Department of Biology

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Marine Biology Section

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Factors influencing the habitat value of tidal marshes for nekton in the Westerschelde estuary

Henrietta Hampel

Promotor: Prof. Dr. Magda Vincx
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This thesis is submitted in partial
fulfilment of the requirement for the
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Summary

An ecotone is a zone where two ecosystems overlap and which supports species from both ecosystems besides the species found only in that zone. Ecotones may have a higher diversity than the surrounding ecosystems since species may invade this area from both sides. However, lower species diversity may also be characteristic to ecotones since, due to the transitional position and unfavourable environmental conditions only a few generalist species may be adapted to cope with such an environment.

Intertidal saltmarshes are considered ecotones due to their positions between the terrestrial and marine or estuarine ecosystems. In the saltmarshes the environmental conditions (e.g. tide, exposure time, temperature, salinity) are constantly changing. Due to the constantly changing environment several factors may influence the habitat value of saltmarshes for nekton species. This study focuses on three aspects that effect the habitat value of the intertidal marshes in the Westerschelde estuary: short-term temporal changes, small and large-scale spatial variation and marsh age.

Influence of short term temporal changes on the marsh habitat value

The aim of **Chapter 2** (in press, Estuarine, Coastal and Shelf Science) was to investigate the effect of short-term temporal variation on the marsh faunal assemblages. The objectives included the description of the change of species densities and community structure during tidal, diel and semi-lunar cycle. Three null-hypotheses were formed as follow: 1- Number of migrating individuals does not differ between the different hours of the tidal cycle. 2- There is no difference in density of the main marsh visiting species during day and night. 3- There is no difference in nekton species densities and community structure between spring and neap tide. Samples were collected during seven tidal cycles from spring tide till neap tide to cover the period of a semi-lunar cycle in August 1994. On consecutive days, day and night samples were taken at spring and at neap tide. Similar to other investigations this study showed the existence of a strong tidal influence on the migration of nekton in and out of the marsh habitat. During the tidal cycles two different tidal-migration modes were observed. The mysid shrimp, *Mesopodopsis slabberi* showed a maximum abundance around high tide. For the remaining common species, the mysid *Neomysis integer*, the shrimp *Palaemonetes varians*, the crab *Carcinus maenas*, the common goby *Pomatoschistus microps* and the amphipod *Corophium volutator* highest numbers were recorded during lower water heights. These species migrate at the edge of the tides maximizing the utilization of the marsh creek habitat. This indicates the importance of tidal creeks for several species. A diel variation of the faunal assemblages was also observed. The total density of nekton and the densities of *Crangon crangon*, *P. microps*, *C. volutator*, *P. varians*, and *C. maenas* were higher during the night hours both at spring and at neap tide. In other studies, *Crangon crangon* and *Corophium volutator* were reported to be more active during night hours, which may explain the higher abundance in the marsh creek. During spring tide a difference in community composition was noticed between the night and the day samples. At neap tide, day and night differences were less clear. The effect of the semi-lunar cycle on the nekton assemblages was also observed. Recorded total densities were generally higher during spring tide and lower during neap tide although at maximum water levels, a decrease in total density was observed. A multivariate analysis indicated a change in community composition between spring and neap tides. The first null-hypothesis was rejected since strong tidal influence was observed leading the activity of several species in the studied intertidal creek. Observations showed the most of the main species migrate in the first and the last hours of the tidal cycle while others like *Mesopodopsis slabberi* occurred in maximum numbers at high water. The second null-hypothesis was not proved because several species showed density differences during day and

night. Diel changes influenced the density of some species however the few sampling occasion do not let further conclusions. The third null-hypothesis was rejected due to the observation that most of the species had different densities at spring and at neap tide and the community structure also differed between the lunar phases. However explanation of this finding is still lacking therefore there is a need for more occasions with given set of conditions in order to reach firm conclusions and to show robust patterns.

In **Chapter 3** (submitted to Aquatic Sciences) changes in the diet of the common goby over a complete semi-lunar cycle were investigated to obtain a better understanding of the influence of tidal, diel and semi-lunar cycles on marsh habitat usage. The study aimed to describe the feeding habit of juvenile *Pomatoschistus microps* during the semi-lunar period, to investigate the separate and combined effect of the tidal, diel and semi-lunar cycle on the feeding behaviour of juvenile gobies and to quantify the change in tidal food consumption. Null hypotheses were set as follow: 1- There is no difference in feeding habit between flood and ebb period. 2- Gobies feed similar during day and night. 3- No difference of the feeding habit of *P. microps* exists between spring and neap tide period. 4- There is no combined effect of the different short term cycles on the foraging habit of the common gobies. *Pomatoschistus microps* was chosen because this is a typical intertidal species that uses the marshes as a nursery and a foraging ground. Individuals enter the marsh creek at the beginning of the tidal cycle with a relatively empty stomach and leave the marsh with a higher stomach content. This indicates the strong dependence of the feeding habit on the tidal cycle and the intense utilisation of the area as a foraging ground. A diel effect on the feeding habit of *P. microps* was present. In marsh creeks common gobies generally foraged more intensively during day than during night. The influence of the diel cycle was inferior in comparison with the tidal influence. This seems obvious as the tides form the main environmental influence on the habitat and the ecology of marsh species. A significant difference in foraging activity occurred also between spring and neap tide. The common goby migrated in lower abundances into the creek during spring tide but foraged more intensively. Both at spring and neap tide, a significant difference was found in the fullness index between day and night. At spring tide, gobies fed more during day while at neap tide they foraged more intensively at night. No clear explanation could be given for the combined effect of the diel and the semi-lunar cycle.

Influence of spatial variation on the marsh habitat value

Hydrology strongly influences the formation of the typical physiographic features in the marsh (creeks, ponds, pans and vegetated marsh flat) creating small-scale habitats. These marsh features can have distinct environmental parameters and represent different habitats for species utilizing the marsh. In estuaries, another physical factor besides hydrology is the large-scale salinity change, which is considered to strongly influence the faunal assemblages. In **Chapter 4**, (submitted to Hydrobiologia) the aim of the study was to investigate the effect of salinity changes combined with the small-scale spatial variation on the marsh habitat value. The first objective of this study was to examine how the fish and macrocrustacean marsh fauna within one estuary differ between salinity regions including the fresh water area. The second objective was to determine the differences in the utilization of three marsh habitats (large and small creek and the marsh pond) by nektonic species. The following null-hypotheses were set: 1- There is no difference in epibenthic species composition between the marshes with different salinity. 2- Same species utilize the three marsh habitats like large and small channel and marsh pond. Samples were taken between spring and autumn 2000 in five marshes along the salinity gradient of the Schelde river. The euhaline Zwin, the polyhaline Zuidgors, the mesohaline Waarde and Saeftinghe and the freshwater Grembergen were chosen. In each marsh different habitats (large creek, small creek and marsh pond) were sampled. Similar environmental conditions may have resulted that the main species (*Platichthys flesus*, *Dicentrarchus labrax*, *Pomatoschistus microps*, *Carcinus maenas*, *Palaemonetes varians*) migrating in the marsh utilised both large and small creeks. Only *Anguilla anguilla* was not captured in the small creek habitat although this species has a wide environmental tolerance. In accordance with other investigations only few species utilised the marsh ponds. In the tidal pools, only *Palaemonetes varians* appeared in high numbers. Among fish species the common goby *Pomatoschistus microps* and *Gasterosteus aculeatus* were present although the latter one was captured only a few times. The tidal freshwater marsh had a species poor fauna and only low numbers of fish were caught. Besides some freshwater species, *Anguilla anguilla* was still an important fish. Amongst the poly- and mesohaline marshes no differences could be detected in nekton species composition. The dominant species were the flounder *Platichthys flesus* and the seabass *Dicentrarchus labrax*. In the euhaline marsh, *P. flesus* was not captured and numbers of *D. labrax* were low. This pattern could the resulted of the salinity preference of flounder. The utilisation of the marsh creek by seabass may be less intense in the euhaline area although the lower catching efficiency of the fyke nets seems to have biased this result. Species are able to adapt and invade marsh areas where environmental variables constantly change are probably also capable of using different marsh habitats under a wide range of salinity.

Food availability will also strongly influence the utilisation of an area by fish and macrocrustaceans. Macrobenthos is an important food source for nekton species. To better understand the potential of the marsh as feeding grounds **Chapter 5** focuses on the main macrobenthic prey species. The objective of this chapter was to investigate temporal and spatial variation of macrobenthos. The study also aimed to compare the macrobenthic density and biomass between the marsh and the intertidal flat especially focused on a few taxa, which are an important food source for the marsh visiting fish species. Null-hypotheses were: 1- Macrobenthos exhibit similar seasonal pattern in every marsh. 2- There is no change in the density, biomass and diversity of macrobenthos in the marshes with different salinity. 3- There is no difference in density and biomass of *Nereis diversicolor, Corophium volutator, Macoma baltica* and Oligochaeta between the intertidal flat and the marsh creeks. Samples were taken in the five marshes along the salinity gradient of the Schelde river every six weeks from May till October 2000. Macrobenthic total and species densities and the biomass of the four dominant taxa (the amphipod *Corophium volutator*, the polychaete *Nereis diversicolor*, the mollusc *Macoma baltica* and Oligochaeta) were measured and diversity indices were calculated. In Saeftinghe and Waarde the macrobenthic density peak occurred during summer while in Zuidgors and Zwin densities declined towards autumn. Higher macrobenthic biomass was measured during the second part of the sampling period due to abundance of *Nereis diversicolor* and *Macoma baltica*. The biomass of the four taxa was highest in August in every marsh except in Saeftinghe where the biomass peaked in October. The abundance of macrofauna fluctuated along the salinity gradient without any spatial trend due to the dominance of oligochaetes. In contrast, the diversity and the total biomass increased towards the euhaline area. Among the main taxa the density and biomass of *N. diversicolor* and *M. baltica* showed a significant positive correlation with salinity. The sampled marshes supported higher densities and biomass of these two species and a lower density and biomass of *C. volutator* than the intertidal flat of the Westerschelde estuary during early autumn 2000.

Chapter 6 presents the feeding habit of the main predator fish species through qualitative stomach analysis in different salt marshes situated along the salinity gradient of the Westerschelde estuary. The objectives of the study were to assess the importance of marsh creeks as feeding grounds for larger seabass and flounder and to define the relative importance and impact of *Platichthys flesus* and *Dicentrarchus labrax* as predators on the infauna and the nursery/refuge function of the creeks for juvenile fish and crustaceans. The following null-hypotheses were set: 1- There is no difference in niche breadth of *P. flesus* and *D. labrax* in the marshes with different salinity. 2- There is no difference in fullness index of the two fish species between the marshes. 3- Predation of flounder and seabass does not affect significantly the macrobenthic stock in the intertidal creeks. 4- Due to the presence of the predatory fish marsh creek does not represent a good nursery area for other species. The study focused on flounder and seabass because these species occur in higher abundances and their postlarvae use marshes as nurseries. Qualitative stomach analyses showed that the two most important benthic prey items for flounder were *Corophium volutator* and *Nereis diversicolor*. *D. labrax* preyed upon on wider range of species and the main prey items were *C. volutator*, *N. diversicolor*, *Crangon crangon*, *Carcinus maenas* and *Orchestia* species. In the diet of *Anguilla anguilla* oligochaetes, *C. maenas*, *N. diversicolor* and *Orchestia* spp. were important. Both the stomach content diversity of *D. labrax* and *P. flesus* showed differences between the five marshes. The stomach content diversity indices of flounder in Waarde were generally lower and differed significantly from Saeftinghe and Zuidgors, which had similar indices. *D. labrax* had significantly different diet diversity indices between Waarde and Zuidgors although no typical species change could be attributed to the observed patterns. The fullness indices of the stomachs of the flounder and seabass in the marshes along the salinity gradient did not show significant differences indicating that these two species find similar foraging opportunities in all areas. The similar high macrobenthic stock in all five marshes also supports this conclusion. The minimum consumption of flounder, seabass and European eel from the macrobenthic stock showed that these predators do not control the marsh infauna. The food was abundant and the availability of the potential prey did not restrict the utilization of the marsh creeks by fish. No correlations were found between the abundances of macrobenthos and fish. The very high abundances of the benthic food items might contribute to the fact that the typical nursery species like *C. crangon*, *C. maenas*, postlarvae of *P. flesus* and *D. labrax* and *Pomatochustus microps* were not preyed upon significantly. The spatial or temporal segregation of these species from the predator fish increases the survival of the former and support the hypothesis that marsh creeks offer good refuge opportunities.

Marsh age as an influencing factor on marsh habitat value

During the maturation process, the physical and chemical characteristics of a marsh system change constantly which consequently influence the potential of an area as a habitat for fish and macrocrustaceans. **Chapter 7** (in press, ICES Journal of Marine Science) aimed to compare a mature and developing marsh creek as a habitat for nekton species. The objective of the study was to investigate whether there are differences in utilisation of a mature and a developing marsh creek. The null-hypotheses were as follow: 1- There is no difference in total and species densities between the two areas. 2- Biomass of nekton species did not differ in the mature and developing marsh creek. 3- Common gobies exhibit similar growth during the sampling period in the two areas. To investigate the effect of marsh age on the nursery function, a mature (Saeftinghe) and a developing marsh (Sieperda) of the Westerschelde estuary were sampled between April and October 1999. Density and biomass of nekton species and the length-frequency distribution of the most common marsh fish, *Pomatoschistus microps* were recorded. The densities of the main nursery species (*P. microps, Dicentrarchus labrax, Crangon crangon, Carcinus maenas*) and the total nekton density were higher in the mature marsh although no significant difference was found. In Saeftinghe, a density peak was mainly due to large numbers of the mysid, *Neomysis integer*. In Sieperda, maximum abundance of the mysid, *Mesopodopsis slabberi* caused the peak density. This difference in species dominance was observed in all samples. Total and most species biomasses were significantly higher in the mature marsh. Mysid shrimp (*N. integer*) and fish (mainly *P. microps*) were the main contributors to the biomass in the mature marsh. Herring, sprat (Clupeidae) and shore crab, *Carcinus maenas* were more important in Sieperda. In the mature marsh the observed length of the juvenile common goby increased during the sampling period while in the developing marsh the length of the gobies remained small. These observations indicate that fish and macrocrustaceans do migrate in the developing marsh but the utilisation of the marsh creek is still less intense compared to the mature marsh.

1 Tidal marshes as habitats for aquatic organisms: their roles and factors influencing their usage

1.1 General characteristics of the intertidal marshes

1.1.1 Definition of salt marshes

Salt marshes are defined as areas with alluvial sediments deposited on the shore by the sea and subjected to tidal or weather-effected inundation by more or less diluted sea water. The moisture conditions of the soil vary from continuously waterlogged to at least temporarily moist. Salt marshes have soils with a chloride content varying in space and time and, consequently, are occupied by plant communities completely or mainly consisting of halophytes (Beeftink, 1977).

Salt marshes occur on intertidal shores in mid and high latitude regions worldwide (Kennish, 2001) since mangroves, which dominate the tropical zones, cannot survive temperatures below minus 4 °C. Marshes develop under the following conditions: (1) in the sheltered region behind offshore bars or islands, (2) in protected bays and (3) along the shores of estuaries protected from the major wave action (Chapman, 1974). European salt marshes are classified in several types. Different environmental conditions form the estuarine, the Wadden, the lagoonal, the beach plain, the bog and the polder-land types (Beeftink, 1977).

1.1.2 Development and characteristics of the marshes

Several factors influence the salt marshes and control their development such as, tidal characteristics, surface drainage, pedological conditions, sediment accretion, wave and current action, erosion, fresh water inflow, salinity, nutrient concentrations, shoreline structure and marsh topography (Mitsch and Gosselink, 1993; Lewis, 1994; Eisma, 1998).

The formation of the salt marshes starts with sediment acceleration on a sheltered shore where a few vascular plant species may establish (Figure 1). As the surface rises the profile of the cross-section becomes more concave with elevated creeks, low-lying marsh flats and other plant species establish themselves (Beeftink, 1988). Accretion of the sediment may continue further raising the surface. Completion of this process may take several years. The rate of saltmarsh formation is determined by the degree of protection that the site is afforded and the supply of sediment (Long and Mason, 1983). During a marsh development, physical (e.g. sediment accretion, formation of physiographic features), chemical (e.g. soil inorganic and organic composition) and biological (e.g. vegetation and faunal composition) characteristics change.

Several typical features characterise the salt marshes. Hydrology is considered the single most important factor in the development and functioning of wetlands (Mitsch and Gosselink, 1993; Reed, 1993). Salt marshes are affected by both the above-ground and underground water regime. Tides and rainfall affect the conditions above ground. The rainfall is an important factor as it inundates enclosed depressions and influences the salinity of the surface soil. Tides influence the zonation pattern of the vegetation in local or regional (Beeftink, 1977). The flow of water within the estuarine/salt marsh system influences the sedimentation, distribution of suspended materials, flux rates of materials between the estuary and the adjacent water, movement of the biota and erosional processes (Vernberg, 1993; Rozas, 1995).

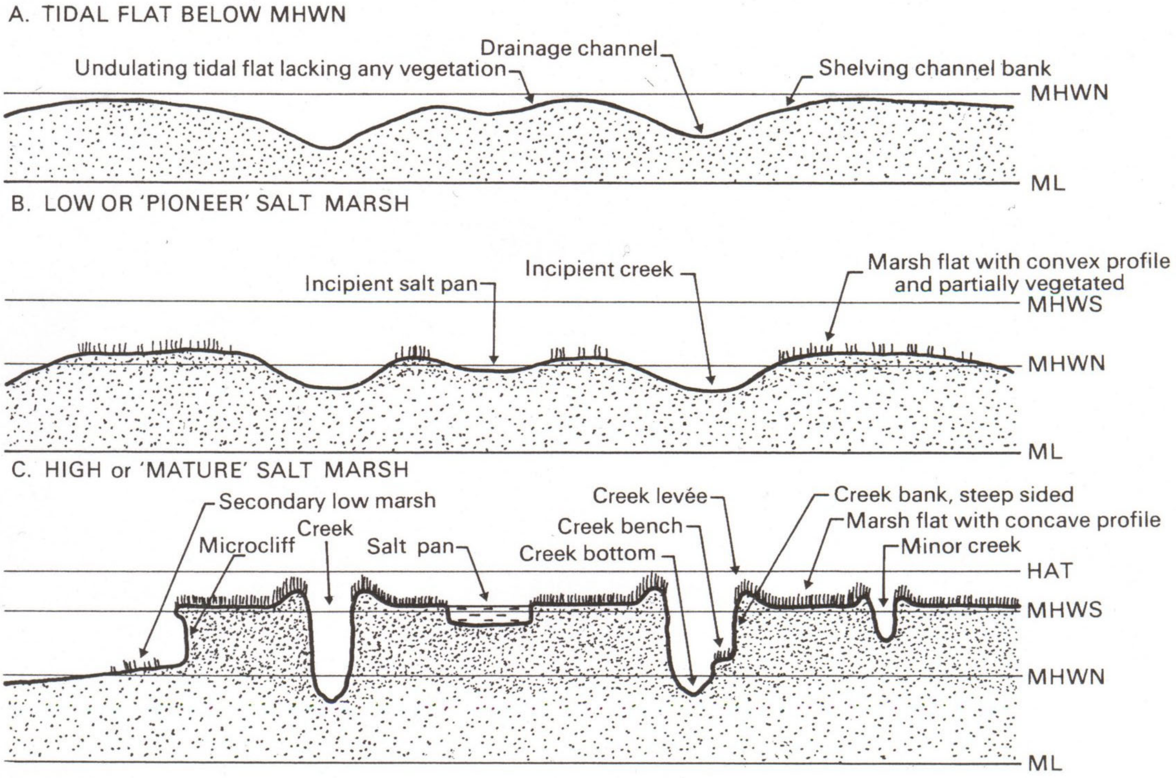

Figure 1. Cross sections of saltmarsh and tidal flat illustrating physiographical features and a hypothetical sequence of saltmarsh development, after the description of Beeftink (1966) and Steers (1977), and flowing the nomenclature of Teal (1962). (A) High level tidal flat. (B) Low level marsh in which plants have colonised the higher points of the tidal flat. (C) high marsh with a fully vegetated surface, except for the creeks and pans (Long and Mason, 1983).

The basic effect of waterlogging in the salt marsh is that oxygen supply is limited and the soil will become anaerobic (Armstrong, 1976). Under these conditions microbial populations develop which make use of electron acceptors other than oxygen for their respiratory oxidations. This results in the conversion of numerous compounds into a chemically reduced state, which is reflected in a lowering of the redox potential of the whole soil (Long and Mason, 1983).

The sediment is transported by the tide and the relative rates of sediment accretion and coastal submergence determine the long-term stability of salt marsh system (Mitsch and Gosselink, 1993). The soil type influences the affinity of various chemical substances to the sediment and the biotic composition of different regions of a salt marsh (Vernberg, 1993). The nutritional state of salt marsh soils depends on series of external and internal processes: input of nutrients, spatial distribution of these nutrients, mineralisation and humification in organic materials, fixation of nutrients onto particles and living materials and output of organic debris offshore all belong to these processes (Beeftink, 1977). Besides mineral particles, marsh soil consists of carbonates and organic matter. Organic matter levels of the soil are very variable but frequently low, although often increasing with elevation (Gray and Bunce, 1972). The organic matter content may decrease with the estuarine gradient. In the Schelde estuary a decrease of one third of the total amount from the mouth upwards to the oligohaline zone was detected (Beeftink, 1965). However, in the salt marshes of the United States (US) sediments typically contain less organic carbon than sediments of tidal freshwater marshes due to the greater annual inputs of riverine and terrestrial carbon (Odum, 1988).

In the salt marshes, the average salinity in the overlying water is in the range of 5-38 psu (Boaden and Seed, 1985). The salinity of surface and soil water varies depending on a number of factors such as rainfall, fresh water input, tidal flooding, evapotranspiration, soil type and vegetation (Vernberg, 1993). In the lower salt marsh soil salinity is relatively constant and exceeds that of the flooding water. At higher elevations, there is an interaction between the influence of flooding and climate, leading a greater variability in soil salinity (Adam, 1990). Along the Western European coast, annual precipitation exceeds annual evapotranspiration, and thus flooding of the marsh mostly results in an input of salt. In many places, however, high evaporation during summer causes the salinity to rise to extremely high values in the surface soil (Beeftink, 1977).

1.1.3 Flora and fauna of salt marshes

1.1.3.1 Flora

Higher salt marsh plants are considered to have developed secondarily and to have ancestors from terrestrial origin. In this secondary evolutionary process the plants tolerate to both the increased soil salinity and the effects of flooding. The majority of salt marsh species have a very wide environmental tolerances (Beeftink and Rozema, 1988).

Salt marsh species composition always varies with elevation (Dijkema, 1984; Adam, 1990; Vernberg 1993): a bare seaward mud or sand flat, then an area of low-growing vegetation that leads to an upland vegetation. The regularly flooded low marsh is characterised with low species diversity and the irregularly flooded high marsh with a higher number of vascular plant species (Niering and Warren, 1980). The salt marsh vegetation further changes with the maturation of the marsh (Long and Mason, 1983) or along the salinity gradient of the estuary (Huiskes, 1988).

The United States (US) salt marshes are dominated by *Spartina* species. Especially the smooth cord grass (*Spartina alterniflora*) inhabits vast areas of salt marshes (Adam, 1990). The smooth cord grass is a native species on the US Atlantic coast but is considered to be a non-native invasive plant on the US Pacific coast.

Spartina species also occur in the Western-European salt marshes. In the United Kingdom (UK) four cord-grass species inhabit the intertidal areas: *Spartina maritima*, *S. alterniflora*, *S.* x *townsendii* and *S. anglica.* The only native species is *S. maritima*. *S. anglica* arose during the end of the nineteenth century in England by hybridization between the indigenous *Spartina maritima* and the introduced East-American *Spartina alterniflora* (Baumel *et al*., 2001). *Spartina alterniflora* was possibly introduced by ships' ballast water from America and rapidly wide spread in Europe. The spread of *Spartina anglica* over the last century has altered salt marsh ecology in northern Europe. This species is more tolerant of tidal submergence and thus colonised mudflats. Consequently the area of mudflats has been reduced replacing the large mudflat fauna by a monoculture of *S. anglica* with few associated animals (Adam, 1990).

In Europe, besides *Spartina* species, marsh vegetation is dominated by several plant communities (e.g. community of *Salicornia europea, Sueda maritima, Puccinellia maritima, Triglochin maritima, Atriplex hastata, Aster tripolium, Scirpus maritimus, Phragmitis australis* etc.) (van Shaik *et al*., 1988) (Figure 2). These plant species form a dense vegetation, which covers the marsh surface. The proximity of the plant stems does not leave space for fish and macrocrustacean to venture deep into the marsh. This fact also contributes to the differences in utilization of habitats by nekton in the US and the European salt marsh.

