Chapter 2

Characteristic aspects of the tidal freshwater zone that affect aquatic primary production

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Abstract

Aquatic-based processes have not been well studied in tidal freshwater habitats even though they are diverse and highly variable systems. This chapter aims at a synthesis of the state of knowledge about aquatic primary production in tidal freshwater ecosystems and the main factors that control this process. Suspended matter is important in tidal freshwater habitats and it is affected by estuarine processes as well as land use and river discharge into the tidal freshwater zone from the catchment area. As a result, variation in the amount and quality of suspended matter influences the variability of light availability. The retention and transformation of nitrogen and phosphorus in the tidal freshwater zone is often intense and wetland vegetation has a major impact on the silica cycle within the tidal freshwater zone of estuaries. Although the primary producers follow a constantly changing equilibrium that is influenced by tide action and river discharge, they show characteristics that contrast with general ideas about primary producers in estuaries. The scarceness of data, together with weaknesses in methodology to measure or model primary production, is however in striking contrast with the complexity and importance of these neglected ecosystems. Nevertheless, within the tidal freshwater zone of the Scheldt estuary, two types of phytoplankton communities have been recorded, indicating that a typology for freshwater tidal systems is waiting to be revealed, taking into account *e.g.* residence time. The dynamic nature of tidal freshwater habitats implies that static, site-bound legislative protection measures tend to be less efficient than a functional approach. Comparative estuarine research offers a good

opportunity to expand our knowledge about the ecological functioning of these important estuarine systems. As an example it is demonstrated here that it is possible to estimate historic suspended matter concentrations.

2.1 Introduction

Tidal freshwater wetlands (hereafter called TFW) were first brought into scientific attention because of their peculiar ecological characteristics (Odum, 1988). In contrast with most estuarine habitats, the tidal freshwater zones have long been regarded as riverine stretches. Consequently, few estuarine ecologists had studied TFW habitats. Probably the first attempt to bring together information on the tidal freshwater region of estuaries in Europe was an ECSA (Estuarine and Coastal Sciences Association) symposium (Meire & Vincx, 1993) held in Gent, Belgium in 1991 (Elliott & McLusky 2002). At that time, tidal freshwater reaches were considered to be specific entities with a combination of riverine and estuarine aspects (Schuchardt *et al.*, 1993). The tidal freshwater region was recognized as a zone which was different from riverine sites due to specific physical processes such as prolonged residence time of water, oscillating water levels, and changing current velocities and directions. All the papers presented at the Gent symposium demonstrated that the tidal freshwater region of estuaries experienced a great deal of natural stress, arising from characteristic chemical and physical processes. A seasonal and spatial oxygen sag is typical of tidal freshwater habitats, often associated with a turbidity maximum, and compounded in many cases by discharges of carbon and nutrients from human habitation (Eliott & McLusky 2002). Phytoplankton-based aquatic primary production in tidal freshwater habitats received little attention, despite its presumed key position in aquatic food webs as well as its importance in ecological functioning.

It was observed that phytoplankton composition and densities were different in TFW compared to phytoplankton communities at the freshwater-saltwater interface or in the upstream (non-tidal) riverine systems (*e.g.* Jackson *et al.*, 1987; Schuchardt & Schirmer, 1991; Rehbehn *et al.*, 1993). Although the factors that determine phytoplankton production in general were already known such as nutrients, temperature, and light (*e.g.* Cloern, 1987), the rates of aquatic primary production, the effects of various factors on primary production, and the impact of primary production on the system were less clear. The importance of the role of autochthonous production in estuarine food chains has been more and more recognized. In contrast to prevailing ideas, the role of allochthonous detritus for the estuarine food chain has been questioned (*e.g.* Sobczak *et al.* 2005), while more evidence is found that aquatic primary production fuels the food web to a greater extent than had formerly been assumed. Even in TFW with overwhelming amounts of detrital carbon from a variety of sources, nutritional

factors associated with phytoplankton were found to be dominant in regulating zooplankton growth (Muller-Solger *et al.* 2002).

In this chapter, the status of aquatic primary production in the tidal freshwater region is reviewed with special emphasis on the factors that control productivity. Production rates and impacts of the production on the system are also evaluated. We begin with a synthesis of the factors influencing pelagic primary productivity. We then focus on the primary production rates and patterns.

2.2 Factors influencing phytoplankton production

Human activity in coastal catchments (*i.e.*, watersheds) greatly increased the fluxes of growth-limiting nutrients from the landscape to receiving waters. This has resulted in greatly increased nutrient concentrations in many of the world's estuaries (Verity, 2002) and coastal ecosystems (Cloern, 2001; Van Beusekom & De Jonge, 2002; Smith *et al.*, 2003). In clear waters, increases in nutrient loading caused predictable increases in the algal biomass (Borum & Sand-Jensen, 1996), sometimes leading to exceptional algal blooms (*e.g.* Richardson, 1997; Dippner, 1998), which may deplete water-column oxygen (Rabalais *et al.*, 1996). In addition, altered proportions between nutrients induce changes in the algal species composition (Officer & Ryther, 1980; Lancelot *et al.*, 1987) and food web structure (*e.g.* Escaravage & Prins, 2002). In contrast, in turbid waters, the effects of increased nutrient loading may not be as pronounced (Cloern, 2001). In these systems, phytoplankton production is often light-limited year-round, and growth is low despite the high levels of nutrient input (Heip *et al.*, 1995). The availability of light and nutrients are main factors that influence pelagic primary production.

2.2.1 Light availability

Light availability to pelagic primary producers of estuarine waters depends on both the mixing depth of the producers and the photic depth of the system (Grobbelaar, 1990). In well-mixed estuaries the mixing depth corresponds with local depth. Stratified estuaries usually are less dynamic than fully mixed ones. A comparative analysis of 26 microtidal (most of them in North America) and 14 macrotidal (mostly European) estuaries revealed that the macrotidal estuaries, which are characterized by high tidal energy, significantly exhibited lower levels of chlorophyll *a* than systems with lower tidal energy, even when nitrogen concentrations were

equal to or higher than in the microtidal systems (Monbet, 1992). This indicates that light conditions are predominantly limiting primary production in dynamic macrotidal and well-mixed estuaries, where the photic depth is determined by turbidity, as was shown in detail by Colijn *et al.* (1987). Therefore it is necessary to understand what determines turbidity in such estuaries and especially in their freshwater reaches.

Turbidity is a cloudiness or haziness of water caused by individual particles (suspended solids). Dissolved materials are not included in this definition, but they can also contribute to light attenuation. In oceans or stagnant waters, turbidity is generally caused by phytoplankton. Estuaries however, especially macrotidal systems (average tidal amplitude at least 2 m, see Elliott & McLusky 2002), are known for their high levels of turbidity, where some fish species are hidden from visual predators (Maes *et al.*, 1998). Indeed estuaries can trap sediments coming both from the saline estuary or from the freshwater catchment area, but local mixing also affects turbidity.

2.2.2 Turbidity at the downstream limits of the freshwater zone

In macrotidal estuaries, the freshwater-saltwater interface is often characterized by a strong estuarine turbidity maximum, of which the mechanisms have been investigated since Postma and Kalle (1955). Sometimes, the turbidity maximum may be independent of salinity, such as in the Tay estuary, where wind-wave resuspension of sediments in shallow water and ebb tide transport to deeper channels keep the turbidity maximum in a longitudinally fixed location (Weir & McManus, 1987). Most often, turbidity maximum can be found where saline water intrudes into the estuary along the bottom, under a layer of less heavy freshwater, thus forming a typical salt wedge. The tip of this salt wedge is in many estuaries the place where this turbidity maximum is most pronounced (*e.g.* Postma & Kalle, 1955; Salomons *et al.*, 1988; Uncles & Stevens, 1993).

