

***Final Draft***  
**of the original manuscript:**

Stegert, C.; Moll, A.; Kreuz, M.:

**Validation of the three-dimensional ECOHAM model in the  
German Bight for 2004 including population dynamics of  
Pseudocalanus elongatus**

In: Journal of Sea Research (2008) Elsevier

DOI: 10.1016/j.seares.2008.10.011

1 Validation of the three-dimensional ECOHAM model in  
2 the German Bight for 2004 including population  
3 dynamics of *Pseudocalanus elongatus*

4 **Christoph Stegert, Andreas Moll and Markus Kreis\***

5 *Institut für Meereskunde, Universität Hamburg (ZMK-ZMAW), Bundesstr. 53,*  
6 *20146 Hamburg, Germany, moll@ifm.uni-hamburg.de.*

7 *\*now at GKSS Forschungszentrum, Max-Planck-Str. 1, 21502 Geesthacht*

8 **1. Abstract**

9 A three-dimensional ecosystem model for the North Sea which includes  
10 competition between *Pseudocalanus elongatus* and the rest of the zooplankton  
11 biomass was applied to describe the seasonal cycle of zooplankton in 2003-  
12 2004. The paper presents the comparison of simulated stage-resolved  
13 abundances with copepod counts at several stations in the German Bight during  
14 the GLOBEC-Germany project from February to October 2004. A validation of  
15 influential state variables gives confidence that the model is able to calculate  
16 reliably the stage development and abundances of *P. elongatus* as well as the  
17 range of bulk zooplankton biomass, and thus the ratio of population biomass to  
18 total biomass. In the German Bight, the population is below 20% in spring. The  
19 ratio increases up to 50% during summer. The number of generations was  
20 estimated from peaks in egg abundance to about 4-8 generations of *P. elongatus*

21 in the southern North Sea. A mean of four generations per year were estimated  
22 in the central North Sea, six to eight generations northwest of the Dogger Bank  
23 (tails end) and five generations in the German Bight.

## 24 **2. Keywords**

25 Stage-structured zooplankton population model, copepod biomass, generation  
26 time, *Pseudocalanus elongatus*, ecosystem model, ECOHAM, North Sea,  
27 German Bight

## 28 **3. Introduction**

29 Copepods as part of the zooplankton bear an important role in the marine food  
30 web as mediators between lower (i.e. phytoplankton) and higher (i.e. fish and  
31 larval fish) trophic levels. They also affect the recruitment success of larval fish,  
32 which undergoes strong inter-annual variability (Alheit et al., 2005). Thus,  
33 copepods have been investigated intensely in the North Sea during the last  
34 decades (Krause et al., 2003). In 2003-2005 an elaborate program of sampling  
35 and field studies in the German Bight was implemented within the GLOBEC-  
36 Germany project, which included studies on zooplankton: its development, the

37 influence of physical processes and the trophodynamic processes linked to larval  
38 fish (i.e. herring and sprat) (Alheit, 2007).

39 In 2004 zooplankton investigations took place during seven cruises between  
40 February to October (Renz et al., 2008). This paper describes a three-  
41 dimensional ecosystem model used for a detailed study of zooplankton and  
42 copepod population dynamics and the influence of physical and biological  
43 environmental factors.

44 Zooplankton population modelling has already been done in the North Sea at  
45 different spatial scales: Slagstad and Tande (1981) developed a process model  
46 for studying the ecophysiology of copepods, Carlotti and Radach (1996) coupled  
47 a population model to a water column model, while Heath et al. (1997) used a  
48 Lagrangean one-dimensional approach based on a three-dimensional Eulerian  
49 hydrodynamical model. Recently, Speirs et al. (2005) described the spatio-  
50 temporal distribution of a copepod population within the North Atlantic. All  
51 these papers dealt with the life cycle of *Calanus finmarchicus*, a larger copepod,  
52 which is found mostly in the northern North Sea. The main food basis of larval  
53 herring and sprat in the German Bight, however, are smaller copepods including  
54 species of the genera *Pseudocalanus* (42%), *Acartia* (11%) and *Temora* (10%)  
55 (Dickmann, 2006).

56 The southern North Sea is influenced by water masses from the Atlantic Ocean  
57 entering through the Strait of Dover in the south and via the Fair Island Current  
58 in the north flowing southward along the British coast as well as by strong,  
59 nutrient-rich fresh water inflow from continental rivers. The North Sea is  
60 characterised by an increase in depth and a decrease in primary production from  
61 the inner German Bight towards the northwest (Rick et al., 2006). This trend is  
62 interrupted by the particularly shallow Dogger Bank area north of the Southern  
63 Bight. Zooplankton in the German Bight is highly diverse and not dominated by  
64 a single species. For our investigation we have chosen *Pseudocalanus elongatus*  
65 since it is one of the most abundant species in the North Sea (Krause et al.,  
66 1995; CPRS, 2004) and its ecophysiology is well studied (Mauchline, 1998).

67 The pelagic species *Pseudocalanus elongatus* belongs to the calanoid copepods.  
68 The eggs are carried by its females. Such sac-spawners are characterised by a  
69 comparatively low egg mortality compared to broadcast spawners as *Calanus*  
70 *sp.*, for example. The nauplii start feeding at the N3 stage (Corkett and  
71 McLaren, 1978) and moult from stage N6 to copepodite stage C1 after about  
72 half of the generation time. Adults reach a total length (TL) of 1-1.7 mm (Frost,  
73 1989) with females being slightly larger than males. In laboratory experiments  
74 Klein Breteler et al. (1995) showed that development times of *P. elongatus* are  
75 strongly influenced by temperature and that this species is more adapted to low  
76 temperatures than *Acartia sp.*, for example. This is also reflected in its numerical

77 dominance in spring and early summer (Fransz et al., 1991), while *Acartia*  
78 reaches maximum abundances in the warmer summer months. Food  
79 concentration, however, affects growth less than it does in other species (Klein  
80 Breteler et al., 1982) as *P. elongatus* has the ability to utilize lipid reserves  
81 (Renz et al., 2008).

82 Our aim was to simulate the development and distribution of *Pseudocalanus*  
83 *elongatus* and to investigate its life cycle in terms of stage development times,  
84 the number of generations per year and the proportion of this particular species  
85 in total zooplankton.

#### 86 **4. The ecosystem model setup**

87 For the zooplankton analysis we used the three-dimensional ecosystem model  
88 ECOHAM3 (Ecological Model, Hamburg), which calculates the cycles of  
89 carbon, nitrogen and oxygen on the Northwest European Continental Shelf with  
90 a horizontal resolution of 20 km (Figure 1, left) (Pätsch and Kühn, 2008). The  
91 biogeochemical model is coupled to the hydrodynamical HAMSOM (Hamburg  
92 Shelf Ocean Model) whose equation system was described in Pohlmann (1996).

93 For the investigation of *Pseudocalanus elongatus* we implemented the model  
94 population in competition to the rest zooplankton (Figure 2) (Moll et al.,

95 submitted 2007). The population was described by ten state variables  
96 representing the naupliar and copepodite stage groups of eggs-N2 (i.e. non-  
97 feeders), N3-6, C1-3, C4-5 and adults each in terms of abundance and biomass  
98 and defined by species-specific (critical moulting) weights as described in  
99 Fennel (2001). Development of *P. elongatus* was described by the change in  
100 mean individual weight through gain (ingestion) and loss (respiration, excretion  
101 and egestion) of matter. Stage transfer was implemented by a sigmoidal function  
102 allowing a statistical scattering of moulting around the critical weight. The  
103 population competed for existing food with the bulk zooplankton variable. This  
104 bulk variable represented the rest of the total zooplankton biomass, though its  
105 dynamics was parameterised towards generic copepod behaviour as this group  
106 constitutes the largest part of zooplankton in the North Sea (Fransz et al., 1991).  
107 Population dynamics of *Pseudocalanus* in the North Sea were parameterised by  
108 Stegert et al. (2007) for zero-dimensional case scenarios in laboratory culture  
109 experiments. When the process equations were adopted for the three-  
110 dimensional environment, some parameter values were changed to fit the  
111 population abundance to the reported annual development. A reduction of the  
112  $Q_{10}$  (2.0 instead of 2.58) and reduced ingestion at higher temperatures adapted  
113 the population to the earlier and colder season. A detailed overview to changes  
114 compared to the zero-dimensional calibration is given in the Appendix.

115 The model system was set up using forcing and boundary conditions of the years  
116 2003-2004 (Table 1). NCEP reanalysis data were used for the meteorological  
117 forcing (i.e. air temperature, cloud coverage, humidity, pressure, radiation and  
118 wind speed) to run a HAMSOM application for these years providing the  
119 necessary hydrodynamic forcing for ECOHAM3. Initial and boundary data were  
120 derived from the World Ocean Atlas 2001 (Conkright et al., 2002) for the  
121 biogeochemical module. A two year spin-up for 2003 with the population  
122 initiated by an overwintering stock of adults according to Moll et al. (2007) was  
123 made previous to the consecutive simulation of the years 2003 and 2004.

## 124 **5. Validation**

125 As temperature and phytoplankton biomass directly influence the development  
126 of zooplankton we compared these variables as well as the total zooplankton  
127 biomass and the *Pseudocalanus* abundance with observed values.

### 128 **5.1. Temperature**

129 The basic step in the validation of an ecological model is the validation of the  
130 hydrodynamics (Skogen and Moll, 2005) as discrepancies in the physical  
131 simulation increase the uncertainty of modelled biological processes. A  
132 validation of the HAMSOM model for different grid setups was presented by



133 Pohlmann (2006) for 2003. The simulation presented in this paper was  
134 compared to weekly sea surface temperature (SST) data of the North Sea for  
135 2004 provided by the Bundesamt für Seeschifffahrt und Hydrographie  
136 (www.bsh.de), which are based on gridded *in-situ* observations, statistical  
137 estimates and radar analysis data (Loewe et al., 2006). The year 2004 was  
138 relatively warm (Figure 3) compared to climatological data for 1971-1993 (~1°C  
139 warmer for most of the year). Particularly high temperatures were found in  
140 August and September with anomalies of 2-3°C above average in the central and  
141 eastern North Sea (Loewe et al., 2006). While the observed strong anomaly was  
142 not simulated in the central North Sea and along the British coast, the model  
143 reproduced the temperature cycle within 1°C deviation in the southern North  
144 Sea.

## 145 **5.2. Phytoplankton**

146 Long-term chlorophyll data were compiled from the ECOMOD data set and  
147 from an ICES data set by Radach et al. (1995) as monthly mean values with  
148 standard deviation. A 1° by 1° box setup for the entire North Sea was chosen,  
149 dividing the North Sea into upper boxes (0-30m) and additional lower boxes  
150 (30m-bottom) in deeper areas (Radach and Pätsch, 1997). Following methods to  
151 validate annual cycles recommended in Radach and Moll (2006) we validated

152 the simulated phytoplankton biomass against these data using a conversion  
153 factor of  $1 \text{ mg Chl m}^{-3}$  equal to  $50 \text{ mg C m}^{-3}$ .