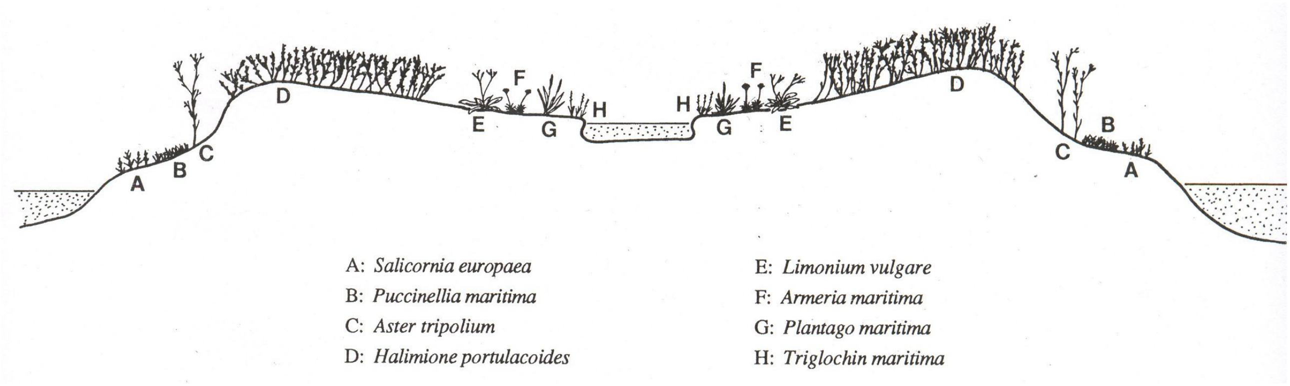

Figure 2. Variation of vegetation associated with microtopography variation on a European saltmarsh (after Adam, 1990).

1.1.3.2 Fauna

Like most highly variable systems, in the salt marshes the faunal species diversity is low and few species occur in high numbers (Nixon and Oviatt, 1973). The salt marsh fauna can be subdivided in various ways: taxonomically, by ecological affinity (e.g. marine, freshwater, terrestrial species), trophically (e.g. primary or secondary consumer), by subhabitat (marsh creek, pond, vegetated surface) occupied or by residence status (permanently resident, visitor) (Adam, 1990). The salt marsh fauna is predominantly marine with affinities to mud and sand-flat communities. The open pioneer zone of salt marshes and the floor of creeks provide an extension of the estuarine mudflat habitat with a basically similar fauna (Jackson *et al.*, 1985). The vegetated salt marsh surface represents a range of microhabitats for fauna (e.g. rooting zone, soil surface under the vegetation) (Adam, 1990). Several species migrate in and out with the tide using the marsh creeks, which include several crustaceans and fish (Boaden and Seed, 1985).

In the US, fauna composition in the salt marshes is well studied. In the east coast of the US, three main macrofaunal taxa (Polychaeta, Bivalvia and Crustacea) were reported by Mannino and Montagna (1997). The most dominant macroinfauna species in the US marshes are the polychaeta *Streblospio benedicti* (Minello *et al.*, 1994; Mannino and Montagna, 1997; Alphin and Posey, 2000), *Heteromastus filiformis*, *Capitella capitata* (Minello *et al.*, 1994; Havens *et al.*, 2002), *Laeonereis culveri* and *Neanthes succinea* (Lerberg *et al.*, 2000), the bivalves *Mulinia lateralis* (Mannino and Montagna, 1997), the crustaceans *Ampelisca abdita* (Mannino and Montagna, 1997), *Orchestia* spp. (Alphin and Posey, 2000), *Gammaridae* spp. (Angradi *et al.*, 2001), the oligochaeta *Tubificoides* spp. (Alphin and Posey, 2000) and the isopods *Cyathura polita* (Angradi *et al.*, 2001).

North American marshes are inhabited by a high number of nektonic, mainly fish species. *Palaemonetes pugio* (Kneib, 1984; Rozas and Reed, 1993; Kneib and Knowlton, 1995; Hanson *et al.*, 2002), *Palaemonetes vulgaris* (Rountree and Able, 1992a) *Callinectes sapidus* and *Uca* spp. (Minello, 1999; Rozas and Zimmerman, 2000; Hanson *et al.*, 2002), *Penaeus* spp. (mainly *P. aztecus*) (Kneib, 1984; Hettler, 1989; Rountree and Able, 1992a, Rozas and Zimmerman, 2000) are the main nektonic crustacean species. From the east coast of the US, Able *et al.* (2001) reported 40 species, Rountree and Able (1992a) found 64 species in a marsh creek, Baltz *et al.* (1993) found 57 fish species in microhabitats of a Louisiana marsh. The most common fish species are *Mugil* spp. (Weinstein *et al.*, 1980; Rozas and Reed, 1993; Rozas and Zimmerman, 2000), *Menidia* spp. (Rountree and Able, 1992a), *Gobiosoma* spp. (Weinstein *et al.*, 1980; Rozas and Reed, 1993), *Leiostomus* spp. (Weinstein *et al.*, 1980; Weinstein and Brooks, 1983; Rountree and Able, 1992a; Rozas and Zimmerman, 2000). *Fundulus* spp. dominate the marshes in the US where *F. heteroclitus* is the most common at the east-coast marshes (Kneib, 1984, 1986; Hettler, 1989; Hanson *et al.*, 2002). Some other *Fundulus* species such as *F. grandis* (Rozas and Zimmerman, 2000), *F.*

pulverous and *F. similis* also inhabit the east coast marshes although with lower density and less widespread (Rozas and Reed, 1993). *F. parvipinnis* dominates the southern California marshes (Desmond *et al*., 2000). At the west coast of the US, Desmond *et al*. (2000) found only 11 species inhabiting marsh creeks (e.g. *Clevelandia ios, Gillichthys mirabilis, Fundulus parvipinnis*). *G. mirabilis, F. parvipinnis, Mugil cephalus* were still reported as dominant species by West and Zedler (2000).

The West-European salt marsh macroinvertebrate fauna includes the crustaceans *Crangon crangon* (Cattrijsse *et al*., 1994; Costa *et al*., 2001), *Palaemon* spp. (Frid and James, 1989), *Orchestia gamarellus* (Frid, 1988; Lefeuvre *et al*., 2000), *Corophium volutator* (Jackson *et al*., 1985), *Uca tangeri* (Costa *et al*., 2001), *Carcinus maenas* (Frid and James, 1989; Costa *et al*., 2001) *Neomysis integer*, *Mesopodopsis slabberi* (Cattrijsse *et al*., 1994) all of which intensively use the salt marshes. The typical members of the macroinfauna are the molluscs *Macoma baltica* (Frid, 1988; Frid and James, 1989, Thorin *et al*., 2001), the polychaetes *Capitella capitata*, *Nereis diversicolor* (Jackson *et al*., 1985; Frid, 1988; Frid and James, 1989; Costa *et al*., 2001), *Pygospio elegans, Eteone longa* (Thorin *et al*., 2001) and Oligochaeta (e.g. *Tubifex* spp.) (Jackson *et al*., 1985; Frid, 1988; Frid and James, 1989).

In the Western European marshes, fish communities are dominated by few species. Lefeuvre *et al*. (2000) reported 23 fish species colonising the salt marshes in the Bay of Mont Saint Michel. Among these species *Liza ramada* and *L. aurata*, gobies (*Pomatoschistus minutus* and *lozanoi*) and *Dicenthrarchus labrax* were the most abundant. In a salt marsh of the Mira estuary, in Portugal, Costa *et al*. (2001) observed *Halobatrachus didactylus*, *Pomatoschistus* spp., *Solea vulgaris*, *D. labrax* and mullets (e.g. *Liza aurata, L. saliens, L. ramada, Mugil cephalus* and *Chelon labrosus*) as resident fish species utilizing the salt marsh as feeding ground. Similar species were found in salt marshes of the Westerschelde, The Netherlands, *Platichthys flesus*, *D. labrax, Pomatoschistus microps* and *Clupeidae* species (e.g. *Clupea harengus, Sprattus sprattus*) (Cattrijsse *et al*., 1994; Beyst *et al*., 1999). In the intertidal marsh of the Cadiz Bay, Spain, Drake and Arias (1991a,b) reported 39 fish species. The ten most abundant ones were *P. microps, Atherina boyeri, L. ramada*, *L. aurata*, *Sardina pilchardus, Engraulis encrasicholus, Anguilla anguilla, Syngnathus typhle, Liza saliens* and *Solea senegalensis*.

Some species like *Streblospio benedicti*, *Heteromastus filiformis*, *Capitella capitata, Carcinus maenas* (Frid and James, 1989; Rountree and Able, 1992a; Costa *et al*., 2001), *Rhitropanopeus harrisii* (Ruiz *et al*., 1993; Rozas and Minello, 1998; Minello, 2000, Meyer *et al*., 2001), *Mugil cephalus* and *Clupea harengus* (Drake and Arias, 1991a,b; Rountree and Able, 1992a; Cattrijsse *et al*., 1994; Szedlmayer and Able, 1996; Beyst *et al*., 1999; Able *et al*., 2001) were found both in the North American and European marshes. Other species probably occupy similar niches in the salt marshes for example *Fundulus heteroclitus* in the North American and *P. microps* in the European marshes (Cattrijsse *et al*., 1994; Laffaille *et al*., 2000).

1.1.4 Scientific investigations in the Westerschelde estuary focused on the marsh habitat

The delta of the Schelde River has been significantly modified after 1953 by the Delta Plan considering only the point of view of safety and flood control (Engels, 1989). Over the years ecological considerations have gained importance partly due to the accumulating knowledge of estuary functioning. These investigations cover a very wide range. Research have been carried out on the higher tropic level in the estuarine intertidal and subtidal areas focused on macrobenthic (Ysebaert *et al*., 1990; Ysebaert and Meire, 1991; Seys *et al*., 1997; Thoolen *et al*., 1997; Ysebaert, 2000), hyperbenthic (e.g. Mees and Hamerlynck, 1992; Mees *et al*., 1993; Mees *et al*., 1995;

Fockedey and Mees, 1997) epibenthic (e.g. Hamerlynck *et al*., 1993; Maes *et al*., 1997; Maes *et al*., 1998; Hostens, 2000) and bird communities (e.g. Meire *et al*., 1994; Schekkerman *et al*., 1994; Van den Bergh *et al*., 1998).

In contrast to the estuary subtidal and intertidal flat, salt marshes are hardly studied. Intertidal marshes are still found along the whole Schelde River up to the freshwater part. Nowadays the conservation of these areas is a high concern in estuarine management. For effective conservation and mitigation of marsh habitat loss, extensive research is required to describe the community structures, food web and to understand the functioning of these habitats. The vegetation coverage was described by van Schaik *et al*. (1988) providing detailed vegetation maps about several marshes along the Westerschelde estuary. However no extensive investigation has been done yet with respect to the macrobenthic community structure in the marsh creeks. The pioneering research of the marsh aquatic fauna started only at the beginning of the 90's. Cattrijsse *et al*. (1994) studied the nekton species in the mesohaline Saeftinghe, which is the largest saltmarsh left in Western Europe (Dijkema, 1984). They monitored the changes of the nekton community structure during a two-year period. Cattrijsse (1994) described the main species using the marshes as nursery habitats like *Crangon crangon*, *Carcinus maenas*, *Pomatoschistus microps* and *Dicentrarchus labrax* and investigated their feeding habit. Stikvoort and Winder (1998) studied the newly formed Sieperda marsh between 1995 and 1996 and gave a description of the development of this area focusing mainly on morphology and vegetation. Macrobenthic density and biomass was also assessed but no information was provided about hyper- and epibenthos. Stikvoort (2000) published another report about this marsh but information is very general about the marsh system. Van Oevelen *et al*. (2000) reported mainly the change of the physical characteristics of the realigned area like Sieperda marsh and compared to other marshes in the world. Verbeek and Storm (2001) also investigated the hydrology and morphodynamics of the newly formed Sieperda marsh but none of the mentioned work described the aquatic species that utilise the marsh habitat. Additionally no research has been done to describe the macro, hyper- or epibenthic communities in the freshwater marshes of the Schelde River. The lack of data about the aquatic fauna, their utilisation of the marsh habitat and the need of the better understanding of the functioning of the Westerschelde marshes made it essential to continue the research on this important area.

1.1.5 Functions of the intertidal marshes

1.1.5.1 Organic matter and nutrient transport

Bays and estuaries, their surrounding salt marshes and mudflats are among the most productive systems of the biosphere (Craft *et al*., 1988; Mitsch and Gosselink, 1993; Vernberg, 1993). In the US marshes, vascular plants annually generate an above-ground biomass of between 0.3 and 3.7 kg m^{-2}, with an equivalent or greater amount below ground (Mitsch and Gosselink, 1993). When other sources of primary production are considered, the total contribution of marshes to the productivity of estuarine systems in even greater. Marshes may contribute more to total ecosystem primary production than suggested by the absolute area they occupy within estuaries (Kneib, 1997b).

In the salt marshes, fluxes of particulate organic matter (POM), dissolved organic matter (DOM) and inorganic nutrients occur between salt marshes and coastal environments (Laffaille *et al*., 1998) however, the investigations of the energy flow through the salt marshes yielded different hypotheses. Teal (1962) studied the North American *Spartina alterniflora* salt marshes and concluded that the tides remove 45% of the production before the marsh consumers have a chance to use it and therefore it enables the estuaries to support an abundant fauna. This view contributed to the origin of the ‘outwelling’ idea, which stated that most fertile zones in coastal water are capable of supporting expanded fisheries result either from “upwelling” of nutrients from deep water or from “outwelling” of nutrients or organic detritus from shallow water traps (e.g. reefs, banks, seagrass beds, salt marshes) (Odum and de la Cruz, 1967; Odum, 1968; 1980). Several studies support the suggestion of an organic matter export from salt marshes (Teal, 1962; Nixon, 1980; Gordon and Cranford, 1994; Lefeuvre and Dame, 1994; Costa *et al*., 2001).

In contrast, other studies have indicated that the ‘outwelling’ paradigm does not occur worldwide. Even in the US, Hackney (1977) showed import of POM into the salt marshes and Dame (1989) also proved that *Spartina* marshes could act as sinks for nutrients. It is only since the 80’s that European researchers have participated in this debate. European studies indicated that macro-detritus mineralisation takes place almost completely within the marsh itself, which results in import of POM and nutrients (Vegter, 1975; Haines *et al*., 1977; Lammens and van Eeden, 1977; Wolff, 1977; Wolff, 1979; Woodwell *et al*., 1977; Dankers *et al*., 1984; Danais, 1985; Hemminga *et al*., 1992, 1993, 1996; Dame and Lefeuvre, 1994; Bouchard and Lefeuvre, 2000). These differences in POM or nutrient transport are mainly due to the fact that marshes differ in many ways in the US and in Europe. European salt marshes lie between the mean high water neap tide and the mean high water spring tide level (Beeftink, 1977; Lefeuvre *et al*., 1994), partly covered by pioneer vegetation, which floods only at high spring tides. While in the USA, marshes are situated at the mean tidal level and their surface is dominated by *Spartina alterniflora*, which floods twice a day providing large amounts of POM (Lefeuvre *et al*., 1999).

Studies indicated that organic matter and nutrient budgets depend on latitude, tidal amplitude, plant communities and geomorphologic characteristics of each individual system (Damme and Gardner, 1993; Lefeuvre and Dame, 1994). Primary production, horizontal turbulent mixing, marsh level, sinking and resuspension of particulate matter, biotic transformation (e.g. bacterial breakdown) during transport (Wolff *et al*., 1979) and the maturation status of the marsh (Dame and Allen, 1996) all influence the direction of the POM and nutrient transport. Therefore neither the hypothesis of POM exporting nor the importing can be generalised for every system.

Organic matter can be transported not only in the form of nutrient and detritus as mentioned above but also faunal species can be responsible for transport in river system (Elliott *et al*., 1997; Maes and Ollevier, 2000) and in salt marshes (Lefeuvre *et al*., 1999). Forman (1981) and Laffaille *et al*. (1998) showed that fish invade salt marshes during flood, forage there and export the ingested food to the coastal waters upon leaving the marsh part o. Not only fish but also macrocrustacean like *Crangon crangon* can be responsible for export of biomass from tidal marsh creeks (Cattrijsse *et al*., 1997). Fish and macrocrustacean thus act as biotic vectors of OM.

1.1.5.2 Salt marsh functions for nekton species

It is well known that many fish and macrocrustacean species spend part of their life in salt marshes and estuaries (Weisberg *et al*., 1981; Boesch and Turner, 1984). Transient nekton fauna comprise marine, freshwater and diadromous species. Permanent residents tend to be small (<150 mm adult size) and are usually represented by relative few species (Potter *et al*., 1990; Whitfield, 1990). Fishes use estuaries as pathways in migrations (McDowall, 1976; Pihl *et al*., 2002) as foraging grounds (Thorpe, 1994) and as nurseries (Elliott *et al*., 1990; Costa and Cabral, 1999; Hostens, 2000). The trophic function cannot be separated from the nursery role but this concerns also older as well as young individuals, which exploit an area as feeding ground for longer period

(Lefeuvre *et al.*, 1999). It is also difficult to determine the refuge role as habitat usage therefore this function is normally integrated as a part of the nursery function.

Tidal marshes are known to play a nursery role for many fishes and macrocrustaceans, including important commercially-fished species (Shenker and Dean, 1979, Weinstein, 1979; Minello and Zimmerman, 1983; Boesch and Turner, 1984, Davis, 1988; Drake and Arias, 1991b; Rountree and Able, 1992a; Cattrijsse *et al.*, 1994; Costa *et al.*, 1994; Rozas, 1995; Kneib, 1997a, Dionne *et al.*, 1999). Nurseries are defined as areas where juveniles aggregate and are spatially or temporally separated from the adults (Pihl *et al.*, 2002). Nursery habitats function in many ways to enhance the growth and survival in the early life stages of the species (Baltz *et al.*, 1993), which are known to increase recruitment success of the species (Rothschild, 1986).

The nursery function includes protection for young individuals through a lowered predation pressure (Shenker and Dean, 1979; Minello and Zimmerman, 1983; Boesch and Turner, 1984; Minello *et al.*, 1989; Thomas 1989; Kneib, 1993; Paterson and Whitfield, 1996; Whitfield, 1998; Halpin, 2000; Paterson and Whitfield, 2000; Costa *et al.*, 2001). Supporting these observations, generally fewer large piscivorous fish species were found in tidal marshes (Rozas and Hackney, 1984; Mathieson *et al.*, 2000). Different marsh habitats like the marsh edge (Zimmerman and Minello, 1984; Baltz *et al.*, 1993; Rozas and Reed, 1993; Peterson and Turner, 1994), vegetated surface (Minello and Zimmerman, 1983; Minello *et al.*, 1989; Thomas, 1989) and shallow areas (Gleason, 1986; Gleason and Wellington, 1988; Kneib, 1993; Halpin, 2000) could also function as nurseries. The turbidity in shallow water may be important to young fishes because it can provide a degree of protection from visual predators (Cyrus and Blaber, 1987). Especially this is the case in the European marshes where nekton is mainly restricted to the tidal channels. In these creeks the high turbidity (Cattrijsse *et al.*, 1994) provides the protection for nursery species.

Besides the protective function of a nursery area, salt marshes offer good foraging ground for several species (Gleason, 1986; Gleason and Wellington, 1988; Rozas and Odum, 1988; Allen *et al.*, 1994; Craig and Crowder, 2000; Laffaille *et al.*, 2002). Researchers observed that gut fullness of fishes (Butner and Brattstrom, 1960; Kneib and Stiven, 1978; Weisberg *et al.*, 1981; Currin *et al.*, 1984; Rozas *et al.*, 1988; Rozas and LaSalle, 1990; Rountree and Able, 1992b) and macrocrustaceans (Ryer, 1987; Fitz and Wiegert, 1991; Cattrijsse *et al.*, 1997) is greater on high or ebbing tides than during low or flooding tides. In the nursery area, growth rates of larval fish are positively related to flooding duration whereas mortality rates show a negative relationship. The higher growth rates and lower mortalities during longer flooding periods are attributed to increased prey availability (Kneib, 1993). Young aquatic predators migrating into intertidal creeks may enhance their access to prey that become concentrated within the marsh creek (Kneib, 1997b). Several transient nekton species feed on marsh fishes and invertebrates. Fish could prey upon infaunal marsh species (Kneib and Stiven, 1978), which additionally may structure the benthic community. Observations showed that fish guts contained a greater volume of marsh resident species at ebbing tide than did those collected during flooding (Rountree and Able, 1992b). In the US marshes, cyprinodontid fishes and palaemonid shrimp occur frequently in the stomach of estuarine predators (Rozas and Hackney, 1984; Smith *et al.*, 1984; Cadigan and Fell, 1985; Minello *et al.*, 1989; Juanes and Conover, 1995; Kneib, 1997b). In the Western-European marshes, among the predator fish species the seabass, *Dicentrarchus labrax* (Drake and Arias, 1991a, 1991b; Cattrijsse *et al.*, 1994; Gardner, 1996; Laffaille *et al.*, 1998, 2000; Costa *et al.*, 2001) and the flounder, *Platichthys flesus* (Gardner, 1996; Laffaille *et al.*, 2000) inhabit frequently at high densities the mudflats and the tidal marsh creeks. The diet of these predators comprises mainly macrocrustacean species (e.g. *Crangon crangon*, *Carcinus maenas*, *Neomysis integer*, *Orchestia gammarellus*) and annelids (e.g. *Nereis diversicolor*, Oligochaeta) (Kelley, 1988; Raffaelli *et al.*, 1990; Cattrijsse *et al.*, 1994; Gardner, 1996; Laffaille *et al.*, 2000) both occurring in high density in the marshes.

Even though salt marshes represent good refuge area for the visiting species, the lower predation risk is sometimes combined with lower food availability (Halpin, 2000). Fish tend to choose a lower predation risk over a higher food reward (Power, 1984, Holbrook and Schmitt, 1988). When predation risk is constantly high, growth rates play an important part in determining the habitat use (Halpin, 2000). Density of juveniles reflects recruitment, mortality and emigration, thus density of specific cohorts can be an important indicator of nursery habitat value (Minello, 1999; Minello *et al*., 2003). The relative nursery value of any habitat also could be obtained from analysis of diet (Rozas and LaSalle, 1990; Moy and Levin, 1991) bioenergetics (Deegan, 1993; Madon *et al*., 2001), ecophysiological responses (Miller *et al*., 2000), stable isotopes (Kwak and Zedler, 1997; Wainright *et al*., 2000) otholith microchemistry (Thresher, 1999; Gillanders and Kingsford, 2000) and trace elements in body tissue (Courtney *et al*., 1994).

1.2 Factors influencing the marsh faunal assemblage and the feeding habit of some fish species

1.2.1 Influence of short-term temporal changes (tidal, diel and lunar cycle)

Long-term temporal changes of the marsh fauna are well studied. Several investigations deal with long term seasonal changes of macrobenthic communities (e.g. Wiltse *et al*., 1984; Jackson *et al*., 1985; Frid and James, 1989; Sarda *et al*., 1995) and nekton assemblages (Kneib, 1984, 1997a; Hettler, 1989; Drake and Arias, 1991a; Cattrijsse *et al*., 1994; Costa and Cabral, 1999; Desmond *et al*., 2000; Minello, 2000; Hanson *et al*., 2002). There are fewer studies which focus on short-term temporal changes like the influence of tidal, diel and lunar cycle. The major characteristic of wetlands is that they are subjected to periodical inundations by the tides (Beeftink and Rozema, 1988). The hydrology of each estuarine marsh produces a hydroperiod or pattern of marsh flooding. Marsh hydroperiod controls habitat use by nekton, because most natant organisms can occupy the marsh only when it is flooded (Rozas, 1995). Several species migrate into the marsh with flood where they forage (Rozas and LaSalle, 1990) or seek refuge. The diurnal or nocturnal lifestyle of several species (Gibson, 1993) may also influence the faunal composition and feeding habit of some species in the intertidal marshes. The lunar cycle is the third short term cycle which determines the availability of marsh habitats through the duration and frequency of the floodings. At neap tide, a smaller area for a shorter period will be flooded than during spring tide (Long and Mason, 1983), which can influence the utilisation of the marsh by the visiting species. Investigations are scarce about the influence of diel and lunar cycles on the community structure and feeding habit of nekton. Moreover prior to this study no integrated work exists, to investigate the combined effect of the three concurrent cycles.

