	2,1	21,2	15,5	35,0	20,8	1,3	1,2	2,1	9,6	9,4	-	0,8	-	0,6
Bulimina marginata	16,7	17,8	11,5	17,3	8,8	5,9	0,7	0,9	3,4	5,5	6,6	-	0,6	2,7	1,9
Cassidulina laevigata	28,1	24,7	18,1	19,5	5,3	9,7	1,7	4,8	2,6	22,5	23,4	6,9	10,2	0,8	0,6
Cibicides lobatulus	0,6	-	0,3	-	0,2	-	1,0	-	0,3	-	1,9	4,4	7,2	2,7	4,8
Cribrostomoides kosterensis	-	-	-	-	-	-	-	-	0,3	-	5,0	7,3	8,0	-	1,9
Eggereloides medius	2,5	1,9	12,0	13,3	15,4	20,8	29,9	32,5	22,1	7,2	6,9	0,9	-	4,4	1,3
Eggereloides scaber	-	-	-	2,5	-	3,5	-	-	6,8	-	-	-	-	14,8	1,9
Elphidium albiumbilicatum	-	-	0,3	-	-	-	-	-	-	-	0,3	-	7,4	-	4,5
Elphidium excavatum	1,5	4,5	2,9	2,5	-	-	-	0,9	-	-	0,9	26,5	18,7	44,2	42,4
Elphidium magellanicum	-	-	-	-	-	-	-	-	-	0,3	-	5,0	6,3	-	1,9
Gavelinopsis praegeri	-	-	-	-	-	-	-	-	-	0,3	0,9	11,7	8,3	0,3	1,9
Globobulimina turgida	0,6	1,6	10,3	3,7	0,5	0,6	1,0	0,3	-	1,7	4,7	-	-	-	-
Glomospira charoides	-	-	0,9	-	0,5	0,6	6,7	6,3	0,5	-	-	-	-	-	-
Haplophragmoides bradyi	-	0,5	0,9	0,9	7,1	8,8	27,9	14,8	11,1	7,5	2,5	-	-	-	-
Hyalinea balthica	18,5	15,2	8,3	9,0	6,0	6,2	0,7	0,3	3,2	8,2	5,3	-	1,1	-	0,3
Melonis barleeanum	0,3	1,1	5,4	1,2	2,1	1,8	-	1,8	4,2	1,0	-	-	-	-	-
Planorbulina mediterranensis	-	-	-	-	-	-	-	-	-	0,3	-	9,1	8,3	0,3	1,0
Psammosphaera fusca	-	-	-	-	-	1,2	0,7	4,2	9,5	0,3	0,3	-	-	0,8	0,6
Saccammina sphaerica	-	-	-	-	1,4	4,1	13,8	13,3	10,5	-	-	-	-	-	-
Textularia bocki	0,3	-	-	-	-	-	-	-	-	0,3	-	5,0	2,5	2,2	1,9
Uvigerina celtica	10,2	12,2	0,3	-	0,9	0,3	1,3	0,3	1,1	0,7	0,3	-	-	-	-

3.2.2 1992/93 Survey

The identified species in the 1992/93 survey (Bergsten et al., 1996) were a total of 97 assigned to species level and 11 to genus level, with 36 species being agglutinated and 61 being calcareous foraminifera (Table A2). The absolute abundance of the total fauna of the 1992/93 survey ranged from 51 to 184 ind. g^{-1}, with no apparent trend for the distribution of high and low abundances (Figure 8). The relative abundance of agglutinated species ranged between 5 and 75 % with a higher abundance at the deeper stations and a lower abundance along the Danish- and Norwegian slope.

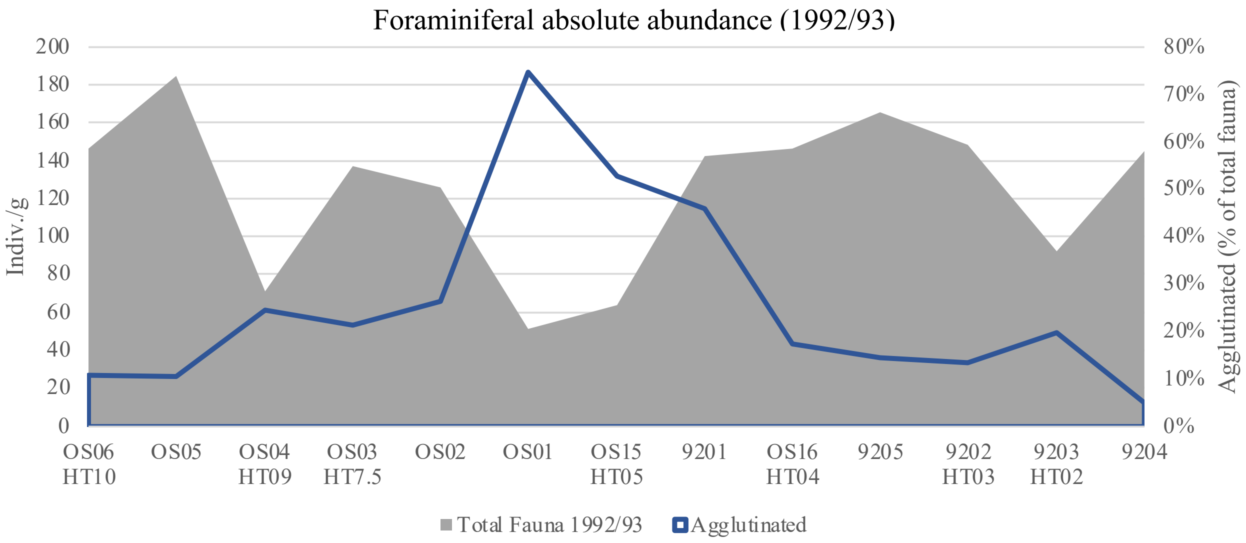


Figure 8. Absolute abundance of total fauna of 1992/93 along the transect between Hirtshals-Torungen.

3.2.2.1 Total Fauna

A total of 19 species remained for further analysis within the total fauna of 1992/93 (**Table 6**). The dominant species (>10 %) within the total fauna are *Brizalina skagerrakensis* (as *Bolivina* *skagerrakensis*: Bergsten et al, 1996*), B. marginata, C. laevigata, E. excavatum, Globobulimina turgida, H. bradyi, H. balthica, L. goësi, M. barleeanum, U. peregrina,* and *E. medius* (as *V. media:* Bergsten et al., 1996). Accessory species (5-10 %) are *Ammonia beccari, E. magellanicum, G. praegeri, G. charoides, P. subcarinata, S. sphaerica, T. bocki, Trifarina angulosa* and *E. medius/E. scaber* (as *E. scabrus:* Bergsten et al., 1996). None of the rare species (>2 %) were present in at least five samples and were thus excluded from further analysis.

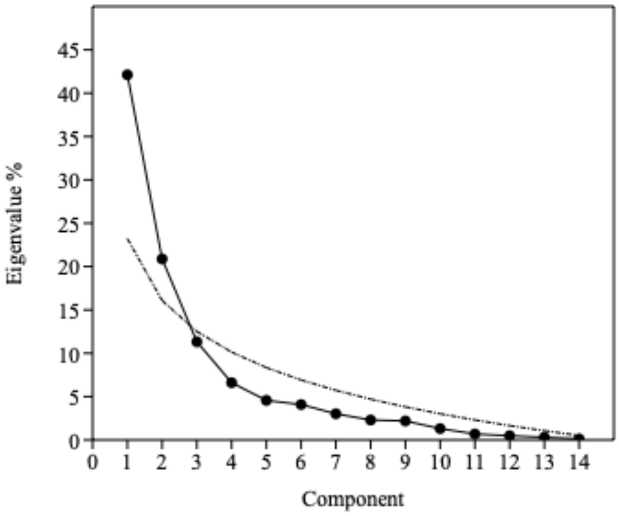
Table 6. Total fauna 1992/93: selected species present >5 % (yellow and green) at a minimum of one station or >2 % (red) in five stations in total fauna 1992/93 (%). Corresponding stations from the 2020 *survey are written in italics.*

