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Analysis of remineralisation, lability, temperature sensitivity and structural composition of organic matter from the upper ocean

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ABSTRACT

Organic carbon (OC) synthesised by plankton is exported out of the surface layer as particulate (POC) and dissolved (DOC) organic carbon. This "biological pump" constitutes a major pathway in the global marine carbon cycle, each year exporting about 10 Pg C into the ocean interior, where it is subsequently remineralised via biological decomposition. Remineralised inorganic nutrients and carbon are, ultimately, again brought to the surface by advection and turbulent mixing which closes the OC-cycle in the upper ocean. Thus, remineralisation rates of OC are a critical component of the biological pump. These rates are regulated by the lability of the material and the environmental conditions in the ambient water. Temperature is particularly important in regulating the rate of microbial respiration and, thus, remineralisation rates. A significant temperature dependence of the microbial metabolic activity in the ocean interior is expected, as this is a feature observed elsewhere in the biosphere. Such temperature dependence of microbial remineralisation of POC and DOC will alter the amount of material available for transport by the biological pump to the deep ocean. Very few studies on the lability of OC and temperature sensitivity of microbial degradation processes in the mesopelagic zone (~100–1000 m) have, to date, been carried out. Here, we present a comprehensive new experimental data set from all major ocean basins and quantify remineralisation rates of OC and their temperature sensitivity in long-term incubations of water from the upper 350 m. Microbial respiration was measured by non-invasive oxygen optodes and oxygen consumption was used as a constraint for determining the remineralisation rates and temperature sensitivity by two complementary methods. First, we analysed the oxygen consumption from a multi-component OC-model where the concentration, remineralisation rates and temperature sensitivity of two bio-available (labile) pools of organic carbon were fitted to the data via a non-linear fitting procedure. Thereafter, a continuous OC-model was fitted to the data through an inverse method and information about lability, temperature sensitivity and structural composition of the OC-pool was analysed together with the results from the two-pool solutions. Median values of remineralisation rates from all experiments on material characterising sinking POC were found to be 0.6 and 0.05 $days^{-1}$ for the two decomposable pools corresponding to turnover times of 2 and 21 days, respectively. Accordingly, solutions from the continuous model resulted in median turnover times between 6 and 11 days. Similar analyses were carried out for the OC-pool characterising DOC. A significant bio-available OC-pool was found to be present in the surface layer with a median value from all experiments of 30 μM TOC. The median values of all remineralisation rates from the two bio-available OC-pools were found to be 0.2 and 0.02 $days^{-1}$, corresponding to turnover times of 5 and 56 days, respectively, in good agreement with previous studies. The corresponding temperature sensitivities, characterised by a Q_{10}-value, were found to be about 1.9 for the POC-fraction whereas the DOC fraction was characterised with values above 2.8 for the continuous OC-models. The analysis of the structural composition indicated that the TOC distribution in the surface layer was characterised by more heterogeneous material in terms of lability compared with the POC material sampled from the upper 350 m. Finally, we analyse the potential impact of the calculated temperature sensitivity on the general OC-cycling in the upper ocean and show that the implied reduction in OC-flux in a warmer ocean may have significant impact on nutrient cycling in general and also tends to reduce future ocean carbon uptake significantly.

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Introduction

Organic carbon (OC) in the ocean is mainly produced by photosynthesis in the euphotic zone and on a global scale this corresponds to an annual production of about 50 Pg C, a number comparable to terrestrial OC production (Field et al., 1998). About 80–90% of this newly produced OC is rapidly respired and thereby provides an important energy source for heterotrophic production in the surface layer. The remaining fraction is transported deeper into the ocean, either as sinking particulate organic carbon (POC) or as dissolved organic carbon (DOC) transported by turbulent mixing and advection. Together, the production and export of OC constitute the so-called organic "biological pump", an efficient pathway for transporting carbon from the surface layer deeper into the ocean. The strength of the biological pump plays a major role in the global carbon cycle and even small changes may have a significant impact on the air–sea exchange of CO_2 and thereby the atmospheric greenhouse gas concentration. The export of OC from the surface layer is therefore an important component in the global marine carbon cycle, each year transporting about 10 Pg of OC into the ocean interior (Martin et al., 1987; Laws et al., 2000; Dunne et al., 2007).

In contrast to surface processes, however, this deep branch of the biological pump is poorly understood. Relatively few studies have focused on processes regulating the cycling of carbon and nutrients in the ocean interior and, in particular, processes involved in the remineralisation of dissolved or sinking particulate organic matter. For example, Robinson and Williams (2005) found from a literature survey that respiration studies only accounted for about one per cent of the number of studies of primary production and respiration studies below the surface layer is even less well represented. Thus, heterotrophic processes taking place in the water column are heavily under-sampled in comparison with autotrophic processes despite the critical role of remineralisation processes for the cycling of carbon and nutrients (Boyd and Tull, 2007).

On a global scale, the ocean has until now absorbed about 30% of all combined historic anthropogenic carbon emissions (Sabine et al., 2004). However, feedbacks between a warmer climate and the carbon cycle will change the efficiency of the ocean carbon sink and, thereby, potentially influence the future atmospheric pCO_2 level. Previous quantifications of these feedbacks have shown that ocean carbon uptake during this century might be less than expected due to feedbacks between ocean stratification and biological production in the ocean surface layer (Sarmiento et al., 1998; Friedlingstein et al., 2006) or relationships between increased CO_2 levels and acidification (Hofmann and Schnellhuber, 2009; Schmittner et al., 2008). Because impacts from a warmer ocean on biological pump processes, including remineralisation, may reduce future carbon uptake significantly, such feedbacks have been identified as important uncertainties in predicting future atmospheric CO_2-levels (IPCC, 2007). Therefore, these processes are now considered as key research areas (Doherty et al., 2009) in terms of understanding and predicting the capacity of the future ocean to act as a natural carbon sink.

Despite the importance of remineralisation rates for the carbon turnover and flux into the interior of the ocean, the temperature sensitivity of the remineralisation processes in the mesopelagic zone is currently unknown. Parameterisations of these processes in global ocean models are generally either not explicitly included (Dunne et al., 2007) or based on relationships established from phytoplankton dynamics (e.g. Eppley, 1972).

Analyses of sediment trap data show a rapid decrease of the POC flux below the surface layer implying that a major fraction of sinking organic matter is remineralised in the upper 500 m (Martin et al., 1987). Recent analyses of sedimented material retrieved from free-drifting traps show large spatial variability (Buesseler et al., 2007) and also rapid remineralisation in the upper few hundred meters (Lampitt et al., 2008) indicating a highly dynamic biogeochemical regime in the upper mesopelagic zone. Variations in organic carbon export are regulated by a number of physical and biological factors, e.g. light, mixing and nutrient levels regulating algal production, but also algal community structure and phytoplankton cell sizes (Boyd et al., 2008), algal aggregation and ballasting effects from calcium carbonate shells can influence sinking velocities of exported material (Trull et al., 2008). In addition to vertical POC transport due to sinking, a significant amount (10–20%) of OC is exported from surface waters as DOC through ocean mixing (Hansell and Carlson, 1998). Degradation of OC by zooplankton and bacterial solubilisation ultimately transforms organic matter into inorganic substances (Boyd and Tull, 2007). Temperature affects heterotrophic metabolic activity and, therefore, changes in ambient temperature can influence the remineralisation rate of OC.

The mesopelagic pools of particulate and dissolved OC are interconnected through aggregation/disaggregation of POC to DOC (DOC is operationally defined as organic material passing through a filter pore size of 0.2–0.7 μm) and production of POC through biological uptake of DOC (Aristegui et al., 2002). The DOC concentration in the upper mesopelagic zone, in general, decreases down through the water column towards its biological refractory deep-sea background level at the bottom of the meso-pelagic zone. This decrease is, accordingly, related to DOC generated from sinking POC and advection/turbulent mixing of DOC balanced by sinks due to microbial consumption and adsorption onto POC. OC in the mesopelagic can be characterised by its bio-availability where (newly produced) labile OC is consumed on time-scales of hours to days whereas consumption of semi-labile OC occurs on time-scales of months to years (Archer et al., 1997).

Temperature sensitivity of the heterotrophic transformation of OC to dissolved inorganic carbon (DIC) can be characterised by a Q_{10} factor where Q_{10} describes the rate change for a 10 °C increase in temperature. The Q_{10} terminology has been widely used to describe the overall temperature response of more complex biological systems (Davidson and Janssens, 2006). In general, temperature sensitivity studies of marine microbial processes have thus far focused either on processes in the surface layer (e.g. White et al., 1991; Pomeroy and Wiebe, 2001; Lomas et al., 2002) or in sediments (e.g. Thamdrup and Fleischer, 1998) where the OC content is relatively enriched compared to the mesopelagic zone. The Q_{10} factor in these studies has been found to range between 1.7 and 3.9 in the surface layer and 1.8–3.2 in the sediments. Studies of the metabolic balance suggest that higher temperatures will increase community respiration more than the corresponding primary production (Rivkin and Legendre, 2001; López-Urrutia et al., 2006; Wohlers et al., 2009), resulting in an overall reduction in ocean carbon uptake. Analysis of bacterial activity from the deep sub-polar ocean (Middelboe and Lundsgaard, 2003) demonstrated a Q_{10} of 3.0 with implications for the deep ocean DOC distribution (Bendtsen et al., 2002). The sinking flux of POC in the mesopelagic zone is also influenced by zooplankton respiration (Steinberg et al., 2008) and associated temperature dependence (Ikeda, 1985) and, therefore, the temperature sensitivity of the microbial respiration might not be representative of the total pelagic response to temperature changes.

The implications of temperature sensitivity of the respiration of organic matter in the mesopelagic zone on the carbon cycle has a terrestrial parallel in the respiration of soil organic matter, where experimental studies have shown a significant temperature dependence (Melillo et al., 2002; Fang et al., 2005) and model studies

have identified soil respiration as a critical process for land carbon storage (Lenton and Huntingford, 2003). Theoretical considerations result in Q_{10} values of about 2 here (Davidson and Janssens, 2006), assuming typical temperature ranges and activation energies for soil organic matter. However, the composition of terrestrial soil and in particular other characteristics such as water availability also affect the temperature sensitivity of the respiration of soil carbon. Global climate change simulations with terrestrial biosphere components show that feedbacks from climate on soil respiration decrease the land carbon storage (Dufresne et al., 2002; Friedlingstein et al., 2006; Sitch et al., 2008). Thus, soil respiration acts as a positive feedback in the climate system. A temperature sensitivity of remineralisation of POC and DOC in the mesopelagic region of the ocean could, correspondingly, reduce the flux of carbon to the deep ocean and, thereby, also act as positive feedback in the climate system. Increasing remineralisation rates of organic matter in a warmer ocean will affect the cycling of DIC and nutrients in the upper ~500 m and this feedback has been found to have a significant impact on oceanic carbon uptake in global model studies (discussed in Section 'Environmental impact and climate change').

Here, we present a new data set of measurements of temperature sensitivity of remineralisation of POC and DOC from the upper mesopelagic zone and in the surface layer from all major ocean basins. Remineralisation rates were determined by inverse methods for quantifying the temperature dependent remineralisation of organic matter. We determine the remineralisation rates, temperature sensitivity and structural composition by analysing time series of oxygen consumption in the incubation experiments by two independent methods. First, we apply a multi-component OC-model and determine the corresponding OC-pools, remineralisation rates and Q_{10} values by a non-linear optimisation method and, then, we apply a continuous OC-model and determine the distribution by an inverse method. The two methods provide complementary information about the best fit OC-distributions. Finally, we discuss the results and assess the potential environmental impact from the estimated temperature sensitivity.

Materials and methods

To investigate the temperature sensitivity of microbial respiration in the upper mesopelagic zone and ocean surface layer, we made 38 long-term incubation experiments on water samples taken from between 10 and 350 m from all major ocean basins on the 2006–2007 circumnavigating Galathea3 expedition (Fig. 1, Tables 1 and 2). Five experiments were made at stations on the shelf (water depth between 200 and 500 m), two experiments at stations with intermediate water depths (500–1000 m) and the

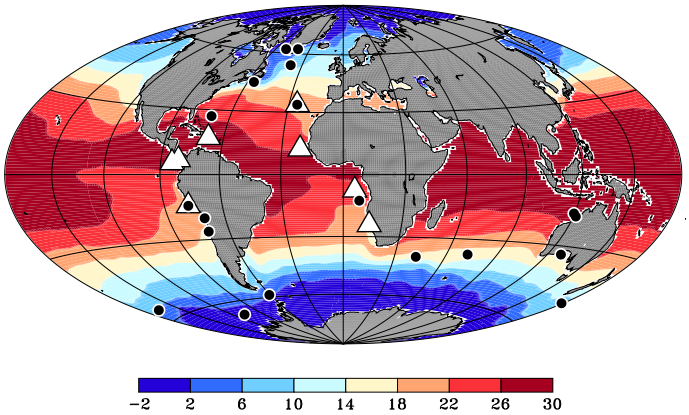

Fig. 1. Dark-incubation experiments on concentrated particulate material from large volume water samples (POC_{TF}) from the upper 350 m were taken at 8 stations in the Atlantic and Pacific (white triangles), and water samples (TOC_{MIX}) from 10 to 60 m depth were dark-incubated from 19 stations in all major ocean basins (black dots). Filled contours show the annual mean temperature (Levitus and Boyer, 1994) at a depth of 30 m.

Table 1
POC_{TF}-incubations on the Galathea3 expedition. The station ID refers to the station number on the expedition. *In situ* depth, total water depth, potential temperature (θ), salinity (S) and oxygen (O_2) concentration from the CTD-profile.

No.	Station name	Station ID	Latitude	Longitude	Date	Depth [m]	Water depth [m]	θ [°C]	S	O_2 [μmol kg^{-1}]
1	NA subtropical gyre	26VD.2006.5.1	33° 45.74′N	25° 25.49′W	22/09/06	100	5217	18.760	36.592	221.1
2	NA subtropical gyre	26VD.2006.5.1	33° 45.74′N	25° 25.49′W	22/09/06	200	5217	17.550	36.509	204.1
3	N. equatorial Current	26VD.2006.5.11	12° 12.34′N	21° 1.55′W	26/09/06	150	4841	13.482	35.365	74.7
4	N. equatorial Current	26VD.2006.5.11	12° 12.34′N	21° 1.55′W	26/09/06	250	4841	12.234	35.291	59.8
5	N. equatorial Current	26VD.2006.5.11	12° 12.34′N	21° 1.55′W	26/09/06	350	4841	11.286	35.310	41.0
6	Angola Current	26VD.2006.6.4	7° 25.72′S	5° 32.75′E	9/10/06	100	4435	15.211	35.555	48.8
7	Angola Current	26VD.2006.6.4	7° 25.72′S	5° 32.75′E	9/10/06	200	4435	13.279	35.315	45.9
8	Benguela upwelling	26VD.2006.6.8	24° 9.05′S	13° 17.96′E	12/10/06	100	434	12.214	35.087	141.6
9	Benguela upwelling	26VD.2006.6.8	24° 9.05′S	13° 17.96′E	12/10/06	200	434	11.196	35.005	61.4
10	Benguela upwelling	26VD.2006.6.8	24° 9.05′S	13° 17.96′E	12/10/06	300	434	10.330	34.919	40.0
11	Peru/Chile Current	26VD.2007.14.85	14° 9.82′S	77° 25.72′W	24/02/07	111	5153	13.712	34.932	4.1
12	Peru/Chile Current	26VD.2007.14.85	14° 9.82′S	77° 25.72′W	24/02/07	200	5153	12.550	34.896	3.3
13	Eastern eq. Pacific A	26VD.2007.15.3	5° 17.58′N	84° 6.99′W	9/03/07	50	3076	18.451	34.734	83.6
14	Eastern eq. Pacific A	26VD.2007.15.3	5° 17.58′N	84° 6.99′W	9/03/07	100	3076	14.341	34.934	30.9
15	Eastern eq. Pacific A	26VD.2007.15.3	5° 17.58′N	84° 6.99′W	9/03/07	200	3076	12.824	34.865	14.5
16	Eastern eq. Pacific B	26VD.2007.15.8	6° 39.65′N	80° 59.06′W	10/03/07	50	2970	17.362	34.826	47.4
17	Eastern eq. Pacific B	26VD.2007.15.8	6° 39.65′N	80° 59.06′W	10/03/07	100	2970	14.719	34.952	29.5
18	Caribbean Sea	26VD.2007.15.21	17° 1.79′N	67° 47.65′W	14/03/07	100	5075	26.122	36.593	176.2
19	Caribbean Sea	26VD.2007.15.21	17° 1.79′N	67° 47.65′W	14/03/07	200	5075	19.983	36.681	146.2

Table 2
TOC_{MIX}-incubations on the Galathea3 expedition. The station ID refers to the station number on the expedition. *In situ* depth, total water depth, potential temperature (θ), salinity (S) and oxygen (O_2) from the CTD-profile.

