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Mesopelagic respiration near the ESTOC (European  
Station for Time-Series in the Ocean, 15.5 °W,  
29.1 °N) site inferred from a tracer conservation model

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## Abstract

Remineralization of organic matter in the mesopelagic zone (ca. 150–700 m) is a key controlling factor of carbon export to the deep ocean. By using a tracer conservation model applied to climatological data of oxygen, dissolved inorganic carbon (DIC) and nitrate, we computed mesopelagic respiration at the ESTOC (European Station for Time-Series in the Ocean, Canary Islands) site, located in the Eastern boundary region of the North Atlantic subtropical gyre. The tracer conservation model included vertical Ekman advection, geostrophic horizontal transport and vertical diffusion, and the biological remineralization terms were diagnosed by assuming steady state. Three different approaches were used to compute reference velocities used for the calculation of geostrophic velocities and flux divergences: a no-motion level at 3000 m, surface geostrophic velocities computed from the averaged absolute dynamic topography field, and surface velocities optimized from the temperature model. Mesopelagic respiration rates computed from the model were  $2.8\text{--}8.9 \text{ mol O}_2 \text{ m}^2 \text{ y}^{-1}$ ,  $2.0\text{--}3.1 \text{ mol C m}^2 \text{ y}^{-1}$  and  $0.6\text{--}1.0 \text{ mol N m}^2 \text{ y}^{-1}$ , consistent with remineralization processes occurring close to Redfield stoichiometry. Model estimates were in close agreement with respiratory activity, derived from electron transport system (ETS) measurements collected in the same region at the end of the winter bloom period ( $3.61 \pm 0.48 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ). According to ETS estimates, 50% of the respiration in the upper 1000 m took place below 150 m. Model results showed that oxygen, DIC and nitrate budgets were dominated by lateral advection, pointing to horizontal transport as the main source of organic carbon fuelling the heterotrophic respiration activity in this region.

*Keywords:* Mesopelagic respiration; tracer conservation model; horizontal advection; North Atlantic subtropical gyre; ESTOC

### *Highlights:*

- Model-derived mesopelagic respiration at ESTOC is in agreement with *in vitro* estimates
- Half of the mesopelagic respiration takes place below 150 m
- Horizontal transport is the main source of organic carbon fuelling respiration

## 29 **1 Introduction**

30 The sunlit surface waters of the ocean are responsible for an annual photosynthetic fixation of  
31 ~50 Pg of carbon, which represents about half of the global primary production (Field et al.,  
32 1998). A fraction of the produced organic matter, ca. 5–12 Pg (Henson et al., 2011), is ex-  
33 ported to deeper layers of the oceans where it fuels the metabolism of the heterotrophic mi-  
34 crobial community. Part of the exported material is remineralized within the mesopelagic or  
35 'twilight' zone (ca. 150 – 700 m), where light penetrates but is not sufficiently intense to  
36 support net photosynthesis. This zone acts as a hub between surface and deeper layers, po-  
37 tentially controlling the export of carbon to the deep ocean through the strength of recycling  
38 processes. Recent studies have shown that mesopelagic bacterial communities can be more ac-  
39 tive than previously thought, as they support respiration rates equivalent to those of epipelagic  
40 communities (Arístegui et al., 2009, Weinbauer et al., 2013). However, organic carbon supply  
41 estimates, accounting for both sinking particulate (POC) and dissolved organic carbon (DOC),  
42 are consistently insufficient to satisfy the estimated carbon demand of the mesopelagic com-  
43 munities (Arístegui et al., 2002, Burd et al., 2010). This imbalance could be compensated by  
44 other sources of organic carbon, such as non-sinking or suspended POC, which escape capture  
45 by sediment traps (Herndl and Reinthaler, 2013, Baltar et al., 2010, Alonso-González et al.,  
46 2009), and active biological flux by zooplankton (Putzeys et al., 2011, Giering et al., 2014).  
47 Moreover, the discrepancy could also be the result of methodological uncertainties in the de-  
48 termination of planktonic metabolic rates.

49 Prokaryotic respiration is a crucial term in the mesopelagic carbon budget. It is frequently  
50 derived from bacterial carbon production estimates and assumed bacterial growth efficiency, or  
51 calculated from measurements of enzymatic ETS (electron transport system) respiratory activ-  
52 ity. Respiration estimates derived from ETS depend on the conversion factor used to transform  
53 ETS activities into oxygen consumption rates (the R:ETS ratio). Recent studies pointed out that  
54 this ratio can vary about one order of magnitude depending on the physiological state of the  
55 heterotrophic communities (Arístegui et al., 2005, Reinthaler et al., 2006). Respiration rates

56 based on biogeochemical approaches, which integrate larger temporal and spatial scales and a  
57 broader array of processes, could help to reconcile the different estimates (Burd et al., 2010).  
58 Biogeochemical calculations were initially restricted to certain locations where the age of the  
59 water masses can be calculated with relative confidence (Jenkins, 1982), or where the seasonal-  
60 ity of biogeochemical tracers is large enough to infer annual averaged respiration rates (Jenkins  
61 and Goldman, 1985, Martz et al., 2008). However, in regions where horizontal transport is  
62 significant, conservation models can be used to infer respiration rates despite relatively weak  
63 seasonality in tracers concentrations (Fernández-Castro et al., 2012).

64 The ESTOC (European Station for Time-Series in the Ocean, Canary Islands, 15.5°W,  
65 29.16° N) site is located in the eastern boundary region of the North Atlantic subtropical gyre  
66 (NASE), and it is indirectly influenced by the coastal African upwelling, which exports nutri-  
67 ents and organic matter towards the centre of the gyre by filaments and Ekman transport (Neuer  
68 et al., 1997, Pelegrí et al., 2005, Álvarez Salgado et al., 2007). Here we adapt the 1D tracer  
69 conservation model described in Fernández-Castro et al. (2012) to quantify mesopelagic respi-  
70 ration at the ESTOC site. This estimate is compared to the averaged respiration derived from  
71 ETS measurements carried out at this location in March 2000, coinciding with the end of the  
72 late winter bloom.

## 73 **2 Methods**

### 74 **2.1 Model description**

A tracer conservation model was applied to temperature, oxygen, dissolved inorganic carbon (DIC) and nitrate ( $\text{NO}_3$ ) data from the ESTOC region in order to infer mesopelagic (150-700 m) respiration. The model was adapted from Fernández-Castro et al. (2012) and includes the main physical process which are relevant below the mixed layer: vertical diffusion, vertical advection (Ekman transport) and horizontal advection. The temporal evolution of a tracer profile ( $C = C(t, z)$ ) –where  $C$ ,  $t$  and  $z$  represent temperature or tracer concentration, time, and, vertical

coordinate, respectively— is described by the following equation:

$$\frac{\partial C}{\partial t} = -u \frac{\partial C}{\partial x} - v \frac{\partial C}{\partial y} - w \frac{\partial C}{\partial z} + K \frac{\partial^2 C}{\partial z^2} + J_C \quad (1)$$

75 where  $u(z)$  and  $v(z)$  are the longitudinal and latitudinal geostrophic velocities, respectively;  
 76  $\partial C/\partial x$  and  $\partial C/\partial y$  the longitudinal and latitudinal gradients of temperature or tracer concen-  
 77 tration;  $K$  vertical diffusivity;  $w$  vertical velocity and  $J_C(z)$  represents the sources minus sinks  
 78 term. For temperature  $J_C$  represents the effect of the solar shortwave radiation that penetrates  
 79 below the mixed layer depth, whereas for oxygen, DIC and  $\text{NO}_3$  it represents the net effect of  
 80 photosynthesis and respiration computed diagnostically at the end of the simulation. The tem-  
 81 perature model was used to optimize  $K$  and the tracer models were used to infer net respiration  
 82 rates. The vertical domain of the model extended from the base of the mixed layer down to  
 83 1000 m, with a vertical resolution of 2 m.

The model was initialised with annual profiles of temperature and tracers. It was then run for 365 days with a time step of  $dt = 0.005$  days forced with annually-averaged physics (see below). At the end of this period a new tracer profile was produced. The profile of the biological production–consumption term was then inferred from the difference between the initial (observed, obs.) and the final (modelled, mod.) profile under the assumption of steady state:

$$J_C(z) = -\frac{C_{\text{obs}}(z) - C_{\text{mod}}(z)}{365 \text{ d}} \text{ (mmol m}^{-3} \text{ d}^{-1}) \quad (2)$$

84 Depth-integrated rates between 150 and 700 m are reported in the text in order to avoid bound-  
 85 ary effects when calculating mesopelagic respiration.

Vertical diffusivity ( $K$ ) was treated as an unknown constant in our model and it was computed from the optimization of the temperature ( $T$ ) model run. The optimal  $K$  was estimated by minimizing the following cost function:

$$\text{Cost} = \left( \frac{1}{550 \text{ m}} \int_{150 \text{ m}}^{700 \text{ m}} \left( \frac{T_{\text{obs}}(z) - T_{\text{mod}}(z)}{\max(T_{\text{obs}}(z)) - \min(T_{\text{obs}}(z))} \right)^2 dz \right)^{1/2} \quad (3)$$

86 Averaged annual temperature, oxygen and  $\text{NO}_3$  profiles were derived from the World Ocean  
 87 Atlas 2009 (WOA09, Locarnini et al. (2010), Garcia et al. (2010b,a)) and computed as the  
 88 mean profile of the four grid points nearest to the ESTOC site (see Figure 1). The DIC profile  
 89 was calculated in a similar way using data from the Global Data Analysis Project (GLODAP)  
 90 climatology (Key et al., 2004). The standard deviation was used as the error estimate.