	OS06 *HT10*	OS05	OS04 *HT09*	OS03 *HT7.5*	OS02	OS01	OS15 *HT05*	9201	OS16 *HT04*	9205	9202 *Ht03*	9203 *HT02*	9204
Ammonia beccari	-	-	-	-	-	-	-	-	-	-	-	5,9	-
Bulimina skagerrakensis	2,6	8,1	18,6	41,7	36,0	4,4	6,2	3,7	6,5	0,9	0,8	0,2	0,1
Bulimina marginata	12,8	16,5	7,2	3,9	3,4	0,1	2,1	10,1	1,4	2,3	2,2	1,6	0,5
Cassidulina laevigata	20,4	22,3	14,0	17,1	18,2	-	8,4	6,5	16,1	23,6	33,3	1,9	0,9
Elphidium excavatum	5,2	3,3	0,5	0,2	1,0	0,6	0,8	0,2	14,5	4,2	20,9	46,7	74,5
Elphidium magellanicum	-	-	-	-	-	-	-	0,2	1,6	2,1	4,5	8,4	4,9
Gavelinopsis praegeri	0,1	-	0,1	-	-	-	-	0,1	3,5	3,7	6,6	1,9	0,4
Globobulimina turgida	6,2	4,7	9,7	0,6	0,1	0,3	0,5	16,8	19,0	30,0	0,8	0,1	0,1
Glomospira charoides	0,1	0,1	-	0,8	1,2	9,5	1,5	-	-	-	-	-	-
Haplophragmoides bradyi	0,5	0,8	5,6	5,5	6,2	33,2	16,2	1,4	-	-	-	-	-
Hyalinea balthica	14,4	5,6	5,3	3,1	2,2	0,8	5,6	2,9	3,2	1,1	1,7	0,1	0,3
Liebusella goësi	2,5	1,6	7,4	0,2	0,1	-	0,6	24,5	1,5	1,8	0,4	-	-
Melonis barleeanum	9,4	7,4	13,1	4,4	3,0	3,4	6,2	8,8	1,4	0,4	-	-	0,1
Pullenia subcarinata	0,1	-	-	0,3	1,3	5,1	2,2	-	-	0,1	-	-	-
Saccammina sphaerica	-	-	-	0,1	-	6,9	0,6	-	0,1	-	-	-	-
Textularia bocki	0,2	-	0,1	-	-	-	-	0,1	8,0	0,8	4,9	1,8	0,8
Trifarina angulosa	5,3	0,8	0,2	0,1	0,2	-	-	0,1	0,2	0,0	0,2	-	0,1
Uvigerina peregrina	9,8	16,5	0,4	0,5	0,5	-	1,8	0,6	-	1,2	0,6	-	-
Eggereloides medius	2,1	7,2	9,8	8,9	11,2	6,6	17,8	11,3	5,1	6,8	6,6	6,1	-
E. medius/E. scaber	4,4	-	-	-	-	-	-	-	-	-	-	7,4	-

3.3 Faunal Assemblages and Distribution

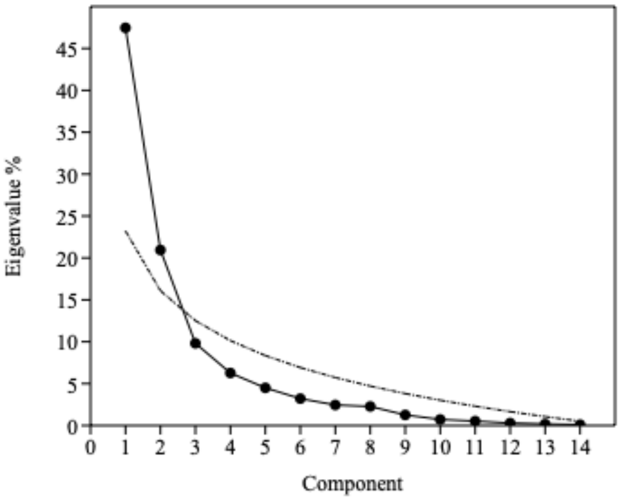
3.3.1 2020 Survey

Based on the PCA-analysis, the first three components within the total fauna and dead fauna of 2020 explain 74.2 % and 78.2 % of the variance within the data, respectively (Figure 9 & Fig. 10). For the living fauna of 2020, the first four PC explain 74.2 % of the variance within the data (Figure 11).



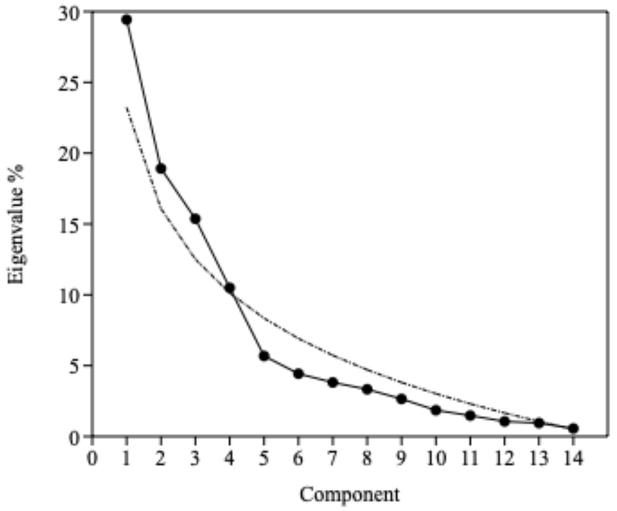
PC	Eigenvalue	% variance
1	10.951	42.119
2	5.42787	20.876
3	2.94432	11.324
4	1.71752	6.6058
5	1.18667	4.5641
6	1.06164	4.0832
7	0.784972	3.0191
8	0.598421	2.3016
9	0.569966	2.1922
10	0.340937	1.3113
11	0.178616	0.68699
12	0.126752	0.48751
13	0.0791759	0.30452
14	0.0321455	0.12364

Figure 9. Scree-plot of variance in R-mode PCA-analysis of the total fauna in the 2020 survey.



PC	Eigenvalue	% variance
1	10.9158	47.46
2	4.81737	20.945
3	2.25639	9.8104
4	1.44151	6.2674
5	1.03391	4.4953
6	0.738779	3.2121
7	0.563747	2.4511
8	0.523164	2.2746
9	0.290521	1.2631
10	0.165947	0.72151
11	0.120625	0.52446
12	0.0668871	0.29081
13	0.0416955	0.18128
14	0.0236211	0.1027

Figure 10. Scree-plot of variance in R-mode PCA-analysis of the dead fauna 2020 survey.



PC	Eigenvalue	% variance
1	9.12293	29.429
2	5.86417	18.917
3	4.76359	15.366
4	3.25315	10.494
5	1.76121	5.6813
6	1.37339	4.4303
7	1.18195	3.8127
8	1.03219	3.3297
9	0.820739	2.6475
10	0.574032	1.8517
11	0.457075	1.4744
12	0.328983	1.0612
13	0.292946	0.94499
14	0.173645	0.56014

Figure 11. Scree-plot of variance in R-mode PCA-analysis of the living fauna in the 2020 survey.

From the CABFAC-analysis, by selecting factors explaining at least 5 % of the data (**Table 7**), three factors were used to represent total- and dead fauna of 2020 each explaining 91.7 % and 90.7 %, respectively. Four factors were used for the living fauna of 2020 explaining in total 93.2 % of the variance. Each factor from the CABFAC-analysis represents an assemblage based on species scores that most strongly characterize each factor.

Table 7. Factors with respective explained variance (%) from CABFAC factor analysis.

		2020	
PC / Variance (%)	Total Fauna	Living Fauna	Dead Fauna
1	67.04	65.99	62.33
2	15.87	13.14	18.18
3	8.46	8.18	10.22
4	3.64	5.91	4.1
5	1.98	2.4	2.51
6	1.33	1.81	1.42
7	1.04	1.41	0.67
8	0.65	1.15	0.57

3.3.1.1 Total fauna

From the species factor scores shown in **Table 8**, three assemblages can be identified: *Cassidulina laevigata* assemblage (Factor 1), characterized by the species *C. laevigata, B. marginata, H. balthica, B. skagerrakensis; Elphidium excavatum* assemblage (Factor 2), characterized by *E. excavatum* and *Ammonia* spp.; and *Haplophragmoides bradyi* assemblage (Factor 3), characterized by *H. bradyi, E. medius,* and *S. sphaerica* species. The distribution of total fauna assemblages along the transect Hirtshals-Torungen is plotted in Figure 12, where the *E. excavatum* dominated the Danish slope, *H. bradyi* dominates the deepest part of the basin (below 400 m) and *C. laevigata* assemblage mainly dominates the Norwegian slope of the Skagerrak but is also seen at station HT04 (374 m depth) at the transition between the deeper water and the Danish slope (Fig. 2).

Table 8. Factor scores in CABFAC on stations total fauna 2020.

	Factor 1	Factor 2	Factor 3
Agglutinated other	0.34648	1.349	-0.10089
Ammonia spp.	-0.50115	1.7711	0.023741
Brizalina skagerrakensis	1.7649	-0.015186	-0.36984
Bulimina marginata	2.1788	0.10099	-0.066833
Cassidulina laevigata	2.3867	0.67201	-0.35007
Cibicides lobatulus	-0.11473	1.3968	0.079116
Cribrostomoides kosterensis	0.14208	1.0159	0.30324
Cribrostomoides subglobosum	0.27321	-0.29566	-1.3082
Eggereloides medius	0.69543	1.1097	-2.2565
Eggereloides scaber	-0.57601	1.0384	-1.3056
Elphidium albiumbilicatum	-0.15507	1.0293	0.13209
Elphidium excavatum	-0.12136	2.8564	0.2507
Elphidium magellanicum	-0.090013	0.94933	0.19737
Gavelinopsis praegeri	-0.06335	1.2753	0.29547
Globobulimina turgida	1.4594	-0.1048	0.35648
Glomospira charoides	-0.48296	-0.06226	-1.3551
Haplophragmoides bradyi	0.052698	-0.38349	-2.4355
Hyalinea baltica	2.0577	-0.18048	-0.12341
Libusella goësi juv.	0.85663	-0.18684	0.060228
Melonis barleeanum	0.40815	-0.31855	-1.3716
Planorbulina mediterranensis	-0.060905	1.0675	0.26883
Psammosphaera fusca	-0.69358	0.50363	-1.4031
Reophax fusiformis	0.60392	1.2704	0.43971
Reophax rostrata	0.89129	-0.11095	0.45034
Saccammina sphaerica	-0.79365	-0.13554	-2.087
Uvigerina celtica	1.1496	-0.29427	-0.57022

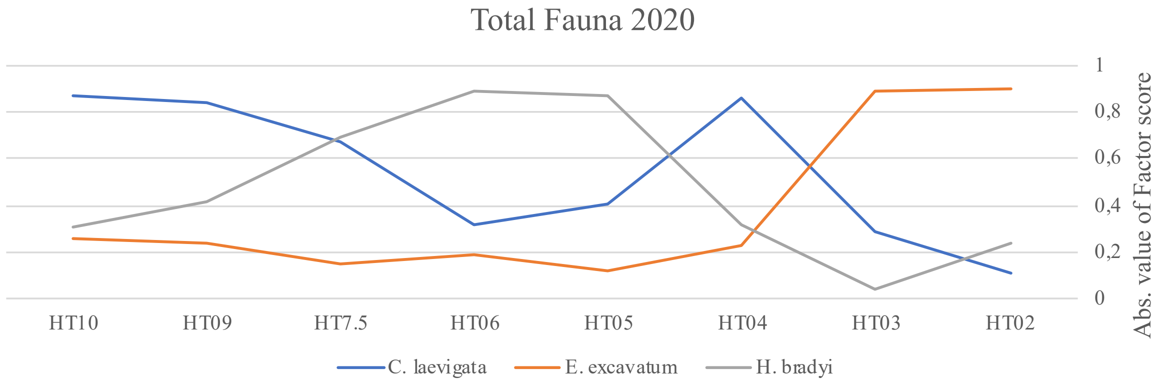


Figure 12. Assemblage distributions of total fauna of 2020 survey along the transect Hirtshals (right)-Torungen (left) based on absolute values of factor scores from CABFAC-analysis.

