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# Seasonal bottom water respiration in the North Sea–Baltic Sea transition zone: rates, temperature sensitivity and sources of organic material

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ABSTRACT: Seasonal respiratory oxygen consumption was measured by bottle incubation of bottom water from 5 stations in transects across the Baltic Sea–North Sea transition zone. Respiration was measured at 3 temperatures (*in situ* temperature and in a 5°C colder and 5°C warmer incubation), to determine temperature sensitivity. The seasonal range in oxygen consumption was 9 to 90 mg $O_2$ $m^{-3}$ $d^{-1}$ corresponding to mineralization rates between 2.8 and 28 mg organic C $m^{-3}$ $d^{-1}$. The total below-halocline mineralization was estimated to be 53 g organic C $m^{-2}$ $yr^{-1}$ in the area; and 38 g C $m^{-2}$ $yr^{-1}$ when the estimate was adjusted to the mean annual temperature. Temperature sensitivity, expressed in terms of a $Q_{10}$ value, was 3.0 ± 1.1 averaged over 23 experiments. The specific decay rate of organic C ranged between 0.0027 and 0.094 $d^{-1}$. To determine the seasonal lability of organic matter, the specific decay rates were normalized to a reference temperature of 10°C using the observed $Q_{10}$ values, and these estimates showed a range of decay rates between 0.0040 $d^{-1}$ (January) and 0.049 $d^{-1}$ (August). The C/N ratio of particulate organic matter (POM) ranged between 7 and 22. The highest decay rates were associated with low (<10) C/N ratios; the C/N ratios increased during the incubations. Measurements of the POM pool showed no decline during the incubations. The initial pool of POM in the bottles could not account for the observed oxygen consumption — which on average corresponded to 183% of the POM pool, indicating that dissolved organic matter (DOM) is the most important carbon source for bottom water respiration in this area.

KEY WORDS: Respiration · Kattegat · Carbon budget · Incubations · Bottom water · $Q_{10}$



## INTRODUCTION

Mineralization of organic matter is a universal process that regulates the amount of organic carbon in ecosystems. In most ecosystems, the mineralization of organic carbon more or less balances primary production over varying time scales, and very few ecosystems accumulate organic matter at significant rates. Eutrophication of marine ecosystems is therefore typically coupled with enhanced respiration rates, balancing the increased input of organic matter into the ecosystem (Rosenberg 1985, Nixon 1995). The oxygen content in aquatic systems is limited by low solubility of oxygen in water (typically less than 10 ppm at 100% saturation) and therefore, hypoxic conditions can develop relatively quickly when oxygen consumption exceeds inputs by physical ventilation (i.e. turbulent mixing and advection) and photosynthetic oxygen production. Hence, hypoxia has often been recognized as the most severe problem associated with high respiration rates due to eutrophication, particularly in estuaries and coastal zones, where hypoxia has negative effects on the ecosystem and leads to increased mortality in benthic communi-

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ties (Diaz & Rosenberg 1995, 2008, Diaz 2001, Kemp et al. 2009). Even though respiration is a critical process in the marine ecosystem, with implications for oxygen conditions and also for global carbon dynamics (Laws et al. 2000, Kwon et al. 2009), surprisingly little is known about its regulating factors. Photosynthetic production of organic carbon and remineralization back to inorganic carbon are equally important processes regulating the amount of organic matter and its turnover rate in the ecosystem. However, Robinson & Williams (2005) found that studies of respiration in the literature only accounted for about 1% of the studies of primary production. The same bias is evident for the transition zone between the Baltic Sea and the North Sea, where primary production has been measured in numerous studies and monitored regularly during the past 4 decades (Conley et al. 2002, Rydberg et al. 2006) and where spatial and temporal patterns have been resolved in comprehensive data series. In comparison, respiration in this area has been covered in very few studies (e.g. Granéli 1992, Kruse & Rasmussen 1995), none of which has resolved the turnover rates of organic carbon or its spatial variability. Hypoxia is a recurrent problem in the bottom waters of many sub-areas of the transition zone — particularly in the southern Belt Sea and Western Baltic Sea (Conley et al. 2007). Bendtsen et al. (2009) showed that the residence time of the bottom water was closely related to the oxygen concentration in the hypoxic season from August to October. Because of this long residence time, even small changes in the respiration rate (due to changes in the input of organic matter or due to changes in the bottom water temperature) can have strong effects on the extent and duration of hypoxia (Bendtsen & Hansen 2013). In this perspective, studies of bottom water respiration covering inter-annual, seasonal and spatial variability are urgently needed in order to understand how variations in oxygen concentration are linked to variations in bottom water respiration, and thereby to the productivity and turnover of organic carbon in the water column. It is also unknown how closely variation and long term trends in oxygen conditions are coupled to long term changes in the productivity of the entire system. There is clear evidence that primary production increased between 1950 and 1990 due to increasing eutrophication (Richardson & Heilmann 1995, Andersson 1996) and that the oxygen content decreased during the same period (Andersson & Rydberg 1988, Rydberg et al. 1990). It is also well documented that trends in nutrient concentrations have reversed again, and have been declining since the 1990s due to the implementation of management plans (Carstensen et al. 2006). However, it has not been documented if there are corresponding trends in water column respiration rates. It is also largely unknown how other factors such as temperature and degradability of organic carbon control the dynamics of the respiration and its potential effect on oxygen conditions in the area. Previous studies of carbon dynamics suggest that the total organic matter mineralization in the heterotrophic bottom water is about 45 g C $m^{-2}$ $yr^{-1}$ (Hansen & Bendtsen 2013). Seasonal variation in remineralization rates due to variations in organic matter input has not been resolved. Sediment trap studies from this area (Olesen & Lundsgaard 1995) show a pronounced seasonality in the quantity and composition of sinking particulate organic matter (POM), reflecting the seasonal succession of the plankton community (Wassmann 1991). Sedimentation rates peak during the spring bloom, when sinking phytoplankton with low C/N ratios dominate the flux, whereas detritus with higher C/N ratios dominate during the rest of the year (Olesen 1993, Olesen & Lundsgaard 1995). However, observations showing that most of the spring bloom material may be recovered from the sediment as live diatoms after the spring bloom (Hansen & Josefson 2001, 2003) suggest a low degradability of the material as it sinks through the bottom water layer. During the rest of the season, the POM concentration is relatively constant (Olesen & Lundsgaard 1995), and this indicates either a constant flux and remineralization, or that seasonal variations in input are balanced by corresponding changes in remineralization (i.e. due to seasonal temperature variation; Hansen & Bendtsen 2013).

Temperature sensitivity can be quantified by the $Q_{10}$ factor, which describes the rate of change in the system per 10°C temperature increase. $Q_{10}$ values for pelagic respiration have been observed ranging between 2 and 3.5 (Robinson & Williams 1993, Lefevre et al. 1994, Lomas et al. 2002). Temperature sensitivity is critical for describing seasonal variation in remineralization rates in this area where the seasonal temperature range is about 10°C. It has been suggested that respiratory processes have higher temperature sensitivity than primary production (Pomeroy & Deibel 1986, López-Urrutia et al. 2006) and this could potentially alter the overall balance between autotrophy and heterotrophy due to global warming. Bendtsen & Hansen (2012) showed that a 3°C warming during the next century would have a dramatic negative impact on the oxygen conditions in the Baltic Sea–North Sea transition zone.

The carbon sources sustaining bottom water respiration are also largely unknown. The transport of particulate material in and out of the transition zone is probably limited, since the typical residence time of 1 to 2 wk for sinking particulate organic carbon (POC) is significantly less than the bottom water residence time of 2 to 3 mo (Bendtsen et al. 2009), which suggests that POM is primarily respired and recycled within the Baltic Sea–North Sea transition zone. However, dissolved organic matter (DOM) may also contribute as a carbon source for bottom water respiration. The concentration of DOM is typically about 100 µM organic C (Osburn & Stedmon 2011), which is about 7 times the typical POC concentration of about 15 µM organic C (Olesen & Lundsgaard 1995), and is transported through the system via water exchange between the Baltic Sea and the North Sea. The concentration is highest in the surface waters originating from the Baltic Sea, with concentrations of 250 to 300 µM organic C (Osburn & Stedmon 2011). A significant fraction has a terrestrial origin, and its degradability is probably low as the various fractions of this DOM has been characterized and successfully used as a conservative tracer of the water exchange (Stedmon et al. 2010). Nevertheless, these concentrations emphasize the role of the Kattegat and Belt Sea as transit areas of DOM. Thus, even low remineralization rates of this material, or transformation between DOM and POM could significantly influence overall rates of bottom water respiration and oxygen consumption. If allochthonous material contributes to bottom water respiration, this would imply a decoupling between oxygen consumption and the primary production of the system. Mineralization of DOM also concerns organically bound nitrogen (DON), and its degradation therefore releases inorganic nitrogen — possibly influencing primary productivity in a system where nitrogen is the limiting nutrient. However, the degradability of the DOM and POM pools has not been studied, and the relative contribution of the 2 pools to bottom water respiration remains unresolved. Thus, bottom water respiration has previously not been explicitly linked to the productivity of the ecosystem because basic knowledge of the sources of organic matter, their turnover rates and temperature sensitivity is lacking.