Monthly solar shortwave radiation for the period 1996-2001 from the CORE.2 Global Air-  
 Sea flux dataset (<http://rda.ucar.edu/datasets/ds260.2/>) was used to calculate the  
 annual mean insolation at the ESTOC site ( $191.1 \pm 4.8 \text{ W m}^{-2}$ ), by fitting the seasonal cycle  
 to an harmonic function. The effect of the solar shortwave radiation that penetrates below the  
 mixed layer ( $J_C$  term for the temperature model) was computed as:

$$J_C^T(z) = \frac{1}{\rho(z)C_p(z)} \frac{\partial I(z)}{\partial z} \quad (4)$$

91 where  $\rho$  is the water density computed from temperature and salinity profiles using the Millero  
 92 and Poisson (1981) formulation,  $C_p$  is the specific heat (Fofonoff and Millard, 1983), and  $I(z)$  is  
 93 the shortwave radiation flux computed by using the attenuation model of Paulson and Simpson  
 94 (1977) for Type I water and the surface shortwave radiation value.

95 Ekman downwelling/upwelling velocity,  $w$ , was computed from the wind stress monthly  
 96 climatological data included in the International Comprehensive Ocean-Atmosphere Data Set  
 97 (Leetmaa and Bunker, 1978), with a spatial resolution of  $2^\circ \times 2^\circ$ , and then annually aver-  
 98 aged. The ESTOC site is characterized by a weak downwelling with a mean annual velocity of  
 99  $-3.8 \pm 15.0 \text{ m y}^{-1}$ . The Ekman velocity was set to zero at the surface and increased linearly to  
 100 the Ekman depth, considered as 30 m, and decreased linearly to zero down to 250 m (Ono et al.,  
 101 2001). As depth-dependent  $w$  requires horizontal convergence or divergence for volume con-  
 102 servation, horizontal advection included a correction term. This was accomplished numerically  
 103 by implicitly evaluating  $w\partial C/\partial z$  at the grid box interfaces.

104 Horizontal gradients of temperature, oxygen and  $\text{NO}_3$  were calculated using the four grid  
 105 points surrounding ESTOC from the WOA09 climatology, whereas the GLODAP database was

106 used for DIC. Longitudinal gradients were computed as the difference between the temperature  
107 and tracer concentration averages at the B,D and A,C locations for each depth divided by the  
108 averaged distance:  $(\partial C/\partial x)(z) = (\overline{C_{B,D}(z)} - \overline{C_{A,C}(z)})/dx$  (see Figure 1). Similarly, latitudinal  
109 gradients were calculated as the difference between the averages at the A,B and the C,D lo-  
110 cations:  $(\partial C/\partial y)(z) = (\overline{C_{A,B}(z)} - \overline{C_{C,D}(z)})/dy$ . The standard deviations associated with each  
111 average were propagated in order to compute gradient uncertainties.

112 Horizontal velocities,  $u$  and  $v$ , were assumed to be geostrophic and computed from the  
113 thermal wind equations using the neutral density profiles derived from temperature and salinity  
114 WOA09 fields according to Jackett and McDougall (1997). Standard deviations in the density  
115 field were propagated in order to evaluate velocity errors. To evaluate the uncertainty due to  
116 the choice of reference level, three different reference velocities were used for the integration  
117 of the thermal wind equations. First, no-motion was assumed at 3000 m in accord with other  
118 studies in the North Atlantic (Siegel and Deuser, 1997, Alonso-González et al., 2009). Second,  
119 geostrophic surface currents derived from the averaged field of 15 years (1996-2010) Absolute  
120 Dynamic Topography (ADT) data provided by AVISO (<http://www.aviso.altimetry.fr>)  
121 were used as the reference for the integration. As spatial resolution of the AVISO database  
122 ( $1/4^\circ$ ) is higher compared to the WOA09 database ( $1^\circ$ ), surface geostrophic velocity vectors  
123 were averaged inside the model box (A,B,C,D in Figure 1). Finally, the optimal surface ref-  
124 erence velocities ( $u_s, v_s$ ) were also diagnosed from the temperature model by minimizing the  
125 cost function in equation 3.

126 Deviations from the steady state in the temperature model, i.e. differences between the  
127 observed and the modelled temperature profile at the end of the simulations, can occur due  
128 to inaccuracy or oversimplification of the modelled physical processes. These limitations can  
129 possibly affect the determination of the biological rates for the different tracers ( $C$ ). We evaluate  
130 the detection limit for the biological rates by rescaling the change in the temperature profile due  
131 to unaccounted physical processes as:



$$J_C^{\text{Det. Lim.}}(z) = \frac{1}{365 \text{ d}} \frac{|T_{obs}(z) - T_{mod}(z)|}{\max(T_{obs}(z)) - \min(T_{obs}(z))} \times (\max(C_{obs}(z)) - \min(C_{obs}(z))), \text{ (mmol m}^{-3} \text{ d}^{-1}) \quad (5)$$

132 Tracer concentration changes lower than  $J_C^{\text{Det. Lim.}}$  are likely due to model inaccuracy and  
 133 can not be attributed to biological uptake or production.

134 Furthermore, in order to determine the standard deviation of the model terms and depth-  
 135 integrated rates, 2000 Monte Carlo simulations were performed for each model run with model  
 136 variables randomly generated by assuming normal distributions. For the tracers, tracers gradi-  
 137 ent and velocity profiles, and other variables obtained from databases (solar radiation,  $w$ ), the  
 138 calculated standard deviation was used to generate random inputs. For the optimized  $K$  and  
 139 surface velocities ( $u_s$ ,  $v_s$ ), uncertainties corresponding to 50% and  $0.2 \text{ cm s}^{-1}$  were assumed,  
 140 respectively.

## 141 2.2 Electron transport system respiratory activity

142 Water samples for the determination of ETS respiratory activity were collected at 15 depths,  
 143 from the surface down to 1000 m, during 9 samplings conducted between 12<sup>th</sup> and 23<sup>rd</sup> March  
 144 2000. Depending on depth, 5 to 20 l of seawater were pre-filtered through a  $200 \mu\text{m}$  mesh and  
 145 poured into acid-cleaned plastic carboys, before being filtered through 47 mm Whatman GF/F  
 146 filters, at a low vacuum pressure ( $<1/3 \text{ atm}$ ). The filters were immediately stored in liquid nitro-  
 147 gen until assayed in the laboratory (within a 2-3 weeks). ETS determinations were carried out  
 148 according to the Kenner and Ahmed (1975) modification of the tetrazolium reduction technique  
 149 proposed by Packard (1971) as described in Arístegui and Montero (1995). An incubation time  
 150 of 15 min at  $18^\circ\text{C}$  was used. ETS activities measured at  $18^\circ\text{C}$  were converted to respiratory  
 151 activities at in situ temperatures by using the Arrhenius equation. A mean activation energy of  
 152  $16 \text{ kcal mol}^{-1}$  was used (Arístegui and Montero, 1995).

## 153 **3 Results**

### 154 **3.1 Implementation of the tracer conservation model**

155 Figure 2 and Table 1 show the geostrophic velocities and flux divergence for temperature,  
156 oxygen, DIC and  $\text{NO}_3$  computed by using three different reference velocities: a no-motion  
157 level at 3000 m, surface geostrophic velocities computed from the averaged ADT field, and  
158 surface velocities optimized from the temperature model (see Methods). The results obtained  
159 by using the three different approaches are described in the following sections.

#### 160 **3.1.1 No-motion level at 3000 m**

161 The geostrophic flow calculated by integrating the thermal wind equations considering a no-  
162 motion level at 3000 m was directed southwards from the surface ( $v_s = -2.67 \pm 0.37 \text{ cm s}^{-1}$ ,  
163 Table 1) down to 1000 m (Figure 2). The longitudinal component was insignificant at the sur-  
164 face ( $u_s = 0.03 \pm 0.52 \text{ cm s}^{-1}$ ) and directed westward at greater depths. The heat flux divergence  
165 indicated a net cooling of the water column by advection. The longitudinal component of the  
166 heat flux divergence ( $-u \frac{\partial T}{\partial x}$ ) was negative throughout the water column, whereas the latitudinal  
167 component ( $-v \frac{\partial T}{\partial y}$ ) was negative in the upper 200 m and close to zero at greater depths. Both  
168 components contributed to the depth-integrated (150–700 m) net cooling, which was  $-203 \pm 66$   
169  $^\circ\text{C m y}^{-1}$  (Table 1). The latitudinal oxygen flow divergence showed positive values (conver-  
170 gence) from the surface down to 800 m, whereas the longitudinal component was negative  
171 throughout the water column, resulting in a net oxygen gain of  $1.97 \pm 3.17 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ .  
172 The opposite pattern was observed for DIC and  $\text{NO}_3$ , resulting in a net loss of both tracers  
173 ( $-1.22 \pm 1.21 \text{ mol C m}^{-2} \text{ y}^{-1}$  and  $-0.35 \pm 0.52 \text{ mol N m}^{-2} \text{ y}^{-1}$ ). However, differences in the  
174 vertical distribution of the flow divergences were observed. Whereas DIC loss was maximum  
175 at the surface and decreased with depth (similar to the oxygen gain),  $\text{NO}_3$  divergence was neg-  
176 ative, mainly between 200 and 800 m.

