

# Mesozooplankton in the Scheldt estuary

Carbon flows through the lower trophic levels

V. T. Langenberg



Source Scheldt river at St. Quentin , France



## Titel

Mesozooplankton in the Scheldt estuary

## Opdrachtgever

L. A. van Duren

## Project

1200254-003

## Kenmerk

1200254-003-ZKS-0001

## Pagina's

25

## Trefwoorden

Zooplankton, ecosystem functioning, secondary production, carbon flows

## Samenvatting

Om te begrijpen hoe de hogere trofische niveaus (zowel beschermde, commerciële en invasieve soorten) zich ontwikkelen bij het huidige beheer van de Schelde is het essentieel om informatie te verkrijgen over de lagere trofische niveaus. Het mesozooplankton vormt daarbij een onmisbare schakel tussen de primaire producenten en hogere niveaus en is dus onmisbaar om veranderingen in vis-, zeezoogdier- en vogelpopulaties te begrijpen.

Dit rapport presenteert een overzicht van de bestaande literatuur betreffende het mesozooplankton voorkomen en functioneren in het zoute, brakke en zoete deel van de Schelde.

Met betrekking tot de uitwisseling van nutriënten en koolstof tussen de verschillende trofische niveaus in het pelagiaal van de Schelde bleek het mesozooplankton een essentiële rol te vervullen binnen het ecosysteem functioneren. De zoöplankton gemeenschappen vertonen een gradiënt in functie van saliniteit, reageren relatief snel op milieuveranderingen (zoals debiet, ratio fytoplankton/detritus, opgelost zuurstof en troebelheid) en vertegenwoordigen een belangrijke bijdrage tot de biodiversiteit van het dierlijke leven in de Schelde.

Daarnaast kunnen verschillende gelatineuze mesozooplankton soorten (dinoflagellaat *Noctiluca scintillans*, de appendiculair *Oikopleura dioica*, en enkele kwalachtigen) domineren en zelfs tot een bloei ontwikkelen en daardoor een sterk sturende rol vervullen in het Schelde systeem. Deze soorten en hun rol zijn echter nauwelijks onderzocht.

Bij elkaar genomen bleek het precies vaststellen van een voldoende duidelijk beeld van het mesozooplankton compartiment en het trofisch functioneren ervan in het pelagische deel van het estuarium mede daardoor niet mogelijk.

Gezien de hoge complexiteit van uiteenlopende habitattypen (en de connecties daartussen) maakt de integratie van zoöplanktondata en systeemmodellen noodzakelijk. Het is dan wel nodig dat de huidige kennis aangevuld wordt met veld- en experimentgegevens over met name de drooggewichten, en seizoensdynamiek in voorkomen en groei van de belangrijkste zooplankton soorten door de Schelde heen.

Versie	Datum	Auteur	Paraaf	Review	Paraaf	Goedkeuring	Paraaf
1	2009-10-18	V. T. Langenberg					

**Titel**

Mesozooplankton in the Scheldt estuary

**Opdrachtgever**

L. A. van Duren

**Project**

1200254-003

**Kenmerk**

1200254-003-ZKS-0001

**Pagina's**

31

**Status**

voorlopig

Dit document is een voorlopig rapport, niet een definitief rapport, en uitsluitend bedoeld voor discussiedoeleinden. Aan de inhoud van dit rapport kunnen noch door de opdrachtgever, noch door derden rechten worden ontleend.

## Inhoud

<b>1 Introduction</b>	<b>1</b>
<b>2 Description Scheldt</b>	<b>2</b>
2.1 Biogeochemical structuring	4
2.2 Phyto and microzooplankton	7
<b>3 Mesozooplankton</b>	<b>8</b>
3.1 Communities and environment	8
3.2 Density and weights	10
3.3 Mesozooplankton dynamics	10
3.4 Feeding and grazing	11
3.5 Diet of mesozooplankton	12
<b>4 Trophic status</b>	<b>14</b>
<b>5 Mesozooplankton importance to higher trophic levels</b>	<b>16</b>
<b>6 Trends and future</b>	<b>17</b>
<b>7 Importance to management</b>	<b>19</b>
<b>8 Research needs knowledge gaps</b>	<b>20</b>
<b>9 References</b>	<b>21</b>



## 1 Introduction

The Scheldt estuary is one of few remaining estuaries with an extensive salt, brackish and fresh water tidal reach in Europe. Due to urban waste water drainage and agricultural run-off from its densely populated catchments it was considered as one of the most eutrofied systems in the world during the 2<sup>nd</sup> half of the 20<sup>th</sup> century (Heip 1988). Substantial emission reductions have lead to a gradual improvement of the Scheldt ecosystem since the mid-seventies.

Generally, the Scheldt estuary combines favorable conditions for herbivorous food webs (abundant nutrients) with those for a microbial loop (detritus and dissolved organic matter, mainly import from upstream rivers) and a so-called multivorous food web may be established (Legendre & Rassoulzadegan, 1995).

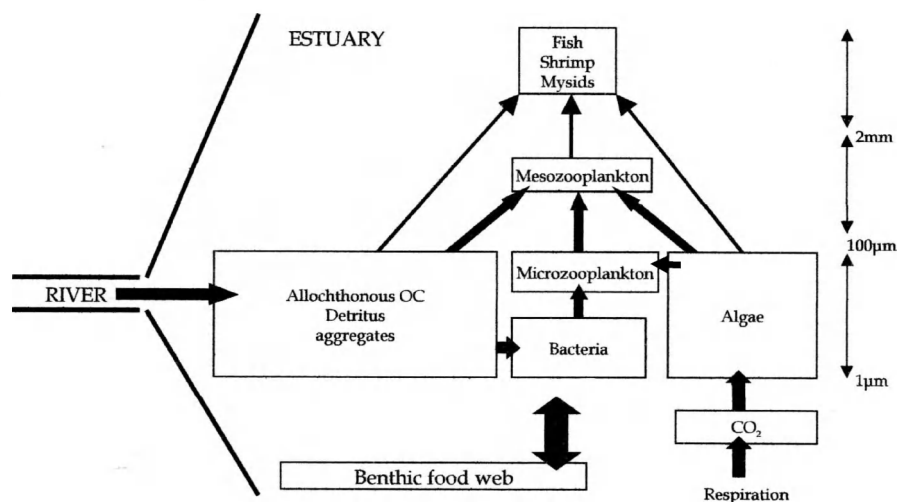


Figure 1. Schematic overview of the multivorous foodweb in estuaries.

Compared to other European coastal systems, the Scheldt system is a rather well-studied system. Several biogeochemical models and budgets and estimates on the Scheldt's metabolic status have become available (Soetaert & Herman, 1995a/b; Hellings et al., 2001; Vanderborght et al., 2002; Gazeau et al., 2005). Nevertheless, only recently some direct measurements have been carried out (Gazeau et al., 2005; Van den Meersche et al., 2009). Furthermore, disclosures of in depth knowledge of the role and performance of those biota in the Scheldt linking primary producers or other carbon sources (especially the mesozooplankton) to higher trophic levels are scanty, at times isolated, descriptive, or assumed similar to ecosystem structure of other estuaries.

The Mesozooplankton in the Scheldt are important consumers of phytoplankton, microzooplankton and other organic carbons and suspended detritus, and while linking these producers and sources with higher trophic levels such as hyperbenthos and fish (Fockedeij & Mees, 1999) they have a significant impact on the biogeochemical cycles of carbon and other elements and the trophic state of the whole system. (figure 1).

To understand their impact in the dynamic and changing environment of the Scheldt it is therefore important to know the relative importance of local phytoplankton or imported detritus

and the associated microbial loop in driving the heterotrophic production of the mesozooplankton. After understanding their contribution to vertical and horizontal flux in relation to that of the microzooplankton the current functioning of the Scheldt system can be properly assessed.

In this overview we bring together several newly available data syntheses on current Scheldt system's characteristics and on most important mesozooplankton species and the biogeochemical fluxes they mediate. We perform assessments on essential rates of biological processes that in turn may help determining and parameterize the key processes for incorporation in an ecological model.

## 2 Description Scheldt

The Scheldt estuary is a relatively small sized, macrotidal estuary crossing the border between Belgium and Netherlands, and discharging into the Southern bight of the North Sea. The river Scheldt, crossing Northern France, Belgium, and the southwest of the Netherlands, has a length of 350 km and a catchment area of ca. 22,000 km<sup>2</sup> consisting mainly of alluvial plains. The Scheldt can be divided into the nontidal upper Scheldt and a tidal portion (length of ca. 160 km) that extends from Vlissingen near the mouth to Ghent. Thereafter, sluices stop the tidal influence. This study covers the tidal river in Belgium (henceforth named Zeeschelde) and the Scheldt estuary in the Netherlands (henceforth named the Westerschelde). These geopolitical zones corresponds rather well with on one hand the marine and mesohaline (salinity >10) zone, and on the other hand the oligohaline (salinity 0-10) and the freshwater zone of the estuary (Figure 2). Strongest salinity gradient can be found between km 50 (the Dutch-Belgian border) and km 80. The mean depth is 10 m.

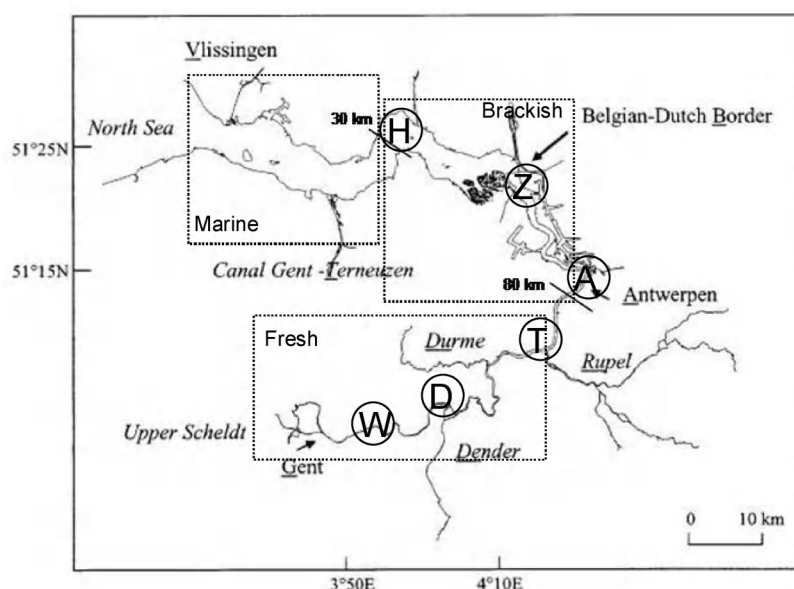


Figure 2. Map of the Scheldt, with indication of main cities and the tributaries (*italic*); underlined characters are used in Figure 3. Indicated are marine, brackish and fresh water mesozooplankton communities, respectively at 0-30, 30-80 and 80-160 km upward from Vlissingen. Also indicated are H=Hansweert, Z=Zandvliet, A=Antwerpen, T=Temse, D=Dendermonde and W=Wetteren.



