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- Dense gravity currents increase mixing in stagnant basins in the central Baltic Sea
- Intrusions of oxygenated water impact methane dynamics in anoxic basins
- Mixing intensity, methane oxidation, and abundance of methanotrophs show a positive correlation

Supporting Information:
- Supporting Information S1

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Dense bottom gravity currents and their impact on pelagic methanotrophy at oxic/anoxic transition zones

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Abstract We show that inflows of oxygenated waters into sulfidic layers have a strong impact on biogeochemical transformation at oxic/anoxic transition zones. Taking the pelagic methane dynamics in the Gotland Basin as an example, we performed our studies when one of the largest inflows ever recorded entered the Baltic Sea in March 2015. An inflowing gravity current transported oxic waters into the sulfidic deep layers and freshly generated a near-bottom secondary redox interface. At the upper slope, where the inflowing water masses were vigorously turbulent and the main and secondary redox interfaces in close contact to each other, methane oxidation rates inside the transition zone were found to be higher compared to the weakly turbulent basin interior. At the main redox interface in the basin center, lateral intrusions of oxygenated waters into intermediate water depth may have stimulated the growth of the methanotrophic community and their activity.

1. Introduction

Interfaces between oxic and anoxic water bodies represent distinct zones in which the activity of specially adapted microbes often controls biogeochemical transformations. Anoxic basins as the Black Sea, the Cariaco Basin, and the Baltic Sea represent ideal locations to examine these processes, the involved microorganisms, and the influence of their metabolism on the turnover of different substances. From studies in these basins it is, e.g., well known that microbial activity in the oxic/anoxic transition zone mediates the carbon, nitrogen, sulfur, and trace metal cycles [*Yakushev et al.*, 2007; *Dellwig et al.*, 2012; *Kuypers et al.*, 2003; *Blumenberg et al.*, 2007].

Here we focus on microbial methane turnover processes at a redox interface that was newly generated by the intrusion of oxic waters into a stagnant pool of sulfidic water. This study was carried out in the Baltic Sea, a nontidal semienclosed brackish basin connected to the oceanic waters of the North Sea by a system of narrow straits in the West (Figure 1). The central basins of the Baltic Sea are generally characterized by a stable halocline, which suppresses turbulent mixing and therefore inhibits the chemical communication between near-surface and deep waters [*Reissmann et al.*, 2009]. A recent long-term tracer experiment [*Holtermann et al.*, 2012; *Holtermann and Umlauf*, 2012] revealed that basin-scale vertical mixing is largely due to boundary mixing in the vicinity of the lateral slopes, while mixing in the stratified interior of the basin is generally negligible. The reduced downward mixing of oxygen results in a redox stratification of the water column with oxygenated surface waters above the anoxic (sulfidic) deeper layers [*Schmale et al.*, 2010]. A redoxcline, typically located at about 100 m water depth, separates the two water masses. The lower (anoxic) region of this redox interface is characterized by a pronounced turbidity peak [*Jakobs et al.*, 2014] that was previously reported also for other anoxic systems like the Black Sea [*Blumenberg et al.*, 2007] and the Cariaco Basin [*Wakeham et al.*, 2012]. Although the processes inducing these turbidity anomalies are currently not fully understood, it has been speculated that transport of reduced chemical species across the redoxcline and subsequent precipitation of metal oxides and colloidal sulfur might be the cause [*Dellwig et al.*, 2010; *Kamyshny et al.*, 2011].