2.2.2.1 *Mechanisms*

Three processes explain the turbidity maximum at the freshwater-saltwater interface: residual gravitational circulation, tidal velocity asymmetry, and tidal mixing asymmetry. The importance of each of these mechanisms varies and is subject of discussion. The residual gravitational circulation is caused by a baroclinic, density driven pressure gradient. This pressure forces the near-bottom horizontal velocity upstream where it meets the freshwater flow going downstream. If the pressure gradient is strong enough, the resulting flow shows a

gravitational circulation within the vertical plane. This mechanism stands apart from tidal action and it can dominate in microtidal estuaries or where topographic depth profiles show major changes (*e.g.* Schubel & Carter, 1984). The tidal velocity asymmetry is, *e.g.* in the Elbe (Burchard & Baumert, 1998), a much more important process causing a turbidity maximum. Due to the convective instability of the near-bottom flow at flood tide, the vertical velocity profile is much more uniform at flood than at ebb tide. As a consequence, velocity profiles are bottom-intensified during flood and surface-intensified during ebb. As the suspended matter concentrations (SPM) are usually higher toward the bottom, this asymmetry in flow patterns can lead to upstream net transport of SPM. The third mechanism, tidal mixing asymmetry, originates from the stable stratification of the ebb current (faster flowing freshwater at the surface moves over slower moving salty layers at the bottom). At the resulting density interface, vertical mixing is suppressed such that almost all SPM is kept below that interface in the region of slow velocities. The consequence is again net upstream SPM transport. These processes result in a residual near-bottom upstream current that traps SPM. If either the residual gravitational circulation or the tidal velocity asymmetry would be reduced, then the turbidity maximum would weaken or even vanish (Burchard & Baumert, 1998).

On top of and combined with these turbidity-generating mechanisms, another sediment-based process is important. Since Eisma (1986) the cohesive behavior of sediment (clay, silt and sometimes fine sand) and organic matter (debris or even living bacteria), clustering together to form porous flocs of varying size and composition, a process known as flocculation, has received increasing interest. In low energy conditions at low SPM concentrations, such as in many rivers and small microtidal estuaries, floc size and composition are rather constant, as the flocculation time is relatively large (Winterwerp *et al.*, 2006). On the contrary, in high energy conditions at high SPM concentrations, as met in many macrotidal or large estuaries, variation is huge. A conceptual diagram, suggesting that floc size changes with SPM values and turbulence shear (Fig. 2.1), is, without disregarding the gained knowledge on the role of ionic strength, still used as a basis for further research into the causes and characteristics of flocculation (Winterwerp *et al.*, 2006).
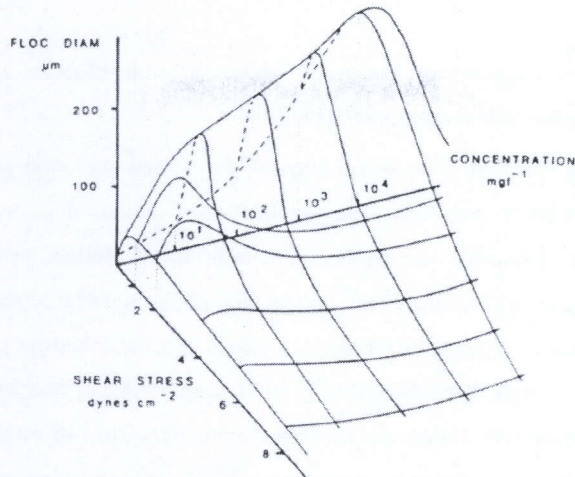
Fig. 2.1: Diagram showing floc diameter as a function of shear stress and suspended matter concentration. Source: (Dyer, 1989)

2.2.2.2 Variation

Although the residual current is quite stable on a long-term multi-tidal cycle scale, especially when the bottom topography enhances salinity stratification, short-term variation in the location and characteristics of the turbidity maximum can be considerable due to changes in gravitational circulation and turbidity maximum formation in general (*e.g.* Schoellhamer, 2001). Thus, migration distances of a turbidity maximum within an estuary can be considerable. When the tidal range increases in the neap-spring cycle, the high current velocities required to make resuspension of deposited SPM are sustained for longer periods. For instance in the lower Forth estuary an increase of tidal range from 4.0 to 4.8 m resulted in an increase of an order of magnitude in net landward sediment transport (Lindsay *et al.*, 1996). This illustrates that spring cycles can be of dominating influence in sediment transport. At spring tide the turbidity maximum, fed by strong upwelling, can migrate upwards of the freshwater-saltwater interface and enter the freshwater zone, as has been described, *e.g.* for the Tamar estuary (Uncles & Stevens, 1993).

Concerning spatial variation, it has been shown that shallow areas tend to be more flood-dominated than deeper areas (Wang *et al.*, 2002), so that the shallow areas are more prone to upwelling by the stronger flood currents. For pelagic primary production, a favorable mixing depth does not necessarily go hand in hand with an optimal photic depth, although sediment-dwelling algae can be important primary producers (V. de Jonge pers. comm.).

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2.2.2.3 Combining comparative estuarine research and historic reconstruction: an opportunity for light environment assessment

Although there is a reasonable understanding of the spatial variation and mechanisms of turbidity, and of its short-term variation, the long-term evolution of turbidity patterns is, however, less clear. Estuaries are naturally in constant evolution, and it is difficult to determine trends of the light environment. Succeeding in this reconstruction is very important, however, for instance in constructing reference conditions for estuarine primary production, the basis of the food web. Linking turbidity with morphological and hydrological aspects provides some opportunities. Using consistently derived data from 44 estuaries in Europe and the Americas in an inter-estuarine comparison, SPM concentrations were shown to be significantly related to tidal intrusion length, tidal range, and residence time (Uncles *et al.*, 2002). Longer estuaries generate faster tidal currents for a given tidal range at their mouth and, in the presence of a supply of erodible fine sediment, therefore produce greater concentrations of suspended matter that can accumulate in turbidity maximum zones. The same is true if the tidal range is increased for estuaries with a given length (the inter-estuarine relation between SPM, mean tidal spring range, and tidal intrusion length could explain 74% of the variation). Thus, a large microtidal estuary can be as turbid as a small macrotidal estuary (*e.g.* Chesapeake Bay compared to the small Yeo estuary). It also explains exceptions in the comparative study by Monbet (1992), *e.g.* why in the microtidal but very long Hudson River estuary high nutrient concentrations do not give rise to high chlorophyll values. These relations can be applied to reconstruct historic SPM concentrations, if the temporal development of the determining parameters is known.

For the heavily impacted Scheldt estuary such results are available. Documentation of the morphology of the Scheldt in 1650, 1800, and 1968 AD (Coen, 1988) provided information that Van der Spek (1997) needed to develop a hydrological reconstruction of the tidal characteristics. The evolution of the tidal range of the Scheldt estuary (Fig. 2.2a), applied to Uncles *et al.* (2002) (Fig. 2.2b) indicated—although with a large degree of error due to the log-log-transformed axes on a smoothed kriging surface plot—that the SPM concentration at the mouth in 1650, was only about one third to one quarter to what it is at present. It seems logical that further upstream, the difference between the historic situations must have been even larger, as the tidal range is amplified closer to the upper limits of tidal influence (Fig. 2a). Although this is only a rough estimate, not taking into account *e.g.* the evolution of the

tidal intrusion length, it is nevertheless a strong indication that the light environment in the Scheldt estuary was indeed negatively affected by large-scale embankments between 1650 and 1968.
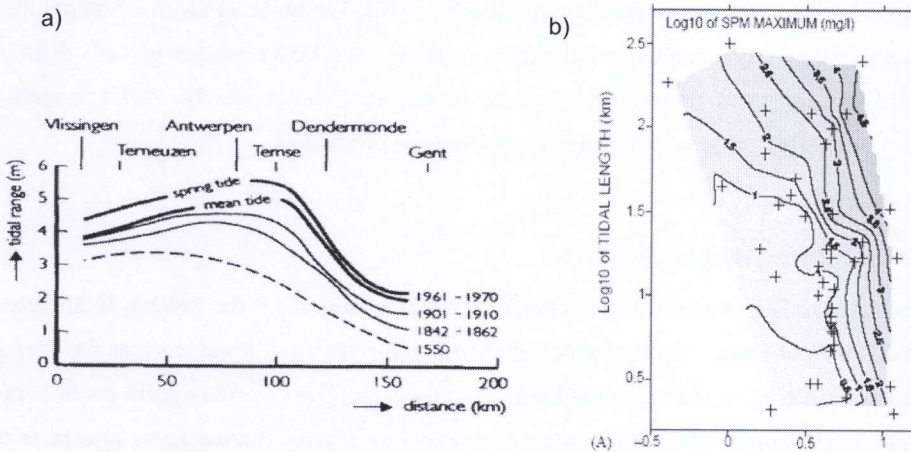
a)

b)

Fig. 2.2: **Combining historic reconstruction and estuarine comparative results: a) Reconstruction of the variation in mean tidal range along the Scheldt estuary (Source: Van der Spek 1997); b) Estuarine suspended matter (SPM) maxima as a function of tidal length and mean spring tidal range at the estuarine mouths. Source: (Uncles *et al.*, 2002)**

2.2.3 Turbidity in the freshwater zone

2.2.3.1 Tidal influence

As the tidal wave progresses through an estuary farther inland, it becomes increasingly reflected against the shoreline, and hence distorted. The steeper water level gradient during the short flood tide phase causes larger maximum current velocities during the flood than during the longer ebb phase. In TFW zone this tidal asymmetry reaches its maximum (*e.g.* Meire *et al.*, 2005). As a result the residual sediment transport of this mechanism, called tidal pumping, is directed upstream, contributing to the existence of the turbidity maxima in TFW zone (*e.g.* Salomons *et al.*, 1988; Grabemann & Krause 2001). Sediment transport is exponentially proportional to current velocity, which strongly amplifies the inequality between flood and ebb transport.