3.3.1.2 Living fauna

The four assemblages distinguished within the living fauna of the 2020 survey (Table 9) are: *Haplophragmoides bradyi* assemblage (Factor 1), characterized by *H. bradyi, C. subglobosum, P. bulloides, M. barleeanum, E. medius*, and *G. charoides*; *Eggereloides scaber* assemblage (Factor 2), characterized by *E. scaber, Ammonia spp., P. fusca,* and *N. turgida*; *Bulimina marginata* assemblage (Factor 3), characterized by *B. marginata, H. balthica*, *G. turgida, L. goësi juv.,* and *R. rostrata;* and finally, the *Cassidulina laevigata* assemblage (Factor 4), characterized by *C. laevigata, R. fusiformis, E. medius, G. praegeri, E. excavatum, C. lobatulus,* and *T. bocki.*

The *E. scaber* assemblage is dominant in the upper Danish slope (HT02), while *C. laevigata* assemblage is dominant at the lower Danish slope, and *H. bradyi* assemblage dominates the deepest part of the basin (Fig. 13). Finally, the *B. marginata* assemblage is mainly found at the Norwegian slope, but also dominates at the transition zone at station HT04.

Table 9. Factor scores in CABFAC on stations living fauna 2020.

	Factor 1	Factor 2	Factor 3	Factor 4
Agglutinated other	-0.45468	1.2678	1.1176	-0.51342
Ammonia spp.	-0.13288	2.3712	-0.19385	-0.53907
Brizalina skagerrakensis	0.17448	-0.10249	0.94985	1.2402
Bulimina marginata	0.20793	-0.10729	2.264	-0.22421
Cassidulina laevigata	1.3811	-0.65681	1.4268	2.3197
Cassidulina neoteretis	-0.038751	-0.015342	0.22215	-0.054799
Cibicides lobatulus	-0.19927	0.0057676	-0.18538	1.5836
Cribrostomoides subglobosum	1.8973	-0.24834	0.36761	-0.51654
Eggereloides medius	1.7716	1.4966	0.72707	1.8719
Eggereloides scaber	0.91717	2.4997	-0.17382	-0.75853
Elphidium excavatum	-0.0093359	0.86543	-0.56246	1.6067
Gavelinopsis praegeri	-0.16101	0.20839	-0.37454	1.7116
Globobulimina turgida	-0.57915	0.078809	1.9429	0.053003
Glomospira charoides	1.6385	-0.076416	-0.89575	0.15266
Haplophragmoides bradyi	2.512	-0.26809	0.033454	-0.4176
Hyalinea baltica	0.37289	0.31192	2.1344	-0.82063
Libusella goësi	0.017746	-0.20967	1.3686	-0.34164
Libusella goësi juv.	-0.13434	-0.097084	1.7217	-0.70905
Melonis barleeanum	1.8158	-0.17517	0.42428	-0.62007
Nonionella turgida	-0.10112	1.8045	-0.14752	-0.41022
Planorbulina mediterranensis	-0.10653	-0.25482	-0.26839	1.4809
Psammosphaera bowmanni	-0.070951	1.2661	-0.10351	-0.28784
Psammosphaera fusca	0.17204	1.8391	-0.21797	-0.41399
Pullenia bulloides	1.8947	-0.15755	-0.72487	0.026875
Pyrgo williamsoni	0.40088	1.1626	0.093457	-0.021217
Quinquerloculina seminula	-0.014325	1.4345	-0.15364	0.052773
Reophax fusiformis	-1.0432	1.3549	0.92301	2.0487
Reophax rostrata	-0.77012	-0.055027	1.65	-0.33004
Textularia bocki	-0.21564	0.0084546	-0.083707	1.5096
Trochammina rotaliformis	1.2186	0.012947	-0.65563	-0.019339
Uvigerina celtica	1.159	-0.35912	1.2423	-0.15996

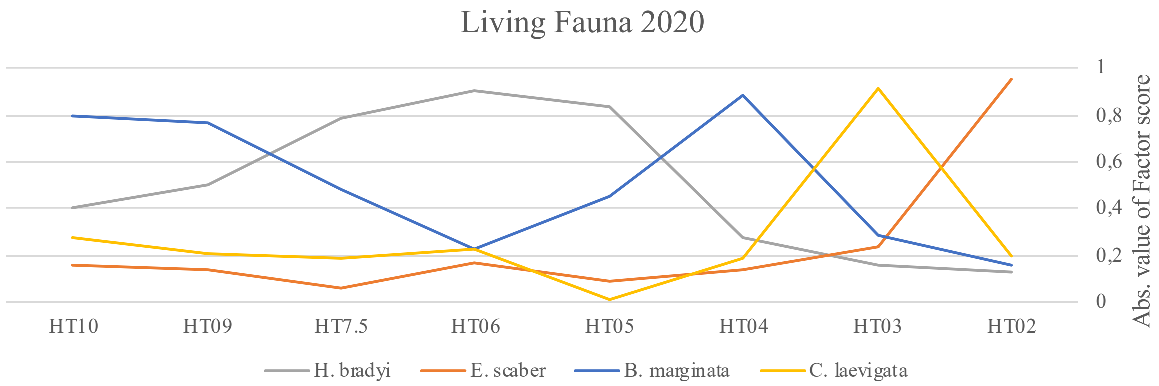


Figure 13. Assemblage distributions of living fauna of 2020 survey along the transect Hirtshals (right)-Torungen (left) based on absolute values of factor scores from CABFAC-analysis.

3.3.1.3 Dead fauna

The three assemblages identified within the dead fauna of 2020 (Table 10) are: the *Cassidulina laevigata* assemblage (Factor 1), characterized by *C. laevigata, H. balthica, B. marginata, and B. skagerrakensis;* The *Elphidium excavatum* assemblage (Factor 2), characterized by *E. excavatum* and *Ammonia* spp.; The *Eggereloides medius* assemblage (Factor 3), characterized by *E. medius, H. bradyi, S. sphaerica,* and *P. fusca.*

The distribution of dead faunas shows the same pattern as for the total fauna of 2020, however, with different dominant species in the deep basin (Fig. 14). Within the dead fauna the deep basin is dominated by *E. medius*, whereas for the total fauna it is *H. bradyi* (present mainly amongst living faunas), although, both species are characteristic of the deepest basin (Table 10).

Table 10. Factor scores in CABFAC on stations dead fauna 2020.

	Factor 1	Factor 2	Factor 3
Agglutinated other	0.15449	1.3734	-0.35251
Ammonia sp.	-0.39525	1.6015	-0.0048253
Brizalina skagerrakensis	1.9138	-0.22086	-0.51315
Bulimina marginata	2.0617	0.1823	-0.14096
Cassidulina laevigata	2.4908	0.63498	-0.043392
Cibicides lobatulus	-0.099027	1.3866	-0.11867
Cribrostomoides kosterensis	0.1403	1.0819	0.13071
Eggereloides medius	0.65264	0.30584	-2.5526
Eggereloides scaber	-0.33554	0.87006	-1.0043
Elphidium albiumbilicatum	-0.16263	1.1104	0.068067
Elphidium excavatum	0.17816	2.7759	0.25852
Elphidium magellanicum	-0.13351	1.0245	0.11607
Gavelinopsis praegeri	-0.066322	1.2342	0.1743
Globobulimina turgida	1.1879	-0.18301	0.18352
Glomospira charoides	-0.3255	-0.03548	-1.0773
Haplophragmoides bradyi	0.029211	-0.25683	-2.3563
Hyalinea baltica	2.1438	-0.17599	0.047766
Melonis barleeanum	0.4623	-0.18445	-0.78659
Planorbulina mediterreanensis	-0.12051	1.0937	0.1573
Psammosphaera fusca	-0.54243	0.17373	-1.5257
Saccammina sphaerica	-0.7377	-0.10599	-2.2788
Textularia bocki	-0.1469	1.0861	0.081528
Uvigerina celtica	0.9232	-0.16046	0.008548