Due to reduced vertical mixing, deep water renewal in the central Baltic Sea occurs primarily through saline and oxygen-rich intrusions of North Sea waters, which propagate as dense bottom currents from the western Baltic Sea toward the deep basins of the central Baltic Sea (Figure 1). These energetic near-bottom flows have been shown to be vigorously turbulent [*Umlauf et al.*, 2007] and may entrain large amounts of ambient water along their pathway, thus modifying their physical and biogeochemical properties. Hot spots for such water mass transformations are the submarine channels in the western Baltic Sea [*Umlauf and Arneborg*, 2009;

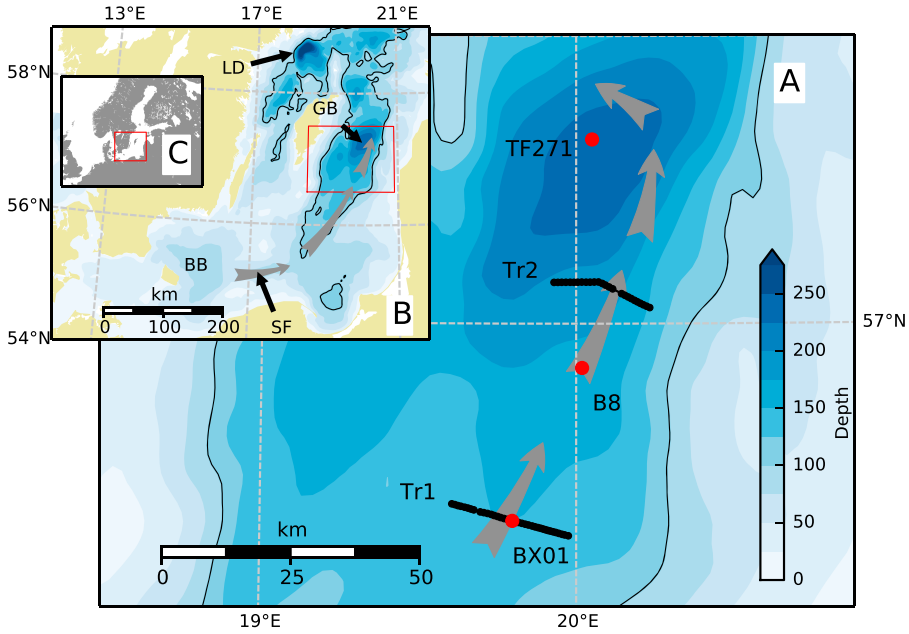

Figure 1. Bathymetric map of the central Baltic Sea with station positions. Red dots = station positions. Black lines = transect locations. The pathway of inflowing bottom currents is indicated by the gray arrows. BB = Bornholm Basin, SF = Slupsk Furrow, GB Gotland Basin, and LD = Landsort Deep.

Reissmann et al., 2009] and the Slupsk Furrow [*Meier et al.*, 2006] that forms the entrance to the Gotland Basin (Figure 1). Particularly strong inflow events of this type with the potential to significantly modify the deep water oxygen concentrations in the central Baltic Sea over extended periods are referred to as Major Baltic Inflows (MBIs) [*Matthäus and Franck*, 1992]. Triggered by special hydrographic and meteorological conditions, MBIs are rare events that, in recent decades, occurred only intermittently on decadal time scales [*Feistel et al.*, 2008]. Due to their unpredictable nature, detailed direct observations of the physical structure and biogeochemical properties of the intruding water masses during a MBI are so far largely missing.

Aerobic oxidation of methane in the water column is mediated by methane-oxidizing bacteria (MOB) of type I, II, and X [*Hanson and Hanson*, 1996]. Studies of the deep anoxic basins in the central Baltic Sea at the Gotland Deep and Landsort Deep (Figure 1) showed that aerobic microbial methane oxidation at the oxic/anoxic transition zone constitutes the pivotal filter mechanism that inhibits the transport of methane from the methane-enriched deep water to the sea surface. Different oxidation rates observed between these deeps were explained by regional differences in the intensity of vertical mixing, which influence the transport of methane across the oxic/anoxic transition zone [*Jakobs et al.*, 2013]. In contrast to other basins with pronounced redoxclines (Black Sea [*Blumenberg et al.*, 2007] and Cariaco Basin [*Taylor et al.*, 2001; *Lin et al.*, 2008]), methane oxidation in the central Baltic Sea is only mediated by type I methanotrophic bacteria [*Schmale et al.*, 2012; *Jakobs et al.*, 2013, 2014; *Berndmeyer et al.*, 2013]. The reduced diversity of the MOB community at the oxic/anoxic transition zone is assumed to be the result of increased sulfide concentrations [*Jakobs et al.*, 2013; *Labrenz et al.*, 2010], exceeding the toxicity threshold of type II and X methanotrophs.