In this study, we present a comprehensive dataset of bottom water respiration rates based on bottle incubations that, to our knowledge, are the only measurements of pelagic respiration in this area during a full seasonal cycle. The data cover both the seasonal and spatial variability transecting the estuarine gradient between the Baltic Sea and the North Sea. From the observed oxygen consumption in the incubation experiments, we calculated the pool of degradable organic carbon and its specific decay rate at 3 temperatures (*in situ* temperatures and in a warmer and a colder incubation), in order to determine the temperature sensitivity of the process. We compared our estimate of the pool of degradable organic carbon with measurements of POC obtained during the incubations to study the role of POC as a carbon source for respiration. Finally, we discuss carbon sources and their degradability in the water column in relation to the hydrography of the Baltic Sea–North Sea transition zone.

## MATERIALS AND METHODS

### Study area

This study was conducted in the Kattegat and the Belt Sea, located in the transition zone between the Baltic Sea and the North Sea (Fig. 1). The area is relatively shallow, with water depths generally less than 70 m. There is a highly productive frontal zone at the border between the Kattegat surface water and the North Sea and Skagerrak water. Throughout the study area, from the front to the Fehmarn Belt in the western Baltic Sea, there is a persistent halocline at about 15 m that separates the inflowing high saline bottom water from the outflowing brackish Baltic surface water. Surface salinity ranges from about 7 in the western Baltic Sea to about 25 near the front, and the salinity below the halocline is generally more than 25 throughout the transition zone. Primary production occurs both in the surface layer and in the pycnocline layer during the summer, but the bottom layer is considered to be heterotrophic. The average transport time of the bottom water across the study area is about 1 mo during the winter, and 2 to 3 mo during the summer (Bendtsen et al. 2009). However, storm events may cause a renewal of the entire bottom water volume within a period of only days (Matthäus & Franck 1992, Stigebrandt 2001). The strong stratification limits the ventilation of bottom water, and seasonal (August to October) hypoxia frequently occurs near the bottom in the southernmost part of the Belt Sea. The stations visited in this study are also part of the National Danish Monitoring Program, and have been sampled regularly during the past 3 decades. Temperature, salinity, chemistry, plankton biomass and primary production data are available from the Danish national marine database (www.dmu.dk/vand/havmiljoe/mads/).

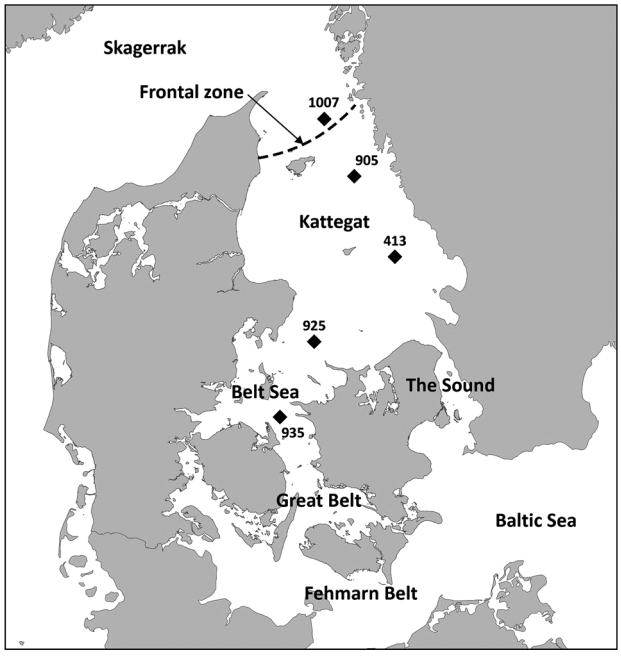


Fig. 1. Study area in the Baltic Sea–North Sea transition zone. Symbols mark positions of the sampling stations: Stn 1007 (57° 32.00′ N, 11° 19.50′ E), Stn 905 (57° 11.06′ N, 11° 39.62′ E), Stn 413 (56° 40.10′ N, 12° 07.00′ E), Stn 925 (56° 07.86′ N, 11° 09.47′ E), Stn 935 (55° 39.05′ N, 10° 45.36′ E). The frontal zone marks the approximate border between the Kattegat surface waters and the North Sea waters

### Experimental design

Seasonal respiration was studied from oxygen uptake during long-term (5 to 7 wk) incubations of bottom water collected from 5 stations (Fig. 1) located along a transect from the northern Kattegat to the Great Belt. Samples were collected during 5 cruises with RV 'Gunnar Thorson', between August 2006 and July 2007 (Table 1). In order to avoid sampling too close to the pycnocline or the sea bottom (where organic matter may be enriched), we sampled the water at 30 m depth (approximately in the middle of the bottom water layer). On each occasion, 25 l water samples were taken from a single CTD cast (with a Seabird sea logger, SBE25). Profiles of salinity, temperature, oxygen and fluorescence from the sea surface to the bottom were recorded from the same CTD cast.

### Incubations

All water samples were incubated at 3 temperatures; as close as possible to *in situ* temperature, 5°C above (+5°C), and 5°C below (–5°C) *in situ* temperature in order to determine the temperature sensitivity of oxygen consumption. Water for the (+5°C) incuba-

Table 1. Measurements of the experimental incubations indicating elapsed time since initial sampling date (1st sample = 0 d). Oxygen concentrations, salinities, and concentrations of particulate organic carbon (POC) and nitrogen (PON) represent the initial measured values. Water depths are as follows: Stn 1007, 42 m; Stn 905, 77 m; Stn 413, 55 m; Stn 925, 42 m; Stn 935, 47 m. 'ND' = no data

| Cruise, sampling dates | Measurements (day) | | | | Incubation temp. (°C) | | | Stn | *In situ* temp. (°C) | Salinity | $O_2$ concentration (µM) | Concentration of organic matter (µM) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1st | 2nd | 3rd | 4th | Low | Mid | High | | | | | POC | PON |
| Cruise 1, 22–23 Aug 2006 | 0 | 14 | 28 | 42 | 10 | 15 | 20 | 1007 | 17.8 | 33.0 | 236 | 16.5 | 2.31 |
| | | | | | | | | 905 | 9.65 | 33.6 | 204 | 7.5 | 1.10 |
| | | | | | | | | 413 | 8.49 | 33.3 | 197 | 19.7 | 2.17 |
| | | | | | | | | 925 | 10.1 | 32.4 | 207 | 22.7 | 2.53 |
| | | | | | | | | 935 | 12.3 | 30.2 | 207 | 35.7 | 3.64 |
| Cruise 2, 17–18 Oct 2006 | 0 | 7 | 21 | 35 | 10 | 15 | 20 | 1007 | 15.4 | 33.1 | 254 | 10.1 | 0.89 |
| | | | | | | | | 905 | 14.8 | 33.4 | 216 | 18.0 | 1.48 |
| | | | | | | | | 413 | 13.9 | 32.9 | 171 | ND | ND |
| | | | | | | | | 925 | 14.2 | 29.7 | 136 | ND | ND |
| | | | | | | | | 935 | 13.9 | 29.1 | 138 | 17.5 | 1.97 |
| Cruise 3, 29–31 Jan 2007 | 0 | 14 | 28 | 48 | 3.5 | 9.5 | 13.5 | 1007 | 7.31 | 32.1 | 294 | 21.5 | 1.24 |
| | | | | | | | | 905 | 7.13 | 32.5 | 297 | 11.1 | 0.6 |
| | | | | | | | | 413 | 7.05 | 28.9 | 291 | 14.7 | 1.14 |
| | | | | | | | | 925 | 4.74 | 24.2 | 341 | 21.7 | 1.53 |
| | | | | | | | | 935 | 4.83 | 20.7 | 338 | 25.0 | 2.07 |
| Cruise 4, 23–24 Apr 2007 | 0 | 20 | 35 | 49 | 3 | 9 | 12 | 1007 | 6.71 | 32.9 | 295 | 35.2 | 3.78 |
| | | | | | | | | 905 | 6.46 | 32.3 | 287 | 52.0 | 4.88 |
| | | | | | | | | 413 | 6.49 | 33.5 | 236 | 18.5 | 2.17 |
| | | | | | | | | 925 | 6.75 | 31.4 | 188 | 81.6 | 8.98 |
| | | | | | | | | 935 | 6.66 | 30.6 | 210 | 36.8 | 4.34 |
| Cruise 5, 5–6 Jul 2007 | 0 | 17 | 28 | 41 | 6 | 13 | 19 | 1007 | 15.12 | 32.7 | 244 | 8.4 | 1.01 |
| | | | | | | | | 905 | 11.85 | 33.2 | 247 | 12.9 | 1.59 |
| | | | | | | | | 413 | 9.58 | 32.6 | 248 | 12.5 | 1.41 |

