**An ecological model for the Scheldt Estuary and tidal rivers ecosystem
Spatial and temporal variability of plankton**

Naithani, J.; de Brye, B.; Buyze, E.; Vyverman, W.; Legat, Vincent; Deleersnijder, Eric

DOI

[10.1007/s10750-016-2710-1](https://doi.org/10.1007/s10750-016-2710-1)

Publication date

2016

Document Version

Accepted author manuscript

Published in

Hydrobiologia: the international journal on limnology and marine sciences

Citation (APA)

Naithani, J., de Brye, B., Buyze, E., Vyverman, W., Legat, V., & Deleersnijder, E. (2016). An ecological model for the Scheldt Estuary and tidal rivers ecosystem: Spatial and temporal variability of plankton. *Hydrobiologia: the international journal on limnology and marine sciences*, 775, 51-67. <https://doi.org/10.1007/s10750-016-2710-1>

Important note

To cite this publication, please use the final published version (if applicable).
Please check the document version above.

Copyright

Other than for strictly personal use, it is not permitted to download, forward or distribute the text or part of it, without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license such as Creative Commons.

Takedown policy

Please contact us and provide details if you believe this document breaches copyrights.
We will remove access to the work immediately and investigate your claim.

An ecological model for the Scheldt Estuary and
tidal rivers ecosystem: spatial and temporal
variability of plankton

J. Naithani^{1,*}, B. de Brye¹, E. Buyze², W. Vyverman², V. Legat¹,
and E. Deleersnijder^{3,4}

¹*Université catholique de Louvain, Institute of Mechanics, Materials
and Civil Engineering (IMMC), 4 Avenue G. Lemaître, B-1348
Louvain-la-Neuve, Belgium*

²*Section Protistology and Aquatic Ecology, Department of Biology,
University of Ghent, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium*

³*Université catholique de Louvain, Institute of Mechanics, Materials
and Civil Engineering (IMMC) & Earth and Life Institute (ELI), 4
Avenue G. Lemaître, B-1348 Louvain-la-Neuve, Belgium*

⁴*Delft University of Technology, Delft Institute of Applied
Mathematics (DIAM), Mekelweg 4, 2628CD Delft, The Netherlands*

*Corresponding author: jaya.naithani@uclouvain.be

February 2016

Abstract

This paper presents the formulation, structure and governing equations of an ecosystem model developed for the Scheldt estuary and the tidal river network. The model has twelve state variables: nitrate, ammonium, phosphate, dissolved silica, freshwater and marine phytoplankton (chlorophytes and diatoms), freshwater zooplankton (ciliates, rotifers and copepods) and benthic detritus. The ecological model is coupled to the 1-D tidal resolving version of the Second-generation Louvain-la-neuve ice-ocean Model (SLIM)¹. The model successfully simulates the observed longitudinal and seasonal variation of plankton in the Scheldt estuary. The phytoplankton production in the estuary is governed by temperature, underwater available light, turbidity, nutrients and discharge. Of all these factors, discharge seems to be dominant. High discharge increases the turbidity in the water column and thus reduces the underwater light, while low discharge means decreased nutrients. The marine phytoplankton species were present as far to the upstream limits of the brackish waters, with diatoms dominating in the spring and chlorophytes in early summer. The freshwater phytoplankton are seen from late spring to

¹<http://www.climate.be/SLIM>.

summer. Freshwater zooplankton followed the evolution of freshwater
phytoplankton.

Key words: ecological model; SLIM, Scheldt estuary; tidal river; chlorophytes;
diatoms; ciliates; rotifers; copepods

Introduction

Originating from France, the Scheldt river flows through Belgium, enters the
Netherlands and discharges into the North Sea (Figure 1). In Belgium its main
tributaries are Dender, Durme and Rupel. The Scheldt estuary is a macro-tidal
estuary, extending from the mouth at Vlissingen (0 km) to Ghent (160 km) (Chen
et al., 2005; Meire et al 2005). The tidal wave is semidiurnal. The mean tidal range
at Vlissingen is 4.5 m, 5.85 m near Antwerp (78.5 km) and 2 m near Ghent (Van Rijn,
2010). The tidal wave also enters its major tributaries Rupel (and its tributaries:
Dijle, Zenne, Kleine Nete, Grote Nete) and Durme (Meire et al., 2005). The estuary
has extensive salty (Western Scheldt, >15 PSU, 0 to around 55 km), brackish (Sea
Scheldt, 0.5 – 15 PSU, between around 55 to 90 km) and freshwater (Upper Sea
Scheldt, <0.5 PSU from around 90 km) tidal reaches (Chen et al., 2005; Meire et
al., 2005; Dijkman & Kromkamp, 2006). The extent of salinity intrusion strongly

55 depends on the freshwater discharge. During high discharge (from around November
56 till March) periods, the transect up to around 58 km from the mouth consists of
57 freshwater (< 0.5 PSU). The salinity gradient along the length of the estuary effects
58 the freshwater as well as the marine plankton (Muylaert et al., 1997; 2000a; Muylaert
59 & Sabbe, 1999; Koeman et al., 2004; Lionard et. al., 2005a; Dijkman & Kromkamp,
60 2006). The salinity stress (osmotic) is seen to increase their respiration (Flameling
61 & Kromkamp, 1994; Griffin et al., 2001; Lionard et. al., 2005a).

62 Another important characteristic of the whole Scheldt estuary is the high water
63 column turbidity (Baeyens et al., 1998; Chen et al., 2005; Gazeau et al., 2005;
64 Kromkamp & Peene, 1995, 2005; Dijkman & Kromkamp, 2006; Gource et al., 2013).
65 According to Baeyens et al. (1998) and Dijkman & Kromkamp, (2006) the zone from
66 55 km to 78 km from the sea corresponding roughly with the salinity zone from 10
67 to 2 psu, is the zone of highest turbidity. High turbidity results in high values of
68 light attenuation and decreases photosynthesis in spite of high nutrients (Cloern,
69 1987; Muylaert et at., 1997, 2005a; Chen et al., 2005; Kromkamp & Peene, 1995,
70 2005; Dijkman & Kromkamp, 2006; Brion et al., 2008). The zone of high turbidity
71 also corresponds to high salinity zone for freshwater species and low salinity zone
72 for marine species, thereby reducing their growth in this region.

73 Ecological models for the Scheldt river estuary range from very simple to

74 more complex ones. With time both kind of models continue to be developed.
75 Soetaert et al. (1994) and Soetaert & Herman (1995) developed an ecosystem
76 model to study the phytoplankton production, nitrogen dynamics and carbon
77 flows, respectively in the Westerschelde. Desmit et al. (2005) presented a
78 zero-dimensional model for phytoplanktonic production of the complete 160 km tidal
79 Scheldt estuary from Vlissingen until Ghent. They investigated how short-term,
80 tidally driven physical forcings interfere with the incident sunlight energy to
81 sustain phytoplankton production in the nutrient-rich, well-mixed tidal estuary.
82 Using a simple light-limited primary production model to estimate phytoplankton
83 growth rates in the freshwater tidal reaches of the Scheldt estuary Muylaert et al.
84 (2005a) observed two phytoplankton blooms in the freshwater tidal reaches, one
85 in March and another one in July-August. According to them the first bloom,
86 which was situated in the upstream reaches of the freshwater tidal zones, was
87 imported from the river Scheldt and the second bloom, which was situated more
88 downstream in the freshwater tidal reaches, appeared to have developed within the
89 estuary. Vanderborght et al. (2002; 2007) proposed a reactive-transport model to
90 investigate nutrients and carbon budgets of the estuary. Arndt et al. (2007; 2009)
91 presented a two-dimensional, nested grid, hydrodynamic, and reactive-transport
92 model of the estuary and its tributaries. Hofmann et al. (2008) constructed
93 a 1-D, biogeochemical, pelagic, reactive-transport model of the mixed, turbid,

94 heterotrophic Scheldt estuary. Other studies include a phytoplankton production
95 model incorporating an increasingly complex description of underlying biological
96 mechanisms such as intracellular fluxes and microbial loop (Arndt et al., 2011;
97 Gypens et al., 2012).

98 This study presents a one-dimensional ecological model of the entire Scheldt
99 river estuary. The ecosystem model simulates the dominant phytoplankton and
100 zooplankton groups observed in the Scheldt estuary, particularly in the upper
101 freshwater reaches. The chemical and biological processes are simulated for the
102 tidal Scheldt and its tributaries extending from Vlissingen near the mouth of the
103 estuary to Ghent. **The ecosystem model is coupled to SLIM (see below for a short**
104 **explanation).** The aim of this study is to provide a detailed description of the
105 biological processes contained in the ECO-SLIM model along with the simulations
106 for the year 2003.