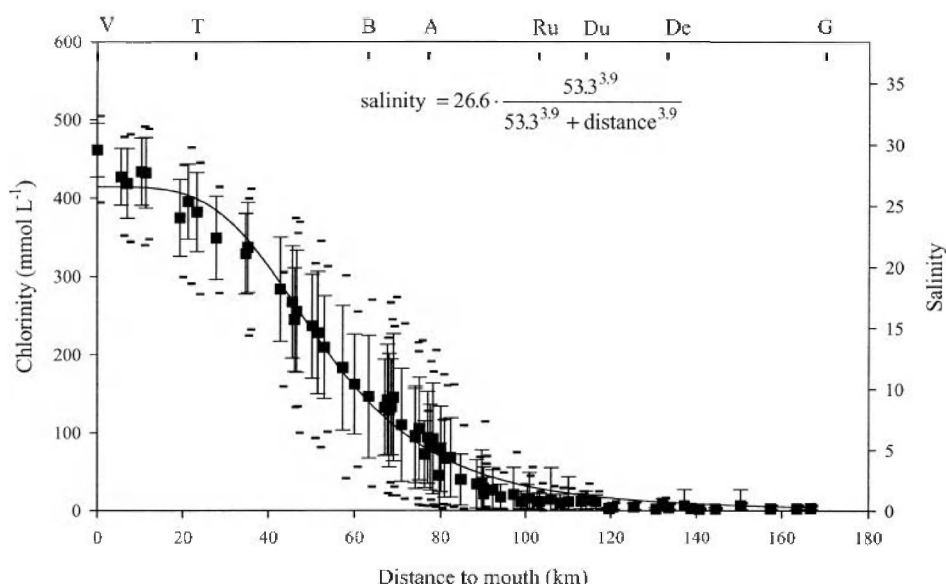


Figure 3. Chlorinity and salinity along the estuarine axis, with sigmoid best-fit equation. Denoted for each sampling station are the mean values 6 standard deviation, and the 5 and 95 percentiles (horizontal dashes); the number of measurements in a station varied from 22 to 2,200. Characters at the top of the graph denote the positioning of cities or confluences with tributaries, as represented in Fig. 2. (From Soetaert et al, 2006)

The Westerschelde is up to 5.5 km wide (Table 1.), and is less turbid and has lower nutrient concentrations than the Zeeschelde. It is also characterized by large intertidal flats with microphytobenthos mats. The Zeeschelde is much narrower, and has nutrient and organic matter concentrations that are extremely high. Also, the upstream zone (80-160 km distance from river mouth) contains mostly freshwater and is here considered part of the estuary because it is still under tidal influence. Tidal amplitude is 4 m at the mouth of the estuary, increases to 5.3 m at km 90 and still is 2 m in Gent.

Table 1. Some characteristics of the Scheldt estuary at several locations (from Meire et al., 2005)

	Vlissingen	Terneuzen	Hansweert	B-NL border	Kruibeke	Temse	Dendermonde	Melle
Distance from the mouth (km)	0	23	36	49	82	97	120	154
Mean tidal range (m)	3.82	4.19	4.48	4.85	5.20	5.14	3.74	1.96
Mean depth (m)	25	55	25	20	13	10	6	15
Width (m)	5000	5500	4300	2500	350	250	100	50
Flood volume (10 <sup>9</sup> m <sup>3</sup> )	1.04	0.67	0.40	0.14	0.04	0.03	0.006	0.006

According to Van den Meersche et al., (2009), Azémar et al. (2002), and Soetaert et al. (1993), the Scheldt may be roughly divided into three different sub regions depending largely on the physico-chemical characteristics of the Scheldt water (predominantly Salinity, Dissolved oxygen and Temperature) at different distances from the river mouth at Vlissingen (figure 2).

## 2.1 Biogeochemical structuring

Since the 70's, gradients of several important biogeochemical variables in time and space have been presented in several works some are conclusively summarised and analysed by e.g., Heip & Herman (1995), Tackx et al (2004), Lionard et al (2005), Soetaert et al. (2006), Meire & Maris (2008). They used a variety of data sources from The Netherlands Institute of Ecology (NIOO-CEME), the Dutch governmental agency Rijkswaterstaat (RIKZ—DONAR database), and several data sets contributed by Belgian universities and governmental agencies. (MONEOS, OMES).

Figure 4 and 5 taken from Soetaert et al (2006) show the development of the general water quality across the Scheldt (for some variables trends were given covering the last 35 years).

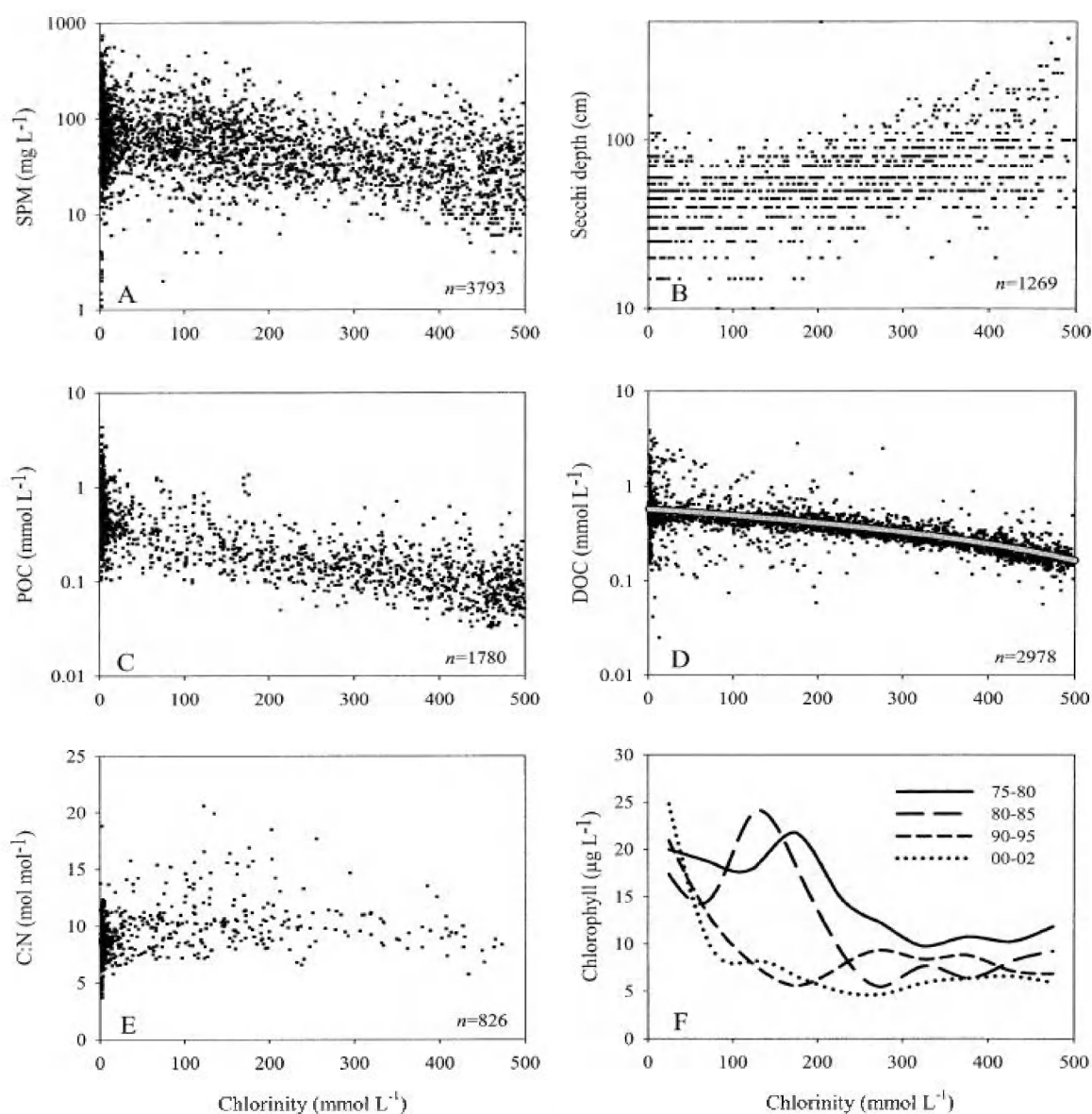


Figure 4. Constituent distributions along the chlorinity gradient from period 1990–2002. (A–E). All data shown; number of observations ( $n$ ) is indicated. (D) Conservative behavior of DOC indicated with gray solid line. (F) Chlorophyll concentrations in 50 mmol L<sup>-1</sup> chlorinity intervals averaged over 5 yr; data upstream from Rupelmonde were excluded.