tions was acclimated to temperatures slightly higher (1 to 2°C) than the subsequent incubation temperature for about 3 h, at which point the jar was shaken to degas the water before setting up the incubation in order to avoid air bubbles that could otherwise form due to oversaturation of $O_2$ and $N_2$ when the water sample was closed and subsequently warmed up. Twenty-seven 500 ml glass bottles with glass stoppers were incubated for each water sample collection (9 for each temperature). The water was carefully siphoned from the 25 l jars into bottles, allowing overflow in the same way as recommended for filling bottles for Winkler titration (Grasshoff et al. 1983). The initial concentration of $O_2$ in the incubations was determined by Winkler titration of 5 replicate samples. These samples were siphoned into 100 ml Winkler titration bottles between filling of the 27 incubation bottles in order to get the closest match with the initial $O_2$ concentration in the incubation bottles. Samples for the initial concentration of POM were also sampled concomitant with the filling of the incubation bottles. Filling of all bottles was completed within 10 min, and the 25 l jar was regularly stirred to avoid sedimentation of POM. The bottles were closed with glass stoppers and kept in the dark, submersed in an 80 l plastic box during the incubation to dampen minor temperature fluctuations in the climate chamber. Incubation temperatures were regularly recorded, and showed a variation less than ±0.5°C in the 80 l box during the 7 wk incubation.

We measured the initial concentration of $O_2$, POC and particulate organic nitrogen (PON); concentrations were subsequently measured 3 more times during the incubations. During each measurement, 3 bottles were stopped, and each bottle was sampled individually for nutrients while samples for oxygen were siphoned into 100 ml glass bottles as described above (i.e. all incubation results were derived from triplicate water samples). The remaining water in the 3 replicate bottles (500 to 1000 ml) was pooled and filtered onto pre-combusted GF/C-filters and stored at −21°C for later measurements of POC and PON.

### Concentration experiments

In order to determine the relationship between the concentration of POM and oxygen consumption, we conducted 2 experiments in which the concentrations of POM were manipulated. The POM fraction (>5 µm) and the fraction >0.7 µm in water sampled at Stn 925 in August 2006 was concentrated by reverse filtration and by GF/F filtration onto pre-combusted GF/F 0.7 µm pore size filters, respectively, resulting in a concentration ranging from 1 to 35 times the natural concentration. Subsequently, a series of incubations of water with varying concentrations of the 2 particle size classes of POM were incubated in duplicates in 100 ml bottles, following the same procedure described for the *in situ* temperature incubations. Initial concentration of oxygen, POC and PON were measured, and after 7 d we stopped the experiment and measured the concentrations of oxygen and ammonium ($NH_4^+$). In order to test how the filtration of POM onto GF/F filters affected the overall oxygen consumption, we compared oxygen consumption in natural bottom water with the oxygen consumption in a corresponding volume of filtrate of the water sample containing a suspended GF/F filter with the particulate fraction of the organic matter.

### Analysis

Oxygen concentration was measured following the standard Winkler titration method as described by Grasshoff et al. (1983) using 100 ml titration bottles, and titrated using a titrator (Metrohm-702 SM titrino) with a precision of 2 µl. The concentration of the $Na_2SO_3^-$ reagent was 0.1 mol $l^{-1}$; molarity was determined daily prior to each sampling for oxygen measurements. Analysis of nutrients included nitrite ($NO_2^-$) nitrate ($NO_3^-$), $NH_4^+$ and phosphate ($PO_4^{3-}$). The samples were stored at −21°C before analysis on an autoanalyser (Scalar Sandplus Analyser) following the standard procedure described for the National Danish Monitoring Programme (Pedersen et al. 1998). The concentrations of POC and PON were measured on an Eager 200 CHNS-elemental analyser calibrated against a methionine standard.

### Calculation of the remineralization rates

Because the degradable fraction of the dissolved organic carbon (DOC) and POC is unknown and cannot be measured directly, we calculated this pool from the course of the oxygen consumption. It was assumed that the oxygen consumption could be ascribed to the mineralization of a single labile pool of organic carbon (OC) characterised by a single remineralization rate (α):

$$\frac{dOC}{dt} = -\alpha OC \quad (1)$$

and the corresponding model solution for oxygen was determined, assuming a remineralization ratio of

$\eta_{O2:C} = 1.2$ between $O_2$ and organic carbon (Hansen & Bendtsen 2013). We limited the number of free variables by assuming that the remineralized organic carbon fraction could be described by a single pool. Although more pools may be a better description of the various organic carbon compounds constituting the OC pool, this would require more frequent measurements than available here. As shown below, the fitting to a single pool of organic carbon describes the incubation experiments well, and this supports the simple model chosen here. OC was described by Eq. (1), and the corresponding oxygen consumption was then determined from:

$$O_2(t) = O_2(t_0) - \eta_{O2:C}\, OC(t_0)\,(1-\exp(-\alpha t)) \quad (2)$$

where $O_2(t_0)$ is the initial measured $O_2$ concentration, and the 2 unknown values in Eq. (2) ($OC(t_0)$ and $\alpha$) were determined by a Levenberg-Marquardt non-linear least-square method (Press et al. 1986) which for each temperature minimizes the sum of the residuals between the measurements ($y_i$) and model solutions ($y_m$) defined by $\chi^2 = \Sigma[(y_i - y_m)/\sigma_i]^2$, where the standard deviation $\sigma_i$ was represented by the maximum of the standard error of the triplicate measurements and the uncertainty associated with the measurement procedure, which was set to 5 µmol $kg^{-1}$ $O_2$. The initial $OC(t_0)$ represents the labile pool of organic carbon which can be respired on time scales comparable to the incubation period, and therefore it only constitutes a fraction of the total organic carbon in the water. A large fraction of DOC and POC is either refractory or only very slowly decomposable (Bauer et al. 1992) and this fraction is therefore not contained in $OC(t_0)$.

As the initial concentrations $OC(t_0)$ in the incubation bottles are the same at all 3 temperatures, a best fit solution was sought that minimised the sum of $\chi^2$ for all 3 temperatures in an interval of $OC(t_0)$, and $\alpha$ was then determined for each temperature. In general, this procedure resulted in best fit $OC(t_0)$ values in a relatively narrow interval for the 3 temperatures; the best fit value found for the minimum of the sum of $\chi^2$ for the 3 residuals (at the 3 temperatures) is referred to as OC best fit ($OC_{bf}$) below.

### Calculation of $Q_{10}$ factor

The $Q_{10}$ values, corresponding to the best fit solutions of the remineralization rates, were determined from the remineralization ratios at 2 temperatures: $Q_{10} = (\alpha_2/\alpha_1)^{10/(T_2 - T_1)}$. The $Q_{10}$ values were calculated for the temperature interval $[T_{-5}:T_{+5}]$. In order to test if cooling or warming of the samples affected the temperature sensitivity differently, we also calculated and compared the $Q_{10}$ values for the temperature intervals $[T_{-5}:T_0]$ and $[T_0:T_{+5}]$. The calculation of the $Q_{10}$ ratio was in general not sensitive to the common value of $OC_{bf}$ within the range of best fit values found for each of the 3 temperatures. The fitting procedure was carried out for all incubation experiments.

## RESULTS

### Hydrography

The salinity of most water samples ranged between 29 and 33.6, and the CTD profiles (not shown) indicated that the water column was stratified by a strong halocline. These conditions are representative of the typical hydrography in the Kattegat. However, on one sampling occasion the water column was completely mixed due to a storm event in the southern Kattegat and Great Belt (Stns 925 and 935) in January 2007, as indicated by an unusual low salinity of 20 in the sampled bottom water; the storm also caused visible resuspension of the sediment at the sea surface (Table 1). The observed *in situ* temperature ranged between 4.8 and 17.8°C, which is similar to the average seasonal temperature range of 4 to 16°C for bottom water in the area. In July and August, the bottom water temperature showed a declining gradient from north to south, reflecting inflow of relatively warm bottom water, heated during the summer, and replacement of colder water masses in the southern part of the area. The typical transport time in the bottom layer from the front in the northern Kattegat to the Great Belt is about 2 to 3 mo, and this causes a corresponding delay in the seasonal temperature signal in the Great Belt. The sampled water was generally well oxygenated with more than 50% oxygen saturation. Initial measured POC concentrations ranged between 7.5 µM and 82 µM POC with a mean value of 23 µM (Table 1). The exceptionally high values of 82 and 52 µM were measured in samples taken during the sedimentation of the spring bloom, which was caught in the sampled bottom water at Stns 925 and 905 (April 2007). During the rest of the seasons the POC concentrations showed much less variation. The C/N ratio of the POM was generally higher than the Redfield ratio (6.6) with a mean value of 9.9 and a range of 6.0 to 18.5. Samples from January 2007 showed higher C/N ratios than during the rest of the seasons, with values exceeding 12 for all stations.