107 **The Model**

108 **The domain**

109 The model domain (Fig. 1) consists of the entire Scheldt estuary from Vlissingen
110 (0km) until Ghent (160km). This includes a river network comprising of the Scheldt
111 river and its bifurcation (the Lys) at Ghent, the Rupel and its tributaries (the

112 Dijle, the Zenne, the Nete, the Grote Nete and the Kleine Nete), the Durme and
 113 the Dender. The Scheldt estuary is divided into three different zones: the saline
 114 lower estuary, the brackish upper estuary and the freshwater tidal river. The lower
 115 estuary extends along 55 km from the mouth near Vlissingen to the Dutch-Belgian
 116 border. The width of the estuary is 8 km at the mouth and decreases gradually to
 117 about 1.5 km near the Dutch-Belgian border. The tidal amplitude increases in this
 118 section (from 1.75 at the mouth to 2 m at Bath for the $M2$ component of the tide)
 119 due to bank convergence, shallow areas and partial reflexion. The lower estuary is
 120 influenced by strong tidal mixing. The upper estuary is about 38 km long extending
 121 from the Dutch-Belgian border to Rupelmonde, where its width is reduced to 100 m.
 122 This part is somewhat stratified from time to time (Winterwerp et al., 2003). In this
 123 section, the $M2$ tidal amplitude increases up to 2.3 m to the south of Antwerp, then
 124 decreases slightly upstream. Finally, the freshwater tidal riverine zone, extending
 125 from Hemiksem to sluices near Ghent (where its width reduces to 50 m). In this part
 126 river banks are well defined and the tidal amplitude decreases gradually because of
 127 dissipative processes (the amplitude of $M2$ tide is about 1 m at the Ghent sluices).

128 **The physical model (SLIM)**

129 The physical model consists of 1D cross-section integrated mass and momentum
 130 conservation equations (de Brye et al., 2010). The model is based on the 1D shallow

131 water equations with varying cross section. The downstream boundary lies at the
132 mouth of estuary, located around Vlissingen. The M2 and S2 tides are imposed
133 here according to the observation for Vlissingen. In the upstream of the model, far
134 from the tidal influence, near Ghent and at the extremities of the main tidal rivers
135 network, daily averaged discharges are imposed. The details about the SLIM model
136 and the parameterization can be found in de Brye et al. (2010).

137 **Ecological model**

138 The ecological model (Figure 2) simulates four dissolved inorganic nutrients:
139 nitrate (NO_3), ammonia (NH_4), phosphate (PO_4) and dissolved silica (DSi).
140 Phytoplankton (*PHYTO*) module includes freshwater chlorophytes (*CHL*), marine
141 chlorophytes (*CHLM*), freshwater diatoms (*DIA*) and marine diatoms (*DIAM*).
142 Zooplankton module (*ZOO*) consists of ciliates (*CIL*) and rotifers (*ROT*) as
143 micro-zooplankton, and copepods (*COP*) as meso-zooplankton. These are the
144 dominant plankton groups found in the freshwater tidal reaches of the Scheldt
145 estuary (Muylaert and Sabbe, 1999; Muylaert et al., 2000a; 2009; Lionard et al.,
146 2005a; Dijkman and Kromkamp, 2006; Lionard et al., 2008a; Tackx et al., 2004).
147 Only freshwater zooplankton are simulated in the model. The marine zooplankton
148 are not simulated. Macro-zooplankton or planktivorous-fish are not explicitly
149 modelled but its influence in terms of predation pressure on other zooplankton is

150 taken into account and is used as the closure term.

151 Growth in the model is a function of the availability of light, nutrients and
152 temperature. Respiration is influenced by a salinity function. This term acts to
153 increase the rate of respiration as the salinity changes above/below an optimum
154 salinity for freshwater/marine planktons. Parameterization for respiration in the
155 model includes activity and maintenance respiration (Weger et al., 1989; Langdon
156 1993; Krompkamp & Peene, 1995). The activity respiration depends on the gross
157 production, whereas the maintenance respiration depends on total biomass. All
158 biological rates in the model are doubled when temperature increases by 10 °C
159 (Eppley, 1972; Kremer & Nixon, 1978). For marine diatoms a different temperature
160 function is used. This temperature function ensures a spring and late summer
161 high biomass as measured in the upstream parts of the estuary and the North Sea
162 (Fransz & Verhagen, 1985; Admiraal, 1977; Montagnes & Franklin, 2001; Baretta
163 et al., 2009).

164 Zooplankton graze only on freshwater phytoplankton (marine zooplankton are
165 not simulated). Excretion and respiration of organisms and the remineralisation of
166 the detritus are added directly to the inorganic nutrient pool. A small percentage of
167 faeces and dead organic matter is immediately remineralised to inorganic nutrients,
168 while the rest contributes to the detrital pool and is defined as particulate organic

169 matter (*POM*) in the model. The direct regeneration is a function of temperature
 170 and represents the effect of the microbial food web, which is not explicitly included
 171 in the model. The *POM* settles to the sediments. The model is closed by predation
 172 by macrozooplankton/zooplanktivorous fish. Predation on zooplankton by fish is
 173 defined similarly to grazing on phytoplankton by zooplankton. For predation, the
 174 fish biomass is considered similar to copepod biomass.

175

176 The general equation describing a nonconservative variable is defined as:

$$\frac{\partial}{\partial t}(A \text{ VAR}) + \frac{\partial}{\partial x}(Au\text{VAR} - Ak\frac{\partial \text{VAR}}{\partial x}) = A R_{\text{VAR}} \quad (1)$$

177

178 where VAR can be any model dependent variable such as *PHYTO*, *ZOO*,
 179 nutrients, *POM* and *BD*. The left-hand side terms represent any local change
 180 in the VAR and advection and diffusion of the VAR. The right-hand side of the
 181 equation represents the biological rates of the VAR. Biological variables (except for
 182 nutrients) are expressed in units of concentration of carbon ($\mu g C l^{-1}$).

183

184 Biological rates effecting the local change in phytoplankton are growth,
 185 respiration, extracellular excretion, mortality and grazing.

$$\begin{aligned}
R_{PHYTO} = & GROWTH_{PHYTO} - RESP_{PHYTO} \\
& - ECE_{PHYTO} - MORT_{PHYTO} \\
& - GRAZ_{PHYTOZOO}
\end{aligned} \tag{2}$$

186

187 Phytoplankton growth rate, $GROWTH_{PHYTO}$ ($\mu gCl^{-1}d^{-1}$), is considered to be
188 influenced by nutrients, light intensity and temperature.

$$GROWTH_{PHYTO} = GROWTH_{mPHYTO} * \min(F(N), F(I)) * F(T) * PHYTO \tag{3}$$

189

190 where $GROWTH_{mPHYTO}$ is the maximum growth rate constant (d^{-1}) of
191 phytoplankton at 0 °C. $F(N)$ describes the effect of nutrients availability.

192

193 The effect of nutrients, $F(N)$, on growth is modelled according to Michaelis-Menten
194 formulation. The nitrogen limitation includes a "gourmet term of ammonium"
195 (preference of phytoplankton for ammonia over nitrate, Wroblewski, 1977). The
196 nutrient dependency is defined as:

$$\begin{aligned}
F(N) = \min & \left[\left(\frac{NO_3}{NO_3 + K_{NO_3PHYTO}} \exp(-\Psi NH_4) \right. \right. \\
& \left. \left. + \frac{NH_4}{NH_4 + K_{NH_4PHYTO}} \right), \right. \\
& \left. \left(\frac{PO_4}{PO_4 + K_{PO_4PHYTO}} \right), \left(\frac{Si}{Si + K_{SiPHYTO}} \right) \right] \quad (4)
\end{aligned}$$

197

198 The constants and parameters are defined in Table 2. Ψ is the ammonium inhibition
199 coefficient. Silica limitation acts only on diatoms.

200

201 Light limitation to growth, $F(I)$, is modelled as an exponential decrease of light
202 intensity with depth (Lambert–Beer’s equation). This is defined as:

$$F(I) = \frac{1}{k_e H} \left(\arctan \frac{I_o}{2I_k} - \arctan \left(\frac{I_o \exp(-k_e H)}{2I_k} \right) \right) \quad (5)$$

203

204 The light attenuation coefficient $k_e = k_{e1} + k_{e2} * SPM$. k_{e1} is the background
205 attenuation and k_{e2} is the specific contribution of SPM .