154 The simulated phytoplankton stock size generally corresponded to the observed  
155 with a better simulation in the coastal area (Figure 4). Highest deviations were  
156 found in the stratified area (boxes 46-48, 50, 57-58 and 65-66), where the model  
157 exceeded the (partly sparse) observed data. In part of the southern coastal area  
158 (boxes 77, 78 and 80) the simulated concentration was in the lower range of the  
159 data. The timing of the spring bloom matched the observation for the coastal  
160 boxes, but was ahead of time in some of the offshore boxes. Increased autumn  
161 chlorophyll concentrations could be reproduced for the outer German Bight but  
162 not within the Elbe outflow box 71. The phytoplankton is expected to control the  
163 timing and the amount of the zooplankton biomass.

### 164 **5.3. Total zooplankton biomass**

165 The total zooplankton biomass was compared to monthly mean values derived  
166 from abundance counts obtained from CPR surveys as provided by Broekhuizen  
167 et al. (1995) and interpolated to the same box setup mentioned above.

168 The zooplankton biomass resembled the observed annual cycle for most boxes  
169 (Figure 5). The winter standing stock was generally above observations. The  
170 spring maximum in the central North Sea was also higher than observed values,

171 but still within a range of factor 2 (boxes 46-59 and 65-66). Also, the onset was  
172 too early in these boxes, which was not the case in any other box. Highest  
173 differences were found in the coastal area, where the simulated zooplankton  
174 biomass was above observations (a factor of 2-3 for boxes 51, 61, 70 and 82 and  
175 a factor of 4 for the box 71, which contains the river Elbe outflow).

#### 176 **5.4. *Pseudocalanus* abundance**

177 Measurements of copepod abundances were available from the GLOBEC  
178 Germany surveys in 2004. Counting was done during seven cruises between  
179 February and October at numerous stations in the German Bight (Figure 1,  
180 right). Copepodite abundances were compared to Bongonet field data, while for  
181 the nauplii sampling Multinet hauls were used (Renz et al., 2008).

182 Comparing the annual cycle of model stage abundances with those from field  
183 samples we found, that the model computed the high variability of individuals  
184 per square meter (data: 0-10<sup>6</sup> Ind m<sup>-2</sup>, Figure 6). Although the model tended to  
185 generate abundances higher than those observed. Comparing the annual  
186 development of *Pseudocalanus* the simulation showed more peaks within the  
187 annual cycle. The simulated maximum abundance was found in June (nauplii)  
188 and July (adults and nauplii) for all stations, while observations showed maxima  
189 of various magnitude in different months. Nauplii maxima were observed in

190 June at stations 7, 31 and 42 with  $100-560 \times 10^3$  Ind  $m^{-2}$ , which were matched by  
191 the simulation (Figure 6, top). High nauplii abundances were also observed in  
192 April at stations 31 and 32, while modelled nauplii increased about one week  
193 later. At stations 22 and 32 maxima were present in August, when the simulation  
194 showed the third peak. Abundances of young copepodites remained low in most  
195 hauls ( $<50 \times 10^3$  Ind  $m^{-2}$ ), whereas the model calculated maxima of  $130-300 \times 10^3$   
196 Ind  $m^{-2}$  for early July. Observed peaks of this magnitude were found in August  
197 at stations 15, 22 and 42, and at station 41 in May and June, a few days before  
198 the simulation reached its maximum.

199 Larger copepodites and adults showed similar patterns (Figure 6, bottom).  
200 Simulated abundances exhibited a development of consecutive cohorts with two  
201 major peaks at the start of June and in mid-July with  $40-60 \times 10^3$  Ind  $m^{-2}$  and  $80-$   
202  $100 \times 10^3$  Ind  $m^{-2}$ , respectively, for both stage groups. Maxima of this size were  
203 mainly observed in the coastal region, whereas the inner German Bight (station  
204 7) exhibited lower abundances in observation and simulation. Highest observed  
205 abundances of copepodites and adults were found in May at stations 20 and 41,  
206 and in June at stations 15, 20, 31 and 41, when the simulation exhibited a local  
207 minimum. In August at stations 22 and 41 simulation results quantitatively  
208 corresponded to the observed peaks. Only some very high numbers observed at

209 station 41 exceeded simulated maxima of  $114 \times 10^3$  Ind  $m^{-2}$  and  $91 \times 10^3$  Ind  $m^{-2}$   
210 for C4-5 and adults, respectively.

## 211 **6. Simulated zooplankton development**

212 The horizontal distribution and seasonal development of phytoplankton biomass,  
213 *Pseudocalanus* non-feeders and adults as well as the bulk zooplankton is given  
214 in Figure 7. The zooplankton biomass started to increase in April 2004 (week  
215 17) in the coastal area of the German Bight after the first peak of the  
216 phytoplankton spring bloom appeared. However, the onset of the *Pseudocalanus*  
217 population occurred almost one week earlier. Mature adults originating from the  
218 overwintering stock started reproduction at the onset of the spring bloom in the  
219 third week of April. At temperatures of 8-12°C in May it took about six weeks  
220 for the first generation of the population to reach maturity and the second and  
221 stronger peak in population abundance happened in early June (week 23).

222 In contrast, bulk zooplankton steadily increased in biomass and reached its  
223 maximum in early June when the phytoplankton already decreased. This  
224 maximum lasted for about two weeks after which the zooplankton biomass  
225 continuously decreased until the end of the year. A third maximum of  
226 *Pseudocalanus* adults appeared in the mid of July co-occurring with a summer

227 increase in phytoplankton (week 29). This peak was as high in abundance as the  
228 previous one, yet more confined to the German Bight and the continental coast.  
229 Further, but distinctly narrower peaks were found in autumn particularly in the  
230 shallow Dogger Bank area, where phytoplankton concentrations remained high  
231 (cf. week 35). The time of increase in bulk zooplankton biomass from week 17  
232 to week 23 was shorter than its decreasing period (week 23 to 35). A sudden  
233 increase was also found for the population state variables in each successive  
234 peak (Figure 6).

235 The simulated zooplankton development showed that distributions of bulk  
236 zooplankton and *Pseudocalanus* population differed both in space and time, and  
237 consequently, the ratio of summed population biomass to the total zooplankton  
238 (Figure 7, right column). In April and May its maximum percentage of about  
239 25% was located in the Dutch coastal region. With increasing bulk zooplankton  
240 biomass in the coastal areas the population percentage maximum shifted to the  
241 offshore region. Highest percentage was found in the central North Sea at the  
242 end of July (~50% of the total zooplankton biomass) and decreased in the later  
243 summer.

244 Stegert et al. (2007) found the generation time to be a robust parameter to  
245 represent the population development. As a proxy for the number of generations  
246 per year the peaks in egg abundance were taken, with double peaks counting as

247 one generation given they occur within a certain period of days. The Belehradek  
248 function was used to calculate this number of days according to the temperature  
249 dependent generation time  $D$  with parameter values estimated by Klein Breteler  
250 et al. (1995) for saturated food concentrations,  $D = 9398 \cdot (T + 8)^{-1.98}$ .

251 We assumed that no further generation can appear within this time span. The  
252 regional distribution of annual generation numbers estimated for the southern  
253 North Sea is shown in Figure 8, varying between four and eight generations. We  
254 estimated a mean of four to five generations per year in the central North Sea  
255 and in the German Bight. Between these regions a belt of six to eight  
256 generations extended from the Dogger Bank northeast to the Fisher Banks. A  
257 detailed inspection of single stations along a transect from the open North Sea  
258 (box 1) to the German Bight (box 9) is given in the lower panels of Figure 8.  
259 Each vertical line represents the onset of a new generation calculated from the  
260 abundance of the non-feeders. The comparison of the development of  
261 *Pseudocalanus* at these stations revealed differences in development: An early  
262 population increase appeared in February in the German Bight, which was not  
263 present in the central North Sea. Development was also faster in the southern  
264 area. The two major peaks occurred there at the end of April and in early June,  
265 while in the central North Sea it happened eight and seventeen days later. In

266 autumn the development in the German Bight stagnated while in the offshore  
267 region further peaks were found.

## 268 **7. Discussion**

269 The validation showed that the model is able to simulate annual cycles of  
270 phytoplankton and zooplankton biomass in the range of long-term monthly  
271 mean values. Simulated phytoplankton was within observed ranges for ~70% of  
272 the data. Monthly mean values based on less than 15 observations (pale bars in  
273 Figure 4) were not considered. The zooplankton biomass was simulated within a  
274 factor of two compared to monthly mean CPR data at about 80% of the observed  
275 data. For the southern boxes 75-77 and 80-81 (Figure 5) the simulation showed  
276 similar annual cycles for phytoplankton and zooplankton biomass compared to  
277 observations. In the stratified area both plankton state variables increased  
278 prematurely due to remarkably high SST in 2004 and early stratification.  
279 Sharples et al. (2006) found a strong correlation for the onsets of stratification  
280 and spring bloom in a thirty year simulation run for the northern (stratified)  
281 North Sea. Likewise Mills et al. (1994) found a similar correlation from  
282 observations north of the Dogger Bank. Observations at Helgoland Reede  
283 revealed an earlier onset of the spring bloom for the years 2000-2004 compared  
284 to the previous decade (Loewe et al., 2006).



285 For the *Pseudocalanus* population we used the extensive GLOBEC-Germany  
286 data set for validation and investigation of abundance development and  
287 distribution (Tamm et al., 2007). The logarithmic regression plot of model  
288 results versus data for all stations (at the specific day) showed that the model  
289 resembled observed abundances of *Pseudocalanus elongatus* nauplii and adults  
290 only in orders of magnitude (Figure 9). Differences in the simulation of adults  
291 were found towards a tendency of overestimation. However, for the copepodite  
292 stage groups (c1-3 and C4-5) the model tended to underestimate abundances.  
293 For a closer investigation of these differences the abundances are plotted with  
294 distinction of time and position (Figure 9 bottom). Overestimated values mostly  
295 belong to the coastal region (dark marks) in October (\*). Although, such autumn  
296 increase was also observed at stations 9, 15 and 22 within GLOBEC in 2004,  
297 which agrees with previous investigations described by Wiborg (1954) and by  
298 Fransz and van Arkel (1983). In autumn temperatures of 13-15°C in the German  
299 Bight (cf. Figure 3) allow optimal development of individuals resulting in a  
300 faster succession of generations and increased abundances as shown by Moll  
301 and Stegert (2007). Very low abundances in the model were found in February  
302 (x), May (o), June (∇) and September (□) for the C1-3 and the C4-5 stages. Low  
303 February values resulted from the parameterisation of overwintering, which was  
304 realised by limiting reproduction in winter so that individuals were summed in  
305 the model stage group for adults.

