

Mechanisms controlling the air–sea CO₂ flux in the North Sea

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Abstract

The mechanisms driving the air–sea exchange of carbon dioxide (CO₂) in the North Sea are investigated using the three–dimensional coupled physical–biogeochemical model ECOHAM. We validate our simulations using field data for the years 2001–2002 and identify the controls of the air–sea CO₂ flux for two locations representative for the North Sea’s biogeochemical provinces. In the seasonally stratified northern region, net CO₂ uptake is high (2.06 mol m^{–2}a^{–1}) due to high net community production (NCP) in the surface water. Overflow production releasing semi–labile dissolved organic carbon needs to be

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considered for a realistic simulation of the low dissolved inorganic carbon (DIC) concentrations observed during summer. This biologically driven carbon drawdown outcompetes the temperature-driven rise in CO₂ partial pressure (pCO₂) during the productive season. In contrast, the permanently mixed southern region is a weak net CO₂ source (0.78 mol m⁻²a⁻¹). NCP is generally low except for the spring bloom because remineralization parallels primary production. Here, the pCO₂ is dominated by temperature.

Key words: CO₂ air-sea flux, continental shelf pump, biogeochemical modelling, ECOHAM, North Sea

1. Introduction

2 The role of coastal shelf seas in the exchange of CO₂ between atmosphere
3 and ocean has been in the focus of many investigations over the past few years
4 (Borges, 2005). Despite evidence of the shelf seas' significant contribution,
5 global estimates of current and future ocean carbon uptake often neglect shelf
6 areas (e.g. *Takahashi et al.*, 2009). The North Sea and other shelf seas have
7 been identified as continental shelf pumps, transferring atmospheric CO₂ into
8 the ocean interior via physical and/or biological mechanisms (e.g. *Tsunogai*
9 *et al.*, 1999; *Thomas et al.*, 2004; *Borges et al.*, 2005). The mechanisms of
10 this CO₂ uptake and their seasonality, however, are still poorly understood.

11 The North Sea constitutes of two biogeochemical provinces (*Thomas*
12 *et al.*, 2004): In the shallow southern North Sea, biological uptake and re-
13 lease of dissolved inorganic carbon (DIC) occur in a single compartment
14 with a mixed water column throughout the year. As a result, after the initial
15 DIC drawdown during the spring phytoplankton bloom the DIC remains at

16 intermediate levels throughout the mixed water column (Fig. 1). In the sea-
17 sonally stratified northern part, primary production draws down DIC in the
18 surface mixed layer. Organic material sinks into the subsurface layer where
19 remineralization releases DIC with no contact to the atmosphere. Low DIC
20 levels prevail in the surface layer, while the DIC-enriched deeper waters are
21 exported to the adjacent North Atlantic. In fall, mixing and remineralization
22 restore uniform high winter DIC levels in both regions (Bozec et al., 2006).
23 Weak annual net air-sea CO₂ fluxes have been reported for the southern
24 regions, while the North has been identified as a strong sink for atmospheric
25 CO₂ (Thomas et al., 2004).

26 In this study, we unravel the biogeochemical dynamics controlling the
27 air-sea CO₂ fluxes in detail for two representative locations in the North Sea
28 employing a three-dimensional coupled physical-biogeochemical ecosystem
29 model.

30 **2. Methods**

31 *2.1. The model*

32 We use the three-dimensional ecosystem model ECOHAM (ECOlogical
33 model, HAMBurg; Pätsch and Kühn, 2008), consisting of a biogeochemical
34 model coupled to the hydrodynamical HAMBurg Shelf Ocean Model (HAM-
35 SOM; Backhaus, 1985; Pohlmann, 1996). Simulations for the years 2001-
36 2002 comprise carbon (C), nitrogen (N) and oxygen cycles including state
37 variables DIC, total alkalinity (TA), bulk phytoplankton, bulk zooplankton,
38 bacteria, detritus and dissolved organic matter (DOM).

39 DIC is calculated prognostically while TA is restored to yield daily val-
40 ues. A relaxation time of 14 days allows for short-term variability. Restoring
41 (TA) and initial values (DIC and TA) within the North Sea are taken from
42 observational data (Thomas et al., 2005, 2009) obtained during four cruises
43 in August/September 2001, November 2001, February 2002 and May 2002
44 at 97 stations on a $1^\circ \times 1^\circ$ grid (see Thomas, 2002, for details). For the
45 adjacent regions of the North Atlantic, DIC initial and boundary condi-
46 tions are taken from CDIAC (Carbon Dioxide Information Analysis Center:
47 www.cdiac.ornl.gov; data from NDP 076). Here, above 100 m water depth
48 DIC values are derived using the T-S-nitrate correlation proposed by Lee
49 et al. (1999) with T, S and nitrate data from Conkright et al. (2002). The
50 latter data are also used as boundary conditions for nitrate. TA initial and
51 restoring values for the adjacent North Atlantic are taken from CDIAC NDP
52 076. For all other state variables, reflecting boundary conditions are used be-
53 cause of the lack of sufficient data. The model is forced by six-hourly wind
54 stress, air pressure and temperature, humidity, cloudiness and six-hourly
55 short wave radiation recalculated to two-hourly resolution. Data stem from
56 the ERA-40 reanalysis data provided by the European Centre for Medium-
57 Range Weather Forecasts with a spatial resolution of 1.125° (ECMWF, 2005).
58 River inputs of DIC, particulate organic C and N, nitrate and ammonium are
59 taken from Pätsch and Lenhart (2004) as daily data for the German, Dutch
60 and Belgian rivers. For the Scandinavian and British river loads, data from
61 Heath et al. (2005) representing annual loads of the year 1990 are used.