No.	Station name	Station ID	Latitude	Longitude	Date	Depth [m]	Water depth [m]	θ [°C]	S	O_2 [μmol kg^{-1}]
1	NA subpolar gyre A	26VD.2006.2.13	62° 30.59′N	40° 31.57′W	21/08/06	30	349	3.212	34.208	306.5
2	NA subpolar gyre B	26VD.2006.4.2	62° 6.58′N	50° 58.29′W	12/09/06	30	1360	6.298	34.214	295.2
3	NA subpolar gyre C	26VD.2006.4.4	53° 46.92′N	38° 23.1′W	14/09/06	30	2796	12.555	34.571	249.0
4	NA	26VD.2007.18.4	44° 20.05′N	56° 10.47′W	16/04/07	30	2424	3.473	33.283	328.7
5	NA subtropical gyre	26VD.2006.5.1	33° 45.7′N	25° 25.49′W	22/09/06	30	5217	24.400	37.032	196.0
6	Carribean Sea	26VD.2007.17.94	27° 1.85′N	70° 5.41′W	7/04/07	30	5489	23.148	36.710	197.5
7	Angola Current	26VD.2006.6.6	12° 30.7′S	7° 48.42′E	10/10/06	30	3595	20.173	36.075	192.9
8	Leeuwin Current A	26VD.2006.7.53	17° 28.37′S	121° 25.84′E	10/11/06	30	195	26.217	34.704	193.5
9	Leeuwin Current B	26VD.2006.7.91	16° 15.31′S	119° 38.15′E	15/11/06	30	1142	28.193	34.639	192.5
10	Southern Ocean A	26VD.2006.7.8	39° 33.89′S	42° 44.63′E	23/10/06	30	2267	12.696	34.838	268.9
11	Southern Ocean B	26VD.2006.7.15	37° 15.62′S	72° 30.38′E	27/10/06	30	4171	13.607	35.167	251.5
12	Southern Ocean C	26VD.2006.8.16	33° 29.82′S	128° 23.58′E	29/11/06	30	961	17.959	35.770	226.3
13	Southern Ocean D	26VD.2007.12.1	49° 41.72′S	178° 52.62′E	12/01/07	30	626	8.484	34.385	279.0
14	Southern Ocean E	26VD.2007.12.8	55° 35.22′S	167° 32.15′W	14/01/07	30	4818	7.623	35.020	282.7
15	Southern Ocean F	26VD.2007.12.15	66° 35.37′S	108° 55.81′W	20/01/07	30	4575	0.337	33.920	342.4
16	Southern Ocean G	26VD.2007.12.47	58° 48.09′S	60° 53.84′W	30/01/07	60	3213	0.085	33.910	327.8
17	Humbolt upwelling A	26VD.2007.13.2	26° 18.27′S	71° 15.77′W	12/02/07	30	4740	16.889	34.444	245.0
18	Humbolt upwelling B	26VD.2007.14.8	20° 3.34′S	70° 45.27′W	17/02/07	10	1477	18.859	34.744	243.8
19	Peru/Chile Current	26VD.2007.14.85	14° 9.82′S	77° 25.72′W	24/02/07	30	5153	17.315	35.123	1.1

remaining (31) incubation experiments made in the open ocean (depths of 1000–5200 m). Samples were taken at locations representing different productivity regimes and usually during the most productive season. The study included upwelling areas in the Benguela and the Peru/Chile currents, sub-polar and oligotrophic Atlantic Ocean waters, the Southern Ocean and waters in the oxygen minimum zones of the eastern equatorial Atlantic and Pacific.

Sample collection

Water was collected with 30-l rosette (SBE-32) mounted Niskin bottles. Two sets of incubation experiments were carried out on the total OC pool; (1) samples of OC concentrated by tangential filtration from large volume samples taken in the upper 350 m, referred to as POC_{TF}-incubations, and (2) samples of total OC from raw water samples in the upper mixed layer (10–60 m), referred to as TOC_{MIX}-incubations. Incubation periods reflected the assumed timescale for sinking POC in the upper 3–500 m (2–4 weeks for the POC_{TF}-incubations) and the seasonal timescale for advection of DOC below the mixed layer (~3 months for the TOC_{MIX}-incubations), respectively.

Large volume samples (between 10 and 150 l) for POC_{TF}-incubations were taken from various depths in the upper 50–350 m in waters ranging in temperature from 10.3 to 26.1 °C (Table 1). For filtration of larger volumes, separate casts were made for each depth level and water from several Niskin bottles was stored in darkness in 20 l bottles on deck during the filtration period. POC_{TF} was concentrated from these by 0.2 μm tangential filtration of large volumes (10–150 l) with a 0.2 μm tangential flow ultrafiltration system (Millipore Pellicon II) and carried out within 18 h after the first cast was made (concentration factors for each experiment are listed in Table S1). The filter was regularly cleaned by filtering 20 l of demineralised water and subsequently filtering from the deepest water samples with the lowest POC-concentration towards the shallowest samples. Before each filtration, the filter was flushed by several liters of the sample which was not used. POC_{TF} incubations were made in 25 ml and 50 ml bottles and the bottles were kept under water in the incubators. Incubations (in triplicate) for determining the temperature sensitivity of remineralisation of POC_{TF} (2–4 weeks) were made at 8 stations and a total of 19 depths.

Samples in the surface layer for TOC_{MIX} incubations were taken at 19 stations at depths of 10–60 m in triplicate (Table 2). Large zooplankton were removed by 50 μm filtration. Thereafter, the samples were incubated in 250 ml glass bottles with ground glass stoppers, which were kept submerged during the incubation. Bottles were stored in darkness in 125 l Refritherm 200 temperature controlled (within 0.1 °C) incubators. Before TOC_{MIX}-incubations, the pre-filtered water was stored in 15 l bottles in darkness at 20–30 °C for about 24 h (cf. Table S2) and rotated vertically three times during that period to avoid bubble formation when incubated warmer than *in situ* temperature.

Oxygen measurements and long-term incubations

Long-term incubations were made onboard the ship and the incubators were held at 5 different temperatures at 5 °C intervals from 5 to 25 °C (4.7 ± 0.3 °C, 9.9 ± 1.1 °C, 14.9 ± 0.1 °C, 20.7 ± 0.1 °C and 25.3 ± 0.1 °C; mean and std. dev. for all experiments carried out during the expedition). Samples were incubated at three temperatures (T_{-5}, T_0, T_{+5}) with T_0 being the incubator temperature closest to *in situ* temperature (θ) unless θ was close to the coldest (warmest) incubator temperature, in which case, the incubations were carried out at the lowest (highest) of the three temperatures. Oxygen concentration was measured regularly by optode sensors (see below) and all experiments were carried out in triplicate. Oxygen was measured in glass bottles with a Presens, Fibox 3 temperature compensated optical oxygen meter where a planar oxygen sensor was glued inside the glass vials with non-reactive acetic acid RTV silicone glue (Silikonkautchuk-Verbindung Tube, 90 ml, R&S Components), and the oxygen was measured by a 2 mm polymer optical fibre. Long term control measurements conducted over a 3 month period with the same bottles and procedure were made with de-mineralised water to investigate whether there was any consumption of oxygen due to the glue or other factors around the handling of the samples. No significant change in oxygen concentration was recorded (the mean change in oxygen concentration in the triplicate samples after 69 days was found to be 0.2 μmol kg^{-1} O_2 and the maximum change among individual bottles was less than 1.2 μmol kg^{-1} O_2 over the whole period). This confirmed that the glue was non-reactive. Measurements were made in a temperature regulated laboratory container (with air temperature of 20 °C) and, to control the temperature during the non-invasive optical measurements, samples were placed directly from the incubators into a temperature regulated water bath (~40 l) at the incubation temperature (within

0.9 °C of the temperature in the incubators). During measurements, the samples were held at constant temperatures (within ±0.09 °C, s.d.) by circulating water through the water bath (Neslab RTE-7).

Measurements of inorganic nutrients, bacterial abundance and POC

The water samples for nutrients were immediately frozen. Subsequently, the water was analysed for nitrate, nitrite, ammonium, and phosphate by wet-chemistry methods according to Grasshoff et al. (1983). Measurements, instruments and detection limits of inorganic nutrients are further described in Richardson et al. (2014). Samples (5 ml) were preserved with filter-sterilised glutar-aldehyde and bacterial abundance determined by flow cytometry (FACS Calibur, Becton Dickinson; Kragh et al., 2008). POC concentration was determined in the initial water used for the POC_{TF}-incubations on material collected on 0.7 μm GF/F filters following passage of a volume of the 0.2 μm pre-concentrated water. Inorganic nutrients were measured on water taken directly from the Niskin bottles and also from the initial water of the POC_{TF}-incubations. Nutrient determinations were also made on the incubation water of both POC_{TF} and TOC_{MIX} at the end of the experiments.

Model calculations

Lability, i.e. remineralisation rate, and the temperature sensitivity during remineralisation of organic matter were first analysed by a multi-component organic carbon model where a temperature sensitivity was imposed *a priori* and the corresponding Q_{10} factor was determined from an optimal non-linear fitting procedure. Thereafter, the incubation experiments were analysed by a general model where the heterogeneity of the organic material was described in the model by a continuous distribution function of organic carbon as a function of decay rate. The structure of the distribution function characterising the lability was determined through an inverse calculation and temperature sensitivity was here determined without *a priori* assumptions concerning the specific functional temperature dependence. The two methods are summarised below and described in detail in the appendices.

Two-pool remineralisation model of TOC

The total amount of bio-available organic carbon in seawater is here defined as TOC and, in general, can be described as the sum of all labile TOC-fractions. A corresponding general multi-component model for the remineralisation of TOC can then be formulated (Appendix A). Here we apply a reduced model with only two bio-available OC-pools. This two-component model, with both a labile and a semi-labile pool of OC, was fitted to the oxygen measurements (a two-component model was found to significantly better describe the data than a single OC-pool model). Such multi-component OC-models have previously been applied in the analysis of *in vitro* incubation experiments of pelagic samples (e.g. Hopkinson et al., 2002). Remineralisation rates were determined from oxygen measurements where it was assumed that oxygen consumption reflected the bio-available fraction of organic matter which could be remineralised on time scales from days to months. Due to the complex mixture of organic substances in seawater, the OC pool was here treated as a composite of homogeneous OC fractions, each pool characterised by its initial concentration and remineralisation rate. In principle, the number of bio-available fractions should reflect the nature of each component but, here, we simplified the general system and only considered the case with two bio-available OC fractions.

Assuming that the TOC can be described by two pools of organic matter, the time-dependent (t) model solution for oxygen becomes:

$$O_2(t) = O_2(t_0) - \eta(TOC_1(t_0)[1 - \exp(-\alpha_1 t)] + TOC_2(t_0)[1 - \exp(-\alpha_2 t)]) \quad (1)$$

where α_i is the remineralisation rate for each pool and the associated remineralisation e-folding time is defined as $\tau_i = 1/\alpha_i$ ($i = 1, 2$), and η is the constant remineralisation ratio between oxygen and the TOC pools. The initial pools (at time = t_0) of bio-available TOC ($TOC_1(t_0)$ and $TOC_2(t_0)$) were assumed to be the same at all temperatures. A temperature dependent model was explicitly included in the analysis where the remineralisation rate was described as:

$$\alpha_i = \alpha_0(i) Q_{10}(i)^{\frac{T-T_0}{10}}, \quad i = 1, 2 \quad (2)$$

and T and T_0 (°C) are the incubation and reference temperatures, respectively. This resulted in six free parameters to be determined for each experiment ($TOC_1(t_0)$, $TOC_2(t_0)$, $\alpha_0(1)$, $\alpha_0(2)$, $Q_{10}(1)$ and $Q_{10}(2)$). The best fit solution was determined by a non-linear least-square method (Appendix B).

A model with a continuous OC-distribution function

The bio-available pool of organic carbon can, in general, be described by a continuous OC-distribution characterised by its lability, i.e. decay rates (α). Contrary to the discrete multi-component OC-model outlined above, such models do not require assumptions about a specific number of bio-available pools. Thus, they may be more robust estimators of processes relating to organic matter. In particular, fitting of multi-component models has been shown to be sensitive to noise in the measurements and defining the number of active pools is therefore difficult (Yeramian and Claveria, 1987; Forney and Rothman, 2012a). We apply the methods and programs described in Forney and Rothman (2012a) to determine the concentration density function $\rho(\ln\alpha)$ where $\rho(\ln\alpha)$ represents the distribution of bio-available organic carbon as a function of the natural logarithm of the decay rates (Appendix C). We refer to this solution as the "OC-distribution" below.

Solutions of the continuous OC-model

The numerical solution of the continuous OC-model (cf. Appendix C) is in general also sensitive to noise in the data but numerical methods have been developed for making robust estimates with low sensitivities to noise. We follow the method described by Forney and Rothman (2012a) and apply the regularisation method where both the residual error between the model solution and observations (i.e. defined by the summed squared error of the OC-solution and observations at the different measurement times during the experiment) and the roughness (or complexity) of the solution is minimised. The roughness is defined by the norm of the first derivative of the model solution, i.e. the constraint seeks an acceptably smooth distribution of the concentration density function $\rho(\ln\alpha)$.

In the study of terrestrial litter decomposition by Forney and Rothman (2012a), it is suggested that best fit solutions based on the regularisation method should be considered as a robust description of $\rho(\ln\alpha)$ and, therefore, superior compared to other fitting methods. However, those workers also showed that a simple log-normal distribution in many cases fits their data as well as the regularisation method. There are good reasons for choosing this particular functional relationship of the concentration density function and these are discussed further below. Therefore, we also investigate how solutions to the inverse Laplace transform

obtained by the regularisation method compare with a fit to a simple log-normal distribution of the OC defined by:

$$\rho(\ln\alpha) = \frac{1}{\sqrt{2\pi}\sigma}\exp(-(\ln\alpha-\mu)^2/2\sigma^2) \quad (3)$$

In this case, the solution is simply described by two parameters; the median value (μ) and the standard deviation (σ) of the log rates. The solutions obtained by the two methods are analysed and the temperature sensitivity and the turnover time are calculated from the log-normal distributions.