306 An important parameter concerning the abundance is the mortality. Several  
307 investigations on calculation of *Pseudocalanus* mortality were performed  
308 (Ohman et al., 2002; Eiane and Ohman, 2004). We used constant stage  
309 dependent mortality rates of 0.13-0.17 (Table 2). Reported mean mortality rates  
310 vary between 0.04 and 0.2, while instantaneous rates vary strongly in time  
311 (Ohman and Wood, 1996).

312 Further differences in simulated abundances compared to observations result  
313 from the strong stage succession in the model when peak abundances alternate  
314 with minima (Figure 6). Thus, we additionally considered monthly mean values  
315 for comparison in Figure 10 (right column). Here the model produced more  
316 congruent values compared to observations. Throughout the year observed  
317 abundances of all stages varied more strongly in space compared to the  
318 simulation.

319 The key question of interest is how *Pseudocalanus* is distributed in the German  
320 Bight. The variability of observations allows different interpretations: Patches of  
321 high abundances with strong lateral gradients are well-known (Wiebe and  
322 Benfield, 2003). Such patches of copepods were reported for a scale of 10-1000  
323 m (Wroblewski, 1977), which cannot be resolved by the 20 km resolution of the  
324 model grid. Furthermore, we are not able to discern from the data how many of

325 such patches exist. This should be studied further in a nested grid model  
326 application.

327 The temporal variability of abundance as calculated by the model was only  
328 partially reflected in the observations. For this purpose a data set at Helgoland  
329 Reede with three observations per week was considered. Comparison of the  
330 simulated abundance to the 2004 time-series showed a similar structure of  
331 several abundance peaks (Figure 11). Such periodic development of abundances  
332 and the impact of advection at that specific location was discussed in the past  
333 (Halsband-Lenk et al., 2004; Wesche et al., 2007). Such development was also  
334 observed at other locations, i.e. for *Pseudocalanus* at the L4 station in the  
335 English Channel (Green et al., 1993), for copepods off Stonehaven (northern  
336 North Sea off Aberdeen) and also in the western Mediterranean Sea (Fernandez  
337 de Puellas et al., 2007). Thus, for stage-resolved population models we propose  
338 a validation based on at least weekly samples at single stations to resolve the  
339 temporal distribution.

340 Another goal was to find the proportion in total zooplankton. *Pseudocalanus*  
341 *elongatus* is reported to be a highly abundant species making up to 46% of the  
342 copepod stock (Fransz et al., 1991). The simulated proportion in terms of  
343 biomass varied considerably in space and time and amounted up to 50%. We

344 found no quantification in terms of biomass in the literature. Thus, this model  
345 provides a tool to estimate biomass ratios in space and time.

346 The numbers of generations were estimated by computed local maxima in egg  
347 abundance. It shows areas of best development with more generations at the tails  
348 end region of the Dogger Bank. This method outlines the general distribution  
349 pattern which is hard to estimate from observations and information on number  
350 of generations is rare. This model study enabled the first estimations for every  
351 grid box. The abundance peaks during the spring bloom were detected well at  
352 most stations, but identification of single peaks was more difficult in autumn,  
353 when generation times partly became shorter at higher temperatures. We found  
354 encouragement for the validity of our simulation approach from reported values  
355 of four to five generations near Norway (Corkett and McLaren, 1978), five  
356 generations in the western North Sea (Evans, 1977), and six (Green et al., 1993)  
357 to nine (Corkett and McLaren, 1978) in the English Channel. For the year 2004  
358 Renz et al. (2008) estimated four to five generations in the German Bight which  
359 was in agreement to the simulation.

## 360 8. Conclusions

361 The numerical modelling of zooplankton biomass and copepod population  
362 dynamics with ECOHAM3 was compared with monitoring data in the German  
363 Bight. The validation was based on monthly mean values and showed that the  
364 phytoplankton stock and the total zooplankton biomass corresponded in  
365 magnitude to long term observations for most boxes. Thus, the model was able  
366 to simulate realistic hydrographic and lower trophic forcing fields for the  
367 development and distribution of *Pseudocalanus elongatus* as one characteristic  
368 copepod species. Comparing the model stage group abundances with GLOBEC-  
369 Germany field data we found, that the model reasonably well reproduced the  
370 variability of the data which were in the range of 0-6  $\log_{10}$  Ind  $m^{-2}$ , but tended to  
371 generate generally higher adult abundances and lower smaller copepodites. The  
372 simulation spatial variance but more peaks within the annual cycle compared to  
373 the field observations. A satisfying comparison was provided at Helgoland  
374 Reede with three observations per week, which showed a similar structure in the  
375 number of annual peaks.

376 The model simulated a biomass ratio of up to 50% for *Pseudocalanus elongatus*  
377 of the total zooplankton biomass in summer. Finally, model estimates of egg  
378 abundance peaks were taken as proxies to estimate the number of generations  
379 per year. We estimated a mean of four generations per year in the central North

380 Sea, six to eight generations northwest of the Dogger Bank and five generations  
381 in the German Bight. The area with the highest number of generations per year  
382 was also the area of highest percentage of the population.

## 383 **9. Acknowledgements**

384 This work was done within the BMBF funded project GLOBEC Germany. The  
385 authors thank Jasmin Renz for help with the GLOBEC data concerning  
386 *Pseudocalanus elongatus* and for helpful comments that improved the  
387 manuscript. We appreciate the discussion within the zooplankton workgroup and  
388 especially Jörg Dutz, Jasmin Renz, and Christian Möllmann. For help  
389 concerning the model simulations at the super-computer we thank our  
390 colleagues Wilfried Kühn and Johannes Pätsch. We also thank Ilse Hamann for  
391 helpful improvements on the text.

## 392 **10. Appendix**

393 The development of *Pseudocalanus elongatus* was parameterised by Stegert et  
394 al. (2007) partly based on literature data and partly based on calibration towards  
395 stage durations as measured by Klein Breteler et al. (1995). The abundance was  
396 not considered there and had to be adjusted for this simulation. Adaptation to

397 lower temperatures was realised by changes in the temperature function for  
 398 ingestion and a lower half-saturation value was applied to maintain growth at  
 399 lower food concentrations reflecting lipid storage (Table 2). The ingestion  
 400 function is given as

$$401 \quad g = P_1 \cdot \frac{F^{P_3}}{P_2^{P_3} + F^{P_3}} \cdot Q_0^{(T-TR)/10} \cdot f_{T,red}$$

402 where  $F$  is the food concentration,  $T$  is the temperature and  $f_{T,red}$  a decreasing  
 403 function for  $T > 15^\circ\text{C}$ . A lower  $Q_{10}$  of 2.0 reduced ingestion at high  
 404 temperatures, while the stronger function  $f_{T,red}$  supported reduced growth at high  
 405 temperatures (Figure 12).

406 The total abundance is strongly affected by mortality and reproduction.  
 407 Mortality rates (Table 2) were calibrated to fit mean abundances from time  
 408 series at Helgoland Reede. As adults were parameterised towards female  
 409 weights, this stage was also parameterised to reflect female physiology, i.e. all  
 410 adults were considered as females as proposed in Moll et al. (submitted 2007).  
 411 Non-vital eggs were associated with detritus to account for males and non-  
 412 reproductive females. A reproductive success of 0.6 with a sex ratio of 0.5  
 413 equals the reproductive females of 0.3 reported in Stegert et al. (2007).

414 **11. References**

- 415 Alheit, J., 2007. Progress of the German GLOBEC project. *International GLOBEC Newsletter*, 13 (2): 57-78.
- 416 Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V. and Wasmund, N., 2005.
- 417 Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES*
- 418 *Journal of Marine Science*, 62: 1205-1215.
- 419 Broekhuizen, N., Heath, M.R., Hay, S.J. and Gurney, W.S.C., 1995. Modelling the dynamics of the North Sea's
- 420 mesozooplankton. *Netherlands Journal of Sea Research*, 33 (3-4): 381-406.
- 421 Carlotti, F. and Radach, G., 1996. Seasonal dynamics of phytoplankton and *Calanus finmarchicus* in the North
- 422 Sea as revealed by a coupled one-dimensional model. *Limnology and Oceanography*, 41 (3): 522-539.
- 423 Conkright, M.E., Locarnini, R.A., Garcia, H.E., O'Brien, T.D., Boyer, T.P., Stephens, C. and Antonov, J.I., 2002.
- 424 *World Ocean Atlas 2001: Objective analyses, data statistics, and figures CD-ROM documentation.*
- 425 *National Oceanographic Data Center Internal Report (NOAA Atlas NESDIS)*, 17: 17.
- 426 Corkett, C.J. and McLaren, I.A., 1978. The biology of *Pseudocalanus*. *Advances in Marine Biology*, 15: 1-231.
- 427 CPRS, 2004. Continuous Plankton Records: Plankton atlas of the North Atlantic Ocean (1958-1999). *Marine*
- 428 *Ecology Progress Series, Supplement*: 1-75.
- 429 Dickmann, M., 2006. Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardine pilchardus* W.) larvae
- 430 in the Baltic Sea and in the North Sea. Ph.D. Thesis, University of Rostock, Rostock.
- 431 Eiane, K. and Ohman, M.D., 2004. Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus*
- 432 and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. *Marine Ecology Progress*
- 433 *Series*, 268: 183-193.
- 434 Evans, G.T., 1977. A two layer shear diffusion model. *Deep-Sea Research*, 24 (10): 931-936.
- 435 Fennel, W., 2001. Modelling of copepods with links to circulation models. *Journal of Plankton Research*, 23
- 436 (11): 1217-1232.
- 437 Fernandez de Puellas, M.L., Alemany, F. and Jansá, J., 2007. Zooplankton time-series in the Balearic Sea
- 438 (Western Mediterranean): Variability during the decade 1994–2003. *Progress in Oceanography*, 74:
- 439 329-354.
- 440 Fransz, H.G., Colebrook, J.M., Gamble, J.C. and Krause, M., 1991. The zooplankton of the North Sea.
- 441 *Netherlands Journal of Sea Research*, 28 (1/2): 1-52.
- 442 Fransz, H.G. and van Arkel, W.G., 1983. Fluctuation and succession of common pelagic copepod species in the
- 443 Dutch Wadden Sea. *Oceanologica Acta, Vol. spec*: 78-91.
- 444 Frost, B.W., 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Canadian Journal of*
- 445 *Zoology*, 67: 525-551.
- 446 Green, E.P., Harris, R.P. and Duncan, A., 1993. The seasonal abundance of the copepodite stages of *Calanus*
- 447 *helgolandicus* and *Pseudocalanus elongatus* off Plymouth. *Journal of the Marine Biological*
- 448 *Association of the United Kingdom*, 73: 109-122.
- 449 Halsband-Lenk, C., Carlotti, F. and Greve, W., 2004. Life-history strategies of calanoid congeners under two
- 450 different climate regimes: a comparison. *ICES Journal of Marine Science*, 61: 709-720.
- 451 Heath, M.R., Edwards, A.C., Pätsch, J. and Turrell, W.R., 2002. Modelling the behaviour of nutrient in the
- 452 coastal waters of Scotland. *Report of the Fisheries Research Services*, 10: 1-106.
- 453 Heath, M.R., Robertson, W., Mardaljevic, J. and Gurney, W.S.G., 1997. Modelling the population dynamics of
- 454 *Calanus* in the Fair Isle current off northern Scotland. *Journal of Sea Research*, 38: 381-412.
- 455 Klein Breteler, W.C.M., Fransz, H.G. and Gonzales, S.R., 1982. Growth and development of four calanoid
- 456 copepod species under experimental and natural conditions. *Netherlands Journal of Sea Research*, 16:
- 457 195-207.
- 458 Klein Breteler, W.C.M., Gonzales, S.R. and Schogt, N., 1995. Development of *Pseudocalanus elongatus*
- 459 (Copepoda, Calanoida) cultured at different temperature and food conditions. *Marine Ecology Progress*
- 460 *Series*, 119: 99-110.
- 461 Krause, M., Dippner, J.W. and Beil, J., 1995. A review of hydrographic controls on the distribution of
- 462 zooplankton biomass and species in the North Sea with particular reference to a survey conducted in
- 463 January-March 1987. *Progress in Oceanography*, 35: 81-152.
- 464 Krause, M., Fock, H., Greve, W. and Winkler, G., 2003. North Sea Zooplankton: a review. *Senckenbergiana*
- 465 *Maritima*, 33 (1-2): 71-204.
- 466 Loewe, P., Becker, G., Brockmann, U., Dick, S., Frohse, A., Hermann, J., Klein, B., Klein, H., Nies, H.,
- 467 Schmolke, S., Schrader, D., Schulz, A., Theobald, N. and Weigelt, S., 2006. Nordseezustand 2004,
- 468 Bundesamt für Seeschifffahrt und Hydrographie (BSH), Hamburg.