206

207 The temperature-dependent term, $F(T)$, is defined using the "Q₁₀" relation:

208

$$F(T) = e^{(k_T T)} \quad (6)$$

209

210 Temperature function for marine diatoms is defined as:

211

$$F(T_{DIAM}) = e^{(-(T - T_{opt_{DIAM}})^2 / (wt_{DIAM})^2)} \quad (7)$$

212

213 Respiration rate, $RESP$ ($\mu gCl^{-1}d^{-1}$), of phytoplankton depends on temperature

214 and salinity stress. It is defined as:

$$RESP_{PHYTO} = \left(RESP_{b0} * F(T)_{RESP} * PHYTO + RESP_{p0} * GROWTH_{PHYTO} \right) * F(S) \quad (8)$$

215

216 The term $F(S)$ is the respiration response to salinity. For freshwater-adapted

217 phytoplankton it is $F(S)_{fresh} = 1.07^S$. For marine or saltwater-adapted

218 phytoplankton it is $F(S)_{marine} = 1 + 5 * 0.85^S$. The respiration rate increases as

219 salinity increases/decreases for freshwater/saltwater species, and, therefore, the
220 growth declines.

221

222 Extracellular excretion rate of phytoplankton, ECE ($\mu gCl^{-1}d^{-1}$), is defined as:

223

$$ECE_{PHYTO} = k_{ECE} * GROWTH_{PHYTO} \quad (9)$$

224

225 Mortality rate, $MORT$ ($\mu gCl^{-1}d^{-1}$), is the loss of phytoplankton by natural death
226 and is defined as a quadratic equation and depends on temperature.

227

$$MORT_{PHYTO} = MORT_{PHYTO0} * F(T) * PHYTO * PHYTO \quad (10)$$

228

229 Loss of phytoplankton by grazing is described after the zooplankton equation.

230 Equations similar to (2) are written for CHL , $CHLM$, DIA and $DIAM$.

231

232 The rates effecting the local change in zooplankton are grazing, respiration,
233 excretion, fecal pellet, mortality and predation.

$$\begin{aligned}
R_{ZOO} = & GRAZ_{PHYTOZOO} - RESP_{ZOO} \\
& - EXC_{ZOO} - FEC_{ZOO} \\
& - MORT_{ZOO} - PRED_{ZOOZOO}
\end{aligned} \tag{11}$$

234

235 The first term is the grazing of phytoplankton by zooplankton, second and third
236 terms represent the respiration and metabolic excretion, fourth term formulates
237 egestion of fecal pellets by zooplankton and fifth term represent the loss due to
238 mortality. The last term is the predation on zooplankton by other zooplankton
239 groups. This term is a loss term for both ciliates and rotifers, and, for copepods it
240 is a gain term.

Grazing rate, $GRAZ$ ($\mu gCl^{-1}d^{-1}$), is described with a temperature-dependent term (Q_{10}) and an Ivlev equation with a fixed feeding threshold (Ivlev, 1945; Parsons et al., 1967). $PHYTO_{min}$ is the threshold below which zooplankton do not graze.

$$\begin{aligned}
GRAZ_{PHYTOZOO} = & max\left(0, g_{maxPHYTOZOO} * F(T) \right. \\
& \left. * \left[1 - e^{-\lambda*(PHYTO_{min}-PHYTO)}\right] * ZOO\right)
\end{aligned} \tag{12}$$

241

242 $g_{maxPHYTOZOO}$ is the maximum grazing rate constant, (d^{-1}). Marine phytoplankton
243 species are not grazed.

244

245 Respiration rate of zooplankton is defined as: $RESP_{ZOO} = RESP_{ZOO0} * F(S)_{fresh} *$
246 $F(T)_{RESP} * ZOO$, excretion rate is defined as: $EXC_{ZOO} = n_{eZOO} * GRAZ_{PHYTOZOO}$
247 and the egestion of fecal pellets is defined as: $FEC_{ZOO} = n_{fZOO} * GRAZ_{PHYTOZOO}$.
248 Mortality of zooplankton is defined with the similar expression as that for
249 phytoplankton. Equations similar to (11) are written for freshwater CIL , ROT
250 and COP .

251

252 The nutrients equation include the uptake by phytoplankton, the metabolic loss
253 terms of all biological variables, a percentage of their mortality, a percentage of feces
254 of zooplankton, and the remineralized detritus.

$$\begin{aligned}
R_{NUT} = & \sum_{PHYTO=1}^4 \left[-GROWTH_{PHYTO} + RESP_{PHYTO} \right. \\
& \left. + ECE_{PHYTO} + p_{MORT} * MORT_{PHYTO} \right] / R_{C:NUT} \\
& + \sum_{ZOO=1}^3 \left[EXC_{ZOO} + RESP_{ZOO} + p_{FEC} * FEC_{ZOO} \right. \\
& \left. + p_{MORT} * MORT_{ZOO} \right] / R_{C:NUT} \\
& + r_D * F(T_{rem}) * (POM + BD) / R_{C:NUT}
\end{aligned} \tag{13}$$

$R_{C:NUT}$ is the ratio of carbon to respective nutrient in the plankton. Equations
similar to 13 are written for NO_3 , NH_4 , PO_4 and DSi . Silica equation
includes the biological terms only from diatoms, rotifers and copepods. The
 $(-GROWTH + RESP)$ term in NO_3 equation is multiplied by (RN_{PHYTO}) , while
in the NH_4 equation this term is multiplied by $(1 - RN_{PHYTO})$. (RN_{PHYTO})
is the ratio of nitrate uptake to total nitrogen uptake for phytoplankton
and is defined as: $RN_{PHYTO} = \frac{\frac{NO_3}{(NO_3 + K_{NO_3PHYTO})} \exp(-\Psi NH_4)}{\frac{NO_3}{(NO_3 + K_{NO_3PHYTO})} \exp(-\Psi NH_4) + \frac{NH_4}{(NH_4 + K_{NH_4PHYTO})}}$.
Nitrification and denitrification processes are modelled as simple first
order processes affected only by temperature. Nitrification of ammonia is
parameterized as: $NIT = NIT_0 * F(T) * NH_4$. Denitrification is defined as:
 $DENIT = DENIT_0 * F(T) * NO_3$. Nitrification of ammonia is added to the NO_3

266 equation.

267

268 Particulate organic matter or pelagic detritus (μgCl^{-1}), is formed mainly
269 by dead organic matter and zooplankton feces, the rest of what is not directly
270 remineralized in the water column.

$$\begin{aligned} R_{POM} = & \sum_{PHYTO=1}^4 (1 - p_{MORT}) * MORT_{PHYTO} \\ & + \sum_{ZOO=1}^3 \left[(1 - p_{MORT}) * MORT_{ZOO} \right. \\ & \left. + (1 - p_{FEC}) * FEC_{ZOO} \right] \\ & - REM_{POM} - SED_{POM} \end{aligned} \tag{14}$$

271

272 where REM_{POM} is the rate of decomposition of POM defined as
273 $r_D * F(T)_{rem} * POM$ and SED_{POM} is the POM sedimenting to the bottom
274 defined as $-(w_{sPOM}/H) * POM$. Decomposed inorganic nutrients are released back
275 into the water column.

276

277 Benthic detritus ($mgCm^{-2}$), in the sediments is formed mainly by settling of
278 POM/pelagic detritus out of the water column. It is decomposed to further release

279 the dissolved inorganic nutrients to the water column.

280

$$R_{BD} = H * \left[SED_{POM} - \frac{REM_{BD}}{H} \right] \quad (15)$$

281

282

283 REM_{BD} is the decomposition rate of BD defined as $r_{Ds} * F(T_{rem}) * BD$.

284

285 The parameter values used in the model (Table 2) are derived from literature

286 or calibrated within literature ranges. These literature ranges are discussed here.