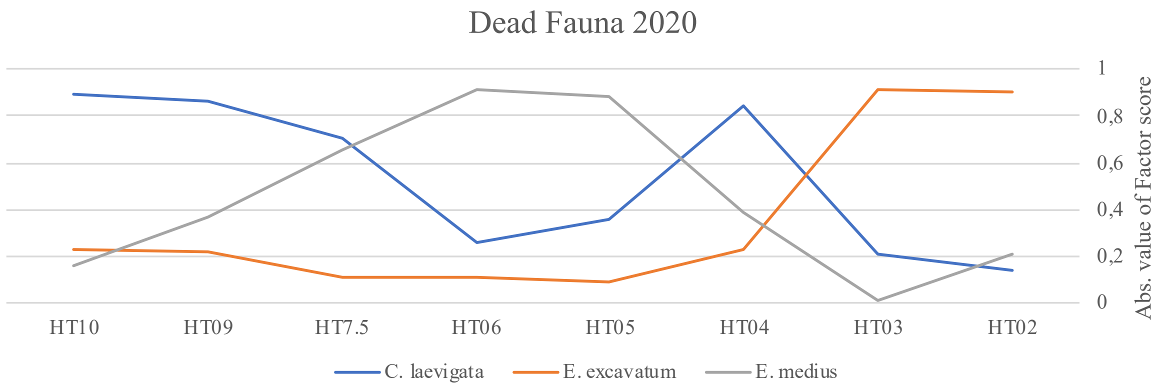
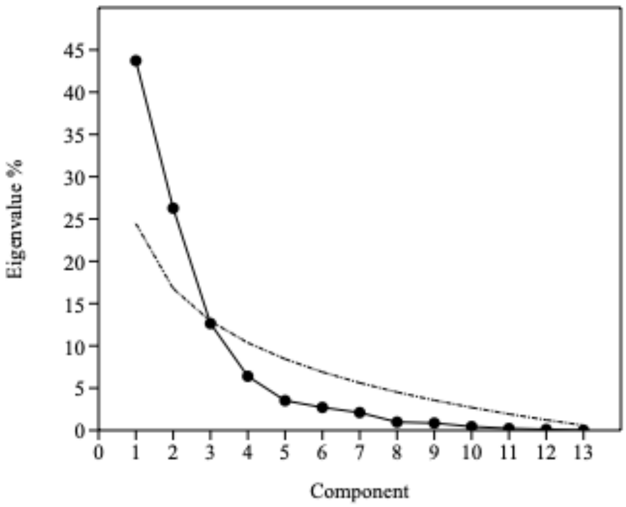


Figure 14. Assemblage distributions of dead fauna of 2020 survey along the transect Hirtshals (right)-Torungen (left) based on absolute values of factor scores from CABFAC-analysis.

3.3.2 1992/93 Survey

Based on the PCA-analysis, the first three components within the total fauna of 1992/93 explain 74.0 % of the variance within the data (Figure 15). For the CABFAC factor analysis, the three first factors, all above 5 %, explain 73.5 % of the variance within the data.



PC	Eigenvalue	% variance
1	7.30432	38,4
2	4.76608	25,1
3	1.98036	10,4
4	1.73607	9.1372
5	1.24589	6.5573
6	0.878693	4.6247
7	0.491845	2.5887
8	0.238809	1.2569
9	0.164637	0.86651
10	0.120448	0.63393
11	0.0568938	0.29944
12	0.015955	0.083974
13	0.00238352	0.018335

Figure 15. Scree-plot of variance in R-mode for the total fauna 1992/93.

From the CABFAC factor analysis, by selecting factors explaining at least 5 % of the data (**Table 11**), three factors were used to represent three assemblages within the total fauna of 1992/93, explaining 89.2 % of variance within the data.

Table 11. Factors with respective variance (%) from CABFAC factor analysis.

PC / Variance (%)	1992/93 Total Fauna
1	64.48
2	16.72
3	7.99
4	3.20
5	2.73
6	1.68
7	1.47
8	0.73
9	0.49
10	0.23

3.3.2.1 *Total fauna 1992/93*

The three assemblages distinguished within the total fauna of 1992/93 (Table 12) are: *Globobulimina turgida* assemblage (Factor 1), characterized by *G. turgida, C. laevigata,* and *B. marginata; Elphidium excavatum* assemblage (Factor 2), characterized by *E. excavatum* and *E. magellanicum,* and *Haplophragmoides bradyi* assemblage (Factor 3), characterized by *H. bradyi, B. skagerrakensis,* and *V. media.*

The *E. excavatum* assemblage dominates along the Danish coast and is being exchanged by the *G. turgida* assemblage in the deeper part of the Danish slope (Fig. 16). The deepest part of the basin (below 500 m) is dominated by *H. bradyi* assemblage, and the Norwegian slope is dominated the *G. turgida* assemblage.

Table 12. Factor scores in CABFAC on stations total fauna 1992/93.

	Factor 1	Factor 2	Factor 3
Ammonia beccari	-0.25026	-0.55468	0.11249
Bolivina skagerrakensis	0.95232	0.20482	1.8643
Bulimina marginata	1.5347	-0.15228	0.10344
Cassidulina laevigata	2.091	-0.86781	0.28444
Elphidium excavatum	-0.31979	-3.542	0.17069
Elphidium magellanicum	-0.28201	-1.7661	-0.088475
Gavelinopsis praegeri	0.25854	-0.99488	-0.33661
Globobulimina turgida	2.1319	-0.036577	-0.88797
Glomospira charoides	-0.55297	-0.044556	1.4149
Haplophragmoides bradyi	-0.37659	0.24176	2.6538
Hyalinea balthica	1.1499	-0.018763	0.48284
Libusella goësi	1.4494	0.34505	-0.4692
Melonis barleeanum	1.1134	0.45017	1.0292
Pullenia subcarinata	-0.44263	-0.041726	1.1905
Saccammina sphaerica	-0.48274	-0.079071	0.97732
Textularia bocki	0.127	-1.0529	-0.23026
Trifarina angulosa	0.38614	-0.0018597	-0.13908
Uvigerina peregrina	0.97053	0.13119	-0.11032
Verneulina media	0.92835	-0.60636	1.5707
V. media/Eggereloides scabrus	-0.03268	-0.57827	-0.0074887

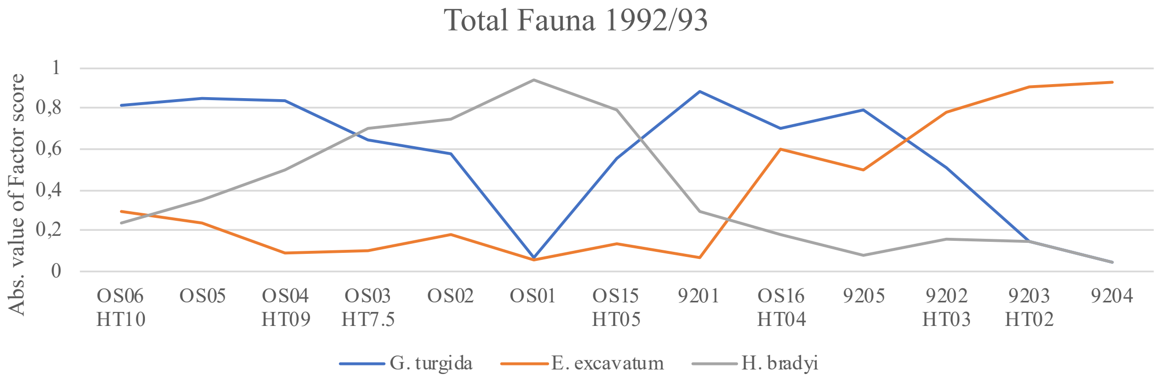


Figure 16. Assemblage distributions of total fauna of 1992/93 survey along the transect Hirtshals (right)-Torungen (left) based on absolute values of factor scores from CABFAC-analysis.

The identified assemblages and corresponding major contributing species in the different data sets based on CABFAC factor analysis are summarized in Table 13. The assemblages are present at four geographically separated zones, the Norwegian slope, the deeper basin, the lower Danish slope, and the upper Danish slope (Table 13). The Norwegian slope and the transition zone consist of the same re-occurring assemblage and is therefore summarized in the same column. The species that are present in all datasets are underlined to emphasize similarities between the data sets.

Table 13. Summary of species considered major contributors (Factor scores above 1.5 (or below -1.5) within identified assemblages based on CABFAC-analysis. Underlined species are species that are both considered major contributors (Factor scores above 1.5 (or below -1.5) and that are present within all datasets from both surveys. * V. media: Bergsten et al., 1996.