62 In the model, C- and N-cycles are coupled via several fixed C/N-ratios for
63 phytoplankton, zooplankton and bacteria. Detritus and DOM have flexible

64 C/N-ratios, since the C and N contents are simulated independent from each
65 other.

66 *2.2. Overflow production*

67 Shifts in environmental factors such as light and nutrients can cause the
68 excretion of organic carbon from phytoplankton cells (Mague et al., 1980).
69 This extracellular release of organic carbon leads to the formation of high
70 molecular dissolved organic matter with a negligible content of nitrogen
71 ("overflow production", Fogg, 1983). This enhanced exudation of DOC is
72 often observed when inorganic nutrients become depleted but photosynthe-
73 sis continues. The excess DIC uptake without corresponding nutrient uptake
74 is therefore also referred to as "carbon overconsumption" (Toggweiler, 1993),
75 and facilitates a non-Redfield pathway for carbon fixation. As physiological
76 basis e.g. Geider and MacIntyre (2002) discuss the glycolate metabolism as
77 a means of reducing oxidative stress at high irradiance (Kozaki and Takeba,
78 1996) due to photorespiration.

79 For the fate of the extracellular DOC from overflow production two path-
80 ways are discussed (Schartau et al., 2007). The excess DIC can be transferred
81 to the labile DOC pool which is taken up by bacteria (e.g. Kähler and Koeve,
82 2001). Alternatively, a fraction of the exuded DOC consisting of polysaccha-
83 rides can fuel the formation of transparent exopolymer particles (TEP; Mop-
84 per et al., 1995; Zhou et al., 1998). For *Phaeocystis* colonies, for instance,
85 fixation of carbon well above the Redfield ratio is linked to increased produc-
86 tion of mainly polysaccharidic mucilaginous matrix under low nutrient, high
87 light conditions (see Bozec et al., 2006, and references therein), which again
88 may lead to enhanced TEP formation (Mari et al., 2005). Field observations

89 in various areas including the Northeast Atlantic and the English Channel
 90 show that the increase of DOC during the productive season significantly
 91 exceeds the corresponding DON increase multiplied by the Redfield ratio
 92 (Williams, 1990; Kähler and Koeve, 2001). The two pathways have different
 93 implications for export of carbon from the upper ocean depending on which
 94 form of carbon, DOC vs. POC, is finally produced.

95 This study intends to elucidate whether non-Redfield processes need to
 96 be taken into account for (future) modelling studies in highly dynamic ocean
 97 regions like shelf seas. Consequently, for this application C and N uptake
 98 by phytoplankton are decoupled to permit overflow production of C-rich,
 99 N-deplete DOM, while the formulation is deliberately kept simple.

100 Total net primary production (flux dic_phc) consists of a Redfield-based
 101 portion (NPP_{red} ; flux dic_phc_{red}) and the overflow production (flux dic_phc_{exc})

$$dic_phc = dic_phc_{red} + dic_phc_{exc} \quad . \quad (1)$$

102 Nutrient-limited primary production is applied in both the phytoplankton C
 103 and N equations of state, applying the Redfield ratio for conversion between C
 104 and N units. It is formulated as Michaelis-Menten equation for two nutrients

$$dic_phc_{red} = T_{fac} \cdot F_{light} \cdot v_P \cdot (Q1 + Q2) \cdot phc \quad , \quad (2)$$

105 where $Q1 = \frac{\frac{n3n}{K_1}}{1 + \frac{n3n}{K_1} + \frac{n4n}{K_2}}$ and $Q2 = \frac{\frac{n4n}{K_2}}{1 + \frac{n3n}{K_1} + \frac{n4n}{K_2}}$ describe limitation of primary
 106 production by nitrate ($n3n$) and ammonium ($n4n$) availability, respectively.
 107 phc is the phytoplankton concentration, T_{fac} and $F_{light} \cdot v_P$ are the tempera-
 108 ture factor and the light-dependent phytoplankton growth rate, respectively
 109 (see Tab. 1 and Pätsch and Kühn (2008) for model equations and parameter
 110 values).

111 Similar to Anderson and le B. Williams (1998) and Smith et al. (2005), the
 112 excess primary production is formulated as fraction f_{exc} of the difference be-
 113 tween production limited by both nutrients and light and nutrient-saturated,
 114 only light-limited production (Bratbak and Thingstad, 1985)

$$dic_phc_{exc} = f_{exc} \cdot (1 - (Q1 + Q2)) \cdot T_{fac} \cdot F_{light} \cdot v_P \cdot phc \quad . \quad (3)$$

115 This overflow production is immediately released from the algal cells as
 116 semi-labile organic carbon (soc ; flux phc_soc). It is then degraded to la-
 117 bile DOC (flux soc_doc) available to bacteria at a rate δ_{soc} corresponding to
 118 degradation on time scales of three months:

$$\frac{\partial soc}{\partial t} = phc_soc - soc_doc = dic_phc_{exc} - \delta_{soc} \cdot soc \quad . \quad (4)$$

119 It does not increase phytoplankton biomass and constitutes a carbon flux
 120 outside the Redfield-coupled C and N fluxes in the model. This formulation
 121 represents the first pathway for extracellular organic carbon produced by
 122 overflow production. TEP formation, although likely to be of significance
 123 (Schartau et al., 2007), is omitted for the benefit of simplicity.

124 2.3. Analysis

125 Net community production (NCP) is the difference between simulated net
 126 primary production (NPP) and heterotrophic pelagic and benthic respiration
 127 (R): $NCP = NPP - R$. The pCO_2 is calculated from simulated DIC and TA.
 128 We decompose the variability of the ΔpCO_2 ($pCO_{2,sea} - pCO_{2,air}$) into the
 129 variabilities induced by variations of surface DIC, TA, temperature (T) and
 130 salinity (S): the simulated ΔpCO_2 is recalculated as function of each indi-
 131 vidual property varying over time t , while the other three are held constant

132 (t_0 =January 1), e.g.

$$\delta pCO_2(DIC) = \Delta pCO_2(DIC_t, TA_{t_0}, T_{t_0}, S_{t_0}) . \quad (5)$$

133 Two three-dimensional simulations with and without overflow production
134 each including 3 spin-up years were performed with the coupled model. We
135 assess model performance by comparing three crucial parameters of the C
136 system, DIC, pCO₂ and temperature, to observational data from four cruises
137 in August/September 2001, November 2001, February 2002 and May 2002
138 (see Thomas et al., 2005; Bozec et al., 2006, for details). The study focuses on
139 two locations representative for conditions in the northern (57.1°N, 2.25°E,
140 location N) and southern North Sea (53.9°N, 3.25°E, location S; Fig. 2) to
141 investigate the drivers of the air-sea CO₂ flux, in particular vertical water
142 column structure, rather than providing budgets on a basin-wide scale. The
143 two locations are chosen at a distance from the coast in order not to be
144 affected by river inputs, and close to observational stations to ensure compa-
145 rability between simulations and observations. They provide windows to the
146 North Sea biogeochemical system for assessing model results in detail before
147 analyzing the air-sea CO₂ flux in the southern and northern North Sea.