287 The range of maximum growth rate constants of phytoplankton at 20 °C is 0.5 d^{-1}

288 - 5 d^{-1} (Parsons et al., 1984). The values for the half saturation constants for

289 nutrients uptake used here are within the range found in the literature (Di Toro et

290 al., 1971; Di Toro, 1980; Fransz & Verhagen, 1985; Muylaert et. al., 2000b; Kishi

291 et. al., 2007). k_{e1} is chosen to be the summer value given by Fransz & Verhagen

292 (1985). Light saturation constant ranges from 20 – 300 $\mu E m^{-2} s^{-1}$ (Ignatiades &

293 Smayda, 1970; Montagnes & Franklin, 2001). The basic respiration is a function

294 of total biomass (0 - 10 %) and the activity respiration depends on production

295 (30 - 55 %) (Laws & Caperon, 1976; Kromkamp & Peene, 1995; Soetaert et al.,

296 1994). About 5% of the production in phytoplankton is excreted in soluble form

297 (Mague et al., 1980; Fransz & Verhagen, 1985). Kremer & Nixon (1978) show that
 298 maximum grazing rate constant values lie in the range of 0.10 - 2.50 d^{-1} . Tackx
 299 (1987) and Klepper et al. (1994) estimated that the range of maximum grazing
 300 rate constants of zooplankton at 15 °C is 0.5 - 2.0 d^{-1} . For the Ivlev constant,
 301 Kremer & Nixon (1978) reported the range of 0.4 - 25.0 $(mgC/l)^{-1}$. All Q_{10} -values
 302 are approximately 2, except the one for remineralization that is about 3 (Fransz
 303 and Verhagen, 1985). This is because the bacterial growth in the Scheldt estuary
 304 is among the highest reported in the literature (Goosen et al. 1995). All rate
 305 constants are defined at 0 °C. Fractions of mortality and fecal pellets remineralized
 306 directly in the water column and contributing to the inorganic nutrient pool is
 307 considered to be 40 %. Sedimentation of *POM* used in the literature varies from
 308 1 - 1.5 $m d^{-1}$ (Smetacek, 1980; Fransz & Verhagen, 1985; Blauw et al., 2009).
 309 The mineralization rate coefficient used for *POM* is 0.12 d^{-1} . The same rate was
 310 adapted for the bottom sediments/benthic detritus. Nitrification and denitrification
 311 rates are taken from Blauw et al. (2009). Carbon to nutrient ratios are taken from
 312 Lingeman-Kosmerchock (1978), Los (1982), Fransz & Verhagen (1985).

313 Model forcing

314 For the Scheldt and its tributaries, upstream discharges are interpolated from daily
 315 averaged data from the Hydrological Information Center (HIC, 2015). The discharge

316 of the Ghent–Terneuzen canal are interpolated from the daily averaged data collected
317 by the Netherlands institute for inland water management and treatment (RWS,
318 2015). Discharge is a time dependent forcing. The water discharge of the river
319 Scheldt (Figure 3) and its tributaries (not shown) show a pronounced seasonal cycle,
320 with high flow occurring in early winter and low in summer. Because of the strong
321 correlation between discharge and the phytoplankton growth observed in the Scheldt
322 estuary (Muylaert et al., 2001, 2005a, 2005b; Arndt et al., 2007; Lionard et al 2008b),
323 daily discharge is applied on the boundary of all the tributaries of the Scheldt.

324 The incident light intensity, water temperature and SPM are given as
325 time-dependent external forcing. Water temperature and solar radiation (Figure 4)
326 are obtained from (Waterbase, 2015; Scheldtmonitor, 2015; NCEP, 2015). Maximum
327 temperature was observed in the month of August while solar insolation was at
328 its maximum in the month of June. SPM in the estuary shows large spatial and
329 seasonal variation (Chen et al., 2005; Desmit et al., 2005; Lionard et al., 2005a;
330 2008b; Muylaert et al., 2005a; 2005b; Arndt et al., 2007; Gource, 2011). SPM was
331 interpolated using the data from (NIOO, 2015) and above mentioned literature.

332 Initial and boundary conditions

333 Monthly plankton values for the tributaries are sparse, therefore, a constant value
334 of biological state variables ($1 \mu g Cl^{-1}$) was considered for initial as well as for the

boundary conditions. Winter values of nutrients for the year 2003 were considered as the boundary conditions (Van der Zee et al., 2007; Carbonnel et al., 2009; ScheldtMonitor). These values were applied at the boundaries of all the rivers and at Vlissingen. Winter averaged boundary values were applied as the initial conditions for these nutrients. The salinity is set to 33 at its marine boundary (Vlissingen) and to 0 at the freshwater boundary at Ghent and at the boundaries of all the rivers. A spin-up of one year was considered before the actual simulation, once the parameters were fixed. The model is not found to be sensitive to the initial phytoplankton values, since the simulation starts in January and the first bloom starts in spring, giving enough time for the biology to establish.

Results

Figure 5 shows the longitudinal variation of model simulated and measured salinity averaged over the year 2003. Starting from around 33 pps at Vlissingen, the annual averaged salinity reduces to around 2 pps at 90 km from the sea. Salinity is significant in the freshwater tidal zone during summer, when the discharge is at its minimum.

The ecological model captured the basic features of the Scheldt river estuary, notably, the spatial and seasonal gradients in various variables (Figures 6 - 8). These

353 variations are discussed in the following sections.

354 **Phytoplankton**

355 Freshwater phytoplankton biomass (Figures 6a, 6c, 7a and 7c) starts developing
356 in June when the light and temperature conditions start becoming favorable for
357 growth. It is seen from around 50 km to around 150 km. Because of relatively
358 higher discharge in June the maximum biomass is displaced further downstream
359 to around 90 km (Figures 6a and 6c). Afterwards as the discharge decreases the
360 biomass increases. The maximum freshwater phytoplankton biomass is seen in
361 August upstream of 120 km (Figures 6a and 6c). During this period the water
362 temperature was maximal and the discharge was minimal. Because of low discharge
363 and low SPM, the light penetration in the water column was high. The saline
364 intrusion during low discharge might also be responsible for the freshwater biomass
365 being constrained to more upstream locations. The maximum freshwater biomass
366 occurs in summer (June-September), when all the necessary conditions for growth
367 (nutrients, light, temperature, salinity and discharge) are at their optimum level
368 (Figures 6a, 6c, 7a and 7c).

369 Sudden decrease in biomass in early July and early September, (Figures 6a,
370 6c, 7a and 7c) in the freshwater phytoplankton in spite of favorable light and
371 temperature conditions, cannot be accounted for only by grazing. This might

372 be because of the consumption of already low levels of nutrients because of low
373 discharge.

374 Marine phytoplankton are seen as far up to the brackish zones (Figures 6b, 6d,
375 7b and 7d). Marine diatoms start developing from April onwards and show their
376 peak biomass in May and decrease afterwards, while marine chlorophytes are seen
377 in summer with a maximum in July.

378 Likewise to phytoplankton carbon, the chlorophylla concentration was highest in
379 the freshwater zone, decreased in the brackish zone and showed secondary maxima in
380 the marine waters (Figures 6j and 7j). Primary production was highest in summer in
381 the freshwater upstream parts, while it was highest in spring near the mouth of the
382 estuary (Figures 6a - 6c and Figures 7a - 7d). During late autumn growth is limited
383 because of increased discharge and unfavorable light and temperature conditions.

384 **Zooplankton**

385 The freshwater zooplankton community followed the evolution of freshwater
386 phytoplankton in time and space (Figures 6e, 6g, 6i, 7e, 7g and 7i). They were found
387 from late spring to the beginning of autumn, being maximum in summer. They are
388 high in the upstream parts in late summer and have lower biomass in late spring and
389 early summer and are displaced further downstream. Their abundance decreased
390 downstream near Antwerp. Copepods show higher abundance than ciliates but much

391 less than those of rotifers. Ciliate abundance (Figures 6e and 7e) stays relatively
392 constant compared to rotifers and copepods (Figures 6g, 6i, 7g and 7i), since they
393 are quickly grazed down upon by rotifers. This imply the top-down control of rotifers
394 on ciliates in summer.

395 **Particulate organic matter and Benthic detritus**

396 The POM (mainly carbon) is present only in the spring and summer as a result
397 of planktons in the estuary (Figures 6f and 7f). Benthic detritus (Figures 6h and
398 7h) depends on the POM formation and river discharge. The deposition of benthic
399 detritus is present throughout the growth season, around June-September in the
400 freshwater parts and in the spring near the sea. High discharge leads to the reduction
401 of its deposition. They both (*POM* and *BD*) decrease in autumn and disappear
402 afterwards.

403 **Nutrients**

404 The evolution of nutrients (Fiigure 8) is in agreement with measurements. Nutrients
405 in the estuary are being supplied continuously from the river Scheldt and its
406 tributaries except for a small time, when they are consumed in the upstream regions
407 of the Scheldt in late spring and summer. During this period the supply of nutrients
408 is already low because of low discharge. Nutrients level increase again in autumn,

409 when the discharge increases. After this time the photosynthetic activity reduces
410 because of low temperature and low light environment. Another minima in the
411 nutrients is observed in the downstream areas around 30 km in summer because of
412 the consumption by marine phytoplankton species. However, in these downstream
413 locations they continue to stay low in autumn.

414 **Sensitivity analysis**

415 Model sensitivity was tested for a few parameters found crucial for the plankton
416 biomass along the length of the Scheldt estuary.