177 The tracer conservation model was first run for temperature in order to diagnose vertical  
178 diffusivity ( $K$ ). The computed optimal value was  $3.9 \text{ cm}^2 \text{ s}^{-1}$  (Table 2), 5-10 fold higher com-

179 pared to diffusivity values obtained in the area by tracer release experiments (Schmitt et al.,  
180 2005) and microstructure observations (Fernández-Castro et al., 2014). There was a good  
181 agreement between the observed and the modelled temperature profiles (Figure 3), the cost  
182 function being 1.8% (see Methods). The advective (horizontal + vertical) and diffusive terms  
183 dominated the temperature budget, and the optimization of  $K$  maximises diffusivity because  
184 the cooling caused by geostrophic advection divergence was compensated by diffusion in order  
185 to minimise the net change at the end of the simulation.

186 The oxygen model showed an accumulation of oxygen from the initial to the final pro-  
187 file. In order to maintain the steady state, this accumulation was compensated by biological  
188 uptake. The  $J_{O_2}$  term showed net oxygen consumption from 100 m down to 1000 m, as the  
189 result of positive advection divergence down to 600 m, and the positive diffusion divergence  
190 below this depth. The DIC and  $NO_3$  simulations resulted in losses of both tracers. This was  
191 mainly driven by advection in the upper 600 m and by diffusion below, and it was balanced  
192 by respiration processes. The respiration signal was also vertically decoupled for both trac-  
193 ers, as  $NO_3$  respiration maximum was located deeper due to differences in the advective flux  
194 divergence. Depth-integrated respiration rates were  $-2.72 \pm 3.90 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ,  $2.46 \pm 1.62$   
195  $\text{mol C m}^{-2} \text{ y}^{-1}$  and  $0.54 \pm 0.64 \text{ mol N m}^{-2} \text{ y}^{-1}$  for oxygen, DIC and  $NO_3$ , respectively (Table 2).  
196 Despite the high uncertainty associated to these figures, the computed rates were about 5-10  
197 fold higher than the detection limit computed from the temperature model runs (see Methods  
198 and Table 2). The respiration stoichiometry ratios were  $O_2:C = 1.1 \pm 1.7$ ,  $O_2:N = 5.0 \pm 9.4$  and  
199  $C:N = 4.6 \pm 6.2$ , largely consistent with respiration rates close to Redfield proportions ( $O_2:C =$   
200  $1.4$ ,  $O_2:N = 9.2$ ,  $C:N = 6.6$ ). For this model configuration, the geostrophic horizontal transport  
201 dominated the tracer budgets, being responsible for 72%, 49% and 65% of the respiration rate  
202 diagnosed for oxygen, DIC and  $NO_3$ , respectively. Note that the horizontal advection term in  
203 Table 2 does not correspond directly to geostrophic advection, as it includes any divergence re-  
204 quired to ensure mass conservation (see Methods). Vertical diffusion accounted for 27%, 52%  
205 and 37%, respectively, whereas the contribution of the Ekman transport (vertical advection)  
206 was very low.

### 207 **3.1.2 Surface velocities derived from absolute dynamic topography**

208 The surface geostrophic flow calculated from the averaged ADT field had a similar south-  
209 wards component ( $v_s = -2.39 \pm 0.78 \text{ cm s}^{-1}$ ) compared to that obtained from the reference  
210 no-motion level at 3000 m (Table 1). However, in this case a significant eastward compo-  
211 nent ( $u_s = 1.11 \pm 0.66 \text{ cm s}^{-1}$ ) was also computed. The eastward flow was caused by the  
212 contribution of velocity vectors computed in the northern part of the model box (see Figure  
213 1). The geostrophic flow was also directed southeastwards at deeper levels (Figure 2), re-  
214 sulting in positive heat flux divergence (net heating,  $233 \pm 67 \text{ }^\circ\text{C m y}^{-1}$ ), mainly driven by the  
215 longitudinal component. Contrary to the previous approach, oxygen convergence and DIC  
216 and  $\text{NO}_3$  divergences were enhanced by the eastward component, which resulted in higher  
217 depth-integrated respiration rates ( $8.71 \pm 2.81 \text{ mol O}_2 \text{ m}^2 \text{ y}^{-1}$ ,  $-2.92 \pm 1.22 \text{ mol C m}^2 \text{ y}^{-1}$  and  
218  $-1.04 \pm 0.49 \text{ mol N m}^2 \text{ y}^{-1}$ ). The optimal  $K$  value diagnosed from the temperature model was  
219  $0.4 \text{ cm}^2 \text{ s}^{-1}$  (Table 2), in better agreement with the observations. However, the temperature  
220 model cost function was 3.0%, slightly higher than in the previous configuration. The temper-  
221 ature and oxygen (DIC and  $\text{NO}_3$ ) profiles showed accumulation (loss) at the end of the sim-  
222 ulations (Figure 4). Due to the lower diffusivity, advection was the most important driver for  
223 these patterns. Depth-integrated respiration rates were  $-8.86 \pm 3.93 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ,  $3.09 \pm 1.63$   
224  $\text{mol C m}^{-2} \text{ y}^{-1}$  and  $1.07 \pm 0.68 \text{ mol N m}^{-2} \text{ y}^{-1}$ . These values were higher compared to the pre-  
225 vious approach, although the model uncertainty was also larger as illustrated by the higher  
226 detection limits (Table 2). The respiration stoichiometry ratios were  $\text{O}_2:\text{C} = 2.9 \pm 2.0$ ,  $\text{O}_2:\text{N} =$   
227  $8.3 \pm 6.4$  and  $\text{C}:\text{N} = 2.9 \pm 2.4$ . In this case the relative contribution of the geostrophic trans-  
228 port to the diagnosed respiration rates was more important, reaching  $> 95\%$  for all the tracers.  
229 Together, vertical diffusion and advection, represented  $< 5\%$  of the tracers budget.

### 230 **3.1.3 Surface velocities optimized from the temperature model**

231 Due to the sensitivity of our model to the geostrophic transport and, in turn, to the used ref-  
232 erence velocities, we performed a triple optimization process for diffusivity ( $K$ ) and surface

233 reference velocities ( $u_s$ ,  $v_s$ ). During this process, the temperature model cost function was  
234 evaluated for a set of plausible  $K$ ,  $u_s$  and  $v_s$  values (Figure 5). The diagnosed optimal param-  
235 eters were  $K = 1 \text{ cm}^2 \text{ s}^{-1}$ ,  $u_s = 0.4 \text{ cm s}^{-1}$  and  $v_s = -2.4 \text{ cm s}^{-1}$ . Optimal diffusivity values  
236 lower than  $1 \text{ cm}^2 \text{ s}^{-1}$ , in good agreement with the observations, were only possible for eastward  
237 (positive) velocities lower than the value of  $u_s = 1.11 \text{ cm s}^{-1}$  computed from the ADT field.  
238 Lower cost values were also computed for close to zero or negative  $u_s$ , but in this case optimal  
239 diffusivity was unrealistically high, and therefore these possibilities were discarded.

240 The latitudinal component of the geostrophic transport was also southwards in the upper  
241 600 m, due to similar surface values in comparison to the previous approaches (Figure 2). The  
242 longitudinal component was westwards, except at the surface and below 700 m, and velocity  
243 values were lower compared to the previous approaches. The net heat flux divergence was neg-  
244 ative through the water column, and the depth-integrated net change ( $-73 \pm 57 \text{ }^\circ\text{C m y}^{-1}$ ) was  
245 smaller compared to the first approach (no-motion level at 3000 m). The net flux divergences  
246 for oxygen, DIC and  $\text{NO}_3$  showed a similar pattern compared to the first approach, because in  
247 this case both longitudinal and latitudinal flux divergences were reduced.

248 Despite the lower diffusivity, initial and final temperature profiles were in close agreement  
249 in this simulation, with a computed cost of 1.6% (Figure 6 and Table 2). Temperature changes  
250 due to horizontal advection were smaller compared to the other two approaches, because the  
251 optimization process reduced the heat advection flux divergence, instead of maximising the  
252 compensatory diffusion. This was mainly accomplished by the optimization of the longitudinal  
253 component of the flow, which was the main component of the heat divergence term. The model  
254 results for oxygen, DIC and  $\text{NO}_3$  were very similar to those from the first approach, although  
255 small differences were noticed in the vertical distribution of the biological term, due to the  
256 different interplay of diffusive and advective processes. Depth-integrated respiration rates were  
257  $-4.39 \pm 7.02 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ,  $2.00 \pm 2.63 \text{ mol C m}^{-2} \text{ y}^{-1}$  and  $0.57 \pm 1.05 \text{ mol N m}^{-2} \text{ y}^{-1}$ , very  
258 similar to the first approach, whereas the stoichiometric ratios were  $\text{O}_2:\text{C} = 2.2 \pm 4.5$ ,  $\text{O}_2:\text{N} =$   
259  $7.7 \pm 18.8$  and  $\text{C}:\text{N} = 3.5$ . In this case, the geostrophic transport flux divergence represented  
260 50 – 60% of the computed respiration.

261 Due to the good agreement between the results derived from this approach and the no-  
262 motion level at 3000 m, the realistic optimized  $K$  value, and the lower detection limits, we  
263 decided to use the mesopelagic respiration rates computed with this configuration for compar-  
264 ison with estimates derived from ETS observations.