	Norwegian slope / transision zone	**Deeper basin**	**Danish slope**	**Upper Danish slope**
Total fauna 2020 *0-3 cm*	*HT04, HT09, HT10*	*HT06, HT06, HT7.5*	*HT02, HT03*	
	C. laevigata B. marginata H. balthica B. skagerrakensis	H. bradyi E. medius S. sphaerica	E. excavatum Ammonia sp.	
Living fauna 2020 *0-3 cm*	*HT04, HT09, HT10*	*HT06, HT06, HT7.5*	*HT03*	*HT02*
	B. marginata H. balthica G. turgida L. goësi juv. R. rostrata	H. bradyi C. subglobosum P. bulloides M. barleeanum E. medius G. charoides	C. laevigata R. fusiformis E. medius G. praegeri E. excavatum C. lobatulus T. bocki	E. scaber Ammonia sp. P. fusca N. turgida
Dead fauna 2020 *0-3 cm*	*HT04, HT09, HT10*	*HT06, HT06, HT7.5*	*HT02, HT03*	
	C. laevigata H. balthica B. marginata B. skagerrakensis	E. medius H. bradyi S. sphaerica P. fusca	E. excavatun Ammonia sp.	
Total fauna 1996 *0-3 cm*	*OS6, OS5, OS4, 9201, OS16, 9205*	*OS03, OS2, OS1, OS15*	*9202, 9203, 9204*	
	G. turgida C. laevigata B. marginata	H. bradyi B. skagerrakensis E. medius*	E. excavatum E. magellanicum	

4 Discussion

4.1 Hydrography

The hydrographic profile of 2020 (Fig. 3) represents the fall season during which the foraminiferal samples were collected for the 2020 survey. This allows for comparing the hydrographical conditions with the concurrent living (stained) fauna of 2020. For consistency, the 1992 hydrographical conditions were plotted from ICES data to reflect the sampling (summer, May - Aug) season of 1992/93 survey, for which hydrographic data taken during the sampling were missing (Fig. 4). To enable a more relevant comparison of the years 1992 and 2020, i.e., without the seasonal discrepancy, the annual mean conditions were also considered (Fig. 5). Therefore, discussed below are firstly the long-term hydrographical trends based on monthly means from 1950 to 2020, secondly the difference between the annual mean conditions of 1992 and 2020 (grey rectangles, Fig. 5). After that, the hydrographical conditions of the two surveys are discussed (Fig. 3 and 4).

4.1.1 Long-term hydrographic series for 1950-2020

Over the period 1950 through 2020 there is long-term trend of increasing temperature and salinity, and a decreasing oxygen concentration that can be traced in both the surface- and deep water (Fig. 5). The surface warming of ~1°C indicates a greater warming than the average increase of ~0.11°C per decade in the North Atlantic surface waters (period 1950-2020) (Dunn et al., 2021). A shift to higher temperatures is seen in the late 1980s, where the surface water stayed above 7 °C throughout the period 1989-1990 (Fig 5a, red line), is accompanied by a temporary salinity increase in the late 1980s to early 1990s (Fig 5b, black dotted line). Furthermore, the bottom oxygen concentration shows a significant drop during a four-year period between 1986-1991, otherwise replenished roughly every two years (Fig. 5c, blue line). The late 1980s has been described as having the highest recorded temperature and lowest recorded oxygen (4.8 ml/l) in the Skagerrak basin since the 1950s and was followed by a large inflow of Atlantic Water in 1991 (Aure & Dahl, 1994; Danielssen, 1996). This is period in the late 1980s is concurrent with the regime shift described by Edwards et al. (2002), during which a high NAO index with associated warm winters and an increased influx of warm, nutrient rich Atlantic water was recorded in the Skagerrak (especially in deeper water ~200 m) (Saetre et al. 2003). A simultaneous increase in phytoplankton biomass, as well as an introduction of an unprecedented number of oceanic species, e.g., oceanic tunicates, and a more northward distribution of tropical fish species have also been recorded (Edwards et al., 2002, and ref therein).

As seen from the rapid decrease in temperature (Fig. 5a), the bottom water exchanges occurred approximately thirteen times over the period 1950-2020. Ljøen and Svansson (1972) identified the first three of these events of bottom water exchange in the Skagerrak in the period 1950-1969. A simultaneous drop in salinity and increase in oxygen is expected, as the cascading inflows consist of mixed surface water from the central North Sea. However, the frequency of variation between the temperature (~5 years) and the and oxygen (~2 years) in the deep water suggest an additional mechanism for oxygen replenishment (e.g., in 1999) other than the cascading inflows of water from the central North Sea, perhaps from phytoplankton blooms in the surface waters. Furthermore, some years do not display a simultaneous drop in salinity (e.g., 2005 and 2013) which could indicate shift in water source of the cascading inflows or varying precipitation. The less saline inflow could originate from the central and southern North Sea, whereas the more saline inflows could originate from the Norwegian sea, meaning Atlantic water entering through the Norwegian Trench.

With a warming of the Atlantic water combined with warmer winters (preventing cooling of North Sea water) could result in reduced bottom water exchange, both in frequency but also in the extent to which the exchange occurs. Longer time periods of failed deep-water exchange could result in decreased oxygen concentration in the deep water of the Skagerrak, especially with an increased nutrient input to the basin. However, as there is an alternative oxygenation process occurring approx. once every two years, the significance of on the oxygenation in the deep basin by cascading inflows is difficult to determine.

4.1.2 Comparison of the annual mean hydrography for 1992 and 2020

As previously mentioned, by comparing the annual mean of the years 1992 and 2020, the seasonal differences can be disregarded. Although there has been an overall change in temperature, salinity, and oxygen, both years show very similar hydrographical conditions. Both surveys were conducted after the shift of 1980s, which could explain the similarity in hydrographical conditions between the years. However, the extended period with no significant oxygen replenishment between 1986-1991 (described above) is worth noting once more. Events of bottom water exchange occurred in 1991 and 2018, one and two years before 1992 and 2020 respectively. The deep water (>400 m) in 2019 had an oxygen concentration of 5.3 ml l^{-1}. Assuming a depletion rate of 0.04 ml l^{-1}month^{-1}in the deep basin (Aure & Dahl, 1994) and an similar initial oxygen content of the intermediate water (~6 ml l^{-1}), suggest the deep water had been stagnant for ~18 months. Considering these specifics, the most significant difference between the conditions of 1992 and 2020 is in the period prior each survey, as the years 1986-1991 show a significant reduction in oxygen concentration.

4.1.3 Hydrographic measurements during sampling in 2020 and 1992

As seen in the hydrography data collected in October 2020, the three major water masses are visible within the data (Fig. 3) and are mostly consistent with long-term variability within the basin. However, the low saline water supplied by the Baltic Current (BC) is normally more defined and concentrated along the Norwegian coast but due to the stormy weather in October 2020, the surface water is splayed out across the surface covering a major part of the basin. This can also occur during events of upwelling along the Norwegian coast, where low-saline water is occasionally driven away from the coast (Rhode, 1996). The Skagerrak Deep Water is a major part of the basin and is part of the deep reaching anti-cyclonic circulation (Rodhe, 1996) reach to about 400 m. Based on the homogeneity in temperature, oxygen concentration, and pH of this water mass and consistent salinities >35 PSU confirms a strong dominance of Atlantic water, supplied by the STC (Conradsen et al., 1994). Within the Skagerrak Deep Water is a distinct layer below 400 m. Based on the salinity, the origin is also Atlantic water, however, the decrease in oxygen and increase in pH indicate that this water has been stagnant for a longer period compared to the water at 50-400 m. The oxygen also showed lower concentrations along the Danish and Norwegian slopes, and roughly follow the same distribution as the pH and turbidity within the intermediate and deep water. The turbidity reflects the amount of suspended material in the water and could therefore indicate higher supply of organic matter which during degradation by organisms consumes oxygen and lower the pH. The highest turbidity is seen at station HT02 within the coastal water closest to the Danish coast, but with no lowering in oxygen and pH as oxygen is likely provided more continuously to the surface water. This is most likely the North Jutland Current (NJC) with a mix of fresh water from South Jutland Current (SJC) and a large supply of Atlantic water from the Southern Trench Current (STC) with related to relatively high current velocities (Keld Conradsen et al., 1994); van Weering et al., 1987, and ref therein). Stations HT02 and HT03 also contain the highest fraction of sand (>60 %, Table 1) compared to the deeper stations (0-20 %), indicating a more dynamic environment with higher current velocities and reworking of the sediments.

The summer of 1992 showed a shallower pycnocline (20 - 30 m) compared to October 2020 (50 – 100 m) (Fig. 4) reflecting seasonal difference between the sampling campaigns. The higher surface temperatures in 1992 were accompanied by lower salinities, resulting in a stronger stratification at that time (Fig. 4a). This stratification is also reflected in the Figure 5a, with a large temperature difference between the surface and bottom water. The oxygen distribution varies between the two periods. In 1992, there was continuous decrease in oxygen content with depth, whereas in 2020, beside the high oxygen concentration in the surface water, there is an elevated oxygen concentration in the intermediate waters (200-400 m), likely indicating presence of well-oxygenated Atlantic water (Danielsen et al., 1996).

4.2 Foraminiferal data

As the samples of 1992/93 only were analyzed for total fauna (Bergsten et al. 1996), it is only possible to compare the total assemblages between 1992/93 and 2020. However, it is still interesting to compare the living-, dead-, and total fauna within the 2020 survey to evaluate potential taphonomical effects on the fauna. A good correlation between the living- and total fauna would increase the reliability of using the fossil assemblages as a proxy. However, as the living fauna in this study only represents a single season, some foraminifera might have had their highest abundances during different times of the year and thus were not covered by this study.

4.2.1 Abundance and Controlling Factors

4.2.1.1 Food availability

As seen in the data from 2020, the peak abundance for stained tests is at the transition between the deeper basin and the Danish slope (374 m at station HT04). High densities of standing crop have generally been found between 200 and 500 m on the Danish slope and broadly correlates with high organic detritus, acting as food for the foraminifera, supplied by the South Jutland Current and resuspending of organic material by trawling, which is present in the study area (Alve & Murray, 1995; Alve and Murray, 1997). A maximum of stained individuals of 18 ind. cm^{-3} recorded in this study is low in contrast to a peak abundance of stained foraminifera recorded in a study in 1994 at 332 ind. cm^{-3} (Alve and Murray, 1997), however, this was recorded for fractions > 63 µm which would capture living juveniles and smaller thin-shelled species not observed herein (e.g. *Nonionella iridea*: Alve, 1996; Polovodova Asteman et al., 2017) or underrepresented (*S. fusiformis*) in the >125 µm sediment fraction in this study.