417 **Effect of irradiance**

418 The tests with changes in I_{kPHYTO} are summarised in Figure 9 and Table 3.
419 Increasing the optimum light intensity for chlorophytes decreased their biomass
420 and increased the biomass of freshwater diatoms. Increasing the optimum light
421 intensity for diatoms decreased their biomass and increased the biomass of freshwater
422 chlorophytes. While the biomass of marine chlorophytes remain unchanged.
423 Increasing the optimum light intensity simultaneously for chlorophytes and diatoms,
424 increased the biomass of freshwater diatoms only. The biomass of ciliates/rotifers
425 decreased/increased for all the three cases, while the biomass of copepods increased
426 only for the first case and decreased for the rest two cases. These tests imply that

427 light can be a crucial limiting factor for growth in summer.

428 **Effect of fish predation**

429 Reducing the biomass of planktivorous fish, increased the biomass of copepods.
430 Biomass of marine species and ciliates remain unchanged, while the biomass of the
431 other planktons decreased. Although fish has no direct influence on the biomass
432 of chlorophytes, its biomass too is reduced (Figure 10). The increased biomass of
433 copepods increased the grazing pressure on other plankton. The amount of carbon
434 grazed by copepods was much higher than the amount of increased biomass of
435 copepods in carbon. This might have reduced the losses (mortality, respiration,
436 excretion, etc.) and the nutrient regeneration by them. This in turn further reduced
437 the biomass of plankton other than copepods.

438 **Discussion**

439 Freshwater phytoplankton are separated by their marine counterparts by a salinity
440 range which is too high for the growth of freshwater species and too low for
441 the growth of marine species. Salinity alone, however, is not responsible for the
442 disappearance of phytoplankton biomass in the brackish waters around 90 km from
443 Vlissingen. The depth of the estuary is maximum around Antwerp. It is the low
444 light conditions in the deeper waters along with high SPM concentration that makes

445 them disappear in the brackish waters.

446 The absence of freshwater plankton biomass in early spring might be because
447 of almost zero initial boundary values of the biomass and because of the absence
448 of transport from the river Scheldt. According to Muylaert et al. (2000a) the
449 phytoplankton in the uppermost parts of the estuary near Ghent are the ones
450 imported from the river Scheldt, the import being more important in spring than in
451 summer. This import is considered negligible in the present study.

452 Phytoplankton blooms were able to develop in the upper estuary in summer
453 in spite the high rotifer populations and their strong grazing impact. Implying
454 the dominance of discharge over grazing, in shaping the phytoplankton blooms.
455 However, the fact that rotifers graze equally on phytoplankton, detritus and ciliates
456 might also account to its high values in the Scheldt and less detrimental influence to
457 phytoplankton blooms. Most of the riverine input of nutrients are depleted either
458 by consumption or by dilution in the upstream reaches of the Scheldt.

459 In conclusion the model simulated the observed seasonal blooms of
460 phytoplankton and zooplankton production. The longitudinal variation in the
461 variables indicates the influence of salinity, SPM and discharge, while the seasonal
462 variation is influenced by temperature, light and discharge. Longitudinal and
463 seasonal input of the data in the present study is considered constant and is set

464 at a non-zero minimum value. The initial boundary conditions seem to be playing
465 a role in the space-time evolution of the simulations. This is evident in the absence
466 of biomass at the extreme boundaries. In future it is envisaged to perform the
467 simulations using the seasonal variation of all the state variables as initial values at
468 the boundaries of all the rivers and at the mouth of the estuary. This will take care of
469 the winter-spring biomass of zooplankton and the spring freshwater phytoplankton
470 biomass transported from the rivers to the estuary, mainly from the Ghent river
471 (Muylaert et al., 2000a; Lionard et al., 2005b; Carbonnel et al., 2009).

472 The Scheldt estuary ecosystem experiences a very high frequency variations of
473 the physical parameters. It is very difficult to separate/define the influence of one
474 forcing parameter independently of the other. Each parameter influences in a special
475 way in the presence or absence of other parameter. Their dominance is difficult to
476 be interpreted or defined at times. On the contrary each has its well defined role.

477

478 **Acknowledgements**

479

480 The author Jaya Naithani is grateful to Dr Klaas Deneudt for all the help provided
481 in locating the data. Thanks are also due to the two reviewers for their careful,
482 critical and constructive comments. This research was conducted in the framework
483 of the Interuniversity Attraction Pole TIMOTHY (IAP VI. 13), funded by Belgian

484 Science Policy (BELSPO), and the project "Taking up the challenge of multi-scale
485 marine modelling", which is funded by the Communauté Française de Belgique under
486 contract ARC10/15-028 (Actions de recherche concertées) with the aim of developing
487 and applying SLIM. Computational resources were provided by the supercomputing
488 facilities of the Université catholique de Louvain (CISM/UCL) and the Consortium
489 des Equipement de Calcul Intensif en Fédération Wallonie Bruxelles (CECI) funded
490 by the Fond de la Recherche Scientifique de Belgique (FRS-FNRS).

491 References

- 492 [1] Arndt, S., Regnier, P., & J.-P. Vanderborgth, 2009. Seasonally-resolved nutrient
493 export fluxes and fluxes and filtering capacities in a macro tidal estuary. *Journal*
494 *of Marine Systems*, 78, 42-58.
- 495 [2] Arndt, S., Vanderborgth, J.-P., & P. Regnier, 2007. Diatom growth
496 response to physical forcing in a macrotidal estuary: coupling hydrodynamics,
497 sediment transport and biogeochemistry. *Journal of Geophysical Research* 12
498 doi:10.1029/2006JC003581.
- 499 [3] Arndt, S., G. Lacroix, N. Gypens, P. Regnier & C. Lancelot, 2011.
500 Nutrient dynamics and phytoplankton development along the estuary-coastal zone
501 continuum: A model study. *Journal of Marine Systems*, 84, 49-66.
- 502 [4] Baeyens, W., B. van Eck, C. Lambert, R. Wollast & L. Goeyens, 1998. General
503 description of the Scheldt estuary. *Hydrobiologia*, 366, 1-14.

- [5] Blauw, A.N., H.F.J. Los, M. Bokhorst & P.L.A. Erftemeijer, 2009. GEM: a genetic ecological model for estuaries and coastal waters, *Hydrobiologia*, 618, 175-198.
- [6] Brion, N., Andersson, M.G.I., Elskens, M., Diaconu, C., Baeyens, W., Dehairs, F., & J.J. Middelburg, 2008. Nitrogen cycling, retention and export in a eutrophic temperate macrotidal estuary. *Marine Ecological Progress Series*, 357, 87-99.
- [7] Carbonnel, V., M. Lionard, K. Muylaert & L. Chou, 2009. Dynamics of dissolved and biogenic silica in the freshwater reaches of a macrotidal estuary (The Scheldt, Belgium). *Biogeochemistry*, 96, 49-72.
- [8] Chen, M.S., Wartel, S., Van Eck, B., & D.V. Maldegem, 2005. Suspended matter in the Scheldt Estuary. *Hydrobiologia*, 540, 79-104.
- [9] Cloern, J.E., 1987. Turbidity as a control on phytoplankton biomass and productivity. *Continental Shelf Research*, 7, 1367-1381.
- [10] de Brye, B., A. de Brauwere, O. Gourgue, T. Kärnä, J. Lamprechts, R. Comblen & E. Deleersnijder, 2010. A finite-element, multi-scale model of the Scheldt tributaries, river, estuary and ROFI, *Coastal Engineering*, doi:10.1016/j.coastaleng.2010.04.001.
- [11] Desmit, X., Vanderborght, Regnier, P., & R. Wollast, 2005. Control of phytoplankton production by physical forcing in a strongly tidal, well-mixed estuary. *Biogeosciences*, 2, 205-218.
- [12] Dijkman, N. & J.C. Kromkamp, 2006, Photosynthesis characteristics of the phytoplankton in the Scheldt estuary: community and single-cell fluorescence measurements. *European Journal of Phycology*, 41, 425-434.
- [13] Di Toro, D.M., D.J. O'Connor & R.V. Thomann, 1971. A dynamic model of the phytoplankton population in the Sacramento-San Joaquin Delta. *Advances*