### 265 **3.2 Mesopelagic respiration derived from ETS respiratory activity**

266 The vertical distribution of averaged respiration rates derived from ETS measurements carried  
267 out at the ESTOC site from 12<sup>th</sup> to 23<sup>rd</sup> March 2000 is shown in Figure 7. ETS respiration rates  
268 were higher above 100 m (ca.  $0.1 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) and progressively decreased down to 200  
269 m (ca.  $0.05 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ). Below this depth, respiration rates showed small vertical vari-  
270 ability ranging between  $0.007$  and  $0.016 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ . The averaged depth-integrated (20–  
271 1000 m) respiration rate was  $8.57 \pm 0.76 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$  ( $23.5 \pm 2.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ), 50% of  
272 the total respiration ( $4.50 \pm 0.52 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ) occurring between 150 and 1000 m.

273 The vertical distribution of ETS mesopelagic respiration was in close agreement with the  
274 biological terms derived for oxygen and DIC from the tracer conservation model, especially  
275 between 150 and 700 m. Modelled respiration for  $\text{NO}_3$ , subjected to larger uncertainty, showed  
276 a deeper maximum at around 400 m. Note that the upper limit for the model configuration  
277 was the mixed layer depth, and that the region above 150 m is likely affected by bound-  
278 ary effects, because the concentration is forced to climatological values in this layer where  
279 air-sea gas exchange is not considered. Depth-integrated (150–700 m) ETS respiration was  
280  $3.61 \pm 0.48 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$  ( $2.56 \pm 0.34 \text{ mol C m}^{-2} \text{ y}^{-1}$  and  $0.388 \pm 0.052 \text{ mol N m}^{-2} \text{ y}^{-1}$ , us-  
281 ing Redfield stoichiometry for the conversion), in close agreement with model estimates for  
282 oxygen ( $2.8$ – $8.9 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ) and DIC ( $2.0$ – $3.1 \text{ mol C m}^{-2} \text{ y}^{-1}$ ), and slightly lower for  $\text{NO}_3$   
283 ( $0.56$ – $1.07 \text{ mol N m}^{-2} \text{ y}^{-1}$ ) (Table 2).

## 284 4 Discussion

### 285 4.1 Comparison of mesopelagic respiration inferred from the tracer conservation model 286 and ETS measurements

287 Respiration estimates derived from the tracer conservation model and ETS measurements ac-  
288 count for distinct processes occurring at different temporal and spatial scales. ETS measure-  
289 ments were carried out near the ESTOC site during the late winter bloom, which constitutes the  
290 most productive season in the region (Neuer et al., 2007), whereas the tracer conservation model  
291 integrates larger temporal and spatial scales implicit in the climatologies. Furthermore, whereas  
292 ETS measurements account for the potential respiration of the  $< 200 \mu\text{m}$  size-fraction micro-  
293 bial plankton (see Methods), the model quantifies total respiration processes relevant on annual  
294 time-scales. The comparison of the ETS measurements reported here with ETS respiration of  
295 the larger size-fraction ( $> 200 \mu\text{m}$ ), quantified for the same cruise, ( $0.52 \pm 0.15 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ,  
296 Putzeys et al., 2011), indicates that the smaller size organisms dominate ( $\approx 87\%$ ) mesopelagic  
297 respiration. Despite the mentioned limitations, mesopelagic respiration derived from the tracer  
298 conservation model for the three tracers was in close agreement with ETS respiration estimated  
299 in the same region in March 2000 ( $3.61 \pm 0.48 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ , or  $4.13 \pm 0.50 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$   
300 both size-fractions included), when a R:ETS = 0.086, representative for low bacterial activity,  
301 (Packard et al., 1988) was used.

302 A previous estimate of global respiration in the dark ocean (below 200 m depth) ( $5 \text{ mol C m}^{-2} \text{ y}^{-1}$ ,  
303 Arístegui et al., 2003a), derived by up-scaling ETS measurements using the same R:ETS ratio,  
304 was also in good agreement with several estimates based on geochemical tracers (Jenkins, 1982,  
305 Jenkins and Wallace, 1992, Carlson et al., 1994). However, an R:ETS ratio of  $0.68 \pm 0.11$  was  
306 inferred from the comparison of oxygen consumption estimates and ETS measurements carried  
307 out in the mesopelagic south of the Canary Islands, leading to an estimate of mesopelagic res-  
308 piration of  $68 \pm 8 \text{ mmol C m}^{-2} \text{ d}^{-1}$  ( $24.8 \pm 2.9 \text{ mol C m}^{-2} \text{ y}^{-1}$ ) (Arístegui et al., 2005), one order  
309 of magnitude higher than the values reported here. The region south of the Canary Islands  
310 is generally more productive (Arístegui et al., 1997), compared to the northern region, due to

311 the nearby upwelling system and also to the intense mesoscale activity generated downstream  
312 of the islands (Aristegui et al., 1994, Sangrà et al., 2009). For this reason, the measurements  
313 reported by Aristegui et al. (2005) probably describe a relatively fast-growing heterotrophic  
314 community as a result of the enhanced phytoplankton productivity that generally characterizes  
315 this region. The good agreement between ETS and model derived respiration, despite the differ-  
316 ent temporal and spatial scales implicit in both estimates, suggest that the seasonal variability  
317 of mesopelagic remineralization processes in this region is relatively weak. This is consistent  
318 with previous studies reporting a small seasonal variability in POC sinking fluxes (Helmke  
319 et al., 2010) and suspended POC concentrations (Neuer et al., 2007) at the ESTOC site.

## 320 **4.2 The mesopelagic carbon budget in the eastern and western subtropical North At-** 321 **lantic**

322 Mesopelagic respiration rates reported in this study were in close agreement with geochemical  
323 estimates, based on  $^3\text{He}/^3\text{H}$  water masses age and apparent oxygen utilisation (AOU) determi-  
324 nations, carried out below 100 m in the beta triangle region, located west of the ESTOC site  
325 ( $5.7 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ , Jenkins, 1982). Our estimates were also very similar to the value reported  
326 for the Sargasso Sea, in the subtropical Northwestern Atlantic (NASW), by using the seasonal  
327 variation of oxygen concentration below 100 m ( $4.1\text{--}5.9 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ , Jenkins and Gold-  
328 man, 1985). Despite the similarities between mesopelagic respiration reported for the eastern  
329 and western subtropical North Atlantic, the two regions are characterized by important differ-  
330 ences regarding the sources of the organic carbon fuelling remineralization processes in the  
331 mesopelagic zone.

332 Our model results indicate that oxygen, DIC and  $\text{NO}_3$  budgets at ESTOC were mainly dom-  
333 inated by lateral processes, due to the southward transport along the Canary Current. We are  
334 aware that these results are sensitive to the calculation of geostrophic flux divergences, which  
335 were derived from global climatologies, and for this reason subjected to important uncertain-  
336 ties (see Methods and Table 2). However, our results were consistent when different approaches  
337 were used to determine the reference velocities used for the calculation of geostrophic trans-



338 ports (Table 2). In agreement with previous studies (Arístegui et al., 2003b, Álvarez Salgado  
339 et al., 2007, Alonso-González et al., 2009), our results point out to the horizontal transport as  
340 the main source of organic carbon for the mesopelagic respiratory activity in this region.

341 Vertical fluxes of sinking particulate organic carbon determined by surface-tethered sedi-  
342 ment traps deployed at 200 m at ESTOC, covering seasonality during three years, ranged be-  
343 tween 0.097 and 0.173 mol C m<sup>-2</sup> y<sup>-1</sup>) (Helmke et al., 2010), which is about one order of mag-  
344 nitude lower compared to our estimates of mesopelagic respiration (2.00–3.09 mol C m<sup>-2</sup> y<sup>-1</sup>)  
345 (Figure 8). By using a box model approach, Alonso-González et al. (2009) estimated the lateral  
346 transport and consumption of suspended particulate organic carbon, between 100 and 700 m,  
347 in the southern Canary Current region away from the influence of the eddy field. According  
348 to these authors, the organic carbon supply by this process was 0.52 mol C m<sup>-2</sup> y<sup>-1</sup>. Moreover,  
349 by comparing the AOU and DOC distributions, Arístegui et al. (2003b) calculated that DOC  
350 transported from the coastal African upwelling account for 27% of the mesopelagic respiration  
351 in this region. By extrapolating this result to our data, we estimated a contribution of DOC  
352 ranging between 0.54 and 0.81 mol C m<sup>-2</sup> y<sup>-1</sup>. Putzeys et al. (2011) calculated the active flux  
353 mediated by diel migrant zooplankton to be 0.053–0.15 mol C m<sup>-2</sup> y<sup>-1</sup> close to the ESTOC site.  
354 The sum of all these processes (1.2–1.7 mol C m<sup>-2</sup> y<sup>-1</sup>), which was in good agreement with the  
355 mass balance reported by Alonso-González et al. (2009) (0.88–1.87 mol C m<sup>-2</sup> y<sup>-1</sup>), accounts  
356 for 38–83% of the diagnosed respiration for the ESTOC site (Figure 8). These results highlight  
357 the lateral supply of DOC and suspended POC as the two major contributors to the mesopelagic  
358 carbon budget in this region, whereas vertical passive and active fluxes only account for less  
359 than 20% of the carbon demand.