Estimation of organic carbon fraction from oxygen measurements

The application of the inverse method above requires that the decay of organic matter is known during the experiment. However, in the incubation experiments only oxygen consumption is measured. Therefore, changes in oxygen concentration have to be converted to a corresponding change in the total amount of organic carbon. We assume a similar "Redfield"-ratio between oxygen and organic carbon consumption as in the multi-pool solutions above (i.e. $\eta(O_2{:}OC) = 138/106$) and, then, that a lower boundary of the bio-available OC is defined from the maximum oxygen consumption among the three temperatures in each incubation exper-

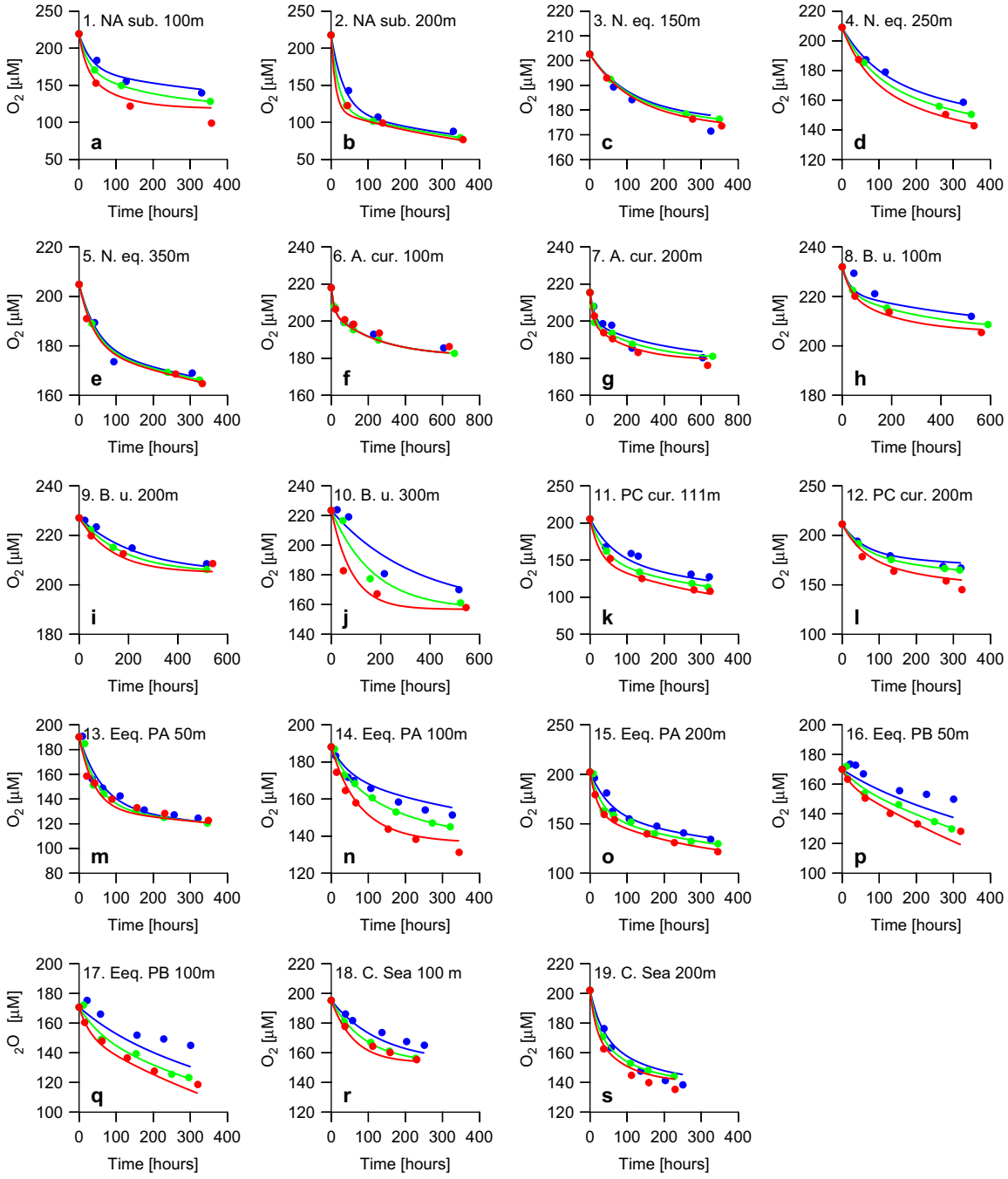

Fig. 2. Oxygen consumption from the POC_{TF}-incubations. Measurements of oxygen (the average values of triplicate measurements are shown with bullets and the associated standard errors are shown with vertical bars) at T_{-5}, T_0 and T_{+5} are shown as blue, green and red dots, respectively. The corresponding best fit solutions for the two-pool OC-model are shown with blue, green and red lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

iment. This assumption implies, however, that all bio-available organic carbon has been remineralised. This is, in general, not the case and, therefore, we make an estimate of the total bio-available OC pool by first comparing the estimate from the oxygen consumption with the bio-available OC-pools obtained from the two-pool model solutions above. Based on this comparison, we assume a representative upper boundary for the bio-available OC-pool. This assumption is discussed further below.

Calculation of Q_{10} and bulk turnover time scales

The temperature sensitivity and the turnover scale can be calculated from the mean and standard deviation of the log normal distribution. If the distribution responds equally to temperature changes across all decay rates, the resulting distribution after a temperature increase would simply be reflected in a corresponding change in the median value (μ) of the log-normally distributed decay rates (see e.g. Forney and Rothman, 2012b). We assume that the remineralisation rate can be described by the empirically derived Arrhenius (1889) formula:

$$\alpha = \alpha_0 \exp\left(\frac{-E_a}{RT}\right) \quad (4)$$

The remineralisation rate is characterised by a constant rate (α_0) and the temperature dependence is then described through an activation energy (E_a) divided by the absolute temperature (T) and the gas constant ($R = 8.314\ \mathrm{J\ K^{-1}\ mol^{-1}}$). This relationship has been shown to describe temperature sensitivity during remineralisation of organic matter in several studies (Davidson and Janssens, 2006). The sensitivity of the remineralisation rate to a given temperature change (ΔT) can, then, be calculated as:

$$Q_{\Delta T} = \exp\left(\frac{E_a \Delta T}{RT(T+\Delta T)}\right) \quad (5)$$

This temperature sensitivity is normally described as a Q_{10}-factor, i.e. Q_{10} describes the increase of the remineralisation rate for a $\Delta T = 10$ °C temperature change. The temperature sensitivity in the incubation experiments is determined around the mean value T_0. From Eq. (5), it can be seen that the Q_{10} value decreases when temperature increases but this inherent temperature effect can be shown to be relatively small for typical ocean temperatures and is not considered further in this study.

The Arrhenius formula is applied for calculating the temperature sensitivity by taking the logarithm of Eq. (4): $\ln(\alpha) = \ln(\alpha_0) - -E_a\ R^{-1}\ T^{-1}$, and then determining the ratio ($-E_a\ R^{-1}$) from the slope of the line of $\ln(\alpha)$ plotted against the inverse absolute temperature. The value of $\ln(\alpha)$ is known from the triplicate experiments at the three different temperatures and we then apply a linear regression through the three values for determining the activation energy (E_a). The assumption that the log-normal distribution is equally affected across all decay rates is considered in the discussion section.

The turnover time (τ) of the distribution of the remineralisation rates (α) is calculated from the log-normal distribution (Forney and Rothman, 2012b);

$$\tau = \exp(-\mu)\exp\left(\frac{\sigma^2}{2}\right) \quad (6)$$

This relationship implies that a broad OC distribution, characterised by a large standard deviation, increases the turnover time significantly.

Results

Two pool OC-model solution

A significant temperature dependent remineralisation rate ($Q_{10} > 1.5$) was found in 15 out of 19 POC_{TF} incubations (Fig. 2) and the OC-model generally resulted in a low misfit between observations and fitted model solutions. There was no significant difference between the Q_{10}-value of the two POC_{TF}-pools with median values of 1.6 and 1.8 of the labile and semi-labile pool, respectively (Table 3). There was a significant difference between the remineralisation rates of the two pools which in general differed by an order of magnitude (Fig. 4a). On average, 41% of the OC was in the most labile OC-pool with a median remineralisation rate of 0.6 $\mathrm{days^{-1}}$ (cf. median values in Table 3).

A significant temperature dependent remineralisation rate was also found in all 19 TOC_{MIX} incubations and the OC-model resulted in a low misfit between fitted model solutions and observations (Fig. 3). On average, 25% of the OC was in the most labile OC-pool with a median remineralisation rate of 0.2 $\mathrm{day^{-1}}$. The semi-labile pool had a median initial pool of 22.5 $\mu\mathrm{mol\ kg^{-1}}$ and a median remineralisation rate of 0.02 $\mathrm{day^{-1}}$ (Table 4).

There was a significant difference between the temperature dependencies of the two TOC_{MIX}-pools with median Q_{10}-values of 2.0 and 5.3 for the labile and semi-labile pools, respectively. The best fit solution also showed a significant difference between the remineralisation rates of the two TOC_{MIX} pools which, in general, differed by an order of magnitude (Fig. 4b). The Q_{10} values were weakly constrained in some incubation experiments because of the proportionality of α to both Q_{10} and α_0 and the relatively small remineralisation rates (i.e. long turnover time scale) compared to the incubation period (cf. Eq. (2)). In such cases, a relatively large uncertainty was associated with the best fit solution. This was taken into account when representative values of α and Q_{10} were calculated (cf. Table 3), and only best fit values below the limiting conditions of Q_{10} (<10) and α (<1/360 days) were considered.

Table 3
Average values (±s.e.m.) and medians (±standard error of the sample median) of the best fit solutions of the two-pool OC-model. Values are shown for the bio-available initial values, where the TOC_{MIX} and POC_{TF}-values are given as *in situ* concentrations (considering the concentration factor for POC_{TF}), the remineralisation rate (α), the Q_{10} value for each OC-pool and n is the number of constrained best fit parameters.

OC-model	Unit	2-Pool POC_{TF}		n	2-Pool TOC_{MIX}		n
		Average	Median		Average	Median	
$TOC[t_0]$ (1)	[$\mu\mathrm{mol\ kg^{-1}}$]	1.4 ± 0.4	1.0 ± 0.5	16	9.0 ± 1.4	7.7 ± 1.8	17
$\alpha(1)$	[$\mathrm{days^{-1}}$]	0.72 ± 0.01	0.56 ± 0.01	16	0.32 ± 0.1	0.20 ± 0.1	17
$\tau(1)$	[days]	1.4	1.8	16	3.1	5.0	17
$Q_{10}(1)$	–	2.0 ± 0.3	1.6 ± 0.4	16	2.8 ± 0.6	2.0 ± 0.6	17
$TOC[t_0](2)$	[$\mu\mathrm{mol\ kg^{-1}}$]	3.2 ± 1.1	1.4 ± 1.4	16	21.7 ± 0.8	22.5 ± 1.0	12
$\alpha(2)$	[$\mathrm{days^{-1}}$]	0.065 ± 0.002	0.048 ± 0.003	16	0.019 ± 0.004	0.018 ± 0.004	12
$\tau(2)$	[days]	15.4	20.8	16	52.6	55.6	12
$Q_{10}(2)$	–	2.3 ± 0.4	1.8 ± 0.5	16	4.8 ± 0.6	5.3 ± 0.8	8

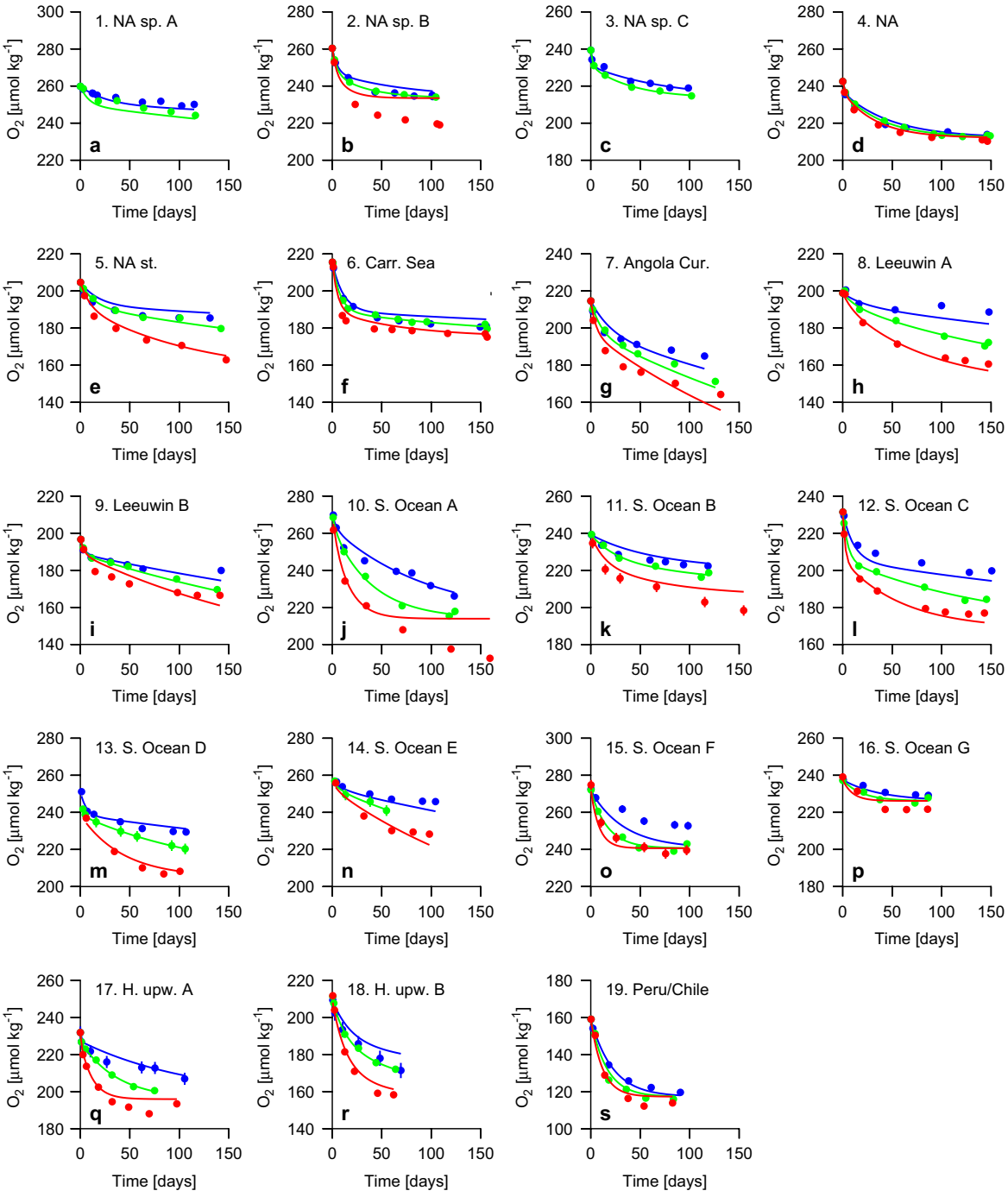

Fig. 3. Oxygen consumption from the TOC_{MIX}-incubations. Measurements of oxygen (the average values of triplicate measurements are shown with bullets and the associated standard errors are shown with vertical bars) at T_{-5}, T_0 and T_{+5} are shown as blue, green and red dots, respectively. The corresponding best fit solutions for the two-pool OC-model are shown with blue, green and red lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Bio-available pools for continuous OC-model calculations

For use in the OC-model calculations, a lower boundary and an estimate of the total amount of bio-available OC in the samples were derived. The lower boundary was determined from the actual oxygen consumption during the experiments and represents the bio-available OC which was actually remineralised during the incubation period. The estimate of the upper boundary is described below and represents the total bio-available OC-pool, i.e. including material remineralised on longer time-scales than the incubation period. This procedure is necessary because there are no methods available at present to identify the bio-available OC-fraction of marine OC-samples.

The maximum amount of oxygen consumed (ΔO_2) during the experiments was converted to an amount of bio-available OC by the Redfield ratio (η), i.e. $OC = \Delta O_2/\eta$. In general, the maximum oxygen consumption was found in the warmest incubations. This value gave a lower boundary on the amount of bio-available OC in the bottles and this was compared to the sum ($\sum$TOC, i.e. corresponding to all the concentrated OC in the POC_{TF}-incubations) of

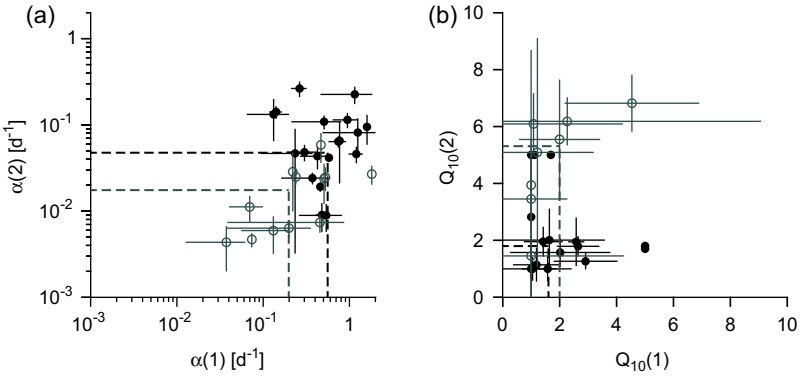

Fig. 4. (a) Best fit solutions (±s.e.m.) of remineralisation rates of labile $\alpha(1)$ and semi-labile $\alpha(2)$ pools for POC_{TF} (black, bullets) and TOC_{MIX} (grey, circles). (b) Corresponding pairs of best fit Q_{10}-values for the two pools are shown for POC_{TF} and TOC_{MIX} for experiments where Q_{10} for both pools are constrained in the fitting procedure. Median values are indicated by dashed lines.

Table 4
Average (±s.e.m.) and median values (±standard error of the sample median) of activation energy (E_a), Q_{10} and turnover time (τ) for the best-fit log-normal distribution in the two cases with a minimum-OC and an intermediate OC-pool, respectively.

OC-model	Variable	Unit	Log-normal POC_{TF}		Log-normal TOC_{MIX}	
			Average	Median	Average	Median
Minimum OC-model	E_a	[kJ mol^{-1}]	54,700 ± 7800	53,500 ± 10000	122,000 ± 15000	112,000 ± 19,000
	Q_{10}	–	2.4 ± 0.3	2.1 ± 0.3	8.8 ± 2.4	5.1 ± 3.0
	τ	[days]	9.6 ± 2.0	6.1 ± 2.5	480 ± 170	130 ± 200
Intermediate OC-model	E_a	[kJ mol^{-1}]	51,100 ± 8000	46,700 ± 10000	136,000 ± 16000	133,000 ± 20,000
	Q_{10}	–	2.3 ± 0.2	1.9 ± 0.3	11.4 ± 3.5	6.8 ± 4.4
	τ	[days]	20.7 ± 5.2	10.8 ± 6.5	4900 ± 1800	555 ± 2300

the OC-pools determined from the corresponding two-pool OC-model of the POC_{TF} or TOC_{MIX} incubation (Fig. 5). The median values for the POC_{TF}-incubations were found to be 43.7 ± 7.1 μM and 51.3 ± 10.8 μM for $\Delta O_2/\eta$ and ΣTOC, respectively, and the median values for the TOC_{MIX} incubations were correspondingly 29.4 ± 2.5 μM and 32.3 ± 5.3 μM.