- 529 in Chemistry Series, Non-equilibrium Systems in Natural Water Chemistry, 106,
530 Americal Chemical Society, Washington, D.C., 131-180.
- 531 [14] Di Toro, D.M., 1980. Applicability of cellular equilibrium and monod theory
532 to phytoplankton growth kinetics. *Ecological Modelling*, 8, 201-218.
- 533 [15] Eppley, R. W., 1972. Temperature and phytoplankton growth in the sea.
534 *Fishery Bulletin*, 70: 1063-1085.
- 535 [16] ESRL, 2015. <http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html>.
- 536 [17] Flameling, I. A. & J. Kromkamp, 1994. Responses of respira- tion and
537 photosynthesis of *Scenedesmus protuberans* Fritsch to gradual and steep salinity
538 increases. *Journal of Plankton Research* 16: 1781–1791.
- 539 [18] Fransz, H.G. & J.H.G. Verhagen, 1985. Modelling research on the production
540 of phytoplankton in the southern bight of the north sea in relation to riverborne
541 nutrient loads. *Netherlands Journal of Sea Research*, 19, 241-250.
- 542 [19] Gazeau, F., Gattuso, J.-P., Middelburg, J.J., Brion, N., Schiettecatte, L.-S.,
543 Frankignouille & A.V. Borges, 2005. Planktonic and whole system metabolism in
544 a nutrient-rich estuary (the Scheldt Estuary). *Estuaries*, 28, 868-883.
- 545 [20] Goosen, N.K., P. van Rijswijk & U. Brockmann, 1995. Comparison of
546 heterotrophic bacterial production rates in early spring in the turbid estuaries
547 of the Scheldt and the Elbe. *Hydrobiologia*, 311, 31-42.
- 548 [21] Gource, O., 2011. Finite element modelling of sediment dynamics in the Scheldt.
549 PhD Thesis, UCL, pp. 151.
- 550 [22] Gource, O. W. Baeyens, M.S. Chen, A. de Brauwere, B. de Brye, E.
551 Deleersnijder, M. Elskens & V. Legat, 2013. A depth-averaged two-dimensional
552 sediment transport model for environmental studies in the Scheldt Estuary and
553 tidal river netsork. *Journal Marine Systems*, 128, 27-39.

- [23] Gypens, N., E. Delhez, A. Vanhoute-Brunier, S. Burton, V. Thieu, P. Passy, Y. Liu, J. Callens, V. Rousseau, & C. Lancelot, 2012. Modelling phytoplankton succession and nutrient transfer along the Scheldt estuary (Belgium, The Netherlands). *Journal of Marine Systems*. <http://dx.doi.org/10.1016/j.jmarsys.2012.10.006>.
- [24] HIC, 2015. <http://www.hydra.vlaanderen.be/hic/servlet/index>.
- [25] Hofmann, A.F., K. Soetaert, & J.J. Middelburg, 2008. Present nitrogen and carbon dynamics in the Scheldt estuary using a novel 1-D model. *Biogeosciences*, 5, 981-1006.
- [26] Ignatiades, L. & T.J. Smayda, 1970. Autecological studies on the marine diatom *Rhizosolenia fragilissima* Bergon. I. The influence of light, temperature and salinity. *Journal of Phycology*, 6, 332-33.
- [27] IRMB (Institut Royal Meteorologique de Belgique) (2003– 2004) Bulletins mensuels, Observations climatologiques, parties I et II. Institut Royal Meteorologique de Belgique, Bruxelles (In French/Dutch).
- [28] Ivlev, V.S., 1945. The biological productivity of waters. *Usp. soverm. Biol.*, 19, 98-120.
- [29] Klepper, O., M.W.M. van der Tol, H. Scholten, & P.M.J. Herman, 1994. SMOSES: a simulation model for the Oosterschelde ecosystem. *Hydrobiologia*, 282:283, 437-451.
- [30] Koeman, R.P.T., Brochard, C.J.E., Fockens, K., Verweij, G.L., & Esselink, P., 2004. Biomonitoring van Fytoplankton in de Nederlandse Zoute Wateren 2003 Kite Diagrammen, Koeman en Bijkerk, Ecologisch onderzoek en advies, Haren: The Netherlands.
- [31] Kremer, J.N. & S.W. Nixon, 1978. A Coastal Marine Ecosystem: Simulation and Analysis. *Ecological Studies*, vol. 24. Springer-Verlag, Heidelberg, p. 217.

- 580 [32] Kromkamp, J.C. & J. Peene, 1995. Possibility of net phytoplankton primary
581 production in the turbid Schelde estuary (SW Netherlands). *Marine Ecology*
582 *Progress Series*, 121, 249-259.
- 583 [33] Kromkamp, J.C. & J. Peene, 2005. Changes in phytoplankton biomass
584 and primary production between 1991 and 2001 in the Westerschelde estuary
585 (Belgium/The Netherlands). *Hydrobiologia*, 540, 117-126.
- 586 [34] Langdon C., 1993. The significance of respiration production measurements
587 based on both carbon and oxygen. In: L1 WKW, Maestrini SY (eds) *Measurement*
588 *of primary production from the molecular to the global scale*. Vol 197 ICES MSS,
589 International Council for the Exploration of the Sea, Copenhagen, p 69-78.
- 590 [35] Laws.E. & J. Caperon, 1976. Carbon and nitrogen metabolism by *Monochrysis*
591 *lutheri*: measurement of growth-rate dependent respiration rates. *Marine Biology*,
592 36, 85-97.
- 593 [36] Lingeman-Kosmerchock, M., 1978. Phytoplankton cells, their nutrient contents,
594 mineralisation and sinking rates. Delft Hydraulics Laboratoty report R1310, Delft.
- 595 [37] Lionard, M., Muylaert, K., van Gansbeke, D. & W. Vyverman, 2005a. Influence
596 of changes in salinity and light intensity on growth of phytoplankton communities
597 from the Schelde river estuary (Belgium/The Netherlands). *Hydrobiologia*, 540,
598 105-115.
- 599 [38] Lionard, M., Azémar, F., Boulêtreau, Muylaert, K., Tackx, M. & W. Vyverman,
600 2005b. Grazing by meso- and microzooplankton on phytoplankton in the upper
601 reaches of the Schelde estuary (Belgium/The Netherlands). *Estuarine, Coastal*
602 *and Shelf Science*, 64, 764-774.
- 603 [39] Lionard, M., Muylaert, K., Tackx, M. & W. Vyverman, 2008a. Evaluation of
604 the performance of HPLC-CHEMTAX analysis for determining phytoplankton

- 605 biomass and composition in a turbid estuary (Schelde, Belgium). *Estuarine,*
606 *Coastal and Shelf Science*, 76, 809-817.
- 607 [40] Lionard, M., Muylaert, K., Hanoutti, A., Maris, T., Tackx, M. & W. Vyverman,
608 2008b. Inter-annual variability in phytoplankton summer blooms in the freshwater
609 tidal reaches of the Schelde estuary (Belgium), *Estuarine, Coastal and Shelf*
610 *Science*, 79, 694-700.
- 611 [41] Los, F.J., 1982. Mathematical simulation of algae blooms by the model BLOOM
612 II. Delft Hydraulics Laboratory Publ. no 316, Delft.
- 613 [42] Meire, P., T. Ysebaert, S. van Damme, E.V. den Bergh, T. Maris & E. Struyf,
614 2005. The Scheldt estuary: a description of a changing ecosystem. *Hydrobiologia*,
615 540, 1-11.
- 616 [43] Muylaert, K., Van Kerckvoorde, A., Vyverman, W. & K. Sabbe, 1997.
617 Structural characteristics of phytoplankton assemblages in tidal and non-tidal
618 freshwater systems: a case study from the Schelde basin, Belgium. *Freshwater*
619 *Biology*, 38, 263-276.
- 620 [44] Muylaert, K. & K. Sabbe, 1999. Spring phytoplankton assemblages in and
621 around the maximum turbidity zone of the estuaries of the Elbe (Germany), the
622 Schelde (Belgium/The Netherlands) and the Gironde (France). *Journal of Marine*
623 *Systems*, 22, 133-149.
- 624 [45] Muylaert, K., Sabbe, K. & W. Vyverman, 2000a. Spatial and temporal
625 dynamics of phytoplankton communities in a freshwater tidal estuary (Schelde,
626 Belgium). *Estuarine, Coastal and Shelf Science*, 50, 673-687.
- 627 [46] Muylaert, K., Mieghem, R.V., Sabbe, K., Tackx, M. & W. Vyverman, 2000b.
628 Dynamics and trophic roles of heterotrophic protists in the plankton of a
629 freshwater tidal estuary. *Hydrobiologia*, 432, 25-36.