148 **3. Results & Discussion**

149 *3.1. Model assessment*

150 Near-surface temperature (T) is well captured by the model (Figs. 3–
151 5) with the exception of August/September at location N (Fig. 5b). The
152 simulated monthly mean and in-situ T at the day of observation are 2°C and
153 1.5°C lower than observed, respectively. These differences might reflect biases

154 in the ERA-40 air temperature forcing. Also, at this time the simulated
155 vertical temperature gradient in the water column is smaller than observed
156 (Fig. 4g). In spring, T at both locations is simulated correctly, but the water
157 column is more strongly stratified compared to the observations (Fig. 3f, 4f).
158 T values $<0.5^{\circ}\text{C}$ lower than observed in February (Fig. 5d) are within the
159 accuracy of circulation models (e.g. Pohlmann, 2006). More details on the
160 circulation model can be found in Pohlmann (1996, 2006).

161 The simulations successfully reproduce the observed DIC patterns in both
162 the southern and northern North Sea (Figs. 1, 3-5). Two biogeochemical
163 provinces are well distinguished: in the deeper North ($54.5\text{-}61^{\circ}\text{N}$) a verti-
164 cal DIC gradient establishes in summer because of biological drawdown and
165 stratification, whereas the shallow South ($51\text{-}54.5^{\circ}\text{N}$) is characterized by a
166 vertically homogeneous distribution (Figs. 1, 3 and 4).

167 Simulated surface and mixed-layer DIC levels are most sensitive to the
168 strength of overflow production. At location N, the simulation with Redfield-
169 based primary production (NPP_{red}) considerably overestimates summer sur-
170 face DIC levels by approx. $40 \mu\text{mol kg}^{-1}$ (Fig. 5c). At this time, primary
171 production is limited by inorganic nutrients, therefore the underestimated
172 mixed-layer temperature (Fig. 4g) alone cannot explain such high simulated
173 DIC levels. Observed lower DIC levels can be reproduced both in magni-
174 tude and seasonality by permitting overflow production ($f_{exc} = 0.75$). In
175 contrast, at location S, NPP_{red} ($f_{exc} = 0$) reproduces observed DIC levels at
176 all depths very well (Figs. 3a-d, 5a), while permitting overflow production
177 underestimates summer DIC levels. In agreement with observational results
178 comparing C-based NCP and NCP estimated by converting nutrient data

179 using the Redfield ratio for the same area and time (Bozec et al., 2006), we
180 take overflow production into account for the northern regions only (north
181 of 54.5°N).

182 Simulated DIC values are higher than observed in winter in particular
183 at location N (Fig. 5c). As the seasonal cycle of DIC is well captured and
184 subsurface DIC levels in summer are lower than observed (Fig. 4c and d),
185 vertical transport of C from deeper layers during fall/winter appears not to
186 be the main cause. Thus the overestimation likely reflects high DIC restor-
187 ing values at the model boundaries. Given continued uptake of DIC despite
188 inorganic nutrient limitation, the stronger stratification (Fig. 4f and g) in
189 the model leads to an overall shallower mixed layer and might result in lower
190 annual primary production and less vertical export via sinking organic mat-
191 ter. Underestimated sinking would also explain the low simulated DIC con-
192 centrations below the mixed layer (Fig. 4c). The applied sinking velocities
193 (Tab. 1; Pätsch and Kühn, 2008) are identical with values used by Fennel
194 et al. (2006) for the Middle Atlantic Bight, and are low compared to other
195 studies (e.g. Pätsch et al., 2002). In addition, TEP formation from exuded
196 DOM, which constitutes the second pathway for overflow production (Schar-
197 tau et al., 2007), might induce enhance sinking and lead to additional C
198 export to the subsurface layer. However, since the simulated nitrate profiles
199 are overestimated compared to the observations (not shown), it is also likely
200 that the model simulates water masses with a different biogeochemical sig-
201 nature entering from the outer shelf/North Atlantic area across the northern
202 boundary of the North Sea. Sensitivity studies investigating the effect of
203 different sinking velocities for organic matter as well as different remineral-

204 ization rates show only small variations in DIC, $\Delta p\text{CO}_2$ and air–sea CO_2 flux
205 in general, and in particular compared to the effect of changing the degree
206 of overflow production.

207 At location S, DIC levels after the spring bloom are slightly higher than
208 observed (Fig. 5a, dotted line). During spring, the simulated DIC gradient
209 from low surface levels to winter levels at depth contrasts the observed uni-
210 form low DIC profile (Fig. 3b), in consequence of the similar, but reversed
211 temperature gradient (Fig. 3f). The corresponding observations show that
212 the water column was well mixed and the biologically mediated drawdown of
213 DIC affected the entire water column. The simulated stronger stratification
214 at this time of the year might lead to an underestimated spring bloom DIC
215 drawdown and cause the slightly higher than observed DIC levels.

216 The simulated $\Delta p\text{CO}_2$ (Fig. 6a and e) agrees well with observations in
217 both magnitude and seasonal cycle, further confirming the distinction be-
218 tween NPP_{red} at location S, and overflow production at location N. It un-
219 derestimates the observed $\Delta p\text{CO}_2$ in summer at location N and in winter at
220 location S because of lower than observed T. Overestimated $\Delta p\text{CO}_2$ values in
221 winter at location N and in spring at location S reflect higher than observed
222 DIC.