### Incubations

There was a consistent decline in oxygen concentration in all incubations (Fig. 2). Total oxygen consumption was on average 24.8 µM $O_2$ (range 2.6 to 54.0 µM) during the 5 to 7 wk incubation, and there was a pronounced temperature effect showing reduced (increased) consumption rates in the colder (warmer) incubations in comparison with the *in situ* temperature. An average over all the experiments showed a doubling in the total oxygen consumption in the warm incubations (32.1 µM $O_2$) compared with the cold incubations (17.8 µM $O_2$). However, during most of the experiments — and in particular in the warm incubations — the oxygen consumption slowed down toward the end of the incubations but did not stop completely (Fig. 2).

By assuming that the oxygen consumption was due to decay of a single pool of suspended organic material, and that the initial pool of organic matter in the sampled water was the same in all bottles at all incubation temperatures, we calculated the initial pool of organic carbon available for remineralization ($OC_{bf}$) and the decay rate (α) of the organic carbon for each station (Table 2). The mean value of α at *in situ* temperature across the seasons was 0.035 $d^{-1}$. The lowest values were found during winter (0.0027 $d^{-1}$ to 0.010 $d^{-1}$) and the highest in October (0.053 $d^{-1}$ to 0.094 $d^{-1}$) (Fig. 3). The initial remineralization rates of OC ($\alpha \times OC_{bf}$) at *in situ* temperatures ranged between 2.8 mg C $m^{-3}$ $d^{-1}$ and 28 mg C $m^{-3}$ $d^{-1}$ (Fig. 4). These rates correspond to an initial oxygen consumption between 9 and 90 mg $O_2$ $m^{-3}$ $d^{-1}$. The lowest rates were observed in July (5.1 mg C $m^{-3}$ $d^{-1}$) and January (5.8 mg C $m^{-3}$ $d^{-1}$), and the highest rates during late summer in August (20.6 mg C $m^{-3}$ $d^{-1}$) and October (16.6 mg C $m^{-3}$ $d^{-1}$); rates during the spring (9.4 mg C $m^{-3}$ $d^{-1}$) were close to the annual mean (12 mg C $m^{-3}$ $d^{-1}$) (Table 2, Fig. 4). There were no significant differences among stations, although remineralization rates tended to be highest in the southernmost stations (Stns 925 and 935) in the Great Belt compared to the Kattegat (Stns 1007, 905 and 413). Assuming that the samples are representative

Table 2. Estimated values of the initial pool of organic carbon ($OC_{bf}$) and specific turnover rates ($d^{-1}$) of organic carbon (α) at the 3 experimental incubation temperatures: cold (5°C lower than *in situ*), *in situ*, and warm (5°C higher than *in situ*) ± standard deviation and the associated summed $\chi^2$ for the 3 fits (cf. 'Materials and methods'). The temperature sensitivities of α expressed as a $Q_{10}$ value have been estimated for the entire temperature range. $\alpha_{10°C}$ expresses the turnover rate of the organic carbon at 10°C and is calculated from the α value in the incubation at 10°C, or the incubation temperature closest to 10°C and subsequently normalized to 10°C using the $Q_{10}$ value from the same experiment. The respiration rate expresses the carbon mineralization at *in situ* temperatures and is calculated from ($OC_{bf} \times \alpha_{in\ situ}$). Mean values represent the arithmetic mean across all experiments. Cruise numbers are as in Table 1

| Cruise | Stn | $OC_{bf}$ (µmol $l^{-1}$) | $\alpha_{cold}$ ± SD ($d^{-1}$) | $\alpha_{in\ situ}$ ± SD ($d^{-1}$) | $\alpha_{warm}$ ± SD ($d^{-1}$) | $Q_{10}$ | $\chi^2$ | $\alpha_{10°C}$ ($d^{-1}$) | Respiration rate (mg C $m^{-3}$ $d^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 1007 | 33 | 0.043 ± 0.0060 | 0.054 ± 0.011 | 0.088 ± 0.027 | 2.1 | 0.6 | 0.043 | 21 |
| 1 | 905 | 31 | 0.048 ± 0.0076 | 0.063 ± 0.010 | 0.15 ± 0.079 | 3.1 | 1.1 | 0.048 | 23 |
| 1 | 413 | 27 | 0.047 ± 0.0079 | 0.025 ± 0.0045 | 0.11 ± 0.029 | 2.4 | 0.7 | 0.047 | 8.2 |
| 1 | 925 | 37 | 0.049 ± 0.0061 | 0.051 ± 0.0064 | 0.090 ± 0.015 | 1.8 | 0.7 | 0.049 | 23 |
| 1 | 935 | 43 | 0.036 ± 0.0041 | 0.055 ± 0.0068 | 0.11 ± 0.017 | 3 | 0.8 | 0.036 | 28 |
| 2 | 1007 | 22 | 0.031 ± 0.0075 | 0.053 ± 0.012 | 0.093 ± 0.024 | 3 | 0.4 | 0.031 | 14 |
| 2 | 905 | 15 | 0.033 ± 0.010 | 0.071 ± 0.023 | 0.13 ± 0.051 | 3.9 | 0.5 | 0.033 | 13 |
| 2 | 413 | 15 | 0.031 ± 0.0095 | 0.094 ± 0.034 | 0.15 ± 0.062 | 4.9 | 0.3 | 0.031 | 17 |
| 2 | 925 | 19 | 0.026 ± 0.0066 | 0.086 ± 0.024 | 0.11 ± 0.032 | 4.2 | 0.4 | 0.026 | 20 |
| 2 | 935 | 21 | 0.034 ± 0.0077 | 0.077 ± 0.019 | 0.093 ± 0.025 | 2.7 | 0.4 | 0.034 | 19 |
| 3 | 1007 | 43 | 0.0062 ± 0.0013 | 0.010 ± 0.0017 | 0.017 ± 0.0028 | 2.8 | 0.5 | 0.013 | 5.2 |
| 3 | 905 | 116 | 0.0020 ± 0.0004 | 0.0027 ± 0.00040 | 0.0042 ± 0.0005 | 2.2 | 0.2 | 0.0040 | 3.8 |
| 3 | 413 | 33 | 0.0031 ± 0.0025 | 0.0087 ± 0.0019 | 0.016 ± 0.0024 | 5 | 0.8 | 0.0063 | 3.5 |
| 3 | 925 | 91 | 0.0020 ± 0.0005 | 0.0075 ± 0.00070 | 0.0093 ± 0.0007 | 4.6 | 0.5 | 0.0041 | 8.2 |
| 3 | 935 | 99 | 0.0020 ± 0.0005 | 0.0072 ± 0.00060 | 0.0095 ± 0.0007 | 4.7 | 0.3 | 0.0041 | 8.5 |
| 4 | 1007 | 87 | 0.0068 ± 0.0008 | 0.0062 ± 0.00080 | 0.010 ± 0.0010 | 1.5 | 0.6 | 0.015 | 6.4 |
| 4 | 905 | 18 | 0.013 ± 0.0039 | 0.019 ± 0.0048 | 0.034 ± 0.0081 | 2.5 | 0.5 | 0.029 | 4.1 |
| 4 | 413 | 28 | 0.018 ± 0.0029 | 0.031 ± 0.0047 | 0.040 ± 0.0065 | 2.3 | 0.7 | 0.038 | 10 |
| 4 | 925 | 49 | 0.020 ± 0.0018 | 0.028 ± 0.0027 | 0.039 ± 0.0035 | 2 | 0.6 | 0.042 | 16 |
| 4 | 935 | 30 | 0.022 ± 0.0034 | 0.029 ± 0.0040 | 0.048 ± 0.0074 | 2.1 | 0.6 | 0.048 | 10 |
| 5 | 1007 | 43 | 0.0074 ± 0.0014 | 0.011 ± 0.0018 | 0.017 ± 0.0019 | 2.3 | 0.7 | 0.011 | 6.0 |
| 5 | 905 | 38 | 0.0094 ± 0.0017 | 0.015 ± 0.0021 | 0.023 ± 0.0026 | 2.4 | 0.3 | 0.015 | 6.8 |
| 5 | 413 | 23 | 0.0076 ± 0.0027 | 0.0098 ± 0.0029 | 0.029 ± 0.0053 | 3.8 | 0.3 | 0.012 | 2.8 |
| Mean: | | 42 | 0.022 | 0.035 | 0.061 | 3.0 | | 0.027 | 12 |