In general, there was a good agreement between the amount of oxygen consumed during the experiments and the total OC-pools determined by the two-pool OC model. Those experiments where the total OC-pools were significantly larger than what could be explained by the oxygen consumption were either experiments where there was still a significant decrease in the oxygen concentration or experiments where the total OC-pools were poorly constrained by the data, i.e. solutions with relatively low remineralisation rates. A few experiments provided a lower estimate of the total OC-pools than the actual amount of oxygen consumed and this indicated that the solution determined by the incubation at the middle temperature (T_0) and the subsequent fit of the Q_{10} value underestimated the total bio-available OC-pools. However, there was in general a good agreement between oxygen consumption and the amount of bio-available OC determined from the two-pool model. Only 9 out of 38 experiments had total OC-pools larger than could be explained by 130% of the scaled oxygen consumption (Fig. 5, dashed line). Thus, the major part of the bio-available OC could be estimated as being within the range of 100–130% of the oxygen consumption. The role of the size of the estimated bio-available OC pool for the model solutions is considered below by comparing the best fit log-normal distributions of the "minimum" OC-pool case based on the actual oxygen consumption during the experiments and a solution where the total OC-pool was assumed to be determined as being equal to 130% of the oxygen consumption, i.e. implying a residual bio-available OC-fraction which was not remineralised during the limited incubation period. These two cases are referred to below as the "minimum-OC" (min-OC) and the "intermediate-OC" (intOC) case, respectively.

Continuous log-normal distributions and regularised solutions

The log-normal distribution and the regularised solution were fitted to the estimated remaining fraction of the bio-available OC-pool. In general, both provided a solution in good agreement with the estimated OC-pool from the incubation experiments (an example is shown in Fig. 6a). The regularised solution, in general, resulted in a non-symmetric OC-distribution and although the log-normal distribution per definition is symmetric, it closely followed the regularised solution in many cases (cf. Fig. 6b). Both solutions characterised the OC-pool as a continuous distribution dependent on the natural logarithm of the remineralisation rates. A general agreement was seen when the continuous distribution was compared to the discrete two-pool solutions obtained from the multi-pool method above. For example, the two remineralisation rates obtained by the two-pool method from the 20 °C experiment in the equatorial Pacific spanned an interval around the maximum of both the regularised and the log-normal distribution (Fig. 6b, vertical lines). Results from the more general continuous distributions are discussed below.

Residuals of log-normal and regularised distributions

In the study of Forney and Rothman (2012a), the solutions determined by the regularisation method were compared with a fitting method where the data were described by a log-normal distribution. For terrestrial OC, they found a general accordance and also that the log-normal distribution in many cases provided a better fit than the regularised solution. However, they recommended that before a log-normal distribution is applied, the solutions should be compared with the more general, and therefore in

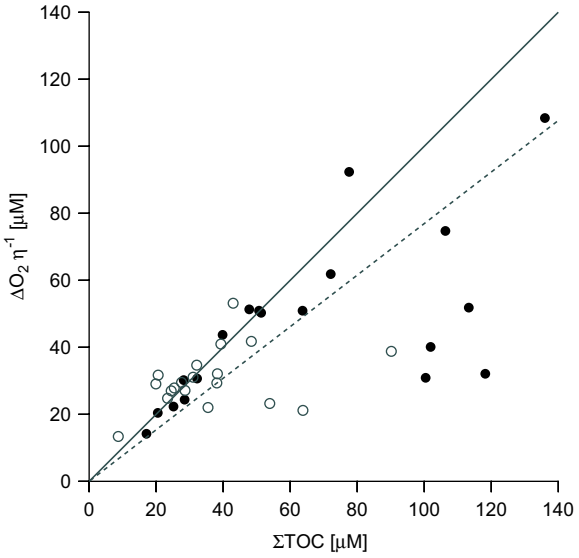

Fig. 5. Oxygen consumption in the POC_{TF} (bullets) and TOC_{MIX} (circles) incubations, scaled with the Redfield ratio η, is shown versus the corresponding best fit total organic carbon from the two-pool solutions (ΣTOC). Lines are indicated showing the ratios 1:1 (solid) and 1:1.3 (dashed), respectively.

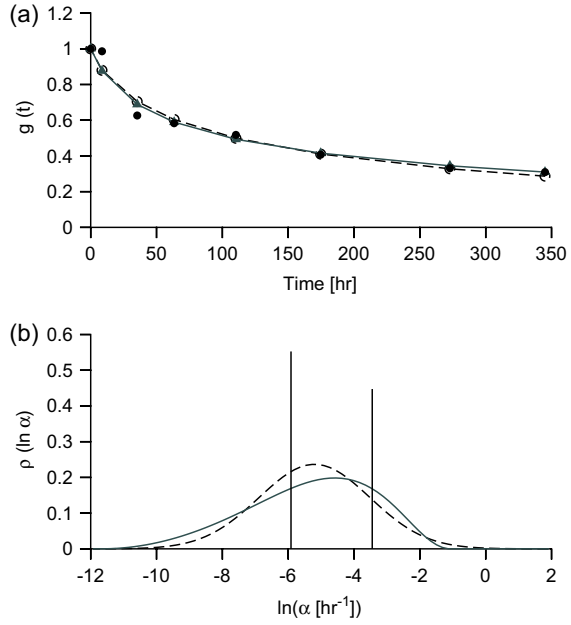

Fig. 6. Best fit solutions for POC_{TF}-incubations from the Eastern equatorial Pacific at 20 °C (exp. no. 44). (a) Measurements of oxygen (bullets), normalised by 130% of the total oxygen consumption during the experiment (i.e. intOC-case), are shown with best fit solutions of the regularised solution (grey solid line, circles), the best fit lognormal distribution (dashed black line, triangles). The normalised solutions are shown by $g(t)$, i.e. the remaining fraction of bio-available OC at the time t. The corresponding distributions are shown in (b) together with the normalised discrete two-pool solution (vertical solid lines).

principle more robust, regularised method. Following this recommendation, we first made a comparison between the two methods. Thereafter, we considered the role of increasing the amount of bio-available OC for the solution based on the log-normal distribution.

Residuals from the regularised solutions were in general comparable to the log-normal solutions for the POC_{TF}-incubations and, in several experiments, the log-normal distribution showed a significantly smaller residual than the regularised solution (Fig. 7, bullets). This can be explained by the general goodness of fit of the log-normal distribution where the two free parameters (μ and σ) are sufficient to describe the data, whereas the criteria of a minimum in the complexity of the regularised solution (i.e. a minimum of the first derivative of the distribution with respect to $\ln\alpha$) led to higher residuals. For some experiments, the residual of the log-normal distribution was larger than the regularised solution but this was only in cases with a relatively low residual (i.e. χ^2(log-normal) < 0.04). This distribution of the residuals supported that the POC_{TF}-distributions could be as well explained by a log-normal distribution as a regularised solution.

The residuals of the TOC_{MIX}-incubations were also relatively low for both solutions. However, in general, the regularised solution was significantly smaller than the solution obtained by the log-normal distribution (Fig. 7, open circles). This indicates that TOC_{MIX} incubations may be better described by a non-symmetric solution than the log-normal distribution because, for example, the distribution of the OC-pools may be skewed or characterised by multiple local maxima. The residuals of the log-normal distributions are, however, still acceptably small, i.e. comparable to the residuals of the POC_{TF}-fits. Therefore, the log-normal distribution is also applied for describing the TOC_{MIX}-incubations. The limitations indicated by the better fit from the regularised solutions are discussed further below.

Sensitivity of solutions to the estimated total OC pool

The residuals of the intermediate-OC cases were smaller than in the minimum-OC cases and by comparing the residuals from all the 57 POC_{TF} and 57 TOC_{MIX} separately (note that we apply each experiment individually in the fitting procedure of the continuous models, i.e. 3×19 experiments, each determined by triplicate measurements, for both the POC_{TF} and TOC_{MIX} data), it was found that the residuals decreased by about 30% (found by linear regression with a r^2 of 0.69 and 0.65 for POC_{TF} and TOC_{MIX}, respectively). This showed that a better fit could be obtained by the intermediate-OC cases and indicated that the minimum-OC underestimated the total amount of bio-available OC.

The mean value of the log-normal distribution was significantly decreased in the intermediate-OC case of the POC_{TF}-incubation and a linear regression showed a close relationship (not shown) between the solution obtained in the two cases given by: $\mu(\text{intOC}) = 0.92 \times \mu(\text{minOC}) - 1.00$, ($r^2 = 0.96$). The negative intercept (-1.0) implies that the mean decay rate in all the POC_{TF}-incubations decreased by a factor of about 3 (i.e. $\exp(-1)$) when the bio-available OC pool was increased by 30%. A similar decrease of the mean decay rate was seen for the TOC_{MIX}-incubations and a similar linear regression resulted in a relationship given by: $\mu(\text{intOC}) = 1.04 \times \mu(\text{minOC}) - 0.65$, ($r^2 = 0.98$). Furthermore, although the intercept was larger than in the POC_{TF}-incubations, it still resulted in a decrease of the decay rate by about a factor of 2.

A similar comparison of the influence of increasing the bio-available OC-pool on the standard deviation of the log-normal distribution was made. In the POC_{TF}-incubations, a linear regression of the standard deviations in the two cases resulted in: $\sigma(\text{intOC}) = 1.13 \times \sigma(\text{minOC}) + 0.68$, ($r^2 = 0.78$). Thus, a larger bio-available OC-fraction also implied a broader OC-distribution because less bio-available compounds are included together with the bio-available material. A corresponding broadening of the OC-distribution was found for the TOC_{MIX}-incubations ($\sigma(\text{intOC}) = 0.86 \times \sigma(\text{minOC}) + 0.88$, ($r^2 = 0.90$)).

Decay rates and structural composition

The mean decay rate of the total OC-pool is given by: $\langle\alpha\rangle = \exp(\mu + \sigma^2/2)$. Thus, the mean decay rate is significantly influenced by the standard deviation of the distribution because of the

relatively large weight from the high decay rates in the log-normal distribution. The relationship between the median value (μ) and the squared standard deviation ($\sigma^2/2$) showed no significant relationship in the POC_{TF} incubations (Fig. 8a). However, the standard deviation was seen to increase when the median decay rate of the TOC_{MIX}-incubations decreased. This indicated that the slowly decaying samples were characterised by a relatively broader distribution than the faster decaying samples (Fig. 8b). No significant difference was found between the minimum-OC case and the intermediate OC-case.

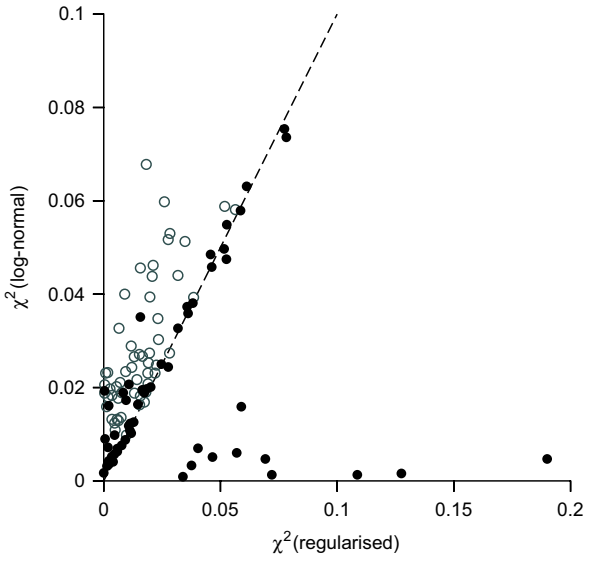

Fig. 7. Residuals (χ^2) from fitting all 114 experiments to a continuous OC-distribution to a log-normal distribution versus the residuals from fitting to a regularised solution (intOC-case). Values are shown for the POC_{TF}-incubations (bullets) and TOC_{MIX}-incubations (open circles), respectively.

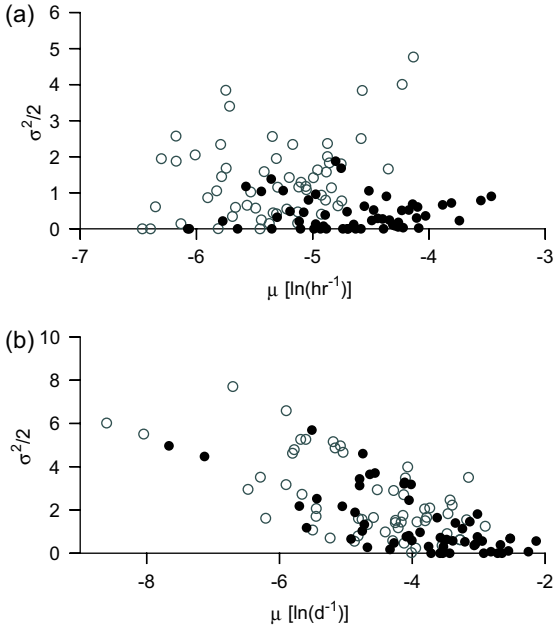

Fig. 8. Scatterplot of the mean value versus the squared standard deviation of the best fit log-normal distribution (the minimum-OC case and intOC-case are shown with bullets and circles, respectively) of the remineralisation rate to all POC_{TF} (a) and TOC_{MIX}-incubations (b), respectively. The median values (μ) of the remineralisation rates are shown.

Temperature sensitivity of the log-normal distributions

The median value (μ) of the best fit log-normal distribution in each incubation experiment at the three temperatures was applied for analysing the temperature dependent sensitivity of the OC-pool. In general, the incubations resulted in a best fit solution where the median decay rate of the distribution showed a gradual increase when temperature increased, i.e. in the T_{-5}, T_0 and T_{+5} incubations (cf. example shown in Fig. 9a). If temperature affected the remineralisation rates equally across the whole OC-distribution, the corresponding log-normal distribution would simply be shifted by a constant value of ln(α) (Forney and Rothman, 2012b). However, in many experiments, the standard deviation of the distribution also changed, typically about 20%, but no systematic correlation to temperature change was found. This modest change of the width of the distribution indicates an additional structural change between the distributions at the three temperatures, but as there were no systematic changes we disregard this effect and calculate the temperature sensitivity from the median values of the distributions.

Temperature sensitivity was defined in terms of the Arrhenius activation energy (E_a) and it was determined from the slope of the linear regression of ln(α) versus the inverse absolute temperature in each set of incubation experiments (Fig. 9b). The corresponding Q_{10} value was calculated from Eq. (5) and the Q_{10} value was then related to the mean turnover time (τ) of the distribution according to Eq. (6).

A significant difference was seen between the POC_{TF} and TOC_{MIX} incubations in terms of Q_{10}-values and turnover times for the individual set of incubation experiments (Fig. 10). POC_{TF}-incubations were characterised by a relatively modest scatter in both turnover times and Q_{10} values in the minOC-case (intOC-case), characterised by median values of 6.1 (11.8) days and 2.1 (1.9), respectively (Table 4).

The TOC_{MIX}-incubations were correspondingly characterised by a significantly higher turnover time (median value of 130 (155) days) and Q_{10}-value (median value of 5.1 (6.8)). However, the TOC_{MIX} distributions were more scattered and the average and

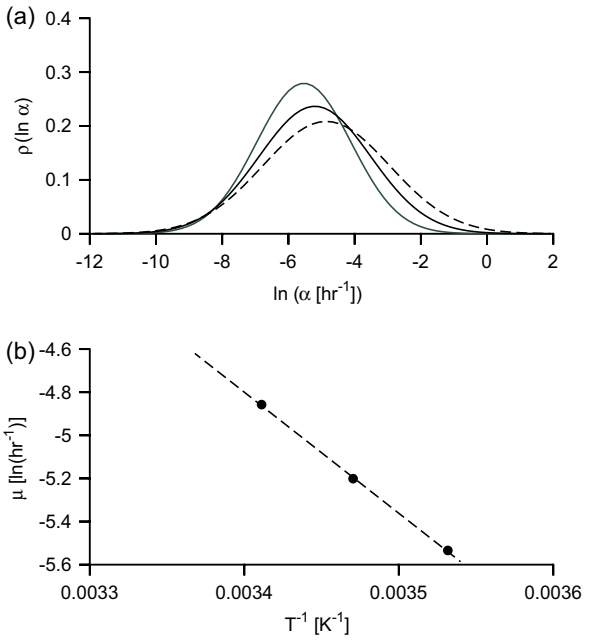

Fig. 9. (a) Best fit log-normal solutions for POC_{TF}-incubations (intOC-case) from the Eastern equatorial Pacific at 15 °C (grey line), 20 °C (black) and 25 °C (dashed line) (exp. no. 43–45). (b) Linear regression of the corresponding median remineralisation ratios (μ) against the inverse incubation temperatures.