4.2.1.2 Carbonate dissolution

Dissolution effects are mainly expressed in two ways: a lower abundance of a species in the dead fauna compared to the living fauna or a relative increase of agglutinated species over calcareous ones, as agglutinated species are less prone to dissolve. The relative abundance of agglutinated foraminifera in the total fauna (Figure 6) is the highest within the deeper basin, where species e.g., *H. bradyi* and *E. medius* are dominant, at up to 34 %. When looking at the relative abundance of agglutinated foraminifera and the relation between stained and non-stained tests, the non-stained test shows a similar distribution pattern as that of the total fauna (Figure 7), with a peak in the deep basin and a continuous decrease toward the Norwegian and Danish coasts. The stained agglutinated tests have its highest abundance within the deep basin, but also show a higher abundance closer to the Norwegian- and Danish coasts respectively. A similar pattern was described by Alve and Murray (1997) where it was stated that carbon dissolution in the deep basin of Skagerrak increases the relative abundance of agglutinated tests (Alve and Murray, 1997). Carbon dissolution may occur because of a range of different reasons: increased temperature, decrease in salinity (Saraswat et al., 2015), decreased oxygen or decreased pH with depth (Bernhard et al., 2021). By conducting a culture study of living benthic foraminifera *Rosalina globularis*, Saraswat et al. (2015) concluded that benthic foraminifera have a lower pH tolerance level of ~7.5 during salinity induced pH changes (i.e., lowering of pH induced by an influx of low saline water). As the pH stayed well above this level in the entire basin in (lowest pH of 8.1) and salinities stayed above 35 PSU at all stations (at depth of sediment collection), salinity induced pH changes, and thus pH induced decalcification, along the Hirtshals-Torungen transect seems unlikely, and would therefore not explain the discrepancy between the abundance distribution of living and dead agglutinated species. A lower pH within the sediments could also lead to dissolution of buried tests.

4.2.1.3 Transport

As shown in (Figure 6) the difference in absolute abundance between the stained and non-stained tests varied greatly within the 2020 total fauna. This is expected with a low sedimentation rate, especially in the deep basin, as several blooming seasons would be represented within the top 0-3 cm, and thus surface sediments will accumulate empty tests. A further explanation of the discrepancy between stained- and non-stained abundance concerns foraminiferal tests being transported from other areas. Although transported individuals were identified and excluded from the analyses in this study, Alve and Murray (1997) states that although foraminiferal tests can be transported as bedload, sand sized foraminiferal test are mainly transported as suspension load, leading to minimal damage on the test. The Danish slope has been attributed as a depositional sink for transported foraminiferal tests, especially of *Elphidium excavatum* (Alve & Murray, 1997; Conradsen et al., 1994; Klitgaard-Kristensen et al., 2002; Nordberg et al., 1999). Based on the regional distribution of living foraminifera, *E. excavatum* and *E. scaber* have been suggested to originate from the southern North Sea (Alve and Murray, 1997). In the current study, the different abundances of *Elphidium excavatum* in non-stained (>40 %) and stained (6 %) assemblages along the Danish slope are significant, suggesting a transportation of empty tests into the area or reworking of the sediments, or both. For *Eggereloides scaber*, however, the abundance is higher in the stained fauna, compared to the non-stained and is thus considered to belong to the in-situ fauna.

4.2.1.4 Sediment Migration and Bioturbation

Sediment migration complicates the picture, as some species have been shown to have an abundance maximum further down in the sediments. Corliss & van Weering (1993) analyzed four sediment cores for living fauna at different depths in Skagerrak. In a core taken on the border between Skagerrak and Kattegat, living *Elphidium excavatum, Ammonia bavatus, B. marginata* had an abundance maximum at 15 cm sediment depth (Corliss & van Weering, 1993). This area has a similar sediment regime with that of the southern slope of the Norwegian trench, i.e., represent well sorted silty sands. Other species showed bimodal maximum at 210 m water depth, one maximum at the surface and another at 10-15 cm, e.g., *B. skagerrakensis, C. laevigata,* and *H. balthica* (Corliss & van Weering, 1993). At depth of 530 m, species *B. skagerrakensis* and *Globobulimina auriculata* had significantly high abundances below 3 cm in the sediment (Corliss & van Weering, 1993). Polovodova Asteman and Schönfeld (2016) also report living (stained) benthic foraminifera present down to 10 cm in the sediment to the west off Skagen within the Skagerrak-Kattegat front where sediments were characterized by high bioturbation and sediment transport.

4.3 Assemblage distribution across the basin: comparing 1992/93 and 2020

Three distinct assemblages were identified for the total fauna of the 2020 and the 1992/93 surveys with similar geographical distributions. Although the assemblages are generally similar between the surveys, as they share many species, there are some differences in the constellations of the most characteristic species within each assemblage. The living fauna consist of one additional assemblage, dividing the Danish slope into two parts. These are compared and discussed below.

4.3.1 Haplophragmoides bradyi assemblage: the deep Skagerrak basin

In the deep basin (>400 m, stations HT05, HT06, and HT7.5, and OS15, OS01, OS02, OS03, and OS04, for the 2020- and 1992/93-surveys respectively) the total fauna is characterized by the *Haplophragmoides bradyi* assemblage with *H. bradyi* and *E. medius* as the two main contributing species (Fig. 12). The deep basin shows stable conditions mainly characterized by the Atlantic water with little no seasonal variability and is affected occasionally by winter inflows from the central North Sea (as seen in Fig. 3-5). This area is characterized by fine grained sediments with a coarser sediment fraction > 63 µm being 0.6-3.9 % (Table 1) and high organic matter content (Alve & Murray, 1995). The area has the lowest absolute foraminiferal abundance along the transect and the highest relative abundance of agglutinated species. The low absolute abundance in this area has been suggested to be partly related to the high sediment accumulation rate compared to the slopes (Bergsten et al., 1996, and ref. therein). A major difference in the assemblage composition between the surveys is presence of *B. skagerrakensis* in the 1992/93 dataset, and *Saccammina sphaerica* in the 2020, in addition to the two above-mentioned species.

The relative abundances of *S. sphaerica* are similar at ~7 % in both surveys (Table 3 and 6), whereas the relative abundance of *B. skagerrakensis* is considerably higher within the 1992/93 total fauna (maximum of 20 % in 2020, and maximum of 42 % in 1992/93, Table 3 & 6). In the compilation study by Conradsen et al. (1993), the deep basin was dominated by *B. skagerrakensis*, however, they had very limited samples taken below 300 m, and no samples were taken below 560 m water depth (Conradsen et al., 1993). *Brizalina skagerrakensis* have previously been associated with the deeper part of the Skagerrak (Murray, 1991) and was suggested to arrive to the Skagerrak deep basin c. 2300-1700 years BP, associated with an increased outflow from the Baltic Sea and a regime shift from low to high productivity in the area (Polovodova Asteman et al., 2017). It was further suggested that this increase in primary productivity contributed to the high abundance of some agglutinated species seen today, e.g., *E. medius* (Polovodova Asteman et al., 2017). Although on very different timescales, a decrease in *B. skagerrakensis* from 1992/93 to 2020 in the deep basin (HT7.5) could therefore be related to a lower primary productivity in 2020. As mentioned in Section 4.1.1., the late 1980s to early 1990s displayed a high influence of warm, nutrient rich Atlantic water, which when upwelled to the surface could contribute to a higher primary production.

The living and total fauna of 2020 share the same geographical distribution, however, with other characteristic species. These are *H. bradyi, C. subglobosum, P. bulloides, M. barleeanum, E. medius, and G. charoides.* In a study of the living fauna in the Skagerrak basin by Corliss & van Weering (1993), the deep basin (621 m) was characterized by different species (the three identified species with the highest abundances were *P. quinqueloba, B. skagerrakensis, M. barleeanum)*, however, they grouped all the agglutinated species into one group. The cause of higher relative abundance of calcareous species (e.g., *P. bulloides, M. barleeanum)* in the living fauna (Fig. 7) is difficult to evaluate (See Section 4.2.1.2 & 4.2.1.3) but could be due to transportation of living calcareous species into the basin or dissolution of calcareous tests, or both.

4.3.2 Elphidium excavatum assemblage: the Danish slope

At the upper Danish slope (HT02 and HT03, and 9202, 9203, and 9204 for 2020 and 1992/93 survey respectively) the total fauna is characterized by the *Elphidium excavatum* assemblage (Fig. 12 & 16), including *E. excavatum* and *Ammonia* spp. in 2020, *and E. excavatum and E. magellanicum* in 1992/93 surveys. The assemblage is found at water depth of 58-192 m and as suggested by the high turbidity (Fig. 3e), the Danish slope is characterized by high amounts of particulate matter near the sediment surface and is also reflected in the sediments that contain >60 % of the coarse sediment fraction (Table 1). This area, with its strong influence of inflowing Atlantic water provided by the STC (197 m, HT03) and NJC from the southern North Sea (67 m, HT02), is affected by large seasonal and annual variability in terms of salinity, temperature, and current flow, especially in the uppermost 50 m (Conradsen et al.

1994, and references therein). The area has been suggested to be a depositional sink for organic material and foraminiferal tests, with a source from the southern North Sea (Alve & Murray, 1997). However, a major part of the suspended matter was estimated to originate from “a more westerly direction” (Rodhe & Holt, 1996), i.e. possibly the central North Sea.