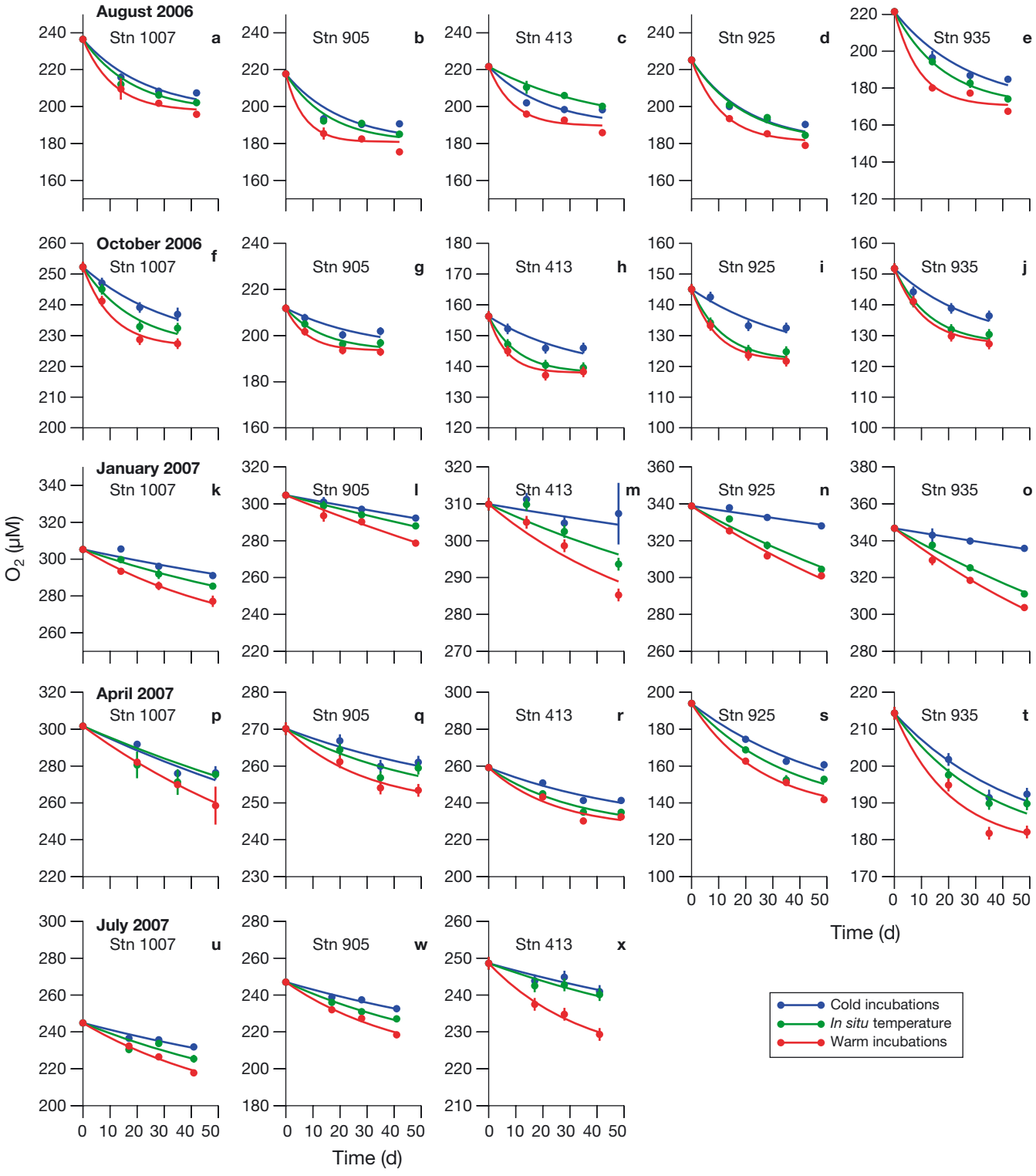


Fig. 2. Changes in oxygen concentrations during incubation for each station (Stns 1007, 905, 413, 925 and 935; columns) and each season (rows). Blue symbols: observed oxygen concentrations in the cold incubations (5°C lower than *in situ* temperatures); green symbols: corresponding oxygen concentration at *in situ* temperatures; red symbols: oxygen concentrations in the warm incubations (5°C higher than *in situ* temperatures). Error bars show standard deviation of triplicates. Lines indicate best fit solutions for each of the 3 incubation temperatures following Eq. (2) and assuming first order decay of one pool of organic matter

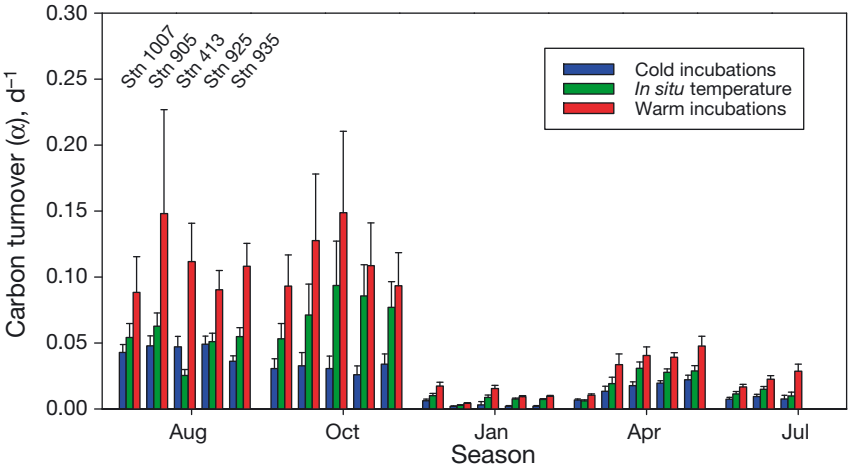


Fig. 3. Estimated turnover rates of organic carbon (α) in the incubations, station by station and season by season, estimated from oxygen consumption rates. Colors represent cold, *in situ* and warm incubation temperatures. Error bars represent standard error of the α-estimate

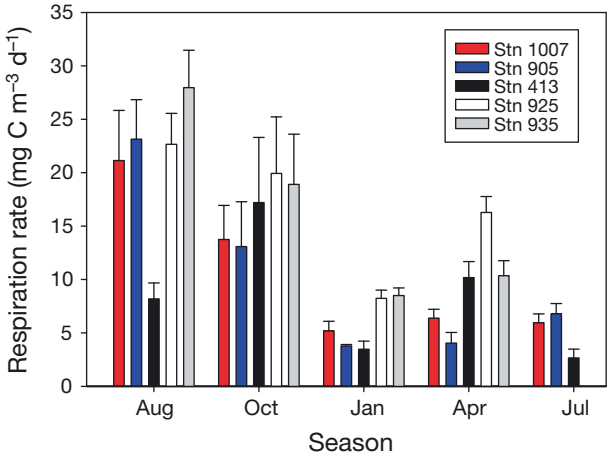


Fig. 4. Initial remineralization rates of organic carbon (mg C $m^{-3}$ $d^{-1}$) in the incubations ($\alpha \times OC_{bf}$) estimated from oxygen consumption station by station and season by season. Colors mark the different stations along the north-south transect

of the seasonal cycle, these rates correspond to an annual remineralization of 53 g C $m^{-2}$ $yr^{-1}$ (12 mg $m^{-3}$ × 365 d $yr^{-1}$ × 12 m) assuming an average bottom layer thickness of 12 m.

The decay rates of organic material were on average 3 times faster in the warm (+5°C) incubations compared to the cold (–5°C) incubations, corresponding to a $Q_{10}$ value ranging between 1.5 and 4.9 and a mean value of 3.0 ± 1.1 (Table 2). There was no systematic difference whether the $Q_{10}$ value was calculated for the –5°C to *in situ* temperature range, for the *in situ* to +5°C, or across the entire incubation temperature range from –5 to +5°C. The value of $OC_{bf}$ was on average 42 µM organic C, ranging from 15 to 116 µM organic C (Table 2), and therefore the estimated pool of organic carbon was on average almost twice as high (183%) as the average measured value of POC (23 µM). Correspondingly, data from the individual experiments showed that values of $OC_{bf}$ were larger than the initial measured values of POC in 18 out of 21 experiments, with values of $OC_{bf}$ being up to 10 times larger than the measured value of POC — suggesting that sources of organic matter other than the particulate fraction contributed significantly to the total oxygen consumption. $OC_{bf}$ values were closest to the measured values of POC in April (113% of the measured value). Three samples from April with the highest POC concentrations (37 to 82 µM) all contained diatomaceous material, and these 3 samples were the only examples of measured values of POC being higher than the estimated values of $OC_{bf}$.