360 In NASW, which is located further from productive areas, seasonal ventilation is considered  
361 the main source for oxygen in the mesopelagic zone (Jenkins and Goldman, 1985). Vertical  
362 fluxes of sinking particulate organic carbon determined by sediment traps at BATS (Bermuda  
363 Atlantic Time-Series Study, 31.7°N-64.2°W) are 3-4 fold higher than the values reported for  
364 ESTOC (0.3–0.8 mol C m<sup>-2</sup> y<sup>-1</sup>, Neuer et al., 2002, Helmke et al., 2010, Owens et al., 2013)  
365 (Figure 8). At BATS, the vertical export of dissolved organic carbon due to entrainment into

366 the thermocline during winter mixing has been estimated to be  $0.99\text{--}1.21 \text{ mol C m}^{-2} \text{ y}^{-1}$  (Carl-  
367 son et al., 1994). More recently, Emerson (2014) estimated as 13% the contribution of DOC  
368 to the variation in AOU below 100 m. Considering the value of total mesopelagic respiration  
369 estimated by Jenkins and Goldman (1985) ( $4.1\text{--}5.9 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ), we computed the contri-  
370 bution of DOC to total respiration as  $0.38\text{--}0.54 \text{ mol C m}^{-2} \text{ y}^{-1}$ , slightly lower than the previous  
371 estimate by Carlson et al. (1994). On the other hand, the active carbon flux by migrating zoo-  
372 plankton in this region has been quantified as  $0.06 \text{ mol C m}^{-2} \text{ y}^{-1}$  (Steinberg et al., 2000). The  
373 sum of all these fluxes ( $0.74\text{--}2.07 \text{ mol C m}^{-2} \text{ y}^{-1}$ ) accounts for 18 – 70% of the organic carbon  
374 demand between 100 and 800 m ( $2.93\text{--}4.21 \text{ mol C m}^{-2} \text{ y}^{-1}$ , Jenkins and Goldman, 1985) (Fig-  
375 ure 8). The lack of agreement between carbon sources and sinks in the BATS region has been  
376 attributed to inefficient performance of sediment traps (Buesseler et al., 2007), intense shallow  
377 remineralization between the euphotic depth (ca. 100 m) and the depth of the shallower trap  
378 (150 m), and also to the carbon supply through lateral processes (Emerson, 2014). Although,  
379 as far as we know, the lateral transport of organic carbon at this site has not been evaluated so  
380 far, its contribution to the mesopelagic carbon budget is probably lower compared to ESTOC.  
381 This argument is supported by the comparison of vertical profiles of POC collected at both  
382 sites (Figure 9). Whereas the fluxes of sinking particulate organic carbon are much lower at  
383 ESTOC, depth-integrated (150–700 m) averaged POC concentration at this site ( $2.65 \text{ mol m}^{-2}$ ,  
384 Neuer et al., 2007) is about 6-fold higher compared to BATS ( $0.41 \text{ mol m}^{-2}$ ), which may re-  
385 flect the accumulation of slow-sinking suspended particles exported from the adjacent, coastal  
386 upwelling region.

387 Recent studies argue against the common assumption that oligotrophic subtropical regions  
388 are relatively homogeneous regarding the contribution of the marine biota to the ocean carbon  
389 cycle (Mouriño-Carballido and Neuer, 2008, Neuer et al., 2002). In support of this, our re-  
390 sults highlight the importance of regional variability in the contribution of different processes  
391 of organic matter transport and cycling in the mesopelagic zone in these regions. Together with  
392 synthesis and remineralization of organic matter in shallow waters, respiratory activity in the  
393 mesopelagic controls the amount of carbon to be exported from the sunlit surface waters to the

394 deep ocean (Kwon et al., 2009). Quantifying its magnitude, but also understanding geograph-  
395 ical differences in the relevance of the vertical and horizontal processes involved in the supply  
396 of organic carbon in this layer, is crucial to determine the role of the open-ocean marine biota  
397 in the global carbon cycle.

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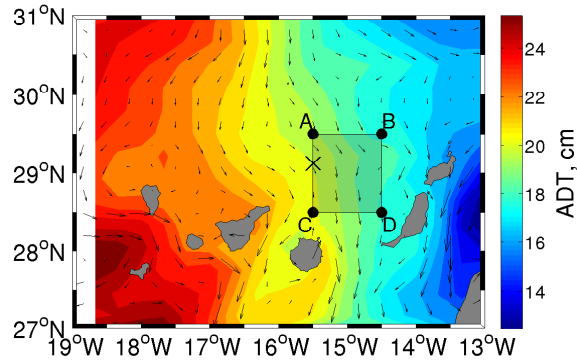
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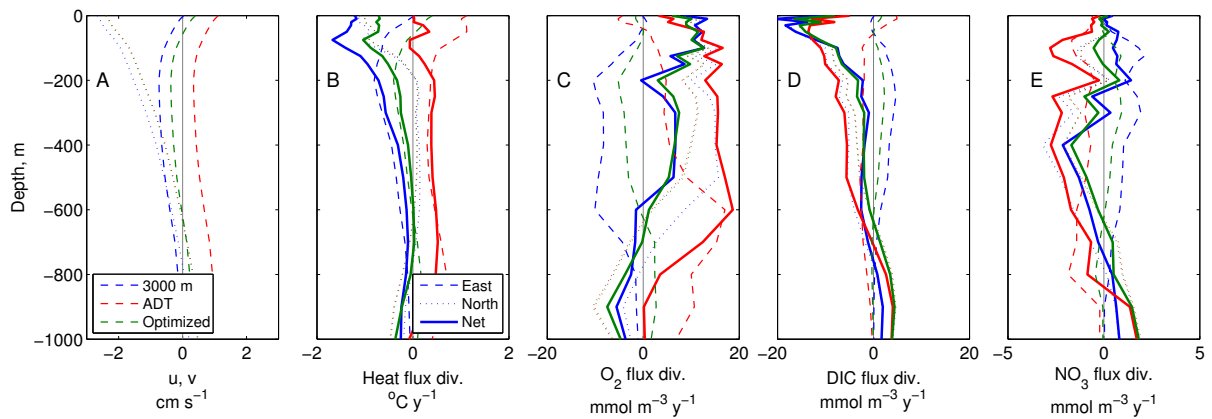
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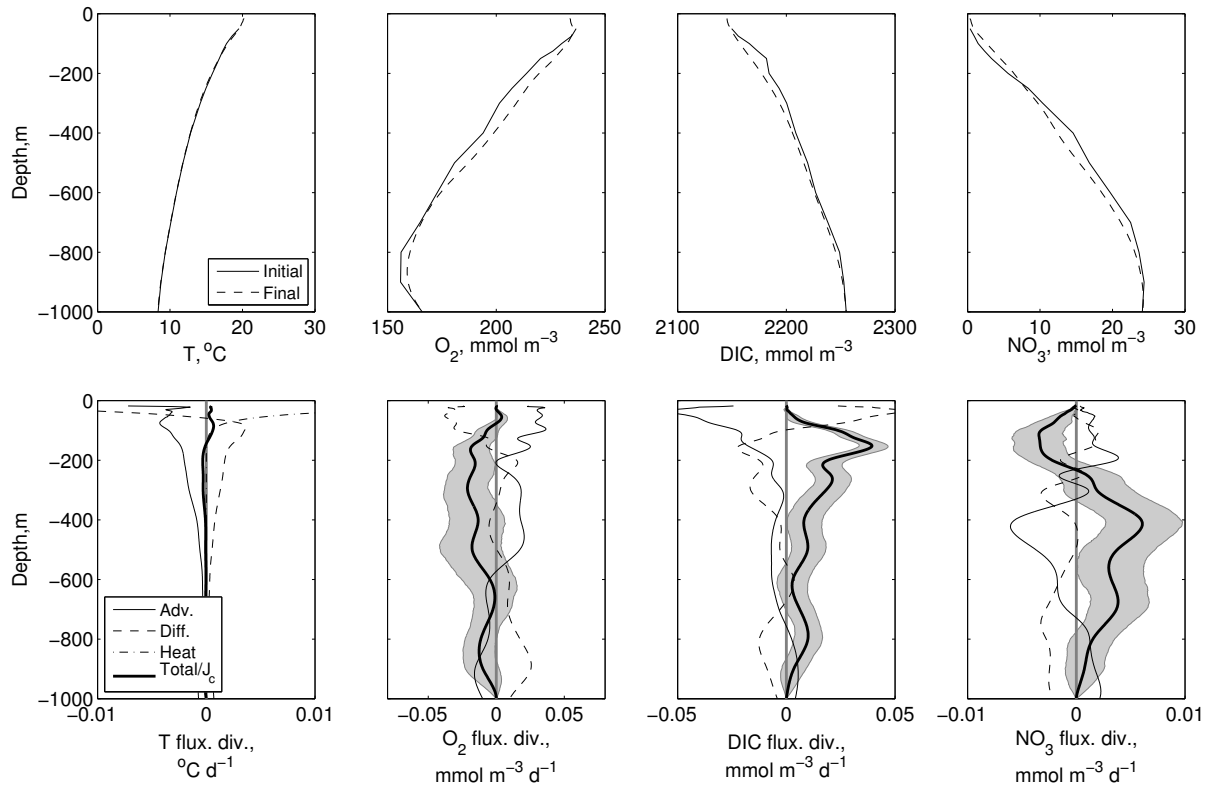
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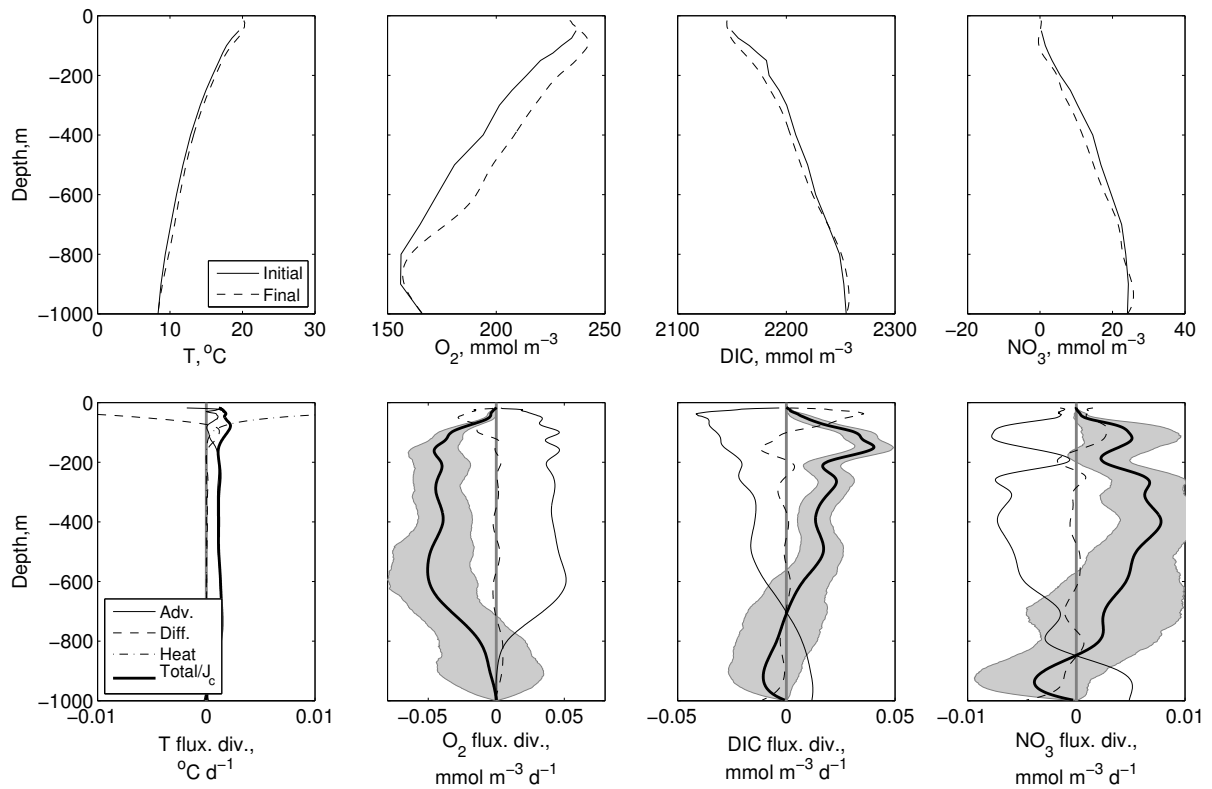
**Figure 1:** Location of the ESTOC site (×). Letters (A, B, C and D) indicate the four gridpoints from the World Ocean Atlas 2009 and GLODAP databases located closest to ESTOC. Background color is the averaged field of absolute dynamic topography (ADT) for the period 1996-2010 computed from the AVISO dataset. Arrows correspond to geostrophic surface velocities also derived from AVISO.