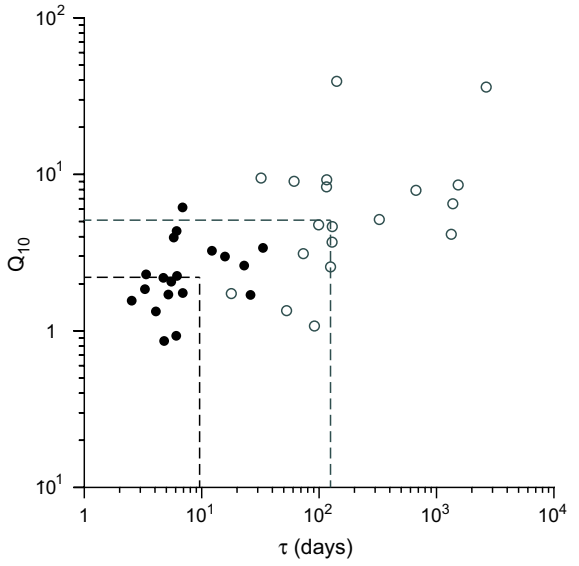

Fig. 10. Calculated Q_{10} values calculated from best fit log-normal solutions (minOC-case) of POC_{TF} (black bullets) and TOC_{MIX} incubations (grey circles) shown against the turnover time (τ).

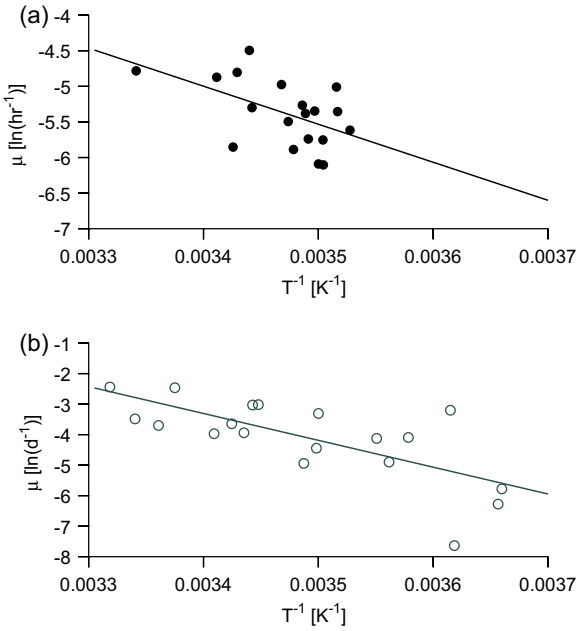

Fig. 11. Median values (μ) of best fit log-normal distributions (minOC-case) at *in situ* temperature for all POC_{TF} (a) and TOC_{MIX} (b) experiments, respectively. The natural logarithm of the remineralisation rates is shown versus the inverse absolute temperature (K^{-1}) and linear regression lines, corresponding to Q_{10} values of (a) 1.9 and (b) 2.8 for the two set of experiments, are shown (solid lines).

median values had significantly larger standard errors. This indicated that the turnover times and Q_{10} values were more diverse for this pool of OC.

Temperature sensitivity was also analysed by relating the remineralisation rate at *in situ* temperatures to the inverse *in situ* temperature across all the POC_{TF} and the TOC_{MIX} experiments, respectively (Fig. 11). Here the logarithm of the mean remineralisation rate in the log-normal distribution (i.e. μ) at the three temperatures in each set of incubation experiments was linearly interpolated to the *in situ* temperature and analysed with respect to the inverse absolute temperature (cf. the method applied for each set of experiments shown in Fig. 9b).

The resulting linear regression for the POC_{TF}-experiments (minOC-case) showed a significant negative correlation with a slope corresponding to an activation energy of 44,400 kJ mol^{-1} ($r^2 = 0.28$, $n = 19$, Fig. 11a). A representative Q_{10} value for all the POC_{TF}-experiments was then calculated at the median value of all the *in situ* temperatures of 13.7 °C, resulting in an overall Q_{10}-value of 1.9.

Correspondingly, a linear regression was made for the TOC_{MIX} experiments and the slope of the linear regression also showed a significant negative correlation corresponding to an activation energy of 73,100 kJ mol^{-1} ($r^2 = 0.50$, $n = 19$, Fig. 11b) and the Q_{10} calculated at the median *in situ* temperature of 13.6 °C was then found to be 2.8.

Inorganic nutrients and bacterial abundance

Inorganic nitrogen (NO_2^-, NO_3^-, NH_4^+) and phosphoros (PO_4^{3-}) were measured at the start and end of 12 of the POC_{TF}-incubations and all TOC_{MIX}-incubations (Tables S3 and S4, supplementary material). Both dissolved inorganic nitrogen (DIN) and phosphoros (DIP) showed consistent changes within each experiment at the three temperatures and, in general, their concentrations increased during the incubations. Relatively small variations in DIN and DIP were recorded among the triplicate measurements in both the POC_{TF}- and TOC_{MIX} incubations, supporting the consistent changes recorded from the oxygen measurements.

Bacterial abundance was measured in 13 of the 19 TOC_{MIX} incubations and showed a consistent decrease between the initial conditions and the final concentrations (Supplementary Fig. S1). The initial abundance of suspended bacteria varied between 10^5 and $5 \cdot 10^5$ cells ml^{-1} at the start of the experiments and exhibited relatively low values (below 10^5 cells ml^{-1}) after 2–3 months of incubation. There could, however, have been a buildup of bacteria attached to the inside of the incubation bottles which may not be reflected by the measurements.

Discussion

The temperature sensitivities of POC_{TF} and TOC_{MIX} remineralisations were found in relatively long-term *in vitro* incubation experiments carried out on board the ship but there are unresolved processes related to the experimental set-up which could affect the measured remineralisation rates in comparison to *in situ* conditions. These issues are also relevant for other experimental setups and are, therefore, discussed further below. Thereafter, we discuss the analysis of the POC_{TF} and TOC_{MIX} incubations by the two fundamentally different OC-models and summarise the complementary information about lability, temperature sensitivity and structural composition of the remineralised organic matter. Finally, we relate these findings to potential feedbacks which may exist between microbial remineralisation of organic matter and the carbon and nutrient cycling in the upper meso-pelagic.

General limitations of in vitro experiments

Duration of the incubation period

Several issues have to be considered before results from our *in vitro* experiments can be related to *in situ* conditions and one of the main assumptions concerns the incubation period. The duration of the incubation period was about 3–4 weeks for the POC_{TF}-experiments and 3–4 months for the TOC_{MIX}-experiments. These incubation periods were motivated by the assumed remineralisation period for sinking POC in the upper 3–500 m of the water column and the seasonal timescale for advection of DOC below the mixed layer, respectively. Reported sinking velocities of POC span

a wide range of values between 1 and 1000 m day^{-1} (Arístegui et al., 2009; Trull et al., 2008) and the assumed sinking velocity used here of about 10–20 m day^{-1} is, therefore, at the low end of this interval. This sinking rate and the corresponding timescale are justified by the observed large vertical gradient of the POC flux in the upper ocean derived from sediment traps which is in accordance with a relatively low sinking velocity in the upper mesopelagic zone. When POC sinks through the upper seasonal thermocline, it experiences large temperature changes and this is only indirectly considered in the experiments. However, the Q_{10} value is calculated over an interval of 10 °C between the coldest and warmest incubation experiment. This temperature range covers a typical temperature change between the surface and 300 m. Furthermore, the median Q_{10} values obtained from all POC_{TF} experiments also cover a relatively large range of temperatures (i.e. between 10 and 26 °C, cf. Table 1). Therefore, we consider the Q_{10}-value for the POC_{TF} as representative for the temperature dependent microbial response to sinking organic matter in the upper ocean.

The long incubation periods gave a robust estimate of the initial pool of bio-available organic carbon which could be respired on these time scales. By comparing the total amount of remineralised OC calculated from the oxygen consumption with the total amount of bio-available OC determined from the two-pool solutions, it was found that the average oxygen consumption accounted for 85% and 91% of the total OC in the model solutions of the POC_{TF}- and the TOC_{MIX}-incubations, respectively. In general, the two-pool solutions provided a good description of the time-dependent oxygen consumption and, together with the estimates above, this showed that the major fraction of bio-available OC was consumed during the experiments. However, both sets of experiments indicated that there was a small, but significant, amount of OC left in the end of the incubations (Figs. 2 and 3).

Bottle effects and changes in microbial community

Although the incubations lasted for weeks to months, the remineralisation rates were primarily constrained by the relatively large oxygen consumption seen in the beginning of the experiments. In the case of the POC_{TF}-incubations, the largest change in oxygen concentration occurred during the first approximately 50 h whereas only small changes were seen in the remaining period of the experiments (Fig. 2). Correspondingly, the largest change occurred during the first weeks in the TOC_{MIX}-incubations and only relatively small changes were seen in the last several months of the incubations (Fig. 3). Thus, remineralisation rates and their temperature dependence were mainly constrained from measurements in the first part of the experiments and, therefore, less sensitive to possible microbial community changes which could have occurred during the last part of the incubations. However, long term incubations may alter the conditions in the bottles significantly compared to the natural environment. Robinson and Williams (2005) consider various methods for measuring respiration in surface waters and describe errors associated with containment in *in vitro* experiments. They distinguish between errors associated with changes in the omission of part of the heterotrophic community and changes due to the bottles themselves, i.e. so-called bottle effects. Here we disregard effects from omission of larger heterotrophic organisms in the incubations due to the relatively coarse pre-filtering of the TOC_{MIX}-incubations and the relatively large depths of the POC_{TF}-samples.

Bottle effects have been analysed in long-term incubations of plankton, including phytoplankton, and it has been shown that phytoplankton production on the bottle walls may influence the incubations significantly when the incubations last for more than about 24 h (Chen et al., 1997; Sanford et al., 2001). However, García-Martín et al. (2011) investigated bottle effects in dark respiration incubations, corresponding to the incubations carried out in this study, and found no significant bias associated with bottle size (investigating bottles between 50 and 570 ml) or duration of the incubation (incubations between 2 and 48 h). Our incubations lasted for 1–3 months and, therefore, there may have been bottle effects which have not been accounted for in the analysis and these could have influenced the semi-labile remineralisation rates compared to the natural environment. Thus, we assume that bottle effects are negligible in the analysis and we argue that bottle effects would have a minor influence on the remineralisation rate of the most labile part of the OC-pool and also only have a minor effect on the temperature sensitivity as this depends on the relative change of the remineralisation rates.

Lee and Fuhrman (1991) analysed the influence of long-term dark incubations on the bacterial community structure in relatively large (20 l) containers and found only minor changes in species composition after two days of incubation. However, other studies have shown a significant change in the microbial community composition and, for example, Gattuso et al. (2002) incubated water in darkness from a lake in 60 ml bottles and found a significant change in bacterioplankton abundance and composition after 55 h of incubation. Longer-term incubations were investigated by Massana et al. (2001) by dark incubating water samples from the Southern Ocean for 10 days and they also found significant changes in prokaryotic community composition often associated with a decrease in bacterial diversity. Baltar et al. (2012) also found marked changes in the prokaryotic community structure in 10–23 day long dark incubations of water samples from a lake. However, they also found that oxygen consumption remained stable for up to 10–23 days. These studies underline the difficulties in applying *in vitro* methods for obtaining bacterial respiration because bacterial communities in incubation bottles cannot be expected to remain comparable to their natural counterparts on the species level when incubation periods extend beyond several days. Whether this causes a serious problem in terms of quantifying the bacterial oxygen consumption on larger spatial scales is currently not known and remains a subject for future studies. In this study, we assume that bacterial consumption is regulated by the lability of the organic material and is not substantially influenced by the bacterial community composition. Thus, an advantage of long term incubations is that they allow a quantification of the bio-available OC-pool on time-scales comparable to the incubation time-scale, but a drawback is the uncertainty about the representativeness of the decay rates of the more semi-labile substances. We note, however, that these considerations regarding potential bias resulting from changes in the microbial community also apply to many experiments where temperature influence on biological processes is investigated, e.g. temperature manipulated marine mesocosm experiments (e.g. Wohlers et al., 2009).

Changes in the bacterial community may also be expected when temperature changes *in situ*, for example due to climate change. We observed that the activity of the microbial communities in both the POC_{TF}- and the TOC_{MIX} incubations across all locations in the data set, i.e. covering a climate gradient from the subpolar northern Atlantic and Southern Ocean to the equatorial ocean, showed almost the same temperature dependency as obtained from each individual community in the manipulated experiments (Fig. 11). This supports the assumption that, although temperature affects the specific community composition, the overall activity of the community responds in a more general way to temperature changes.

We, therefore, assume that a change in the microbial community would only have a minor impact on the *relative* temperature sensitivity determined from the data analysis. It should also be noted that these considerations and limitations also are relevant for other long-term incubation experiments, i.e. on soil organic matter.

Tangential flow ultra filtration and decay of POC

Tangential flow ultra filtration (TFF) has been applied for separating size fractions of various substances in marine water samples in several studies but the filtration process involves several steps which may influence the subsequent incubations. Buesseler et al. (1996) found different filter efficiencies between membranes and systems from different manufacturers and, in general, it has been found that TFF requires careful handling and protocols for obtaining reliable results (Benner, 2002). Benner et al. (1997) applied optical and electron microscopy to analyse the retained material and found that even relatively fragile materials were recovered intact during TFF. In addition, those workers showed that the relative fraction of low molecular weight material (LMW) decreased during filtration, i.e. the retentate accumulated larger fractions, as expected. Guo et al. (2000) investigated the role of the concentration factor for the permeate of low molecular weight material and found that the concentration factor may influence the LMW in the permeate significantly. They also found that only a small amount of HMW permeated across the ultrafilter membrane.

In the current study the larger fractions of organic material was accumulated in the retentate which was subsequently incubated. The retentate is, therefore, expected to contain mainly the larger fractions of material but also a potential accumulated fraction of material with size classes less than the cut-off filter size (i.e. DOC). However, as the concentration factor on average was 31 ($n = 19$, Table S1) for all the POC_{TF}-experiments this small-size material can be expected to be relatively small. Thus, it can be assumed that the incubated retentate would mainly contain the larger fractions of the OC-pool. The accumulated DOC is also expected to contribute relatively less to the oxygen consumption compared to POC (Aristegui et al., 2002) and this supports our assumption that the POC_{TF}-incubations are representative for the larger size fractions of the OC-pool below the surface layer.

The two-pool solutions were analysed for a possible correlation between the concentration factor and the size of the OC-pools. Such a correlation would be expected to be found if accumulated DOC contributed significantly to the amount of respired oxygen in the incubations. A linear regression between the concentration factor and the respective pools $POC_0(1)$, $POC_0(2)$ and their sum (i.e. $POC_0(1) + POC_0(2)$, cf. Table S1) showed no significant correlation (i.e. a $r^2 < 0.05$ in any of the three cases). This supported the assumption that significant amounts of bio-available DOC were not accumulated during the TFF. Furthermore, the analysis of remineralisation rates and temperature sensitivities mainly depends upon the lability of the material and, therefore, the absolute amount of POC_{TF}, which may be more susceptible to small changes of the membrane or contamination, will not be so critical for the analysis. Thus, our POC_{TF}-incubations can be assumed to represent the lability of the larger size fractions of the OC-pool (i.e. $>\sim 0.2$ μm). This is also supported by the relatively small amount of total POC_{TF} found in the two-pool model solutions (i.e. total median value of 3.2 ± 1.5 μmol kg^{-1}, Table 1) and also the relatively homogenous material in terms of labilities which was found from the continuous model solutions.

Pressure effects on microbial metabolic activity

A special difference between terrestrial and marine studies of organic matter decay is the large pressure difference between *in situ* and *in vitro* conditions in marine incubations. Previous studies have found a pressure effect on bacterial metabolic activity where incubations at *in situ* pressure were found to have a higher rate than incubations carried out at atmospheric pressure (Lochte and Turley, 1988; Tamburini et al., 2003). However, we assume that this would have a minor influence on the determination of the *relative* temperature sensitivity between incubations carried out on waters taken from the same depth – especially considering that the relatively small pressure changes involved in the experiments (30–350 m) are within the range of pressure change routinely experienced by higher organisms, e.g. zooplankton.