- 469 Mauchline, J., 1998. The biology of Calanoid Copepods. Academic Press, San Diego, 710 pp.
- 470 Mills, D.K., Tett, P.B. and Vovrino, G., 1994. The spring bloom in the south western North Sea in 1989.
- 471 Netherlands Journal of Sea Research, 33 (1): 65-80.
- 472 Moll, A., Kreuz, M., Kühn, W., Krause, M. and Greve, W., submitted 2007. Seasonal dynamics of
- 473 *Pseudocalanus elongatus* in the North Sea using the ecosystem model ECOHAM3 with competing bulk
- 474 zooplankton. Part 1: Description and validation of the embedded population model. Journal of Marine
- 475 Systems.
- 476 Moll, A. and Stegert, C., 2007. Modelling *Pseudocalanus elongatus* population dynamics embedded in a water
- 477 column ecosystem model for the northern North Sea. Journal of Marine Systems, 64 (1-4): 35-46.
- 478 Ohman, M.D., Runge, J.A., Durbin, E.G., Field, D.B. and Niehoff, B., 2002. On birth and death in the sea.
- 479 Hydrobiologia, 480: 55-68.
- 480 Ohman, M.D. and Wood, S.N., 1996. Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in
- 481 a temperate fjord. Limnology and Oceanography, 41 (1): 126-135.
- 482 Pätsch, J. and Kühn, W., 2008. Nitrogen and carbon cycling in the North Sea and exchange with the North
- 483 Atlantic - a model study, Part I. Nitrogen budget and fluxes. Continental Shelf Research,
- 484 doi:10.1016/j.csr.2007.12.013.
- 485 Pätsch, J. and Lenhart, H.-J., 2004. Daily loads of nutrients, total alkalinity, dissolved inorganic carbon and
- 486 dissolved organic carbon of the European continental rivers for the years 1977-2002. Berichte aus dem
- 487 Zentrum für Meeres- und Klimaforschung. Reihe B: Ozeanographie, 48: 159.
- 488 Pohlmann, T., 1996. Predicting the thermocline in a circulation model of the North Sea - Part I: Model
- 489 description, calibration and verification. Continental Shelf Research, 16 (2): 131-146.
- 490 Pohlmann, T., 2006. A meso-scale model of the central and southern North Sea: Consequences of an improved
- 491 resolution. Continental Shelf Research, 26: 2367-2385.
- 492 Radach, G. and Moll, A., 2006. Review of three-dimensional ecological modelling related to the North Sea shelf
- 493 system. Part II: Model validation and data needs. Oceanography and Marine Biology: An Annual
- 494 Review, 44: 1-60.
- 495 Radach, G. and Pätsch, J., 1997. Climatological annual cycles of nutrients and chlorophyll in the North Sea.
- 496 Journal of Sea Research, 38: 231-248.
- 497 Radach, G., Pätsch, J., Gekeler, J. and Herbig, K., 1995. Annual cycles of nutrients and chlorophyll in the North
- 498 Sea (Part 1). Berichte aus dem Zentrum für Meeres- und Klimaforschung. Reihe B: Ozeanographie, 20
- 499 (1): 172.
- 500 Renz, J., Mengedocht, D. and Hirche, H.-J., 2008. Reproduction, growth and secondary production of
- 501 *Pseudocalanus elongatus* Boeck (Copepoda, Calanoida) in the southern North Sea. Journal of Plankton
- 502 Research, doi: 10.1093/plankt/fbn016.
- 503 Rick, H.-J., Rick, S., Tillmann, U., Brockmann, U., Gärtner, U., Dürselen, C.-D. and Sündermann, J., 2006.
- 504 Primary productivity in the German Bight (1994-1996). Estuaries and Coasts, 29 (1): 4-23.
- 505 Sharples, J., Ross, O.N., Scott, B.E., Greenstreet, S.P.R. and Fraser, H., 2006. Inter-annual variability in the
- 506 timing of stratification and the spring bloom in the North-western North Sea. Continental Shelf
- 507 Research, 26: 733-751.
- 508 Skogen, M.D. and Moll, A., 2005. Importance of ocean circulation in ecological modelling: An example from
- 509 the North Sea. Journal of Marine Systems, 57 (3-4): 289-300.
- 510 Slagstad, D. and Tande, K.S., 1981. A mathematical model of the assimilation process in the copepod *Calanus*
- 511 *finmarchicus* (Gunnerus): computer simulations discusses in relation to experimental results. Kieler
- 512 Meeresforschungen Sonderhefte, 5: 229-239.
- 513 Speirs, D.C., Gurney, W.S.C., Heath, M.R. and Wood, S.N., 2005. Modelling the basin-scale demography of
- 514 *Calanus finmarchicus* in the north-east Atlantic. Fisheries Oceanography, 14 (5): 333-358.
- 515 Stegert, C., Kreuz, M., Carlotti, F. and Moll, A., 2007. Parameterisation of a zooplankton population model for
- 516 *Pseudocalanus elongatus* using stage duration laboratory experiments. Ecological Modelling, 206 (3-4):
- 517 214-234.
- 518 Tamm, S., Moll, A. and Zabanski, S., 2007. The GLOBEC-Germany database. GLOBEC International
- 519 Newsletter, 13 (2): 57-58.
- 520 Thomas, H., Bozec, Y., Elkalay, K. and de Baar, H.J.W., 2004. Enhanced open ocean storage of CO<sub>2</sub> from shelf
- 521 sea pumping. Science, 304 (14 May 2004): 1005-1008.
- 522 Wesche, A., Wiltshire, K.A. and J., H.H., 2007. Overwintering strategies of dominant calanoid copepods in the
- 523 German Bight, southern North Sea. Marine Biology, 151 (4): 1309-1320.
- 524 Wiborg, K.F., 1954. Investigations on zooplankton in coastal and offshore waters of western and northwestern
- 525 Norway with special reference to the copepods. Fisk Dir. Skr. (Ser. Havunders.), 11 (1): 1-246.
- 526 Wiebe, P.H. and Benfield, M.C., 2003. From the Hensen net toward four-dimensional biological oceanography.
- 527 Progress in Oceanography, 56: 7-136.

528 Wroblewski, J.S., 1977. Vertically migrating herbivorous plankton - their possible role in the creation of small  
529 scale phytoplankton patchiness in the ocean. In: N. Andersen and B. Zahurane (Editors), Oceanic  
530 sound scattering prediction. Plenum Press, pp. 817-847.  
531  
532

## 533 **12. Figure captions**

534 **Figure 1: Left: Model topography of the northwest European Continental**  
535 **shelf (NECS). Right: Zoom on the area of interest with station**  
536 **grid of zooplankton sampling during GLOBEC Germany cruises**  
537 **in the German Bight in 2004.**

538 **Figure 2: Conceptual diagram of the coupled three-dimensional physical-**  
539 **biogeochemical model ECOHAM3 with implemented population**  
540 **model of *Pseudocalanus elongatus* shown for the carbon cycle.**

541 **Figure 3: Monthly mean sea surface temperatures [°C] for each season**  
542 **from simulation (left) and observations by Loewe (2006) (right).**

543 **Figure 4: Validation of chlorophyll-*a* [mg Chl m<sup>-3</sup>] for the German Bight:**  
544 **Annual cycles derived from model phytoplankton (red lines, 1**  
545 **mg Chl = 50 mg C) compared to box averages of observed values**  
546 **(dots) with 17/83% quantiles as bars (pale bars indicate values**  
547 **based on <15 observations).**

548 **Figure 5: Validation of total zooplankton biomass [mg C m<sup>-3</sup>] for the**  
549 **German Bight: Annual cycles of simulated biomass (red lines)**  
550 **compared to box averages of observed values (dots). Monthly**  
551 **mean observations based on CPR counts derived by Broekhuizen**  
552 **et al. (1995).**

553 **Figure 6: Comparison of simulated (lines) and observed (crosses)**  
554 ***Pseudocalanus elongatus* abundances ( 10<sup>3</sup> Ind m<sup>-2</sup>). Upper panel:**  
555 **Nauplii (green) and C1-3 (red), lower panel: C4-5 (cyan) and**  
556 **adults (magenta).**

557 **Figure 7: Spatial distribution of plankton state variables in the North Sea**  
558 **every two weeks from April to August for (left to right)**  
559 **phytoplankton, *Pseudocalanus elongatus* non-feeders [E-N2], *P.***  
560 ***elongatus* adults, bulk zooplankton and percentage of *P.***  
561 ***elongatus* to the total zooplankton biomass.**

562 **Figure 8: Number of estimated *Pseudocalanus* generations in the North**  
563 **Sea. Top: Spatial distribution of the number of generations in**  
564 **2004. Bottom: Simulated development of eggs and non-feeders**  
565 **(N1-N2) abundance at selected stations from the central North**  
566 **Sea (top) to the inner German Bight (bottom) with local**

567 abundance maxima indicated by vertical lines and estimated  
568 number of generations.