223 *3.2. $p\text{CO}_2$ and air–sea CO_2 exchange*

224 *3.2.1. Southern North Sea*

225 In the southern North Sea, NPP_{red} is high from the spring bloom in
226 March/April until fall, and low during winter (Fig. 6b). It is lower than R
227 throughout the year except for the period of the spring bloom and isolated
228 events during summer. With carbon fixation strictly coupled to inorganic

229 nutrient availability, remineralization within the mixed water column and the
230 sediment sustains a constantly high level of regenerated primary production
231 throughout the season.

232 As a result, NCP is positive only during the spring bloom, and the an-
233 nual NCP of $-1.01 \text{ mol C m}^{-2} \text{ a}^{-1}$ classifies the water column as weakly het-
234 erotrophic: remineralization of organic carbon exceeds uptake of inorganic
235 carbon. The surplus organic matter required to sustain the heterotrophic
236 status is supplied by advection from river inputs, the coastal regions, and
237 the North Atlantic via the English Channel. Other studies estimate an
238 autotrophic state for the southern North Sea (Bozec et al., 2006) and the
239 Southern Bight (Schiettecatte et al., 2007), in the latter case because of a
240 stronger spring bloom. Near-shore areas such as the Belgian coastal zone
241 have been estimated as net heterotrophic (Borges and Frankignoulle, 2002;
242 Borges et al., 2008). The simulated NPP_{red} of $191.5 \text{ g C m}^{-2} \text{ a}^{-1}$ is in the
243 lower range of observed primary production (Joint and Pomroy, 1993; Reid
244 et al., 1990), which usually shows high interannual variability (Borges et al.,
245 2008). A higher C uptake during the spring bloom would increase primary
246 production and might shift NCP values towards autotrophy.

247 Surface waters are characterized by CO_2 undersaturation in winter (Fig. 6a),
248 a short, but significant pCO_2 decrease in spring and an increase to strong
249 supersaturation during summer and fall. Changes in DIC ($\delta\text{pCO}_2(\text{DIC})$,
250 Fig. 6d) dominate the ΔpCO_2 only during November to April: in spring,
251 the positive NCP causes the DIC drawdown; in winter, DIC levels mainly
252 increase due to remineralization in November/December ($\text{NCP} < 0$) or advec-
253 tive and atmospheric inputs in February/March ($\text{NCP} > 0$, Fig. 6c). However,

254 a strong net effect of advective DIC transport on the DIC concentration can-
255 not be identified: the net change in concentration within the surface layer
256 due to advective transport is $-0.07 \text{ mmol C m}^{-2} \text{ d}^{-1}$. In the absence of
257 strong biological DIC uptake ($\text{NCP} \approx 0$) during the remainder of the year the
258 ΔpCO_2 signal is dominated by the effects of temperature ($\delta \text{pCO}_2(\text{T})$), lead-
259 ing to CO_2 supersaturation and release of CO_2 to the atmosphere in summer
260 and fall. During winter, decreasing temperatures eventually result in CO_2
261 uptake (Fig. 6a and d). Benthic calcification as driver of the ΔpCO_2 , as sug-
262 gested by Borges and Frankignoulle (2003) for the English Channel, would
263 decrease TA and lead to a net release of CO_2 to surrounding water. Since the
264 observed TA is used for restoring, any potential effect is implicitly included
265 in the model. For this location, benthic calcification does not seem to be of
266 importance in driving the air-sea CO_2 flux.

267 At the annual scale, $0.78 \text{ mol C m}^{-2} \text{ a}^{-1}$ are released to the atmosphere.
268 This value is the result of a delicate balance between the strength of net
269 carbon fixation, i.e. NCP, and the dominating temperature effect. Close to
270 neutral air-sea CO_2 exchange has been reported by other studies (Thomas
271 et al., 2004; Schiettecatte et al., 2007; Borges et al., 2008), partly with oppos-
272 ing, yet weak fluxes. Recent studies also show interannual variability of the
273 NCP and air-sea CO_2 exchange (Borges et al., 2008). These ambiguous find-
274 ings could be due to the fact that governing processes balance closely and the
275 net CO_2 flux is small, which is confirmed by all studies. In the present study,
276 this balance is robust over a range of primary production levels simulated in
277 sensitivity runs.

278 *3.2.2. Northern North Sea*

279 In the upper 0–30 m of the northern North Sea, simulated primary pro-
280 duction increases sharply during the spring bloom (Fig. 6f). After inorganic
281 nutrients are exhausted, primary production recedes with overflow produc-
282 tion constituting approx. 50% of total NPP during summer, or 34% at the
283 annual scale. About 60% of the annual primary production are respired in
284 the surface layer. The remaining organic material mostly sinks out of the
285 surface layer. A smaller amount of DIC is supplied by advection during
286 summer (Fig. 6g), which further stresses the importance of biological mech-
287 anisms for the DIC drawdown as opposed to physical transport. With an
288 average daily flux of $4.62 \text{ mmol C m}^{-2} \text{ d}^{-1}$ over the year, however, the net
289 change in concentration due to advection is small. The resulting surface layer
290 NCP is strongly positive throughout the productive season from April until
291 September until mixing starts in fall. NCP peaks during the spring bloom,
292 when respiration lags behind primary production by approx. two weeks. The
293 simulated annual primary production of $205 \text{ g C m}^{-2} \text{ a}^{-1}$ ($135 \text{ g C m}^{-2} \text{ a}^{-1}$
294 NPP_{red} only) is well within the range of observations of 119–200 $\text{g C m}^{-2} \text{ a}^{-1}$
295 (Reid et al., 1990; Joint and Pomroy, 1993) considering that these field stud-
296 ies do not account for overflow production.