Influence from suboxia on remineralisation

The incubations of POC_{TF} were saturated with oxygen during the filtration process and, therefore, the rates derived from the two incubation experiments from the suboxic station off Chile (Table 1, exp. no. 11–12) with *in situ* oxygen concentrations below 5 μM have been influenced by the large change in oxygen concentration in the incubation samples compared to the *in situ* conditions. For example, a sediment trap study in the eastern tropical North Pacific indicated that suboxic microbial remineralisation of organic carbon preferentially utilises nitrogen-rich organic compounds and, thereby, changes the remineralisation rates between carbon and nutrients accordingly and, at the same time, apparently lowers the remineralisation rate (Mooy et al., 2002). Therefore, these two POC_{TF} incubations might not be representative of the *in situ* remineralisation taking place in the suboxic areas.

Microbial adaptation to temperature

Temperature changes will affect many parts of the ecosystem. In particular, there may be large scale changes in the microbial community in a warmer ocean. This, could, in principle, modify the temperature sensitivity of the remineralisation rate through microbial adaptation to a warmer temperature level. Evolutionary temperature adaptation has been argued to explain the relatively small temperature sensitivity found among fish species in polar and tropical areas compared to the temperature sensitivity within a specific species (Clarke and Johnston, 1999), and similar adaptation could also be taking place for communities in the mesopelagic zone.

However, temperature changes of a few degrees Celsius, expected by the end of this century, are small changes compared to seasonal and inter-annual variability and also to the variation in temperature experienced by microorganisms attached to sinking POC through the thermocline. The relatively short time scale of microbial colonisation of 1–2 days found in *in vitro* aggregates in the study of Arístegui et al. (2009) suggests that the attached microbial community would be represented by surface bacteria and these attached communities are, therefore, not expected to adapt to temperature changes below the euphotic zone. In addition, we find a consistent and significant temperature sensitivity across all experiments despite a large *in situ* temperature interval from different oceanic regions (Fig. 11). Thus, we do not predict temperature adaptation to influence the general temperature sensitivity of the microbes relevant for the processes studied here. Additional support for this assumption comes from the observation that no such adaptation is identified in our incubations, although they were carried out over a relatively long time scale (months) compared to a typical bacterial regeneration time scale of hours to days.

The positive correlations found between *in situ* temperatures and remineralisation rates (Fig. 11) indicate that bacterial metabolic rates are significantly influenced by the local temperature and that the impact from the latitudinal temperature gradient in the upper ocean has not been compensated for through microbial adaptation. This interpretation is in accordance with earlier studies showing the significance of temperature for regulating the bacterial activity on organic matter in the upper ocean (Rivkin and Legendre, 2001). The possibility of a gradual microbial adaptation to temperature changes in the surrounding environment, e.g. due to climate change, cannot, of course, be dismissed, and such precaution is also relevant for interpretation of corresponding terrestrial studies of microbial temperature sensitivity. The temperature sensitivity of remineralisation of organic matter in the ocean corre-

sponds to the sensitivity found for terrestrial soil with Q_{10}(soil) ranging within 2.0–2.3 (Fang et al., 2005) indicating that the microbial response to temperature changes in the ocean is comparable with microbial response in other parts of the biosphere.

Other heterotrophic respiration

The sinking flux of POC in the mesopelagic zone is influenced by several biological and chemical processes including microbial degradation and zooplankton grazing (Tamburini et al., 2003). Therefore, the temperature sensitivity of the microbial respiration may not be representative for the total pelagic response to changes of the deep ocean temperature. Comparison between two stations in the Pacific showed that the integrated mesopelagic zooplankton carbon demand ranged between one and one third of the corresponding bacterial consumption (Steinberg et al., 2008). Earlier studies of the temperature sensitivity of zooplankton has found Q_{10} values of about 1.9 (Ikeda, 1985) and this has to be considered when results of microbial temperature sensitivity are assumed to represent the ecosystem response in the mesopelagic zone.

Remineralisation rates related to other measurements

Remineralisation rates and export estimates

TOC_{MIX}-samples include both POC and DOC but, because DOC is generally the largest OC-pool in the surface layer, we compare the solution for the TOC_{MIX} incubations with previous studies of the seasonal DOC-cycling below. The remineralisation rate of the semi-labile pool in the two-pool OC model (0.019 day^{-1}, i.e. an e-folding time of 56 days) is comparable to previous model studies where an e-folding time of DOC of about 3 months was found in the equatorial Pacific (Archer et al., 1997). Robinson et al. (2002) carried out short term dark incubations and quantified community respiration in the mixed layer on a transect in the eastern Atlantic basin during the period May–June. They found an average mixed layer respiration rate of 2.5 ± 2.1 μM O_2 day^{-1} which is comparable to the median value of the respiration rates in our experiments of the most labile component in the TOC_{MIX} incubations of 2.1 μM O_2 day^{-1} (i.e. 7.7 × 0.2 × 1.38 μmol O_2 kg^{-1} day^{-1}, cf. Table 4). They also found a significant correlation between respiration rates and surface chlorophyll values. We found no such correlation between surface chlorophyll and either the most labile TOC_{MIX}-pool or the corresponding decay rate. However, their data were more confined in space and time and this may explain their high correlation.

Also the two-pool TOC_{MIX}-solutions can be compared to results from the long-term incubation study by Hopkinson et al. (2002) of DOC collected in the Mid-Atlantic Bight. In their study, they fitted a three component OC-model, with two labile and one refractory pool, to measurements of DOC. Thus, their model is directly comparable to the two-pool OC-model applied here as adding a refractory component to the OC-pool in Eq. (A.1) does not affect the solution in terms of oxygen (cf. Eq. (1)). They found e-folding times of 4 days and 54 days for the remineralisation of DOC in their two labile OC-pools. These values are almost identical to the median values of 5 days and 56 days we find for the two pools in all the TOC_{MIX}-experiments. The turnover time of the TOC_{MIX}-incubations, found by fitting the log-normal distribution, resulted in a longer turnover time of about 4 months and 1.5 year for the minimum and intermediate OC-model, respectively. This shows that the decomposition of bulk TOC from the surface layer is, in general, associated with a relatively slow decay.

These relatively large e-folding time scales are in accordance with parameterisations of DOC-cycling in large scale ocean models (Najjar et al., 2007; Hansell et al., 2012). However, the discrepancy between the timescales inferred from the two-pool and the continuous OC-models indicate a large heterogeneity of the surface TOC-pool. The median values of the two-pool solutions only considered those solutions where the remineralisation rates were well-constrained and excluded solutions with very slowly decaying material. This would bias the median value towards faster decay rates. However, over half of the incubations were well constrained (i.e. 12 out of 19). Therefore, decay of surface TOC may be better represented by the relatively short decay timescales of 5 days and 56 days for the two pools, and these timescales would imply that global model studies with decay timescales on the order of a year would overestimate the export of DOC into the upper ocean. The solutions from the two models indicate that the surface TOC-distribution is relatively heterogeneous in terms of decay rates and that further investigation is required before a representative global parameterisation of TOC-remineralisation can be made.

The median value of bio-available TOC_{MIX} estimated from the two-pool model and the oxygen consumption of about 30 μM of bio-available organic carbon in the mixed layer is in agreement with previous findings from the Mid Atlantic Bight where the averaged respired DOC-pool during long-term incubations was found to be 35.6 μM (Hopkinson et al., 2002).

Few long-term incubations studies of remineralisation of POC have been carried out in the upper meso-pelagic zone. Williams and Purdie (1991) measured oxygen utilisation rates from *in vitro* short term incubations (12–24 h) of water samples from the oligotrophic northern Pacific and found an average daily respiration in the depth range between 90 and 250 m of 0.01 μmol C kg^{-1} h^{-1} (using an $\eta_{O2:C}$ = 138/106), comparable to the average remineralisation rate found in our study if scaled with an initial POC_{TF} value representative for oligotrophic waters (i.e. about 2 μmol C kg^{-1}). Correspondingly, independent estimates of organic carbon export from the distribution of the isotope ^{7}Be (77-day mean life) also resulted in a comparable respiration rate of 0.004 μmol C kg^{-1} h^{-1} (i.e. corresponding to an e-folding time of 10 days for POC values of 1 μM) in the 100–200 m depth interval in the subtropical North Atlantic (Kadko, 2009).

The spatial variability of the organic carbon flux (Buesseler et al., 2007) and the unavoidable limitations of *in vitro* incubation experiments have to be considered as potential sources of uncertainty in the comparisons with other measurements. The POC_{TF} incubations reported here were generally made during the growth season in highly productive areas such as the Benguela, Peru/Chile and equatorial upwelling systems and this could explain some of the high values. However, high POC_{TF} reactivity could also be caused by concentrated bacterial biomass (>0.2 μm), concentrated background DOC for material with sizes in the interval between 0.2 and 0.7 μm or "wall effects" in the bottles. Increased biomass on the walls of the incubation bottles is known to contribute significantly to the biological consumption or production in incubation experiments (Chen et al., 1997). We assumed that the relative temperature sensitivity of the microbial respiration was independent of whether the biomass was attached to particles, at the incubation bottle walls or free-living in the water. In addition, pressure induced lysis of the microbes could also increase oxygen consumption relative to *in situ* conditions. Nevertheless, we have no reason to believe that this effect would significantly influence the *relative* temperature sensitivity of the remineralisation rates found here.

POC_{TF} compared to GF/F filtered POC

The median values for the initial labile and semi-labile POC_{TF} two-pool sizes (1.0 and 1.4 μmol kg^{-1}, respectively) agree well with the average of the direct measurements of POC (not shown) retained on GF/F-filters (0.7 μm) of 1.5 ± 0.3 μmol kg^{-1} (s.e.m., n = 18) taking into account the differences in filter pore size between the GF/F-filter and the incubated water (0.7 versus 0.2 μm). At some depth levels, more organic matter was remineralised than was captured on the 0.7 μm GF/F filters. This difference may be explained either by the difference between the filter cut off

size of 0.2 and 0.7 μm or by the background concentration of DOC in the concentrated samples. At a few depths, less organic matter was remineralised than the POC measured on the GF/F filter ($POC_{GF/F}$), indicating the presence of a less labile particulate organic carbon fraction. The average molar ratio of the GF/F-filtered POC/PON was 9.3 ± 0.5 (s.e.m) was significantly higher than the C:N Redfield ratio of 6.6 (Redfield et al., 1963) suggesting the dominance of recycled organic material in the POC_{TF}-incubations. The lowest $POC_{GF/F}$:$PON_{GF/F}$ ratios ranged between 4.5 and 8.7 and were found in the Peru/Chile upwelling region and in the eastern equatorial Pacific. The highest value (of 12.2) was measured in the Benguela upwelling region. The particulate C:N ratios can be compared to the corresponding estimate of the C:N ratio of 11.2 ± 2.6 (s.e.m., $n = 11$) of the remineralised material determined by comparing the total change of oxygen and DIN (Table S3) in the warmest incubations ($C{:}N = -\eta_{C:O2}\ \Delta O_2/\Delta DIN$). Similarly, the lower C:N ratio determined for the remineralised material in the TOC_{MIX}-incubations (7.5 ± 2.2, s.e.m., $n = 15$) suggests that this OC-pool contained more fresh material (Table S4). Remineralisation ratios above the Redfield uptake ratio, as measured for the POC, have also been inferred from analysis of global carbon and nutrient data from water samples, from sediment trap data and ecosystem modelling (e.g. Shaffer et al., 1999; Anderson and Pondaven, 2003; Schneider et al., 2003).

Correction of remineralised OC for oxidation of ammonium

Other factors may influence the oxygen consumption in our incubation bottles and, thereby, our calculation of the temperature sensitivity of microbial respiration. The differences in nitrate concentrations between the coldest and warmest incubations at the end of the POC_{TF}-experiments were between 1 and 3 μmol kg^{-1} in all experiments where the DIN pools were recorded (Table S3). In the TOC_{MIX}-experiments, the differences in the ammonium concentration between the three temperatures were found to be less than 2.7 μmol kg^{-1} (Table S4). Therefore, differences in nitrification rates between the three temperatures, when compared to the total oxygen consumption (Figs. 2 and 3), could not account for the temperature sensitivities determined here. The appearance of ammonium in the end of the incubations showed that the remineralisation ratio between O_2 and organic carbon was between 1 and 138/106 because ammonium was not fully oxidised. This influences the estimated total pool of OC-concentration but had a minor effect on the calculations of Q_{10} (estimated to be less than 5% in the two-pool OC-models). Thus, the DIN-pools are not likely to have affected the Q_{10} calculations significantly. There were only measurements of DIN of the initial and final concentration and, therefore, the partial ammonium oxidation could not be directly included in the model solution. However, an upper boundary on the uncertainty of the bio-available OC in the TOC_{MIX}-experiments can be made by accounting for the oxidation of about 2.5 μM ammonium, which then would increase the median value of the total OC-pools in the two-pool solutions by 5 μM to about 35 μM.

Influence from bacterial biomass

Bacterial abundance showed a consistent decrease during the incubations (Fig. S1) and the generally large decrease in abundance of the free-living bacteria and small final oxygen variations between the three temperatures implies that changes in the bacterial biomasses in the incubations could not have accounted for the recorded temperature sensitivities.

Continuous versus discrete multi-component OC-models

A general problem in the study of decaying organic matter is the limited knowledge of the specific distribution of organic molecules in the OC pool. This limitation is, in general, circumvented by considering either the total OC-pool as relevant for the determination of decay rates or, as in this study, by only considering the bio-available pool of organic matter inferred indirectly from oxygen consumption. The estimate of the OC-pool based on oxygen consumption provides a lower boundary on the bio-available OC-pool, whereas the total amount of OC in the samples (i.e. the sum of DOC and POC) would provide an upper boundary. A large fraction of the DOC pool in the deep ocean, however, has timescales associated with its decay of the order of millennia (Druffel et al., 1992) and the contribution of such refractory OC-compounds to the biological activity in the upper aphotic ocean can, therefore, be considered as limited. Long-term dark incubation experiments of OC from various depths in the Mid-Atlantic Bight have confirmed that a significant amount of the DOC is refractory on timescales greater than years to decades (Hopkinson et al., 2002). The total amount of DOC present in water samples from the upper ocean is typically within 50–80 μM and, therefore, water samples in this study contain a large fraction of OC, even in the POC_{TF}-incubations, which could not be identified by measurement of the oxygen consumption. This fundamental uncertainty about the size and structural composition of the bio-available OC-pool motivated the application of different mathematical models in the analysis of the incubation experiments.

The analysis of the POC_{TF} and TOC_{MIX} incubations by two fundamentally different OC-models provided complementary information about the lability, temperature sensitivity and structural composition of the remineralised organic matter. The discrete two-component OC-model resulted in specific sizes and remineralisation rates of two labile pools together with corresponding temperature sensitivities. However, Forney and Rothman (2012a) show in their study that multi-pool solutions are, in general, sensitive to noise in the data such that even the number of active pools best describing a data set is likely to be weakly constrained. In contrast, they showed that continuous models determined by robust inverse methods provide a simple description of heterogeneous material and that these methods are less sensitive to noise in the data and, in general, do not require any *a priori* assumptions about the structure of the OC-pool, i.e. the distribution of bio-available OC. Basically, these solutions only assume that the distribution of the OC-pool can be associated with a remineralisation rate and that remineralisation can be characterised by first order kinetics, i.e. an exponential decay.

The continuous model solutions were first determined by the regularised solution where the optimal solution was determined by minimising both the misfit between model and data and the complexity of the solution (Forney and Rothman, 2012a). This provided a general non-symmetric solution. However, by also fitting a continuous log-normal distribution, it was found that the solutions generally fitted the data better in the POC_{TF}-incubations. The regularised solution, on the other hand, generally had smaller residuals in the TOC_{MIX}-incubations, although the residuals associated with the log-normal distribution still were acceptably small. Similarly, Forney and Rothman (2012b) found in a study of terrestrial litter decomposition that, in many cases, a log-normal distribution may describe the OC-pool as well as the more general regularised solution.

Overall, a log-normal distribution may be the relevant distribution if the outcome of a process can be characterised as resulting from multiplicative rather than additive actions which in many cases would be better described by a normal (Gaussian) distribution. The log-normal distribution has been found to characterise many processes in biology and other sciences where multiplicative actions are causing the distribution, e.g. when chemical reaction rates are determined by the product rather than the sum of chemical concentrations (Limbert et al., 2001). Similar to what has been found for terrestrial decay processes, the goodness of fit of the log-normal distribution suggests that decaying organic carbon in the

marine environment is controlled by many multiplicative actions and feedbacks.