How the sporadic inflow events described above influence the redox chemistry and consequently the biogeochemical transformation processes have been only rudimentarily investigated so far. A few studies focusing on lateral intrusions of oxygenated water into suboxic and anoxic layers in the Black Sea, the Cariaco Basin, and Baltic Sea showed that they influence bacteria community structure [*Lin et al.*, 2008] and affect the biotic and abiotic transformation of manganese and sulfur species [*Glazer et al.*, 2006; *Dellwig et al.*, 2012]. In this context, turbulent mixing of water with different redox properties certainly plays a key role as it increases the fluxes of electron acceptors (e.g., oxygen) and electron donors (e.g., methane) along the concentrations gradients. However, a study that directly couples turbulent mixing with these biogeochemical processes is still missing.

Here we present a recent data set, combining physical, chemical, and microbiological observations obtained during one of the largest MBIs ever recorded. In December 2014, after a stagnation period of 10 years,

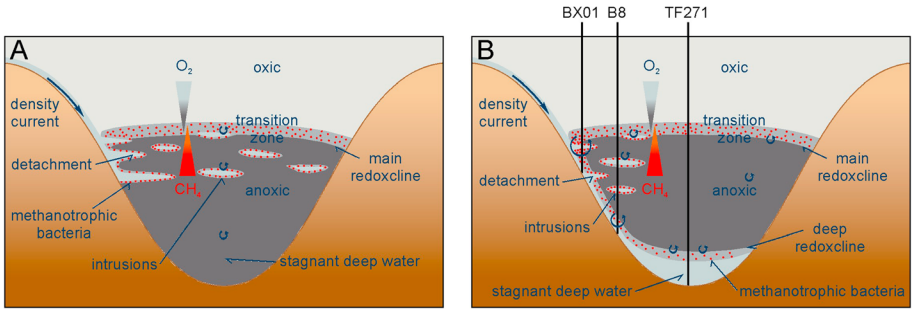

Figure 2. Conceptional model of the inflowing bottom density current and its impact on the methane dynamics (in this case the abundance of methanotrophic bacteria, red dots). (a) Preinflow situation with detachments at the basin slope and intrusions at intermediate water depth. (b) Inflow situation with a dense bottom gravity current that replaces the deep anoxic water in the center of the basin. The different intensity of mixing is indicated by the size of semicircles. Mixing intensities at BX01 = high, B8 = medium, and TF271 = low.

320 km^3 of salty and oxygen-rich water entered the western Baltic Sea and reached our study site in the Gotland Basin (Figure 1) in February/March 2015, exactly coinciding with our ship-based measurements from R/V *Alkor*. This event represented the third largest salt water inflow since the beginning of the records in the year 1880 and was classified as the largest event of this type since 1951 [*Gräwe et al.*, 2015; *Mohrholz et al.*, 2015]. We used this unique opportunity to test our hypothesis that the vigorous near-bottom turbulence associated with the bottom gravity currents has the potential to increase microbial turnover of methane at the oxic/anoxic transition zone between ambient and inflowing water masses. By the use of a free-falling profiler, high-resolution turbulence microstructure measurements were analyzed to study the areal extension of the inflow and its impact on turbulent mixing. Based on these results, three different mixing regimes were identified. Methane oxidation rates as well as the abundance of MOB type I were studied to provide direct insight into the methane dynamics at the newly developed near-bottom redox gradient and the main redox interface in intermediate water depth (see Text S1 in the supporting information for details on the different methods).