297 The net annual NCP is sensitive to the strength of overflow production.
298 The simulated value of $8.01 \text{ mol C m}^{-2} \text{ a}^{-1}$ ($f_{exc} = 0.75$, 0–30 m) exceeds
299 comparable observation–based NCP estimates (Bozec et al., 2006). Compar-
300 ing primary production (PP) levels proves difficult because of limitations and
301 differences in methods estimating production from field observations (Gazeau
302 et al., 2004), and scarcity of adequate data for the North Sea. In particular,

303 the ^{14}C method has inherent conceptual problems since it gives estimates
304 which are intermediate between gross primary production (for short incuba-
305 tions) and net primary production (for long incubations, e.g. Peterson, 1980;
306 Marra, 2002). Furthermore, ^{14}C -based primary production yields results
307 for particulate phytoplankton production only and does not account for dis-
308 solved products e.g. from overflow production. Dissolved PP products have
309 been found a significant part of total PP, and are estimated to account for
310 up to 20% for oligotrophic oceanic (Morán et al., 2002) as well as eutrophic
311 coastal (Marañón et al., 2004) regions. Since in the model all overflow pro-
312 duction remains within the DOC pool, the simulated overflow production
313 also contains a potential particulate fraction created by TEP formation. It
314 is therefore likely to exceed these estimates of only dissolved PP products.
315 Sensitivity runs with a lower percentage of overflow production give lower
316 NCP values closer to other estimates, but overestimate the observed DIC.
317 Since DIC concentrations are affected via both sinking and remineralization
318 rates of POC and DOC, further work is needed, also concerning the fate of
319 DOC from overflow production in the model, to reliably capture the ratio of
320 dissolved and particulate PP.

321 The ΔpCO_2 is characterized by strongly undersaturated levels during the
322 spring bloom, when NCP is highest (Fig. 6e). Throughout the productive
323 season, ΔpCO_2 remains strongly undersaturated at nearly constant levels
324 until the onset of mixing in fall, in contrast to the shallow southern North
325 Sea. The constantly low ΔpCO_2 results from a biologically (NCP>0) driven
326 DIC drawdown, which counteracts the effect of rising temperature on the
327 ΔpCO_2 (Fig. 6h). This DIC drawdown is facilitated by overflow production

328 overcoming inorganic nutrient limitation. Sinking of organic matter and
329 slow degradation rates of semi-labile DOC maintain DIC and thus $\Delta p\text{CO}_2$
330 conditions until the onset of mixing in fall.

331 At the annual scale, $2.06 \text{ mol C m}^{-2} \text{ a}^{-1}$ CO_2 are taken up from the atmo-
332 sphere at location N, which slightly exceeds an uptake of $1.64 \text{ mol C m}^{-2} \text{ a}^{-1}$
333 estimated from observations (Thomas et al., 2005).

334 4. Conclusions

335 The air-sea CO_2 flux in the two biogeochemical provinces of the North
336 Sea is the result of a balance between temperature and biological effects,
337 which strongly depend on the stratification and its consequences for the fate
338 of biological production. In the southern North Sea, primary production
339 over long periods relies on recycled nutrients, preventing high net C fixation.
340 Temperature, and to a certain degree degradation of allochthonous organic
341 matter become the seemingly dominant drivers of the air-sea CO_2 flux. In
342 the northern North Sea, stratification of the water column permits export of
343 organic matter out of the surface layer. Overflow production under inorganic
344 nutrient limitation facilitates continued net carbon fixation counteracting the
345 temperature-driven $\Delta p\text{CO}_2$ increase during summer. The subsurface water
346 masses are enriched in DIC by remineralization, which can then be exported
347 into the North Atlantic, forcing CO_2 replenishment from the atmosphere.
348 Our model results indicate the importance of C overconsumption and dis-
349 solved products of primary production in driving CO_2 fluxes. More inves-
350 tigation are needed, however, to unravel their seasonality and mechanisms
351 under different oceanic conditions.

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501 **Figure captions**

502 **Figure 1:** Observed (a) and simulated (b) monthly mean DIC [$\mu\text{mol kg}^{-1}$]
503 along a section at 2°E in August/September 2001.

504 **Figure 2:** The model domain including the North Sea, showing the
505 section along 2°E (cf. Fig. 1), location N (57.1°N , 2.25°E) and location S
506 (53.9°N , 3.25°E). The grey boxes show the areas used for spatial averages of
507 DIC and ΔpCO_2 in Figs. 5 and 6.

508 **Figure 3:** Simulated dissolved inorganic carbon (DIC; $\mu\text{mol kg}^{-1}$) (a-
509 d) and temperature (T; $^\circ\text{C}$) (e-h) profiles compared to observations (grey
510 dots) at location S (53.9°N , 3.25°E) for (a, e) February 2001, (b, f) May
511 2001, (c, g) August/September 2001, (d, h) November 2001. Simulated val-
512 ues are monthly means with error bars indicating one temporal standard
513 deviation. DIC is shown for two cases, allowing non-Redfield overflow pro-
514 duction (squares) and primary production coupled to nutrient availability
515 via the Redfield ratio (triangles). Simulations for February and May 2001
516 are compared to observations from cruises in 2002 as guidelines.

517 **Figure 4:** Simulated dissolved inorganic carbon (DIC; $\mu\text{mol kg}^{-1}$) (a-
518 d) and temperature (T; $^\circ\text{C}$) (e-h) profiles compared to observations (grey
519 dots) at location N (57.1°N , 2.25°E) for (a, e) February 2001, (b, f) May
520 2001, (c, g) August/September 2001, (d, h) November 2001. Simulated val-
521 ues are monthly means with error bars indicating one temporal standard
522 deviation. DIC is shown for two cases, allowing non-Redfield overflow pro-
523 duction (squares) and primary production coupled to nutrient availability
524 via the Redfield ratio (triangles). Simulations for February and May 2001
525 are compared to observations from cruises in 2002 as guidelines.