The specific turnover rate of organic matter in all the experiments was normalized to a common reference temperature of 10°C, and was calculated using observed $Q_{10}$ values for each individual experiment to normalize α to 10°C ($\alpha_{10°C}$); which, in the following is assumed to represent the lability of the degradable fraction of organic matter $OC_{bf}$. The lability varied one order of magnitude from 0.0040 $d^{-1}$ to 0.049 $d^{-1}$ (Table 2, Fig. 5). The lowest lability (most refractory) was found in the winter with ($\alpha_{10°C}$ = 0.0062 $d^{-1}$) and

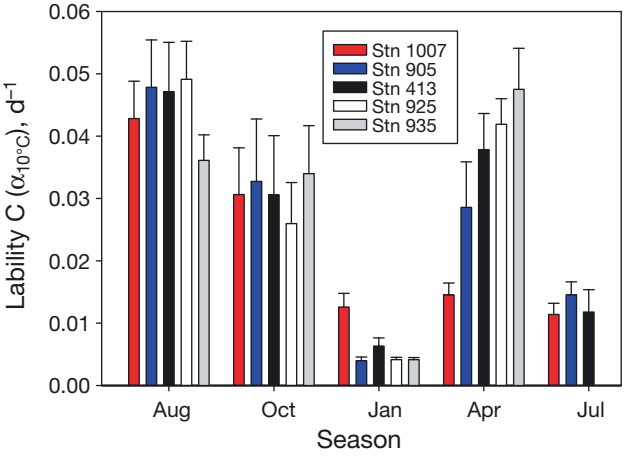


Fig. 5. Lability of organic matter expressed as turnover rates of organic carbon ($d^{-1}$) normalized to a temperature of 10°C ($\alpha_{10°C}$). In each experiment, the value was obtained from the incubation temperature closest to 10°C and subsequently scaled to 10°C using a $Q_{10}$ value of 3. Colors as in Fig. 4

in July ($\alpha_{10°C}$ = 0.0126 $d^{-1}$), whereas the most labile organic material was found in August ($\alpha_{10°C}$ = 0.045 $d^{-1}$) and October ($\alpha_{10°C}$ = 0.031 $d^{-1}$). In April there was a characteristic north-south gradient with the lowest values occurring in the north (Fig. 5).

In 4 out of the 5 seasons (April, July, October and January) we measured the concentrations of POC and PON during the incubation experiments. In the incubations from January there was an initial build-up of POM, whereas in April there was a decrease in POM. During the rest of the 5 to 7 wk incubation period there was no reduction in the pool of POM. In most cases, the C/N ratio of the POM increased during the incubations (Fig. 6). In July, the C/N ratios increased from about 9 to 12 in the cold and *in situ* temperature incubations, while the C/N ratio ended at about 14 in the warm incubation. The October samples showed the same pattern, with C/N ratios increasing from 11 to 15 in the cold and *in situ* temperature incubations, whereas the C/N ratios as high as 25 in the warm incubations. In April the increase was less pronounced, going from 9 to 11 for all temperatures; but in January the C/N ratio remained more or less constant around 15. The highest lability ($\alpha_{10°C}$) of the pool of degradable organic matter $OC_{bf}$ was always associated with C/N ratios below 10 of the measured pool of POM (Fig. 7).

A comparison between the measured standing concentration of POC in the incubations and an estimate of the concentration of POC (cf. Eq. 2, assuming that the oxygen consumption was due to POC degradation alone) shows a consistent pattern in which the measured POC concentration remained almost constant at about 100% of the initial pool throughout all the experiments, whereas the estimated POC concentration declined (Fig. 8). The estimated POC concentration was on average 50% of the initial value for all incubations at 3 to 5°C at the end of the incubations, and correspondingly 20% for all incubations at 6 to 10°C (Fig. 8). For incubations within the temperature range between 12 and 15°C, the oxygen consumption corresponded to a carbon mineralization exceeding the initial pool of POC by about 30%. For the warmest incubations at 18 to 20°C, the mineralization of carbon was almost twice as high (183%) as the concentration of POC. Thus, in these experiments the total oxygen consumption during the 5 to 7 wk incubations corresponded to about twice the POC pool present at the beginning of the experiments, while measurements taken during the experiments showed that the POC pools remained relatively constant. This is discussed further below.

The concentration experiment showed a linear correlation between oxygen consumption and the initial concentration of POC (Fig. 9a), both when the particulate material was concentrated on GF/F filters, and by reverse filtration through a 5 µm

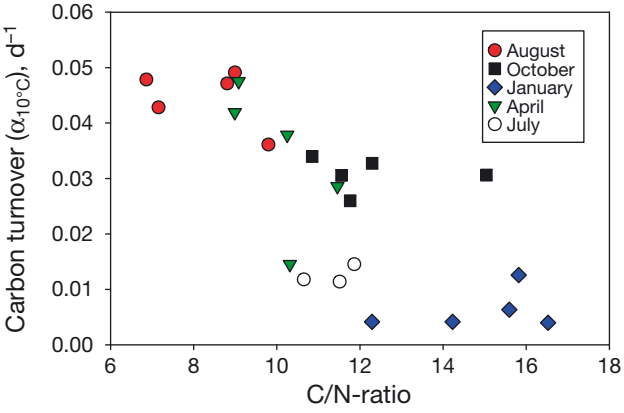


Fig. 7. Carbon lability ($\alpha_{10°C}$) versus the initial composition of the particulate organic matter in terms of C/N ratios for each experiment. Symbols mark the different seasons replicated by stations

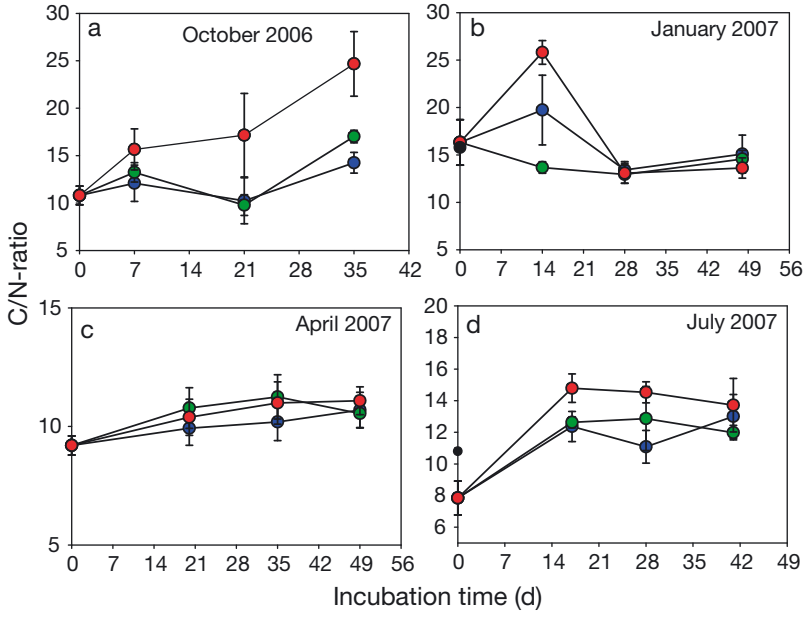


Fig. 6. Molar ratios of carbon and nitrogen (C/N) in the particulate organic matter during the course of the incubations in (a) October, (b) January, (c) April and (d) July. Blue, green and red symbols indicate cold, *in situ* and warm incubations as in Figs. 2 & 3

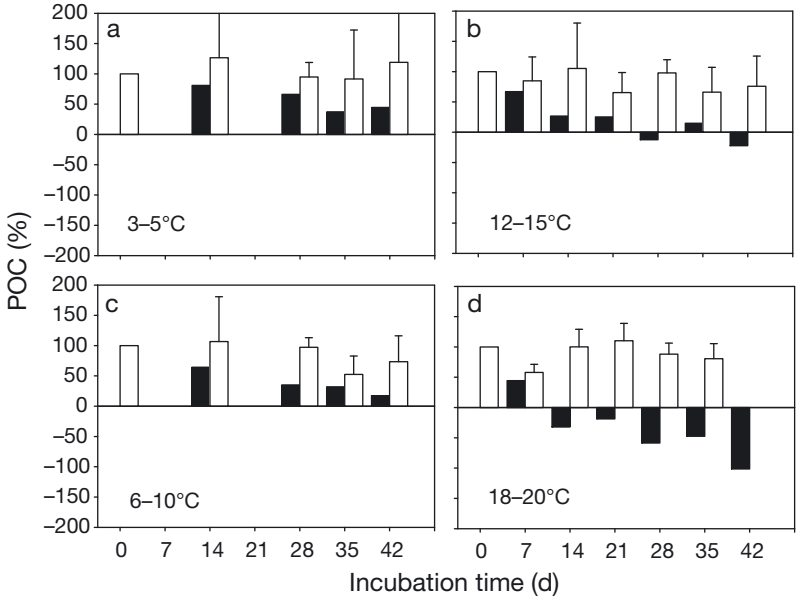


Fig. 8. Relative changes in the particulate organic carbon (POC) concentration during the course of the incubations for all experiments grouped by incubation temperature: (a) temperatures of 3 to 5°C, (b) 6 to 10°C, (c) 12 to 15°C and (d) 18 to 20°C. Open bars show measured values of POC during the incubation expressed as percent of the measured POC at the beginning of the experiment. Filled bars show the expected concentration of POC from the oxygen consumption using a carbon/oxygen mineralization ratio of 1.2. Negative values indicate that the expected POC consumption exceeds the available pool at the beginning of the incubation. Error bars = standard deviation