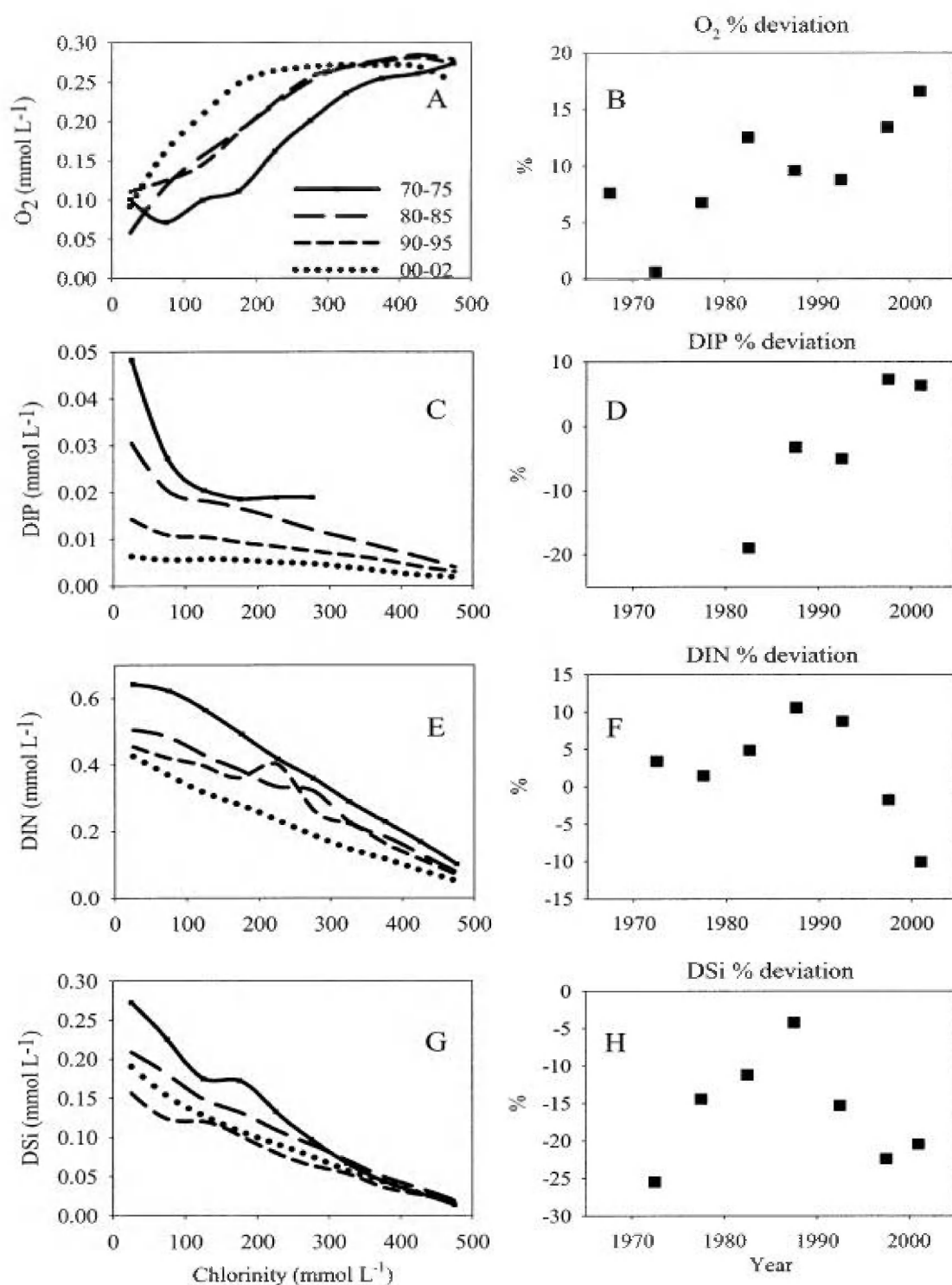


Figure 5. (A, C, E, G) Five-year-averaged concentrations of oxygen and dissolved inorganic nutrients binned in 50 mmol L<sup>-1</sup> chlorinity intervals for four selected periods; data from Rupelmonde were excluded. Plots were smoothed with a spline function. (B, D, F, H), represent percent deviation from conservative behavior, for 5-yr intervals. Positive values indicate that sources to the water are larger than the sinks.

Depending largely on the freshwater discharge, the residence time in the estuary upstream has been estimated between 7 weeks and 3 months, (Soetaert & Herman, 1995b). The river discharge varies from ca. 50 m<sup>3</sup>/s during dry summer to 300 m<sup>3</sup>/s during wet winter months with an annual average between 100 and 200 m<sup>3</sup>/s (Baeyens et al., 1998; Taverniers, 2000; Damme van et al., 2005). The freshwater discharge is small compared to the high tidal discharge with annual average of ca. 50 000 m<sup>3</sup>/s for both ebb and flood tides near the river mouth.

Turbidity and turbulence have a significant effect on the distribution of main mesozooplankton assemblages (Soetaert & Herman, 1994). Suspended matter transport and distribution are mainly driven by the energy distribution pattern in the Scheldt and the level of maintenance dredging. A detailed study on the SPM from Chen et al. (2005) roughly discerns three different zones in the Scheldt

- a. The lower estuary (up to 60 km from river mouth): where tidal energy is important but where the total energy remains at first relatively constant and then increases slightly toward upstream. Marine processes dominate. SPM values are fluctuating around 50 mg/l and seldom up to 100 mg/l.
- b. The middle estuary (60-90km from river mouth)– tidal energy dominates and also the total energy maximum occurs. Average SPM concentration of  $82 \pm 65$  mg/l in the uppermost 10% of the water column, and a range of 150 mg/l to 2.5 g/l in the lowermost 10% of the water column.
- c. The upper estuary – river energy dominates and is characterised by a seaward decreasing fluvial energy. SPM has an average concentration of  $110 \pm 65$  mg/l in the uppermost 10% of the water depth, and a range of 100– 1000 mg/l in the lowermost 10% of the water depth.

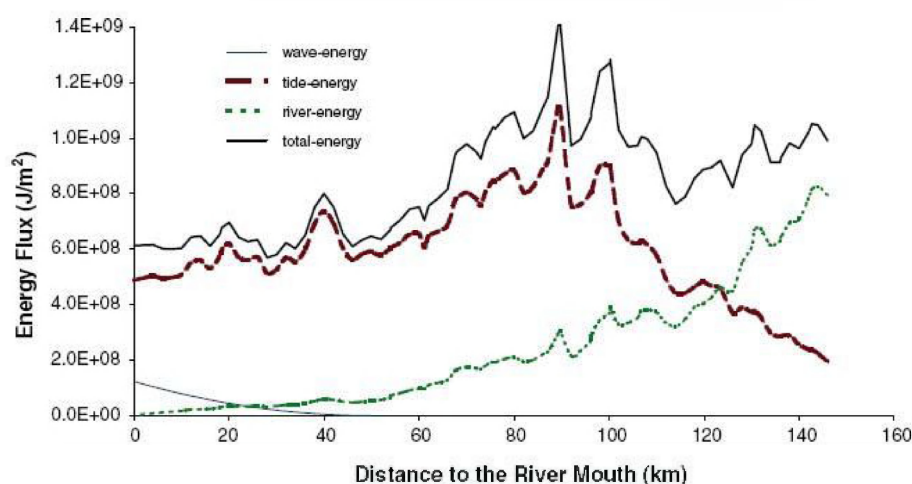


Figure 6. Energy distribution through Scheldt vs. distance (km) from river mouth (From Chen et al., 2005).

The existence of one or more distinct MTZs at the fresh/brackish interface (and one originating from tidal asymmetry) of the Scheldt as indicated by Chen et al. (2005), Soetaert & Herman (1994) and Meire et al. (2005) is questioned By Van den Meersche (2009) as turbidity is extremely high from km 60 upward.

Time series measurements (1990–2000) of suspended matter property show an increasing sand fraction, decreasing organic matter content, as well as a decrease in water transparency. A relation has been postulated with dredging activity for estuarine maintenance operations. Maintenance dredging of the shipping channel and harbors and dumping operations in the Scheldt strengthen marine influence further landward, resulting in a sustained tidal range increment and upstream flow and transport of suspended matter (Chen et al 2005; Baeyens et al., 1998).

On average less than 7% of total SPM in the marine part of the Westerschelde is of organic origin (Soetaert & Herman, 1994).

## 2.2 Phyto and microzooplankton

In general, Chlorophyll a concentrations increase with increasing distance from the mouth, with largest increase just North from Antwerp and upstream, the Zeeschelde. From 5-20  $\mu\text{g l}^{-1}$  to more than 200 around Ghent.

The phytoplankton community averaged over the Zeeschelde reaches concentrations of 50  $\mu\text{g Chl a l}^{-1}$  during spring and summer blooms, and is dominated by diatoms (60-85 % of total standing biomass), followed in abundance by green algae (Chlorophyceae) and other groups (Muylaert et al., 2000b). Cyanobacteria are relatively unimportant.

Similarly, in the Westerschelde, diatoms are the largest group, with important contributions of dinoflagellates and the haptophyte *Phaeocystis* (Kromkamp & Peene, 1995). Phytoplankton blooms occur in spring and summer. The microzooplankton community consists of heterotrophic nanoflagellates and ciliates (Muylaert et al., 2000a).

Generally annual gross phytoplankton production is rather constant for the marine part (200-250  $\text{gC m}^{-2} \text{yr}^{-1}$ ), reduced (80-150  $\text{gC m}^{-2} \text{yr}^{-1}$ ) in the brackish due to higher turbidity, and again higher in the freshwater part of the Scheldt (150-500  $\text{gC m}^{-2} \text{yr}^{-1}$ ). On average for the whole estuary a value of 40  $\text{gC m}^{-2} \text{yr}^{-1}$  was calculated (Heip & Herman, 1995; Kromkamp et al., 1995).

Local primary production upstream areas, mostly characterized by lowered DO values, may occasionally reach even higher values of around 900  $\text{gC m}^{-2} \text{yr}^{-1}$ . These summer blooms in the Zeeschelde seem to be mainly controlled (or terminated) by discharge increase in autumn and the apparent absence of significant herbivory, and therefore blooms here fuel a relatively short foodchain of phytoplankton and bacteria.

Absence of significant herbivory is caused by several reasons:

- Rotifers are the dominant grazers upstream and their total grazing potential is highest in the fresh water communities. However, a short retention time may prevent them to reach sufficiently high populations capable of reducing /controlling phytoplankton (Lionard et al, 2005).
- Lowered DO especially during summer may hamper significant crustacean grazing thus allowing phytoplankton to reach high concentrations (Appeltans et al., 2004).
- Cladocerans seem only important in the most upstream parts, where they are probably imported from the smaller adjacent rivers and streams.

- Grazing Calanoid copepods are generally only present in the brackish parts in spring and, as such, can only have had a minimal impact on estuarine phytoplankton populations, which peak in summer.
- Cyclopoid copepods are sometimes present in high numbers upstream, but the dominant species, *Acanthocyclops robustus*, is known as a carnivore.

### 3 Mesozooplankton

Knowledge on the mesozooplankton is derived from work carried out by Bakker & Pauw, (1975), Soetaert & van Rijswijk (1993), Renz (2006), Peitsch (1995), Escaravage & Soetaert (1995), Van den Meersche et al. (2009), Franz et al. (1991), Azémar et al. (2002 and 2007b), , Lionard et al. (2005), Tackx et al. (1995, 2003, 2004 and 2005), Dauvin & Desroy (2005), Muylaert et al. (2000a), Gasparine et al. (2000), Soetaert & Herman (1994) and Heip & Herman (1995) and Irigoien & Castel (1995). Other information not treated in this chapter may be found in Appendix 1.

#### 3.1 Communities and environment

According to Van den Meersche et al. (2009), Azémar et al. (2002), Soetaert et al. (1992), Soetaert & Herman (1994) the Mesozooplankton in the Scheldt may be roughly divided into three different communities depending largely on the physico-chemical characteristics of the Scheldt water (predominantly Salinity, Dissolved oxygen, SPM and Temperature) at different distances from the river mouth at Vlissingen (figure 2 and Table 2).