569 **Figure 9: Regression plot of *Pseudocalanus elongatus* abundances ( $\log_{10}$   
570  $\text{Ind m}^{-2}$ ) from observations (x-axis) versus simulated abundances  
571 (y-axis). Top panel with indication of state variables and lower  
572 panel with indication of months and area (bold and pale station  
573 circles).**

574 **Figure 10: Distribution in space and time of observed (left) and simulated  
575 (middle and right) abundances of nauplii, C1-3, C4-5 and adults  
576 (top to bottom) of *Pseudocalanus elongatus* as  $\log_{10} \text{Ind m}^{-2}$ .  
577 Simulated abundances were compared to values at the specific  
578 days of observation (middle) and as monthly mean values (right).**

579 **Figure 11: Comparison of simulated copepodite abundance (C1-6, red line)  
580 and samples at Helgoland Reede (black dotted line) as  $\text{Ind m}^{-2}$ .**

581 **Figure 12: Temperature dependent ingestion function in Stegert et al.  
582 (2007) (blue) and this paper (red) with ingestion reduction factor  
583 (dashed) for higher temperatures.**

584 **13. Tables**585 **Table 1: Source and resolution for the ECOHAM3 forcing data sets.**

	Variable	Resolution	Source
Nutrient cycle	NO <sub>3</sub>	Monthly	Conkright et al. (2002)
Carbon cycle	DIC, alkalinity	Seasonal	Thomas et al. (2004)
Silt concentration	SPM	Monthly	Heath et al. (2002)
Atmospheric deposition	NO <sub>3</sub> , NH <sub>4</sub>	Annual	EMEP (www.emep.int)
River loads	NO <sub>3</sub> , NH <sub>4</sub> , DIC, other	Daily	Heath et al. (2002) and Pätsch et al. (2004)

586

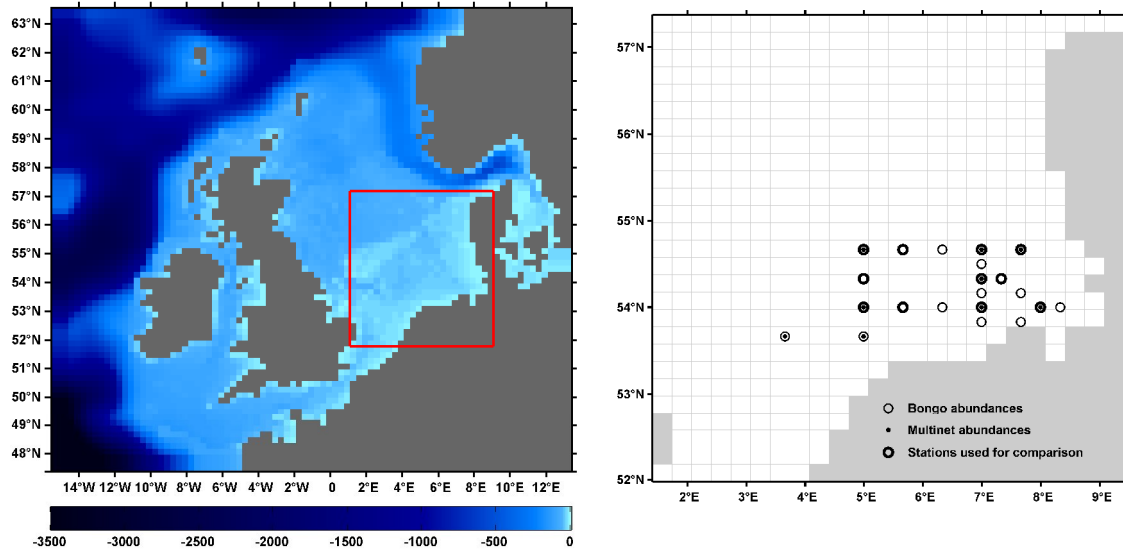
587 **Table 2: Parameter values used for this paper differing from Stegert *et al.***588 **(2007).**

Parameter	this paper				Stegert et al. (2007)			
	N3-6	C1-3	C4-5	C6	N3-6	C1-3	C4-5	C6
<i>max ingestion (P<sub>1</sub>)</i>	1.00	0.60	0.55	0.35	1.00	0.60	0.50	0.30
<i>power coefficient (P<sub>3</sub>)</i>	2.00	2.00	2.00	2.00	1.15	1.40	1.40	1.40
<i>Q<sub>10</sub> value (Qg)</i>	2.00	2.00	2.00	2.00	2.58	2.58	2.58	2.58
<i>Mortality(μ)</i>	0.17	0.16	0.15	0.12	0.03	0.03	0.03	0.03
<i>reproductive female</i>	-	-	-	0.60	-	-	-	0.30