1.2.1.1 Tidal cycle

Pulses of tidal flooding, which characterise the hydrology of estuarine marshes, produce a multitude of wetland functions, including the exchange of nutrients, sediments, organic material and biota between the marsh and the rest of the estuary (Rozas, 1995). Tidal migration is a well-known phenomenon in the estuaries where fish species use the tides in order to forage on the intertidal sand, mudflats or to enter intertidal salt marsh creeks as the tide floods (Elliott *et al*., 2002). In the salt marsh areas, the hydroperiod is also one of the main factors governing the utilisation of marshes by nekton species (Zimmerman and Minello, 1984; Rozas and Reed, 1993; Rozas, 1995). Not all species arrive at or depart from the intertidal marsh at the same time but maximum use of the marsh by nekton occurs around high tide (Kneib and Wagner, 1994). This suggests that during the tidal migration, individuals enter into the marsh at an early tidal stage and leave late in the tidal cycle, which allow maximisation of their habitat use (Kneib and Wagner, 1994). Studies showed this type of tidal migration of fish (Perschbacher and Strawn, 1986; Cattrijsse *et al.*, 1994; Kneib and Wagner, 1994) and macrocrustaceans (Al-Adhub *et al.*, 1975; Fitz and Wiegert, 1991; Cattrijsse *et al.*, 1997).

Tidal migration of the species is the result of seeking foraging area (Craig and Crowder, 2000) or protection. Several fish species like *Fundulus heteroclitus* (Butner and Brattstrom, 1960; Weisberg *et al.*, 1981; Rozas *et al.*, 1988; Allen *et al.*, 1994; Kneib and Wagner, 1994) *F. grandis* (Rozas and LaSalle, 1990), *F. diaphanous* (Rozas *et al.*, 1988) *Leiostomus xanthurus* (Miller and Dunn, 1980) *Bidyanus bidyanus* (Kleypas and Dean, 1983) and *Pomatoschistus microps* (Cattrijsse *et al.*, 1994) following the flooding tide into the marsh had empty guts, while the guts of individuals returning to deeper water on the ebb tide were filled. A maximum consumption is reached at the first hour of ebb (Cattrijsse *et al.*, 1994). A similar result was also found with macrocrustaceans (Ryer, 1987; Fitz and Wiegert, 1991; Cattrijsse *et al.*, 1997). This pattern suggests that the feeding habit of several marsh visiting nekton species is strongly tide dependent.

1.2.1.2 Diel cycle

Species numbers can change according to the diel variation. Night time counts can be characterised by marked reduction or complete absence of day-time observed fish species in a marsh (Shenker and Dean, 1979) or in a mangrove habitat (Rooker and Dennis, 1991). Several fish (Reis and Dean, 1981; Rooker and Dennis, 1991; Rountree and Able, 1992b) and macrocrustacean (Fitz and Wiegert, 1991; Kneib and Wagner, 1994) also exhibit diel variation in their abundance.

The diel differences in abundance of some species are partly attributed to their reproductive cycles. Queiroga *et al.* (1994) observed that change of the abundance of first stage *Carcinus maenas* with the tidal and diel cycles was the result of synchronous larval-releasing activity. Reproductive cycles can cause diel abundance differences although these differences are mainly linked to the feeding habit of the species. Species can be more active to search for food during daylight or the night (Vance, 1992; Burrows *et al.*, 1994). Kneib and Wagner (1994) suggested that nocturnal activity patterns allow nekton to forage in relative safety from visually oriented predators. Opposite to this observation, other studies suggested that if fish search for their prey especially by sight (Hesthagen, 1980), foraging at dusk becomes more difficult. The typical marsh visiting fish species in the Western European intertidal marshes is *Pomatoschistus microps*, which has been described as a daytime active fish (Magnhagen and Wiederholm, 1982; Antholz *et al.*, 1991). *Fundulus heteroclitus*, in the US east coast marshes, was found also to feed more during daylight (Weisberg *et al.*, 1981).

Investigating the dominance of the tidal and diel cycles, Baker-Dittus (1978) presented evidence that the diel feeding cycle of *Fundulus heteroclitus* was not correlated with tidal rhythms. Weisberg *et al.* (1981) also found that the tidal rhythms were more important than the diurnal rhythms in controlling feeding chronology of *F. heteroclitus*. Domination of diel cycle over the tidal rhythm would result a loss of several foraging opportunities (Kneib and Wagner, 1994) and increase utilization of planktonic and subtidal prey (Baker-Dittus, 1978).

1.2.1.3 Lunar cycle

The lunar cycle covers the period from one spring tide to another through the neap tide period. These tides bring different amounts of water to the marsh, which may affect the number of individuals migrating to the creeks, the size of the flooded area and like this the food availability (Long and Mason, 1983). Investigations about the effect of the lunar cycle on the abundance and feeding habit of marsh faunal species are scarce in Europe as well as in the US.

Short-term temporal variation of fish and macrocrustacean abundance in intertidal marsh has been reported by a few scientists (Shenker and Dean, 1979; Fitz and Wiegert, 1991; Kneib and Wagner, 1994). In other habitats, like a small mangrove bordered estuary (Quinn *et al.*, 1981) or a mangrove habitat (Rooker and Dennis, 1991) there was little evidence for lunar periodicity in species abundance. However other observations indicated that the abundance of some fish species was associated with the lunar cycle in a swamp habitat (Davis, 1988). This author found that higher tides provide greater assistance for the movement of juvenile fish to upper in a marsh and also enable them to penetrate further. So if fish rely on tides for transport into the marsh they may benefit from higher tides. And, as a consequence, short-term changes in the composition of the fish fauna can, in part, be attributed to the flood of spring tides and the maximum height of these tides when they enter the marsh.

During the lunar cycle the reproductive activity may influence the occurrence of some species in the intertidal area. The reproductive cycle of *Fundulus heteroclitus* was linked with the lunar-tidal cycle (Taylor, 1986; Taylor *et al.*, 1979; Kneib, 1986) and other species like *Carcinus maenas* also exhibited semi-lunar periodicity of larval release (Queiroga *et al.*, 1994), which may determine the presence of these species in the marshes.

The influence of the lunar cycle on the feeding intensity of marsh visiting fishes has been little studied. Morton *et al.* (1987) reported that feeding index values for most of the salt marsh visiting fishes were higher when the water depth was the highest because larger areas of salt marshes were then available for extended periods. In the estuary, Hamerlynck *et al.* (1993) observed that the feeding intensity of *Pomatoschistus lozanoi* was related to the spring-neap tide and Morgan (1990) found that the prey abundance of this species may be determined by the same cycle.

1.2.2 Spatial elements influence the marsh habitat functioning

1.2.2.1 Large scale spatial variation: Marshes along the salinity gradient

Intertidal saltmarshes function similarly in US and Europe. They act as pollution filter (Hazelden and Boorman, 1999), flood control, they can export organic matter to the adjacent coastal area (Teal, 1962; Lefeuvre and Dame, 1994) and provide nursery ground of young individuals (Davis, 1988; Cattrijsse *et al.*, 1994; Rozas, 1995; Dionne *et al.*, 1999). Besides the similarities same differences can be observed between the European and North American marshes. In the vertical range of a European estuary, from about the level of the mean high water neap tide the mud flats are colonised by terrestrial halophytic vegetations, first *Salicornia* and *Spartina* species. The upper marsh limit is found between the levels of mean high water spring and extreme high water spring (Beeftink, 1977). In contrast, North American marshes are situated lower at the vertical level and the low marsh already appears at the mean high water level. As a result of the difference in the vertical position marshes in the US are flooded twice per day. In Europe marsh surface is covered by water irregularly only during the high spring tide. This characteristic defines the period when marsh surface is available for visiting species. The difference in flooding periodicity can also affect the water supply of the marsh pond habitat and consequently their utilisation by nursery species. *Spartina* species dominate the US salt marshes. Especially the smooth cord grass (*Spartina alterniflora*) inhabits vast areas of salt marshes (Adam, 1990). This plant typically forms monoculture vegetation in the salt marshes. Typical structure of this vegetation is the space between the stems of *S. alterniflora* leaving enough area for faunal species to move between the stems. The type of vegetation strongly influences and structures the faunal community invading this habitat. The vegetated marsh surface is intensively used by fish and macrocrustaceans to forage and seek refuge between the *S. alterniflora* stems (Rozas and Odum, 1987a, 1988; Kneib and Wagner, 1994). In contrast to the US marshes, in Europe the vegetation is diverse including *Halimione*, *Limonium*, *Plantago*, *Armeria*, *Triglochin* species (Beeftink, 1988). These species form a dens vegetation structure on the marsh surface, which restrict the mobile species to venture far from the marsh creek. All these dissimilarities contribute to the differences in the marsh habitat utilisation by nursery species in Europe and North America.

On a smaller scale like an estuary, distribution and abundance of species in estuarine and coastal environments are determined by physical, chemical factors (e.g. salinity, temperature, dissolved oxygen, water transparency, tidal cycles, wave action and wind) (Blaber and Blaber, 1980) and biotic factors (e.g. migration, reproduction, feeding and habitat selection) (Morin *et al.*, 1992). Most researchers found that the effects, which causes the distribution of hyper- and epibenthic species in estuaries are combined (Elliott and Taylor, 1989; Mees and Hamerlynck, 1992; Mees *et al.*, 1993; Maes *et al.*, 1998; Hostens, 2000).

By definition the major characteristic of an estuarine system is the variation in the distribution of salinity (King, 1995). Bulger *et al.* (1993) emphasized that organisms in the coastal wetlands are affected by spatial and temporal dynamics of salinity. Physiological tolerance to salinity and other physiochemical parameters, and life-history strategies determine how animals respond to heterogeneity and dynamics of coastal wetlands. Salinity influences the occurrence of several crustacean species (Sorbe, 1981; Williams and Collins, 1984; Mees and Hamerlynck, 1992; Mees *et al.*, 1993; Moffat and Jones, 1993; Köpcke and Kausch, 1996). Salinity is also considered one of the major factors to define the fish communities in the estuaries (Cyrus and Blaber, 1992; Marshall and Elliott, 1998). Since the fresh-brackish water part of the estuary is a transition zone for several fish species this limits the penetration of fish further into the estuary because of osmo-regulatory problems (Green, 1968).

The general species distribution patterns in an estuary were defined by Remane and Schlieper (1971). The number of species is high in the euhaline part of the estuary dominated by marine species. Absolute values of 5-8 psu appear to represent a critical salinity for many species and mark the area of minimum species richness. The number of species increases again from the freshwater area, which is inhabited mainly by freshwater species. A linear model was suggested by Attrill (2002) to describe the relationship between salinity range and meio- and macrofaunal diversity. He found a similar high diversity in the euhaline and fresh-water part of an estuary and a lower diversity in the brackish part. Opposite to these observations, this pattern was not proved in several estuaries and studies showed a decrease in benthic (Elliott and Taylor, 1989; Ysebaert *et al.*, 1993) and epibenthic (Maes *et al.*, 1998) species number towards the upstream part.

Salinity patterns have been shown to affect nekton growth (Baltz *et al.*, 1998), survival (Weinstein and Walters, 1981) and productivity (Ford and St. Amant, 1971) in the salt marsh. Salinity changes in estuaries have been indicated to coincide with changes in the distribution and abundance of young nekton in the intertidal marshes (Weinstein *et al.*, 1980; Zimmerman *et al.*, 1990 a, b). In the US, researchers found that salinity had a strong association with fish assemblages along a spatial gradient in a marsh network system (Rakocinski *et al.*, 1992; Gelwick *et al.*, 2001). The salinity regime also affects nekton density patterns and the nursery value of the marshes

(Minello *et al*., 2003). In Europe, there have been no studies on this topic although salinity might be hypothesised to be an important environmental parameter structuring marsh faunal communities and influencing the use of the intertidal marshes by nektonic species.

1.2.2.2 Small scale spatial variation: Habitat differences within a marsh

Coastal salt marshes have several typical structural features (Figure 3). The surface is dissected by a dense network of creeks, often dotted with small pans and may include small cliffs or ridges (Long and Mason, 1983; Kneib, 1997b) which offer different habitats for marsh species. The term habitat has been used generally to mean a location where animals live (Minello *et al*., 2003). The different structural characteristics such as creeks, ponds, vegetated surface etc. have different potentials for creating a foraging and refuge area for marsh faunal species, which define the species composition inhabiting a particular marsh habitat.

An early theory was the ideal free distribution concept which Fretwell and Lucas (1970) predicted that organisms would forage in those habitats that provide the highest energetic return as mediated by intraspecific competition. This theory was reconsidered since the ability of organisms to forage optimally is frequently prevented by strong negative interactions with competitors and predators (Werner and Hall, 1988; Lima and Dill, 1990; Peckarsky *et al*., 1993; Turner, 1996). Habitat heterogeneity modifies the outcome of biological interactions such as competition and predation and directly influences foraging behaviour and predator avoidance (Irlandi and Crawford, 1997). Species choose a habitat balancing between predation risk and food reward in order to maximise their growth rate. Similarly a habitat, which offers refuge from predators may offer lower food availability and thus compromise the growth of the individual (Holbrook and Smith, 1988). Since intertidal nekton species are highly mobile they are able to respond to environmental changes and use those habitats in which their growth is maximised (Halpin, 2000). To measure the habitat quality for nekton Minello *et al*. (2003) suggested using habitat specific estimates of survival of nekton species.

In contrast to European research, in the US, investigations have been focused on different marsh habitats. In Europe, the surface of these marshes is flooded only at high spring tides, which restricts species to forage and seek refuge in the creek system. The few occasional floodings of the marsh surface result an infrequent water supply to marsh ponds. This may reduce the species numbers and density in these ponds. Due to these characteristics salt marsh faunal research in Europe has focused mainly on large marsh creeks and investigations considering other habitats are rare (Frid, 1988). However other habitats can be important for some species as nursery or feeding grounds and their utilisation could influence their survival in the marshes.

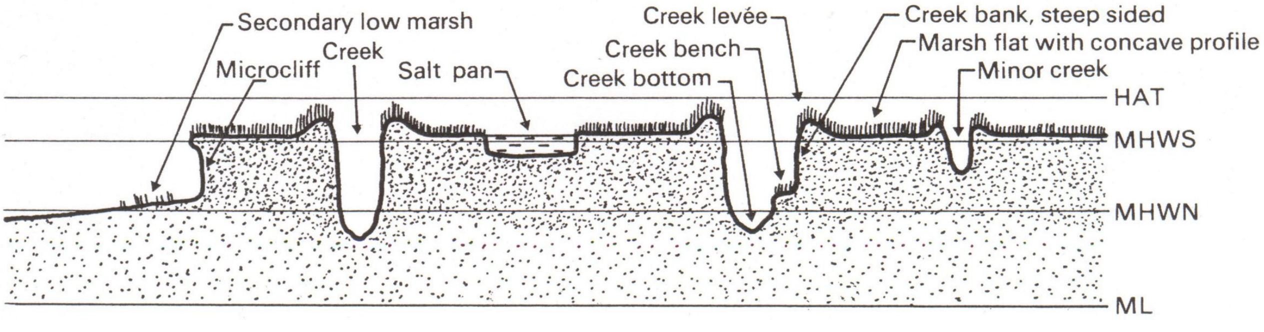

Figure 3. Cross section of a European saltmarsh illustrating physiographical features after the description of Beeftink (1966) and Steers (1977) and following the nomenclature of Teal (1962). HAT-Highest Tide Level, MHWS-Mean High Water Spring Tide, MHWN-Mean High Water Neap Tide (Long and Mason, 1983).

1.2.2.2.1 Creek network

Chapman (1960) identified the creeks and the pans as the principal physiographic features of natural tidal marshes (Figure 4a). Large channels maintain an open connection with the sea or estuary (Kneib, 1997b). Creek channels are the major conduits for the bi-directional flow of tidal water through the marsh system and their drainage patterns depend on the underlying sediments, slope of the intertidal zone, vegetation type and marsh age (Frey and Basan, 1978). The creek network supplies water and sediment to the salt marsh surface and for this reason it has a fundamental importance to the morphological and ecological evolution of the entire salt marsh (Fagherazzi, 2001). For nekton species, channels provide access to the marsh surface (Rozas *et al.*, 1988), pathways for migration, links for species using multiple habitats and transition areas for larvae and juveniles (Williams and Desmond, 2001). Sites with complex networks of channels appear to be used more by fishes than areas with low drainage density (Kneib, 1994).

Tidal creeks can be classified by the concept of stream order. A first stream order creek is defined to have no tributaries. Second order creeks are formed by the joint of two first order channels. The fusion of two second order creeks create the third order channel (Odum, 1984). Tidal creeks of the same stream order have similar physical attributes such as temperature, salinity (Hackney *et al.*, 1976) width, depth, drainage basin size, which all influence their physicochemical and biological properties (Rozas and Odum, 1987b). Therefore nekton communities could vary among marshes of different stream orders (Rozas and Odum, 1987b). The low oxygen environment and the higher temperatures in the smallest intertidal creeks may restrict their use by fish (Desmond *et al.*, 2000). Other observations in the US showed that fish and macroinvertebrates concentrate in the upper reaches of tidal creeks where the creeks become more shallow and narrow in a tidal freshwater area (Rozas and Odum, 1987b) and in a salt marsh (Weinstein, 1979). The factors of importance in this relationship may be the absence of predators in the upper reaches of tidal creeks because of unfavorable physicochemical conditions and/or the physical constraint of shallow water (Shenker and Dean, 1979; Rozas and Hackney, 1984). Another concept is that detritus is concentrated at the head of the marsh creeks (Odum, 1984) and the concentration of fish at the creek headwaters may be a response to high densities of prey that are selecting areas rich in detritus (Rozas and Odum, 1987b).

(a) (b)

Figure 4. Creek network system (a) and marsh ponds situated on the surface of the marsh.

1.2.2.2.2 Marsh microhabitats (ponds, pools and seepage water)

Intertidal creeks rarely drain completely and water continues to trickle from the channels (seepage water) until the next flood. These modest flows often link a series of permanent intertidal pools along the length of the channel. These marsh pools are formed generally in the depressions of a creek or adjacent to the marsh channels. High marsh ponds or pans are permanent or semi-permanent shallow aquatic habitats imbedded within the tidal landscape (Figure 4b). In the literature, sometimes the distinction between the pond and the pool is not clear and the term of 'shallow aquatic microhabitats' is also used.

Populations of nekton, largely resident species, may remain within intertidal pools and shallow flows of creek channels over low tide (Kneib, 1997b). The physical environment of marsh pools can be extremely variable and only a few species have the tolerance to withstand the changes of salinity (Griffith, 1974), temperature (Bulger, 1984), oxygen (Cochran and Burnett, 1996), and sulphide concentrations (Bagarinao and Vetter, 1993). The nekton assemblage included only less than six species in the pools of the North American marshes (Smith and Able, 1994; Rowe and Dunson, 1995) and these species utilised this habitat intensively. These aquatic microhabitats in low-lying areas are important nurseries for the resident nekton of some regularly flooded tidal marshes (Kneib, 1984, 1987, 1997a; Talbot and Able 1984; Smith and Able, 1994; Yozzo *et al.*, 1994). In the salt marshes of the US, natural microhabitats may be only a few millimetres deep but can harbour high densities of young fish and shrimps (Kneib and Stiven, 1982; Kneib, 1984; Smith and Able, 1994; Kneib, 1997a).

In a European salt marsh, the utilization of the seepage water microhabitat by *Crangon crangon* was reported by Cattrijsse *et al.* (1997).

In Europe, the utilization of the higher situated tidal ponds by macrocrustaceans and fish like juvenile mullet, small plaice and flounder, gobiid fish and *Palaemon* species has been reported (Frid, 1988; Frid and James, 1989). Despite the fact that marsh ponds offer refuge from predators, they may compromise growth (Werner *et al.*, 1983; Power, 1984; Holbrook and Schmitt, 1988; Halpin, 2000; Layman *et al.*, 2000). Poulin and Fitzgerald (1989) and Dunson *et al.* (1993) found that abiotic factors play the predominant role in structuring the fish communities in marsh ponds whereas other researchers suggested that biotic interactions might be more important than abiotic parameters (Weisberg, 1986; Dunson and Rowe, 1996). The combined approach showed that both abiotic and biotic factors influence the growth and survival of salt marsh pond species (Rowe and Dunson, 1995; Layman *et al.*, 2000).

1.2.2.2.3 Vegetated marsh surface

In Europe, the marsh surface is less inhabited by larger mobile macroinvertebrate species (Frid, 1988) due to the vegetation structure however small *Carcinus maenas* was reported to make use of these areas to extend their foraging period (Frid, 1988). Similarly, reduced utilisation of the vegetated surface was observed in an Australian salt marsh (Thomas and Connolly, 2001).

In the US, the marshes are dominated by the smooth cord grass, *Spartina alterniflora* (Odum and de la Cruz, 1967). Utilization of submerged aquatic vegetation and its importance was reported by several researchers (Kemp *et al.*, 1984; Orth *et al.*, 1984; Rozas and Odum 1987a; Sogard and Able, 1991). Resident species seize opportunities to move into the intertidal marsh vegetation with flooding tide. Macrocrustacean (Zimmerman and Minello, 1984; Hettler, 1989; Kneib, 1991; Kneib and Wagner, 1994, Minello *et al.*, 1994; Peterson and Turner, 1994; Rozas and Zimmerman, 2000), resident fishes and estuarine dependent transient juvenile fishes (Hettler, 1989; Minello and Zimmerman, 1992; Kneib and Wagner, 1994; Rozas and Zimmerman, 2000) are all commonly found on the vegetated marsh surface. These species mainly belong to the family of Cyprinodontidae and Palaemonidae. Gobiid fishes may be also very abundant within a few metres of the marsh edge (Peterson and Turner, 1994). A reason for the high abundance of fishes and crustaceans occurring on the marsh surface is that it provides a spawning site for many fish species (Able and Castagna, 1975; Taylor *et al.*, 1979; Taylor and DiMichele, 1983; Kneib, 1986). Vegetated marsh surface also offer a food rich place, which becomes available to forage when marsh is flooded (Weisberg *et al.*, 1981; Weisberg and Lotrich, 1982; Bosch and Turner, 1984;

Rozas and Odum, 1988; Fitz and Wiegert, 1991; Rozas and Reed, 1993). When fish had access to the marsh surface during high tide, a much greater volume of food was consumed than when fish were restricted to the subtidal areas (Rozas and LaSalle, 1990; Allen *et al*., 1994). The protection from predators offered by the vegetated marsh surface also contributes to the higher nekton abundance (Boesch and Turner, 1984; Kneib, 1987; Rozas and Odum, 1988). These functions (spawning area, food and refuge) demonstrate the importance of the vegetated surface as a nursery for fish (Kneib, 1984, 1986, 1997a,b, Talbot and Able, 1984; Able and Fahay, 1998) and macrocrustacean species (Zimmerman and Minello, 1984; Kneib, 1987; Thomas *et al*., 1990; Fitz and Wiegert, 1991; Rozas and Reed, 1993; Peterson and Turner, 1994; Minello, 1999). Boesch and Turner (1984) found that the average annual yield of shrimp in the Gulf of Mexico was highly correlated with the area of vegetated wetlands within an estuary, which further indicates the importance of vegetated marshes. Although several advantages make the marsh surface attractive for nekton species, competition between species may be an important interaction when they share the same refuge habitat in the vegetated intertidal (Cross and Stiven, 1999).

1.2.3 Marsh age as parameter influencing the marsh faunal composition

From the beginning of the human history, man always utilized the salt marshes but since the last century, human impact started to alter wetlands very drastically (Nichols *et al*., 1986). Salt marshes have been filled, diked and impounded for purposes of agricultural or urban land claim (Bakker *et al*., 1993; Mitsch *et al*., 1994). The conversion of these areas for agricultural, residential and industrial land removed thousands of square kilometres of coastal salt marshes (Mitsch and Gosselink, 1993; Kennish, 1997, 1999). On a global level, relative sea-level change influenced by an array of anthropogenic factors affect hydrology, soils, plant communities, sediment inputs, accretion rates, subsidence and other components of coastal wetlands (Kennish, 2001).

In Western Europe, the land claim for agriculture or urban use represents the biggest threat for intertidal areas. The loss of marsh areas also occurs with the dike constructions along the rivers to restrict tidal inundation. After the huge flood event in 1953 in the Westerschelde, dikes were built and heightened in the framework of the Delta plan in The Netherlands. This resulted in the loss of 31 950 ha intertidal area in 1960 and an other 19 615 ha in 1990. This represented 39% decrease of the total intertidal areas (Meininger and Snoek, 1992). In the Oosterschelde estuary, the construction of the storm-surge barrier and compartment dams reduced the total area under tidal influence by 22 %, the area of tidal flats by 35 % and salt marsh area by 63 % (Smaal *et al*., 1991). In Belgium, the Sigma plan was born after the flood in 1976 and in the framework of this plan the dikes were heightened and several polders were created to reduce the threat of the flood (Meire *et al*., 1992).