Heterogeneity of OC-pools and temperature sensitivity

A general result from the incubation experiments is the significant heterogeneity of the OC-pools found both in the two-pool solutions and in the continuous distributions. Both the POC_{TF} and TOC_{MIX} results were described well by two OC-pools with order of magnitude differences in the respective decay timescales. Characteristic e-folding time scales for the POC_{TF} incubations were about 10 days for the continuous solutions and these values were in accordance with the respective time scales of 2 and 21 days found for the two pools in the two-pool OC-model. The e-folding time scale for the TOC_{MIX} incubations was characterised by more scattered results, as discussed below, and the time scales of 130 and 555 days found for the cases with the minimum and the intermediate OC-model, respectively, were associated with large uncertainties.

Results from the continuous distributions indicated that the TOC_{MIX} distribution was characterised by a relatively larger standard deviation and, thus, a broad distribution (cf. Fig. 8). This can be interpreted as the TOC in the surface layer being relatively heterogeneous in terms of lability. The shape of the distributions also indicated that the standard deviation was negatively correlated with the median value. This trend could be explained by a mixture of slowly decaying TOC with newly produced and faster decaying organic material. The POC_{TF} did not show a similar trend. This indicates a more uniform origin for POC_{TF}.

Temperature sensitivity of the remineralisation of organic carbon

Results of the temperature sensitivity from the two-pool models were in good agreement with the results from the continuous models. The POC_{TF} incubations resulted in median Q_{10}-values in the two-pool model of 1.6 and 1.8 for the fast and slowly decaying OC-pools, respectively (Table 3 and Fig. 4b). The corresponding Q_{10}-values for the continuous model were found to be 2.1 and 1.9 for the minimum and the intermediate OC-model, respectively (Table 4). When the Q_{10} value was determined from the distribution of remineralisation rates versus *in situ* temperature, a Q_{10} of 1.9 was found. Therefore, we suggest that a value of about 1.9 is representative for the temperature sensitivity of sinking POC. This value is in accordance with previous reported temperature sensitivities found for remineralisation of organic material in the sediment or in the surface layer but here we show that this temperature sensitivity also characterises the temperature sensitivity of organic matter sampled in the upper mesopelagic zone. The positive correlation between remineralisation rate and *in situ* temperature (Fig. 11) suggests that temperature dependent remineralisation rates also characterise differences in remineralisation rates on larger scale, i.e. more efficient remineralisation characterise the decomposition of sinking organic particles in warmer waters.

Results from the TOC_{MIX} incubations indicated relatively large scatter in the two-pool solutions and, in some experiments, the Q_{10} value was weakly constrained by the slowly decaying pool. This resulted in relatively large median values between 2.0 and 5.3 for the fast and slowly decaying pools, respectively (Table 3, Fig. 4b). The fast decaying pool was better constrained by the data (i.e. in 17 out of 19 experiments) and the Q_{10} value was also significantly smaller than for the less labile component and comparable to the Q_{10} values of the more labile POC_{TF} pools. The median values of the continuous model solutions were between 5.1 and 6.8 for the minimum OC- and intermediate OC-model (Table 4), respectively, but these values were associated with a relatively large uncertainty. Results from the two models showed that the overall temperature sensitivity of the TOC_{MIX} pool to be relatively large but associated with a significant scatter (Fig. 10). However, plotting the mean values of the continuous distributions versus *in situ* temperature showed a significant correlation corresponding to a Q_{10} of 2.8. Thus, we suggest that the bulk temperature sensitivity of TOC in the surface layer is characterised by a Q_{10} value of about 3 but the large scatter among the incubation experiments should be taken into account. A similar Q_{10} value of 3 was found for remineralisation of TOC in the seas between the North Sea and the Baltic sea where the composition of TOC is influenced significantly from DOC originating in the Baltic sea (Hansen and Bendtsen, 2014), so the presence of significant amounts of DOC may increase the temperature sensitivity.

Environmental impact and climate change

The Q_{10} values determined here suggest that carbon export from the surface layer may be altered significantly when the environment is exposed to general temperature changes. In coastal and shelf areas, such changes may be critical for the oxygen conditions because of the delicate balance between aerobic remineralisation and ventilation of water masses through physical mixing with surface waters. A general increase of hypoxic areas has been documented worldwide (Diaz and Rosenberg, 2008) and temperature increases in such areas would, in general, increase anoxia due to faster decay of organic matter (Bendtsen and Hansen, 2013).

On a global scale, the impact of changes in remineralisation rate of OC would influence the cycling of carbon in the upper ocean. Higher temperatures would tend to increase remineralisation and, thereby, tend to increase inorganic carbon in the surface waters. This, in turn, would tend to increase surface pCO_2. This would make a feedback between deep remineralisation and air–sea exchange of CO_2 and, thereby, the atmospheric concentration of greenhouse gases. This feedback was analysed in a simple ocean model where a Q_{10} of 2 resulted in an atmospheric pCO_2 increase of 21 ppm on a century time-scale (Matsumoto, 2007). This response was supported by a model study of Kwon et al. (2009) where a more shallow remineralisation depth increased atmospheric equilibrium CO_2-level by about 20–60 ppm. Temperature dependent respiration was also found to affect the cycling of nutrients and carbon in the upper ocean and significantly alter the global net primary production in global change scenarios (Tauscher and Oschlies, 2011). Results from a coupled ocean–atmosphere model during the next century showed that the impact from a temperature dependent remineralisation of OC, together with a general warming of the ocean, reduce the ocean carbon uptake by 0.2 Gt C yr^{-1} by the end of the 21st century (Segschneider and Bendtsen, 2013). Such large changes suggest that temperature dependent remineralisation in the upper ocean should be considered as a significant climate-carbon cycle feedback in the climate system. Corresponding changes may arise during colder climatic conditions, i.e. the glacial periods, where colder water masses would increase remineralisation depth and, thereby, contribute to a lowering of the atmospheric CO_2. This is in accordance with analyses of POC-sedimentation inferred from sediment cores (Kohfeld et al., 2005), increased export production inferred from oxygen isotopes in ice cores (Blunier et al., 2002) and model simulations (Matsumoto, 2007), all of which indicate an increased export during the glacial period. This would be in accordance with a decreased remineralisation of the sinking POC-flux during that time.

The relative role of temperature on primary production and respiration in the surface layer has been studied in previous studies. The study of López-Urrutia et al. (2006) showed a larger temperature dependence of heterotrophic respiration than autotrophic production at the organism level would tend to decrease the ocean uptake of CO_2. Similarly, a larger heterotrophic than autotrophic

temperature dependence was found in a mesocosm experiment (Wohlers et al., 2009). However, an increased primary production (PP) may still counteract the larger temperature effect from respiration and, thereby, limit the positive feedback on the oceanic carbon uptake, described above. Ocean model studies indicate that this is not the case and that effects from temperature changes alone play a minor role for regulating the response of global primary production in climate change scenarios. Tauscher and Oschlies (2011) showed in a sensitivity study that including temperature effects in the parameterization of PP indeed caused an increased PP in a global warming scenario but also that PP on a global scale mainly was influenced by changes in nutrient supply by vertical transports, i.e. effects from increased stratification and transports in the upper part of the main thermocline. Other studies have indicated that PP on a global scale may decrease in a global warming scenario. Although differences exist between ocean models they, in general, agree that export production would decrease in a warmer ocean (Steinacher et al., 2010). This supports the hypothesis that temperature effects on primary production may be less significant for the oceanic carbon uptake than the effect from increased remineralisation rates in a warmer ocean.

Conclusions

A new data set of remineralisation experiments was analysed for lability, temperature sensitivity and structural composition of the OC. The lability of OC was determined by fitting the oxygen measurements with both a discrete two-pool OC-model and a continuously distributed OC-model. Results showed that the bio-available organic carbon was well represented by a continuous log-normal distribution of the OC pool as a function of decay rates. General agreement between the two methods was found but they provided complementary information about the bio-available organic carbon. The discrete two-pool OC-model resulted in specific information about the sizes and temperature sensitivities of the two pools, whereas the continuous OC-model gave corresponding information about bulk turnover timescales and temperature sensitivities. In addition, the continuous OC-model also quantified the heterogeneity of the OC-distribution by the associated standard deviations of the log-normal distributions.

The e-folding decay timescales in the POC_{TF}-incubations were relatively well constrained and characterised by median values of the labile and semi-labile OC in the two-pool model of 2 and 21 days, respectively, and these values embraced the median values of 6–11 days obtained by the continuous log-normally distributed model. Temperature sensitivities were represented by Q_{10} median values between 1.6 and 1.8 in the discrete two-pool OC model and these values were comparable to results from the continuous model with median values of 1.9–2.1. An analysis of the remineralisation rates at *in situ* temperature from all the samples gave an overall Q_{10} value of 1.9. The good accordance between the various methods applied in the POC_{TF}-analysis suggested a representative Q_{10} value of about 1.9 for remineralisation of sinking OC.

The TOC_{MIX}-incubations showed a significant amount of bio-available OC being present in the surface layer with a median value from all the experiments of 30 μM. In the two-pool OC model, the most labile fraction was characterised by a remineralisation time scale of 5 days and a Q_{10} of 2.0 and was, thus, comparable to the values found in the POC_{TF}-experiments. The slowly decaying pool was characterised by a corresponding remineralisation e-folding time of 56 days and a relatively high Q_{10} value of 5.3. High values were also found from the continuous OC-model characterised by median-values of the turnover times of the bulk OC-distribution between 4 and 19 month and a median Q_{10}-value between 5.1 and 6.8. These values were, however, associated with a significant scatter. Characterising remineralisation of DOC in the surface layer on a global scale thus requires further study as the scatter between the experiments indicated that this is a relatively heterogeneous OC-pool. An analysis of the remineralisation rates at *in situ* temperature from all the samples was also made for the TOC_{MIX} incubations and resulted in an overall Q_{10} value of 2.8. Thus, although the TOC_{MIX} incubations indicated a more heterogeneous OC-distribution, the results from the continuous OC-model showed a relatively high temperature sensitivity with Q_{10} values above 2.8.

Analysis of previously reported studies of the impact of temperature dependent OC-remineralisation show that the found temperature dependence potentially may have a large effect on nutrient and carbon cycling. In particular, in a warmer ocean the temperature sensitivity implies a reduced OC-export into the deep ocean. This will tend to reduce oceanic CO_2-uptake and thereby feed back onto the climate system.

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Appendix A

A multi-component OC-model

The total amount of bio-available organic substances in seawater is here defined as TOC and it consists of the sum of all bio-available TOC_i fractions:

$$\mathrm{TOC} = \sum \mathrm{TOC}_i \tag{A.1}$$

A general model for the remineralisation of all bio-available TOC can then be described as:

$$\frac{d\mathrm{TOC}}{dt} = -\sum \alpha_i \mathrm{TOC}_i \tag{A.2}$$

where α_i is the remineralisation rate for each pool and the associated remineralisation e-folding time is defined as $\tau_i = 1/\alpha_i$. The corresponding solution for oxygen is described by:

$$\frac{d\mathrm{O}_2}{dt} = \frac{d}{dt}\left(\sum \eta(\mathrm{O}_2 : \mathrm{TOC}_i)\mathrm{TOC}_i\right) \tag{A.3}$$

where $\eta(O_2{:}TOC_i)$ is the remineralisation ratio between oxygen and the corresponding TOC_i pool. A constant "Redfield" value of $\eta(O_2{:}TOC_i) = 138/106$ (denoted below as η) was assumed for all the respired OC pools. The general solution of Eq. (3) can then be obtained from:

$$\mathrm{O}_2(t) = \mathrm{O}_2(t_0) - \eta \sum (\mathrm{TOC}_i(t_0)[1 - \exp(-\alpha_i t)]) \tag{A.4}$$

where $O_2(t_0)$ is the initial O_2 concentration.

Appendix B

Numerical solution of the two-component OC-model

The best fit solution to Eq. (1) was sought for the reference temperature (T_0) where $TOC_1(t_0)$, $TOC_2(t_0)$, $\alpha_0(1)$ and $\alpha_0(2)$ were determined (green lines in Figs. 2 and 3) by a Levenberg–Marquardt (LM) non-linear least-square method (Press et al., 1986) which for each temperature minimises the sum of the residuals between the measurements (y_j) and model solutions (y_m) defined by $\chi^2 = \Sigma[(y_j - y_m)/\sigma_j]^2$, where the standard deviation σ_j 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. Then, similar best-fit solutions were determined for $Q_{10}(1)$ and $Q_{10}(2)$ where the best fit solution (Eq. (1)) was dependent on both time and temperature in the LM-fitting procedure, and where the misfit χ^2 was determined for all temperature levels. In general, the POC_{TF}-experiments were well constrained by the measurements. However, high Q_{10} values were determined in 5 experiments and an upper boundary ($Q_{10} \leqslant 5$) was, therefore, applied in the fitting procedure. Three experiments could be explained by a single pool of OC ($POC(2) \sim 0$). The relatively small remineralisation rates associated with the semi-labile TOC_{MIX}-pool resulted in only 8 experiments where the remineralisation rate of the slow pool was well constrained and, in two experiments, the oxygen-consumption could be explained by a single OC-pool. Upper boundaries for Q_{10} ($\leqslant 10$) and the remineralisation e-folding time τ ($\leqslant 360$ days) were applied in the fitting procedure. Best fit solutions with these maximum values were considered as poorly constrained by the data and were, therefore, not included when the average values were calculated. The confidence interval associated with the best fit parameter values was determined by calculating the standard deviation from the LM least mean square fit while keeping the other parameters at their best fit value.

Appendix C

Solution of the continuous OC-model

The total amount of bio-available organic matter at a given time (t) is determined by a functional relationship ($f(\alpha,t)$) describing the decay of organic carbon characterised by the decay rate (α) and a corresponding concentration distribution function $p(\alpha)$. The decay is described by the time-dependent remaining organic carbon fraction $g(t)$ where the initial value is defined by $g(t_0)$. When integrated over all decay rates, the remaining fraction of organic matter at a given time is determined by:

$$g(t) = g(t_0) \int p(\alpha) f(\alpha, t) d\alpha \quad \text{(C.1)}$$

Here, we assume that the functional relationship can be described by a continuous superposition of exponential decays as analysed in previous studies (Forney and Rothman, 2012b), i.e. $f(\alpha,t) = \exp(-\alpha t)$. The basic functional dependence of the time-dependent decay is thereby similar to the multi-component OC-models described in Appendix A. Because a large range of decay rates is expected, a shift of variable to the natural logarithm of the decay rate ($\ln(\alpha)$) is first applied by using the transformation; $p(\alpha)d\alpha = \rho(\ln\alpha)\, d\ln\alpha$:

$$\frac{g(t)}{g(t_0)} = \int \rho(\ln\alpha) e^{-\alpha t} d\ln\alpha \quad \text{(C.2)}$$

Eq. (C.2) is the Laplace transform of the concentration density function $\rho(\ln\alpha)$ and the distribution $\rho(\ln\alpha)$ can therefore be determined by the inverse Laplace transform of Eq. (C.2). We apply the methods and programs described in Forney and Rothman (2012a) to determine the concentration density function $\rho(\ln\alpha)$ where $\rho(\ln\alpha)$ represents the distribution of bio-available organic carbon as a function of decay rates.

Appendix D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2014.10.009.

References

Anderson, T.R., Pondaven, P., 2003. Non-Redfield carbon and nitrogen cycling in the Sargasso Sea: pelagic imbalances and export flux. Deep-Sea Research I 50, 573–591.

Archer, D.E., Peeltzer, E.T., Kirchmann, D.L., 1997. A timescale for dissolved organic carbon production in equatorial Pacific surface waters. Global Biogeochemical Cycles 11, 435–452.

Aristegui, J., Duarte, C.M., Agustí, S., Doval, M., Álvarez-Salgado, X.A., Hansell, D.A., 2002. Dissolved organic carbon support of respiration in the dark ocean. Science 298, 1967.

Arístegui, J., Gasol, J.M., Duarte, C.M., Herndl, G.J., 2009. Microbial oceanography of the dark ocean's pelagic realm. Limnology and Oceanography 54, 1501–1529.

Arrhenius, S., 1889. Über die Reaktionsgeschwindigkeit bei der Inversion von Rohrzucker durch Sauren. Zeitscrift für Physicalishe Chemie 4, 226–248.

Baltar, F., Lindh, M.V., Parparov, A., Berman, T., Pinhassi, J., 2012. Prokaryotic community structure and respiration during long-term incubations. MicrobiologyOpen 2012 (1), 214–224.

Bendtsen, J., Hansen, J.L.S., 2013. Effects of global warming on hypoxia in the Baltic Sea–North Sea transition zone. Ecological Modelling 264, 17–26.