When indications are available that, by a specific length-depth relation of an estuary, the lateral and upper boundary reflections of the initial tidal wave can give rise to resonant behavior, the reflection of the tide that case gives rise to a pattern of standing waves. This

pattern can be recognized by observations that the height of the tidal wave is constant over a large longitudinal distance. Standing waves can dominate as an organizing mechanism for sustaining turbidity maxima (Rolinski & Eichweber, 2000). This is likely the case in the Elbe estuary, where three different turbidity maxima upstream of the salt wedge were simulated under low discharge and wind conditions (Rolinski, 1999). The nodes of idealized amplitudes of over-tide velocities coincided with the main dredging sites. Sedimentation prevails at these sites. This indicates that, if resonance occurs, it can provoke considerable shifts in spatial patterns of estuarine ecology, compared to non-resonant conditions.

2.2.3.2 *Influence of river discharge*

The immediate effect of freshwater discharge on the incoming tide is dampening. If discharge increases, the tidal wave—in the absence of obstructing sluices—will not reach as far inland, also causing shifts in tidal characteristics so that discharge from a certain point controls the amplitude of the tide (Godin, 1999), and tidal pumping weakens. But discharge also imports material from the catchment area. According to a model that calculates erosion and sediment transport from land to water bodies (Van Oost *et al.*, 2000; Van Rompaey *et al.*, 2001), the load of sediment entering the streams of the Scheldt catchment is nearly completely induced by human impact. Erosion of arable land clearly was the dominant factor. This eroded material eventually reaches the estuary, whereby the river discharge determines the imported load as well as the residence time in the system. From 1996 to 2000, a period in which the yearly discharge of the Scheldt gradually more than doubled, the suspended matter load discharged into the estuary more than tripled (Struyf *et al.*, 2004). It was demonstrated that the concentrations of SPM increase with increasing discharge (Vanderweijden & Middelburg, 1989). In the Tweed River, a small meso-tidal estuary with low turbidity, 80% of the variance of freshwater turbidity was explained by discharge of the inflow, which had occurred 30 hr earlier (Uncles & Stevens, 1997). This time lag between turbidity and inflow is a feature of fluvial systems, and is likely to increase if the surface of the drainage basin is larger. Generally, the SPM in the TFW has a finer texture than its marine counterpart (*e.g.* Uncles & Stevens, 1997; Chen *et al.*, 2005). Within the TFW, flocculation has been studied much less than in the turbidity maximum at the freshwater-saltwater interface. In the Scheldt estuary, it was observed that the average floc size increased with decreasing salinity with maximum size occurring well within the TFW (Chen *et al.*, 2005). The availability of dominating quantities of small size individual sediment particles and a high concentration of organic matter,

together with reduced energetic conditions relative to the freshwater-saltwater interface, may explain this observation.

SPM of the TFW zone is usually rich in organic matter. In the Scheldt estuary, a combination of isotope and budget studies indicated that up to one quarter of the SPM could consist of anthropogenic organic matter, *i.e.* during the winter (Van Damme *et al.*, 2005). In summer, anthropogenic organic matter was as high as 10%. This indicated that the implementation of wastewater treatment can attribute slightly but directly to the improvement of light conditions for pelagic primary production in the TFW. In the brackish part of the Scheldt, organic matter is already degraded to such an extent that this factor is of no importance anymore.

The combination of tide and discharge, under normal discharge conditions, causes a specific springtide-neap tide pattern (Fig. 2.3). During spring tides, the flow of river water masses and the transport of suspended particles from the freshwater zone to the brackish and marine zone are slowed due to the increase in estuary water volume (Guézennec *et al.*, 1999). Concurrent with this spring tide phenomenon, strong tidal currents generate maximum suspended load concentrations, so that the tidal pumping can even stop the net downward sediment transport.
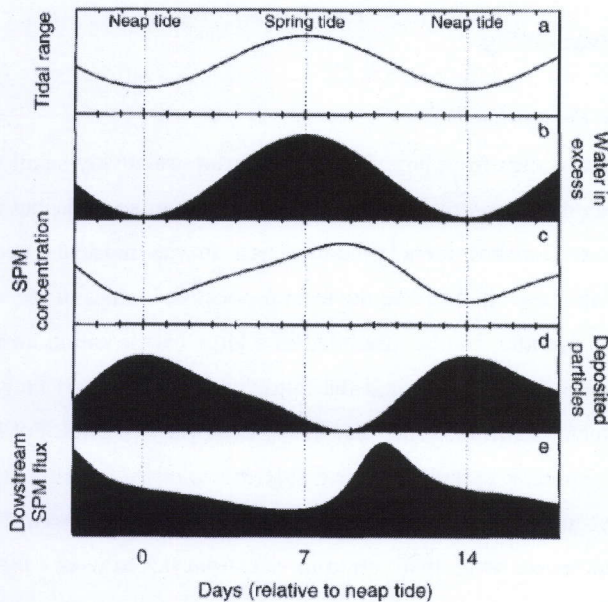

Fig.2.3: **Conceptual sketch of particulate transfer during spring-neap periods onto the upper Seine estuary. Downstream suspended matter flux is maximum during the spring-neap tide transition. Source: (Guézennec *et al.*, 1999)**

At the end of the spring tide period, when the SPM concentration is at its springtide-neap tide peak and the low tide level drops, the transport of SPM downstream reaches its maximum. This period is of short duration, as sedimentation prevails during neap tides.

Extreme river discharges, however, cause a dispersal of SPM from the turbidity maximum to a location further downstream. If this dispersal reaches the sea, then the estuary is flushed substantially and the water is temporarily much clearer. Whereas salinity responds relatively rapidly to changes in runoff, *e.g.* in the Weser and the Tamar estuary within days or even hours (Grabemann *et al.*, 1997), reestablishment of the turbidity maximum after a river spate can require weeks or even months. For the Seine it has been shown that human impact, resulting in a reduction of estuarine space, shifted the main deposition zone of mud brought by winter floods all the way down to the open marine zone, where sandy zones received increasing quantities of silt (Lesourd *et al.*, 2001). The threshold circumstances between net filling or emptying of the TFW by SPM need further integration, but this requires not only a well described relation between turbidity and hydraulic morphology characteristics such as residence time and tidal asymmetry, but, simultaneously, a quantified relation between sediment input in the estuary, discharge, and land use in the catchment area.

2.2.4 Nutrient availability

2.2.4.1 Input from the catchment area

Estuaries concentrate waters from large land surfaces into relatively small water bodies. The constant replenishing of the supply of nutrients from mainly the river, but also directly from the land and the sea, makes them generally rich in the nutrients needed for primary production, and so they are cited among the most productive biomes of the world (Costanza *et al.*, 1997). Whereas turbidity can be generated to a large extent within estuaries, the relation between the estuarine water quality and the nutrients (N, P, and Si) they receive from the surrounding catchment is stricter, especially in the freshwater reaches. For instance, although the control of N export is complex, among-system variation for large rivers is predicted relatively well by simple models of human activity. Using data from 249 predominantly north-temperate catchment areas that varied in size from 0.1 to over 1,000,000 km^2, it was found that the relationship between human population density and nitrate export becomes weaker at smaller scales, and that for catchments less than 100 km^2, it explained only 8% of the 1000-fold variation in nitrate export into the estuary (Caraco *et al.*, 2003).