2. Results and Discussion

2.1. Temporal Development of the Inflow and Its Impact on Mixing

Prior to the main inflow in December, oxic intrusions from a number of previous, smaller inflow events reached the Gotland Basin, and interleaved with the sulfidic ambient water body below the redoxcline (Figure 2a). The signature of these intrusions is particularly evident in the small-scale anomalies characterizing the temperature profile below the redoxcline at the central station TF271 (Figure 3a). The oxygen imported by these events was, however, rapidly exhausted, and sulfidic conditions were reestablished already after a few weeks [*Nausch et al.*, 2015]. Nevertheless, the turbidity layers created at the secondary redox interfaces between the intruding and the ambient waters persisted until the main inflow reached the Gotland Basin (Figure 2b) and significantly increased the overall turbidity in the region below the redoxcline (Figure 3a) compared to the stagnation period before the inflow (Figure 3b) [*Jakobs et al.*, 2014].

The dense bottom waters associated with the main inflow, which will be the main focus of our study, passed the Danish Straits in December 2014 [*Mohrholz et al.*, 2015; *Gräwe et al.*, 2015]. The inflow continued to propagate as a dense bottom current through the western Baltic Sea, the Bornholm Basin, and the Slupsk Furrow, reaching the central station TF271 near the deepest point of the Gotland Basin (Figure 1) in the second half of February 2015.

As schematically depicted in Figure 1a, the inflowing dense water passed through a wide submarine channel in the southern part of our study area before entering the central part of the Gotland Basin. Data from the cross-channel transect Tr1 (Figure 1a) reveal an approximately 10–20 m thick bottom layer of dense inflow water that is easily distinguished from the ambient fluid by its higher temperature (Figure 4a). Note that positive temperature anomalies are also found above the dense bottom flow, indicating the presence of intrusions that have detached from the interface of the bottom gravity current [e.g., *Baines*, 2001]. Figure 4e shows