The wetlands were considered important areas for conservation by the Ramsar Convention in 1971. Reestablishment of intertidal marshes started in the US with extensive planting of *Spartina* spp. (Boston, 1981). Later several methods were used to create new marshes or mitigate the wetland loss (Streever, 2000; Rozas and Minello, 2001). Restoration and creation technologies are important tools for mitigating unavoidable losses of tidal marshes (Lewis, 1990; Kentula *et al*., 1992; Broome and Craft, 2000), although some scientists doubt that creation and restoration projects can equitably replace the functional value of natural systems because of the complexity and uniqueness of natural wetlands. Quantifying community responses to restoration is critical to determine the success or failure of a project (Short *et al*., 2000). Monitoring activities in salt marshes often include assessments of vegetation (Burdick *et al*., 1997) hydrology (Roman *et al*., 1995) soil chemistry (Portnoy, 1999) and abundance of nekton and invertebrate communities (Dionne *et al*., 1999;

Raposa, 2000) however it is difficult to measure the functional values of a wetland system (Delaney *et al*., 2000).

The post restoration monitoring is important to indicate the success of the marsh creation by studying the change of the habitat values or to compare the status of restored marshes the reference areas. The emphasis is given to monitor re/creation and most of the studies comparing marshes with different age have been carried out in artificially created areas (Moy and Levin, 1991; Levin *et al*., 1996; Minello and Webb, 1997; Williams and Zedler, 1999; Alphin and Posey, 2000). This fact is due to the importance of recreation but also to the circumstance that natural (i.e. without human interference) formation and development of intertidal marshes are rarely observed since estuaries and coastal areas are strongly controlled by human activities in both the United State and Europe.

Scientific investigations mainly focus on whether the restored or naturally formed young ecosystems have similar structural characteristics and would function equivalently as a reference or matured area. And if not, how much time is required to reach similar functional equivalency (Havens *et al*., 1995, 2002).

Since it usually is difficult to measure the functions (rates, processes) (Minello and Webb, 1997; Delaney *et al*., 2000; West *et al*., 2000) in most cases structural attributes are used to indicate difference or similarities between restored and natural (Zedler and Lindig-Cisneros, 2000) or young and matured marsh. Useful indicators of salt marsh structure include: the composition, percent cover, biomass, density, and vertical structure of the vegetation, three soil attributes (texture, nitrogen pools, and organic matter concentrations), fish and invertebrate abundance and measure of their growth or size distributions, and topographic complexity (e.g. tidal creek density) (Seneca *et al*., 1976; West *et al*., 2000; Zedler and Lindig-Cisneros, 2000).

Plant species composition, stem density, percent cover, and biomass are probably the most widespread descriptors of salt marsh structure (Zedler and Lindig-Cisneros, 2000). The plant community in created and restored marshes develops quickly, often achieving structural and some functional similarity to the natural marshes within a few years after establishment (Seneca *et al*., 1985; Broome *et al*., 1986; Broome and Craft, 2000).

Soil attributes include texture, nutrient and organic matter content. These characteristics are important for establishing the vegetation in the low and the high marshes (Boyer and Zedler, 1998; Zedler and Lindig-Cisneros, 2000). Williams and Zedler (1999) found that hydrology was the driving force in determining channel physical characteristics, regardless of its restoration status.

In tidal marshes of the US, habitat complexity proved to be a good indicator of faunal use. Complexity measurements can include area-perimeter ratio, marsh-water edge ratio, angle of exposure and elevation (Delaney *et al*., 2000). Creek network development also plays an important role to support higher abundances of fishes and invertebrates (Minello and Zimmerman, 1992) and more plant species (Zedler *et al*., 1999). Some researchers indicated the relatively few creeks and ponds and little marsh edge habitat as the main important reasons of the lack of functional equivalency between the created and reference areas (Minello *et al*., 1994; Delaney *et al*., 2000; Streever, 2000).

The development of the benthic invertebrate community in a restored marsh depends on the formation of wetland soil characteristics, especially an organic rich surface layer, particle size distribution (Kneib, 1984; Levin *et al*., 1998) and root density of marsh plants (Lana and Guiss, 1992). In the marsh creation, marshes are initially colonised by opportunistic benthic species that are succeeded by more stable and mixed assemblages (Moy and Levin, 1991). These assemblages have similar species composition as reference areas (Sacco *et al*., 1994) but restored marshes had lower densities than natural ones (Cammen, 1976; Sacco, 1989; Moy and Levin, 1991; Minello and Zimmerman, 1992; Sacco *et al*., 1994; Simenstad and Thom, 1996). A clear relationship between the age of the restored marsh and infaunal density was not always found. Marsh vegetation and physical factors are more important than the age of the marsh in determining macrobenthic faunal characteristics (Moy and Levin, 1991; Sacco *et al.*, 1994; Simenstad and Thom, 1996; Levin *et al.*, 1998)

Constructed salt marshes are readily occupied by native invertebrates (LaSalle *et al.*, 1991; Scatolini and Zedler, 1996; Posey *et al.*, 1997). Species lists of the constructed areas can be very similar to the ones recorded in the reference sites (Scatolini and Zedler, 1996) but density was generally lower in the constructed marshes (Minello and Zimmerman, 1992; Scatolini and Zedler, 1996; Minello and Webb, 1997). Several researchers found that the density of macroinvertebrates progressively increased with the constructed marsh age (LaSalle *et al.*, 1991; Minello and Zimmerman, 1992; Posey *et al.*, 1997; Craft, 2000).

Fish species appear to utilise restored marshes immediately (Simenstad and Thom, 1996; Williams and Zedler, 1999) with similar abundance as the reference sites (Rulifson, 1991; Minello and Zimmerman, 1992; Burdick *et al.*, 1997; Dionne *et al.*, 1999; Tupper and Able, 2000; Pirri *et al.*, 2001). Other observations indicated that transplanted marshes supported fewer fish than natural ones (Moy and Levin, 1991; Minello and Webb, 1997). Minello and Zimmerman (1992) observed that fish diversity was consistently higher in a transplanted marsh than the reference site. Tidal regime (Burdick *et al.*, 1997; Zedler *et al.*, 1997), channel morphology (Zedler *et al.*, 1997; Williams and Desmond, 2001), density of vegetation (Dionne *et al.*, 1999), marsh surface elevation (Minello and Webb, 1997) and habitat complexity (Havens *et al.*, 1995) are considered to influence the colonisation of the area more than the marsh age or restoration status.

Feeding relationships (Kwak and Zedler, 1997) may indicate differences and similarities between marshes. Allen *et al.* (1994) showed that foraging pattern of *Fundulus heteroclitus* differed between the restored and natural marshes however other observations showed similar diet of this (Moy and Levin, 1991) and other fish species (Tupper and Able, 2000). Pirri *et al.* (2001) also found that length, weights, gut fullness, diet composition of *F. heteroclitus* were similar between restored and unrestricted salt marsh area, indicating that the restored marsh was providing similar energy resources and functioning as a natural foraging habitat for this species.

Most studies measured few of the above-mentioned structural elements and compared different functional equivalencies (nutrient cycles, nursery and foraging function etc.) between restored and reference marshes. As a conclusion, some researchers suggested time periods during which the different functions of restored marshes could reach the same level as the reference areas (Seneca *et al.*, 1976, 1985; Broome *et al.*, 1986; Craft *et al.*, 1988, 1999; Sacco *et al.*, 1994; Minello and Webb, 1997).

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2 Tidal, diel and semi-lunar changes in the fauna assemblage of an intertidal marsh creek

Abstract: *The utilisation of a brackish estuarine marsh by nekton was investigated over a semi-lunar cycle in August 1994. Nekton migrating in and out of the intertidal creeks of the marsh 'Het Verdronken Land van Saeftinghe' in the Westerschelde estuary, SW Netherlands, was sampled passively during 7 complete tidal cycles. Sampling one tidal cycle yielded three consecutive flood samples and four consecutive ebb samples. Sampling occurred every two to three days, covering diel, tidal and semi-lunar situations, thus allowing comparison of tidal, diel and semi-lunar influences on the composition of the intertidal fauna. Two different tidal migration modes were observed. The mysid shrimp Mesopodopsis slabberi showed maximum abundance around high tide. For the remaining common species: the mysid Neomysis integer, the shrimp Palaemonetes varians, the crab Carcinus maenas, the goby Pomatoschistus microps and the amphipod Corophium volutator, highest densities were recorded during lower water heights. The faunal assemblage shifted between the different tidal stages. On two occasions consecutive day and night samples were taken. Total densities were higher during the night samples. During spring tide, a difference in community composition was noticed between the night and the day samples. During neap tide, day-night differences were less clear. Recorded total densities were highest during spring tide and lowest during neap tide. At maximum water levels a drop in total density was observed. A shift in community composition occurred between spring and neap tides. All the three cycles influenced the migration of the species and thus the community composition in the marsh creek.*

2.1 Introduction

Salt marshes have been recognised world-wide as ecosystems that play a vital role in the productivity of estuaries and as a habitat for fish and macrocrustaceans (Kneib, 1997). Most of the information on marsh habitat use by fish and macro-crustaceans has been collected in the US (Rozas and Reed, 1993; Minello 1999; Desmond *et al*., 2000; Rozas and Zimmerman, 2000). The average European salt marsh is situated higher in the intertidal and consequently the vegetated surface has only limited accessibility to nekton species. In Europe observations suggest that organisms largely remain in intertidal creeks rather than venturing onto the vegetated marsh surface (Cattrijsse *et al*., 1994; Mathieson *et al*., 2000).

Availability and use of the marsh habitat are influenced by three concurrent cycles. Each tide brings organisms to the marsh habitats. Shallow creeks, pans, tidal pools, the vegetated surface and other marsh habitats each offer refuge and foraging opportunities for a variety of species (Kneib, 1997). While some aquatic animals are adapted to remain within the marsh proper, most return to the subtidal on ebbing tides. Diel activity patterns, likely associated with feeding rhythms, will cause differences in abundance of certain species within the marsh (Davis, 1988; Rooker and Dennis, 1991; Rountree and Able, 1997). Finally, the lunar cycle determines the temporal and spatial availability of marsh habitats. At neap tide, less marsh area will be flooded while at spring tide total inundation time will be longer. Lunar influences on the nekton abundance and community composition remain largely unstudied.

The intertidal creeks of the salt marshes in the Westerschelde estuary are visited by many organisms: juvenile fish, shrimps and crabs (Cattrijsse *et al*., 1994), mysid shrimps (Mees *et al*., 1993) and amphipods (Cattrijsse *et al*., 1993). Many studies exist about marsh fauna composition however no integrated work on the effect of the three cycles (tidal, diel, lunar) in one sampling area has been published previously. Especially investigations on the lunar effect are lacking. In Europe, in contrasts to the estuaries, the salt marshes are not well studied. In this work, the structure of nekton communities in an intertidal marsh creek during several tidal stages over a semi-lunar cycle was examined. The aim of this study is a more detailed understanding of the habitat use of marsh by estuarine organisms. The objective of the study was to describe tidal, diel and semi-lunar changes in the aquatic fauna entering the marsh with each tide. Three null-hypotheses were formed as follow: 1- Number of migrating individuals does not differ between the different hours of the tidal cycle. 2- There is no difference in density of the main species during day and night. 3- There is no difference in nekton species composition between spring and neap tide.

2.2 Material and methods

2.2.1 Study area

The studied marsh 'Het Verdronken Land van Saeftinghe' lies in the mesohaline part of the Westerschelde estuary, South-West Netherlands (Fig. 1). It is the largest estuarine brackish marsh left in Western-Europe with a surface area of 2800 ha (Dijkema *et al*., 1984).

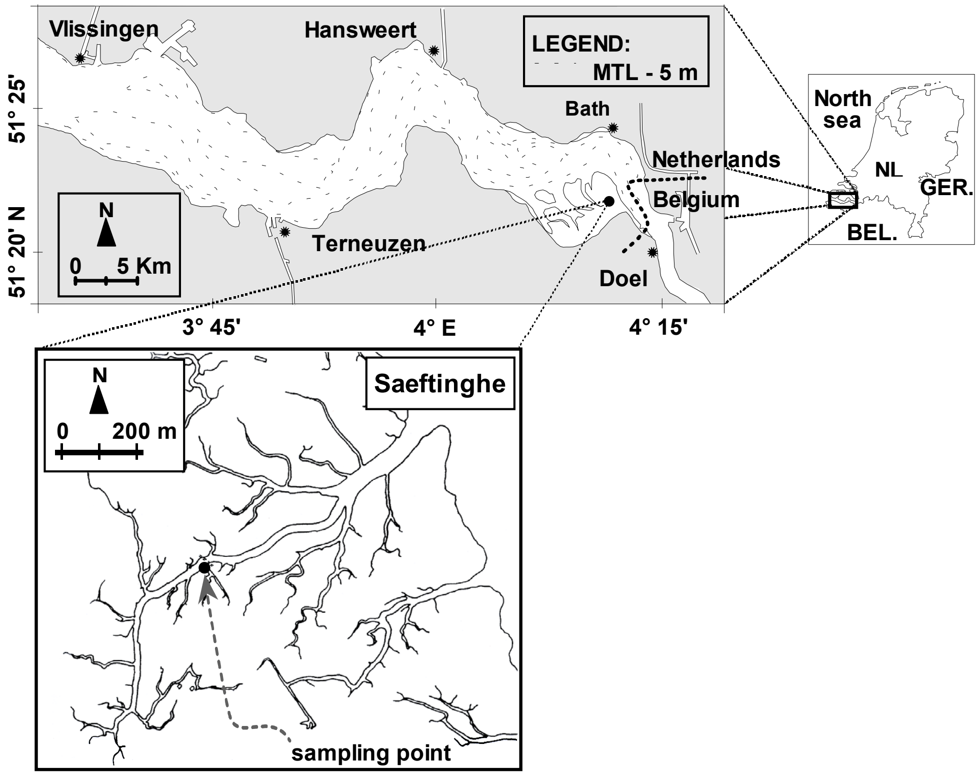


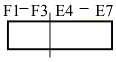
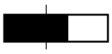
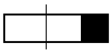
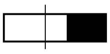
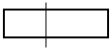
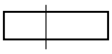
Figure 1. Location of Saeftinghe in the Westerschelde estuary and indication of the sampling point situated on the east side of the marsh.

All samples were collected in an intertidal creek measuring 1600 m long, 38 m wide and 4 m deep at the sampling point. It floods and drains a marsh surface of approximately 75 ha. There is no connection of any other major creek in the marsh and there are no pools at the mouth of the creek or in the channel itself. The migrating individuals therefore can come only from the estuary. The channel showed a sigmoid shape close to the estuary however at the sampling point the creek was straight and the slopes of both banks were symmetrical. Every tidal cycle the creek falls completely dry for at least 5 hours. Water enters the marsh 3 hours before high water and leaves the creek within 4 hours after high water.

2.2.2 Sampling

Sampling took place from a bridge spanning the creek. A stow net with a 1 mm x 1 mm mesh size, an opening of 1 m x 1 m and a length of 5 m was used to sample the migrating nekton. The net was placed on the bottom and mounted on an iron frame. Two weights attached to the sides of the frame prevented the net from being lifted by the currents while ropes kept the net in place during sampling. The opening size of the net, the mesh size and the thickness of the fibre were used to calculate the necessary length of the net in order to keep the pressure inside the net under all current conditions (Tranter, 1979). This reduced the probability that animals avoided the net.

Table 1. Selected sampling days and periods during the semi-lunar cycle with predicted water heights (1)(cm above the Dutch ground level NAP) and observed maximum water height (2) (cm above the Dutch ground level NAP) in the marsh creek in August, 1994. Filled blocks in diurnal phases indicate night hours during the sampling campaign. Tidal phase is labelled with F1-F3 as flood hours and E4-E7 as ebb hours. The moment of high water (HW) is indicated by a vertical line.

Date	*Time*	*Diurnal Phase*		*Moon Phase*	*Lunar Phase*	*Waterheight*	
		Tidal Phase				1.	2.
		HW F1−F3, E4 − E7					
7 Aug	13:30 - 20:45		day	full		297	340
8 Aug	02:20 - 09:35		**night**		spring	319	350
10 Aug	15:30 - 23:00		day		spring	319	380
13 Aug	17:05 - 01:15		day			289	360
16 Aug	20:55 - 04:25		**night**		neap	235	290
17 Aug	09:25 - 17:00		day		neap	224	295
19 Aug	12:00 - 19:30		day	new		276	340

Sampling lasted a complete tidal cycle and yielded 3 flood (F1, F2 and F3) and 4 ebb (E4, E5, E6 and E7) samples on every sampling day. The net fished for one hour, was rinsed and then replaced in the same position. After high water the net was turned to sample the ebb current until all water had left the creek.

Samples were collected every two-three days between 7 and 19 of August 1994 during a semi-lunar cycle from full moon till new moon covering all possible combinations of the tidal, diel and semi-lunar cycles (Table 1). The predicted water height was used to define the sampling days. Each day is a different combination of tidal conditions (e.g. spring tide-day, spring tide-night, neap tide-day etc.) hence no sampling occasion would reinforce the findings of any other day. While some tidal cycles fell during day or night, others included both light and dark conditions. On the 8 and 16 of August the flood tide started during night hours. Since the organisms moved into the creek during night, these days were considered as night samples. On 10 and 13 night hours fell when ebb had started already. Therefore evening hours did not influence the migration hence these days were considered as day samplings.

Temperature, salinity (in practical salinity unit), and dissolved oxygen concentration were measured every sampling hour. Water current speed and water height were measured every 15 min. Current speed was measured with a current meter, placed about 20 cm above the bottom next to the net. Since the net was constructed in such a way to keep the pressure inside the net under all conditions we assumed that the current speed was the same in the mouth of and beside the net. Water height was measured with a ruled stake placed next to the net in the deepest part of the creek. The maximum water height for each sampling day was used as a measure for the lunar phase.

Samples were preserved in a 10% formalin brackish water solution. In the laboratory all samples were sorted and species were identified. In the case of very high abundances, volumetric sub-samples were taken for that particular species.

2.2.3 Data processing and analyses

Every 15 minutes the volume of water filtered by the net and passing through the lower metre of the creek was calculated. At the sampling point, the cross sectional area for every 10 cm water height was measured. Water height, current speed and the cross section measurement allowed calculation of the flow (m^3s^{-1}) at the sampling point.

Species densities were calculated from the volumes of water passing through the net and the number of captured individuals. With ebb tide the creek dries out completely. There is no pond on the marsh surface next to or in the creek therefore animals present at the moment of the high water could only come from the estuary through the channel. The amount of detritus was weighed and the number of individuals that passed the sampling point during each sampling hour was counted for each species. Using the total number of individuals and the total volume of water passing through the net during one hour, the density was estimated in the lower metre of the water column. The densities of the 3 flood samples were summed which yielded an estimate at high water. Densities were also calculated for every ebb hour also using the total number of individuals and volume of water leaving the creek. The sum of these four densities also yielded an estimate at high water. The abundance of the species at the moment of high water of each tidal cycle was calculated by averaging the flood and the ebb estimate.

To examine tidal migration patterns the number of individuals that entered or left the creek during one sampling hour were expressed as a percentage of the total number of individuals that migrated in or out of the creek. The total number of individuals entering the creek during the 3 flood hours was considered to be 100%. The number of individuals captured during each hour of flood was expressed as a percentage of the total number captured during the entire flood tide. Likewise, the total number of individuals captured on leaving the creek with ebb were taken as 100% and the number captured during each ebb hour was expressed as a percentage of that total.

A Spearman-Rank test was used to examine the correlation between the water height and the species numbers during the tidal cycle and between the water height and the species abundances during the semi-lunar cycle. A species-density matrix was constructed with the seven high water density estimates (7 dates). Species that occurred twice or less were eliminated from the data set. Density data were quart-root transformed prior to the multivariate analysis. A data matrix was also constructed for the environmental variables for the seven sampled days. Data were than subjected to ordination techniques from the CANOCO package (Ter Braak, 1987a). Ter Braak (1987b) was followed to decide between linear and unimodal response models. Firstly, a Principal Component Analysis (PCA) was performed using only the species density data of the seven sampling days. Then, environmental variables were incorporated into the analysis and the canonical form of the

PCA (RDA) was run. This revealed a similar distribution of the sampling stations therefore the RDA was used to explain the observed pattern in the species composition.

2.3 Results

2.3.1 Environmental parameters

Variations of environmental parameters during the seven tidal cycles are presented in Figure 2. Maximum water height was reached approximately three hours after water began entering the creek.

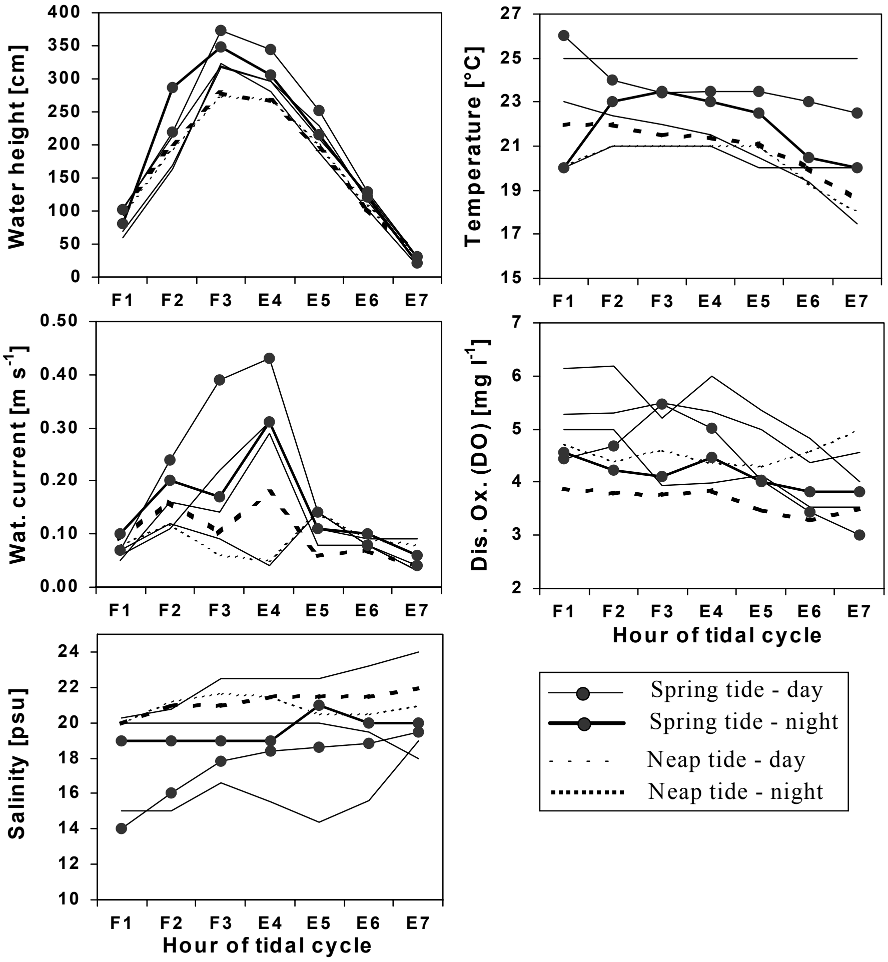


Figure 2. Tidal fluctuation of maximum water height (cm), maximum current speed (m s^{-1}), temperature (°C), salinity (psu), and dissolved oxygen concentration (mg l^{-1}) during the seven tidal cycles (flood hours F1-F3, ebb hours E4-E7). [1]

Water currents generally peaked after high water and decreased gradually until all water had left the creek. Only during 10 August did current speed exceed 0.4 m s^{-1}. During the other sampling dates, maximum current speed varied between 0.1- 0.3 m s^{-1}. In general, temperature decreased towards the end of the tidal cycle. These trends were not observed on all sampling occasions and the difference between the start and final values of the tidal cycle varied with each sampling date.

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[1] After Hampel et al. (2003).

Temperature remained constant during the tidal cycle on two dates (7 and 19). Salinity ranged between 14 and 24 psu. Dissolved oxygen concentration ranged between 3 and 6.2 mg l^{-1} and decrease toward the end of the ebb tide.