Tabel 2. General description of the different Scheldt's communities: Mean biotic and abiotic characteristics, adapted from Soetaert & van Rijswijk (1993) and Van den Meersche et al. (2009). Tdens= Total density mesozooplankton, Cop.dens = copepod density, Tdiv= Shannon-Wiener diversity index. KM Mouth= km distance from rivermouth.

Community	Area KM mouth	Tdens ind l <sup>-1</sup>	Cop. Dens ind l <sup>-1</sup>	Tdiv spec. l <sup>-1</sup>	Sal ‰	Temp °C	DO ‰	Secchi cm	Chloro ug l <sup>-1</sup>	DOC mg l <sup>-1</sup>	POC mg l <sup>-1</sup>
fresh	80-160	1,1	0,9	1,9	3,8	14,0	12,9	58,0	40,2	9,0	7-12
brakish	30-80	8,3	8,2	2,9	17,8	9,5	77,4	55,0	4,9	4,8	4-7
Marine	0-30	14,9	13,1	4,1	26,1	15,7	104,3	115,8	6,6	3,4	1-4

A "marine community" in a river section (generally up to 30 km from river mouth) that is mainly under influence of the North Sea. This community with high density and diversity is present in saline, well-aerated, relatively transparent and warm waters. Its main constituents are the:

#### Harpacticoid copepods

*Euterpina acutifrons*

#### Calanoid copepods

*Acartia clausi*

*Pseudocalanus elongatus*

*Temora longicornis*  
*Centropages hamatus*

*Paracalanus parvus*

**Cyclopoid copepods**

*Oithona nana*

**Appendicularia**

*Oikopleura dioica*

B A “brackish community” in a river section that is variable in size but generally situated at 30-80 km from river mouth). A very dynamic, and somewhat less diverse and dense community with a dominant role for *E. affinis* and *A. tonsa*. The waters are characterized by at times lowered oxygen concentrations (due to lowered aeration) and salinity and temperature but elevated concentrations of suspended matter loads. Its main constituents (with in parenthesis maximum density and months of peak occurrence) are the:

**Calanoid copepod**

*Eurytemora affinis*  
*Acartia tonsa*  
*Acartia bifilosa*  
*Eudiaptomus gracilis*

C A “fresh water community” as of 60 km from the river mouth up to Gent. This tidal river section contains largely fresh water and is furthermore characterized by low oxygen content but elevated chlorophyll concentrations. The community contains generally low densities of mesozooplankton with low numbers of Cyclopoid copepods, high abundance of Cladocerans and at times a high abundance of rotifers. Its main constituents are the:

**Cladocerans**

*Daphnia longispina*  
*Daphnia Magna*  
*Daphnia pulex*  
  
*Bosmina longirostri*  
*Moina brachiata*

**Calanoid copepod**

*Eudiaptomus gracilis*

**Rotifers**

*Brachionus calyciflorus*  
*Keratella quadrata*

**Cyclopoid copepods**

*Acanthocyclops robustus*,  
*Cyclops vicinus*

### *Thermocyclops crassus*

Species specific characteristics are presented in Appendix 1.

## 3.2 Density and weights

As in most European estuaries, the mesozooplankton in the Scheldt is dominated by calanoid copepods (Tackx et al, 1995).

Across the Zeeschelde in 1996, thus including some part of the brackish zone, the total crustacean zooplankton abundance averaged from <10 ind l<sup>-1</sup> in winter to ca. 180 ind l<sup>-1</sup> in spring and 270 ind l<sup>-1</sup> in summer (Tackx et al., 2004).

The marine community can reach during summer periods of highest densities of adults, copepodids and nauplii of especially the smaller copepods *Euterpina acutifrons*, *Acartia clausii* and *Oithona nana* (ca. 70 ind l<sup>-1</sup>) with total copepod dry weights up to 250 mg m<sup>-3</sup>.

The brackish community in comparison may reach in summer period mainly due to *Acartia tonsa* copepod densities and dry weights respectively up to 22 ind l<sup>-1</sup> and 70 mg m<sup>-3</sup>. During winter periods when the large *Eurytemora affinis* peaks densities and dry weights may be higher respectively up to 150 ind l<sup>-1</sup> and 500 mg m<sup>-3</sup> (Soetaert & van Rijswijk, 1993).

Average mesozooplankton dry weights in the marine part of the estuary were 76 mg m<sup>-3</sup> and in the estuary 30 mg m<sup>-3</sup> (Soetaert & Herman, 1994 and 1995a) based from means of length weight regressions (see Klein Bretler et al., 1982 for main marine species *T. Longicornis*, *C. hamatus* and *Pseudocalanus* sp. including nauplii and copepodite stages).

## 3.3 Mesozooplankton dynamics

The mesozooplankton diversity is not determined by long living species in a highly differentiated but stable environment (like for benthic communities). Zooplankton can grow fast and reproduce with a generation time of a few weeks to several months. In rivers and estuaries mesozooplankton undergoes advective and dispersive transport through water movements (Soetaert & Herman., 1994). Consequently local fluctuations or dynamics in growth conditions and mortality mainly determine abundance and diversity. In fact, the levels of stress caused by the estuarine environment significantly affect the main mesozooplankton species. Consequently, the differential mortality of these species results in shifts in dominance within the zooplankton community relative to that in the nearby sea.

The overall mesozooplankton taxa observed are well known from the OMES project. From 60 km upstream a total of ca. 55 rotifera; 19 copepods and 31 cladocerans have been encountered (Soetaert & van Rijswijk, 1993) although new species are still being added to this list (e.g., Azémar et al., 2007).



The marine zone is reported to have high density and diversity; about 13 species of mesozooplankton are known, predominantly copepods. However, a total overview of the species in the marine section of the Scheldt seemed not available.

The residence time in the upstream part of the estuary has been estimated between 7 weeks and 3 months, whereas the most seaward compartment had residence times of 10-15 days (Soetaert & Herman, 1995b). Depending on the seasonal freshwater discharge species assemblages (brackish, marine and fresh communities) may wander through the estuary. E.g., The marine community is in spring normally observed only the most seaward area, may move upward and extend during summer covering the whole lower estuary (0-80 km from river mouth), after which the distribution diminishes, disappearing in seaward direction during winter (Figure 7).

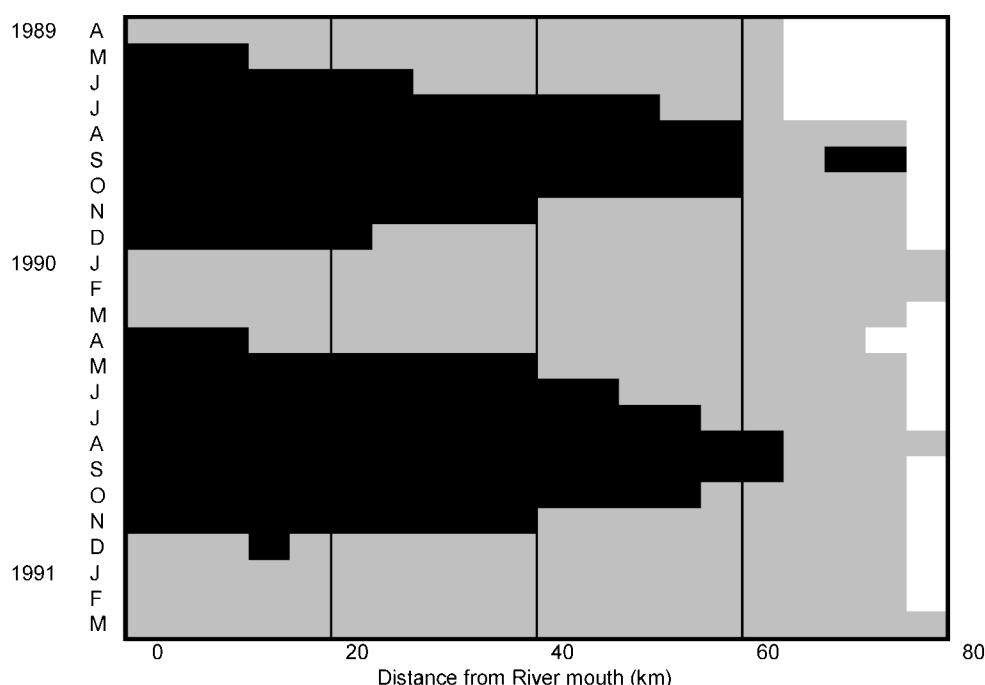


Figure 8. Multi year TWINSPAN analyses showing movement of Marine (black), brackish (grey) and fresh water (white) mesozooplankton communities through lower part of the Scheldt. Simplified and redrawn from Soetaert and van Rijswijk (1993).

A generalised spatio-temporal overview of the main species is presented in Figure 8.

### 3.4 Feeding and grazing

Due to the presence of strong spatial environmental gradients and a high temporal variability related to fluctuating freshwater inputs, the Scheldt estuary resembles very dynamic ecosystems characterized by a high spatiotemporal variability of the planktonic community composition.

It is hence very difficult to obtain consistent series of observations on one prey or predator taxon or even on one prey or predator functional group under estuarine field conditions. Due to this complexity, relatively few predation experiments have been performed using natural estuarine populations (e.g., Tackx et al., 2003, Azémar et al., 2007).

Information on the species characteristics of the different communities is included in appendix 1.