526 **Figure 5:** Simulated surface dissolved inorganic carbon (DIC; $\mu\text{mol kg}^{-1}$)
527 at location S (53.9°N, 3.25°E; a) and location N (57.1°N, 2.25°E; b) for
528 Redfield primary production (dotted line) and non-Redfield overflow pro-
529 duction (dash-dotted line). Simulated near-surface temperatures (T; °C)
530 (dotted line) at location S (c) and location N (d). Simulations for 2001 are
531 compared to observations (open circles) at two stations from cruises in Au-
532 gust/September and November 2001, and February and May 2002 as guide-
533 lines. Simulated values are monthly means averaged over a $1^\circ \times 1^\circ$ area
534 corresponding to these stations, with black error bars indicating one spatial
535 standard deviation. Grey error bars indicate spatial averages \pm one stan-
536 dard deviation of three and nine observational stations in the southern and
537 northern North Sea, respectively (cf. Fig. 2). Grey shaded areas show the
538 corresponding averages \pm one standard deviation of the model data.

539 **Figure 6:** (a, e) Simulated and observed ΔpCO_2 [ppm], net community
540 production (NCP) and air-to-sea CO_2 flux [$\text{mmol C m}^{-2} \text{d}^{-1}$] (positive: CO_2
541 uptake from the atmosphere), (b, f) NCP, net primary production (NPP) and
542 respiration (R; zooplankton, bacteria and benthos), (c, g) sum of horizontal
543 and vertical advective fluxes (running average), at location S and location N
544 in the southern and northern North Sea, respectively, in 2001. Variables are
545 given for the entire water column (a-c; 0-39 m) at location S and for an upper
546 layer (e-g; 0-30 m) at location N. Two observations in May at location S
547 are two passes of the same $1^\circ \times 1^\circ$ area 15 days apart. Error bars indicate
548 spatial averages \pm one standard deviation of the observed ΔpCO_2 within
549 the same areas used in Fig. 5 (cf. Fig. 2). Mean net advective fluxes are -
550 $0.07 \text{ mmol C m}^{-2} \text{d}^{-1}$ (location S) and $4.62 \text{ mmol C m}^{-2} \text{d}^{-1}$ (location N). (d,

551 h) The simulated $\Delta p\text{CO}_2$ is recalculated as function of one varying property
552 out of surface dissolved inorganic carbon (DIC; e.g. $\delta p\text{CO}_2(\text{DIC})$), total
553 alkalinity (TA), temperature (T) and salinity (S), while the other three are
554 held constant at their value of January 1.

Table 1: Selected parameters of the biogeochemical model and their values. All rates are valid for 10°C. The full set of model equations and parameters can be found in Pätsch and Kühn (2008).

description	parameter	value	unit
Remineralization rate benthic carbon	brc	1.00	d^{-1}
Remineralization rate benthic nitrogen	brn	0.85	d^{-1}
Breakdown rate of <i>soc</i> to <i>doc</i>	δ_{soc}	0.0037	d^{-1}
Overflow production	f_{exc}	0 – 1	
Light dependency phytoplankton growth	F_{light}	0 – 1	
Half-saturation constant nitrate uptake	K_1	0.5	mmol N m^{-3}
Half-saturation constant ammonium uptake	K_2	0.05	mmol N m^{-3}
Breakdown rate slowly sinking detritus	μ_4	0.03	d^{-1}
Breakdown rate fast sinking detritus	μ_5	0.01	d^{-1}
Temperature dependency phytoplankton growth	T_{fac}	$1.5^{\frac{T-T_0}{T_0}}$	$T_0 = 10^\circ\text{C}$
Maximum phytoplankton growth rate	v_P	1.1	d^{-1}
Sinking velocity slowly sinking detritus	w_{d1}	0.1	m d^{-1}
Sinking velocity fast sinking detritus	w_{d2}	1.0	m d^{-1}