Table 2 shows the tidal average values of the environmental parameters over the semi-lunar cycle. Both maximum water height and maximum current speed peaked on the 10th August and reached a minimum on the 16th and 17th August. By new moon on the 19th the water height and the current speed had again increased to the same level as at the start of the sampling period. Only water current and water height showed a clear positive correlation. Consequently, only water height was used to indicate the phase of the lunar cycle. Salinity fluctuated between 15.9 and 22.3 without showing any trend over the semi-lunar cycle. Temperature showed a slight decrease towards the end of sampling period. Oxygen concentration fluctuated without any semi-lunar trend between 3.6 and 5.5 mg l^{-1}.

Table 2. Fluctuation of maximum water height (cm), maximum water current (m s^{-1}), average salinity (psu) (±standard error), temperature (°C) (±se), dissolved oxygen (mg l^{-1}) (±se) and the amount of detritus (g m^{-3}) at the moment of the high water at the sampling point over the seven sampling dates.

Variable	*Sampling date*						
	07	*08*	*10*	*13*	*16*	*17*	*19*
Water height (cm)	340	350	380	360	290	295	340
Water current (m s^{-1})	0.29	0.31	0.43	0.31	0.14	0.14	0.18
Salinity (psu)	15.9 ±0.6	20.0 ±0.7	17.6 ±0.7	22.3 ±0.5	21.2 ±0.2	20.9 ±0.2	19.6 ±0.3
Temperature (°C)	25.0 ±0	22.0 ±0.5	23.7 ±0.4	20.9 ±0.7	20.9 ±0.4	20.2 ±0.4	20.4 ±0.2
Dissolved O_2 (mg l^{-1})	4.1 ±0.2	4.2 ±0.1	4.3 ±0.3	5.0 ±0.2	3.6 ±0.1	4.6 ±0.1	5.5 ±0.2
Detritus (g m^{-3})	0.042	0.083	0.033	0.042	0.035	0.005	0.102

2.3.2 Species

Twenty-five taxa were captured containing 21 species. Larval stages of *Carcinus maenas* were treated separately because of their different ecology (Table 3). Three amphipod, 9 decapod, 3 mysid, 2 isopod, 1 polychaete, jellyfish and 5 fish taxa were recorded.

Table 3. List of the species captured during the sampling period.

Taxa-Species
Amphipoda
Corophium volutator
Gammarus salinus
Gammarus zaddachi
Caridea
Crangon crangon
Palaemonetes varians
Brachyura
Carcinus maenas (megalopa)
Carcinus maenas (juvenile)
Eriocheir sinensis
Macropodia rostrata
Portumnus latipes
Rhithropanopeus harrisi
Isopoda
Eurydice pulchra
Lekanesphaera rugicauda
Teleostei
Dicentrarchus labrax
Gasterosteus aculeatus
Platichthys flesus
Pomatoschistus microps
Syngnathus rostellatus
Mysidacea
Mesopodopsis slabberi
Neomysis integer
Praunus flexuosus
Other
Decapoda larvae
Insect
Jelly fish
Nereis diversicolor

The most abundant species include the amphipods *Corophium volutator* and *Gammarus* spp., the caridean shrimp *Crangon crangon*, the palaemonid shrimp *Palaemonetes varians*, the shore crab *Carcinus maenas* (megalopa and juvenile), zoea of the mudcrab *Rhithropanopeus harrisi*, the mysid shrimp *Neomysis integer* and *Mesopodopsis slabberi,* the isopods *Eurydice pulchra* and *Lekanesphaera rugicauda* and the fishes *Pomatoschistus microps*, *Dicentrarchus labrax* and *Platichthys flesus.* The mysid shrimp *Mesopodopsis slabberi* dominated all catches reaching densities between 0.5 to 162.9 individuals m^{-3}.

2.3.3 Tidal pattern

Two different tidal migration patterns were observed (Fig. 3). The common goby exhibited the clearest pattern. From the incoming gobies, most individuals were caught during the first hour of flood while emigration occurred predominantly during the last hour of ebb. This pattern was observed during all tidal cycles. A similar tidal migration pattern was found for *Corophium volutator*, *Palaemonetes varians*, juvenile *Carcinus maenas*, and *Neomysis integer* but for the latter species the pattern was not pronounced during all tidal cycles. A negative significant correlation was detected between the number of *Pomatoschistus microps*, *P. varians* and the water height (Spearman-Rank correlation, p=0.008 and p<0.001 respectively).

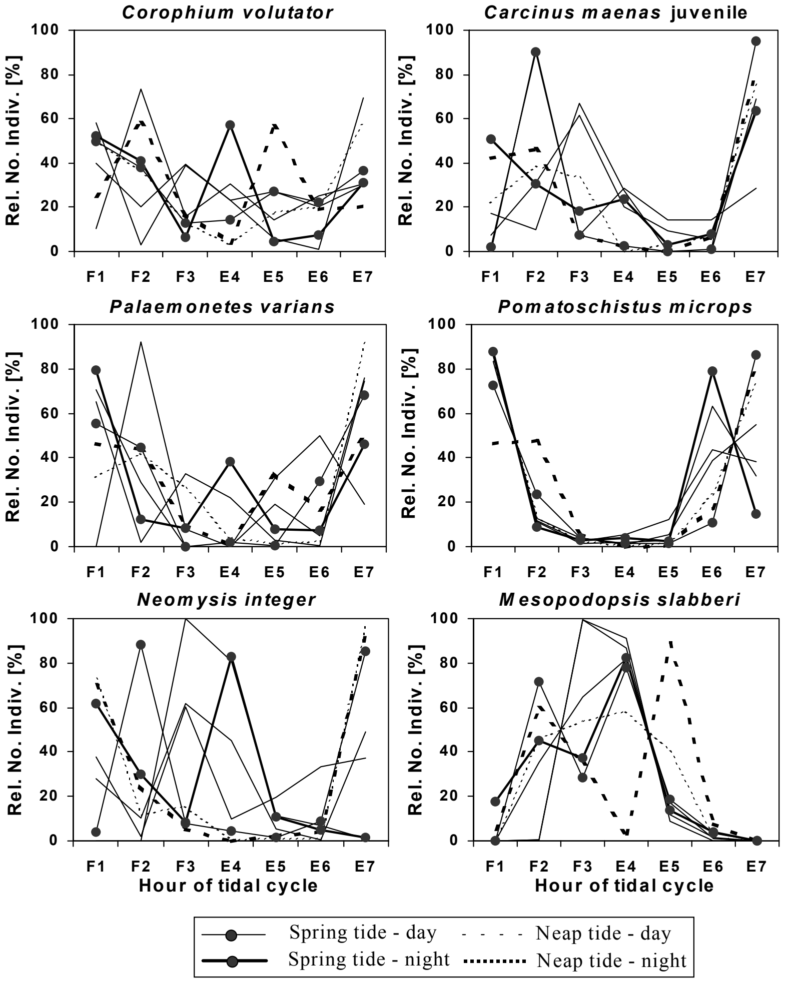

Figure 3. Migration patterns of major nekton species during the seven tidal cycles. Incomming numbers for each flood sample (F1, F2 and F3) and outgoing numbers for each ebb sample (E4-E7) have been expressed as percentages of total immigrating individuals and total emigrating individuals respectively for each sampling date. [2]

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[2] After Hampel et al. (2003).

An opposite pattern was observed for *Mesopodopsis slabberi*, in which abundance maxima generally occurred just before and after high water (Fig. 3). The number of this mysid was positively correlated with water height ($p<0.001$).

2.3.4 Diel pattern

Night-time samples collected following or preceding daytime samples showed diel density changes of some species like *Crangon crangon, Pomatoschistus microps* and *Corophium volutator* (Fig. 4). On 8 August, all common species reached higher densities than during 7 August, yet waterheight and current speed did not differ substantially between these two consecutive tidal cycles (Table 2). Except for the mysids, higher densities were recorded again during the night sample of 16 August when the hydrological conditions were similar to the daytime sample of 17 August.

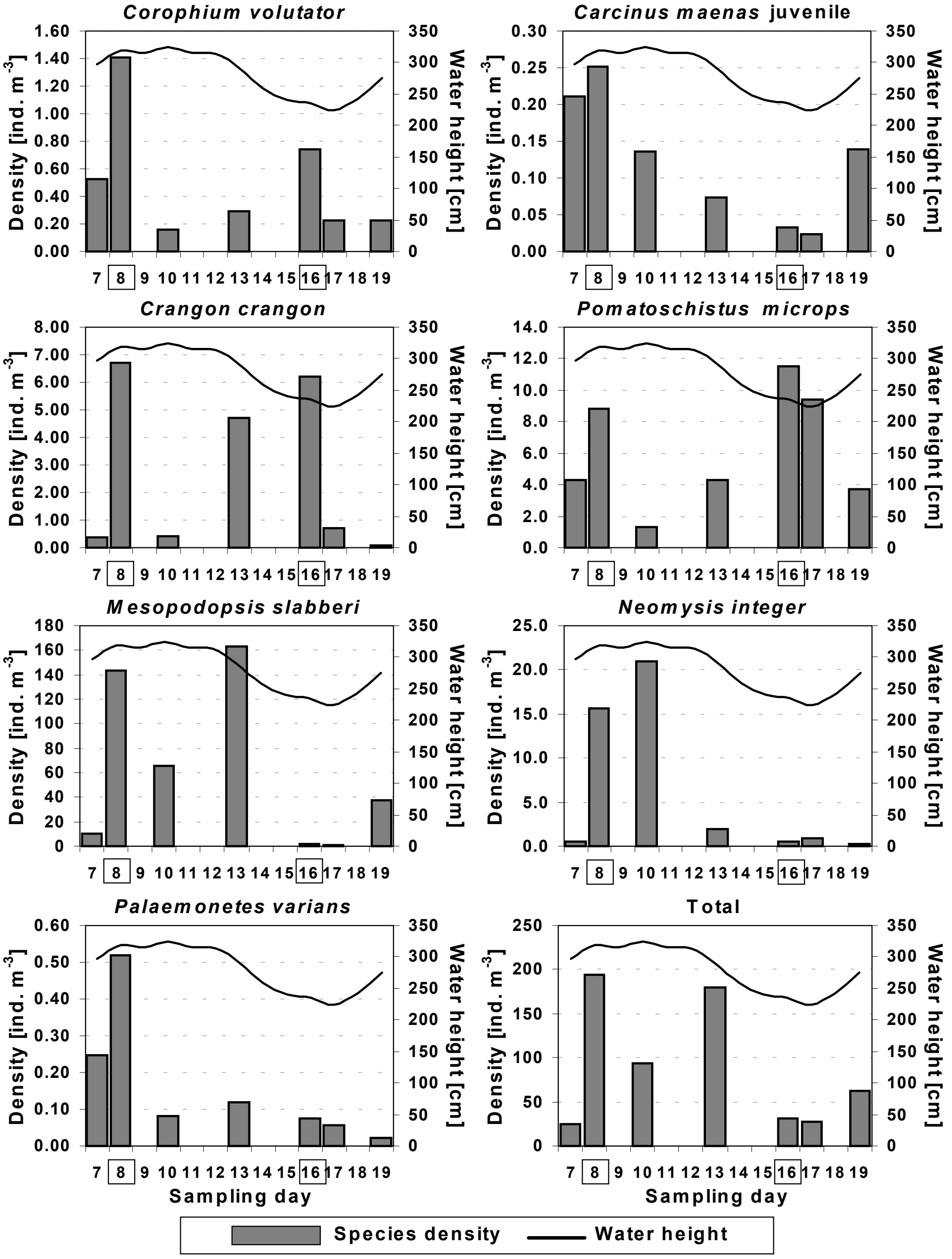

Figure 4. Density fluctuations (ind. m^{-3}) over the seven tidal cycles vs. predicted water height for the major nekton species and total densities. Nocturnal tides on 8 and 16 of August are indicated with a rectangle.

2.3.5 Semi-lunar pattern

Density changes over the semi-lunar cycle for the most common species is shown by Figure 4. Spearman Rank tests showed significant correlations between the observed maximum water height and the daily density estimates for *Neomysis integer* (p=0.04), *Mesopodopsis slabberi* (p=0.01) and *Pomatoschistus microps* (p=0.03). While the correlations were positive for both mysid shrimps, the average daily densities for *P. microps* showed a negative correlation with water levels. Total densities reached a maximum during spring tide. Low densities were recorded during neap tide. On the peak of the spring tide period (10 August) a sharp decline occurred.

2.3.6 Community structure

The correspondence analysis showed that community variation is less than 2 standard deviation units along the first axis thus a linear method was more appropriate for the density data of the semi-lunar cycle. The results of RDA are depicted in Figure 5. Eigen values of first and second axes of the RDA were 0.669 and 0.136 respectively. Around 60% of the variance was explained by the first two axes. Maximum water height and current seemed to influence the community structure during the semi-lunar cycle (Fig. 5). These vectors give large arrows and correlated with the first axes. The vector presenting the water height variable separates the different sampling days according to the registered maximum water level. The fauna sampled on the 10 and 13 separated from the samples collected at neap tide during the 16 and 17 of August.

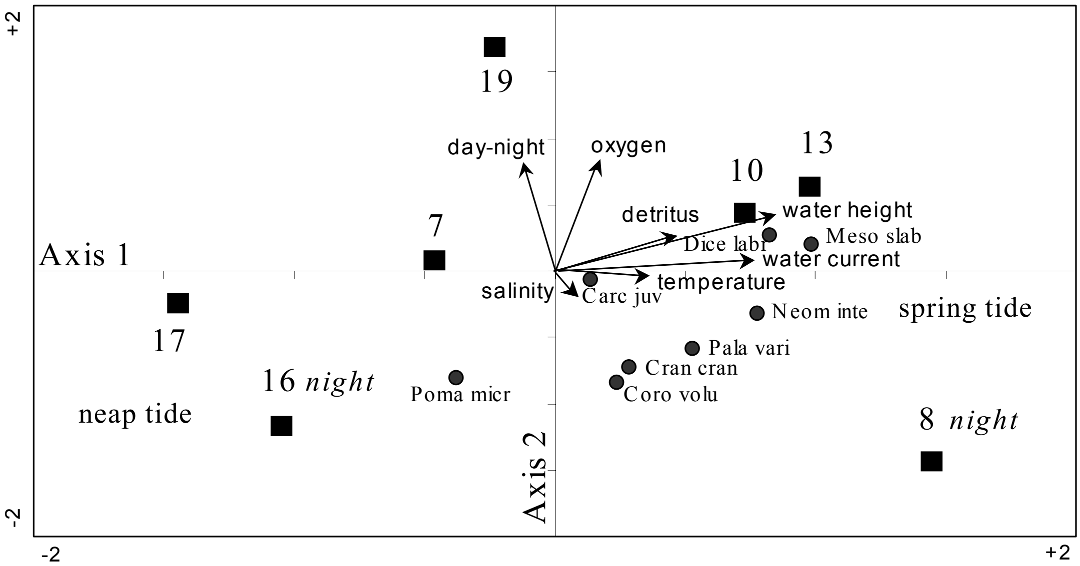

Figure 5. Redundancy Analysis (RDA) plot shows the diel and the semi-lunar changes in the marsh nekton community. Spring tide samples and neap tide samples are situated at opposite corners of the plot. Abbreviations of species names are used as follow: Mesopodopsis slabber (Meso slab), Dicentrarchus labrax (Dice labr), Carcinus maenas juvenile (Carc juve), Neomysis integer (Neom inte), Palaemonetes varians (Pala vari), Crangon crangon (Cran cran), Corophium volutator (Coro volu) and Pomatoschsitus microps (Poma micr). [3]

The day-night vector gave a large arrow and correlated well with the second axis. Besides the water height and current which mainly explain the separation of the sampling days along the first axis, day and night variation seems to determine the position of the stations along the second axis. The day-night differences in community composition can be observed between sampling days 7 and 8 and less pronounced, between 16 and 17. Most of the main species had high density during the

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[3] Figure 5 was modified including the species ordination.

spring tide period and situated on the right side of the ordination plot characterising the spring tide sampling days. Exception was the common goby, *Pomatoschsitus microps*, which had high density during neap tide and plotted in the vicinity of sampling days 16 and 17. *Crangon crangon*, *Palaemonetes varians*, *P. microps* and *Corophium volutator* were positioned on the lower half of the species plot and characterised the night sampling occasions.

2.4 Discussion

Evaluation of the habitat value of an intertidal area for actively migrating species necessitates full appreciation of the habitat use patterns under all temporal circumstances. Seasonal variations in community composition and species abundance of the marsh Saeftinghe have been reported before (Cattrijsse *et al.*, 1994). This field study provides data on small-scale temporal differences in a marsh creek. Day-night related activity patterns might cause significant changes in abundance and species composition. The lunar tidal cycle influences both total access time and total area accessibility of intertidal marsh habitats.

The aim of this study was to focus on the influence of tidal, diel and semi-lunar cycles not the observation of seasonal change hence the number of observations is limited similarly the study of Shenker and Dean (1979). August was chosen for sampling the marsh because during this month the marsh is used the most intensively as nursery by nekton like sea bass, common goby and shore crab. (Cattrijsse *et al.*, 1994). Moreover the density and biomass of infauna also peaks in August (Cattrijsse unpubl.). The whole tidal cycles were covered by the sampling from the beginning till the end of each tidal cycle. During spring as well as neap tide, day and night samples were taken however with some restrictions. At neap tide, high water always occurs during night hence taking night samples does not represent a problem. However during spring tide, high water is always in the early afternoon therefore complete night sampling is not possible. For covering the semi-lunar cycle, samples were taken before, after and at the moment of spring tide and at the neap tide. Sampling the following semi-lunar cycle would have already biased the result by the seasonal influence. Moreover samples taken one year later in the same time would show already temporal changes not the influence of tidal, diel and semi-lunar cycle therefore no replicates were taken. Like this we covered all possible combinations of tidal, diel and semi-lunar changes and thus should be able to picture the habitat value of an estuarine marsh creek in the Westerschelde estuary.

Most of the organisms caught were epibenthic or hyperbenthic species. Hyperbenthos includes all swimming bottom-dependent animals, which perform seasonal or daily vertical migrations above the bottom (Brunel *et al.* 1978). All species caught were small sized and it could be argued that all individuals are transported passively to the marsh creek. Yet, selective tidal transport is a well-documented mechanism by which small organisms reach upstream habitats. In the subtidal of the Westerschelde estuary Mees *et al.* (1993) recorded all the hyperbenthic mysids that were observed in the intertidal. These authors showed a clear spatial distribution of these mysid shrimp along the salinity gradient. This indicates that these animals are able to cope with the currents and able to maintain their position within the subtidal habitat. In the estuary subtidal currents are stronger (0.05-1.35 m s^{-1}) (Stroomatlas, 1992) than in the intertidal creeks (0.03-0.4 m s^{-1}).

Other species captured include juvenile goby, brown shrimp, palaemonid shrimp and the adult shore crab, which belong to the epibenthos. These animals always stay close to the bottom. *Corophium volutator* is a benthic species but with a capability to swim (Hughes, 1988). In the laboratory *C. volutator* rarely swam higher than about 25 cm from the bottom of the container (Meadows and Reid, 1966).

All species considered here thus occur relatively close to the bottom. The tidal migration patterns showed that species migrate actively to the creek and the water current did not transport them passively. It means that nekton species are able to cope with the water current. They keep their position close to the bottom of the creek and will not be lifted into the water column higher than the sampling net. This resulted that the species have been effectively sampled with the net and as such it is believed that the observations of this study reflect the reality.

2.4.1 Tidal changes

Tides were expected to have a profound influence on the species composition of the nekton fauna. Most organisms occurring in the marsh live predominantly in the intertidal, at least during their early life stages (Kneib, 1997). Lowered water levels force the animals to seek refuge in intertidal pools (Rozas and Zimmerman, 2000) or to retreat to the shallow subtidal. With rising water levels the intertidal habitat becomes available. Migrations onto and out of the intertidal are by necessity fully synchronised with the tides.

Focusing on the tidal migration of fishes and crustaceans into and out of marshes Kneib and Wagner (1994) found that individuals enter at an early tidal stage and leave late in the tidal cycle, allowing maximisation of their habitat use. Showing the importance of intertidal European marshes, Cattrijsse *et al.* (1994) mentioned similar tidal migration patterns for non-vegetated intertidal marsh creeks. These authors mentioned that during spring tide most species were generally found to migrate in highest numbers during the first and last hours of the tidal cycle. During the field campaign in the same creek, covering also neap tide and stages in between, the pattern was observed that most of the species occurred during all tidal cycles, regardless of day-night or lunar rhythms.

This pattern was most obvious for *Pomatoschistus microps*, the most common fish species in the marsh. The common goby uses the salt marsh creeks in the Westerschelde estuary as a nursery ground and feeding ground throughout most of its life (Cattrijsse *et al.*, 1994). Their stomach fullness index increases with flood and decreases with ebb indicating that gobies begin to feed when they enter the marsh. A maximum consumption is reached at the first hour of ebb (Cattrijsse *et al.*, 1994, Chapter 3). *Fundulus heteroclitus*, the most common fish in the marshes of the US East Coast, also shows a tide related feeding pattern (Weisberg *et al.*, 1981). In the subtidal of the Westerschelde estuary *P. minutus* is the most abundant fish (Hamerlynck *et al.*, 1993b). When co-existing, *P. minutus* dominates *P. microps* and the latter is pushed to the intertidal zone (Magnhagen *et al.*, 1982a). Possibly, this observation contributes to the explanation of the observed migration pattern.

The shore crab *Carcinus maenas* and the palaemonid shrimp *Paelaemonetes varians* also exhibited tidal migration patterns. Cattrijsse *et al.* (1997) observed that *Crangon crangon* enters the marsh creek for feeding early during flood and leaves late at ebb. However in the present study, this pattern was not clear for the brown shrimp even though migrations closely synchronised with tidal water movements have been observed before for this species (Al-Abhub *et al.*, 1975).

Similar observations have been made for the amphipod *Corophium volutator* (Morgan, 1965). *C. volutator* is a benthic species but a small portion of the population occurs in the pelagic population (Essink *et al.* 1989). Hughes (1988) found that amphipods swim most of the time when water covers the sediment. Swimming is not restricted to one specific life stage and it may be stimulated by several factors. In an estuary, Holmstrom and Morgan (1983) demonstrated that the swimming activity of *C. volutator* has a circa-tidal rhythm with maximum occurrence on ebb tide. Hughes (1988) also recorded the highest density after high water. These studies and our observation also show that *C. volutator* does swim however it may not prove a pure migration pattern. No evidence exists on the swimming distance or the fraction of the population that swims.

Neomysis integer followed the edge of the tidal cycle during most of the sampling days. It is a hyperbenthic euryhaline species and typically occurring in high numbers in estuarine, brackish water (Tattersall and Tattersall, 1951). In the Westerschelde estuary *Mesopodopsis slabberi* and *N. integer* are the major hyperbenthic species (Mees and Hamerlynck, 1992). Mysids are known as good swimmers (Mauchline, 1980) and can avoid nets in areas with high transparency water (Mees and Hamerlynck, 1992). However in the sampled intertidal creek turbidity is high, which excludes the possible avoidance. *M. slabberi* is a less intertidal species (Mees *et al*., 1993) making it less likely to occur in the marsh creek during lowered water levels.

2.4.2 Diel changes

Faunal surveys covering only daytime situations are believed to be less accurate than studies including night time sampling due to the daytime sampling bias and gear avoidance (Rountree and Able, 1997). Sampling during the night always raises the question whether the difference between the numbers of individuals caught is due to visual net avoidance by day. The constant high turbidity in the creek reduces the possibility that light conditions obscure migration patterns. Other studies have documented differences in diel abundance of fish moving in and out of intertidal vegetated habitats. Rooker and Dennis (1991) found that night time counts in a mangrove habitat were characterised by a marked reduction or complete absence of diurnally observed fish species. A similar observation was reported by Shenker and Dean (1979) for fish in an intertidal marsh creek. Changes in the level of activity during night are also known to occur, with some species being more abundant in marsh habitats at night (Rountree and Able, 1993).

This study had limited observation for night sampling but on these days changes in abundance between day and night occurred for at least *Pomatoschistus microps*, *Corophium volutator* and *Crangon crangon*. Kneib and Wagner (1994) suggested that nocturnal activity patterns allow fish to forage in relative safety from visually oriented predators. This is a less satisfying explanation for greater night densities since so many foraging opportunities (high tides during day) would not be used. It is quite unlikely also for *P. microps* that it would refrain from feeding at day and only feed at night. However the consumption of *P. microps* is different between day and night (Chapter 3.), and *P. microps* has been described as a daytime active fish (Magnhagen *et al*., 1982b). Feeding activity thus seems unlikely to explain the higher night abundance. Spawning activity can also be excluded since most individuals are juvenile. An increased predation pressure at night in the subtidal could cause a more intense immigration to the marsh habitat but no data were found to support this.