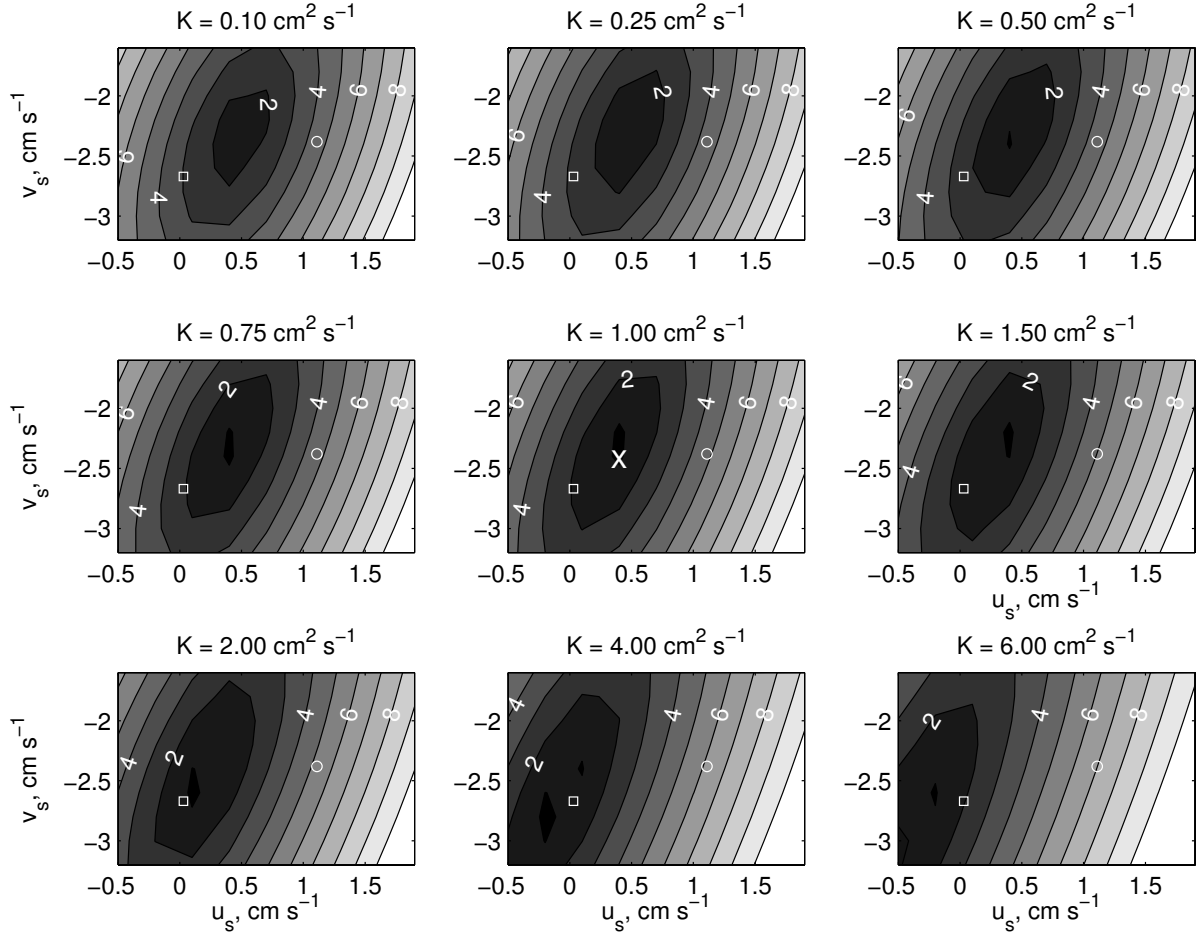
**Figure 2:** Vertical profiles of (A) geostrophic velocities, geostrophic flux divergence of (B) heat, (C) dissolved oxygen, (D) dissolved inorganic carbon, and (E) nitrate. Three different reference velocities were used for the integration of the thermal wind equations: no-motion level at 3000 m (blue), surface geostrophic velocities computed from the averaged absolute dynamic topography field (ADT) (red), and surface velocities optimized from the temperature model (green). The longitudinal (eastward), latitudinal (northward) and net components are represented by the dashed, dotted, and solid lines, respectively.



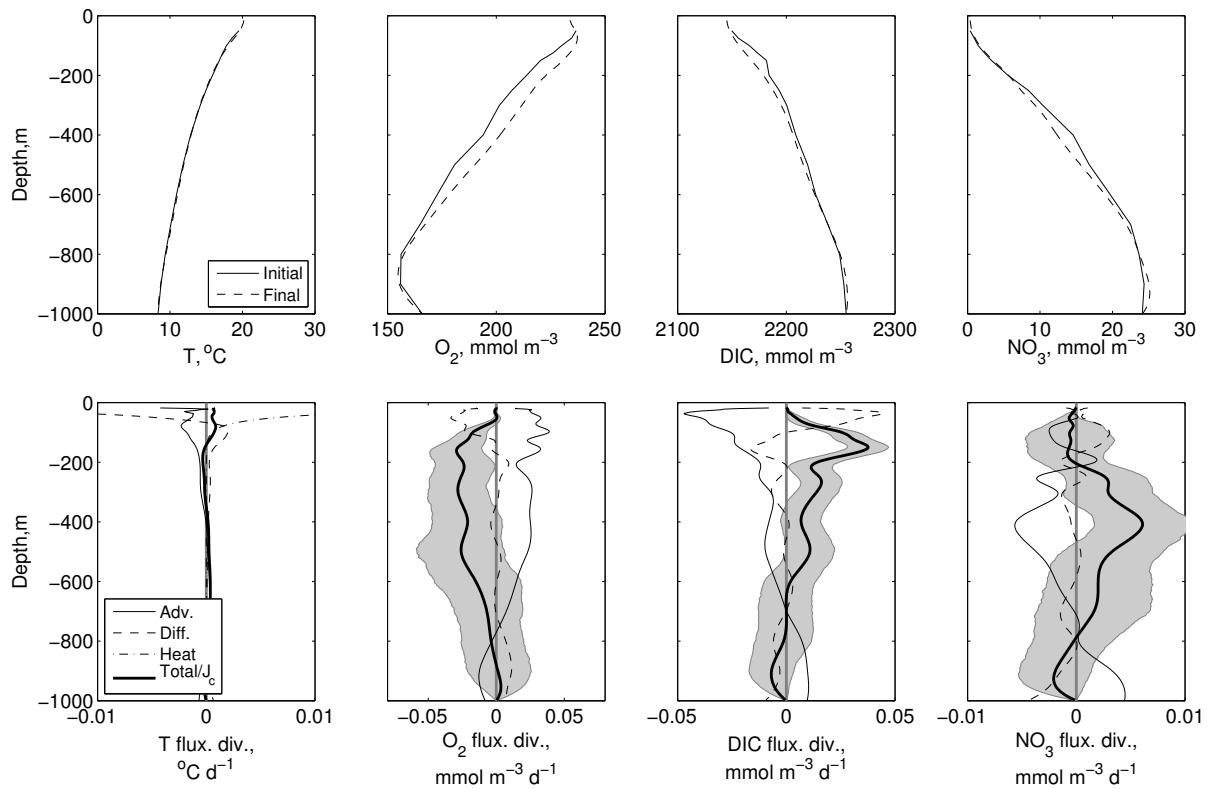
**Figure 3:** Vertical profiles of model results computed by using as reference the no-motion level at 3000 m. Upper panels correspond to initial (solid line, observed) and final (dashed line, modelled) profiles of temperature (T), oxygen ( $O_2$ ), dissolved inorganic carbon (DIC) and nitrate ( $NO_3$ ). Lower panels are total advection flux divergence (Adv., solid line), diffusive flux divergence (Diff., dashed line), solar heating (Heat, dotted–dashed) and the net photosynthesis minus respiration term ( $J_C$ , thick black line) for  $O_2$ , DIC and  $NO_3$ . For temperature the thick black line represents the net (Total) rate of change. The 25% and 75% percentiles of the biological rate diagnosed from the Monte Carlo simulations are delimited by the shaded area.