Growing awareness of the eutrophication problem in coastal zones, estuaries, and rivers has led worldwide to measures to reduce waste loads, such as the Clean Water Act in the USA in 1972 or the European Water Framework Directive (2000/60/EC). As a result, long-term trends of water quality have significantly improved for several estuaries, *e.g.* the Hudson (O'Shea & Brosnan, 2000), where untreated municipal waste loads were reduced from 197 m^3 s^{-1} in 1970 to 0.044 m^3 s^{-1} in 1993. In Europe, the Seine (Billen *et al.*, 2001), the Scheldt (Soetaert *et al.*, 2006) and the Elbe (A. Schoell pers. comm.) all improved from the mid-eighties until the present day. Chinese estuaries, in contrast, over the same period showed their worst decline in water quality ever, *e.g.* dissolved inorganic N concentrations increasing in the Yangtze from 100 to 300 μM and dissolved inorganic P from 25 to 150 μM, leading to a sharp decrease in macro-zoobenthos biomass and causing algal blooms in the adjacent sea (Wang, 2006).

However, a higher proportion of the nutrients loaded to the coastal zone flows through estuarine systems as compared to landscape features located higher in the catchment area. A small increase in the retention of nutrients in the TFW zone may therefore be far more important than a large retention in some buffer strip high up in the catchment, as was indicated for the Hudson (Lampman *et al.*, 1999). This explains the need for understanding nutrient cycling in TFW habitats.

The main regulator of nutrient input from the catchment area into the TFW is discharge. Flow variation can induce several major changes in estuarine water quality and in estuarine functioning. In the freshwater and brackish reaches of the Scheldt estuary, higher discharges apparently improved water quality by diluting nutrient concentrations (Struyf *et al.*, 2004). A positive effect on oxygen concentrations was shown at higher discharge. This masks a problem of increasing total loadings of nutrients. The effect of increasing discharge on the loads of ammonia, nitrate, and silica concentrations is opposite in spring and summer from autumn and winter (Fig. 2.4). With increasing discharge, summer concentrations of dissolved Si (DSi) increased to the level of winter concentrations, indicating reduced consumption of DSi, probably through washout of the diatom community. If future global change would lead to higher discharge, this could flatten out the seasonal cycles for nutrients. The relevance of this phenomenon depends on the importance of the pelagic processes.

2.2.4.2 Pelagic processes

TFW are usually more turbid than their upstream riverine counterparts (M. Lionard pers. comm.). The increased amount of SPM has been related to some changes in the pelagic processes. Ammonium-oxidizing, nitrifying bacteria are associated with suspended particles. These bacteria are chemoautotrophic and therefore must be included as important components of primary production; however, it is not the scope of this study to include chemoautotrophic primary production. It was shown for the river Seine that, while in the river ammonium was slowly nitrified, in the TFW zone, with its longer residence time, nitrification was rapid and complete (Brion *et al.*, 2000).
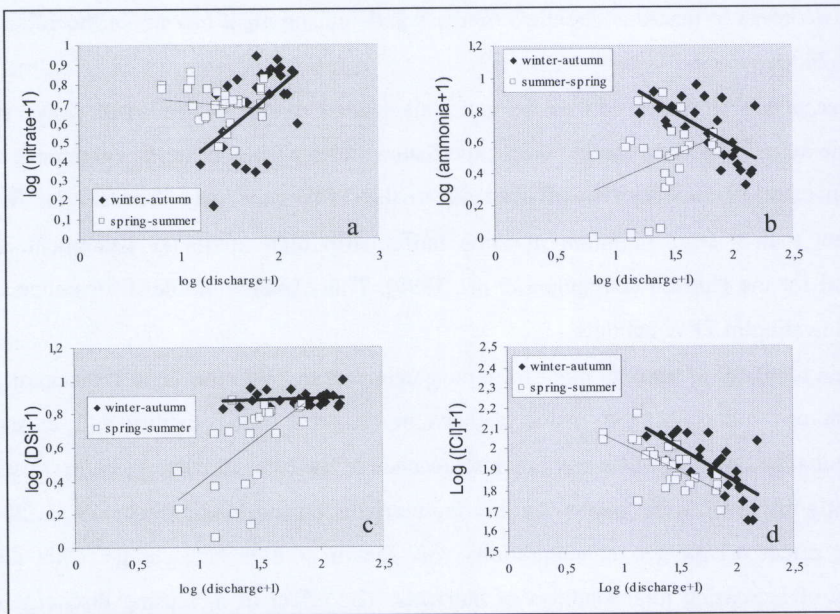

Fig. 2.4: Relation (least-squares linear regression) between total monthly discharge and monthly nutrient concentrations in spring-summer (April-September) and autumn-winter (October-March) in the tidal freshwater zone of the Scheldt estuary (Dendermonde). a) nitrate (summer-spring p=0.40, r^2=0.03; winter-autumn p=0.003, r^2=0.29) b) ammonia (summer-spring p=0.06, r^2 = 0.13, winter-autumn p=0.0001, r^2=0.44) c) silica (summer-spring p=0.0007, r^2=0.39, winter-autumn p=0.53, r^2=0.02) d) chloride (summer-spring p=0.00003, r^2=0.47, winter-autumn p=0.00002, r^2=0.51). Source: (Struyf *et al.*, 2004); see also Chapter 4

Oxygen depletion during summer in the Seine could be attributed to the high demand by nitrification (Garnier *et al.*, 2006). Although this created favorable conditions for water-

column denitrification, chemical or isotopic techniques could not provide evidence for this process in the TFW zone (Sebilo *et al.*, 2006). In the brackish zone, however, a significant departure of the nitrate isotopic composition from what would be expected from simple mixing of freshwater and marine nitrates suggested coupled nitrification and denitrification. The nitrification distribution in the Seine River was in accordance with results from the Elbe River (nitrifier cell count values, which dropped drastically with increasing salinity (Stehr *et al.*, 1995)), and with modelled patterns in the Scheldt River (Soetaert & Herman, 1995b).

Nitrification is not the first cause of oxygen depletion in every estuary. Within the turbidity maximum of the Seine, a lowered biodegradable fraction of particulate organic carbon indicated that freshwater turbidity maxima are sites of preferential degradation, with a bacterial growth of attached bacteria being on average threefold that of free living bacteria (Servais & Garnier, 2006). Extremely high amounts of CO_2 can be emitted from estuaries, with the Scheldt estuary as record holder (Frankignoulle *et al.*, 1998). Within estuaries emissions were maximal in the freshwater part, *e.g.* in the Scheldt partial pressures of 13,000 µatm were not unusual (Hellings *et al.*, 2001). In the Elbe autotrophy prevailed in most of the estuary, except in the freshwater zone, where an average pCO_2 of 1100 µatm was measured (Brasse *et al.*, 2002).

This enhanced mineralization can affect the distribution of nutrient forms. In the Elbe the turbidity maximum showed a clear decrease of particulate organic P (POP) to 20% of total P, which was otherwise the dominant P species at the seaward side of the estuary (51%). Upstream of the turbidity zone the POP fraction increased to 33% (Van Beusekom & Brockman, 1998). Fe-bound P, the dominant inorganic form, increased from 27% of total P at the seaward side to 57% just upstream of the turbidity maximum, and slightly decreased further upstream to 48%. A similar pattern was found for the Scheldt (Zwolsman, 1994), although only the downstream limit of the TFW zone was included in this study, as zones of maximal turbidity or retention studies of whole estuaries received much more attention with respect to P cycling than the TFW itself. It deserves more attention though. In the Scheldt estuary, 53% of dissolved inorganic P (DIP) (14600 kM), 27% of POP (3600 kM) and 25% of total P (18400 kM) of the estuarine input at the river boundary was retained within the TFW zone (Van der Zee *et al.*, 2007). This retention is important, the more so if it is considered that the water quality improvement that is observed in several estuaries, can cause the nutrient limitation in the coastal zone and in estuaries to shift from N to P (Billen & Garnier, 1997; Billen *et al.*, 2005).

In low turbidity microtidal freshwater systems, the fate of nutrients can be different. At the interface between the watershed and the shallow Rhode River estuary, a small oligohaline to mesohaline sub-estuary of Chesapeake Bay, DIP production was the most pronounced feature, fed by enhanced mineralization of settled POP and dissolution of Fe-oxyhydroxides from sediments and wetlands, especially in summer (Jordan *et al.*, 1991). The freshwater zone was thus not retaining P, but merely transforming it from particulate to dissolved forms. Another important feature was the strong uptake of nitrate by enhanced phytoplankton growth. As a result, the N:P ratio was seasonally changed to low values, contrasting sharply with the adjacent Chesapeake Bay. This also illustrates that not only changes in the pelagic compartment determine the fate of nutrients but that the interaction with sediments and marshes have to be considered as well.