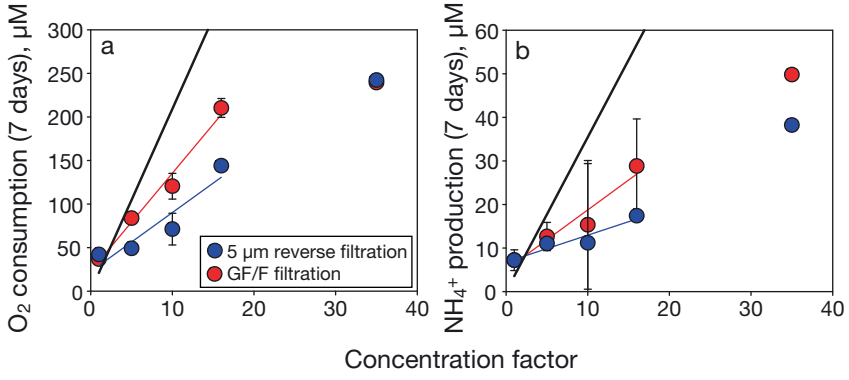


Fig. 9. (a) Oxygen uptake during 7 d of incubation versus the enrichment factor of particulate organic carbon (POC). The POC was enriched by reverse (5 µm) filtration (blue symbols) and by filtration onto pre-combusted GF/F filters retaining approximately the >0.7 µm fraction (red symbols). Lines show linear regressions for the range of enrichment between 1 and 16 times the natural POC concentration at Stn 925 in August. The incubation with 35 times enrichment of POC became almost anoxic during the incubation, and these data were omitted from the regression. Black line shows the expected oxygen consumption when scaled from incubation of the un-manipulated water sample (concentration factor = 1). Error bars show standard deviation of replicates. (b) As (a) but shows the corresponding production of $NH_4^+$ as a function versus the enrichment factor. Black line shows expected $NH_4^+$ production from oxygen consumption in un-manipulated water incubation assuming a mineralization ratio of $O_2$:N of 8

plankton net. For example, the incubation with 16 times enrichment of the >0.7 µM fraction resulted in an oxygen consumption of 210 µM $O_2$, corresponding to a 13.1 times relative increase in oxygen consumption (210 µM $O_2$ / 16 µM $O_2$ = 13.1), where consumption of 16 µM $O_2$ was measured in the corresponding incubation of water from Stn 925 at *in situ* temperature. Similarly, the concentration experiment with a factor of 16 enrichment of the >5 µm fraction showed a 9 times increase in the oxygen consumption. However, at the highest POC concentration (35 times the natural concentration) the oxygen consumption was lower than expected, likely due to oxygen limitation in this experiment. The corresponding changes in the concentrations of $NH_4^+$ show a linear relationship between oxygen consumption and ammonification of organic material (Fig. 9b)

## DISCUSSION

Respiration rates in the bottom waters of the Kattegat and the Belt Sea area are critical for the oxygen conditions in the entire transition zone between the North Sea and the Baltic Sea, because the bottom water ventilation is limited by strong stratification of the water column. The oxygen concentration in the bottom water flowing in to the Kattegat is typically 200 µM (6.2 mg $O_2$ $l^{-1}$) during the summer (Hansen & Bendtsen 2013). According to the observed oxygen consumption rates in August of 0.065 mg $O_2$ $l^{-1}$ $d^{-1}$ [20.6 µg C $d^{-1}$ × ($O_2$:C = 1.2) × (32 g $O_2$ $mol^{-1}$ / 12 g C $mol^{-1}$)], the bottom water mass will reach hypoxia (<2 mg $O_2$ $l^{-1}$) after 65 d [(6.2 – 2) mg $O_2$ $l^{-1}$ / 0.065 mg $O_2$ $l^{-1}$ $d^{-1}$]. The residence time of the bottom water in the Kattegat is typically 60 to 90 d in the summer (Bendtsen et al. 2009) before it is transported from the northern front to the Belt

Sea (Fig. 1). The oxygen consumption rates observed in August will therefore be critical for the oxygen conditions in the Belt Sea — especially in years with calm weather conditions where the residence time is longest (Bendtsen et al. 2009, Hansen & Bendtsen 2013). Thus, the estimated oxygen consumption rates in our incubations agree with the observed oxygen conditions in the area when the hydrography is taken in to account. A model of bottom water respiration in the North Sea–Baltic Sea transition zone; OXYCON (Bendtsen & Hansen 2012, Hansen & Bendtsen 2013) has recently been developed based on various sources in the literature, and subsequently successfully validated in different physical models (Bendtsen & Hansen 2012, Jonasson et al. 2012, Hansen & Bendtsen 2013). The parameterisation of OXYCON assumed that total remineralization of the bottom water layer was 45 g C $m^{-2}$ $yr^{-1}$, and that temperature sensitivity corresponded to a $Q_{10}$ value of 3. These values are in very good accordance with the present estimates of 53 g C $m^{-2}$ $yr^{-1}$ and the calculated mean $Q_{10}$ value, respectively.

### Temperature sensitivity of the pelagic respiration

We consider temperature sensitivity to be well constrained due to the large data set, and the fact that we observed the same $Q_{10}$ value whether we cooled or warmed the samples relative to the *in situ* temperature. The $Q_{10}$ values also fall within the range of previous reported $Q_{10}$ values (i.e. 2 to 3.5) for pelagic respiration (Robinson & Williams 1993, Lefevre et al. 1994, Lomas et al. 2002) and a $Q_{10}$ value of 3.5 and 3.4 can be recalculated from Sampou & Kemp (1994) where plankton respiration from Chesapeake Bay was studied over a range of incubation temperatures (5 to 30°C). Temperature sensitivity is critical for the seasonal variation in oxygen conditions in a heterotrophic plankton system such as in the bottom water in the Kattegat and the Belt Sea area, where it can be expected that higher water temperatures will increase the remineralization rate of organic matter exported from the surface layer, and thereby increase the total remineralization. Bendtsen & Hansen (2012) showed that by extrapolating the present day seasonal oxygen consumption to a future 3°C warmer climate (i.e. applying a $Q_{10}$ = 3), this would increase the area affected by seasonal hypoxia even though the total annual remineralization remained the same. The effect was due to larger seasonal variation because a larger proportion of the total input of organic matter was mineralized in the water column. In the larger perspective, the $Q_{10}$ value is also a central issue for the role of the global marine carbon cycle, because respiration is expected to have higher temperature sensitivity than primary production — thereby making the world's oceans more heterotrophic and reducing carbon sequestering in a future, warmer climate (López-Urrutia et al. 2006). However, as described above, knowledge of the 2 processes (primary production and respiration) is biased, and such predictions are based on relatively few experimental observations of the $Q_{10}$ value for pelagic respiratory processes.

### Mineralization rates of organic carbon

Our estimate of a total annual remineralization rate of 53 g C $m^{-2}$ $yr^{-1}$ is uncertain because it is unknown how well the 5 sampling occasions and 5 stations represented actual seasonal and spatial variation (specifically with respect to water temperature and the concentration and degradability of organic matter); and there are no similar studies with which to compare our results. The mean temperature of all our samples from the Kattegat and the Belt Sea was 9.4°C, whereas data from the national marine database (www.dmu.dk/vand/havmiljoe/mads/) show an annual temperature (2000 to 2006) for the same stations of 8.0°C. By assuming a 1.4°C bias in the data, the total remineralization would then be 38 g C $m^{-2}$ $yr^{-1}$ when using the $Q_{10}$ = 3.0 to scale the seasonal rates. This is less than the area-averaged organic carbon budget of 45 g C $m^{-2}$ $yr^{-1}$ assumed in Hansen & Bendtsen (2013) but, as discussed in the same study, that carbon budget was primarily based on literature studies from the 1990s where the conditions were more eutrophic, and therefore the more recent respiration rates obtained here could be slightly lower due to the less eutrophic conditions. Such long-term variability due to environmental management has to be taken into account when carbon budgets are made for near-coastal areas. With respect to the concentration of organic matter and its specific degradability (lability), we observed considerable variation but with no distinct seasonal pattern. In comparison, Olesen & Lundsgaard (1995) observed a relatively constant POC concentration of about 15 µM organic C at one station during the productive season (March to October), except during the spring bloom when the concentration was higher due to sinking diatomaceous material. We also observed varying degradability of the organic material with low values in January and July, high degradability in August and

October, and variable degradability in April. In general, it could be hypothesised that low lability or degradability is associated with older material (i.e. organic material that has been exposed to pelagic degradation for a longer time) with high C/N ratios. If the particulate material entering into the bottom layer is heterogeneous with different degrees of lability, then the material will gradually be more refractory. This was confirmed in most of our incubations where we observed a gradual increase in the C/N ratio during the incubations (Fig. 6). Varying input rates of organic material from the surface layer could lead to corresponding changes in degradability, where the organic matter suspended in the bottom layer should be more refractory following periods of low input rates from the surface layer. This could be the case for the July samples, whereas the refractory material in the January samples was probably due to re-suspension of 'old material' from the sediment surface. In April, the sedimentary flux typically contained varying fractions of living diatoms, which are not degraded during their descent through the bottom layer (Smetacek 1985, Hansen & Josefson 2003, Josefson & Hansen 2003); therefore, low C/N ratio during this season does not necessarily imply high degradability.