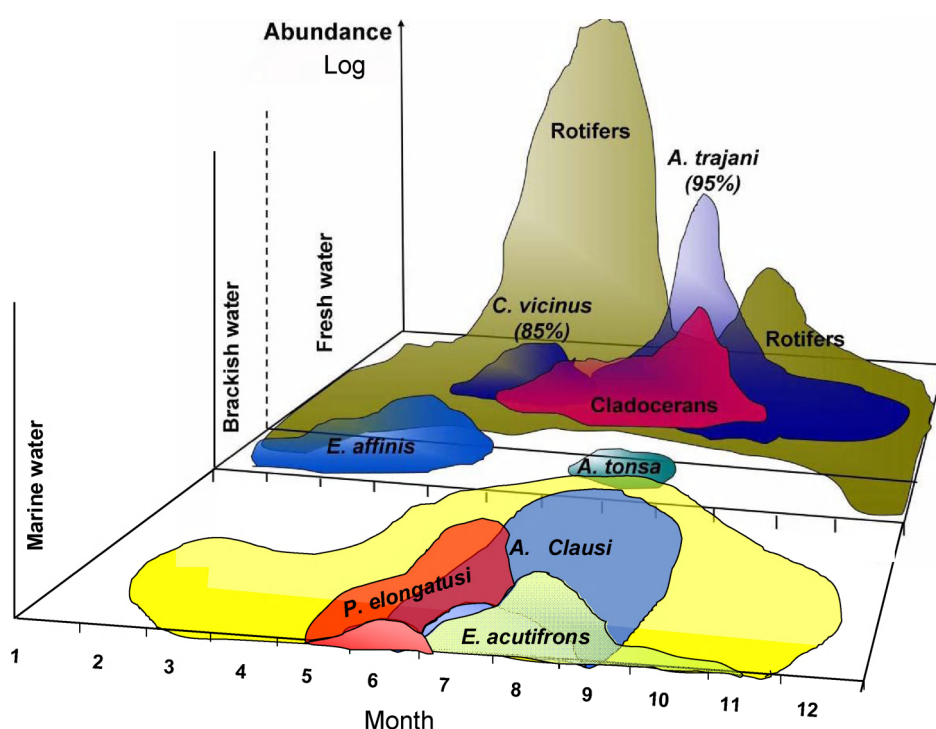


Figure 8. Simplified overview spatio-temporal distribution of key zooplankton species in the Scheldt (redrawn from Meire & Maris, 2008 and based on Azémar, 2006 en Soetaert & van Rijswijk, 1993).

### 3.5 Diet of mesozooplankton

In tidal rivers and estuaries, such as the Scheldt, primary production is generally less than community respiration and metabolism and bacterial secondary production are fueled mainly by external POC and DOC subsidies (Findlay et al. 1991; Soetaert & Herman, 1995a; Heip et al. 1995). As mentioned, a relatively high PCO<sub>2</sub>, bacterial production, oxygen deficiency and respiration (Heip et al., 1995) characterize these systems.

However, the link between high secondary bacterial production on allochthonous material and benefits for eukaryotic secondary producers is not clear.

Depending on the system's specifics (i.e. also systems other than the Scheldt), the scientific discussions involves the following postulations:

- 1 Even in tidal rivers and estuaries with high detritus to phytoplankton ratios, the phytoplankton carbon governs zooplankton dynamics because of nutritional quality aspects and selective feeding (Sobczak et al., 2005).
- 2 In heterotrophic rivers, autochthonous carbon dominates pelagic metazoan food webs because allochthonous carbon, albeit abundant, is mostly refractory and can therefore not easily assimilated by consumers. (Hamilton and Lewis, 1992; Sobczak et al., 2005; Tackx et al., 2003)
- 3 Decoupling of metazoan and detritus dynamics exists
- 4 Mesozooplankton in the Scheldt must consume detrital carbon to obtain sufficient energy (Escaravage and Soetaert, 1995).
- 5 There are major but variable external sources supporting zooplankton (Cole et al., 2006)
- 6 Relative importance of detrital sources depends on trophic status of the system (See modelling efforts of e.g. Sarvala et al, 1999; Cole et al, 2006).

Basically, metazoans may obtain their carbon requirements via four pathways:

- 1 by direct grazing on phytoplankton, predominantly diatoms (herbivory),
- 2 by feeding on particulate detritus (detritivory),
- 3 by feeding on bacteria that consume POC or DOC (bacterivory), or indirectly
- 4 by feeding on bacterivorous microzooplankton

Through analysis of stable isotope coupled with fatty acid in waters from Hansweert up to Wetteren over an annual cycle (Figure 2 and 8), Van den Meersche et al. (2009), recently managed to elucidate the relative importance and interactions between these four carbon pathways. This study included information from studies carried out by Soetaert & Herman (1994), Tackx et al. (2003), Damme van (2005), Middelburg & Herman (2007), and Lionard et al. (2005). After reconciling all pros and cons of both methods and weighing of the results some general conclusions can be drawn:

- 1 Algal material contribute little to total POC pool (except during bloom)
- 2 DOC pool is dominated by allochthonous input
- 3 Bacteria likely profit from both allochthonous DOC en POC but pass little up the foodweb (as in Cole et al., 2006).
- 4 Algal blooms phytoplankton distribution to POC to vary between 17-65%
- 5 The anthropogenic fraction of POC mounts to around 45% in summer to 80% in winter.
- 6 Mesozooplankton receives little carbon through the DOC→bacteria and microzooplankton pathways\*.
- 7 Mesozooplankton directly profit mostly from both herbivory and detrital pathways.
- 8 Mesozooplankton cannot exert significant grazing pressure during phytoplankton blooms in Zeeschelde.
- 9 The more marine Mesozooplankton in the Scheldt is of decreasing while the bacterial loop is of increasing importance.
- 10 Allochthonous and autochthonous contributions to mesozooplankton are of similar magnitude, although algae are preferred.
- 11 80% of the food requirements for *E. affinis* to reach optimal physiological condition is already reached when through grazing 3% of POC load is phyto-C.
- 12 Mesozooplankton selectively feeds on autochthonous carbon even up to high levels of SPM. However, SPM hampering the feeding may differ among species.

- 13 Scheldt detritus is of relatively high quality and nutritional value (as reflected by lowered DO, high N turnover, high bacterial production and where respiration of allochthonous carbon exceeds local primary production).

\* Gasparini et al., 2000 postulated that especially marine copepods may profit indirectly through the *P.globosa* → microzooplankton pathway to compensate for periods of low diatom abundance. This however seemed insufficient and either copepods are food limited during this period or complement their diet with other POC sources.

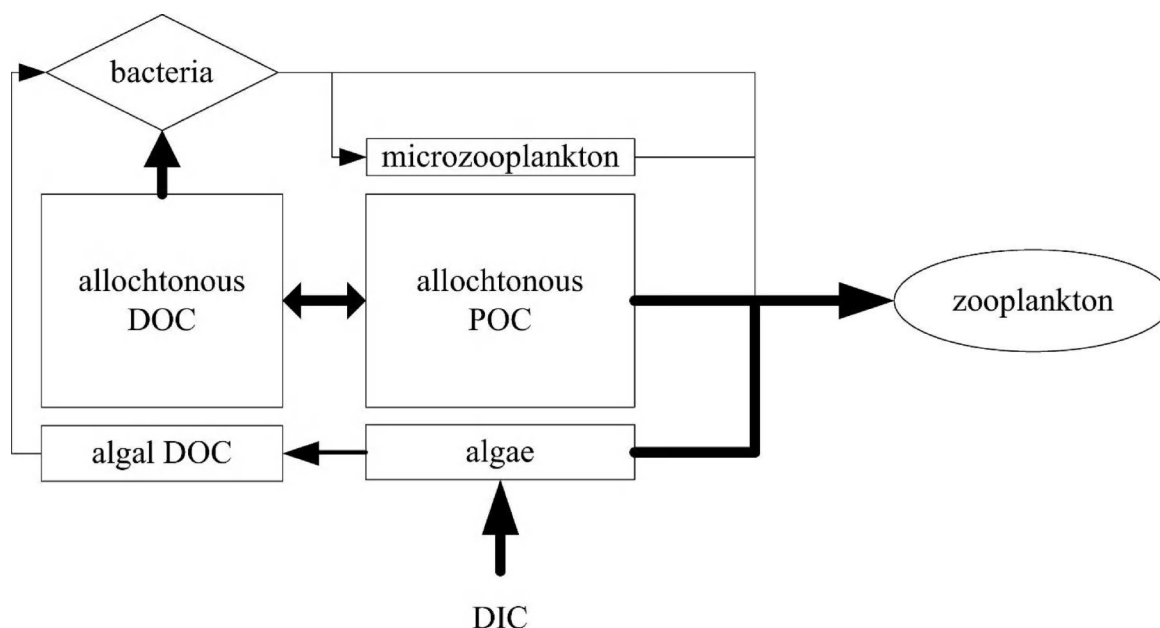


Figure 9. Schematic picture of the lower plankton food web in the tidal Scheldt River and estuary, including main carbon fluxes to mesozooplankton. Thick arrows represent the most important flow paths.

Upper conclusions are based on the findings from locations Hansweert and upriver. It remains to be seen whether the marine mesozooplankton communities depend as heavily on the allochthonous and herbivorous pathways. *E. affinis* and *Acartia* spp. may exhibit highly selective and more efficient feeding patterns for microzooplankton than for phytoplankton (ciliates and nanoflagellates). It is known that in marine areas that for mesozooplankton the small bacterial carbon may through the microzooplankton loop provide up to 30 % of the mesozooplankton carbon uptake.

## 4 Trophic status

The Scheldt is composed of a multitude of different habitat types where large and unpredictable fluctuations in physiological (salinity, light limitation) and physical stress (SPM as function of water movement) limit the biodiversity of the mesozooplankton capable of adapting to these harsh conditions. As a result more species can be found in the fresh and the truly marine habitat. The Scheldt is among the most productive biomes of the world.

However compared to other productive systems such as coral reefs and rainforest, where limited resources are efficiently recycled in a very diverse ecosystem, the relatively species-impooverished and dynamic Scheldt system achieves its productivity through the continuous arrival of new organic/nutrient supplies.

Soetaert & Herman (1995a) showed with ecosystem model MOSES that nearly all imported and *in situ* produced carbon is processed in the estuary and only some refractory carbon may reach the Sea. The high bacterial respiration results at times in a PCO<sub>2</sub> up to 10-15 matm (ca. 2500-3500% oversaturation) and it appears that most carbon input is out-gassed to the atmosphere.

For the whole Scheldt, MOSES furthermore calculated that:

- Net pelagic production is relatively low; 41 gC m<sup>-2</sup> yr<sup>-1</sup>
- For the whole Scheldt the primary formation of org. matter is ca. 72 gC m<sup>-2</sup> yr<sup>-1</sup> (of that ca. 60% is pelagic phytoplankton, 30% benthic algae<sup>1</sup> and 10% pelagic bacterial nitrification)
- 19% of TOC is autochthonous Prim. Prod. The rest is imported<sup>2</sup>
- A mean 380 gC m<sup>-2</sup> yr<sup>-1</sup> (range 200-1200) is lost through community respiration (bacterial mineralization, sedimentation and respiring higher trophic levels)

<sup>1</sup> In the some brackish sections of the Scheldt the pelagic primary production reaches such low values that benthic algae become the major primary carbon source (Soetaert & Herman, 1995a). Their contribution decreases towards the river and the sea depending on decreasing turbidity values and ratio intertidal surface versus water volume (allowing higher phytoplankton production). The benthic primary production estimates on intertidal surface can be modeled consistently (80-120 gC m<sup>-2</sup> yr<sup>-1</sup>) and are comparable e.g., to the ranges 47-314 gC m<sup>-2</sup> yr<sup>-1</sup> (Colijn & Jonge, 1984) and 66-180 gC m<sup>-2</sup> yr<sup>-1</sup> (Jassby et al., 1993) but are higher than the ca. 20 gC m<sup>-2</sup> yr<sup>-1</sup> as reported by Kromkamp et al (1995)

<sup>2</sup> The river Scheldt and point source and tributary waste discharges are the main sources of organic matter to the estuary. This allochthonous source is totaled to ca. 100 103 tonnes of carbon.