2.2.4.3   *Interaction with sediment and wetland vegetation*

A key difference between estuaries and non-tidal rivers is the presence of intertidal habitats, such as mudflats, sand bars, and tidal wetlands. Their interaction with the water column received much attention in estuaries, although the TFW are represented relatively little in these studies. Nevertheless, in TFW, intertidal areas and especially North American wetlands have probably been studied more than the pelagic processes.

Freshwater mudflats are known to be (potential) hotspots of denitrification (Seitzinger, 1988). In the Scheldt estuary, denitrification, nitrification, and ammonification differed by almost an order of magnitude between a freshwater station and intermediate brackish stations (Middelburg *et al.*, 1995). The abundant amounts of available nutrients, the flooding regime, oxygen gradients, and factors enhancing sediment-water column exchange such as bioturbation by benthic invertebrates (*e.g.* Pelegri & Blackburn, 1995) are all factors that favor denitrification in sediments.

A negative relation between salinity and denitrification rates has repeatedly been reported (*e.g.* Seitzinger, 1988). Salinity intrusion can have profound effects on the anaerobic microbial and geochemical dynamics of tidal freshwater sediments. In a flow-through experiment, increased nutrient release (ammonium, silicate, phosphate), decreased methanogenesis and a rapid shift to sulfate reduction, with a coincident increase overall organic matter mineralization, accompanied salinity intrusion into previously freshwater riverine sediments (Weston *et al.*, 2006). The role of oxygen variation in DIP release from

sediments is thus probably larger in TFW than in marine bottom layers, because salinity is already a constant factor of enhanced release in marine zones (Jordan *et al.*, 1991).

Rooted macrophytes link sediment biogeochemistry with the biogeochemistry of the overlying water. As a result, the TFW vegetation can have an important impact on nutrient cycling in estuaries. The ecology of European TFW has, with respect to nutrient cycling and exchange, received little attention in the European scientific community, as compared to the scientific research conducted in North America (*e.g.* Bowden, 1984; 1986; 1987; Chambers & Odum, 1990; Khan & Brush, 1994). The few exchange studies focused upon TFW (*e.g.* Simpson *et al.*, 1983b; Childers & Day, 1988; Bowden *et al.*, 1991) were also mainly American. However, recently, the silica and nitrogen cycling in a Scheldt freshwater marsh have been studied in detail, clearly indicating the buffering role the TFW habitats play in nutrient cycling. This study was triggered by a marsh exchange study, which pointed out that N retention and export of dissolved Si (DSi) were equally important dominant features (Van Damme *et al.*, 2009). A summary of these recent advances in research on N and Si-cycling is provided.

2.2.4.4   *Silica cycling*

TFW contain huge stocks of biogenic Si (BSi), both in sediment and vegetation (Struyf *et al.*, 2005b). Although the total biomass in a reed-dominated TFW is only a fraction of the biomass of a tropical rainforest, the stock of reactive biogenic Si in soil and vegetation is similar (+/- 120 g BSi m^{-2} in vegetation, and 1500 g m^{-2} in the upper 30 cm of soil) (for figures on tropical rainforests: Lucas *et al.*, 1993, Alexandre *et al.*, 1997). Almost all vegetation BSi is in the *Phragmites australis* (hereafter referred to as *Phragmites*) vegetation, where dead shoots can contain up to 8% of BSi relative to dry weight. BSi content in most other species (*Impatiens glandulifera, Salix* spp., *Epilobium hirsutum*) is negligible, while *Urtica dioica* contains relatively high BSi (up to 1% of biomass), but its biomass is not high enough to significantly contribute to the total amount of plant BSi (Struyf *et al.*, 2005b). In a TFW that covered 3500 m^{-2}, 96% of plant BSi was stored in *Phragmites*, while in the total biomass, contribution of reed was only 50%.

BSi is easily soluble if compared to mineral Si, which is considered nearly inert at biological timescales (Van Cappellen, 2003). The high loading of TFW, dominated by *Phragmites*, with such a reactive silica stock, effectively makes them dissolved silica buffers in the estuarine environment. Dissolution of BSi enriches the porewater with dissolved silica compared to the

estuarine pelagic water. Porewater DSi concentrations in the TFW along the Scheldt can be one order of magnitude higher than the concentration of DSi in tidal inundation water in summer. Averaged yearly, the porewater DSi concentrations are about 500 µM (or 14 mg L^{-1}), while DSi concentrations are maximally around 300 µM in the pelagic, and can drop as low as 10 µM in summer there (Struyf et al., 2005a, b).

At high tides, when the wetland is flooded, the porewater is entrained by inundation water with a lower DSi concentration. This mixing of DSi-enriched porewater with DSi-poor flooding water results in a steady outflow of DSi from the wetland towards the main estuarine river. This outflow is mainly focused in the seepage water, which is the water flowing out of the wetland between two bulk-tides, the period of ca. 3 hours during which the wetland is flooded with large volumes of water (Barendregt et al., 2006). The seepage water has been in close contact with wetland sediments and litter. As a result of this BSi-recycling mechanism, TFW act as buffers within the estuarine Si-cycling: they will export most DSi, when the DSi-content in the inundation water and the pelagic is mostly depleted (Struyf et al., 2006). DSi ratio to N and P is extremely important in the occurrence of harmful phytoplankton blooms in the coastal region. As DSi-buffers, tidal wetlands probably partly buffer human over-input of N and P into estuaries. Both sediment and vegetation play a similar role in this mechanism, that of a recyclable stock of Si. However, the rate of BSi dissolution and the amount of BSi stored in both stocks differs.

Phragmites is a relatively small but rapidly recycled sink for Si. Once reed shoots collapse, the BSi in the shoots dissolves very rapidly. Based on decomposition experiments, carried out in both winter and summer at different flooding frequencies (Struyf et al., 2007), after one year all BSi has leached from the decomposing shoots. Taking into consideration the highly dynamic character of the reed vegetation, we can effectively conclude that the *Phragmites* community is almost self-sufficient in regard to Si-use, with almost 100% recycling of biologically fixed Si in a single year. Similar high recycling efficiencies were observed in temperate and tropical forests (Bartoli, 1983; Conley, 2002). Average DSi-release from the *Phragmites* litter layer was approximately 0.07 kg m^{-2} y^{-1}. Sediment on the other hand was by far the largest sink for BSi in freshwater wetlands, mainly from import with deposited sediments (Struyf et al., 2007). BSi dissolves much more slowly than plant BSi: although the source for potential BSi dissolution is more than ten times the potential source for plant BSi dissolution, only about 0.04 kg Dsi m^{-2} y^{-1} is released from the sediment. The complete yearly

flux schedule of Si between the different compartments in a TFW marsh along the Scheldt is shown in Fig. 2.5.
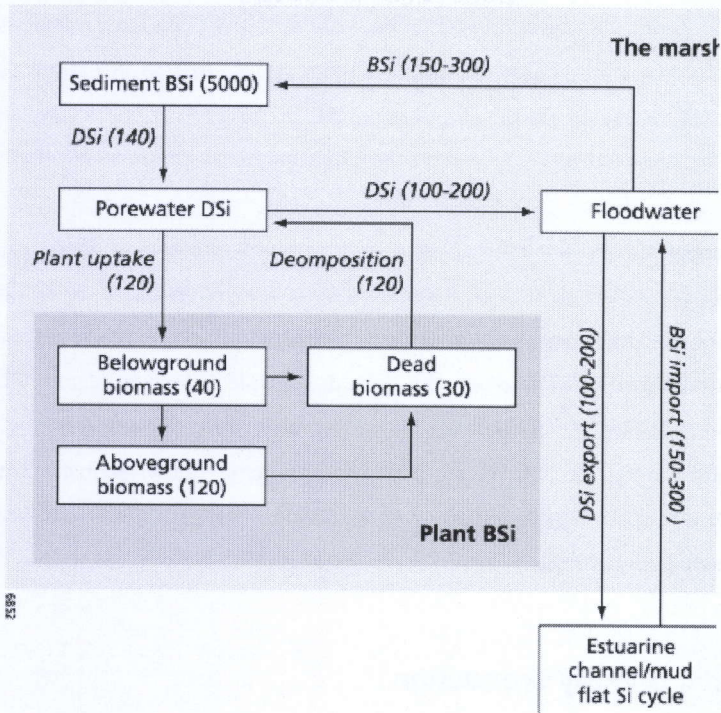

Fig. 2.5: The freshwater wetland Si cycling in a 3500 m² marsh along the Scheldt. All numbers are in kg Si. Fluxes (in italics) are indicated as yearly total fluxes. Stocks of Si in sediment (upper 30 cm) and vegetation are indicated in bold, and are the total stocks for the complete 3500 m² area. Stocks in vegetation are for the peak of the growing season. Stocks in sediment are not subject to seasonal change. The marsh and the estuarine channel are indicated as interacting compartments.