Burrows *et al*. (1994) observed an increase in activity of *Crangon crangon* moving closer to the bottom during night. This night activity could explain the higher catches in the marsh.

Holmstrom and Morgan (1983) in an estuary demonstrated that swimming *Corophium volutator* were present in daylight but more abundant in darkness. Hughes (1988) observed that swimming of benthic amphipods is a nocturnal activity. In this study, more *C. volutator* were caught during night, which can be attributed to the higher night activity. Other species did not show significant changes in abundance between day and night.

2.4.3 Semi-lunar changes

A change in species composition occurred during the seven sampling days. In the days around spring tide, the nekton assemblage was characterised by high densities for most of the species. Species using the intertidal marsh creeks seem to take full advantage of the highest water levels. At the other extreme, abundances were lowest during the lowest water levels, which occurred shortly after neap tide. The samples taken in between the maximum and minimum water levels had intermediate abundances.

The effect of the lunar or semi-lunar cycle on the community structure in tidal marshes is little documented. Existing observations are mainly about fish fauna. Davis (1988) pointed out that higher tides provide greater assistance for the upstream movement of several species causing differences in community structure over the lunar phases. He claims that fish benefit from stronger tides for transport into inundated areas. Shenker and Dean (1979) investigated short-term changes in a fish community of an intertidal marsh creek over a 14 day period but did not suggest that changes were associated with the lunar phase. Kneib and Wagner (1994) also observed little temporal variation in nekton abundance and found no evidence of an effect of a 'sampling week'. Although neither study reported on water levels, the first should have covered both spring and neap tide cycles and the intermediate moments. The latter study might have sampled only in between the moments of extreme water levels. Rooker and Dennis (1991) found little evidence for lunar periodicity on species abundance in a mangrove prop root habitat. Nocturnal fish assemblages of a small mangrove bordered estuary were not found to change between new and full moon phases (Quinn *et al*., 1981). However the reproductive cycle of *Fundulus heteroclitus*, which possibly has similar role in American intertidal areas as *P. microps* in Europe, was observed to be linked with the lunar-tidal cycle, which can influence the occurrence of this species in the intertidal area (Taylor *et al*., 1979; Kneib, 1986).

A full explanation of the observed semi-lunar influence on species composition is lacking. The simplest explanation is the longer habitat accessibility during spring tide however it does not explain why some individuals choose not to enter the marsh at neap tide and wait every 14 days to use the marsh habitat. The stronger water currents and the larger volumes of water moving during spring tide could passively bring more individuals into the intertidal however the observed tidal migration pattern contradicts the full passive tidal migration. Full passive tidal transportation could also not account for the drop in densities observed here at the highest water levels for most of the species (Fig.3). Semi-lunar feeding rhythms have been observed in juvenile gobies (Hamerlynck *et al*., 1993a). Such a variation in feeding rhythm, closely linked to activity, might explain the higher abundances in the intertidal creek. Hamerlynck *et al.* (1993a) also observed a drop in feeding intensity at the highest water levels. The density drop observed here may be linked to this decrease in feeding activity.

The first null-hypothesis was rejected as a strong tidal influence was observed leading the activity of several species in the studied intertidal creek. Observations showed that the most of the main species migrate in the first and the last hours of the tidal cycle while others like *Mesopodopsis slabberi* occurred in maximum numbers at high water. The second null-hypothesis was not proved because several species showed density differences during day and night. Diel changes influenced the density of some species however the few sampling events did able to elaborate further conclusions. The third null-hypothesis was rejected due to the observation that most of the species had different densities at spring and at neap tide and the community structure also differed between the lunar phases. However owing to the lack of more extensive data records a clear explanation of the latter phenomenon could not be with drawn. Therefore there is a need for more occasions with given set of conditions in order to reach firm conclusions and to obtain robust patterns.

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3 Temporal variation of the feeding rhythms in a tidal marsh population of the common goby *Pomatoschistus microps*

Abstract: *Pomatoschistus microps (Teleostei, Gobiidae) is intensively using the intertidal area of the mesohaline marsh 'Het Verdronken Land van Saeftinghe' as a nursery and a foraging ground. The sampling campaign covered the semi-lunar, diel and tidal cycles in August 1994. The density of P. microps and potential hyperbenthic prey species in the marsh creek, fullness index, evacuation rates and daily ration of common goby were calculated. Qualitative stomach analysis was also performed. Mesopodopsis slabberi, Neomysis integer and Corophium volutator were the most dominant prey items in terms of biomass. Numerically, copepods were still dominating the diet during most sampling days. The migrating fish enter the marsh creek with a relatively empty stomach and leave the marsh with a higher stomach content. Pomatoschistus microps seemed to feed more intensively during the day than the night however the influence of the diel cycle is less than the tidal influence on the feeding behaviour of the common goby. A significant difference in foraging activity occurred also between spring and neap tide. The common goby migrated in lower abundance into the creek during spring tide but foraged more intensively. Both at spring and neap tide, a significant difference was found in the fullness index between day and night. At spring tide, gobies feed more during the day while at neap tide they forage more intensively at night. All the three cycles (tidal, diel and semi-lunar) have an influence on the feeding rhythm of the common goby. The tidal influence is greater than the diel variation while the explanation of the combined effect of diel and semi-lunar cycle needs further studies.*

3.1 Introduction

The common goby, *Pomatoschistus microps*, is a small gobiid fish commonly found in all European coastal waters, estuaries, fjords, salt marshes and high shore pools (Petersen, 1919). In the intertidal area of the Westerschelde estuary (SW Netherlands), the common goby is one of the most abundant fish species (Maes *et al*., 1997; Hostens and Mees, 1999; Hostens, 2003).

The biology and ecology of *Pomatoschistus microps* has been intensively studied. The population structure (Bouchereau *et al.,* 1989, 1993; Pampoulie *et al*., 2001), breeding behaviour (Magnhagen, 1998; Pampoulie *et al*., 2001), age-structure, growth and reproduction (Arruda *et al*., 1993), food selection (Magnhagen, 1985) and the diet spectra of newly hatched gobies (Menher, 1992) all received attention. Despite these intensive investigations, no work has been published on the influence of different cycles (tidal, diel and lunar) on the migration or on the feeding rhythm of the common goby.

Three main functions have been ascribed to intertidal migration of fish: reproduction, avoidance of predation and feeding (Gibson, 1993). In the Westerschelde estuary, the common goby uses the marsh creeks between June and October (Cattrijsse *et al*., 1994). During this period several waves of early postlarval gobies enter the marsh creeks and remain there to spend their early life stage. Predation avoidance may result from the huge numbers of juveniles that stay in small pools and seepage water (Cattrijsse *et al*., 1997; Kneib, 1997). The marsh must harbour favourable conditions for nesting but Cattrijsse *et al.* (1994) never found nests. Cattrijsse *et al.* (1994) also mentioned that the common goby utilizes the marsh creeks as feeding grounds, preying mainly upon amphipods and mysids. The common goby shifts its feeding preference from copepods towards mysids and infaunal species during its life span at the size of 20 mm.

In general, three different cycles may influence the migration and feeding habits of intertidal fish species. The tidal effect is the most obvious for the movement of fish into the intertidal areas (Gibson, 1988). The availability of intertidal feeding areas depends upon the tidal phase. Several studies have investigated the tidal influence on the feeding behaviour of fish in the salt marshes (Weisberg *et al.,* 1981; Rozas *et al*., 1988; Rozas and LaSalle, 1990; Rountree and Able, 1992).

A second important cycle is the diurnal variation. The activity of most marine fishes is synchronised with the daily cycle of light and darkness (Gibson, 1993). The diurnal influence on the feeding activity of fish in tidal marshes has received some attention (Kneib and Stiven, 1978; Weisberg *et al*., 1981; Cadigan and Fell, 1985; Antholz *et al*., 1991). Weisberg *et al.* (1981) argued that diel rhythms would result in reduced feeding on the marsh surface.

The semi-lunar phases form a third cyclic effect on the migration and feeding behaviour of intertidal fish however its influence is poorly studied. Changes in abundance of fish species in marsh areas related to the semi-lunar cycle of spring and neap tides have been documented by Rooker and Dennis (1991) and Kneib and Wagner (1994). The influence of the semi-lunar cycle on the feeding activity of fish has not often been investigated. Only Hamerlynck *et al*. (1993) observed a semi-lunar feeding rhythm in juvenile *Pomatoschistus lozanoi* from a sandy beach. Integrated work about the influence of the tidal, diel and semi-lunar cycle on the feeding habit of intertidal fish does not exist.

Marsh creeks and other intertidal habitats are believed to play a significant role in the early life stages of many fish and crustacean species as feeding grounds. A full appreciation of the value of such habitats necessitates more information than tidal feeding rhythms. Day-night changes in feeding activity and fluctuations in stomach contents over a semi-lunar cycle are needed to fully understand the functioning of such feeding grounds and to quantify their importance in the food web of the marsh.

The study aims to describe the feeding habit of juvenile *Pomatoschistus microps* during the semi-lunar period, to investigate the separate and combined effect of the tidal, diel and semi-lunar cycle on the feeding behaviour of juvenile common goby in a salt marsh creek and to quantify the change in tidal food consumption.

3.2 Material and Methods

3.2.1 Study Area

The studied marsh ‘Het Verdronken Land van Saeftinghe’ lies in the mesohaline part of the Westerschelde estuary (Figure 1). It is the largest estuarine brackish marsh in Europe with a surface area of 2800 ha (Dijkema *et al*., 1984). All samples were collected in an intertidal creek measuring 1600 m long and 4 m deep at the sampling point. Every tidal cycle the creek falls completely dry for at least 5 hours. Water starts entering the marsh 3 hours before high water and leaves the creek 4 hours after high water. There is no connection to any other major creek in the marsh and there is no tidal flat and pools at the mouth of the creek. The channel showed a sigmoid shape close to the estuary however at the sampling point the creek was straight and the slopes of both banks were symmetrical.

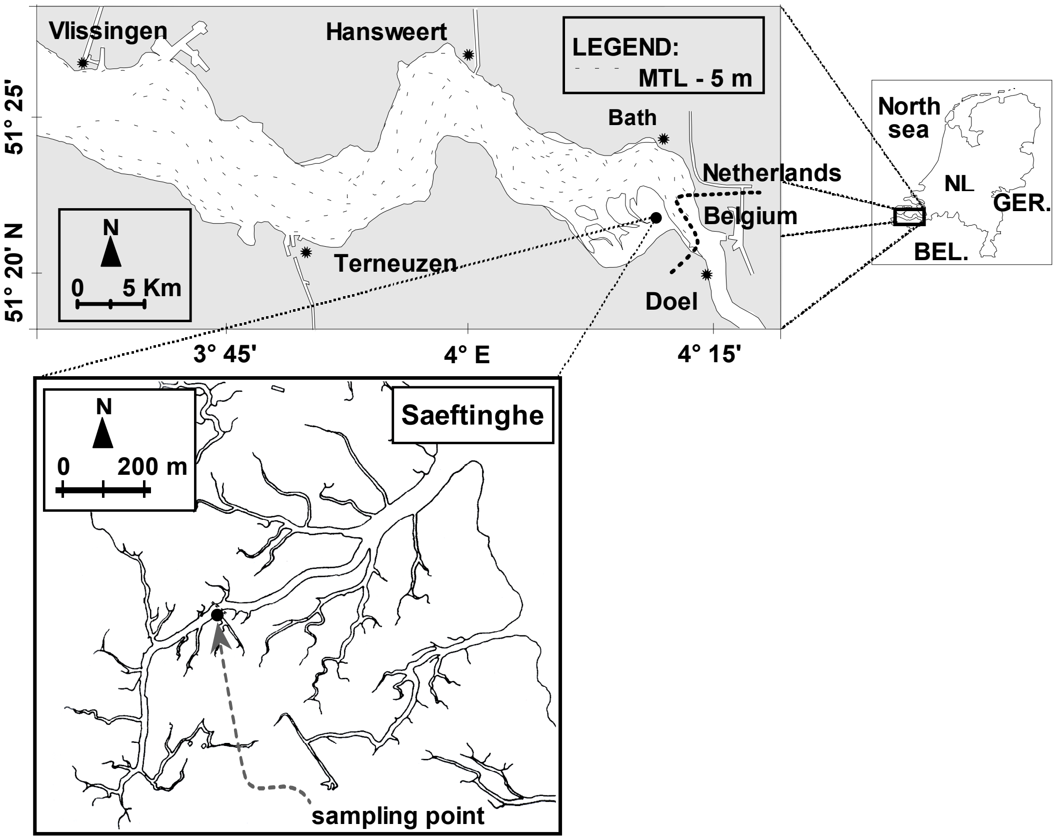

Figure 1. The Westerschelde estuary in the SW Netherlands and the positioning of the marsh 'Het Verdronken Land van Saeftinghe' and the sampling site.

3.2.2 Sampling

Sampling took place from upon a bridge spanning the creek. A stow net with a 1x1 mm mesh size, an opening of 1x1 m and a length of 5 m was used. The net was placed on the bottom to sample passively the migrating fish and the potential hyperbenthic prey species in the first metre of the lower water column. Hyperbenthic species were defined, as animals found in the first metre of the lower water column, larger than 1 mm and capable of actively migrating with the moving water. Two weights attached to the sides of the frame prevented the net from being lifted by the currents, while ropes kept the net in place during sampling. The opening size of the net, the mesh size and the thickness of the fibre were used to calculate the necessary length of the net in order to keep the pressure inside the net under all current conditions (Tranter, 1979). This reduced the probability that animals avoided the net.

The net fished during one hour, was rinsed and then replaced in the same position. After high water the net was turned to sample the ebb current until all water had left the creek. Sampling lasted a complete tidal cycle yielding 3 flood (F1, F2 and F3) and 4 ebb (E4, E5, E6 and E7) samples on every sampling occasion. Water current and water height were measured every 15 minutes. Current speed was measured in every 15 minutes with a current meter, placed about 20 cm above the bottom next to the net. The water height was measured with a ruled stake placed next to the net in the deepest part of the creek.

August was chosen for sampling because in Saeftinghe density and biomass of *Pomatoschistus microps* peaks during this month (Cattrijsse *et al.*, 1994). To cover the semi-lunar cycle, observations were made between 7 and 19 August 1994 from full moon till new moon covering the possible combinations of the diel, tidal and semi-lunar cycles (Table 1). Eight and 10 August were considered as spring tide while 16 and 17 of August were defined as neap tide according to the predicted water height. Due to the weather conditions the spring tide period slightly shifted and peaked on 10 of August.

Table 1. Selected sampling days and periods during the semi-lunar cycle with predicted water heights (1) (cm above the Dutch ground level NAP) and observed maximum water height (2) (cm above the Dutch ground level NAP) in the marsh creek in August, 1994. Filled blocks in diurnal phases indicate night hours during the sampling campaign. Tidal phase is labelled with F1-F3 as flood hours and E4-E7 as ebb hours. The moment of high water (HW) is indicated by a vertical line.

Date	*Time*	Tidal Phase HW F1−F3, E4 − E7	*Diurnal Phase*	*Moon Phase*	*Lunar Phase*	*Waterheight* 1.	 2.
7 Aug	13:30 - 20:45	□□□|□□□□	day	full		297	340
8 Aug	02:20 - 09:35	■■■|■□□□	**night**		spring	319	350
10 Aug	15:30 - 23:00	□□□|□□■■	day		spring	319	380
13 Aug	17:05 - 01:15	□□□|□■■■	day			289	360
16 Aug	20:55 - 04:25	■■■|■■■■	**night**		neap	235	290
17 Aug	09:25 - 17:00	□□□|□□□□	day		neap	224	295
19 Aug	12:00 - 19:30	□□□|□□□□	day	new		276	340

Both at spring and at neap tide day and night samples were taken however with some restrictions. At neap tide high water always occurred around midnight or midday, hence taking full night or daytime tidal samples did not present a problem. During spring tide, high water was always in the late afternoon or early morning. Complete night sampling was thus not possible during spring tide. 8 and 16 August were considered as night samples since the organisms moved into the creek during night. On 10 and 13 of August night hours fell when ebb had started already and evening hours did not influence the migration, hence these sampling days were considered as complete day samplings.

In the field, all the fishes were anaesthetised in a benzocaine (Ethyl amino-4-benzoate)-water solution to prevent regurgitation of the stomach contents. The gobies and the captured hyperbenthic species were preserved in a 10% formalin-brackish water solution.

3.2.3 Data processing and analysis

The number of gobies that entered or left the creek during one sampling hour were expressed as a percentage of the total number of individuals that migrated in or out of the creek. The total number of individuals entering the creek during the 3 flood hours was considered to be 100%. The number of individuals captured during each hour of flood was expressed as a percentage of the total number capturing during the entire flood tide. Likewise, the total number of individuals captured on leaving the creek with ebb were taken as 100% and the number captured during each ebb hour was expressed as a percentage of that total. Using the total number of individuals and the total volume of water passing through the net during one hour, the density was estimated in the lower metre of the water column. The densities of the 3 flood samples were summed which yielded an estimate at high water. Densities were also calculated for every ebb hour also using the total number of individuals and volume of water leaving the creek. The sum of these four densities also yielded an estimate at high water. The abundance of the species at the moment of high water of each tidal cycle was calculated by averaging the flood and the ebb estimate. This calculation was performed for the common goby and also for its preys. The species, which were found in the creek and in the stomachs of the *P. microps* were considered as prey species (Table 3). The densities of these species were summed and defined as the total prey density.

A maximum of 20 fish between 20 mm and 30 mm standard length (SL) were selected at random from all sampling hours of the tidal cycle and their stomach content was analysed. In the laboratory, all prey items encountered were counted, identified, if possible to species level, and the length of each individual was measured. The biomass (mg ADW m^{-3}) of each prey item present in the stomachs was computed with length-ADW (ash free dry weight) regressions established formerly in the laboratory by Hamerlynck and Cattrijsse (1994) and Beyst *et al.* (1999). Stomach contents were placed in pre-weighed aluminium foil cups, dried at 110 °C for 5 hours and cooled to room temperature in a dessicator for 2 hours before weighing.

For statistical analysis stomachs were classified in different groups like flood and ebb, day and night and spring tide-day, spring tide-night, neap tide-day and neap-tide night. Night samples were 8 and 16 of August and day samples were 7, 10, 13, 17 and 19. According to the water height prediction, spring tide samples were taken on 8 and 10 of August and neap tide samples on 16 and 17. Stomachs samples on 7 of August were considered as spring tide-day and on 8 of August as spring tide-night samples. Neap tide-day samples were taken on 17 and neap tide-night samples on 16 of August.

For the quantitative analysis of the stomach contents, the fullness index (FI), was used:

$$\mathrm{FI} = \frac{S_i}{W_i} \times 100 \tag{1}$$

where S_i is the ash-free dry weight (ADW) of the stomach content in milligram (mg) and W_i is the ash-free dry weight of the fish in mg. The mean FI and standard error (se) were determined for every hour of the tidal cycles (F1-E7) and every day of the semi-lunar cycle (7-19 of August).

As a simple measure of niche overlap between spring and neap tide the Renkonen index of similarity (Hurlbert, 1978) was calculated from the numerical and the biomass of different prey types in the diet of gobies.

$$C_{xy} = 1 - \frac{\sum_i | P_{xi} - P_{yi} |}{2} \tag{2}$$

where p_{xi} and p_{yi} are the proportions of the prey species ‘i’ in the total numbers or biomasses of items at spring tide and at neap tide.

To assess niche breadth of the common goby during the semi-lunar cycle the Shannon Wiener diversity index (Pielou, 1966) was calculated for each sampling day.

$$H' = -\sum p_i \times \ln p_i \tag{3}$$

where p_i is the proportion of the individuals found in the ‘i’th species.

For qualitative stomach analysis the food composition was expressed as gravimetric percentage (G%):

$$G\% = \frac{\text{ADW of prey type}_i}{\text{Total ADW of the ingested food}} \times 100 \tag{4}$$

and as a numerical percentage (N%) (Hyslop 1980):

$$N\% = \frac{\text{Number of prey type}_i}{\text{Total number of the prey items ingested}} \times 100 \tag{5}$$

Eggers' (1977) model was followed to estimate the daily ration during the complete tidal cycles. According to this model, the daily ration (R_d) is determined as:

$$R_d = \overline{FI} \times E \times T \tag{6}$$

where $\overline{FI}$ is the average fullness index of all fish collected, E is the instantaneous rate of gastric evacuation and T is time. Calculating the daily ration for the tidal cycle T equalled with 7. Andersen (1984) calculated gastric evacuation for *Pomatoschistus microps* as:

$$E = 7.385 \times TL^{-0.832} \times e^{0.0639\,(T-20)} \tag{7}$$

where TL is the total length of the fish and *T* is the ambient temperature. TL was calculated from TL-SL regressions established in the laboratory.

Number of *Corophium volutator, Nereis diversicolor, Neomysis integer* and *Mesopodopsis slabberi* was counted in the marsh creek in every hour of the tidal cycle. The sum of the counts in the 7 hours of the tidal cycle yielded an estimate of the available prey items in the marsh creek. In the stomach of gobies the number of individuals belonging to these four species was also counted. The minimum consumption of *Pomatoschistus microps* (larger than 20 mm) was calculated from the available number of prey in the marsh channel and the numbers of prey items found in the fish stomachs.

Spearman-Rank tests analysed the correlation between the number of gobies and the average FI's of each hour sample with the recorded water height. To evaluate the semi-lunar influence the same analysis tool was used to test the relationship between the daily densities, the daily average FI's, the daily total prey densities and daily ration vs. the predicted maximum water height during the semi-lunar cycle.

The predicted water heights were used rather than the observed ones because these were more representative of the lunar cycle. Due to meteorological conditions the maximum water heights during the 10 and 13 August were higher than predicted. This caused a shift of the highest water levels after the true springtide. On the 13 the moon was already in its last quarter.

Also the relationship between the average FI's vs. the prey density during the semi-lunar cycle was tested by Spearman-Rank correlation.

Mann–Whitney U tests were applied to test the influence of the tidal, the diel and the semi-lunar cycle on the fullness index. The fullness indices were compared between flood and ebb tide, day and night hours, and between spring and neap tide.

Since the ANOVA analysis was not applicable for the dataset due to the lack of normal distribution and the strong correlation between the mean and the standard deviation the interactions between the different cycles were investigated by using the non-parametric Kruskal-Wallis test. The results of the Kruskal-Wallis test were verified by a post-hoc Multiple Comparisons tests (Conover, 1980).

3.3 Results

3.3.1 Densities of the common goby and its prey species

During all sampling occasions the common gobies exhibited a similar tidal migration pattern (Figure 2). Highest numbers were observed in the earliest flooding water (46-87 %) and during the last hours of the ebbing tide (14-86%). Gobies migrated in low numbers during the high water (minimum 0.12%). A significant and negative relation existed between the number of gobies and the recorded water height of each hour (Spearman-Rank correlation, $p< 0.01$) (Table 2).

Table 2. Results of Spearman-Rank correlation comparing different variables. Significant values are given with bold numbers and direction of the correlation (+ or -) is indicted.

Tidal cycle			**Semi-lunar cycle**		
Variables		p value	*Variables*		p value
No. of fish	Recorded water height	**< 0.001 (-)**	Daily density of fish	Predicted water height	0.21
Average FI	Recorded water height	**0.02 (+)**	Daily average FI	Predicted water height	0.21
			Daily total prey density	Predicted water height	**0.003 (+)**
			Daily ration	Predicted water height	0.06
			FI of fish	Prey density	**0.04 (+)**
			Shannon Wiener index	Prey density	**0.002 (+)**

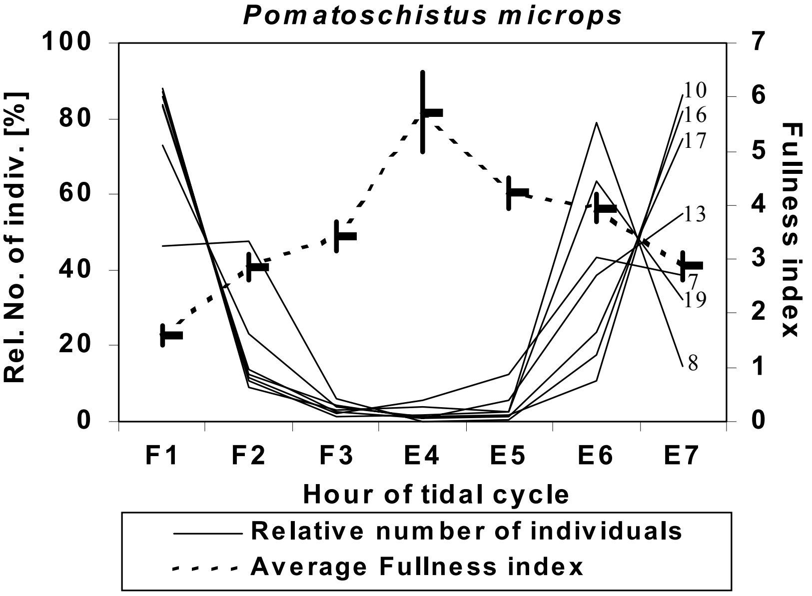

Figure 2. Relative numbers of Pomatoschistus microps (full line), the average fullness index (dashed line) and standard error, for each hour of the tidal cycle. F1-F3 represents the flood hours and E4-E7 the ebb hours of the tidal cycle. The sampling dates are indicated next to each line representing the relative number of individuals.