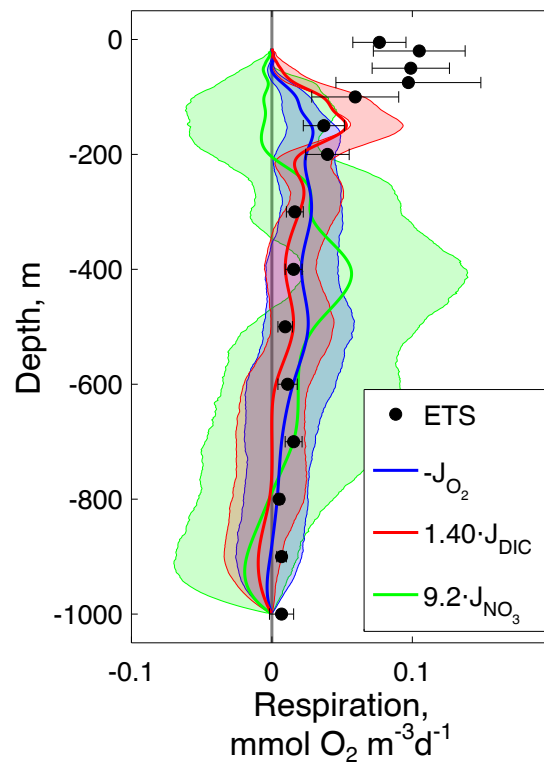
**Figure 4:** Vertical profiles of model results computed by using reference surface velocities derived from the averaged field of absolute dynamic topography (ADT). Upper panels correspond to initial (solid line, observed) and final (dashed line, modelled) profiles of temperature (T), oxygen ( $O_2$ ), dissolved inorganic carbon (DIC) and nitrate ( $NO_3$ ). Lower panels are total advection flux divergence (Adv., solid line), diffusive flux divergence (Diff., dashed line), solar heating (Heat, dotted–dashed) and the net photosynthesis minus respiration term ( $J_C$ , thick black line) for  $O_2$ , DIC and  $NO_3$ . For temperature the thick black line represents the net (Total) rate of change. The 25% and 75% percentiles of the biological rate diagnosed from the Monte Carlo simulations are delimited by the shaded area.



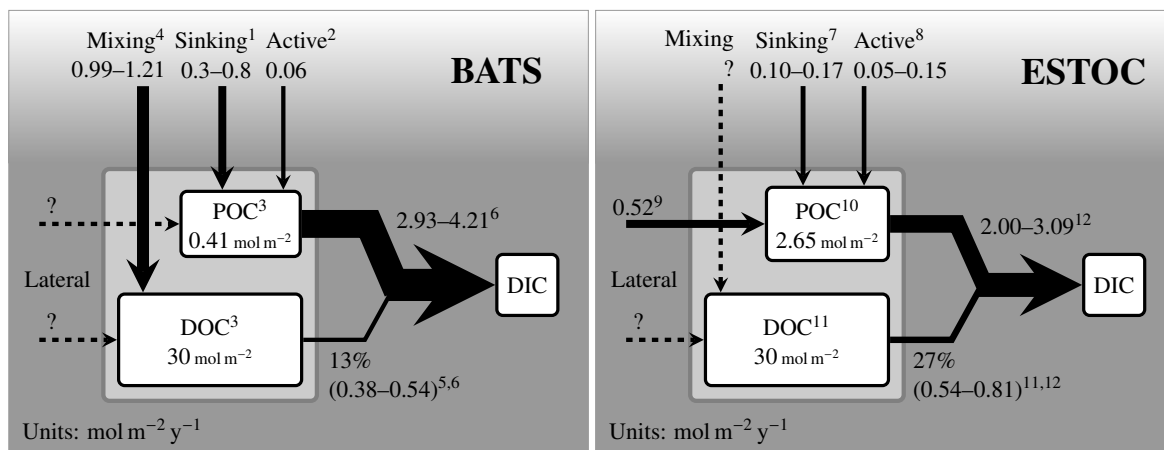
**Figure 5:** Temperature costs function (%) evaluated for a range of vertical diffusivity ( $K$ ) and reference surface velocities used for the geostrophic transport calculation ( $u_s$ ,  $v_s$ ). The  $\square$  and  $\circ$  represent the surface geostrophic velocities calculated from the thermal wind equations by using as reference the no-motion level at 3000 m, and the averaged field of absolute dynamic topography (ADT), respectively (see Table 1). The white  $\times$  indicates the optimal values chosen for  $K$ ,  $u_s$  and  $v_s$ .  $K$  values higher than  $1 \text{ cm}^2 \text{ s}^{-1}$  were considered unrealistic.



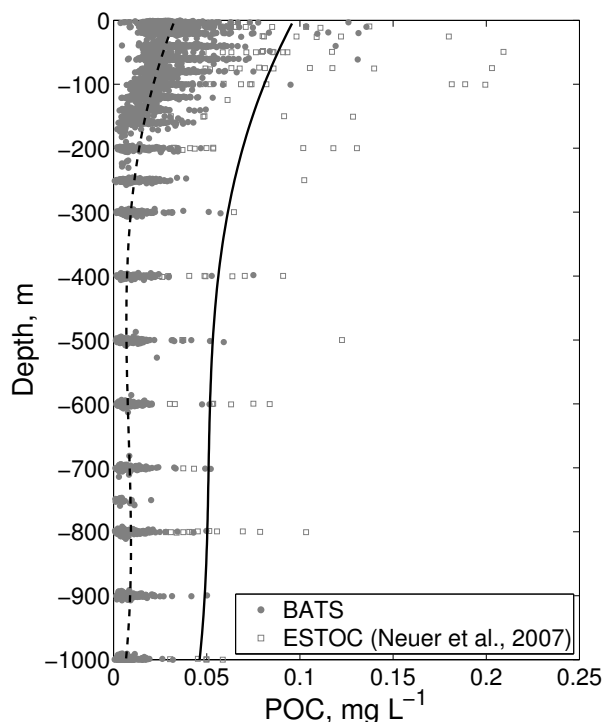
**Figure 6:** Vertical profiles of model results computed by using reference surface velocities diagnosed from the temperature model. Upper panels correspond to initial (solid line, observed) and final (dashed line, modelled) profiles of temperature (T), oxygen ( $O_2$ ), dissolved inorganic carbon (DIC) and nitrate ( $NO_3$ ). Lower panels are total advection flux divergence (Adv., solid line), diffusive flux divergence (Diff., dashed line), solar heating (Heat, dotted–dashed) and the net photosynthesis minus respiration term ( $J_C$ , thick black line) for  $O_2$ , DIC and  $NO_3$ . For temperature the thick black line represents the net (Total) rate of change. The 25% and 75% percentiles of the biological rate diagnosed from the Monte Carlo simulations are delimited by the shaded area.



**Figure 7:** Vertical distribution of averaged respiration rates estimated from the tracer conservation model and from enzymatic electron transport system (ETS) measurements carried out at the ESTOC site. Error bars correspond to standard deviations. Blue, red and green thick lines represent the biological terms for oxygen ( $O_2$ ), dissolved inorganic carbon (DIC) and nitrate ( $NO_3$ ) respectively, computed from the tracer conservation model for the optimal  $K$ ,  $u_s$  and  $v_s$  configuration. The  $J_{DIC}$  term was converted to oxygen units assuming Redfield stoichiometry. The 25% and 75% percentiles of the biological terms diagnosed from the Monte Carlo simulations are delimited by the shaded areas.



**Figure 8:** Mesopelagic carbon budget for the BATS (Bermuda Atlantic Time-Series Study, 31.7°N-64.2°W) and ESTOC (European Station for Time-Series in the Ocean, 15.5 °W, 29.1 °N) sites. Units are  $\text{mol m}^{-2} \text{y}^{-1}$  unless indicated; DIC, dissolved inorganic carbon, POC and DOC, particulate and dissolved organic carbon, respectively. References: <sup>1</sup>Helmke et al. (2010), Owens et al. (2013); <sup>2</sup>Steinberg et al. (2000); <sup>3</sup><http://bats.bios.edu/>; <sup>4</sup>Carlson et al. (1994); <sup>5</sup>Emerson (2014); <sup>6</sup>Jenkins and Goldman (1985); <sup>7</sup>Helmke et al. (2010); <sup>8</sup>Putzeys et al. (2011); <sup>9</sup>Alonso-González et al. (2009); <sup>10</sup>Neuer et al. (2007); <sup>11</sup>Arístegui et al. (2003b); <sup>12</sup>this study.