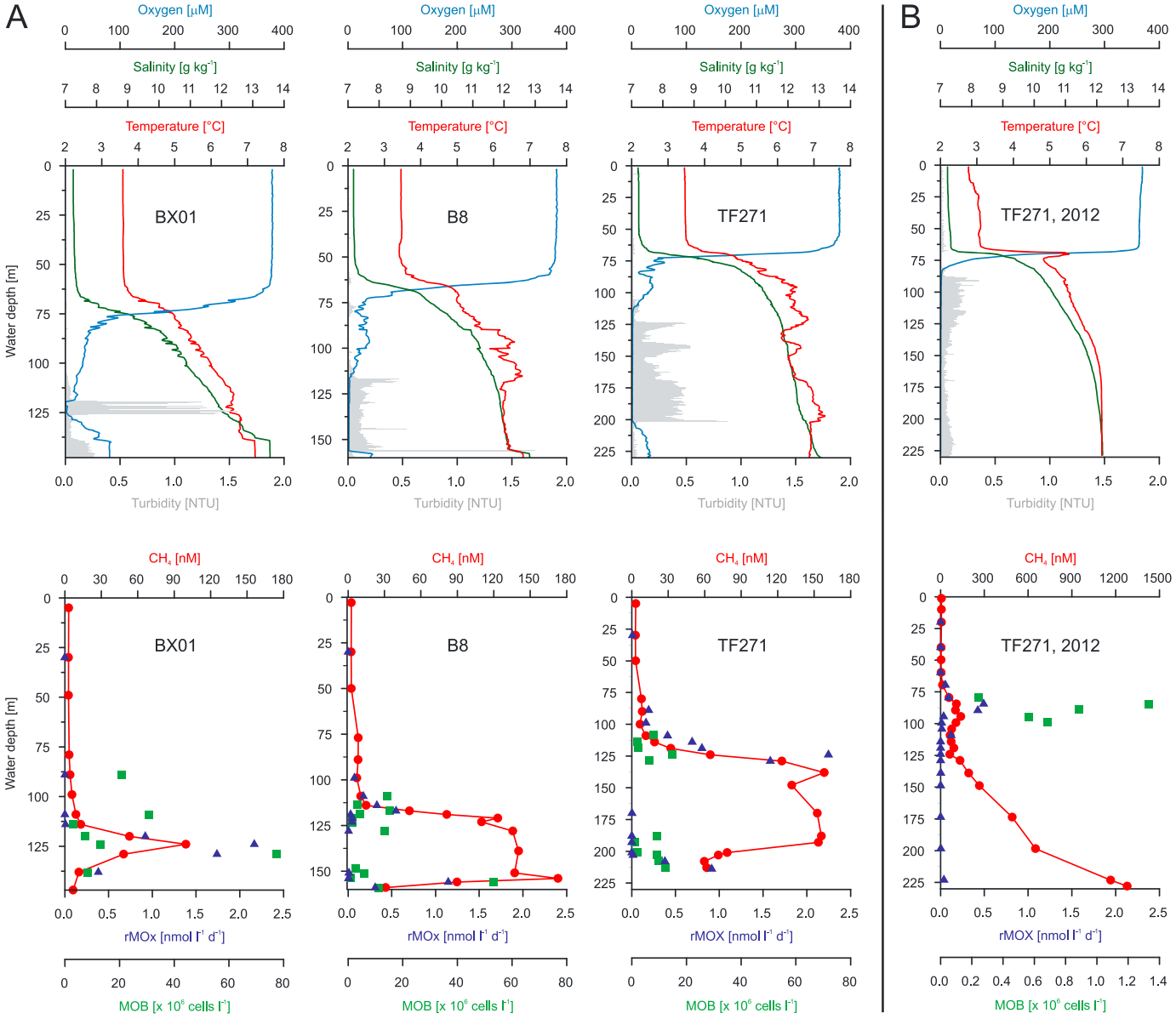

Figure 3. (a) Physical, gas chemical, and microbiological data from the inflow in 2015 for water stations BX01, B8, and TF271. (top row) Vertical profiles of oxygen (blue), salinity (green), temperature (red), and turbidity (gray). (bottom row) Vertical profiles for methane concentration (red), methane oxidation rates (rMOx, blue triangles), and cell number of type I aerobic methanotrophic bacteria (green squares). (b) Same data set from the stagnation period in 2012 (modified after Jakobs *et al.* [2014]). Note the different scales in B for methane concentrations and MOB cell numbers.

that the dense bottom layer is vigorously turbulent, in particular, on the southeastern side of the transect, which mirrors the deflection of the inflowing current by the Coriolis force. Turbulence energy dissipation rates in this region are more than 2 orders of magnitude higher compared to the weakly turbulent ambient waters. As indicated in Figure 4e, also, the density interface separating inflowing and ambient water is strongly turbulent, presumably as a result of interfacial shear instability [*Umlauf and Arneborg*, 2009], providing direct evidence for the mixing of waters with different biogeochemical properties. We propose that the sharp interfacial turbidity peak visible in Figure 4c mirrors the optical signature of the biogeochemical reaction products generated by this process (e.g., precipitation of metal oxides and colloidal sulfur, see above).

After leaving the channel, the gravity current widens and spreads over the eastern slope of the Gotland Basin (Figure 1a). Figure 4b illustrates that at the cross-slope transect Tr2, the inflow already covers a cross-slope