The bacterial activity is high (highest among European estuaries; see Soetaert & Herman, 1995a, Goosen et al., 1999) and DO depletion regularly occurs (Damme van et al., 2005). The huge amount of respiration suggests a true heterotrophic system. Annual gross bacterial production exceeds net primary production, even in the marine part, although differences there are smaller. In de Zeeschelde bacterial production and densities may reach 100 ug C l<sup>-1</sup>d<sup>-1</sup> and 5\*10<sup>6</sup> cells in winter and up to a 5 fold of rate during summer (Goosen et al., 1999). A first rough Net Ecosystem Production of ca. – 40 mmol C m<sup>-2</sup> d<sup>-1</sup> for the whole estuary was estimated by Gazeau et al. (2005).

This high bacterial production itself rather constitutes a dead end in the Scheldt foodweb (see Van den Meersche, 2009; Damme van et al., 2005) since it does not seem to form an important source to higher trophic levels. This assumption is supported by the following findings:

- phytoplankton is important for macrobenthic suspension feeders (both productivity dynamics relate to one another)
- microphytobenthos is important for deposit feeders
- mesozooplankton shows selective feeding

- In paragraph 3.7: mesozooplankton receives little through the DOC→ bacteria pathway.

Interestingly, the mesozooplankton itself constitutes one of the Carbon imports. With an average volume of entering water during flood of ca  $1 \cdot 10^7 \text{ m}^3$  and a mean DW of zooplankton of  $0.076 \text{ g DW m}^{-3}$  (Soetaert & Herman, 1994) a calculated amount of 78 tons of zooplankton dry weight enters the Estuary. An estimated 3% of this amount is retained and lost in the estuary per flood event<sup>1</sup> (Soetaert & Herman, 1994). On a yearly basis this amounts to 1500 tons of dry weight entering and decaying in the Westerschelde.

<sup>1</sup> The high loss rates for truly marine mesozooplankters like *P. elongates*, *C. hamatus*, *P. parvus*, *O. nana* (up to  $-0.4 \text{ d}^{-1}$ ) explains that although these species are important species in the adjacent sea they themselves seem insignificant in the estuary. Published loss rates in Appendix.

## 5 Mesozooplankton importance to higher trophic levels

Compared to allochthonous sources of carbon from upstream catchments and the sea (a modeled  $100 \cdot 10^3 \text{ tonnes yr}^{-1}$ ), the primary formation of carbon within the Scheldt may account to some 20% (ca.  $72 \text{ gC m}^{-2} \text{ yr}^{-1}$  for the Scheldt). A near 60% of this ( $41 \text{ gC m}^{-2} \text{ yr}^{-1}$ ) comes from phytoplankton production. Reasons for this relative low phytoplankton productivity rates are high turbidity and relatively great depth of the estuary, keeping the phytoplankton communities a large amount of time in the dark.

The imported, relatively reactive organic carbon is incorporated into the estuarine foodweb. Internal cycling results in the removal of most organic matter that enters the estuary or is produced *in situ*, while the more refractory matter escapes to sea. This makes the Scheldt, in comparison to many other coastal marine communities across the world, one of the most heterotrophic systems in the world (average respiration/production ratio of 6 with maximum of 35).

Van den Meersche et al. (2009) found that mesozooplankton to rely primarily on selective grazing on phytoplankton and the direct consumption of particulate organic matter, while they appear to receive little carbon via bacteria. The contribution of algae to zooplankton diets as estimated from isotope ratios and fatty acid profiles respectively averaged as high as 41 and 75%, and did not differ greatly among the stations, the taxa and life stages.

The total productivity is not restricted to the lowest trophic level (higher plants and algae) and secondary production (zooplankton and shrimps) as well as production at higher trophic levels (benthos, fish, mammals and birds) are significant due to the availability of large amounts of detritus. It has been postulated, as a Scheldt ecosystem feature, that secondary production at times seems more important than primary production (Baeyens et al., 1998).

Copepods generally constitute the majority of the mesozooplankton in the Scheldt. By eating and being eaten, copepods have implications for the flow of matter and energy in the estuary by coupling the lowest trophic levels with organisms at higher trophic levels. Without this tangible coupling between plants and higher animals, the detritus production will likely increase and consequently carbon accumulates less up the Scheldt foodweb at a level where it can be capitalized upon by the hyperbenthos, birds, mammals and fish.

The importance of the mesozooplankton as food source for shrimps, fish and birds has clearly been demonstrated (Fockede & Mees, 1999). E.g., the copepod stocks constitute the most important component in the diets of herring, sprat and sand eel and are important to the diet of several national and international “red list”, rare and commercial species that depend heavily on the nursery and feeding grounds of the Scheldt estuary.

## 6 Trends and future

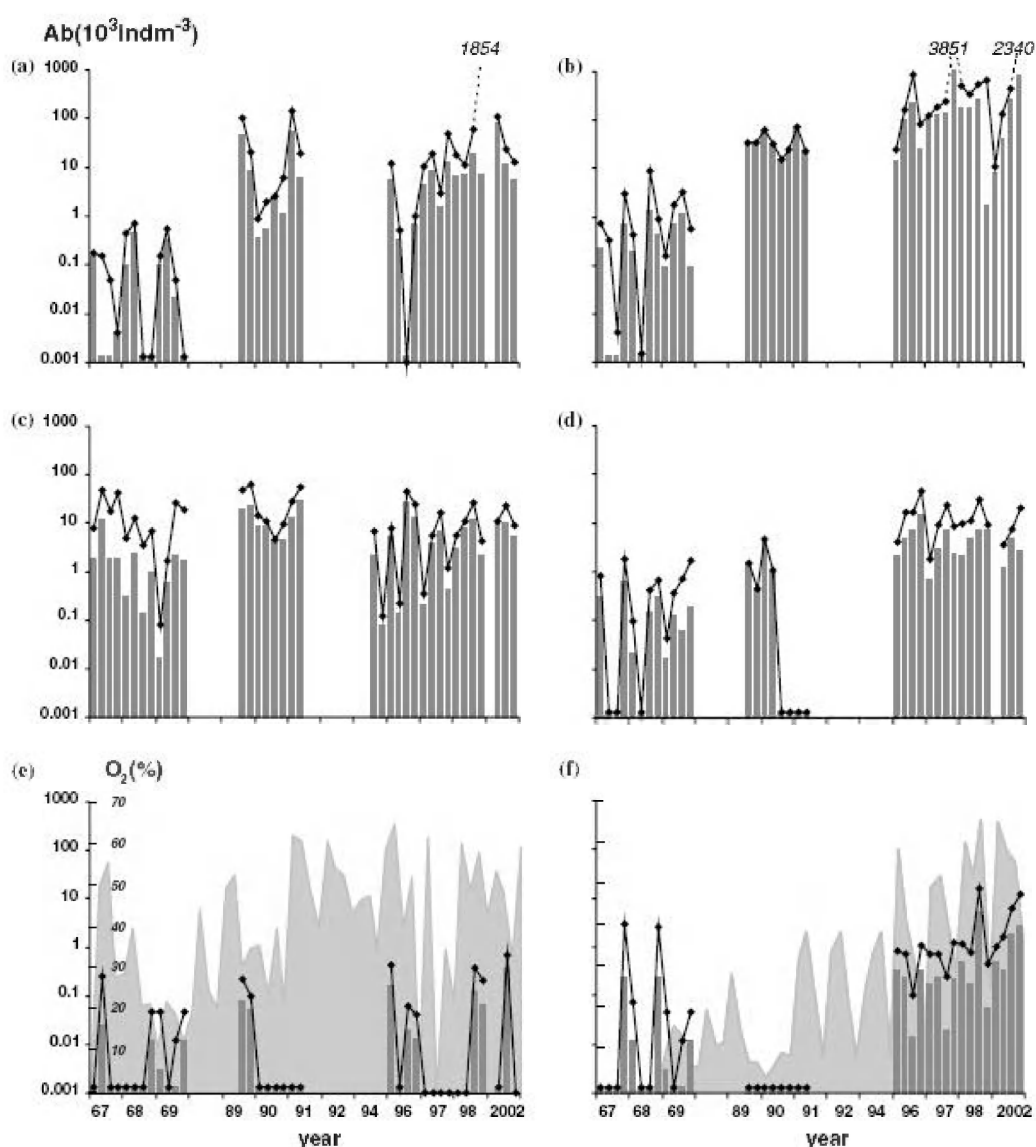


Figure 10. Spring (February–May) mean abundance (bars) and maximum abundance (line with diamonds) of Rotifera (a), Copepoda (c) and Branchiopoda, essentially Cladocera (e) observed in the brackish zone and of Rotifera (b), Copepoda (d) and Branchiopoda (f) observed in the freshwater zone of the Scheldt estuary from 1967 till 2002. Note the logarithmic scale. Shaded area in Fig. 2e, f represents percentage oxygen saturation. (From Tackx et al., 2004)

A compilation of available data in between 1967 and 2002 on spring zooplankton abundance was made for the brackish and the freshwater zone of the Scheldt estuary. The general picture is a significant increase of 1–2 orders of magnitude in abundance for Rotifera, Copepoda and Branchiopoda (mainly Cladocera) in the freshwater zone, while zooplankton abundance in the brackish water zone remained more constant (Figure 10).

While the overall distribution of species within the mesozooplankton communities remained rather constant over the period, the increase in copepod abundance between the brackish and the fresh water zones can be explained by the observation that the dominant spring species *Eurytemora affinis* has shifted its bulk population from the brackish to the freshwater zone since the mid-nineties (Appeltans et al., 2004). Generally, *E. affinis* has optimum at 0 PSU but due to low DO upstream the species in the Scheldt peaked in the brackish zone. Now, because of increased DO it can also be found further upstream in the truly fresh zone. This is comparable to the distribution in the Seine (Dauvin & Desroy, 2005) where it is normally found more upstream.