589

Figure 1

@BCL@140D7F34.doc



@BCL@140D7F34.doc

Figure 2

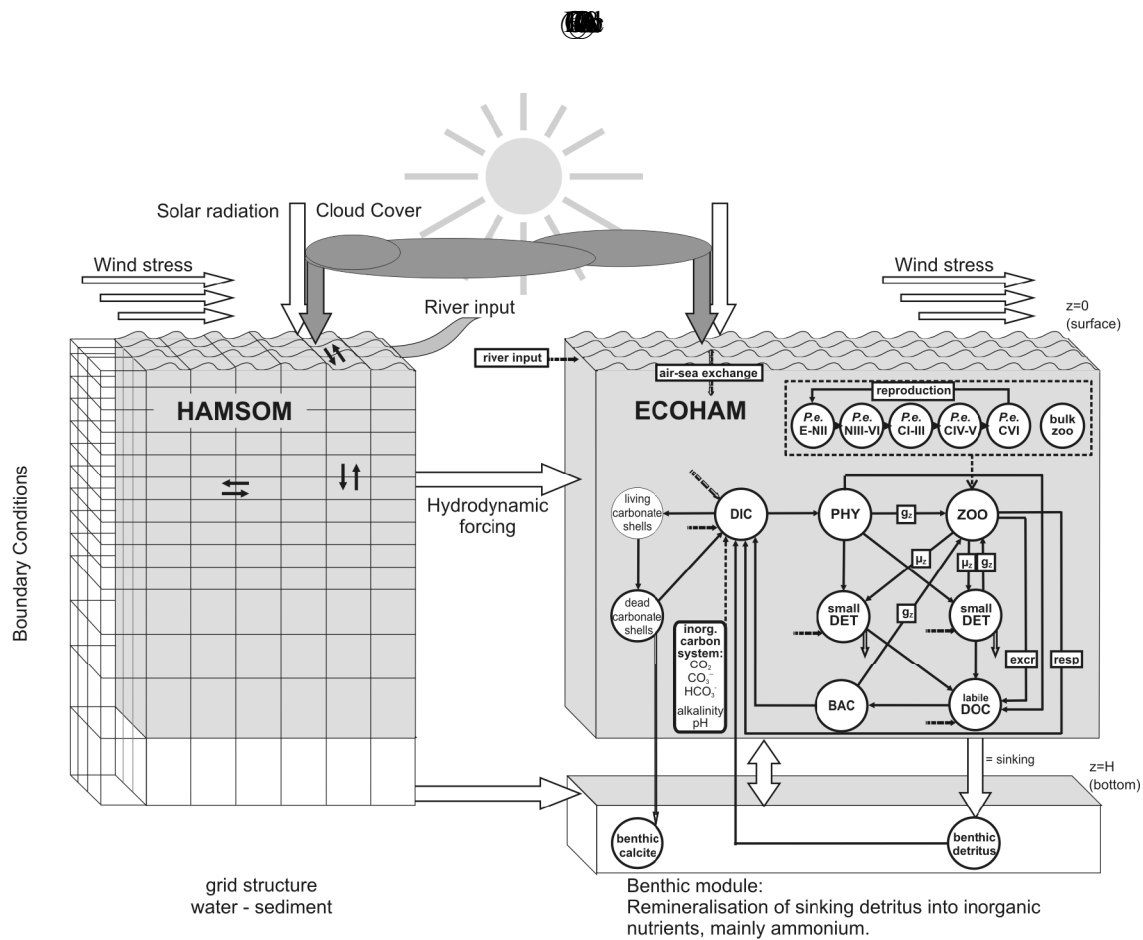


Figure 3

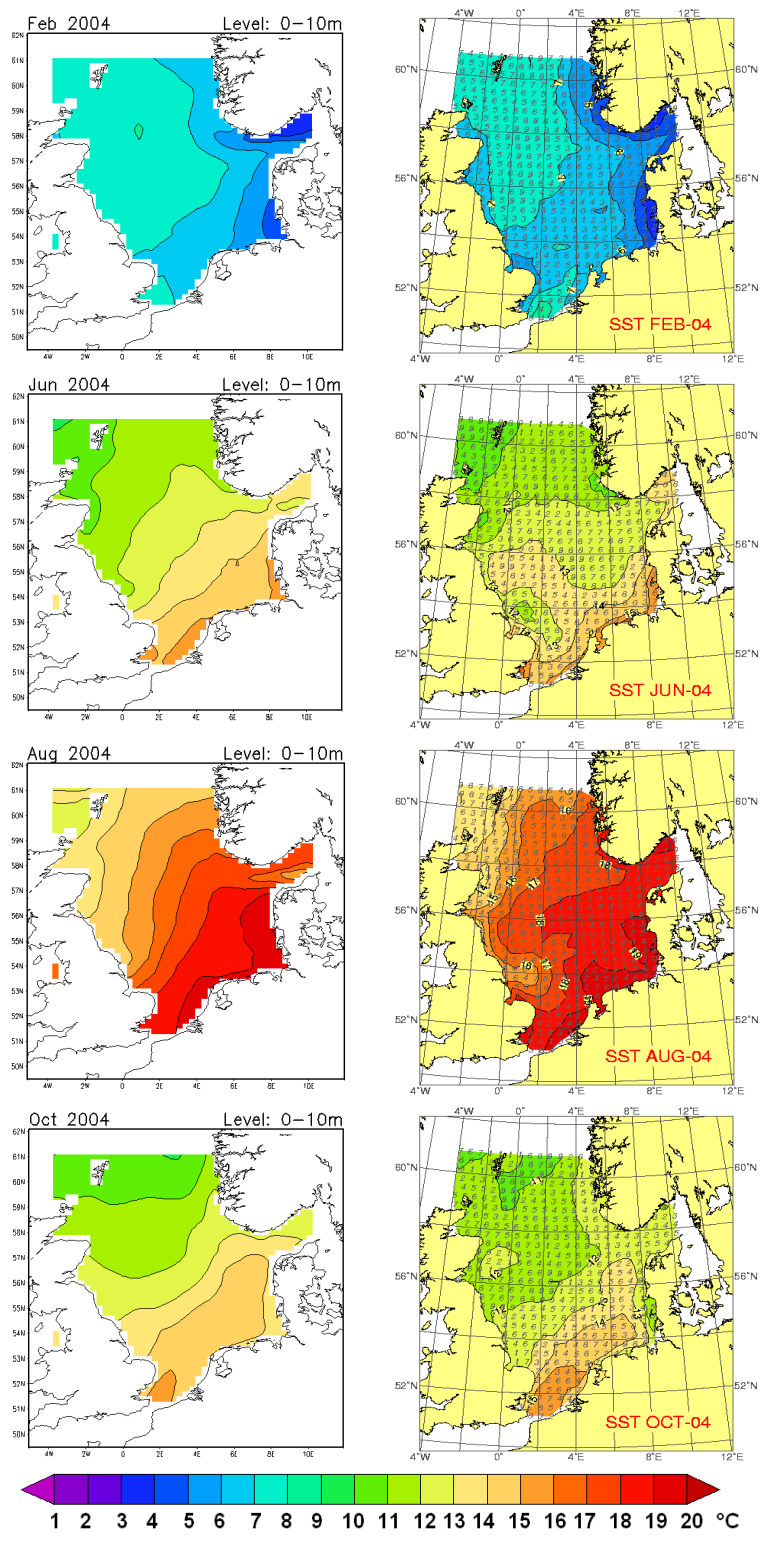




Figure 4

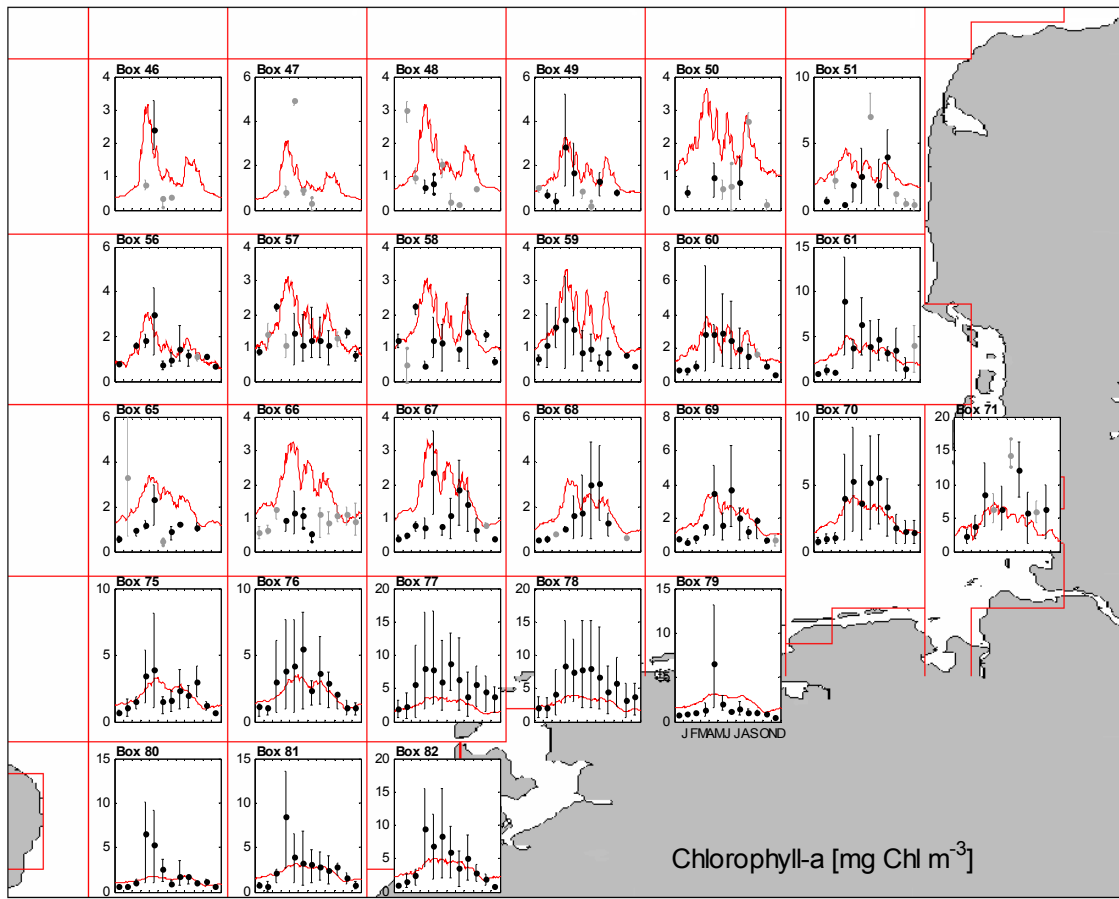


Figure 5

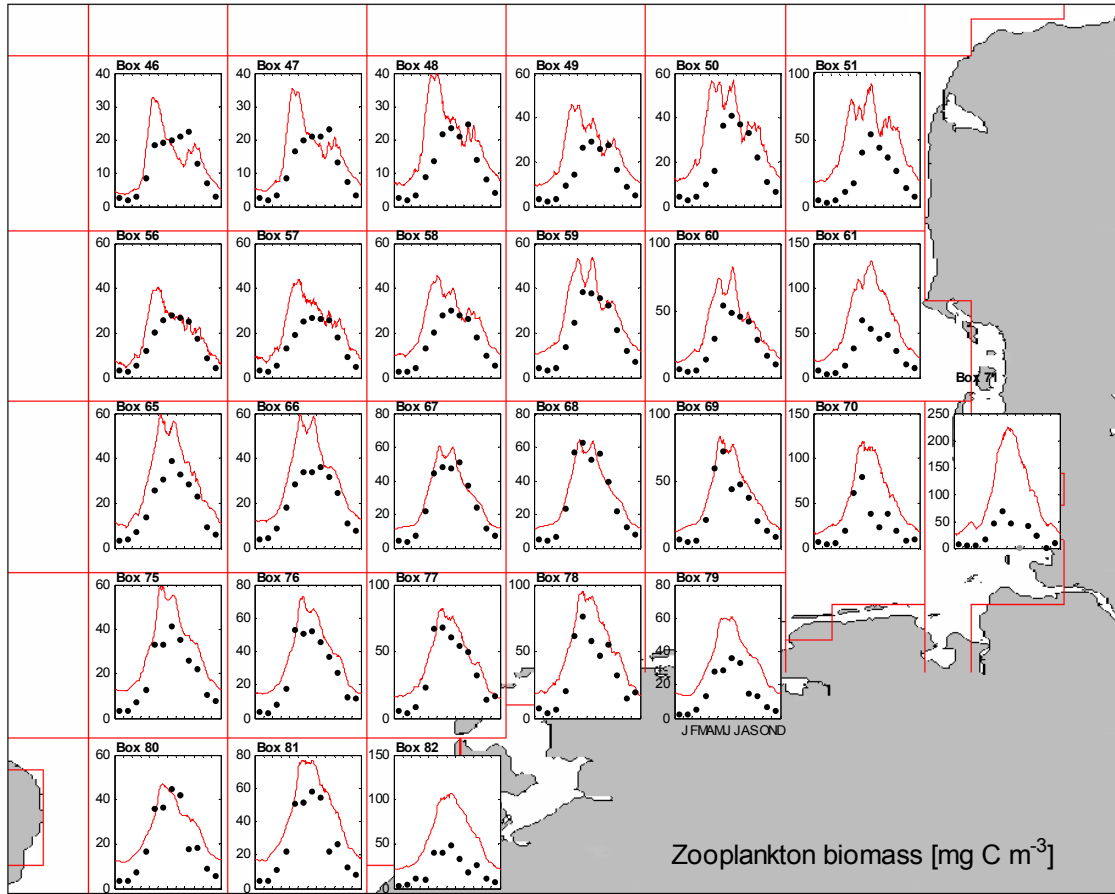
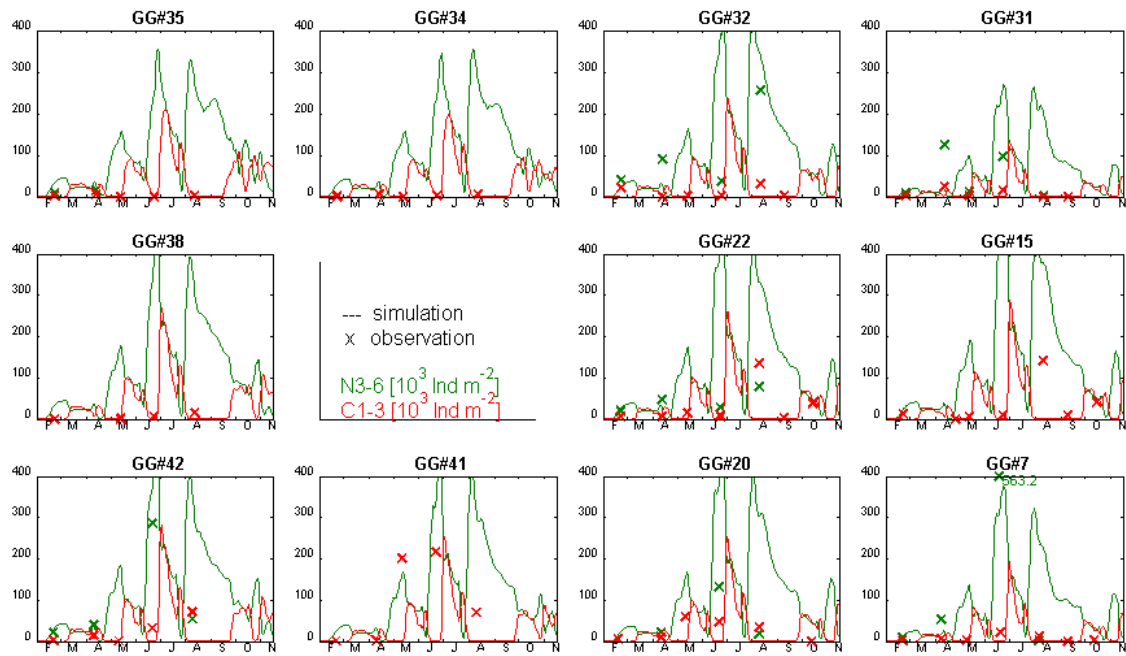