Night-time densities of common goby were higher than the previous or the following daytime densities (Figure 3a). On 7 August, during day at high tide, 4.2 ind. m^{-3} were found while the density at night, on the 8, was estimated to be 8.8 ind. m^{-3}. The night time density of 16 August was 11.5 ind. m^{-3} while it reached only 9.4 ind. m^{-3} the following day on 17.

Over the semi-lunar cycle, the density of *Pomatoschistus microps* seemed to be higher at neap tide than at spring tide (Figure 3a) but no correlation was found with the water predicted height (Spearman-Rank correlation p=0.21) (Table 2). On 10 August, when the water height reached a maximum, the density dropped to 1.3 ind. m^{-3}.

The total density of potential prey species did follow the change of water height during the semi-lunar cycle (Spearman-Rank p=0.03) (Table 2) with higher values at spring tide (maximum 181.9 ind. m^{-3}) than at neap tide (minimum 2.5 ind. m^{-3}) (Figure 3c). At the highest water level (10 of August), a drop of density also occurred (88.4 ind. m^{-3}). The average fullness index of *Pomatoschistus microps* showed a positive correlation with the total density of potential prey during the semi-lunar cycle (Spearman Rank correlation p=0.04) (Table 2).

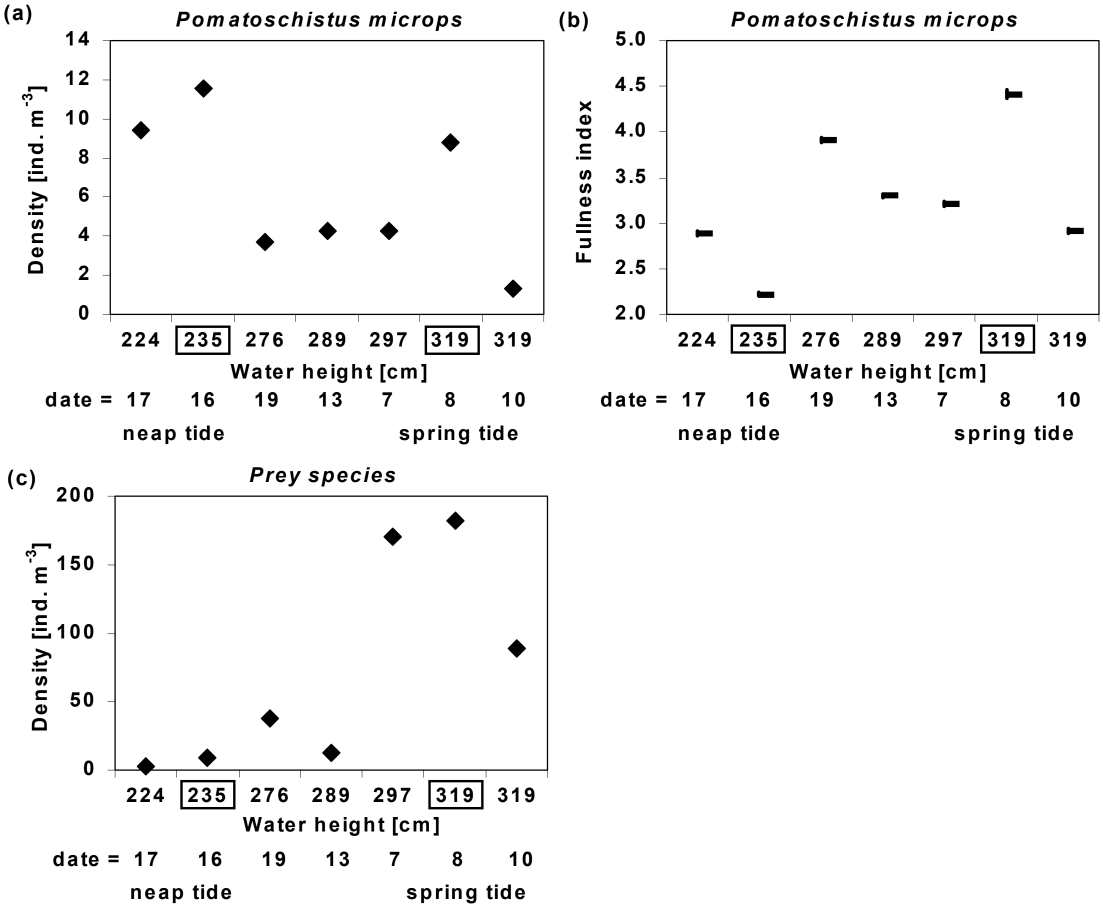

Figure 3. Density of common goby (a), the average stomach fullness index (FI) with standard error (b) and the density of potential prey species occurring in the marsh creek (c) during the semi-lunar cycle. The predicted water height (cm) is representative for the phase of the semi-lunar cycle. Night samplings are labelled with rectangles.

3.3.2 Qualitative stomach analyses

All taxa found in the stomach of *Pomatoschistus microps* are listed in Table 3. Among these taxa the amphipod, *Corophium volutator, Gammarus salinus*, *Gammarus zaddachi*, the mysid *Neomysis integer, Mesopodopsis slabberi,* the isopod *Lekanesphaera rugicauda*, *Eurydice pulchra*, the decapod *Crangon crangon, Carcinus maenas*, the polychaeta *Nereis diversicolor* and insects were also sampled in the marsh creeks.

The qualitative stomach analyses showed that few species were important in the diet of the juvenile gobies (Figure 4). Numerically, copepods (Harpacticoidea and Calanoidea) were dominating the diet during most of the sampling days (16.3-65.7%). *Corophium volutator* and also *Mesopodopsis slabberi* were often taken by the juvenile common gobies (maximum 39.4 and 45.3% respectively). *Nereis diversicolor* was not a common food item in the marsh creek. The two mysid shrimps, *M. slabberi* and *N. integer* and the infaunal amphipod, *C. volutator* were the most dominant prey items in terms of biomass and reached the maximum of 46.6, 38.6 and 59 gravimetric percentages respectively. There were no clear changes in diet composition detected over the semi-lunar cycle.

Table 3. Taxa occurred in the stomachs of *Pomatoschistus microps*. Asterisks label the species captured also in the marsh creek and considered as prey species for *P. microps*.

Amphipoda		**Brachyura**	
Corophium volutator	*	*Carcinus maenas* (juvenile)	*
Gammarus salinus	*	*Carcinus maenas* (megalopa)	*
Gammarus zaddachi	*		
Melita pellucida		**Copepoda**	
Orchestia spp.		Calanoidea	
		Harpacticoidea	
Mysidacea			
Mesopodopsis slabberi	*	**Polychaeta**	
Neomysis integer	*	*Nereis diversicolor*	*
Schistomysis kervillei		*Spio* spp.	
Isopoda		**Others**	
Lekanesphaera rugicauda	*	*Acarina* spp.	
Eurydice pulchra	*	*Cumacean* spp.	
Cyathura carinata		Insect	*
Idotea spp.		Fish eggs	
		Nematoda spp.	
Caridea		Oligochaeta	
Crangon crangon	*	Syphon of bivalve	

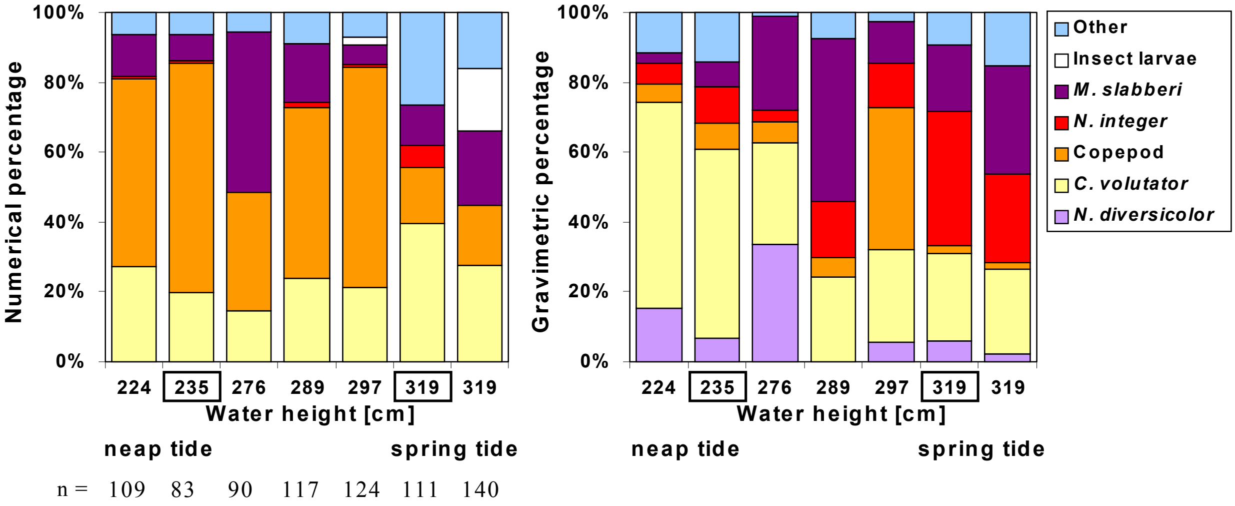

Figure 4. Numerical (N%) and gravimetric (G%) percentage of the stomach content of Pomatoschistus microps over the semi-lunar cycle. Species are labelled as follows: Corophium volutator (C. volutator), Neomysis integer (N. integer), Mesopodopsis slabberi (M. slabberi), Nereis diversicolor (N. diversicolor). Predicted water height (cm) is used to indicate the lunar phase. Night samples are labelled with rectangles and the number of stomachs analysed (n) is indicated under each sampling occasion.

Renkonen index of similarity was calculated for spring tide (8 and 10 of August) and neap tide (16 and 17 of August). Using numerical data the calculation produced a value of 0.57. An index of 0.46 was obtained using biomass data. The index values greater than 0.6 are considered biologically significant. The indices calculated with numerical and biomass data indicated that there was no significant overlap in the diet of *Pomatoschistus microps* during spring tide and neap tide.

Shannon Wiener diversity indices of the stomach content of *Pomatoschsitus microps* showed smaller niche breadth during neap tide (1.15 and 1.09) than during spring tide (1.90 and 1.84) (Table 4). The density of prey species positively correlated with the calculated diversity indices (Spearman Rank correlation, p=0.002) (Table 2).

From the available number of *Corophium volutator, Nereis diversicolor, Neomysis integer* and *Mesopodopsis slabberi* in the marsh creek the common gobies consumed an average of 39.9 %, 32.2 %, 0.5 % and 2.8 % respectively during the semi-lunar cycle.

Table 4. Predicted water height (cm) and Shannon Wiener diversity index of stomach content of *Pomatoschistus microps* calculated during the semi-lunar cycle. Bold letters indicate the night sampling occasions.

Predicted water height	Shannon Wiener index
224	1.15
235	1.09
276	1.25
289	1.42
297	1.19
319	1.90
319	1.84

3.3.3 Quantitative Stomach Analyses

3.3.3.1 Tidal cycle

Every fullness index of the first hour of the seven sampling days were averaged and similar calculations were carried out for the other hours of the tidal cycle. A clear change in the amount of food in the stomachs of the juvenile common gobies was observed (Figure 2) and the Spearman-Rank analysis did show a positive significant correlation with the change of the water height (p= 0.02) (Table 2).

Gobies started to feed upon entering the creek and continued doing so until high water when the overall average fullness index reached a maximum of 5.7. The consumption reduced after that moment and the fullness index started to drop progressively over the ebbing tide.

The tidal effect on the intertidal feeding of the common goby has been tested with a Mann-Whitney U-test, combining all flood FI's and all ebb FI's. The amount of food present in the stomachs was significantly higher during ebb than during the flood period (Table 5, Fig. 5a).

Feeding activity was thus the most intense during flood when gobies entered the creek with low food content in the stomachs and reached a maximum around high water. After that the food items gradually passed through the gastrointestinal canal keeping the total amount of food present during ebb higher than during flood.

3.3.3.2 Diel cycle

To detect the difference in diel feeding activity fish were collected both at daylight and night time tidal cycles. A Mann-Whitney U test indicated a significant (p=0.03) higher feeding activity during day (FI= 3.41) than during night (FI=3.19) (Table 5 and Fig. 5b).

Investigating the combined effect of tidal and diel cycle on the feeding activity of the juvenile gobies, Kruskal-Wallis tests showed a significant difference (p<0.001) between the four groups of day-flood, day-ebb, night-flood and night-ebb (Table 5).

Multiple Comparisons proved significant differences between day-flood and day-ebb and between night-flood and night-ebb samples (Table 5). During both day and night the fullness index was higher during ebb (Fig. 5d). There was no significant difference detected between day-flood vs. night-flood and between day-ebb vs. night ebb indicating that the tidal stimulus was dominant over the diel cycle.

Table 5. Mann-Whitney U test, Kruskal-Wallis and Multiple Comparisons tests showed the effects of tidal, diel and semi-lunar cycles on the fullness index of the common goby.

Mann-Whitney U test			*Kruskal-Wallis test*			*Multiple comparisons*		
Compared groups		p value	Compared groups		p value	Compared groups		Level of significance
Flood	Ebb	**<0.001**	Day-flood	Night-flood	**<0.001**	Day-flood	Night-flood	non significant
Day	Night	**0.03**	Day-ebb	Night-ebb		Day-ebb	Night-ebb	non significant
Spring tide	Neap tide	**<0.001**				Day-flood	Day-ebb	**significant**
						Night-flood	Night-ebb	**significant**
			Spring-day	Neap-night	**0.002**	Spring-day	Spring-night	**significant**
			Spring-night	Neap-day		Neap-day	Neap-night	**significant**
						Spring-day	Neap-day	non significant
						Spring-night	Neap-night	**significant**

3.3.3.3 Semi-lunar cycle

The feeding activity of juvenile *Pomatoschistus microps* was also closely related to the semi-lunar cycle.

A Mann-Whitney U test indicated a significant difference (p<0.001) between spring tide (FI=3.74) and neap tide samples (FI=2.63) (Table 5 and Fig 5c) although a Spearman-Rank test did not show a correlation between the change of the fullness index and the water height during the semi-lunar cycle (p=0.21) (Table 2). Compared to the other spring tide day (8 of August), low average fullness index was observed on 10 August at the peak of the spring tide (observed water height, 380 cm) (Fig. 3b).

A Kruskal-Wallis test detected a combined effect of the lunar phase and the diel cycle (four groups of spring-day, spring-night, neap-day and neap-night) (p=0.002) (Table 5).

Multiple Comparisons showed significant differences between some of these groups (Table 5). Comparing spring-day versus neap-day no significant difference was found in contrast to the spring-night vs. neap-night combination. At daytime *Pomatoschistus microps* seemed to have a similar feeding habit regardless of the lunar phase (FI is around 3). Yet, at spring tide gobies foraged more during night-time (Fig 5e).

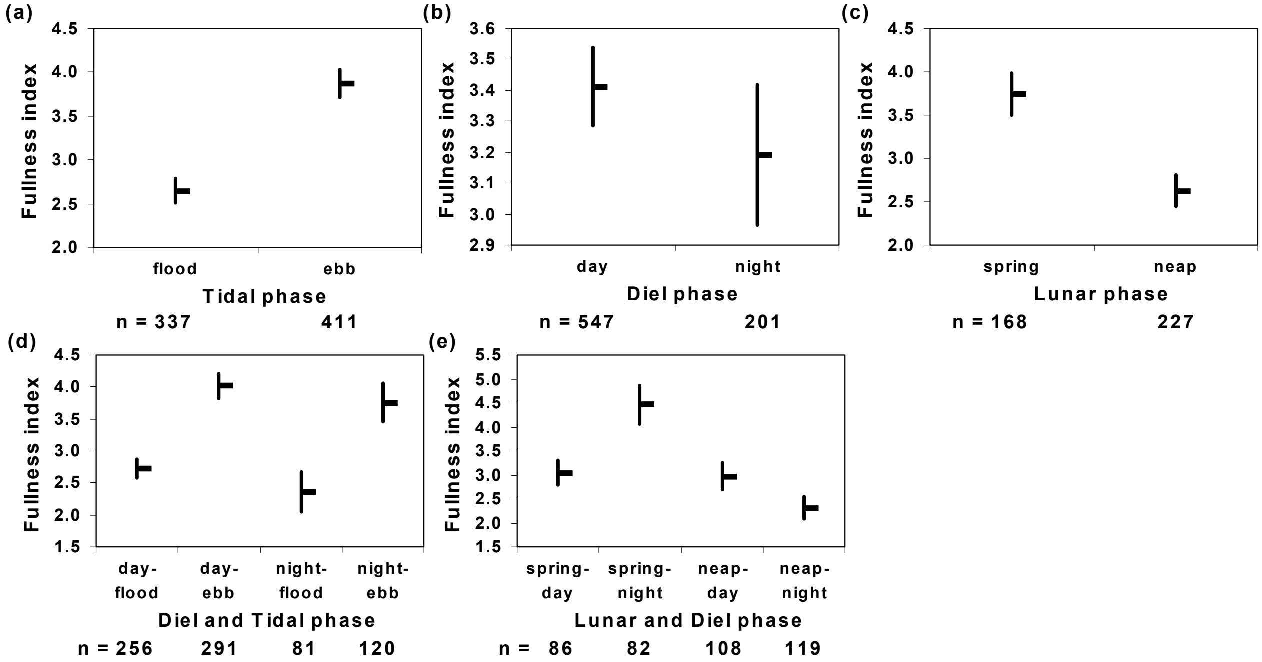

Figure 5. Mean fullness index (FI) ± standard error of the common goby in the two phases of tidal (a) diel (b) and semi-lunar (c) cycles and the combination of diel-tidal (d) and semi-lunar-diel cycles (e). The numbers of observations (n) are indicated below each graph. The similar signs above each average fullness index show the significantly different groups.

3.3.4 Consumption

The daily ration as estimated with the model of Eggers (1977) ranged between 8.2% and 16.5% of the body ash free dry weight (ADW). The fluctuation in the consumption along the semi lunar cycle followed the same trend as shown with the FI. Lower values were calculated at neap tide (minimum 8.2 % ADW of the body weight) and higher consumption was detected at spring tide (maximum 16.5%). Again, a low value occurred at the peak of spring tide (Table 6). Probably this drop caused the lack of correlation between the daily ration and the predicted water height during the semi-lunar cycle (Spearman-Rank correlation, p= 0.06) (Table 2).

Table 6. Sampling dates, predicted water height (cm), water temperature (°C), gastric evacuation (Andersen, 1984) and the daily ration as estimated with Eggers' model along the semi-lunar cycle.

Date	Water height	Water temperature	Gastric evacuation	Daily ration
17	224	24.4	0.45	9.6
16	235	23.2	0.49	8.2
19	276	24.9	0.45	12.3
13	289	24.3	0.47	11.0
7	297	22.8	0.64	14.1
8	319	23.0	0.51	16.5
10	319	23.4	0.58	11.4

3.4 Discussion

Magnhagen (1986) showed that *Pomatoschistus microps* forage mainly on *Corophium*, chironomids, *Nereis*, Harpacticoids and Ostracods in a fjord of south-west Sweden. In the present study copepods and *Corophium volutator* dominated numerically the diet of fish. Gravimetrically *C. volutator, Nereis diversicolor, Mesopodopsis slabberi* and *Neomysis integer* were important. Fish size significantly affects the type and size of prey species taken (Gardner, 1996). Gobies smaller than 20 mm forage mainly on copepods (Cattrijsse pers. comm.) therefore individuals larger than 20 mm were chosen for stomach analysis. Townsend and Hughes (1981) considered that when fish face with a choice of food items, they would accept only those items that would provide the maximum net energy per unit foraging time. Therefore largest fish may be expected to take the largest size prey species, which are available and with which it can morphologically deal with. The size of the fish used for stomach analysis ranged between 20-30 mm to minimise the size effect on the feeding habit.

The Shannon Wiener diversity indices were relatively high showing that gobies are more opportunistic feeders than specialists. Wider niche breadth was observed during spring tide than neap tide. Important prey species (e.g. mysids, *Corophium volutator*) migrate in the creek in higher density during spring tide (Chapter 2), which may cause the observed pattern. At neap tide when the larger preys had lower abundances fish tend to forage more on the available smaller prey items like copepods.

The niche overlap index value between spring and neap tide also indicated that gobies have slightly different feeding habit between spring and neap tide. The observation was probable due to the density differences of prey species, which may also indicates that gobies forage on the prey items that are available. Additionally, turbidity of the marsh creek is high (Chapter 7) resulting longer foraging time, which may cause fish to be more opportunistic feeding on all that is encountered.

From the available number of *Corophium volutator*, *Nereis diversicolor*, *Neomysis integer* and *Mesopodopsis slabberi* in the marsh creek common gobies consumed on average 39.9%, 32.2%, 0.5% and 2.8% respectively during the semi-lunar cycle. These values indicate that gobies did not represent large predation pressure on the mysids. Prey items were very abundant and they did not restrict the utilisation of the marsh creek habitat by *Pomatoschistus microps*. The consumption of gobies from the calculated stock of *C. volutator* and *N. diversicolor* seems high. Sampling method (stow net) resulted in that only the preys swimming in the lower metre of the water column were captured. Since *C. volutator* and *N. diversicolor* are benthic species their calculated density reflected only the part of the population, which swim. These densities are much lower than the ones calculated from macrobenthic samples (Chapter 5). This explains the high consumption of gobies from the available stock of *C. volutator* and *N. diversicolor*.

All organisms living in the intertidal areas are under the dominance of the constant tidal movement and are forced to adapt their life to this changeable environment (Kneib and Wagner, 1994; Rozas, 1995). This study showed clear effects of the tidal, the diel and the semi-lunar cycles on the feeding habit of the common goby. The influence of these cycles was not equal.

3.4.1 Tidal influence

The tidal cycle strongly influences the migration and the feeding activity of the common goby. To maximize the time spent in the marsh creek *Pomatoschistus microps* migrate at the first and last hours of the tidal cycle. When the water starts to enter to the creek, a high number of individuals entered the marsh with relatively little food in their gut. Maximum foraging activity coincided with flood. Two hours before the creek dries out gobies start to leave the marsh with the outgoing tide and their gut contained significantly more food than upon entering to the creek. In the northern Wadden Sea, Norte-Campos and Temming (1994) also found a peak feeding activity of *Pomatoschistus microps* at high tide, which decreased with the outgoing tide. *Fundulus heteroclitus*, which occupies a comparable niche in the North American intertidal marshes, exhibits a similar migration and foraging pattern (Weisberg *et al*., 1981; Allen *et al*., 1994; Kneib and Wagner, 1994). The more subtidal species, *Pomatoschistus minutus*, also shows a peak in feeding activity at high water in the Ythan estuary (Healey, 1971), while in more stable conditions this species has an endogenous circatidal rhythm with peak activity around low water (Gibson and Hesthagen, 1981). Macrocrustaceans also represent a similar foraging pattern as *P. microps*. Cattrijsse *et al*. (1997) reported from the marsh of Saeftinghe that *Crangon crangon* had highest fullness index at high water which gradually decreased during the ebb. Blue crab (*Callinectes sapidus*) also had greater gut fullness during high tide in a salt marsh of the Chesapeake Bay (Ryer, 1987). On the intertidal areas where species have to adapt to the constant change of the environment, the tidal stimulus seems a prime factor to govern the behaviour of nektonic species (Rozas and Reed, 1993; Rozas, 1995).

3.4.2 Diel influence

In Saeftinghe, the common goby was feeding more intensively during day. *Pomatoschistus microps* is active during day hours in the Baltic brackish fjords (Antholz *et al.,* 1991). As gobies search for their prey especially by sight (Hesthagen, 1980), foraging at dusk becomes more difficult. Magnhagen and Wiederholm (1982) observed the same day-active pattern.