The general increase in zooplankton abundance since the 60s in the freshwater zone, the significant recovery of fish life around Antwerp and the reports of several new (alien) rotifers in fresh and brackish water are all likely to be a reflection of ameliorated environmental conditions as a result of restoration efforts and increased water treatment. Generally, pollution levels decreased and oxygen concentration in the fresh water zone have increased from the 90ties onwards. Other important factors that might relate to this zooplankton development upstream did not change significantly. E.g., despite global warming, yearly mean water temperature throughout the Scheldt does not show a clear trend over the last two decades (Onderzoek Milieu-effecten Sigmaplan-OMES database and MWTL database).

CCA analyses on the plankton biota and key physico-chemical variables performed by Tackx et al. (2004) revealed that separate clusters of zooplankters respond differently to changes in eutrophication, temperature fluctuations long and short, DO concentrations and salinity. Furthermore, the ratios phytoplankton/SPM and POC/SPM have great influence on for example the development (size and time) but also the selective feeding capabilities of the mesozooplankton and therefore their success and performance.

These ratios are greatly affected by degree of water treatment, changes in basin geomorphology and continuing dredging activity (intensity and duration).

Although the Chlorophyll concentrations show a decreasing trend throughout the Scheldt (Figure 4), through improved aeration and water transparency by increased water treatment in the upper streams, Areas of elevated phytoplankton abundance may now be better reached and grazed upon by the mesozooplankton. Then more carbon may accumulate at the higher trophic levels, assuming that the developing phytoplankton species do not become a nuisance and that they are digestible by the zooplankton.

Figure 5 also shows that the SiO<sub>2</sub> concentrations in fresh and brackish part of the Scheldt are decreasing and increasingly reach values that are limiting the development of diatoms. Including an improved underwater climate it may promote the development of flagellates rather than diatoms (like what happened during the Veerse Meer transition from turbulent turbid to stagnant clearer waters). A dominance of smaller phytoplankters is less efficiently grazed upon by the mesozooplankton, thus enhancing detritus production. Consequently, the risk of the negative impacts of eutrophication may increase.



Independent time series measurements (1990–2000) of suspended matter property show an increasing sand fraction, decreasing organic matter content, as well as a decrease in water transparency. These results exhibit coherent consequences of estuarine maintenance operations. Maintenance dredging of the shipping channel and harbors and dumping operation in the Scheldt strengthen marine influence further landward, resulting in a sustained tidal range increment and upstream flow and transport of suspended matter (see Chen et al 2005). Consequently this in combination with sea level rise, bottom subsidence and reclamation will lead to a further loss of low dynamic areas (mud flats and shallows) and an increase of high dynamic areas (physically stressed sand flats, deeper waters). E.g., a 0.5 m increase in tidal amplitude since the 60's has been noted at Antwerp. Altogether these factors may determine the spatio-temporal quality and distribution of SPM throughout the Scheldt.

The continuous import of exotic zooplankton species with shipping as main vector is not likely to decrease in the Scheldt. For example the comb jelly *Mnemiopsis leidyi* has been seen in the river mouth and a further expansion in the Scheldt is likely. The role of these gelatinous zooplankters can be devastating to the structure and functioning of the Scheldt system as we know today.

All these evolutions will, in itself, provide an interesting setting for inter specific competition among the presently dominant tolerant zooplankton species and some of the more sensitive ones.

## 7 Importance to management

The pronounced productivity makes the Scheldt an important natural resource. For the sustainable management of this system one needs systematic approaches to describe the current condition of the system, mitigate bottlenecks or threats and predict the impact of natural and anthropogenic pressures.

Several monitoring programmes have been designed to make an inventory of the current situation and to signal potential threats. This also includes approaches like AMOEBE (Algemene Methode voor Oecosysteem-beschrijving en beoordeling. Zie Laane & Peeters, 1993), GONZ (Graadmeter Ontwikkeling Noordzee), BHD-monitoring (Birds and Habitat Directive) and RIVPACS (River Invertebrate Prediction and Classification System) that compare the system's condition with a reference situation. Ultimately, with this information the objective is to reach a preferred ideal situation.

Guarding the development of a limited number of indicators for well-known and likable species relatively high up the foodchain that are characteristic to a system, sensitive and tightly linked to certain pressures and understandable or manageable by a broad group of people seems pragmatic.

These approaches seem however not suitable for such a dynamic system as the Scheldt estuary (Deckere & Meire, 2000)<sup>1</sup>. Moreover, these methods do not fully elaborate on the ecosystem health of the Scheldt, a subject underlying most of the WFD and the MSFD objectives

Ecosystem health relates to the functional and structural characteristics of the system. The determination of ecosystem health, e.g., through certain foodweb characteristics or trophic interactions within the nutrient cycles, can not be determined by a number of indicators as commonly used in the above approaches alone. Ecosystem health implicitly encompasses an integrated approach through which one comprehends the structure, functioning and the resilience of the Scheldt system.

One may classify the system as “good” if it has sufficient resilience to maintain its functional (vigour) and structural (organisation) characteristics within a certain range of stress or capability to naturally restore itself (Costanza & Mageau, 1999; Kolosa & Pickett, 1992).

The functional aspects include the Scheldt’s nutrient cycles as well as primary and secondary production dynamics. Therefore, to determine whether the system resilience may cope with changes in natural and human-induced stress, management that governs this system must have a comprehensive understanding of the main foodweb constituents. This includes knowledge on the secondary production of the zooplankton and its role in structuring the Scheldt’s foodweb. Up to now, this information is too scarce.

<sup>1</sup> When focusing merely on a set of indicators, the condition of the system’s health and functions (ecological and socio-economical) becomes secondary and as such, their development remains largely unclear.

Furthermore, the abundance and fitness of many of these indicator species are sensitive to human activities outside the managed ecosystem (connectivity and quality of migration routes and other habitats).

If one agrees that the return of these indicator species only occurs when the quality of the system is sufficient, there is a chance for these indicators to become metaphors. After all, the different mitigation efforts that are implemented to restore historical populations may be successful even without the return of the indicator species.

## 8 Knowledge gaps

There are numerous descriptive works on the abundance of certain key species (and new arrivals) along the salinity gradient in the Belgium part of the Scheldt (mainly Zeeschelde). However, in-depth studies on the impact of chronic eutrophication in combination with improved water quality upstream on the evolution of the main mesozooplankton species are virtually non-existing.

The evolution of main species should be determined through an integrated monitoring activity covering at least all major phytoplankton and zooplankton populations.

Better relation between physico-chemistry and species assemblages. Now, due to the biased approaches in Scheldt research (long term monitoring exists mainly in the Zeeschelde) the larger context in which mesozooplankton should be assessed is rather left untreated.

A finer spatio-temporal coverage of salinity, DO and other for zooplankton crucial water quality variables may indicate better which mesozooplankters have specific environmental needs for reaching their optimum production and play a significant role in the Scheldt foodweb and which ones are the more flexible or opportunistic species that may just survive under suboptimal circumstances.

Comprehensive knowledge on the population dynamics (structure, life cycles, and *in situ* growth, production, ingestion, and clearance rates) of the major mesozooplankton species in the whole Scheldt is a prerequisite in determining the Scheldt foodweb.

The processes that regulate mesozooplankton abundance in the dynamic Scheldt environment must be clarified better for all three communities. Throughout the Scheldt one must be able to distinguish, preferably through substantial direct physical and biological measurements, between increases in standing stock due to *in situ* growth and to import/export processes.

For understanding foodweb structuring purposes and determining the energy flow through the zooplankton any future plankton sampling should include gelatinous zooplankton constituents as well since these have never been adequately monitored although they may at times be the most dominant zooplankton. E.g., it was noted that blooms of for example *noctiluca miliaris* (sometimes  $> 1000 \text{ ind l}^{-1}$  and dominant) and *Oikopleura dioica* have not yet been included in any ecosystemic analyses. In addition, the potential threat of *Mnemiopsis leidyi* can be followed by methodologies that include the proper sampling of soft-bodied gelatinous zooplankters.

Furthermore, there is a need to cover the Scheldt with standardised methodological approaches. This has mostly not been the case and therefore integrated data assessments are still hampered. There are numerous examples that the integration and standardisation at monitoring level and not at data-assessment level is more efficient and cost-effective.

## 9 References

- Appeltans, W., A. Hannouti, S. Van Damme, K. Soetaert, R. Vanthomme & M. Tackx, 2004. Zooplankton in the Schelde estuary (Belgium/The Netherlands): the distribution of *Eurytemora affinis*: effect of oxygen? *Journal of Plankton Research* 25: 1441–1445.
- Azémar, F., F. Fiers, and M. Tackx, 2002. Zooplankton distribution across the brackish and freshwater zone of the Scheldt estuary, in: (2002). ECSA Local Meeting: ecological structures and functions in the Scheldt Estuary: from past to future, Antwerp, Belgium October 7-10, 2002: abstract book. pp. 70
- Azémar, F., S. Van Damme, P. Meire & M. Tackx, 2007a. New occurrence of *Lecane decipiens* (Murray, 1913) and some other alien rotifers in the Schelde estuary (Belgium). *Belg. J. Zool.* 137(1): 75-83,
- Azémar F., S. Bouletreau, M. Lionard, K. Muylaert, W. Vyverman, P. Meire and M. Tackx, 2007b. Looking for general trends in trophic interactions among estuarine micro- and mesozooplankton. *JPR* vol29 (suppl1) pp: 135-147.
- Bakker, C. & N. de Pauw, 1975. Comparison of plankton assemblages of identical salinity ranges in estuarine tidal and stagnant environments II. *Zooplankton. Neth. J. Sea Res.* 9 (2):145-165.
- Baeyens, W., B. van Eck, C. Lambert, R. Wollast and L. Goeyend, 1998. General description of the Scheldt estuary. *Hydrobiologia* 366: 1-14.
- Chen, M. S., S. Wartel, B. Van Eck, and D. Van Maldegem, 2005. Suspended matter in the Scheldt estuary. *Hydrobiologia*, 540:, 79-104.

Cole, J. J., S. R. Carpenter, M. L. Pace, M. C. Van de Bogert, J. L. Kitchell and J. R. Hodgsonm 2006. Differential support of lake food webs by three types of terrestrial organic carbon. *Ecology Letters*, (2006) 9: 558–568 doi: 10.1111/j.1461-0248.2006.00898.x

Colijn, F. & V. N. de Jonge, 1984. Primary production of microphytobenthos biomass in the Ems-Dollard estuary. *Mar. Ecol. Progr. Ser.* 14: 185-196.

Dauvin, J-C. N. Desroy, 2005. The foodweb in the lower part of the Seine estuary: a synthesis of existing knowledge. *Hydrobiologia* 540:13-27.