Bendtsen, J., Lundsgaard, C., Middelboe, M., Archer, D., 2002. Influence of bacterial uptake on deep-ocean dissolved organic carbon. Global Biogeochemical Cycles 16, 1127. http://dx.doi.org/10.1019/2002GB001947.

Benner, R., 2002. Chemical composition and reactivity. In: Hansell, D.A., Carlson, C.A. (Eds.), Biogeochemistry of Marine Dissolved Organic Matter. Academic Press, London, pp. 59–90.

Benner, R., Biddande, B., Black, B., McCathy, M., 1997. Abundance, size distribution, and stable carbon and nitrogen isotopic compositions of marine organic matter isolated by tangential-flow ultrafiltration. Marine Chemistry 57, 243–263.

Blunier, T., Barnett, B., Bender, M.L., Hendricks, M.B., 2002. Biological oxygen productivity during the last 60,000 years from triple oxygen isotope measurements. Global Biogeochemical Cycles 16, 1029. http://dx.doi.org/10.1029/2001GB001460.

Boyd, P.W., Tull, T.W., 2007. Understanding the export of biogenic particles in oceanic waters: is there a consensus? Progress in Oceanography 72, 276–312.

Boyd, P.W., Gall, M.P., Silver, M.W., Coale, S.L., Bidigare, R.R., Bishop, J.L.K.B., 2008. Quantifying the surface–subsurface biogeochemical coupling during the VERTIGO ALOHA and K2 studies. Deep-Sea Research II 55, 1578–1593.

Buesseler, K.O., Bauer, J.E., Chen, R.F., Eglinton, T.I., Gustafsson, O., Landing, W., Mopper, K., Moran, S.B., Santschi, P.H., VernonClark, R., Wells, M.L., 1996. An intercomparison of cross-flow filtration techniques used for sampling marine colloids: overview and organic carbon results. Marine Chemistry 55, 1–31.

Buesseler, K.O., Lamborg, C.H., Boyd, W.P., Lam, P.J., Trull, T.W., Bidigare, R.R., Bishop, J.K.B., Casciotti, K.L., Dehairs, F., Elskens, M., Honda, M., Karl, D.M., Siegel, D.A., Silver, M.W., Steinberg, D.K., Valdes, J., Mooy, B.V., Wilson, S., 2007. Revisiting Carbon Flux through the ocean's twilight zone. Science 316, 567–570.

Chen, C.-C., Petersen, J.E., Kemp, W.M., 1997. Spatial and temporal scaling of periphyton growth on walls of estuarine mesocosms. Marine Ecological Progress Series 155, 1–15.

Clarke, A., Johnston, N.M., 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology 68, 893–905.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–929.

Doherty, S.J., Bojinski, S., Henderson-Sellers, A., Noone, K., Goodrich, D., Bindhoff, N.L., Church, J.A., Hibbard, K.A., Karl, T.R., Kajfez-Bogata, L., Lynch, A.H., Parker, D.E., Prentice, I.C., Ramswamy, V., Saunders, R.W., Smith, M.S., Steffen, K., Stocker, T.F., Thorne, P.W., Trenberth, K.E., Verstraete, M.M., Zwiers, F.W., 2009. Lessons learned from IPCC AR4. Scientific developments needed to understand, predict and respond to climate change. Bulletin of the American Meteorological Society 90, 497–513. http://dx.doi.org/10.1175/2008BAMS2643.1.

Druffel, E.R., Williams, P.M., Bauer, J.E., Ertel, J.R., 1992. Cycling of dissolved and particulate organic matter in the open ocean. Journal of Geophysical Research 97, 15,639–15,659.

Dufresne, J.L., Friedlingstein, P., Berthelot, M., Bopp, L., Ciais, P., Fairhead, L., Treut, H., Monfray, P., 2002. On the magnitude of positive feedback between future climate change and the carbon cycle. Geophysical Research Letters 29, 1405. http://dx.doi.org/10.1029/2001GL013777.

Dunne, J.P., Sarmiento, J.L., Gnadadesikan, A., 2007. A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor. Global Biogeochemical Cycles 21, GB4006. http://dx.doi.org/10.1029/2006GB002907.

Eppley, R.W., 1972. Temperature and phytoplankton growth in sea. Fishery Bulletin 70, 1063–1085.

Fang, C., Smith, P., Mancrieff, J.B., Smith, J.U., 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433, 57–59.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281, 237–240.

Forney, E.C., Rothman, D.H., 2012a. Inverse method for estimating respiration rates from decay time series. Biogeosciences 9, 3601–3612.

Forney, E.C., Rothman, D.H., 2012b. Common structure in the heterogeneity of plant-matter decay. Journal of the Royal Society Interface 9, 2255–2267.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H.D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.G., Schnur, R., Strassmann, K., Weaver, A.J., Yoshikawa, C., Zeng, N., 2006. Climate-carbon cycle feedback analysis results from the C^{4}MIP model intercomparison. Journal of Climate 19, 3337–3353.

García-Martín, E.E., Serret, P., Pérez-Lorenzo, M., 2011. Testing potential bias in marine plankton respiration rates by dark bottle incubations in the NW Iberian shelf: incubation time and bottle volume. Continental Shelf Research 31, 496–506.

Gattuso, J.-P., Peduzzi, S., Pizay, M.-D., Tonalla, M., 2002. Changes in freshwater bacterial community composition during measurements of microbial and community respiration. Journal of Plankton Research 24, 1097–1206.

Grasshoff, K., Erhardt, M., Kremling, K., 1983. Methods of Seawater Analysis. Verlag Chemie, Basel.

Guo, L., Wen, L.-S., Tang, D., Santschi, P.H., 2000. Re-examination of cross-flow ultrafiltration for sampling aquatic colloids: evidence from molecular probes. Marine Chemistry 69, 75–90.

Hansell, D.A., Carlson, C.A., Schlitzer, R., 2012. Net removal of major marine dissolved organic carbon fractions in the subsurface ocean. Global Biogeochemical Cycles 26, GB1016. http://dx.doi.org/10.1029/2011GB004069.

Hansell, D.A., Carlson, C.A., 1998. Net community production of dissolved organic carbon. Global Biogeochemical Cycles 12, 443–453.

Hansen, J.L.S., Bendtsen, J., 2014. Seasonal bottom water respiration in the North Sea–Baltic Sea transition zone: rates, temperature sensitivity and sources of organic material. Marine Ecology Progress Series 499, 19–34.

Hofmann, M., Schnellhuber, H.J., 2009. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. Proceeding of the National Academy of Sciences of the United States of America 106, 3017–3022. http://dx.doi.org/10.1073/pnas.0813384106.

Hopkinson, H.S., Vallino, J., Nolin, A., 2002. Decomposition of dissolved organic matter from the continental margin. Deep-Sea Research II 49, 4461–4478.

Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Marine Biology 85, 1–11.

IPCC, 2007. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007. The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 996pp.

Kadko, D., 2009. Rapid oxygen utilization in the ocean twilight zone assessed with the cosmogenic isotope 7Be. Global Biogeochemical Cycles 23, GB4010. http://dx.doi.org/10.1029/2009GB03510.

Kohfeld, K.E., Quéré, C.L., Harrison, S.P., Anderson, R.F., 2005. Role of the biology in glacial–interglacial CO_2 cycles. Science 308, 74–78.

Kragh, T., Søndergaard, M., Tranvik, L., 2008. Effect of exposure to sunlight and phosphorus-limitation on bacterial degradation of coloured dissolved organic matter (CDOM) in freshwater. FEMS Microbial Ecology 64, 230–239.

Kwon, E.Y., Primeau, F., Sarmiento, J.L., 2009. The impact of remineralization depth on the air–sea carbon balance. Nature Geoscience 2, 630–635.

Lampitt, R.S., Boorman, B., Brown, L., Lucas, M., Salter, I., Sanders, R., Saw, K., Seeyave, S., Thomalla, S.J., Turnewitsch, R., 2008. Particle export from the euphotic zone: estimates using a novel drifting sediment trap, ^{234}Th and new production. Deep-Sea Research 55, 1484–1502.

Laws, E.A., Falkowski, P.G., Smith, W.O., Ducklow, H., McWilliams, J.C., 2000. Temperature effects on export production in the open ocean. Global Biogeochemical Cycles 14, 1231–1246.

Lee, S., Fuhrman, J.A., 1991. Species composition shift of confined bacterioplankton studied at the level of community DNA. Marine Ecology Progress Series 79, 195–201.

Lenton, T., Huntingford, C., 2003. Global terrestrial carbon storage and uncertainties in its temperature sensitivity examined with a simple model. Global Change Biology 9, 1333–1352.

Levitus, S., Boyer, T.P., 1994. World Ocean Atlas: Temperature, vol. 4. NOAA Atlas NESDIS, Silver Spring, Maryland.

Limbert, E., Stahel, W.A., Abbt, M., 2001. Log-normal distributions across the sciences: keys and clues. Bioscience 51, 341–352.

Lochte, K., Turley, C.M., 1988. Bacteria and cyanobacteria associated with phytodetritus in the deep sea. Nature 333, 67–69.

Lomas, M.W., Glibert, P.M., Shiah, F.K., Smith, E.M., 2002. Microbial processes and temperature in Chesapeake Bay: current relationships and potential impacts of regional warming. Global Change Biology 8, 51–70.

López-Urrutia, Á., Martin, E.S., Harris, R.P., Irigoien, X., 2006. Scaling the metabolic balance of the oceans. Proceeding of the National Academy of Sciences of the United States of America 103, 8739–8744.

Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W., 1987. VERTEX: carbon cycling in the northeast Pacific. Deep-Sea Research 34, 267–285.

Massana, R., Pedros-Alio, C., Casamayor, E.O., Gasol, J.M., 2001. Changes in marine bacterioplankton phylogenetic composition during incubations designed to measure biogeochemically significant parameters. Limnology and Oceanography 46, 1181–1188.

Matsumoto, K., 2007. Biology-mediated temperature control on atmospheric pCO_2 and ocean biogeochemistry. Geophysical Research Letters. http://dx.doi.org/10.1029/2007GL031301.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carbon-cycle feedbacks to the climate system. Science 298, 2173–2176.

Middelboe, M., Lundsgaard, C., 2003. Microbial activity in the Greenland Sea: the role of DOC lability, mineral nutrients and temperature. Aquatic Microbial Ecology 32, 15–163.

Mooy, V.B.A.S., Keil, R.G., Devol, A.H., 2002. Impact of suboxia on sinking particulate organic carbon: enhanced carbon flux and preferential degradation of amino acids via denitrification. Geochimica et Cosmochimica Acta 66, 457–465.

Najjar, R.G., Jin, X., Louanchi, F., Aumont, O., Caldeira, K., Doney, S.C., Dutay, J.-C., Follows, M., Gruber, N., Joos, F., Lindsay, K., Maier-Reimer, E., Matear, R.J., Matsumoto, K., Monfray, P., Mouchet, A., Orr, J.C., Plattner, G.-K., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Weirig, M.-F., Yamanaka, Y., Yool, A., 2007. Impact of circulation on export production, dissolved organic matter, and dissolved oxygen in the ocean: results from Phase II of the Ocean Carbon-cycle Model Intercomparison Project (OCMIP-2). Global Biogeochemical Cycles 21, GB3007. http://dx.doi.org/10.1029/2006GB002857.

Pomeroy, L.R., Wiebe, W.J., 2001. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquatic Microbial Ecology 23, 187–204.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 1986. Numerical Recipes in FORTRAN: The Art of Scientific Computing. Press Syndicate of the University of Cambridge, USA.

Redfield, A.C., Ketchum, B.H., Richards, F.A., 1963. In: Hill, M.N. (Ed.), The Sea, vol. 2. Interscience, New York, pp. 26–77.

Richardson, K., Bendtsen, J., Christensen, J.T., Adjou, M., Lyngsgaard, M.M., Hilligsøe, K.-M., Vang, T., Holtegaard, M., 2014. Localised upwelling and heterogeneity in the plankton food web in a frontal region of the Sargasso Sea: implications for eel early life history? Marine Ecology Progress Series 504, 91–107.

Rivkin, R.B., Legendre, L., 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291, 2398–2400.

Robinson, C., Williams, P.J.B., 2005. Respiration and it measurements in surface marine waters. In: delGiorgio, P.A., Williams, P.J.LeB. (Eds.), Respiration in Aquatic Ecosystems. Oxford University Press, pp. 147–180.

Robinson, C., Serret, P., Tilstone, G., Teira, E., Zubkov, M.V., Rees, A.P., Malcolm, E., Woodward, S., 2002. Plankton respiration in the Eastern Atlantic Ocean. Deep-Sea Research 49, 787–813.

Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L., Wanninkhof, R., Wong, C.S., Douglas, W.R., Tilbrook, B., Millero, F.J., Peng, T.H., Kozyr, A., Ono, T., Rios, A.F., 2004. The oceanic sink for anthropogenic CO_2. Science 305, 367–371.

Sanford, A., Morgan, D., Evans, D., Ducklow, H., 2001. Bacterioplankton dynamics in estuarine mesocosms: Effects of tank shape and size. Microbial Ecology 41, 45–55. http://dx.doi.org/10.1007/s002480000048.

Sarmiento, J.T., Hughes, T., Stouffer, R., Manabe, S., 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. Nature 393, 245–249.

Schmittner, A., Oschlies, A., Matthews, H.D., Galbraith, E.D., 2008. Future changes in climate, ocean circulation, ecosystems, and biogeochemical cycling simulated for a business-as-usual CO_2 emission scenario until year 4000 AD. Global Biogeochemical Cycles 22, GB1013. http://dx.doi.org/10.1029/2007GB002953.

Schneider, B., Schlitzer, R., Fischer, G., Nöthig, E.-M., 2003. Depth-dependent elemental compositions of particulate organic matter (POM) in the ocean. Global Biogeochemical Cycles, 10.1029/2002GB001871.

Segschneider, J., Bendtsen, J., 2013. Temperature dependent remineralization in a warming ocean changes marine ecosystem species composition through Si-limitation and increases surface pCO_2. Global Biogeochemical Cycles 27, 1–12. http://dx.doi.org/10.1002/2013GB004684.

Shaffer, G., Bendtsen, J., Ulloa, O., 1999. Fractionation during remineralisation of organic matter in the ocean. Deep-Sea Research 46, 185–204.

Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I., 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change Biology 14 (1–25), 2015–2039.

Steinacher, M., Joos, F., Frölicher, T.L., Bopp, L., Cadule, P., Cocco, V., Doney, S.C., Gehlen, M., Lindsay, K., Moore, J.K., Schneider, B., Segschneider, J., 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. Biogeosciences 7, 979–1005.

Steinberg, D.K., Mooy, V., Buesseler, K.O., Boyd, P.W., Kobari, T., Karl, D.M., 2008. Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. Limnology and Oceanography 53, 1327–1338.

Tamburini, C., Garcin, J., Bianchi, A., 2003. Role of deep-sea bacteria in organic matter mineralization and adaptation to hydrostatic pressure conditions in the NW Mediterranean Sea. Aquatic Microbial Ecology 32, 209–218.

Tauscher, J., Oschlies, A., 2011. Can we predict the direction of marine primary production change under global warming? Geophysical Research Letters 38, L02603. http://dx.doi.org/10.1029/2010GL045934.

Thamdrup, B., Fleischer, S., 1998. Temperature dependence of oxygen respiration, nitrogen mineralization, and nitrification in Arctic sediments. Aquatic Microbial Ecology 15, 191–199.

Trull, T.W., Bray, S.G., Buesseler, K.O., Lamborg, C.H., Manganini, S., Moy, C., Valdes, J., 2008. In situ measurement of mesopelagic particle sinking rates and the control of carbon transfer to the ocean interior during the Vertical Flux in the Global Ocean (VERTIGO) voyages in the North Pacific. Deep Sea Research II 55, 1522–1539.

White, P.A., Kalff, J., Rasmussen, J.B., Gasol, J.M., 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. Microbial Ecology 21, 99–118.

Williams, P.J.le B., Purdie, D.A., 1991. In vitro and in situ derived rates of gross production, net community production and respiration of oxygen in the oligotrophic subtropical gyre of the North Pacific Ocean. Deep-Sea Research 38, 891–910.

Wohlers, J., Engel, Zöllner, A., Breithaupt, P., Jürgens, K., Hoppe, H.G., Sommer, U., Riebesell, U., 2009. Changes in biogenic carbon flow in response to sea surface warming. Proceedings of the National Academy of Sciences of the United States of America 106, 7067–7072.

Yeramian, E., Claveria, P., 1987. Analysis of multiexponential functions without a hypothesis as the number of components. Nature 326, 169–174.