- [47] Muylaert, K., Van Wichelen, J., Sabbe, K., & W. Vyverman, 2001. Effects of freshets on phytoplankton dynamics in a freshwater tidal estuary (Schelde, Belgium). *Archiv für Hydrobiologie* 150, 269-288.
- [48] Muylaert, K., M. Tackx & W. Vyverman, 2005a. Phytoplankton growth rates in the freshwater tidal reaches of the Schelde estuary (Belgium) estimated using a simple light-limited primary production model. *Hydrobiologia*, 540, 127-140.
- [49] Muylaert, K., R. Dasseville, L. De Brabandere, F. Dehairs & W. Vyverman, 2005b. Dissolved organic carbon in the freshwater tidal reaches of the Schelde estuary. *Estuarine, Coastal and Shelf Science*, 64, 591-600.
- [50] Muylaert, K., Sabbe, K. & W. Vyverman, 2009. Changes in phytoplankton diversity and community composition along the salinity gradient of the Schelde estuary (Belgium/The Netherlands). *Estuarine, Coastal and Shelf Science*, 82, 335-340.
- [51] NCEP, 2015. <http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html>.
- [52] Parsons, T.R., Le Brasseur, R.J. & J.D. Fulton, 1967. Some observations on the dependence of zooplankton grazing on cell size and concentration of phytoplankton blooms. *Journal of Oceanographical Society of Japan*, 23, 10-17.
- [53] Parsons, T.R., Takahashi, M., & B. Hargrave, 1984. *Biological Oceanographic Processes*, third ed. Pergamon Press.
- [54] **RWS**, 2015. Ministerie van Verkeer en Waterstaat, www.waterbase.nl.
- [55] ScheldtMonitor, Onderzoek Milieu-effecten Sigmaplan. Multidisciplinaire studie rond het estuariene milieu van de Zeeschelde. Ecosystem Management Research Group, UA; Protistology and Aquatic Ecology, Ugent; Laboratoire d'Ecologie des Hydrosystèmes, Université Paul Sabatier - France, i.o.v. Vlaamse Overheid; Beleidsdomein Mobiliteit en

- 655 Openbare Werken; Waterwegen en zeekanaal NV, metadata available at
656 <http://www.scheldemonitor.be/imis.php?module=dataset&dased=1381>.
- 657 [56] Smetacek, V.S, 1980. Zooplankton standing stock, copepod faecal pellets and
658 particulate detritus in Kiel Bight. *Marine Biology*, 63, 1-11.
- 659 [57] Soetaert, K. Herman, P.M.J. & J. Kromkamp, 1994. Living in twilight:
660 estimating net phytoplankton growth in the Westerschelde estuary (The
661 Netherlands) by means of an ecosystem model (MOSES). *Journal of Plankton*
662 *Research*, 16, 1277-1301.
- 663 [58] Soetaert, K. & P.M.J. Herman, 1995. Carbon flows in the Westerschelde
664 estuary (The Netherlands) evaluated by means of an ecosystem model (MOSES).
665 *Hydrobiologia*, 311: 247-266.
- 666 [59] Tackx, M. L. M., 1987. Grazing door zooplankton in de Oosterschelde. Ph.D.
667 thesis, Lab. voor ecologie en systematiek, Vrije Universiteit Brussel.
- 668 [60] Tackx, M. L. M., N. de Pauw, R. van Mieghem, F. Azemar, A. Hannouti, S.
669 van Damme, F. Fiers, N. Daro, & P. Meire, 2004. Zooplankton in the Schelde
670 estuary, Belgium and The Netherlands. Spatial and temporal patterns, *Journal*
671 *of Plankton Research*, 26, 133– 141.
- 672 [61] Van der Zee, C., N. Roevros, & L. Chou, 2007. Phosphorus speciation,
673 transformation and retention in the Scheldt estuary (Belgium/The Netherlands)
674 from the freshwater tidal limits to the North Sea. *Marine Chemistry*, 106, 76-91.
- 675 [62] Vanderborght, J.P., Wollast, R., Loijens, M., & P. Regnier, 2002. Application
676 of a transport-reaction model to the estimation of biomass fluxes in the Scheldt
677 estuary. *Biogeochemistry*, 59, 207-237.
- 678 [63] Vanderborght, J.P., Folmer, I.M., Aguilera, D.R. Unhrendt, T., &
679 P. Regnier, 2007. Reactive-transport modelling of C, N, and O_2 in a

- 680 river-estuarine-coastal zone system: Application to the Scheldt estuary, Marine
681 Chemistry, 106, 92-110.
- 682 [64] Van Rijn, L.C., 2010. Tidal phenomena in the Scheldt Estuary. Report,
683 Deltares, pp 105.
- 684 [65] Waterbase, 2015. Ministerie van Verkeer en Waterstaat, www.waterbase.nl.
- 685 [66] Weger, H. G., Herzig, R., Falkowski, P. G., & D.H. Turpin, 1989. Respiratory
686 losses in the light in a marine diatom: measurements by short-term mass
687 spectrometry, Limnology and Oceanography, 34, 1153–1161.
- 688 [67] Wroblewski, J.S., 1977. A model of phytoplankton plume formation during
689 variable Oregon upwelling. Journal of Marine Research, 35, 357-394.

Figure 1: Map of the Scheldt river estuary and its tributaries. The three zones of the estuary (lower, upper and freshwater) are separated by dash-dot lines.

Figure 2: Schematic view of the ECO-SLIM model showing various variables (circles) and processes (boxes) in the model.

Figure 3: Discharge of the river Scheldt for the year 2003.

Figure 4: Irradiance and temperature for the year 2003.

Figure 5: **Longitudinal** variation of the model simulated salinity (-) and measured salinity (*) for the year 2003. X-axis is in kms, with 0 km at Vlissingen and 160 km at Ghent.

Figure 6: The spatio-temporal variation of model simulated variables for the year 2003. Y-axis is in kms, with 0 km at Vlissingen and 160 km at Ghent. The three main rivers Rupel, Durme and Dender join the Scheldt river at around 92, 100 and 123 kms, respectively from Vlissingen.

Figure 7: Temporal variation of model simulated variables (-) and measurements (*) for the year 2003. Freshwater plankton are averaged over the freshwater estuary and the marine phytoplankton are averaged over the marine parts, organic waste and chlorophyll-*a* are averaged over the whole estuary.

Figure 8: **Longitudinal** variation of the model simulated nutrients (-) and measurements (*) for the year 2003. X-axis is in kms, with 0 km at Vlissingen and 160 km at Ghent. The three main rivers Rupel, Durme and Dender join the Scheldt river at around 92, 100 and 123 kms, respectively from Vlissingen.

Figure 9: **Longitudinal** variation of model simulated variables with light saturation constant for phytoplankton changed separately or simultaneously ($I_{kCHL} = 125 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $I_{kDIA} = 75 \mu\text{mol m}^{-2} \text{s}^{-1}$). X-axis is in kms, with 0 km at Vlissingen and 160 km at Ghent.

Figure 10: Time series of model simulated variables when the fish biomass was reduced.

Table 1: Variables and parameters for the SLIM model

Parameter	Units
t , the time	s
x , along-river distance	m
A , the cross-section area	m^2
u , the cross-section averaged velocity	d^{-1}
η , the elevation of the free surface above the reference level	m
H , the total effective depth	m
g , the gravitational acceleration	ms^{-2}
ν , the horizontal eddy viscosity	ms^{-2}
C_h , the Chézy coefficient	
k , the longitudinal diffusivity	$m^2 s^{-1}$
C , the tracer concentration	

Table 2: Parameter values for the ecological model

Parameter	Value
General	
dt , time step	20minutes
k_{e1} , background extinction for water	0.2 m^{-1}
k_{e2} , extinction due to SPM	$0.02 \text{ L mg}^{-1} \text{ m}^{-1}$
I_k , optimum light intensity for phytoplankton	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
I_o , light intensity at the water surface	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
k_T , temperature coefficient for the growth rate and other temperature dependent rates	$0.069 \text{ }^{\circ}\text{C}^{-1}$
k_{TRESP} , temperature coefficient for the respiration rate	$0.045 \text{ }^{\circ}\text{C}^{-1}$
k_{Trem} , for remineralization	$0.1 \text{ }^{\circ}\text{C}^{-1}$
T , water temperature	$^{\circ}\text{C}$
$RESP_{b0}$, maintenance respiration percentage of phytoplankton at 0°C	0.03 d^{-1}
$RESP_{p0}$, percentage of $GROWTH_{PHYTO}$ respired at 0°C	0.03
λ , Ivlev constant	$0.01 (\mu\text{gCl}^{-1})^{-1} \text{ d}^{-1}$
$PHYTO_{min}$, the threshold value of phytoplankton biomass below which zooplankton do not graze	$10 \mu\text{gCl}^{-1}$
$C : Chla$, ratio of carbon to Chlorophyll-a	30 NO DIM
$R_{C:N}$, ratio of carbon to nitrogen	5.88 NO DIM
$R_{C:P}$, ratio of carbon to phosphate	32.25 NO DIM
$R_{C:Si}$, ratio of carbon to silica	2.13 NO DIM
p_{MORT} , percentage of dead organic matter directly remineralised in the water column	0.4 d^{-1}
p_{FEC} , percentage of feces directly remineralised in the water column	0.4 d^{-1}
NIT_0 , nitrification rate coefficient at 0°C	0.0175 d^{-1}
$DENIT_0$, denitrification rate coefficient at 0°C	0.0075 d^{-1}
Chlorophytes, CHL (μgCl^{-1})	
NO_3CHL , half saturation constant for NO_3 uptake by CHL	$10 \mu\text{gNl}^{-1}$
K_{NH_4CHL} , half saturation constant for NH_4 uptake by CHL	$5 \mu\text{gNl}^{-1}$
K_{PO_4CHL} , half saturation constant for PO_4 uptake by CHL	$0.5 \mu\text{gPl}^{-1}$
$GROWTH_{mCHL}$, CHL maximum growth rate constant at 0°C	0.36 d^{-1}
I_{kCHL} , CHL optimum light intensity	$100 \mu\text{mol m}^{-2} \text{ s}^{-1}$
$MORT_{0CHL}$, CHL rate constant at 0°C	$0.000025 (\mu\text{gCl}^{-1})^{-1} \text{ d}^{-1}$
k_{ECECHL} , CHL ratio of extracellular excretion to photosynthesis	0.05
Diatoms, DIA (μgCl^{-1})	
Continued on next page	