Damme, S. van, E. Struyf, T. Maris, T. Ysebaert, F. Dehairs, M. Tackx C. Heip and P. Meire. Spatial and temporal patterns of waterquality along the estuarine salinity gradient of the Scheldt estuary (Belgium and The Netherlands): results of an integrated monitoring approach. *Hydrobiologia* 540:29-45.

Deckere E. de & P. Meire, 2000. De ontwikkeling van een streefbeeld voor het Schelde estuarium op basis van de ecosysteemfuncties, benaderd vanuit de functie natuurlijkheid. Universiteit van Antwerpen: 34pp.

Escaravage, V. & K. Soetaert, 1995. Secondary production of the brackish copepod communities and their contribution to the carbon fluxes in the Westerschelde estuary (the Netherlands). *Hydrobiologia* 311: 103–114

Findlay, S., M. L. Pace, D. Lints, J. J. Cole, N. F. Caraco and B. Peierls, 1991. Weak coupling of bacterial and algal production in a heterotrophic ecosystem—the Hudson river estuary. *Limnol. Oceanogr.* 36: 268–278.

Fockedye, N. & J. Mees, 1999. Feeding of the hyperbenthic mysid *Neomysis integer* in the maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries. *Journal of marine systems*, 22:207-228.

Fransz, H. G., J. M. Colebrook, J. C. Gamble, M. Krause, 1991. The zooplankton of the North Sea. *Neth. J. Sea Res.* 28(1/2): 1-52.

Gasparini, S., M. H. Daro, E. Antajan, M. Tackx, V. Rousseau, J-Y. Parent and C. Lancelot, 2000. Mesozooplankton grazing during the *Phaeocystis globosa* bloom in the Southern bight of the North Sea. *Journal of Sea Research* 43: 345-356.

Gazeau, F., Gattuso, J. P., Middelburg, J. J., Brion, N., Schiettecatte, L. S., Frankignoulle, M., & Borges, A. V. 2005. Planktonic and whole system metabolism in a nutrient-rich estuary (the Scheldt estuary). *Estuaries*, 28(6), 868-883.

Goosen, N. K., J. Kromkamp, J. Peene, P. van Rijswijk and P. van Breugel, 1999. Bacterial phytoplankton production in the maximum turbidity zone of three European estuaries: The Elbe, Westerschelde and Gironde. *Journal of Marine Systems* 22:151-172.

Hamilton, S. K., and W. M. Lewis, 1992. Stable carbon and nitrogen isotopes in algae and detritus from the Orinoco river floodplain, Venezuela. *Geochim. Cosmochim. Acta* 56: 4237–4246.

Heip, C., 1988. Biota and abiotic environment in the Westerschelde estuary. *Hydrological bulleting* (22): 31-34.

- Heip C., & P. M. J. Herman, 1995. Major biological processes in European tidal estuaries: a synthesis of the JEEP-92 project. *Hydrobiologia* 311: 1-7.
- Heip, C. , N. K. Goosen, P. M. J. Herman, J. Kromkamp, J. J. Middelburg and K. Soetaert, 1995. Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr. Mar. Biol. Annu. Rev.* 33: 1–149.
- Hellings, L., F. Dehairs, S. van Damme, and W. Baeyens, 2001. Dissolved inorganic carbon in a highly polluted estuary (the Scheldt). *Limnology and Oceanography* 46:1406–1414.
- Irigoin X. and J. Castel, 1995. Feeding rates and productivity of the copepod *Acartia biflosa* in a highly turbid estuary; the Gironde (SW France). *Hydrobiologia*, 311: 115-125.
- Jassby, A. D., J. E. Cloern and T. M. Powell, 1993. Organic carbon sources and sinks in San Francisco Bay: Variability induced by riverflow. *Mar. Ecol. Prog. Ser.* 95: 39–54.
- Klein Breteler W. C. M., H. G. Franz and S. R. Gonzalez, 1982. Growth and development of four calanoid copepod species under experimental and natural conditions. *Netherlands Journal of Sea Research* 16: 195-207.
- Kromkamp, J., J. Peene, P. van Rijswijk, A. Sandee and N. Goosen, 1995. Nutrients. Light and primary production by phytoplankton and microphytobenthos in the eutrophic, turbid Westerschelde estuary (The Netherlands). *Hydrobiologia* 311: 9-19.
- Kromkamp, J., & J. Peene, 1995. Possibility of net phytoplankton primary production in the turbid Schelde estuary (SW Netherlands). *Marine Ecology-Progress Series*, 121(1-3), 249-259.
- Legendre, L. and F. Rassoulzadegan, 1995. Plankton and nutrient dynamics in marine waters. *Ophelia*, 41(Mar), 153-172.
- Lionard, M., K. Muylaert, W. Vyverman, and D. Van Gansbeke, 2005. Influence of changes in salinity and light intensity on growth of phytoplankton communities from the Schelde river and estuary (Belgium/The Netherlands). *Hydrobiologia*, 540(1-3), 105.
- Meersche K. Van den., 2009. Carbon flows in the planktonic food web of temperate estuaries: A combined approach using stable isotopes, biomarkers and modelling. PhD thesis University of Ghent, Belgium:199pp.
- Meire, P., T. Ysebaert, S. van Damme, E. Van den Bergh, T. Maris, E. Struyf, 2005. The Scheldt estuary: a description of a changing ecosystem *Hydrobiologia*, 540, 1-11
- Meire, P. & T. Maris, 2008. MONEOS. geïntegreerde monitoring van het Schelde-estuarium. Onderzoeksgroep Ecosysteembeheer Universiteit Antwerpen, ECOBE 08-R-113: 176pp.
- Middelburg, J. J. and P. M. J. Herman. 2007. Organic matter processing in tidal estuaries. *Mar. Chem.* 106: 127–147.
- Muylaert, K., R. Van Mieghem, K. Sabbe, M. Tackx, and W. Vyverman, 2000a. Dynamics and trophic roles of heterotrophic protists in the plankton of a freshwater tidal estuary. *Hydrobiologia*, 432(1-3), 25-36.
- Muylaert, K., K. Sabbe & W. Vyverman, 2000b. Spatial and temporal dynamics of phytoplankton communities in a freshwater tidal estuary (Schelde, Belgium). *Estuarine, Coastal and Shelf Science*, 50(5), 673-687.

Peitsch, A. (1995). Production rates of *Eurytemora affinis* in the Elbe estuary, comparison of field and enclosure production estimates. *Hydrobiology* 311 127-137

Renz, J., 2006. Life cycle and population dynamics of the calanoid copepod *Pseudocalanus* spp. in the Baltic Sea and North Sea. Alfred-Wegener-Institut für Polar und Meeresforschung Bremerhaven, PhD Dissertation: 142 pp.

Sarvala, J., K. Salonen, M. Järvinen, E. Aro, T. Huttula, P. Kotilainen, H. Kurki, V. T. Langenberg, P. Mannini, A. Peltonen, P-D. Plisnier, I. Vuorinen, H. Mölsä, and O. V. Lindqvist, 1999: Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web. *Hydrobiologia* 407: 155-179

Sobczak, W. V., J. E. Cloern, A. D. Jassby, B. E. Cole, T. S. Schraga and A. Arnsberg, 2005. Detritus fuels ecosystem metabolism but not metazoan food webs in San Francisco estuary's freshwater delta. *Estuaries* 28: 124–137.

Soetaert, K., & P. Van Rijswijk, 1993. Spatial and temporal patterns of the Zooplankton in the Westerschelde Estuary. *Marine Ecology-Progress Series*, 97(1), 47-59.

Soetaert, K. and P. M. J. Herman, 1994. One foot in the grave: zooplankton drift in to the Westerschelde estuary (The Netherlands). *Mar. Ecol. Prog. Ser.* Vol 105: 19-29.

Soetaert, K. and P. M. J. Herman, 1995a. Carbon flows in the Westerschelde estuary (The Netherlands) evaluated by means of an ecosystem model (MOSES). *Hydrobiologia* 311:247–266.

Soetaert, K. and P. M. J. Herman, 1995b. Estimating estuarine residence times in the Westerschelde (The Netherlands) using a box model with fixed dispersion coefficients. *Hydrobiologia* 311:215–224.

Soetaert, K., J. J. Middelburg, C. Heip, P. Meire, S. Van Damme, and T. Maris, 2006. Longterm change in dissolved inorganic nutrients in the heterotrophic Scheldt estuary (Belgium, The Netherlands). *Limnology and Oceanography*, 51(1), 409-423.

Tackx, M., X. Irigoien, N. Daro, J. Castel, L. Zhu, X. Zhang & J. Nijs, 1995. Copepod Feeding in the Westerschelde and the Gironde. *Hydrobiologia*, 311(1-3), 71-83.

Tackx, M., P. J. M. Herman, S. Gasparini, X. Irigoien, R. Billiones and M. H. Daro. 2003. Selective feeding of *Eurytemora affinis* (Copepoda, Calanoida) in temperate estuaries: Model and field observations. *Estuar. Coast. Shelf Sci.* 56: 305–311.

Tackx, M., N. de Pauw, R. van Mieghem, F. Azemar, A. Hannouti, S. van Damme, F. Fiers, N. Daro, and P. Meire, 2004. Zooplankton in the Schelde estuary, Belgium and The Netherlands. Spatial and temporal patterns. *Journal of Plankton Research*, 26(2), 133-141.

Tackx, M. F. Azémar, S. Boulêtreau, N. De Pauw, K. Bakker, B. Sautour, S. Gasparini, K. Soetaert, S. Van Damme, and P. Meire, 2005. Zooplankton in the Schelde estuary, Belgium and the Netherlands: long-term trends in spring populations, in: Meire, P.; Van Damme, S. (Ed.) (2005). *Ecological structures and functions in the Scheldt Estuary: from past to future*. *Hydrobiologia*, 540(1-3): pp. 275-278

Taverniers, E., 2000. Zeescheldebekken: de afvoer van de Schelde in 1999. Ministerie van de Vlaamse Gemeenschap AWZ Afdeling Maritieme Schelde, Antwerpen.

Vanderborght, J.-P., R. Wollast, M. Loijens, and P. Regnier, 2002. Application of a transport-reaction model to the estimation of the biogas fluxes in the Scheldt estuary. *Biogeochemistry* 59:207–237.

Wollast, R. 1988. The Scheldt estuary, In W. Salomons, B. L. Bayne, E. K. Duursma, and U. Förstner (eds.), *Pollution in the North Sea*. Springer Verlag, Berlin, Germany, p. 183–193.