2.2.4.5 Nitrogen cycling

Wetlands are known to play an important role in the retention of nitrogen along the aquatic continuum, and TFW marshes are no exception. Providing a large surface of sediments and biota to interact with the inundating water, wetlands have the potential to promote processes that change nitrogen speciation, and that increase the potential for retention in vegetation or sediment (Gribsholt et al., 2005; 2006). However, until recently, surprisingly little data supported this hypothesis for TFW marshes.

Recent whole ecosystem N[15] labeling experiments in a small TFW along the Scheldt have provided experimental evidence for the large potential of the freshwater intertidal to enhance

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nitrogen retention and processing (Gribsholt *et al.*, 2005; 2006). The wetlands strongly stimulate the nitrification of ammonia to nitrate, and transformation of nitrogen speciation (through both denitrification and nitrification) was equally important as the (partly temporal) retention of N. Roots, aboveground vegetation, sediment, and plant litter retained about 4% of the added ammonia, while 9% of the added ammonia was nitrified. Although denitrification was not directly measured during the experiment, up to 14% of the added ammonia was estimated to be removed ultimately from the estuarine ecosystem through denitrification in the TFW.

The results suggested that annually about 3% of the yearly ammonium load to the Scheldt is nitrified in TFW. Although the total transformation and retention of N in the freshwater intertidal area is for the moment still very small compared to pelagic processes, future plans to increase the total area of TFW along the Scheldt fourfold (Flemish decree VR/PV/2005/9-point 22 and VR/PV/2005/29-point 114) might alter this. Indeed, for the near future restoration plans along the Scheldt are planned to increase safety against extreme flooding events and to allow the establishment of an estuarine ecosystem. TFW and sediments thus show strong potential benefits.

2.3 Aquatic primary production

Primary production is defined as the rate at which inorganic carbon is incorporated in the food chain through photosynthesis. Gross primary production (GPP) is the rate of photosynthetic energy conversion of light into chemical energy; net primary production (NPP) is gross production minus respiration (Platt *et al.*, 1984). A review on estuarine primary production is given in Heip *et al.* (1995). Here, an update of knowledge on the aquatic primary production in TFW is presented.

Three important compartments may be distinguished: phytoplankton, micro-phytobenthos, and macrophytes. The relative contribution of each of them probably depends mainly on the surface-volume distribution of the system, the tidal amplitude, and the turbidity. Submerged macrophytes preferentially occur in low-hydrologic-energy systems with good light conditions (*e.g.* Capers, 2003). For instance, in the tidal Hudson River, submerged vegetation production was in the same range as phytoplankton production, but due to the scarce distribution of shoal habitat, the area-specific contribution to the system carbon balance was

marginal (Howarth *et al.*, 1996). In systems with higher hydrologic energy, macrophytes are confined to the tidal marshes.

Biomass and production data for micro-phytobenthos in TFW are extremely scarce, in part because extracting them from the sediment is difficult. Nevertheless, a comparison between freshwater and brackish tidal mudflats showed clear differences. Epipelon (defined as organisms moving freely in and on the sediment) and epipsammon (defined as organisms that live in close association with individual sand grains) were the dominant organisms at the brackish sites (Muylaert *et al.*, 2002). In TFW mudflats these groups were nearly absent; instead, the sediments were dominated by pelagic diatoms that settled onto the substrate. This was ascribed to the dynamic character of TFW mudflats. As the level of tidal wetlands increases following an increasing tidal range (Temmerman *et al.*, 2003), while the system remains confined between dikes, the slopes of intertidal mudflats logically must increase. It is hypothesized that this effect is largest in the TFW where the estuary is narrowest, and that micro-phytobenthos is related with mudflat slope. This chapter is further restricted to phytoplankton.

2.3.1 General pattern of pelagic primary production

Information on pelagic primary production in TFW is scarce. In recent years, TFW habitats in the Scheldt estuary have been targeted in several studies. Before studies of pelagic primary production in TFW were undertaken, it was generally believed that primary production of phytoplankton increased towards the mouth of an estuary, where a decrease of nutrient concentrations would be more than compensated for by the increased water transparency (Heip *et al.*, 1995). This picture has changed during the last few years. In the tidal freshwater zone of the Scheldt, NPP can vary from negative (Soetaert & Herman, 1995a) to high positive values (Kromkamp *et al.*, 1995; Mulaert *et al.*, 2005). In the Scheldt, the tidal freshwater zone showed higher values of chlorophyll *a* than the brackish part (Fig. 2.6; Muylaert *et al.*, 2000; Van Damme *et al.*, 2005) and high phytoplankton production values were measured in several studies (Table 2.1). Along the salinity gradient of both the Scheldt and Elbe estuaries, total cell abundance and biomass were highest at the oligohaline stations (Muylaert & Sabbe, 1999). In the Gironde estuary cell numbers and biomass values were an order of magnitude lower but followed the same pattern (Muylaert & Sabbe, 1999). Maximum values of production, biomass or chlorophyll *a* occurred in the TFW zone in the Seine, although measurements were restricted at low discharge regimes (Garnier *et al.*, 2001), in the Weser

(Schuchardt & Schirmer, 1991) and the James River estuary (Moon & Dunstan, 1989). The pattern that has emerged from these studies is that TFW are in general more productive than their brackish or saline counterparts, although a possible dilution effect is not always considered. This decline has been ascribed to osmotic stress at the freshwater-saltwater interface, *e.g.* in the Elbe (Kies, 1997). A specific experiment in the Scheldt estuary, however, showed that, although freshwater and brackish water phytoplankton was negatively affected by, respectively, an increase or decrease in salinity, this effect was not strong enough to explain the phytoplankton distribution along the salinity gradient (Lionard *et al.*, 2005). Neither could suspended matter concentrations explain the difference, as values were similar in the turbidity maximum of the freshwater-saltwater interface and the freshwater zone. In many estuaries, however, the freshwater zone is more shallow than the brackish part, *e.g.* in the Scheldt (Muylaert *et al.*, 2005) and the Elbe (Rolinski, 1999). In those cases a change of the euphotic depth:mixing depth ratio could explain the distribution along the salinity gradient, although the Elbe is less well mixed than the Scheldt. In many cases, the high production rates in the TFW zone were attributed to low freshwater discharge and hence longer residence times (*e.g.* Moon & Dunstan, 1990; Schuchardt & Schirmer, 1991; Muylaert & Sabbe, 1999; Muylaert *et al.*, 2005), thereby often pointing to the fact that blooms occurred during summer or autumn periods, when precipitation was low. On the contrary, when river discharges into the TFW zone were high, low production values were measured in the York River (Sin *et al.*, 1999) and Elbe (Muylaert & Sabbe, 1999) estuaries.