Elphidium excavatum is an extremely tolerant and eurytopic species and is the only dominant species along the Danish coast to a depth of about 200 m, and in the Kattegat in shallow areas with high variability induced by both wind and the water exchange between the Skagerrak and Kattegat (Conradsen et al., 1994). The species is common along the southern North Sea and is also present in the western Baltic Sea (Murray, 1991; Nikulina et al., 2008; Polovodova Asteman et al., 2009).

When comparing the living- and total fauna of 2020, the Danish slope is instead characterized by two assemblages: *E. scaber* assemblage at station HT02 and *C. laevigata* assemblage at station HT03. *Eggereloides scaber* have been associated with areas in with a large influx of organic-rich and sandy-silty substrate and is found at shallow depths of ~30 m in the northern Kattegat (Conradsen et al., 1994). *Cassidulina laevigata* occurs in well-oxygenated environments (Klitgaard-Kristensen et al., 2002) and is observed as a dominant species (>10 %) in the total fauna of 2020 at all stations with an oxygen concentration >5 ml l^{-1}. The exception is station HT02 which, again, might be due to the high influence of transported species (i.e., *Elphidium excavatum*) to the Danish slope. As discussed above, the abundance of *E. excavatum* is low in the living fauna and high in the total fauna. This is most likely due to the abundance maximum of living individuals being well below the analyzed sediments and thus missed (Section 4.2.1.4 Sediment Migration). The high abundance of empty *E. excavatum* tests at the surface (i.e., above the living abundance maximum of 15 cm (Corliss & van Weering, 1994)) could reflect a transport from other areas or related to internal transportation within the area, as the current conditions show a high variability (Bergsten et al., 1996, and ref therein). Alve & Murray (1997) suggests both *E. excavatum* and *E. scaber* to be transported from the southern North Sea, where living and dead individuals of these species are widespread. Furthermore, living assemblages with *Ammonia beccarii* have also been documented in the area (Murray, 1991, and ref. therein).

4.3.3 Cassidulina laevigata vs. Globobulimina turgida assemblage: the Norwegian slope and “transition zone”

The third assemblage is present at two locations, the Norwegian slope (HT10 and HT09 in 2020, and OS06, OS05, and OS03 in 1992/93) and the “transition zone” (HT04 in 2020, and 9201, OS16, and 9205 in 1992/93). The highest contributing species is *C. laevigata* in 2020, whilst in 1992/93 it was *G. turgida,* each naming the assemblages of respective survey, however, both assemblages share many similar species. For example, both areas are characterized by high relative abundance of *Cassidulina laevigata*, *Bulimina marginata,* and *B. skagerrakensis* in both 2020 and 1992/93 (Table 3 & 6). *Bulimina marginata* and *B. skagerrakensis* are both associated with areas with high organic content (Eichler et al., 2014; Klitgaard-Kristensen et al., 2002; Irina Polovodova Asteman et al., 2017). Furthermore, *B. marginata* has been associated with environments of high nutrient availability close to the Skagerrak-Kattegat front where various hydrographic regimes meet (Eichler et al., 2014). Both areas generally contain fine-grained sediments with a high organic content. The exceptions are the stations closest to Norway which are in an area with higher sand content (~50 %, Table 1) further associated with lower organic carbon (Alve & Murray, 1995, and references therein). Here *B. skagerrakensis* have a lower relative abundance (Table 3 & 6), likely due to the lower organic content.

The differences are, though, seen in the relative abundances of *G. turgida, Liebusella goësi* and *Eggereloides medius.* The differences are observed in the transition zone between the deeper basin and the Danish slope. In this area, *G. turgida* had a relative up to 30 % (9205, OS16, 9201) in the 1992/93 survey, while in 2020, the relative abundance was just above 4 % (HT04). *Globobulimina turgida* is an infaunal species that has been shown to utilize nitrogen respiration, a strategy suggested to be used to maintain metabolism during temporary stays in oxygen-free environments (Piña-Ochoa et al., 2010). Koho et al. (2008a) found that deep infaunal species can occupy different sediment depth. In highly eutrophic setting they migrate close to the sediment water interface, whereas they otherwise often are found at 10 cm sediment depth, below the oxygen penetration depth (Koho et al., 2010, and references therein). Nitrate in sediments is produced (e.g., by bacteria) under aerobic conditions and is actively collected by denitrifying foraminifera, such as *G. turgida,* and stored within the cell (Koho et al., 2010). This nitrate can then be utilized when oxygen and nitrate is absent within the sediment. As the process of nitrate uptake and storage is part of nitrogen sequestration into the sediments, denitrifying foraminiferal species can potentially help counterbalance eutrophication (Choquel et al., 2021). The higher relative abundance of *G. turgida* in the top 0-3 cm in 1992/93 compared to 2020 suggest a shallower oxygen penetration depth at the transition zone in 1992/93. This zone could be an area where high nutrient water from the Jutland Current meets the deeper basin water with a lower oxygen content. This combination could lead to temporary oxygen depletion in the sediments and thus a reduced availability of nitrate.

4.4 Critical analysis of uncertainty sources which may have affected this study

Several factors may have affected the results of this thesis, e.g., seasonal discrepancy between the sampling campaign in 2020 and 1992/93. These are discussed below.

4.4.1 Foraminiferal data

The two sampling campaigns were conducted at different seasons (summer of 1990s and fall of 2020), and the apparent low abundance of living individuals in 2020 survey may be a result of fall sampling. The seasonal difference between the sampling campaigns is expected to mainly affect the living assemblage, which is why only the total faunas have mainly been considered when comparing the faunal change between 1992/93 and 2020. Also based on observations in Swedish fjords, autumn (i.e., Sep-Nov) sediment samples contain high abundance of living juvenile foraminifera (Asteman, pers. comm. 2021), which were not captured when analyzing >125 µm fraction in this study. The sediments for the study in Bergsten et al. 1996, were collected during two consecutive years during the summer months, whereas the sediments of this study were collected in late October.

Also, benthic foraminiferal taxonomy may have affected the outcome of this study. For instance, the species *Eggrelloides scabrus* and *E. medius*, and *Nonionella turgida* and *N. auricula*, respectively, were combined and treated as single taxa by Bergsten et al. (1996), due to frequently occurring transitional forms (Nordberg, 1999), but were treated separately in this study.

Another potential problem arises when comparing relative abundance instead of absolute abundance between living-, dead-, and total fauna as an increase in one species drives a decrease in another species.

4.4.2 Methodology

The sediment volume was measured of the already stained sediments, which may not reflect the volume in the original environment, potentially effecting the reliance of comparison between samples (Corliss et al., 1993). Furthermore, the estimated volume of the sediment was done in jars with a diameter of ca 10 cm, lowering the precision significantly.

The comparison of faunas has been largely done by visual inspection of relative abundance, making it time consuming and, at times, confusing. A multivariate statistical analysis that would consider the similarities and dissimilarities between the different faunas (total-, living-, and dead fauna in 2020, and total fauna of 2020 and 1992/93) in terms of species composition and abundance, would simplify the analysis. Furthermore, an analysis considering test construction, shape, ecological preference for each species together with the prevailing hydrographical conditions could help identify and interpret environment, both in terms of taphonomical processes, but also for the paleoenvironmental reconstruction.

5 Summary & Conclusion

In this study, the foraminiferal total fauna is divided into three geographically distinct assemblages that seem to follow a similar distribution to water masses present within the basin, as previously suggested in the study by Bergsten et al. (1996). The total fauna assemblages identified in 2020 share many similar species with the assemblages in the total fauna in 1992/93. However, a clear difference is the decrease in relative abundance of *Globobulimina turgida* in the transition zone between the deep basin and the Danish slope. The long-term hydrographical record between 1950 and 2020 taken in the Skagerrak, shows a clear trend of increasing temperatures accompanied by an increase in salinity and decrease in oxygen concentration in the basin. A period of stagnant waters is revealed between 1986-1991 in the Skagerrak deep basin, which might explain the high relative abundance of denitrifying benthic foraminifer *Globobulimina turgida* in 1992/93 compared to 2020. The stagnant period has been attributed to a higher influence of Atlantic water in the North Sea in the late 1980, bringing warm and nutrient rich water to both the North Sea and Skagerrak. Denitrifying foraminifers might act as an important part of the nitrogen cycle and nitrogen sequestration and have been suggested to be of help counterbalance eutrophication.

Although the taphonomical effects (e.g., dissolution, transportation, and sediment migration) on the total faunal compositions are difficult to assess, they are assumed to have a minor effect on the overall species composition. However, some caution is recommended for the use of certain species as proxies of specific environmental conditions. For example, to better evaluate the importance of sediment migration, the use of longer cores (15-20 cm) in studies of living benthic foraminiferal fauna would be needed. Nonetheless, the correlation of total fauna assemblage to the Skagerrak water masses is still informative as they indicate the influence of the prevailing currents.