Figure 6



**Pseudocalanus N3-6 and C1-3 [ $10^3$  Ind  $m^{-2}$ ]**



**Pseudocalanus C4-5 and adults [ $10^3$  Ind  $m^{-2}$ ]**

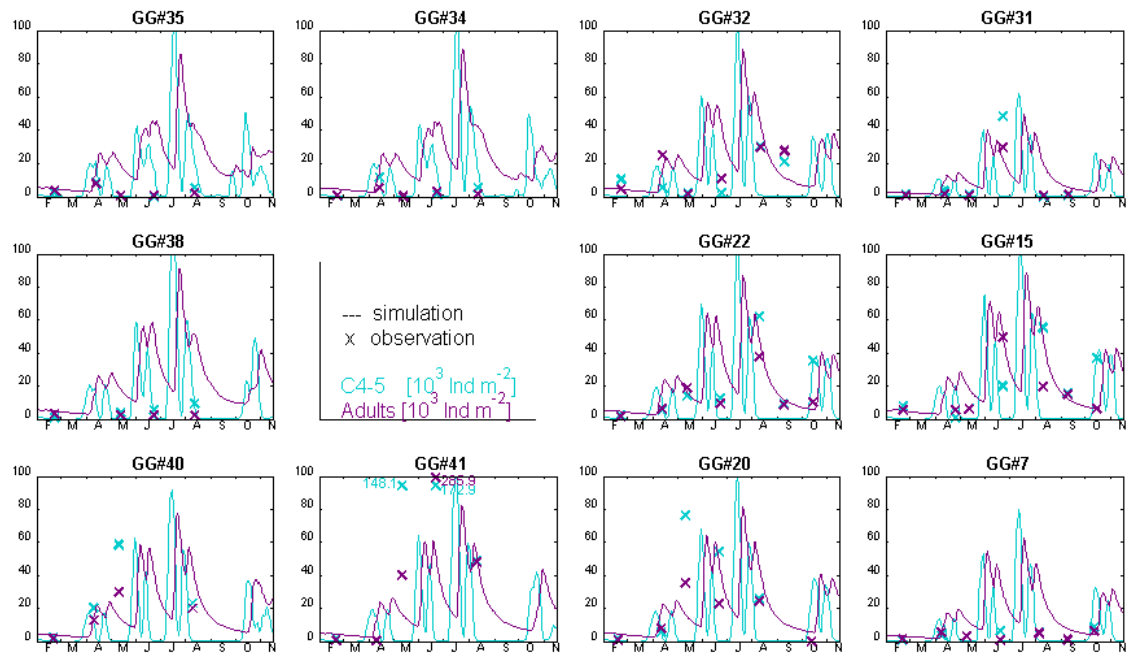


Figure 7

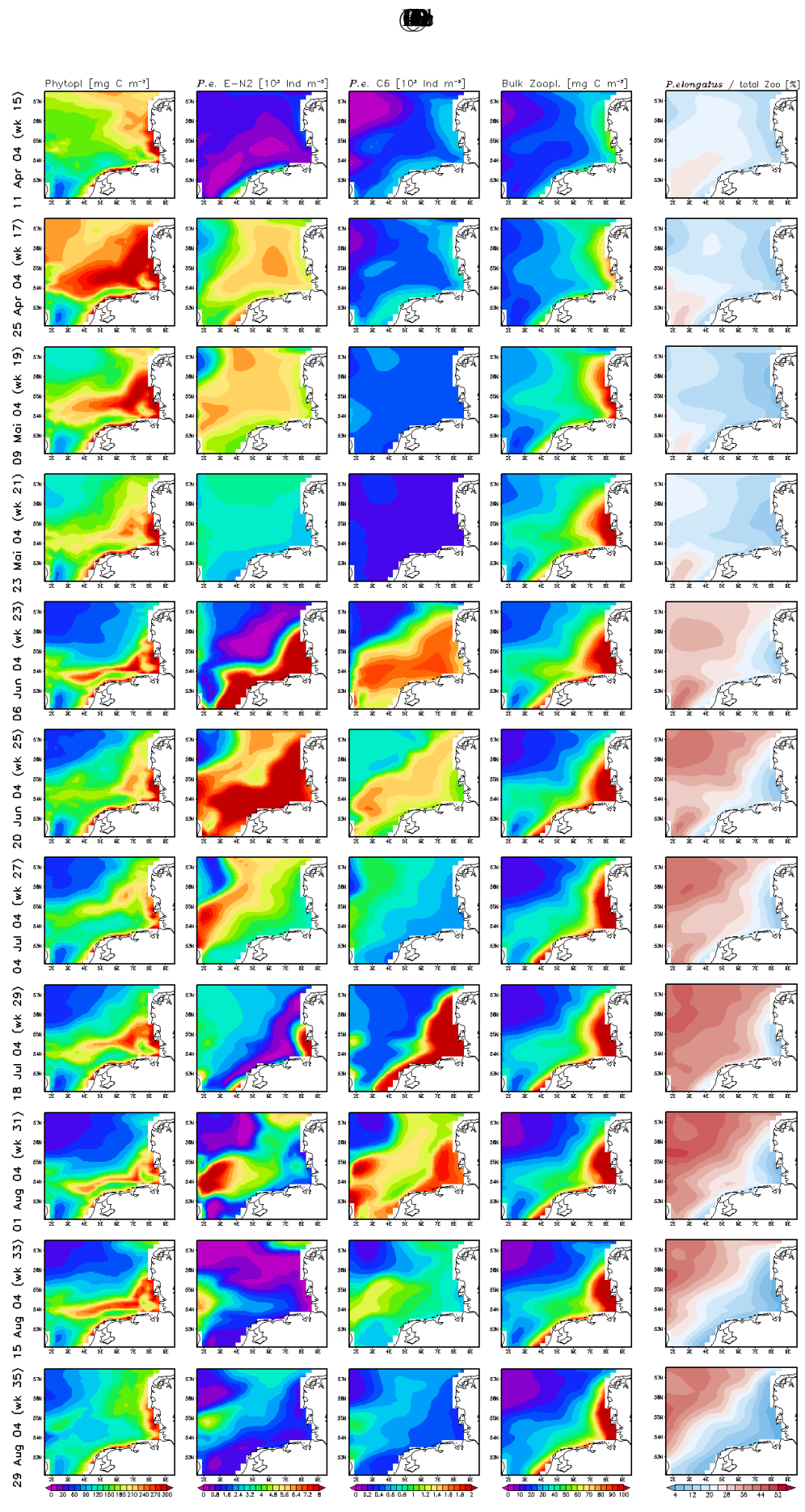


Figure 8

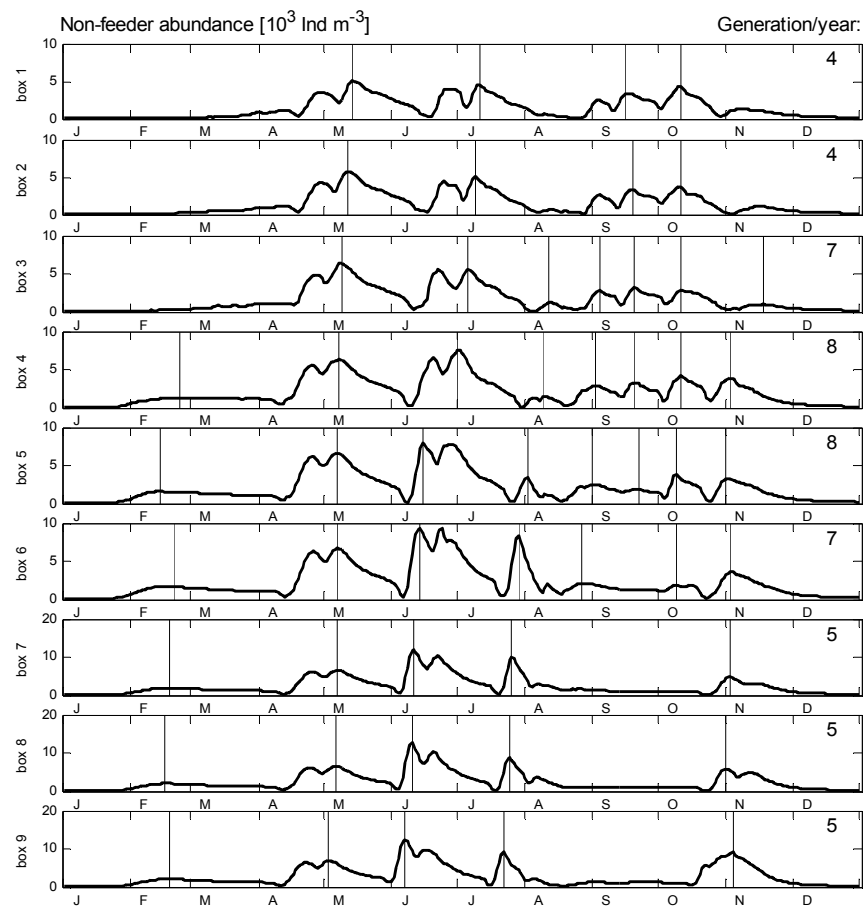
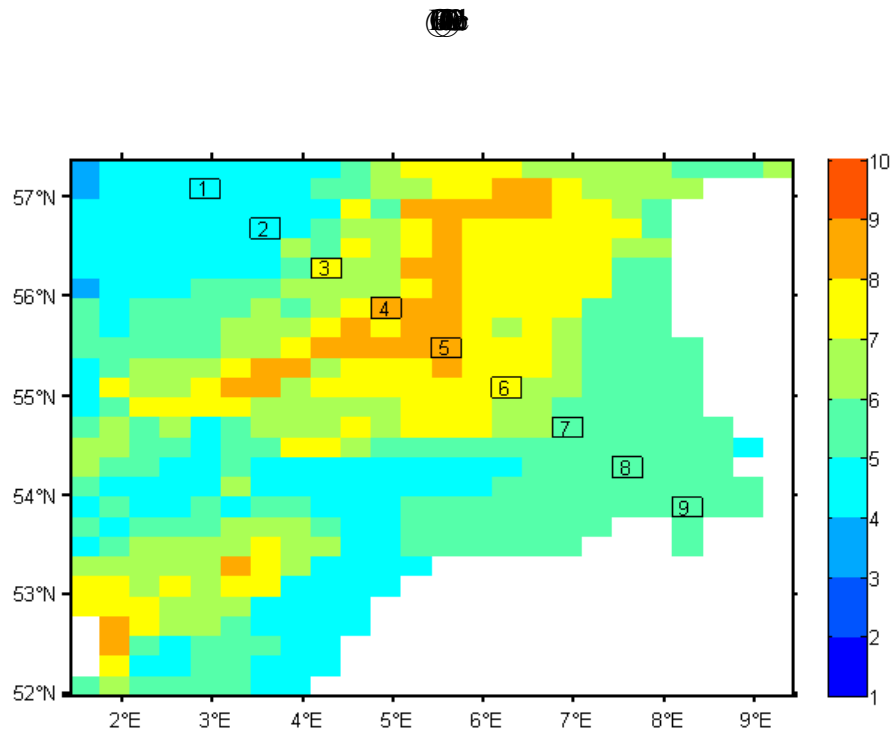