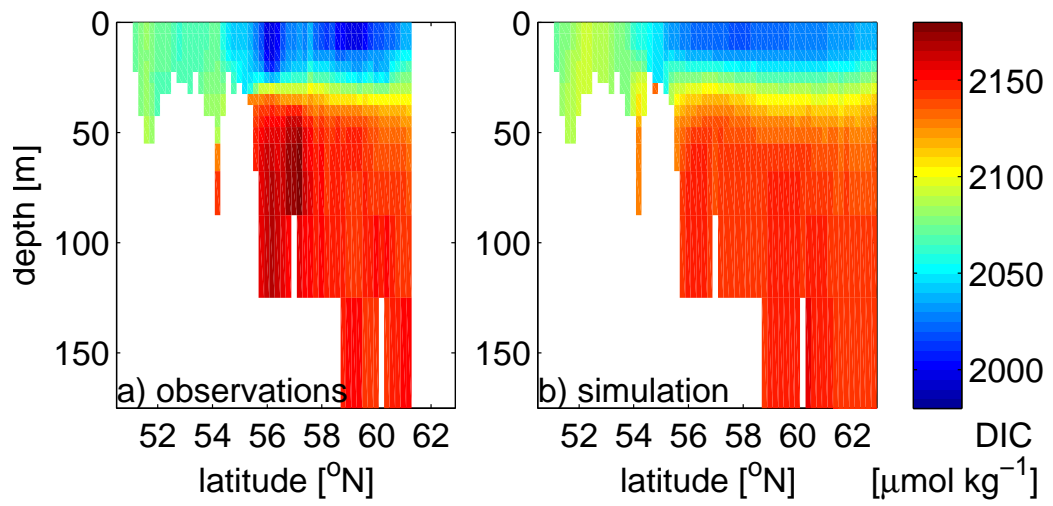


Figure 1a-b

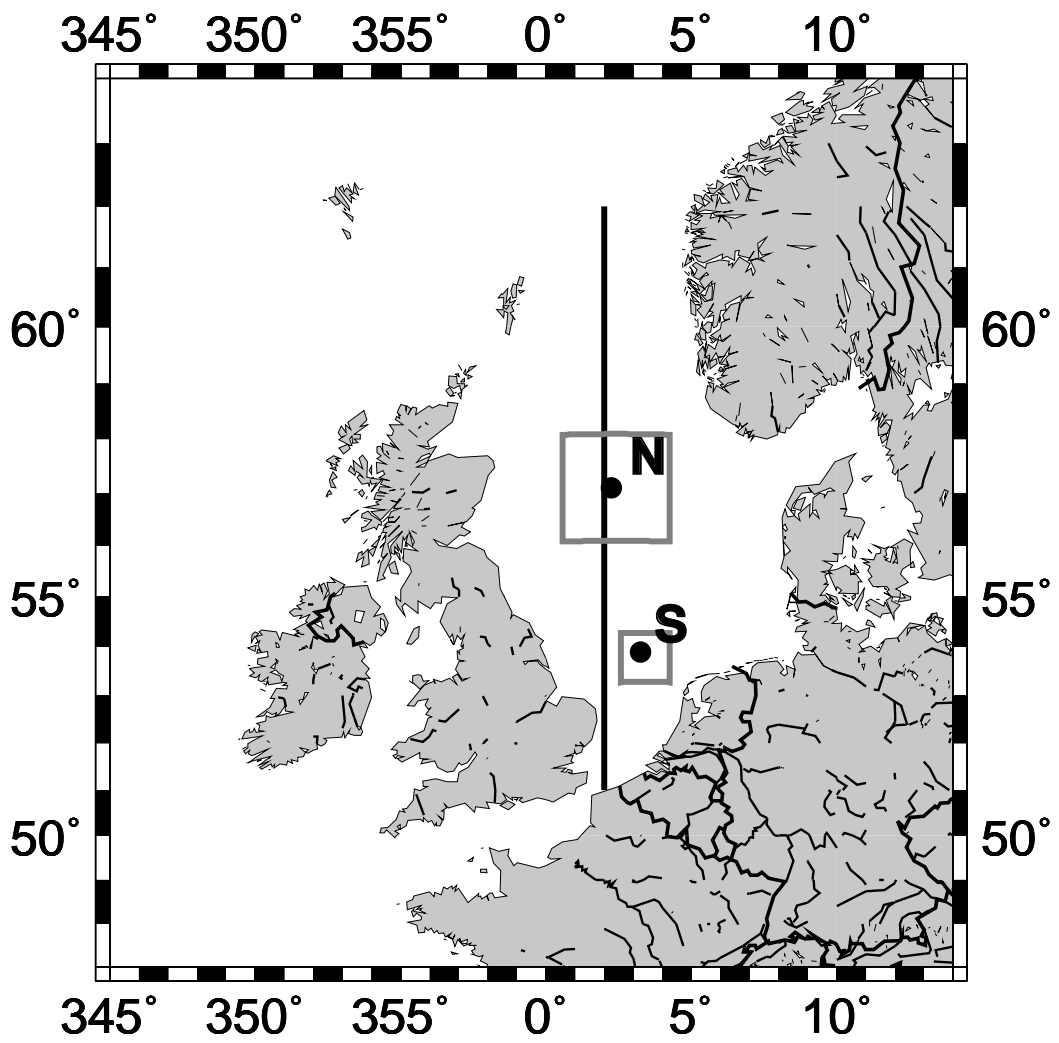


Figure 2

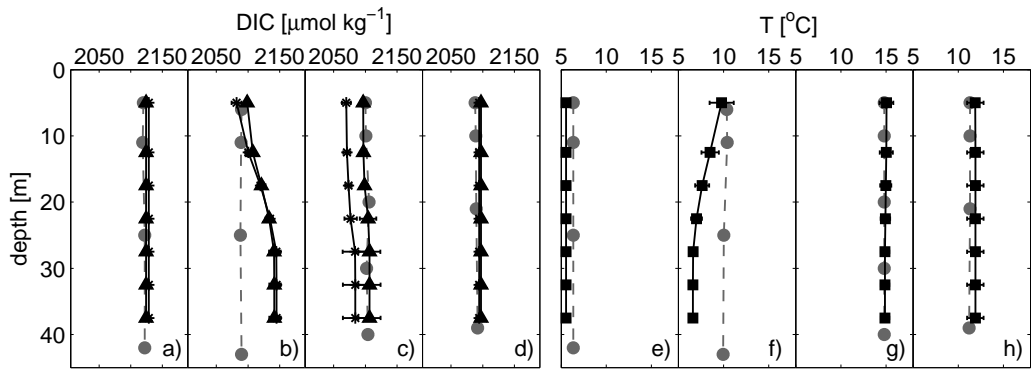


Figure 3a-h