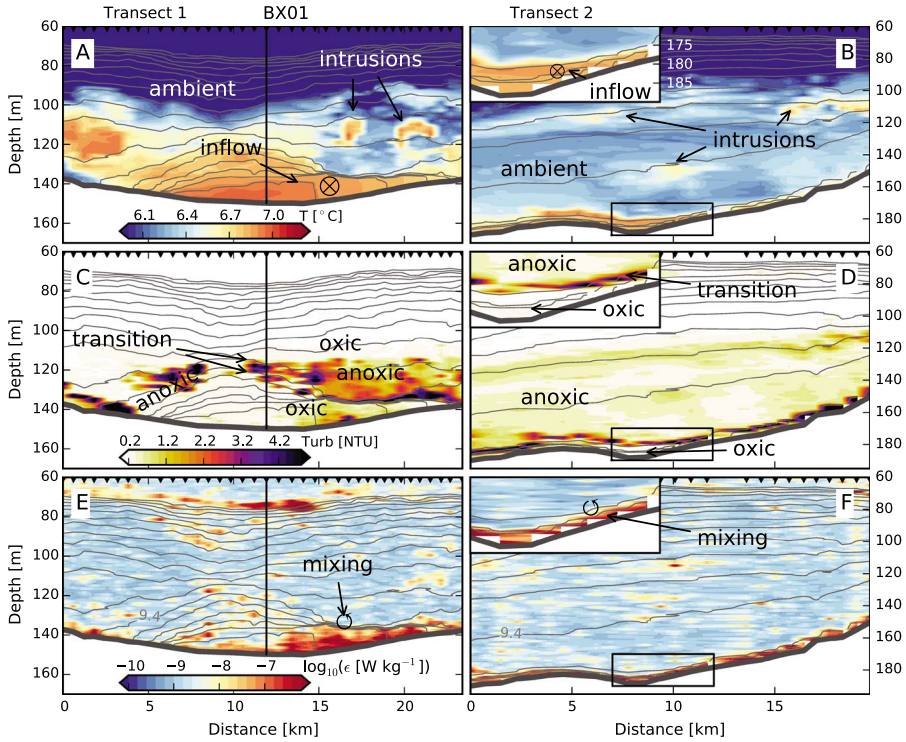

Figure 4. Cross-slope transects of (a and b) temperature, (c and d) turbidity, and (e and f) turbulence dissipation rate on a logarithmic scale for transects Tr1 and Tr2 (positions shown in Figure 1). Black contour lines indicate isopycnals at 0.2 kg m^{-3} intervals. The flow direction of the near-bottom gravity current is shown in Figures 4a and 4b; interfacial mixing between oxic and anoxic waters is symbolically indicated in Figures 4e and 4f. The black vertical lines mark the position of station BX01. Black rectangles in Figures 4b, 4d, and 4f indicate enlarged near-bottom regions.

distance of at least 20 km and rarely exceeds a thickness of 10 m. A closer physical analysis, reported in more detail elsewhere, suggests that the dynamics in this region can be described by available theories for rotating, frictionally controlled bottom gravity currents with a geostrophic balance in the cross-slope direction [e.g., *Wåhlin and Walin*, 2001]. Our direct velocity measurements in the near-bottom region (not shown) indicate that the gravity current travels with a velocity of approximately 0.2–0.3 m s^{-1} along the slope, consistent with the theory mentioned above. Turbulence triggered by bottom friction and interfacial shear instability again separates the gravity current from the weakly turbulent interior although turbulence levels are generally somewhat weaker compared to transect Tr1 (Figure 4f). The sharp turbidity peak on the anoxic side of the interface (Figure 4d) again points at enhanced biogeochemical transformations due to interfacial mixing of sulfidic and oxic water, analogous to our observations at transect Tr1.

In addition to the compact gravity current that travels along the seafloor, temperature and turbidity anomalies in the anoxic intermediate water body also indicate the presence of highly corrugated intrusions that may have detached upstream from the interface of the gravity current (Figure 4). Our turbulence measurements show small-scale patches of enhanced turbulence in the otherwise quiescent interior region above the gravity current. Although not directly associated with the gravity current, they may have been indirectly triggered by it, e.g., through the generation of internal waves and eddies. This suggests an intermittent but persistent mixing between the small-scale intrusions and the ambient waters also in the interior. This mixing is, compared to the near-bottom region, less vigorous but leads on longer time scales to biogeochemical implications similar to those found in the near-bottom region as discussed in more detail below.