Figure 9

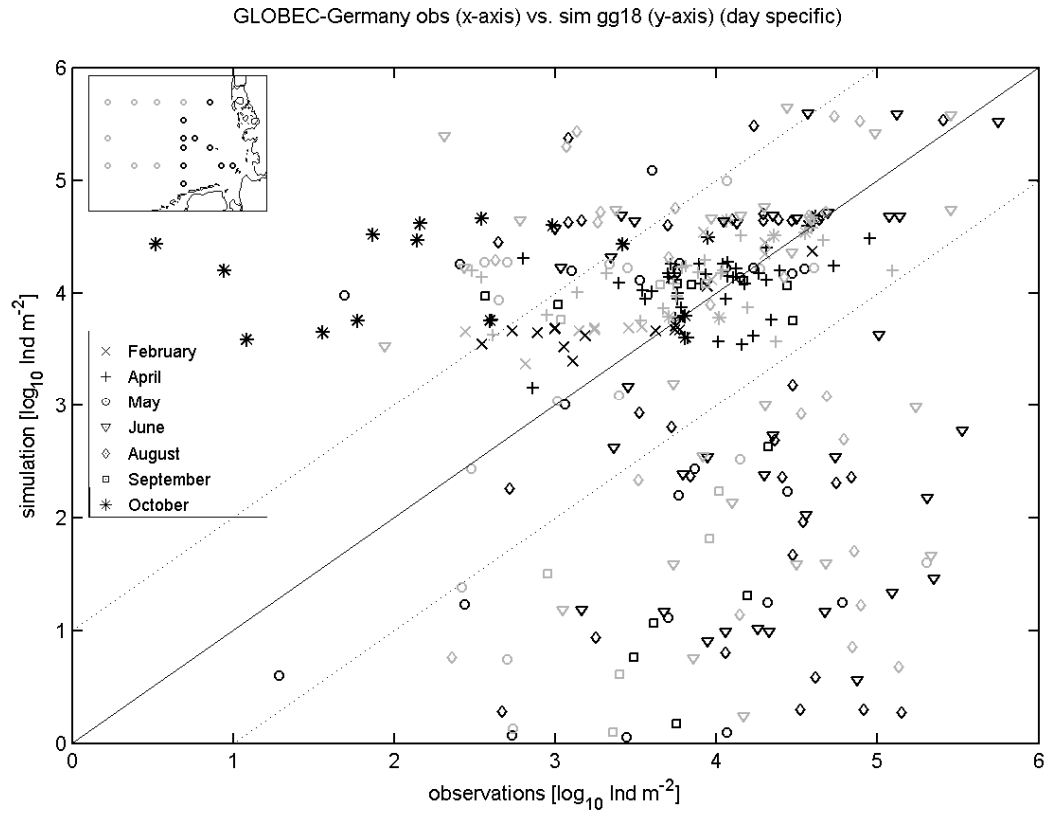
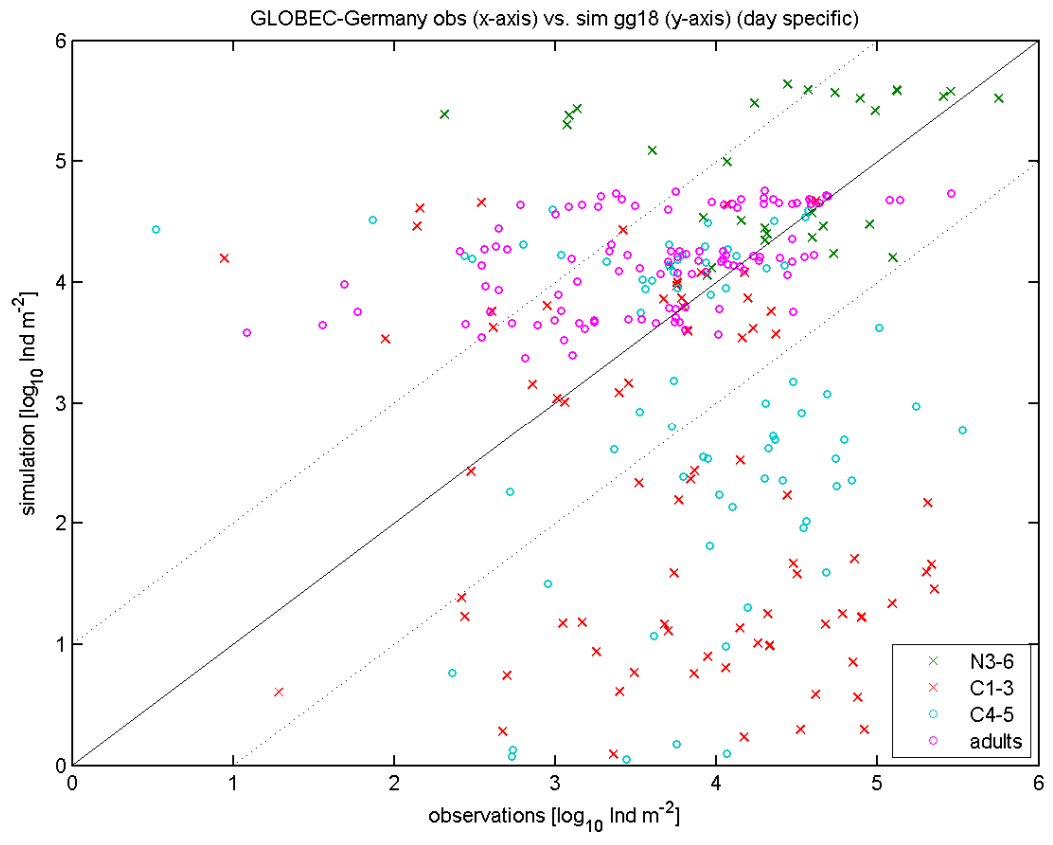


Figure 10

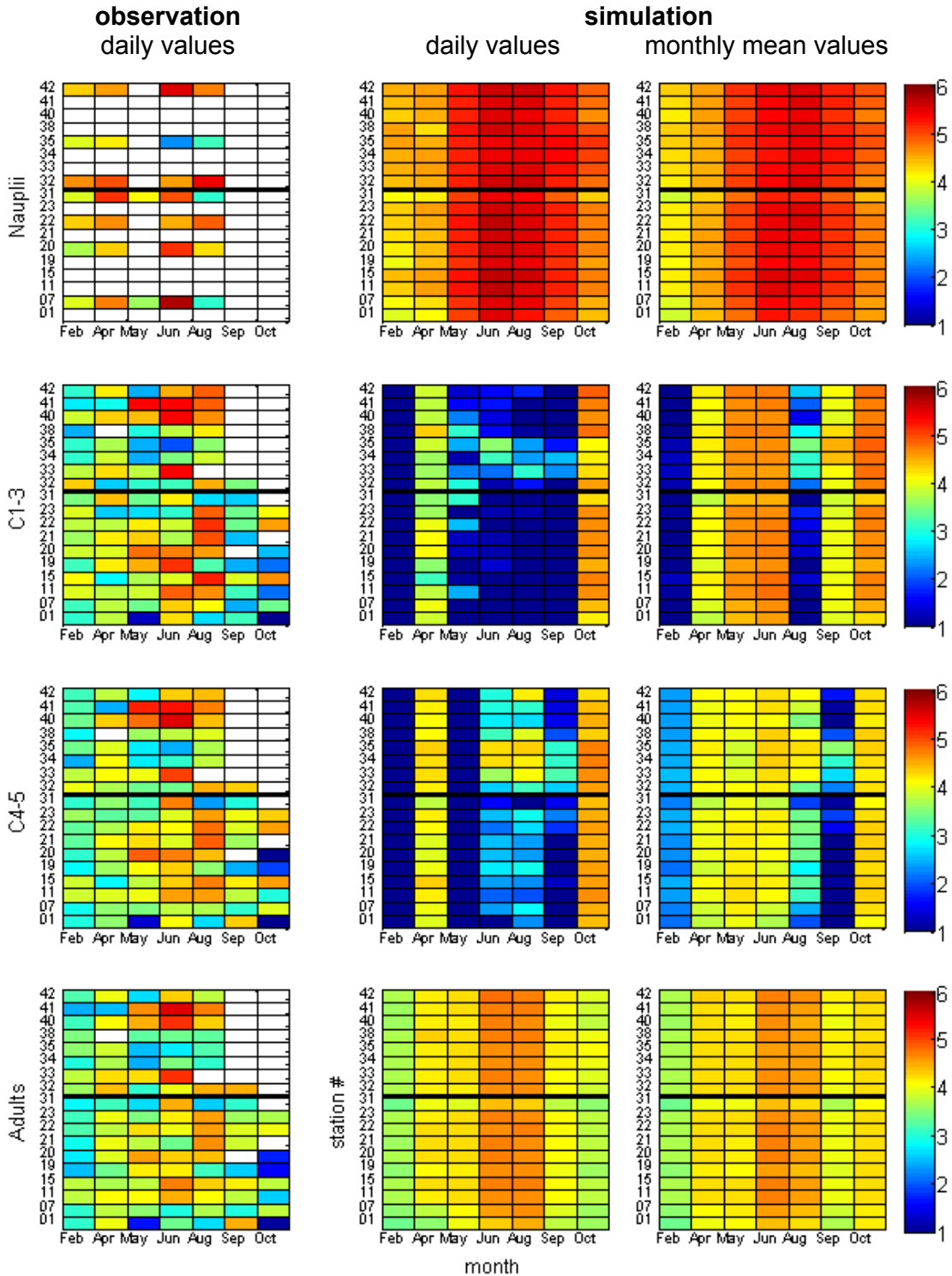


Figure 11

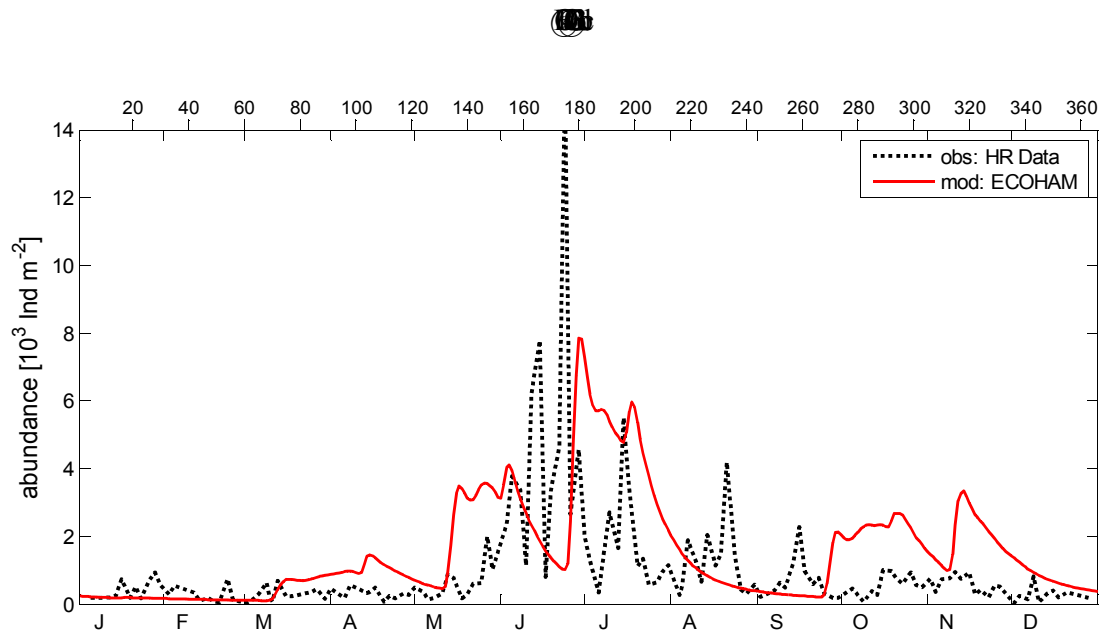




Figure 12