Another uncertainty in the estimate of total remineralization concerns the calculation for the respiration rate. Because it is not possible to directly measure the degradable fraction of the suspended organic carbon, it was necessary for us to estimate this pool of organic carbon. The calculation assumes that the organic matter being respired can be represented by only one homogenous pool undergoing a first order decay. Fitting the data results in an estimate of the initial pool of degradable organic matter ($OC_{bf}$) and its specific decay rate ($\alpha$). However, our experiments show that the composition of POM undergoes changes in terms of the C/N ratios during the 6 to 8 wk of incubation, which implies that the pool of POM is not decaying as one homogeneous pool. Even though POM is probably not the primary source for the respiratory processes, as discussed below, other sources of dissolved organic matter may also change composition during the degradation process. If the total observed oxygen consumption results from several pools of organic matter, each with different degradability, then this could affect the estimated initial respiration rates and thereby our estimate of *in situ* respiration, because our model would not resolve the dynamics of fast-degrading labile compounds during the first week of incubation. On the other hand, our estimates suggest that the total available pool of organic matter has a turnover time ($1\ \alpha^{-1}$) of about 15 d in August and October. If the bottom water respiration to a larger extent was based on labile organic compounds with faster turnover rates, this would require correspondingly higher input rates of DOM to maintain this pool in the heterotrophic bottom layer. The DOM can enter the bottom layer by mixing from the surface layer or by advection from North Sea/Skagerrak where the bottom water layer has been exposed to primary production before its subduction into the Kattegat area. However, the residence time of the bottom water is typically 2 to 3 mo (Bendtsen et al. 2009) and therefore it is unlikely that inputs by mixing and advection can sustain a DOM-pool with faster turnover rates than 15 d. On the other hand, the sinking POM fraction has a typical residence time in the bottom layer of 1 to 2 wk (Olesen & Lundsgaard 1995) and therefore this pool could potentially balance the observed respiration rates.

### Carbon sources for pelagic remineralization in the transition zone

Contrary to our expectations that bottom water respiration was primarily based on POM sinking from the surface layer, our results showed consistently that the POM concentration did not decline during incubation. The longer the incubation experiments lasted, or the warmer the incubations were, the larger the discrepancy was between the amount of organic matter being mineralized and the initial measurements of POM. When the incubations with the warmest temperatures were terminated, the integrated oxygen consumption corresponded to almost twice the initial measured pool of POM — which remained constant throughout the incubation time. We have no measurements of DOM, but given these results we must conclude that DOM (or particulate matter with particle sizes $< 0.7$ µm) is a main source of organic matter for bottom water respiration, and that it is a relatively large pool of about 50 µM organic C on average, with an average turnover time of about 46 d. Turnover rates of DOC of only 3 to 40 d have been observed in surface waters during phytoplankton blooms, and our estimates probably reflect that the bottom water is isolated from the productive surface layer and newly produced DOC from phytoplankton. Our concentration experiments showed that oxygen consumption was also related to the POC fraction (defined by the 0.7 µm pore size of the GF/F filters). In addition, changes in the C/N ratios of the

POM during the incubations also indicated that POM is being transformed, and that there is a transformation between the DOM and POM and an interaction in their degradation. Heterotrophic organisms are of course a part of the measured pool of POM (>0.7 µm), and this can explain the correlation between the respiration rate and the concentration of POM.

We hypothesize that the heterotrophic microbial community are both free living and attached to particulate detritus (marine snow), and that their metabolism is based on the surrounding DOM rather than the particulate detritus itself. Therefore, sinking POM can accomplish a net uptake of DOC from the bottom layer, as illustrated in Fig. 10. For the mesopelagic zone in the open oceans, the opposite scenario has been proposed, whereby dissolution of POM supplies DOM to the deep water (Cho & Azam 1988, Bendtsen et al. 2002). A net uptake of labile DOM by sinking POM will obviously require an input of DOM to the bottom layer by advection or mixing from the surface layer, and this is probably only possible in a relatively shallow area. In the open ocean, mixing from the productive surface layer is insufficient to maintain a high concentration of labile DOM, and at these depths the transformation is probably from POM to DOM. In our study area, the main transport mechanism of DOM to the bottom layer is either accomplished by mixing from the productive surface layer or advection from the high productive frontal zone in the northern Kattegat (where the bottom water originates). Osburn & Stedmon (2011) found that the concentration of DOC ranged between 250 and 300 µM in the surface and about 100 µM in the bottom layer. Our estimate of a labile pool of about 50 µM therefore suggests that about half of the DOC is labile; but as described above, the turnover time is somewhat faster than the turnover time of the bottom waters (50 to 90 d) can account for (Hansen & Bendtsen 2013). However, our study did not include direct measurements of DOM, and this is needed in order to determine the relative significance of DOM and POM as sources of organic matter for pelagic respiration. Because the Baltic Sea–North Sea transition zone is a major transit area for DOM transport, the relative significance of DOM and POM as sources for bottom water respiration is also an important issue for the overall carbon budget in the area, and thereby for oxygen dynamics. Due to sedimentation rates of about 1 m $d^{-1}$ (Olesen & Lundsgaard 1995) and the relatively shallow water depth, the residence time of POM is much shorter than DOM, and therefore POM is a much more local source of organic matter — linking bottom water respiration to local production in the euphotic surface layer. In contrast, the DOM being remineralized could, in principle, originate from remote areas and cause a spatial decoupling of primary production and respiration in the Kattegat. This also implies that remineralization of organic matter can exceed primary production if the area functions as a sink of dissolved allochthonous organic matter being advected into the area from the North Sea and from the central Baltic.

## CONCLUSIONS

The first seasonal study of respiration rates in the bottom waters of the Baltic Sea–North Sea transition zone based on long time bottle incubations suggests that annual mineralization of organic matter is about 38 g C $m^{-2}$ $yr^{-1}$; therefore, this study confirms previous indirect estimates of carbon mineralization.

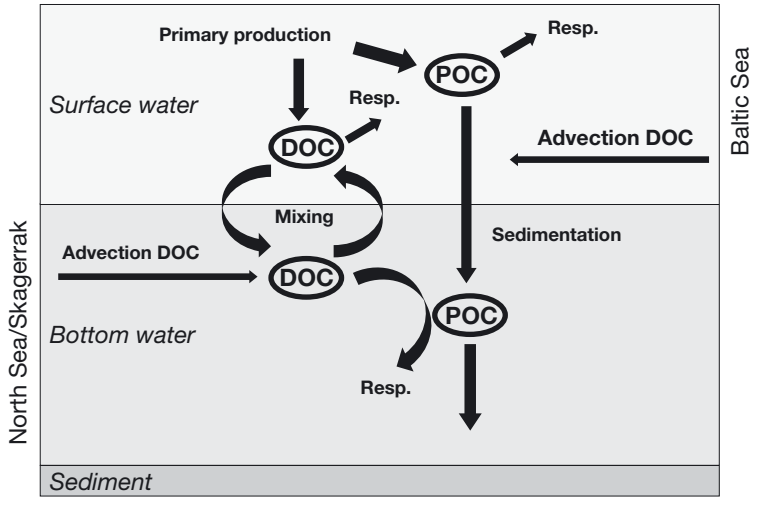


Fig. 10. Conceptual diagram of carbon cycling and transport in the Baltic Sea–North Sea transition zone. Particulate organic carbon (POC) and dissolved organic carbon (DOC) are produced by primary production in the surface water. DOC is also supplied to the surface water by advection from the Baltic Sea and advected to the bottom layer from the frontal area between the Skagerrak and Kattegat. POC enters the bottom water by sedimentation from the surface layer, whereas DOC is supplied to the bottom layer by mixing across the halocline and by advection from the frontal area. Bottom water respiration is maintained by microbial communities associated with sinking POC using labile DOC as a carbon source, and the POC is eventually deposited on the sea floor

There was a clear temperature effect in all of the incubations corresponding to a mean $Q_{10}$ value of 3. C/N ratios generally increased during the incubations, and the end value of ca. 15 was about twice as high as the Redfield ratio. In contrast to our expectations, there was no significant reduction in the concentration of POM during the incubation experiments, and therefore we conclude that labile DOM (<0.7 µM) is a main carbon source for pelagic respiration in the area.

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