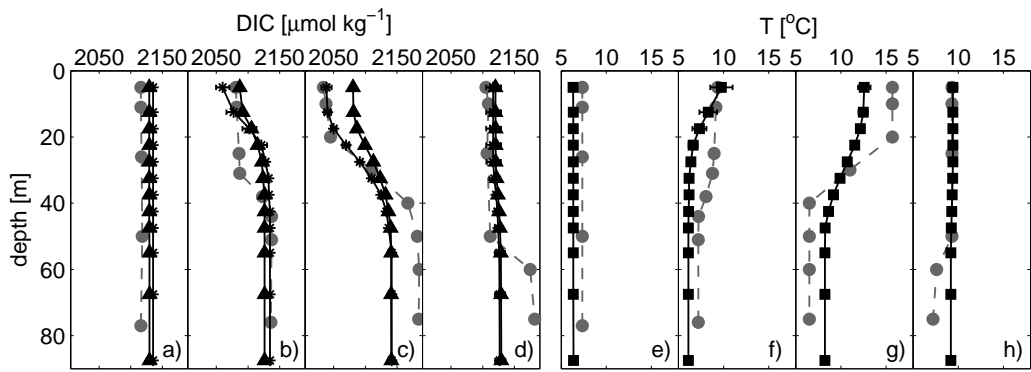


Figure 4a-h

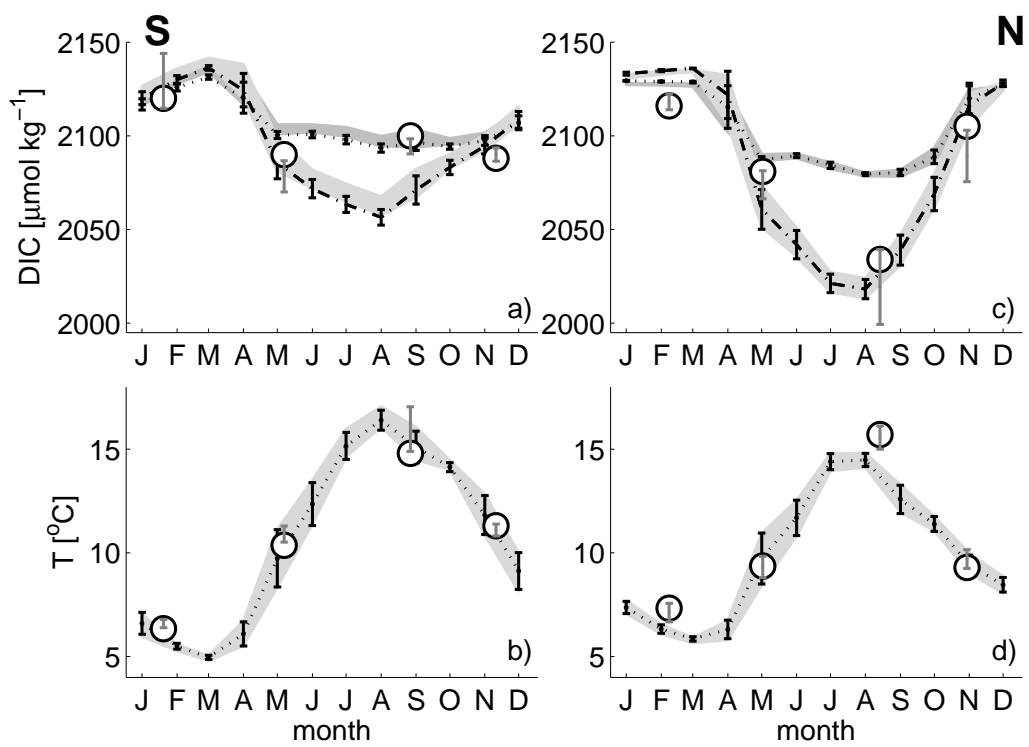


Figure 5a-d

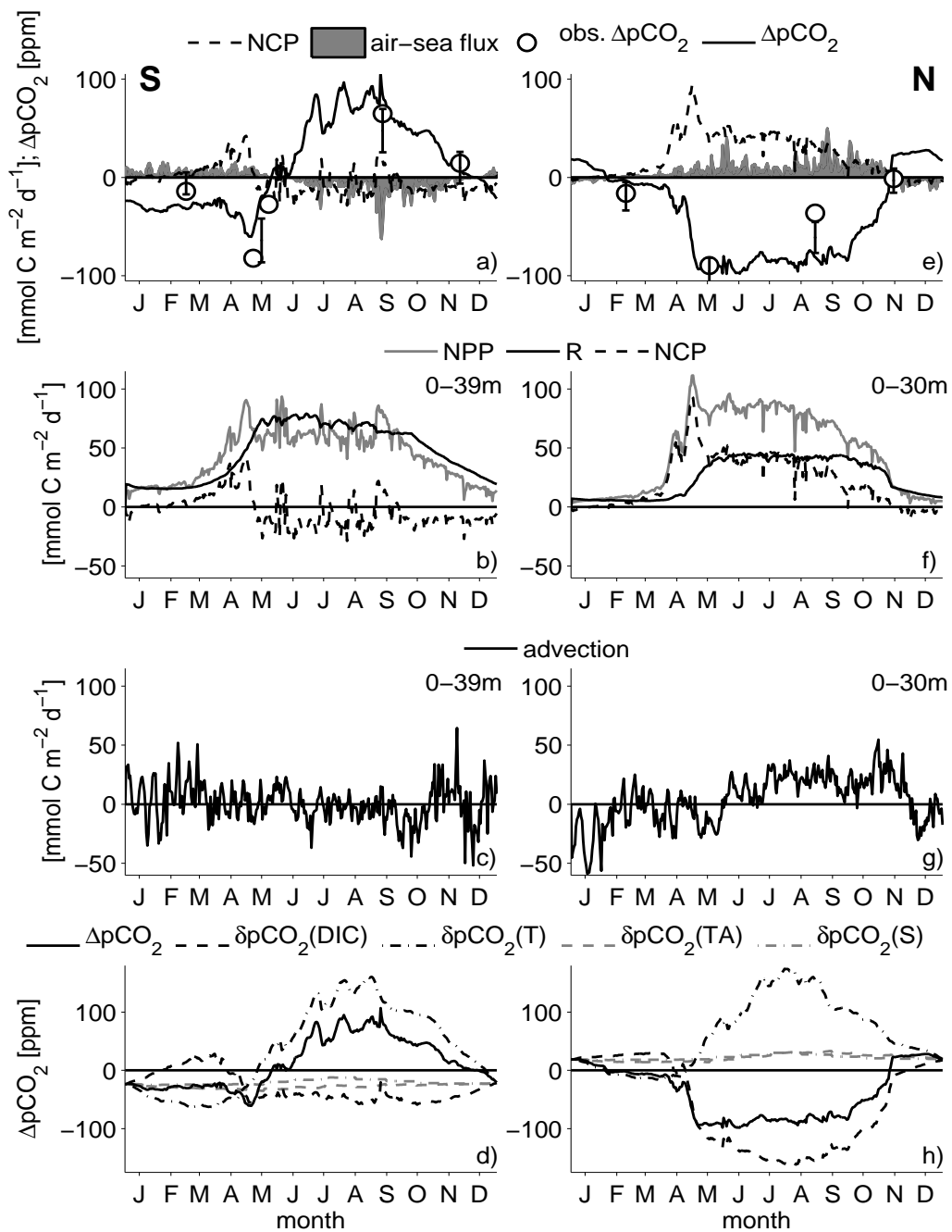


Figure 6a-h