In the Scheldt estuary, clear differences in phytoplankton species composition were observed between the tributary (non tidal) rivers and the TFW zone (Muylaert *et al.*, 1997; Muylaert *et al.*, 2000). Diatoms were found to be the dominant phytoplankton group in the TFW reaches, while chlorophytes dominated the tributary rivers, especially in summer. Changes in phytoplankton community composition along the riverine-estuarine transition were ascribed to different adaptations of the phytoplankton community to the light environment. The general idea was that diatoms are adapted to low light levels and are therefore capable of surviving in the turbid estuary, while green algae depend on relatively high light intensities and would therefore be expected to survive only in the river (Richardson *et al.*, 1983).
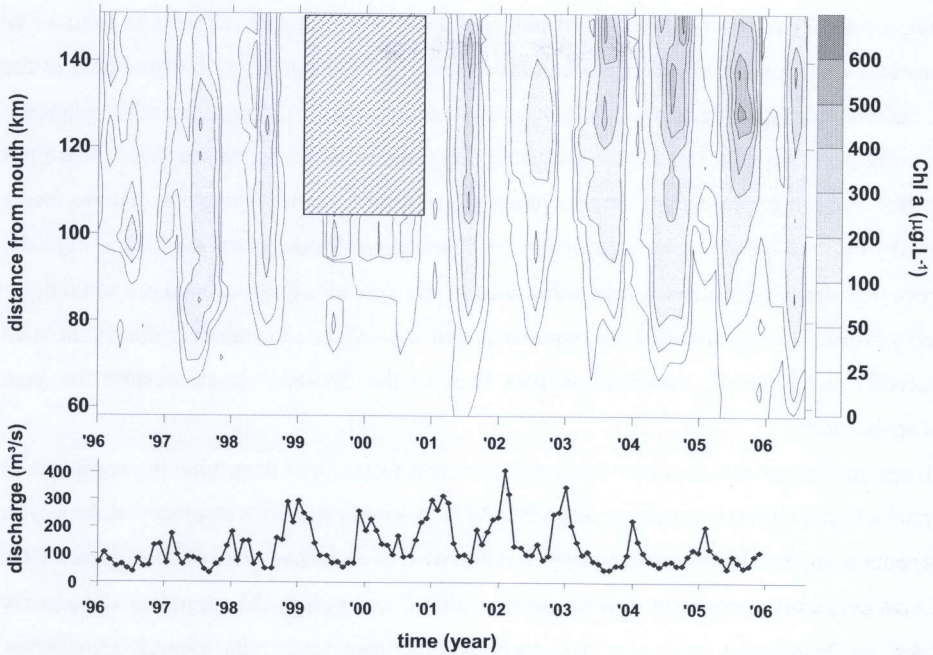
Fig. 2.6: Chlorophyll *a* (Chl *a*) concentrations in the Belgian part of the Scheldt estuary and river discharge (Schelle, source Flemish Administration of Waterways and Sea); update after Van Damme *et al.* (2005); see also Chapter 3

Table 2.1: Phytoplankton production, total cell count, and chlorophyll *a* (Chl *a*) values in tidal freshwater areas; GPP=gross primary production; NPP= net primary production; Chl *a* is expressed as yearly maxima (<) or yearly average values (interval).

		GPP $g\,C\,m^{-2}\,y^{-1}$	NPP $g\,C\,m^{-2}\,y^{-1}$	$g\,C\,m^{-3}\,d^{-1}$	Total cell counts cells ml^{-1}	Chl a $mg\,L^{-1}$
Hudson River	Cole et al. (1992)	130-380	70-204			20-40
	Howarth et al. (1996)	130-380	20			20-40
York River estuary	Sin et al. (1999)	< 30				< 10
Chesapeake Bay	Moon & Dunstan (1990)					< 115
Scheldt	Van Spaendonk et al. (1993)	900				< 270
	Kromkamp & Peene (1995)		388			< 75
	Kromkamp & Peene (2005)		500			28-43
	Soetaert et al. (1995)			-20 - +10		< 50
	Muylaert & Sabbe (1999)				10000-22000	
	Muylaert et al. (2005)		108-294			< 111
Elbe	Muylaert & Sabbe (1999)				100-36000	
	Schuchardt & Schirmer (1991)					50-70
Weser	Schuchardt & Schirmer (1991)					50
Gironde	Muylaert & Sabbe (1999)				800-1100	
Seine	Garnier et al. (2001)			500-1000		

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However, when incubated at a light intensity corresponding to the mean underwater light intensity of the TFW reaches, growth of phytoplankton from the river as well as from TFW reaches was significantly lower than when incubated at a light intensity corresponding to the mean underwater light intensity of the river (Lionard *et al.*, 2005). The phytoplankton community from the tidal freshwater reaches did not appear to be better adapted to low light intensities than the phytoplankton community from the river. Although diatoms were expected to be less sensitive to a reduction in light intensity than green algae, the opposite response was observed. The non-tidal tributaries of the Scheldt estuary turned out to be light-limited as well. This accentuated the hypothesis that the enhanced residence time in the tidal part gives rise to higher production values than in the non-tidal river, despite the high estuarine turbidity.

Depth and residence time thus turn out to be dominant factors that determine the composition and production of pelagic plankton in TFW. When a longer period was observed, however, discrepancies appeared between chlorophyll *a* and discharge values (Fig. 6). Both years 1996 and 2004 were characterized by low discharge values, yet in 2004 chlorophyll *a* values were much higher. Monitoring on a monthly basis does sometimes not provide enough information. In 1996, a specific short-term high-frequency monitoring effort revealed that during a storm at the end of August a peak discharge occurred from 10 to 280 $m^3 s^{-1}$. As a result of this event, diatom biomass dropped from 3.5 to 1.0 mg C L^{-1}, while *Scenedesmus* and coccal green algae in general did not decrease, NPP decreased to roughly 20% of its initial value, and DSi concentrations increased (Muylaert *et al.*, 2001). This drop lasted, in combination with a drop in temperature and irradiance, for the rest of the season. In 1998 another peak discharge event was followed (from 50 to 250 $m^3 s^{-1}$), this time in spring, but this time the effects were less pronounced (Muylaert & Vyverman, 2006).

Because of these clear indications that standing stock, production, and community composition can vary considerably within the TFW, it is surprising that the TFW zone is often considered as a single entity. In many estuarine studies the tidal freshwater zone is not considered over its full length and is considered to only be a boundary of the estuary (*e.g.* Van Spaendonk *et al.*, 1993; Kromkamp *et al.*, 1995; Kromkamp & Peene, 2005; Soetaert & Herman, 1995a; Goosen *et al.*, 1999). When variation was measured within the TFW zone, longitudinal patterns other than increasing upstream trends were found. Within the long TFW zone in the Hudson River, for example, production was higher in the mid-section compared to

the upper limit of tide (Cole *et al.*, 1992). A closer look at the phytoplankton community is therefore an essential step in understanding production variation within the TFW.

2.3.2 Tidal freshwater communities

In the Scheldt estuary, the TFW was characterized by two separate plankton communities (Fig. 2.7) and the distribution of these communities along the longitudinal estuarine axis corresponded with the energy distribution pattern. The TFW has a critical point, upstream of which the discharge energy exceeds the tidal energy and the freshwater velocity becomes larger than the tidal velocity (Chen *et al.*, 2005). Upstream of this critical point the river discharge has a considerable influence on tidal damping, primarily through friction (Horrevoets *et al.*, 2004). This cross point is situated where the cross-sectional area of the estuary approaches the cross-sectional area of the non-tidal upstream boundary. It can rightly be regarded as the boundary between the estuarine and the riverine part of the TFW. This is reflected in the plankton community structure: where tidal energy dominates over river discharge, the phytoplankton community was dominated by the taxa *Actinocyclus normanii* (Gregory ex Greville) Hustedt and *Aulacoseira granulata* (Ehrenberg) Simonsen in winter and by *Cyclotella scaldensis* Muylaert & Sabbe in summer (Muylaert *et al.*, 2000). *Actinocyclus normanii* was also the dominating species during the seasonal chlorophyll *a* maximum within the TFW reaches of Weser and Elbe, which occurred in late summer / autumn (Schuchardt & Schirmer, 1991; Rehbehn *et al.*, 1993). Where river discharge dominated tidal energy, *Stephanodiscus hantzii* Grunow and *Scenedesmus* spp. represented the community, but their densities declined as the tidal energy increased. *Stephanodiscus hantzii* also dominated the limnetic part of the Elbe estuary (Muylaert & Sabbe, 1999).
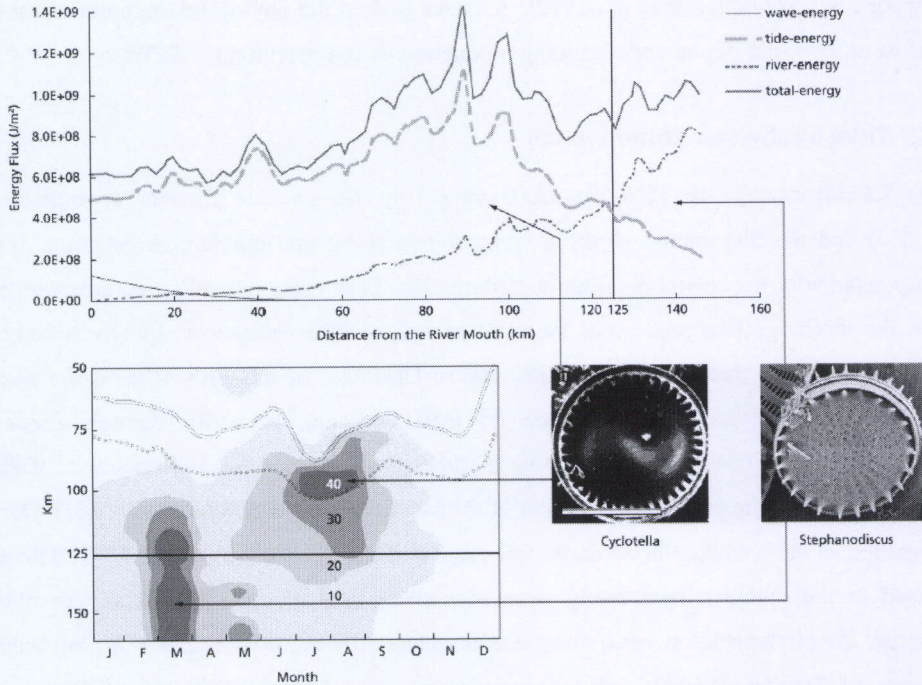
Fig. 2.7: Combining the spatial chlorophyll *a* concentration distribution (below) (Source: Muylaert *et al.*, 2000) and energy distribution in the Scheldt estuary (top) (Source: Chen *et al.*, 2005), with electron microscope images (Source: K. Muylaert pers. comm.) of the dominating species in each bloom. Spring and summer bloom occurred under different energy conditions.