After the gravity current reached the center of the basin, the inflowing water accumulates in a stagnant pool of oxic bottom waters. At the time of our arrival with R/V *Alkor* in the Gotland Basin on 4 March, we detected an oxic near-bottom layer of approximately 30–40 m thickness at station TF271 (local depth: 231 m) that reflected the arrival of the first inflow pulse (Figure 3a). Water mass properties suggest that this layer consisted of a mixture between (i) fresh inflow water, (ii) water from the near-bottom region of the neighboring

Bornholm Basin (Figure 1) that had been flushed out of the basin by the denser inflow water, and (iii) ambient water entrained along the pathway of the inflow. Turbulence energy dissipation rates in this area (data not shown) were 2 to 3 orders of magnitude lower compared to the vigorously turbulent areas along the basin slope (transect Tr1 and Tr2).

Based on the physical investigations above, we define three distinct mixing regimes along the inflow pathway of the gravity current (Figure 2b):

1. Highest mixing rates were found at the southern entrance channel where the vigorously turbulent bottom layer impacted both the main and the deep redoxclines. Transect Tr1 and station BX01 are representative for this type of mixing regime.
2. Mixing with intermediate intensity associated with the bottom gravity current was encountered along the slope transect Tr2 and at station B8. Here the thin oxic bottom current created a sharp redox interface between the intruding and ambient waters.
3. Lowest mixing rates were detected at the deep redoxcline delineating the upper edge of the oxic deep water pool in the center of the basin (station TF271).

2.2. Methane Dynamics at Oxic/Anoxic Transition Zones

Consistent with these physical observations, the inflow of the oxic bottom current into the anoxic deep layers also left a clear imprint on the methane distribution. The vertical distribution at each station shows two sharp methane concentration gradients at the upper main oxic/anoxic transition zone and the newly developed near-bottom redox interface, respectively (Figure 3a). In the intermediate anoxic layer, sandwiched between the oxic near-surface and intruding bottom waters, methane concentrations increased from the shallow station BX01 (maximum 99 nM) toward the basin interior at station TF271 (maximum 158 nM, Figure 3a). The observed bottom water methane enrichment toward the center of the basin (from 7 nM at BX01 to 62 nM at TF271, Figure 3a) can be explained by mixing between the anoxic methane-enriched ambient water and the oxygenated inflowing water mass and, additionally, through a diffusive flux of methane from the sediment into the bottom current [*Piker et al*., 1998].

As described above, multiple intrusions of oxygenated water in the period before the main inflow event that reached our study site end of February induced biogeochemical reactions, causing increased turbidity in the anoxic layer. The impact of these intrusions is also mirrored in the methane budget of the basin. When comparing our results with data acquired during the stagnation period before the inflow (Figure 3b) [*Jakobs et al*., 2014] by integrating the two inventories of methane at station TF271, it can be shown that about 80% of methane in the anoxic layer had been lost. The remarkable loss of methane might be explained by (1) the dilution through the inflows, which brought water into the basin with comparatively low methane content; (2) an inflow-induced flushing of water out of the Gotland Basin, (3) and microbial methane oxidation stimulated by these oxygenated intrusions into the methane-enriched anoxic waters.

Our data obtained along the pathway of the gravity current show that oxic/anoxic transition zones represent hot spots of methane turnover, indicating that methanotrophic communities might develop within days at newly generated redox interfaces (Figure 3a). Methane oxidation rates peaked at these interfaces but generally declined along the inflow pathway from 2.2 nmol l^{-1} d^{-1} at station BX01 in the entrance channel down to 0.9 nmol l^{-1} d^{-1} at station TF271 in the basin center. Oxygen concentrations at the depth of the methane oxidation maxima are in the micromolar range and are therefore unlikely to limit the turnover of methane. Instead, we assume first-order kinetics ($rMOx = k[CH_4]$) [*Valentine et al*., 2001], with methane oxidation rates (rMOx) depending linearly on the in situ methane concentration [CH_4] and the turnover rate constant (k). The latter is defined as the fraction of $^{14}CH_4$ tracer oxidized per unit time and displays the relative activity of the incubated water sample. Although methane concentrations showed slight variations at the depths with maximum oxidation rates (Figure 3a), a positive relationship between mixing intensities and maximum k values implies a higher relative activity in regions affected by enhanced mixing ($k = 0.036\ d^{-1}$ at BX01 versus 0.015 d^{-1} at TF271). Consistent with these trends in methane oxidation rates, MOB showed their highest abundance within the oxic/anoxic transition zone and constantly decreasing cell densities toward the basin interior from 77.3×10^6 cells l^{-1} at BX01 to 12.3×10^6 cells l^{-1} at TF271 (see Figure 3a). Calculations of cell specific oxidation rates at TF271 show that these were 5 times lower at the deep oxic/anoxic transition zone during the inflow compared with the main transition zone (in about 100 m water depth) during