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7 References

Albretsen, J., Aure, J., Saetre, R., & Danielssen, D. (2011). Climatic variability in the Skagerrak and coastal waters of Norway. *ICES Journal of Marine Science*, *69*, 758–763. https://doi.org/10.1093/icesjms/fsr187

Alve, E., & Murray, J. W. (1995). Benthic foraminiferal distribution and abundance changes in Skagerrak surface sediments: 1937 (Höglund) and 1992/1993 data compared. *Marine Micropaleontology*, *25*(4), 269–288. https://doi.org/10.1016/0377-8398(95)00026-7

Alve, Elisabeth, & Murray, J. W. (1997). High benthic fertility and taphonomy of foraminifera: a case study of the Skagerrak, North Sea. *Marine Micropaleontology*, *31*(3), 157–175. https://doi.org/10.1016/S0377-8398(97)00005-4

Aure, J., & Dahl, E. (1994). Oxygen, nutrients, carbon and water exchange in the Skagerrak Basin. *Continental Shelf Research*, *14*(9), 965–977. https://doi.org/10.1016/0278-4343(94)90059-0

Bergsten, H., Nordberg, K., & Malmgren, B. (1996). Recent benthic foraminifera as tracers of water masses along a transect in the Skagerrak, north-eastern North Sea. *Journal of Sea Research*, *35*(1), 111–121. https://doi.org/10.1016/S1385-1101(96)90740-6

Bøe, R., Rise, L., Thorsnes, T. H., de Haas, H., Sæther, O. M., & Kunzendorf, H. (1996). Sea-bed sediments and sediment accumulation rates in the Norwegian part of the Skagerrak. *Norges Geologiske Undersøkelse*, *Bulletin 430*, 75–84.

Conradsen, K. (2008). Recent benthic foraminifera in the southern Kattegat, Scandinavia: distributional pattern and controlling parameters. *Boreas*, *22*, 367–382. https://doi.org/10.1111/j.1502-3885.1993.tb00200.x

Conradsen, Keld, Bergsten, H., Knudsen, K. L., Nordberg, K., & Seidenkrantz, M.-S. (1994). Recent benthic foraminiferal distribution in the Kattegat and the Skagerrak, Scandinavia. *Cushman Foundation Special Publication 32*, 53–68.

Corliss, B., & van Weering, T. (1993). Living (stained) benthic foraminifera within surficial sediments of the Skagerrak. *Marine Geology*, *111*, 323–335. https://doi.org/10.1016/0025-3227(93)90138-L

Danielssen, D. (1996). Long-term hydrographic variation in the Skagerrak based on the section Torungen–Hirtshals. *ICES Journal of Marine Science*, *53*(6), 917–925. https://doi.org/10.1006/jmsc.1996.0113

de Haas, H., van Weering, T. C. E., & de Stigter, H. (2002). Organic carbon in shelf seas: sinks or sources, processes and products. *Continental Shelf Research*, *22*(5), 691–717. https://doi.org/10.1016/S0278-4343(01)00093-0

Edwards, M., Beaugrand, G., Reid, P., Rowden, A., & Jones, M. B. (2002). Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series*, *239*, 1–10. https://doi.org/10.3354/meps239001

EEA. (2008). *Europe's biodiversity- biogeographical regions and seas. Seas around Europe. The North Sea- bottom trawling and oil/gas exploitation*. European Environment Agency. https://www.eea.europa.eu/ds_resolveuid/D7WUV3BQHK

Eichler, P., Pimenta, F., Eichler, B., & Vital, H. (2014). Living Bulimina marginata in the SW Atlantic Continental margin: Effect of the Subtropical Shelf Front and South Atlantic Central Water. *Continental Shelf Research*, *71*, 1. https://doi.org/10.1016/j.csr.2013.09.027

Gustafsson, B. (1997). Interaction between Baltic Sea and North Sea. *Deutsche Hydrografische Zeitschrift*, *49*(2), 165–183. https://doi.org/10.1007/BF02764031

Hirama, M., Toledo, F., Camillo Jr, E., Costa, K., & de Quadros, J. (2010). Q-Mode and R-Mode Factor Analysis in Quantitative Studies of Microfossils of the Late Quaternary in Sediments from the Brazilian Continental Margin. *Terrae*, *7*, 41–49.

Howarth, R., Billen, G., Swaney, D., Townsend, A., NA, J., Lajtha, K., Downing, J., Elmgren, R., Caraco, N., Jordan, T., Berendse, F., Freney, J., Kudeyarov, V., Murdoch, P., & Zhao-Liang, Z. (1996). Regional Nitrogen Budgets and Riverine N & P Fluxes for the Drainages to the North Atlantic Ocean: Natural and Human Influences. *Biogeochemistry*, *35*, 75–139. https://doi.org/10.1007/BF02179825

ICES. (2020). *Greater North Sea Sea Ecoregion – Ecosystem overview. In Report of the ICES Advisory Committee, 2020. ICES Advice 2020, Section 9.1,*. https://doi.org/10.17895/ices.advice.7632

Idronaut. (2020). *OCEAN SEVEN 316Plus*. https://www.idronaut.it/multiparameter-ctds/environmental-ctds/os316plus-environmental-ctd/

Klitgaard-Kristensen, D., Sejrup, H., & Haflidason, H. (2002). Distribution of recent calcareous benthic foraminifera in the northern North Sea and relation to the environment. *Polar Research*, *21*, 275–282. https://doi.org/10.1111/j.1751-8369.2002.tb00081.x

Ljøen, R., & Svansson, A. (1972). Long-term variations of subsurface temperatures in the Skagerrak. *Pergamon Press*, *19*, 277–288.

Murray, J. W. (1991). Ecology and Palaeoecology of Benthic Foraminifera (1st ed.). In *Ecology and Palaeoecology of Benthic Foraminifera* (p. 397). Routledge. https://doi.org/10.4324/9781315846101

Nikulina, A., Polovodova Asteman, I., & J, S. (2008). Foraminiferal response to environmental changes in Kiel Fjord, SW Baltic Sea. *EEarth*, *3*. https://doi.org/10.5194/ee-3-37-2008

Nordberg, K., Löfstedt Filipsson, H., & Malmgren, B. (1999). Oceanographic Conditions in the Deepest Parts of the Kattegat, Scandinavia, Revealed Through Recent Benthic Foraminifera and Hydrography. *Estuarine, Coastal and Shelf Science*, *49*(4), 557–576. https://doi.org/10.1006/ecss.1999.0511

Piña-Ochoa, E., Høgslund, S., Geslin, E., Cedhagen, T., Revsbech, N. P., Nielsen, L. P., Schweizer, M., Jorissen, F., Rysgaard, S., & Risgaard-Petersen, N. (2010). Widespread occurrence of nitrate storage and denitrification among Foraminifera and Gromiida. *Proceedings of the National Academy of Sciences*, *107*(3), 1148. https://doi.org/10.1073/pnas.0908440107

Polovodova Asteman, I., & Schöndeld, J. (2016). *Recent invasion of the foraminifer Nonionella stella Cushman & Moyer, 1930 in northern European waters: evidence from the Skagerrak and its fjords. 35(1)*, 20–25.

Polovodova Asteman, Irina, Nikulina, A., SCHONFELD, J., & Dullo, W.-C. (2009). Recent benthic foraminifera in the Flensburg Fjord (Western Baltic Sea). *Journal of Micropalaeontology - J MICROPALAEONTOL*, *28*, 131–142. https://doi.org/10.1144/jm.28.2.131

Polovodova Asteman, Irina, Risebrobakken, B., Moros, M., Binczewska, A., Dobosz, S., Jansen, E., Sławińska, J., & Bąk, M. (2017). Late Holocene palaeoproductivity changes: a multi-proxy study in the Norwegian Trench and the Skagerrak, North Sea. *Boreas*, *47*. https://doi.org/10.1111/bor.12264

R Core Team. (2021). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. URL https://www.R-project.org/

Rodhe, J. (1996). On the dynamics of the large-scale circulation of the skagerrak. *Journal of Sea Research*, *35*(1), 9–21. https://doi.org/10.1016/S1385-1101(96)90731-5

Rodhe, J., & Holt, N. (1996). Observations of the transport of suspended matter into the Skagerrak along the western and northern coast of Jutland. *Journal of Sea Research*, *35*(1–3), 91–98. https://doi.org/10.1016/S1385-1101(96)90738-8

Sætre, R., Aure, J., & Danielssen, D. S. (2003). Long-term hydrographic variability patterns off the Norwegian coast and in the Skagerrak. *ICES Mar. Sci. Symp.*, *219*, 150–159.

Saraswat, R., Kouthanker, M., Kurtarkar, S. R., Nigam, R., Naqvi, S. W. A., & Linshy, V. N. (2015). Effect of salinity induced pH/alkalinity changes on benthic foraminifera: A laboratory culture experiment. *Estuarine, Coastal and Shelf Science*, *153*, 96–107. https://doi.org/10.1016/j.ecss.2014.12.005

Schlitzer, R. (2021). *Ocean Data View*. https://odv.awi.de

Schönfeld, J., Golikova, E., Korsun, S., & Spezzaferri, S. (2013). The Helgoland Experiment – assessing the influence of methodologies on Recent benthic foraminiferal assemblage composition. *J. Micropalaeontol.*, *32*, 161–182. https://doi.org/10.1144/jmpaleo2012-022

Van Weering, T. C. E., Berger, G. W., & Kalf, J. (1987). Recent sediment accumulation in the Skagerrak, Northeastern North Sea. *Netherlands Journal of Sea Research*, *21*(3), 177–189. https://doi.org/10.1016/0077-7579(87)90011-1

van Weering, T. C. E., Rumohr, J., & Liebezeit, G. (1993). Holocene sedimentation in the Skagerrak: A review. *Holocene Sedimentation in the Skagerrak*, *111*(3), 379–391. https://doi.org/10.1016/0025-3227(93)90142-I

Winther, N., & Johannessen, J. (2006). North Sea circulation: Atlantic inflow and its destination. *Journal of Geophysical Research*, *111*. https://doi.org/10.1029/2005JC003310