**Figure 9:** Vertical distribution of particulate organic carbon (POC) for the BATS and ESTOC sites. Data for BATS correspond to the 1988-2012 period (<http://bats.bios.edu/>), whereas for ESTOC were adapted from Neuer et al. (2007) and correspond to the 1996-1999 period. Polynomial (cubic) fits are shown.



**Table 1:** Geostrophic transports computed by using three different reference velocities: no-motion level at 3000 m, surface geostrophic velocities computed from the averaged field of absolute dynamic topography (ADT), and optimal surface velocities diagnosed from the temperature model.  $u_s$  and  $v_s$  are the eastward and northward surface velocities, respectively. Depth-integrated (150–700 m) longitudinal, latitudinal and net geostrophic flux divergences are shown for temperature (T), oxygen ( $O_2$ ), dissolved inorganic carbon (DIC) and nitrate ( $NO_3$ ).

		Geostrophic velocity reference		
		3000 m	ADT	Optimized
$u_s$ , $cm\ s^{-1}$		$0.03 \pm 0.52$	$1.11 \pm 0.66$	$0.40 \pm 0.20$
$v_s$ , $cm\ s^{-1}$		$-2.67 \pm 0.37$	$-2.39 \pm 0.78$	$-2.40 \pm 0.20$
T	Long. Flux. Div.	$-259 \pm 49$	$209 \pm 56$	$-98 \pm 43$
	Lat. Flux. Div.	$56 \pm 44$	$24 \pm 37$	$25 \pm 37$
	Net Flux. Div.	$-203 \pm 66$	$233 \pm 67$	$-73 \pm 57$
$^{\circ}C\ m\ y^{-1}$	Long. Flux. Div.	$-4.78 \pm 2.08$	$4.80 \pm 2.31$	$-1.50 \pm 1.08$
	Lat. Flux. Div.	$6.75 \pm 2.39$	$3.91 \pm 1.60$	$4.06 \pm 1.63$
	Net Flux. Div.	$1.97 \pm 3.17$	$8.71 \pm 2.81$	$2.56 \pm 1.96$
$O_2$	Long. Flux. Div.	$-4.78 \pm 2.08$	$4.80 \pm 2.31$	$-1.50 \pm 1.08$
	Lat. Flux. Div.	$6.75 \pm 2.39$	$3.91 \pm 1.60$	$4.06 \pm 1.63$
	Net Flux. Div.	$1.97 \pm 3.17$	$8.71 \pm 2.81$	$2.56 \pm 1.96$
DIC	Long. Flux. Div.	$1.65 \pm 0.79$	$-1.28 \pm 1.04$	$0.65 \pm 0.38$
	Lat. Flux. Div.	$-2.87 \pm 0.92$	$-1.64 \pm 0.62$	$-1.70 \pm 0.64$
	Net Flux. Div.	$-1.22 \pm 1.21$	$-2.92 \pm 1.22$	$-1.06 \pm 0.74$
$mol\ m^{-2}\ y^{-1}$	Long. Flux. Div.	$1.65 \pm 0.79$	$-1.28 \pm 1.04$	$0.65 \pm 0.38$
	Lat. Flux. Div.	$-2.87 \pm 0.92$	$-1.64 \pm 0.62$	$-1.70 \pm 0.64$
	Net Flux. Div.	$-1.22 \pm 1.21$	$-2.92 \pm 1.22$	$-1.06 \pm 0.74$
$NO_3$	Long. Flux. Div.	$0.63 \pm 0.34$	$-0.54 \pm 0.43$	$0.23 \pm 0.16$
	Lat. Flux. Div.	$-0.98 \pm 0.38$	$-0.50 \pm 0.25$	$-0.53 \pm 0.25$
	Net Flux. Div.	$-0.35 \pm 0.52$	$-1.04 \pm 0.49$	$-0.30 \pm 0.30$
$mol\ m^{-2}\ y^{-1}$	Long. Flux. Div.	$0.63 \pm 0.34$	$-0.54 \pm 0.43$	$0.23 \pm 0.16$
	Lat. Flux. Div.	$-0.98 \pm 0.38$	$-0.50 \pm 0.25$	$-0.53 \pm 0.25$
	Net Flux. Div.	$-0.35 \pm 0.52$	$-1.04 \pm 0.49$	$-0.30 \pm 0.30$

**Table 2:** Depth-integrated (150–700 m) model terms computed from the model runs using three different reference levels: no-motion level at 3000 m, surface geostrophic velocities computed from the averaged field of absolute dynamic topography (ADT), and optimal surface velocities diagnosed from the temperature model. Optimal diffusivity ( $K_{op}$ ), horizontal advection (H. adv), vertical advection (V. adv), vertical diffusion (V. diff.), solar heating and biological remineralization (Remin.) terms are shown. The model cost for the temperature model and the detection limit for the respiration rates are also shown (see Methods).

		Geostrophic velocity reference		
		3000 m	ADT	Optimized
$K_{op}$ , $cm^2\ s^{-1}$		3.9	0.4	1.0
T	H. adv	$-237 \pm 206$	$198 \pm 183$	$-52 \pm 299$
	V. adv	$31 \pm 119$	$31 \pm 121$	$31 \pm 119$
	V. diff.	$179 \pm 115$	$15 \pm 20$	$42 \pm 32$
	Solar Heat	$0.37 \pm 0.01$	$0.37 \pm 0.01$	$0.37 \pm 0.01$
	Cost	1.8%	3.0%	1.6%
$^{\circ}C\ m\ y^{-1}$	H. adv	$-237 \pm 206$	$198 \pm 183$	$-52 \pm 299$
	V. adv	$31 \pm 119$	$31 \pm 121$	$31 \pm 119$
	V. diff.	$179 \pm 115$	$15 \pm 20$	$42 \pm 32$
	Solar Heat	$0.37 \pm 0.01$	$0.37 \pm 0.01$	$0.37 \pm 0.01$
	Cost	1.8%	3.0%	1.6%
$O_2$	H. adv	$1.56 \pm 4.56$	$8.42 \pm 4.30$	$3.80 \pm 7.41$
	V. adv	$0.41 \pm 1.59$	$0.42 \pm 1.62$	$0.41 \pm 1.60$
	V. diff.	$0.75 \pm 0.84$	$0.02 \pm 0.26$	$0.18 \pm 0.45$
	Remin.	$-2.72 \pm 3.90$	$-8.86 \pm 3.93$	$-4.39 \pm 7.02$
	Det.Lim.	0.38	0.61	0.35
$mol\ m^{-2}\ y^{-1}$	H. adv	$1.56 \pm 4.56$	$8.42 \pm 4.30$	$3.80 \pm 7.41$
	V. adv	$0.41 \pm 1.59$	$0.42 \pm 1.62$	$0.41 \pm 1.60$
	V. diff.	$0.75 \pm 0.84$	$0.02 \pm 0.26$	$0.18 \pm 0.45$
	Remin.	$-2.72 \pm 3.90$	$-8.86 \pm 3.93$	$-4.39 \pm 7.02$
	Det.Lim.	0.38	0.61	0.35
DIC	H. adv	$-5.08 \pm 15.50$	$-6.86 \pm 15.54$	$-5.56 \pm 15.68$
	V. adv	$3.89 \pm 15.34$	$3.89 \pm 15.35$	$3.89 \pm 15.35$
	V. diff.	$-1.27 \pm 0.78$	$-0.12 \pm 0.13$	$-0.33 \pm 0.21$
	Remin.	$2.46 \pm 1.62$	$3.09 \pm 1.63$	$2.00 \pm 2.63$
	Det.Lim.	0.43	1.01	0.40
$mol\ m^{-2}\ y^{-1}$	H. adv	$-5.08 \pm 15.50$	$-6.86 \pm 15.54$	$-5.56 \pm 15.68$
	V. adv	$3.89 \pm 15.34$	$3.89 \pm 15.35$	$3.89 \pm 15.35$
	V. diff.	$-1.27 \pm 0.78$	$-0.12 \pm 0.13$	$-0.33 \pm 0.21$
	Remin.	$2.46 \pm 1.62$	$3.09 \pm 1.63$	$2.00 \pm 2.63$
	Det.Lim.	0.43	1.01	0.40
$NO_3$	H. adv	$-0.35 \pm 0.69$	$-1.03 \pm 0.70$	$-0.50 \pm 1.07$
	V. adv	$0.01 \pm 0.03$	$0.00 \pm 0.02$	$0.01 \pm 0.03$
	V. diff.	$-0.20 \pm 0.18$	$-0.04 \pm 0.06$	$-0.07 \pm 0.09$
	Remin.	$0.54 \pm 0.64$	$1.07 \pm 0.68$	$0.57 \pm 1.05$
	Det.Lim.	0.09	0.22	0.08
$mol\ m^{-2}\ y^{-1}$	H. adv	$-0.35 \pm 0.69$	$-1.03 \pm 0.70$	$-0.50 \pm 1.07$
	V. adv	$0.01 \pm 0.03$	$0.00 \pm 0.02$	$0.01 \pm 0.03$
	V. diff.	$-0.20 \pm 0.18$	$-0.04 \pm 0.06$	$-0.07 \pm 0.09$
	Remin.	$0.54 \pm 0.64$	$1.07 \pm 0.68$	$0.57 \pm 1.05$
	Det.Lim.	0.09	0.22	0.08