stagnant conditions (2015: 0.30×10^{-2} fmol h^{-1}; 2012: 1.57×10^{-2} fmol h^{-1}, 1.3×10^{6} cells l^{-1}) suggesting that not the individual activity of MOB cells but rather the concentration of the MOB cells explains the enhanced methane turnover at the deep transition zone in 2015.

As schematically shown in Figure 2b, we propose that high mixing rates in the entrance channel (station BX01) and the close vicinity of two oxic/anoxic transition zones (see Figure 3a) increased the flux of oxygen and methane into the transition zone and consequently stimulated the growth of the MOB population and their activity. In contrast, low mixing rates in the stagnant interior of the basin reduced the flux of these gases into the transition zone, explaining the relatively small MOB population size and low methane turnover rates observed at station TF271.

It should be noted that although methane oxidation rates and MOB cell numbers at the deep redoxcline were lowest at the central station TF271 compared to the more energetic slope stations (Figure 3a), they were still 2 to 10 times higher compared to those typically found during stagnation conditions in the main oxic/anoxic transition zone of the basin (Figure 3b) [*Jakobs et al*., 2014]. It may be speculated that this effect is caused by the generally enhanced basin-scale mixing rates in the interior during an inflow event compared to the normal situation. A similar picture is visible at the upper redoxcline of our central station TF271 and the slope station B8. Also here, oxidation rates and MOB cell numbers were strongly elevated during the time of the inflow (Figure 3a) compared to the stagnation period (Figure 3b). We suggest that the increased oxidation rates and MOB cell numbers are caused by the multiple lateral intrusions that interleaved with the sulfidic water before the arrival of the main inflow took place (see above). During the time of our measurements, the signatures of these intrusions were still visible as irregular small-scale anomalies in the oxygen and temperature profiles at the depth of the main redoxcline (Figure 3a, compare with the smooth profiles during the stagnation period in Figure 3b). The intermittent turbulent patches triggered by the energetic gravity current (see, e.g., Figure 4e) are likely to mix ambient and intruding waters, potentially fostering microbially mediated methane turnover and other biogeochemical transformations. We assume that this process permanently stimulated the development of the methanotrophic community and that the resulting increase in MOB cell numbers and their activity is still preserved.

3. Conclusion

The activity of water-column methanotrophy is primarily depending on the concentrations of the main redox partners methane [*Kessler et al*., 2011] and oxygen [*Sansone and Martens*, 1978]. Advection and mixing represent the key physical processes transporting these components from one compartment into the other [e.g., *Schmale et al*., 2011]. The importance of oceanographic settings as one of the controlling factors for the efficiency of the pelagic methane filter was recently demonstrated at methane seeps west of Svalbard, where bottom water with a large number of MOB was periodically replaced by a switch in the ocean current regime [*Steinle et al*., 2015]. Our results reveal that the inflow of oxygenated water into sulfidic layers, in the example considered here induced by a strongly turbulent intrusion of oxic waters, can also rapidly change environmental conditions and increase the flux of methane and oxygen along concentration gradients, which is a prerequisite to stimulate aerobic microbial methanotrophy. Since all redox reactions depend on the flux of electron donators and acceptors, we suggest that also other biogeochemical transformations are influenced by these inflow events.

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