Thus, it is likely that in various estuaries the transition point between discharge and tide-dominated hydrology is reflected by a succession between a phytoplankton community of riverine origin to one that is autochthonous to the estuary. Riverine communities of course have their own variability, which can affect input in estuaries, as was demonstrated, *e.g.* in the Seine, where a seasonal succession of diatoms and Chlorophyceae caused silica depletion in summer (Garnier *et al.*, 1995).

Another reflection is that determining the actual phytoplankton species composition is one thing, determining what assemblage corresponds with a good condition is yet something else. In Chesapeake Bay, paleontological indicators in dated sediment cores were used for the purpose of reconstructing a long-term environmental history of the bay. Analysis of the data indicates that sedimentation rates, anoxic conditions, and eutrophication have increased in the Chesapeake Bay since the time of European settlement (Cooper & Brush, 1993). For example, since initial land clearance around 1760, sedimentation rates have increased from as low as

0.02 cm y^{-1} to an average 0.22 cm y^{-1}, indicating an increased risk of light limitation. Diatom community structure showed a steady decrease in overall diversity since 1760 and the centric:pennate ratio increased significantly since 1940. While this approach to characterization of the plankton community provides interesting information, care should be taken, as sea-level changes and estuarine morphological evolution most likely caused shifts in the location of the TFW zones.

A comparison of measured production between freshwater tidal communities is unavailable, although a different response on light conditions and nutrients is expected or demonstrated (*e.g.* Lionard *et al.*, 2005). TFW have specific phytoplankton assemblages. Whether this is incorporated sufficiently in existing ecological models that are used to reconstruct or predict primary production is a relevant question. In many estuaries, an investigation into communities in the freshwater zone is still needed, as the TFW zone of estuaries is in most cases treated as one entity. This lack of basic knowledge is striking, when one realizes that primary production is the basis of the estuarine food chain, and that a shift in balance from autotrophy to heterotrophy can have a significant impact on oxygen concentration and thus on the faunal diversity. Refining the knowledge on primary production is therefore a need that is expressed not only by biologists but also by modellers.

2.3.3 Complications in measuring and modelling

GPP is commonly expressed in terms of specific productivity, *i.e.*, per unit mass of chlorophyll *a*. Chlorophyll *a* is thus used as a proxy for photosynthetically active biomass. In this way, GPP is only a potential value of specific photosynthetic activity (*i.e.* the carbon incorporation rate per unit mass of phytoplankton at well-defined values of light intensity, temperature, and nutrient content). However, in natural systems, these parameters usually vary both in space (for example, light intensity decreases with water depth) and time (*e.g.* according to discharge). To estimate the actual carbon fluxes due to photosynthesis during a given period, gross primary productivity has to be multiplied by the phytoplankton mass and must then be integrated over space and time, leading to the value of GPP. When respiration is determined in an analogue way and subtracted from GPP, NPP is determined as presented in Table 1. Many different methods are used to determine GPP and NPP, making it difficult to develop precise values of GPP or NPP. Some occurring problems are listed in the following sections.

2.3.3.1 Light intensity

GPP is often determined by measuring C^{14} isotope incorporation through incubations. Incubations for measuring GPP have the disadvantage of being static, so that the light intensity is usually not simulated according to the short-term variation of the natural conditions. Model results based on short-term variability data showed that the description of phytoplankton growth must operate at a time resolution sufficiently high to describe the interference between solar and tidal driven physical forcing functions (Desmit *et al.*, 2005). It was shown that in shallow to moderately deep systems, simulations using averaged, instead of time-varying forcing functions, lead to significant errors in the estimation of phytoplankton productivity. The highest errors were observed when the temporal pattern of light penetration, linked to the tidal cycle of solids settling and resuspension, were neglected.

In order to overcome the disadvantage of static incubations, a so-called 'turbulence incubator' was designed (Gocke & Lenz, 2004). The incubator allowed simulating the changing light conditions for vertically mixed phytoplankton cells by moving sample bottles in a controlled way. With this method, significantly higher primary production rates were obtained than in static incubations *ceteris paribus*. Short-term variation was not taken into account in any of the GPP or NPP values in Table 1.

2.3.3.2 Nutrients

If one would implement reference conditions for phytoplankton in Chesapeake Bay, this would require an increase in light transparency of the water column and lower concentrations of dissolved inorganic nitrogen and orthophosphate (Buchanan *et al.*, 2005). Limitation can shift from one element to another if conditions change (*e.g.* Billen *et al.*, 2005). But the fate of lesser limiting nutrients is every bit as important as that of the limiting nutrient (Flynn, 2005). Phytoplankton species have multi-nutrient growth dynamics. Therefore, neglecting a nutrient in monitoring or modelling can have consequences on the modelled primary production results. Soetaert & Herman (1995a, b) obtained the results by a model that took into account N, but not P. As the limitation sequence between these two elements changed in the Scheldt (Billen *et al.*, 2005), this model certainly needs improvement on this point.

Limitation of diatom growth by DSi is a major issue in coastal zones and the marine zone of estuaries, where shifts in community structure have been related to it (*e.g.* Cugier *et al.*, 2005). But also in the TFW, DSi can show depletion (Van Damme *et al.*, 2005), even beyond diatom growth limitation (T. Maris pers. comm.). These shortages occurred during summer

months, concurrently with peaking rates of NPP (between 500 and 1500 g C m^{-2} y^{-1}) (T. Cox pers. comm.). However, the silica processing by the tidal freshwater community probably needs different modeling formulations than the marine zone.

2.3.3.3 *Biomass specific rates*

Due to different estimates of respiration rates, a discrepancy in NPP values between different authors was reported for the Hudson River (Table 1). A common failing is measurement of biomass by chlorophyll (Flynn, 2005). The relationship between chlorophyll *a* and biomass is not constant but may vary over 5- to 10-fold with growth irradiance and nutritional status. The chlorophyll *a*:biomass (chlorophyll *a*:C) ratio is important for determining GPP as well as respiration. With the very specific and variable light conditions and nutrient status in TFW, it is essential to determine local chlorophyll *a*:C ratios. Preliminary results revealed that in the TFW of the Scheldt this ratio ranged between 1 and 70, with a mean of 15 (M. Lionard pers. comm.). These values are exceptionally low. If they can be confirmed, this would imply that modelling of phytoplankton production in TFW needs a full revision.

2.4 Conclusions

This study presented a state-of-the-art synthesis concerning aquatic primary production and its determining factors in the TFW zone of estuaries. Although there was much less information available compared to their more saline counterparts, enough arguments were assembled to illustrate the importance, complexity, variability, and uniqueness of the TFW. All factors that could be related to primary production can strongly interact. There are TFW of all kinds, high or low hydrologic energyc, dominated by tide or discharge, turbid or clear. This diversity is reflected in the community composition of the primary producers, but their adaptive behavior is sometimes contrasting with general ideas.

This synthesis provides a basis for deeper comparative estuarine research that could lead to quantified relations between determining factors. However, the scarceness of data, together with weaknesses in methodology for measuring or modelling primary production, is so striking that it can be postulated that the time is not yet ripe for providing an accurate and detailed picture of primary production in TFW. Nevertheless, the time is ripe for starting to work on it, as it is clear what must be done to fill in the gaps. The basis of the food web, in zones through which the entire discharge of whole catchments passes, offers enough potential

to deserve sound scientific attention. Restoration and management can after all only be successful if at least the actual status is known.