Table 2 – continued from previous page

Parameter	Value
K_{NO_3DIA} , half saturation constant for NO_3 uptake by DIA	$15 \mu g N l^{-1}$
K_{NH_4DIA} , half saturation constant for NH_4 uptake by DIA	$5 \mu g N l^{-1}$
K_{PO_4DIA} , half saturation constant for PO_4 uptake by DIA	$1 \mu g P l^{-1}$
K_{DSiDIA} , half saturation constant for DSi uptake by DIA	$20 \mu g Si l^{-1}$
$GROWTH_{mDIA}$, DIA maximum growth rate constant at $0^\circ C$	$0.42 d^{-1}$
I_{kDIA} , DIA optimum light intensity	$50 \mu mol m^{-2} s^{-1}$
$MORT_{0DIA}$, DIA rate constant at $0^\circ C$	$0.0000025 (\mu g Cl^{-1})^{-1} d^{-1}$
k_{ECEDIA} , DIA ratio of extracellular excretion to photosynthesis	0.05
Marine Chlorophytes, CHLM ($\mu g Cl^{-1}$)	
K_{NO_3CHLM} , half saturation constant for NO_3 uptake by CHLM	$10 \mu g N l^{-1}$
K_{NH_4CHLM} , half saturation constant for NH_4 uptake by CHLM	$5 \mu g N l^{-1}$
K_{PO_4CHLM} , half saturation constant for PO_4 uptake by CHLM	$0.5 \mu g P l^{-1}$
$GROWTH_{mCHLM}$, CHLM maximum growth rate constant at $0^\circ C$	$0.3 d^{-1}$
I_{kCHLM} , CHLM optimum light intensity	$100 \mu mol m^{-2} s^{-1}$
$MORT_{0CHLM}$, CHLM rate constant at $0^\circ C$	$0.00005 (\mu g Cl^{-1})^{-1} d^{-1}$
$k_{ECECHLM}$, CHLM ratio of extracellular excretion to photosynthesis	0.05
Marine Diatoms, DIAM ($\mu g Cl^{-1}$)	
K_{NO_3DIAM} , half saturation constant for NO_3 uptake by DIAM	$15 \mu g N l^{-1}$
K_{NH_4DIAM} , half saturation constant for NH_4 uptake by DIAM	$5 \mu g N l^{-1}$
K_{PO_4DIAM} , half saturation constant for PO_4 uptake by DIAM	$1 \mu g P l^{-1}$
$K_{DSiDIAM}$, half saturation constant for DSi uptake by DIAM	$10 \mu g Si l^{-1}$
$GROWTH_{mDIAM}$, DIAM maximum growth rate constant at $T_{optDIAM}$	$0.7 d^{-1}$
I_{kDIAM} , DIAM optimum light intensity	$50 \mu mol m^{-2} s^{-1}$
$MORT_{0DIAM}$, DIAM rate constant at $T_{optDIAM}$	$0.000053 (\mu g Cl^{-1})^{-1} d^{-1}$
$k_{ECEDIAM}$, DIAM ratio of extracellular excretion to photosynthesis	0.05
$T_{optDIAM}$, optimum temperature for marine diatom growth	$8^\circ C$
wt_{DIAM} , width of influence of $T_{optDIAM}$	$10^\circ C$
Ciliates, CIL ($\mu g Cl^{-1}$)	
$RESP_0$, zooplankton respiration rate at $0^\circ C$	$0.03 d^{-1}$
n_{eZoo} , excretion by zooplankton	0.3
n_{fZoo} , fecal pellet egestion by zooplankton	0.3
$MORT_{0CIL}$, CIL rate constant at $0^\circ C$	$0.00025 (\mu g Cl^{-1})^{-1} d^{-1}$
$g_{maxCHLCIL}$, CIL maximum grazing rate constant on CHL at $0^\circ C$	$0.4 d^{-1}$
Rotifers, ROT ($\mu g Cl^{-1}$)	
$MORT_{0ROT}$, ROT rate constant at $0^\circ C$	$0.000003 (\mu g Cl^{-1})^{-1} d^{-1}$
Continued on next page	

Table 2 – continued from previous page

Parameter	Value
$g_{maxCHLROT}$, maximum grazing rate constant on CHL by ROT at 0 °C	$0.1 d^{-1}$
$g_{maxDIAROT}$, ROT maximum grazing rate constant on DIA at 0 °C	$0.27 d^{-1}$
$p_{maxCILROT}$, ROT maximum grazing rate constant on CIL at 0 °C	$0.2 d^{-1}$
Copepods, COP (μgCl^{-1})	
$MORT_{0COP}$, COP rate constant at 0 °C	$0.00015 (\mu gCl^{-1})^{-1} d^{-1}$
$g_{maxCHLCOP}$, COP maximum grazing rate constant on CHL at 0 °C	$0.1 d^{-1}$
$g_{maxDIACOP}$, COP maximum grazing rate constant on DIA at 0 °C	$0.25 d^{-1}$
$p_{maxCILCOP}$, COP maximum grazing rate constant on CIL at 0 °C	$0.1 d^{-1}$
$p_{maxROTCOP}$, COP maximum grazing rate constant on ROT at 0 °C	$0.15 d^{-1}$
Macro-zooplankton or Fish (μgCl^{-1})	
$g_{maxDIAFISH}$, maximum grazing rate constant on DIA by FISH at 0 °C	$0.1 d^{-1}$
$p_{maxCILFISH}$, maximum grazing rate constant on CIL by FISH at 0 °C	$0.1 d^{-1}$
$p_{maxROTFISH}$, maximum grazing rate constant on ROT by FISH at 0 °C	$0.2 d^{-1}$
$p_{maxCOPFISH}$, maximum grazing rate constant on COP by FISH at 0 °C	$0.4 d^{-1}$
POM (μgCl^{-1}) and BD ($mgCm^{-2}$)	
r_D , remineralization rate constant of <i>POM</i> at 0 °C	$0.016 d^{-1}$
r_{Ds} , remineralization rate constant of <i>BD</i> at 0 °C	$0.016 d^{-1}$
k_{Trem} , temperature coefficient for the rate of remineralisation	$0.1 ^\circ C^{-1}$
w_{sPOM} , sinking velocity of POM	$1.2 md^{-1}$

Table 3: Percentage change in the ecological variables during various sensitivity tests with I_{kPHYTO} and zooplanktivorous fish population as compared to the control run

Variable	I_{kCHL} $125 \mu mol m^{-2} s^{-1}$	I_{kDIA} $75 \mu mol m^{-2} s^{-1}$	$I_{kCHLDIA}$ $125 \& 75 \mu mol m^{-2} s^{-1}$	$FISH$ $FISH = 0.5 * ZOO$
<i>CHL</i>	-12.78	9.07	-13.17	-5.60
<i>CHLM</i>	-23.10	-	-23.10	-
<i>DIA</i>	30.85	-25.70	4.17	-6.64
<i>DIAM</i>	-	-29.14	-29.14	-
<i>CIL</i>	-15.15	-17.86	-34.57	0.38
<i>POM</i>	28.94	-27.22	11.51	-2.12
<i>ROT</i>	23.86	2.64	69.11	-22.82
<i>BD</i>	16.39	-39.69	-20.97	-1.00
<i>COP</i>	3.42	-14.86	-12.69	46.62
<i>Chla</i>	9.05	-21.04	-13.03	-3.15