Other studies showed different observations about gobiid fish. In a tide less environment Berge *et al*. (1983) found *Pomatoschistus minutus* to be mainly night active. Evans (1984) could not detect any diurnal rhythm in feeding activity of this species. *P. lozanoi* also feeds more intensively at night (Hamerlynck *et al.,* 1993). Gibson (1993) stated that the activity of most fish is clearly synchronised with the light-dark cycle, but in the sea there is an additional tidal stimulus.

This study showed that the tidal stimulus is superior over the influence of diel variation on the feeding habit of *Pomatoschistus microps* in the intertidal marsh. A tidal dominance seems reasonable since the utilization of the marshes by fish and macrocrustaceans is restricted to the time of the inundation period (Kneib and Wagner, 1994). Being more influenced by the diel variation rather that the tidal cycle, several foraging opportunities would be lost. Weisberg *et al*. (1981) made similar observations and found that the tidal variation is more important than diurnal rhythms in controlling the feeding of *Fundulus heteroclitus*. These authors and also Clymer (1978) showed that when nocturnal feeding occurred, feeding activity was significantly less than the feeding peaks found during daytime.

3.4.3 Semi-lunar influence

Scientific observations examining the effect of the semi-lunar cycle on the foraging activity of fish species are largely lacking. Campana and Neilson (1985) and Hamerlynck *et al*. (1993) pointed at the existence of bands on the otoliths of fish and the relation of these bands with a semi-lunar periodicity in growth and thus food consumption. These bands consisted of fourteen daily growth rings. Narrow rings alternated with wider rings. Arrellano (1995) prooved that the wider daily growth rings in *Pomatoschistus lozanoi* observed by Hamerlyck *et al*. (1993) coincided with spring tide and the narrower ones with neap tide. These observations thus proofed that food consumption followed a semi-lunar pattern and feeding intensity would differ between neap and spring tide. Hamerlynck *et al*. (1993) indeed observed in the subtidal of a sandy beach of The Netherlands that the feeding intensity of *P. lozanoi* was related to the spring-neap tide. Also Morton *et al*. (1987) reported that feeding index values for most of the salt marsh visiting fishes were higher when water depth reached a maximum because then larger areas of salt marshes were available for extended periods. The data of this study indicated a significant higher fullness index during spring tide although a drop in average FI at the highest water occurred. The highest water levels and currents may represent a stressful environment, influencing the migration and feeding of the fish. Hamerlynck *et al*. (1993) also observed a similar drop in fullness index of *P. lozanoi* at the maximum water levels and currents. While fullness index and consumption generally increase with increasing water levels, above a certain threshold value, feeding is inhibited. Currents indeed increase with the rising water levels during the semi-lunar cycle (pers. obs.).

The change in abundance of the common goby is in accordance with this assumption. In contrast to the fullness index and the daily ration, the density of the common goby was higher at neap tide and lower at spring tide. Fewer individuals entered the creek at spring tide but foraged more intense.

Prey abundance is also determined by the same cycle (Morgan, 1990; pers.obs.). The potential prey species of the common goby were more abundant during spring tide and this could encourage the gobies fish to feed more intensively. Again, the total potential prey density drops sharply at the highest water levels. Other prey items, like benthic (e. g. *Nereis diversicolor*, Harpactiocoidea) and planktonic species (e. g. Calanoidea) represented only a small gravimetric part of the gobies' diet. While hyperbenthic prey abundance may largely explain the observed feeding patterns during the semi-lunar cycle some questions remain unanswered. At spring tide the higher prey density encourage fish to feed more what the higher fullness index and daily ration indicated but the lower density of fish migrating into the marsh creek is not explained. Moreover at neap tide, total density of potential prey species did not differ between day and night. Yet, the feeding intensity of the gobies was higher during neap tide at night.

The daily ration varies with the age of the fish and with the ambient temperature (Norte-Campos and Temming, 1994). Eggers measured a daily ration of 5-12% of body weight for *Pomatoschistus minutus*. In the Wadden Sea, the estimated tidal ration of an average 27 mm *Pomatoschistus microps* was 27.3% at 18.5 °C (Norte-Campos and Temming, 1994). Meyer-Antholz (1987) calculated the 4.8-6.5% daily ration for this species at 14-20.5 °C in the Baltic Sea. The result of this study (8.2-16.5% body weight) falls between these two reported values and followed the same change during the semi-lunar cycle as the fullness index.

This study showed clear effect of tidal, diel and semi-lunar cycle on the feeding habit of *Pomatoschistus microps*. The influence of these cycles is not equal. All organisms living in the intertidal areas are under the dominance of the tidal movement and are forced to adapt their life to the constant movement of tide (Kneib & Wagner, 1994; Rozas, 1995). Because of the strong tidal influence, diel variation is present but inferior to the tidal effects. The semi-lunar cycle clearly influences both the abundance of *P. microps* and its feeding habits, however day-night differences between spring and neap tide are still in question which requires further investigations.

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4 Changes in marsh nekton communities along the salinity gradient of the Schelde river, Belgium and The Netherlands

Abstract: *Nekton was sampled in five marshes along the salinity gradient of the Schelde River. The utilisation of three different habitats (large and small creek, marsh pond) by fish and macrocrustacean species was compared among the five sampling sites. In the larger channels fyke nets were deployed to capture fish and macrocrustaceans leaving the marsh at ebb while block nets were set in smaller intertidal creeks. Fish traps passively sampled fish and shrimp in the marsh ponds. The tidal freshwater marsh had a species poor fauna and only a low number of fish was caught. Besides some freshwater species (Alburnoides bipunctatus, Carassius carassius) the European eel, Anguilla anguilla was still present. The four other marshes had a similar community structure although Platichthys flesus was absent from the euhaline area. Among fish species, dominance of Dicentrarchus labrax, Platichthys flesus and Pomatoschistus microps was observed. Carcinus maenas and Palaemonetes varians were the most abundant macrocrustacean species in every marsh. Between the large and small intertidal creeks there was no difference in nekton species composition. The main species used both habitats. Marsh ponds were utilized intensively only by two species, Pomatoschistus microps and Palaemonetes varians in every marsh.*

4.1 Introduction

Salt marshes are ecotones with variable environmental conditions resulting a comparatively low faunal diversity in these ecosystems (Long and Mason, 1983). Species, which adapt to the highly variable environment can successfully utilize the saltmarshes and reach higher species biomass and density than in other habitats (Vernberg, 1993). Shallow marshes have been reported to be among the most productive zones of estuaries for supporting high standing crop of fish and shellfish (Weinstein *et al*., 1980).

In the North American marshes, the occurrence of nekton species in marsh creeks is influenced by several factors like the presence or absence of vegetation (Rozas and Zimmerman, 2000), the type of the marsh whether natural vs. restored or created (Zedler *et al*., 1997; Williams and Zedler, 1999), the hydrology and channel morphology (McIvor and Rozas, 1996) or the stream order of the marsh creeks (Rozas and Odum, 1987). The tidal creeks can be classified by the concept of stream order. A first stream order creek is defined to have no tributaries. A second order creek is formed by the joint of two first order channels. The fusion of two second order creeks creates the third order channel (Odum, 1984). Tidal creeks of the same stream order have similar physical attributes, which influence the physicochemical and biological properties. These properties differ between stream orders (Rozas and Odum, 1987; Desmond *et al*., 2000), which can have an effect on the utilization of the marsh channels by nekton.

Small-scale spatial variation such as the different structural characteristics of the marsh (creeks, ponds, and vegetated surface) can influence the species composition inhabiting a particular marsh habitat (Rozas *et al*., 1988; Frid and James, 1989; Peterson and Turner, 1994; Smith and Able, 1994; Minello, 1999). In the present study, large creeks, smaller high creeks and marsh ponds were sampled to further evaluate the habitat value of marshes for nekton species. Cattrijsse *et al*. (1994) used a small mesh size (1 mm) to estimate the nursery and feeding ground value of the intertidal marsh creeks. Larger individuals would have been inefficiently caught with their method. Other studies in Europe also mainly focused on larval or post-larvae stage of nekton (Drake and

Arias, 1991a,b; Laffaille *et al*., 2000) and utilisation of marshes by larger individuals has not been reported. By using other techniques this study tried to broaden the knowledge on marsh usage by fish and macrocrustaceans. In North America, marsh habitats different than large creek are equally used by nekton species (Rozas and Reed, 1993; Kneib and Wagner, 1994) but information on the use of other marsh habitats is lacking in Europe (Frid, 1988; Frid and James, 1989). Therefore it is of value to determine differences of habitat utilization by fish, shrimps or crabs, within the marshes.

Studies dealing with the nekton fauna of European tidal marshes have so far not addressed the topic of spatial differences in the aquatic marsh fauna within different regions in the estuary (Drake and Arias, 1991a; Laffaille *et al*., 2000; Lefeuvre *et al*., 2000; Costa *et al*., 2001). Mathieson *et al*. (2000) compared the fauna of several European tidal marshes but did not include this topic. Studies from other part of the word describing faunistic changes in marsh nekton along salinity changes are also few (Rakocinski *et al*., 1992; Gelwick *et al*., 2001). Cattrijsse *et al*. (1994) supplied a detailed description of the aquatic fauna of the brackish marsh of Saeftinghe (The Netherlands) in the Westerschelde estuary but information is lacking on the species occurrence in marshes situated in other salinity ranges within the Schelde river.

The first objective of this study is to examine how the fish and macrocrustacean fauna of tidal marsh creeks within one estuary differ between salinity regions including the fresh water area. The second objective is to determine the differences in the utilization of three marsh habitats (large and small creek and the marsh pond) by nektonic species.

4.2 Study area

In this study five marshes were chosen to investigate possible changes in the fish and macrocrustaceans assemblages along the salinity gradient of the Schelde river (Fig. 1).

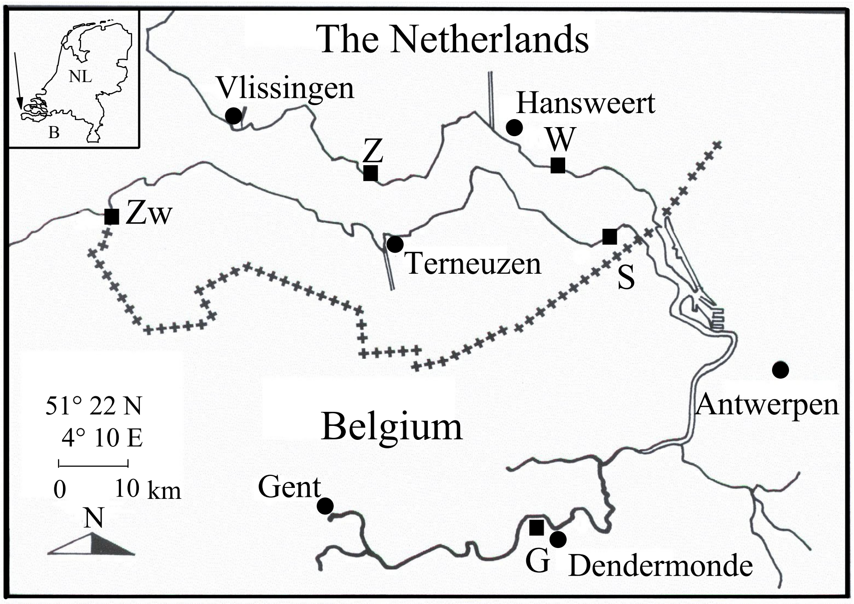

Figure 1. Location of the five marshes sampled along the Schelde river: Zwin (Zw), Zuidgors (Z), Waarde (W), Saeftinghe (S), Grembergen (G).

The river is divided by the saline part of the Westerschelde and the freshwater part of Zeeschelde. Zwin (Zw) is situated at the mouth of the Westerschelde estuary, in the euhaline zone, with the total surface area of 125 ha. The Zuidgors (Z) marsh belongs to the polyhaline zone of the estuary and Waarde (W) to the mesohaline part. The total surface of the two marshes are 50 ha and 107 ha respectively. 'Het Verdronken Land van Saeftinghe' (S) also lies in the mesohaline part of the Westerschelde estuary but with lower salinity as measured in Waarde. Saeftinghe has the largest surface area (2078 ha). In the tidal freshwater part of the Schelde reed and willow marshes are still present. One of the largest tidal freshwater marshes (8.77 ha) is the 'Groot Schoor' or the marsh of Grembergen (G).

4.3 Material and Methods

4.3.1 Sampling in the large intertidal channels

Large intertidal channels were sampled with fyke nets to capture larger fish, which were only occasionally caught by Cattrijsse *et al.* (1994) (Figure 2a). The dimensions of the larger creeks varied between 10-20 m wide and 2-3 m deep. These fyke nets had an opening of 1 m and a mesh size of 15x15 mm.

The nets were 5 m long and contained 6 parlours. At the mouth 3 m long wings enlarged the sampling area of each net. Two fyke nets were set close to the mouth of each creek and two deeper into the marsh. The fyke nets were set before water entered the system and faced the outgoing ebb currents to sample fish and macrocrustaceans leaving the creek with the ebb. Collections were made after the water receded.

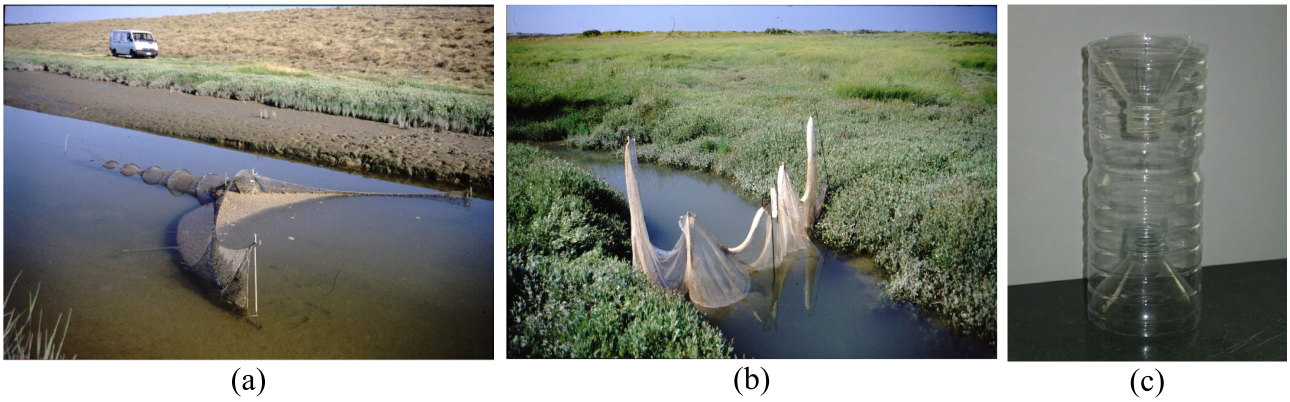
(a) (b) (c)

Figure 2. Fyke net (a) and block net (b) placed in the large and the small intertidal channel. Fish trap (c) sampled the nekton inhabiting the marsh ponds.

4.3.2 Sampling in the small intertidal creeks

Smaller intertidal creeks further along the marsh were sampled with a block net (Figure 2b). These smaller creeks were generally 2 m wide and 1.5-1.8 m deep. This net was constructed of 5 mm gauze and had two lateral wings of 2 m and a central bag. The whole net was 2 m height and the topline was provided with float.

The ground rope was fitted with a heavy chain. The block net was set at high water near the mouth of the creek. The chain in the ground rope was manually placed on the bottom of the creek and sticks kept the net and ground rope in place. After all water had left the creek the net was emptied.

4.3.3 Sampling in the tidal ponds

Tidal ponds inside the marsh were also selected as potential nekton habitats. In Grembergen such pans were not present while in Saeftinghe there was no pond that could easily be accessed. Fish bottle traps were selected to passively catch small fish or macrocrustaceans inhabiting these shallow environments (Figure 2c). The traps were placed at the edge of the pools for 5 hours. The number of the fish traps placed varied between 6 and 10 according to the size of the pan. Fish traps were made of transparent plastic bottles. The neck of the bottle was cut off and inserted backwards into the bottle. The bottom was also opened to insert another neck. This created a trap with two openings of 25 mm, a diameter of 75 mm and a total length of 250 mm.

4.3.4 General material and methods

Samples were collected every six weeks between April and October 2000. During this period epibenthic species showed high density and biomass in the estuary (Maes *et al*., 1998; Hostens, 2000) therefore this period was considered sufficient to sample. The five marshes were sampled on consecutive days during spring tide periods.

Waarde could not be sampled during April while in Grembergen the block net could not be set after that month. Between May and October too dense vegetation prevented the placement of the net in this marsh. Traps were placed in the ponds from July onwards targeting the common goby, *Pomatoschistus microps* utilizing this habitat. Previous observations had shown that early juvenile *P. microps* inhabit the creeks from June onwards (Cattrijsse *et al*., 1994).

At each location dissolved oxygen, salinity and temperature were measured at the moment of high water. Similar environmental parameters were detected in the small and large creeks therefore only the values from the large creeks are presented in this study.

Individuals per fyke net per hour were calculated for the large creek in every month in each marsh. These values were summed up to obtain the total number of nekton in each month in this habitat. Similar calculation was made for the other two habitats such as the small creek and the marsh pond.

To standardise the catches in the different marshes the total number of individuals caught per hour per fyke net was calculated. Block net samples were expressed as number of individuals leaving the creek with the ebb. Fish trap collections were expressed as number of individuals per hour per fish trap.

Different multivariate techniques were used to describe the spatial structure of nekton based on density per station and per month. Prior to the multivariate analysis the data were fourth-root transformed. Two Way Indicator Species Analysis (TWINSPAN, Hill, 1979) and Group Average Sorting cluster analysis based on the Bray-Curtis similarities (Bray and Curtis, 1957) were used as classification techniques.

The choice of the cut levels in the TWINSPAN was based on the rule that the number of observations within each cut level should be approximately equal except for the lowest cut level which contains all the 0 observations. Cut levels chosen for the density in the large creek were 0, 0.65, 0.85, 1.1, 1.4, in the small creek 0, 1.1, 1.4, 1.5, 1.8 and in the marsh pond 0, 0.6, 0.95, 1.0, 1.5.

4.4 Results and discussion

4.4.1 Environmental parameters

Table 1 shows the change of environmental parameters in the five marshes during the sampling period. Samples were collected along the salinity gradient between 0.2-30 psu. In the large channels, salinity ranged from the maximum of 30.8 in Zwin, 25.3 in Zuidgors, over 16.7 in Waarde and 11.4 in Saeftinghe to fresh water, 0.4 psu in Grembergen. Temperature showed a similar temporal variation in all marshes. Generally 11.6-16 °C were measured at spring and autumn while in the summer months the temperature reached 21.9 °C. Exceptions were Zuidgors and Zwin in August when only 15.8 and 16.9 °C were detected respectively. Dissolved oxygen concentration showed the lowest value in Saeftinghe and Grembergen around 4-6.8 mg 1^{-1}, except in October when 7.7-7.2 mg 1^{-1} oxygen were measured respectively. Waarde and Zuidgors had similar dissolved oxygen concentrations ranging between 5.6-8.1 mg 1^{-1}. Approximately 9 mg 1^{-1} oxygen concentrations were measured in Zwin except in April when the concentration stayed only at 4.5. The decrease in oxygen concentration in the upstream part of the estuary is a well-known phenomenon. Large areas of the tidal freshwater parts of the Schelde estuary are anoxic throughout most of the year (Maes *et al.*, 1997).

Table 1. Predicted water height (cm) in the creek and the measured water height in the marsh pond, salinity (psu), dissolved oxygen (mg l^{-1}) and temperature (°C) measured in the water column in the large creek and the marsh pond.

Location	*April*		*May*		*July*		*August*		*October*	
waterheight	*creek*	*pond*	*creek*	*pond*	*creek*	*pond*	*creek*	*pond*	*creek*	*pond*
Grembergen	524		506		532		524		541	
Saeftinghe	424		517		513		515		523	
Waarde			517		521	22	552	30	513	25
Zuidgors	575		555		518	30	562	42	477	28
Zwin	388		423		423	25	451	40	402	30
salinity										
Grembergen	0.3		0.4		0.2		0.2		0.3	
Saeftinghe	11.4		8.4		8.0		10.8		9.0	
Waarde			16.5		14.8	22.5	16.7	17.3	15.9	16.8
Zuidgors	22.6		22.8		25.3	25.8	28.4	25.3	25.0	24.0
Zwin	25.5		27.5		30.8	31.2	28.5	30.1	25.5	25.7
temperature										
Grembergen	13.3		17.0		17.2		20.3		16.0	
Saeftinghe	13.3		17.5		18.8		21.9		15.2	
Waarde			14.0		16.7	25.1	21.2	19.1	12.6	13.0
Zuidgors	12.2		15.1		20.5	22.4	16.9	18.4	13.6	14.3
Zwin	12.7		21.4		21.9	25.5	15.8	16.2	11.6	12.0
oxygen										
Grembergen	4.1		5.2		5.0		4.8		7.2	
Saeftinghe	4.6		6.8		5.6		4.6		7.7	
Waarde			8.0		7.3	5.2	6.2	5.8	6.6	4.2
Zuidgors	5.6		8.1		7.5	6.3	7.3	5.9	6.8	4.2
Zwin	4.2		9.2		8.9	5.6	9.0	7.4	9.2	9.1

In the marsh ponds, salinity showed generally higher values than in the channels. Temperature changes reflected the seasonal trend with the highest values in July (22.4-25.5°C) and lowest in

October (12-14.3 °C). In every marsh, the dissolved oxygen was lower in the marsh ponds than in the creeks.

4.4.2 Temporal variation of the total number of nekton during the sampling period

Species captured during the sampling period are listed in Table 2. Fifteen taxa were captured in the five marshes. *Liza* and *Clupeidae* species were not identified up to species level. Among the 15 taxa only *Dicentrarchus labrax*, *Platichthys flesus*, *Pomatoschistus microps*, *Carcinus maenas* and *Palaemonetes varians* were abundant. Other species were captured only occasionally. *D. labrax* and *P. flesus* were individuals belonging to the 1+ or 2+ year class.

Total number of individuals caught for each sampling technique over the sampling campaign is presented in Figure 3. The total catches of the fyke nets increased over the 5 months reaching maximum 27.7 ind. hour^{-1} net^{-1} in August (Fig 3a). Block net caught the maximum number of individuals (209 per ebb tide) in October (Fig. 3b). The maximum catch of fish traps happened in August (18.5 ind. hour^{-1} trap^{-1}). Cattrijsse *et al.* (1994) have shown that during this period of the year a maximum number of species use the marsh creeks as nursery and feeding ground.

Table 2. List of the species occurring in the five marshes. Abbreviations are used for the indicator species of TWINSPAN.

Teleostei		**Crustacea - Brachyura (crabs)**	
Anguilla anguilla	Angu angu	*Carcinus maenas*	Carc maen
Alburnoides bipunctatus	Albu bipu	*Eriocheir sinensis*	Erio sine
Carassius carassius	Cara cara	**Crustacea - Caridea (prawns)**	
Clupeidae spp.	Clup spp	*Palaemonetes varians*	Pala vari
Dicentrarchus labrax	Dice labr	*Crangon crangon*	Cran cran
Gasterosteus acureatus	Gast acul		
Liza spp.	Liza spp		
Platichthys flesus	Plat fles		
Pleuronectes platessa	Pleu plat		
Pomatoschistus microps	Poma micr		
Syngnathus rostellatus	Syng rost		

4.4.2.1 Intertidal large channels

In the large creeks, numbers of shore crab, *Carcinus maenas* and seabass, *Dicentrarchus labrax* increased towards autumn reaching a total of 9.9 and 16.5 ind. hour^{-1} net^{-1}, respectively (Fig 3a). The abundance of flounder, *Platichthys flesus* was higher in the first three sampling months. Highest occurrence was detected in July (5.7 ind. hour^{-1} net^{-1}). A high number of adult shore crab was observed in autumn in a mesohaline marsh creek, Sieperda, The Netherlands (Chapter 7). Adult *C. maenas* was also abundant on muddy sediment in the Wadden Sea from August till November (Klein-Breteler, 1976). Raffaelli *et al.* (1990) reported that large numbers of flounder appeared in the Ythan estuary in spring (April, May) and all year classes were present until winter. Investigations mainly focused on the larval or postlarval stages of *D. labrax*. Drake and Arias (1991a) found high densities of postlarval seabass from March till July in a salt marsh in Spain. Aprahamian and Baar (1985) observed postlarvae in the Severn estuary, UK during August and September. In the Westerschelde estuary, high density of postlarvae of seabass migrated in the salt marsh creek from August till November (Cattrijsse *et al.*, 1994) and the juvenile of this species reached the highest abundances from December till March in the estuary subtidal (Hostens, 2003).

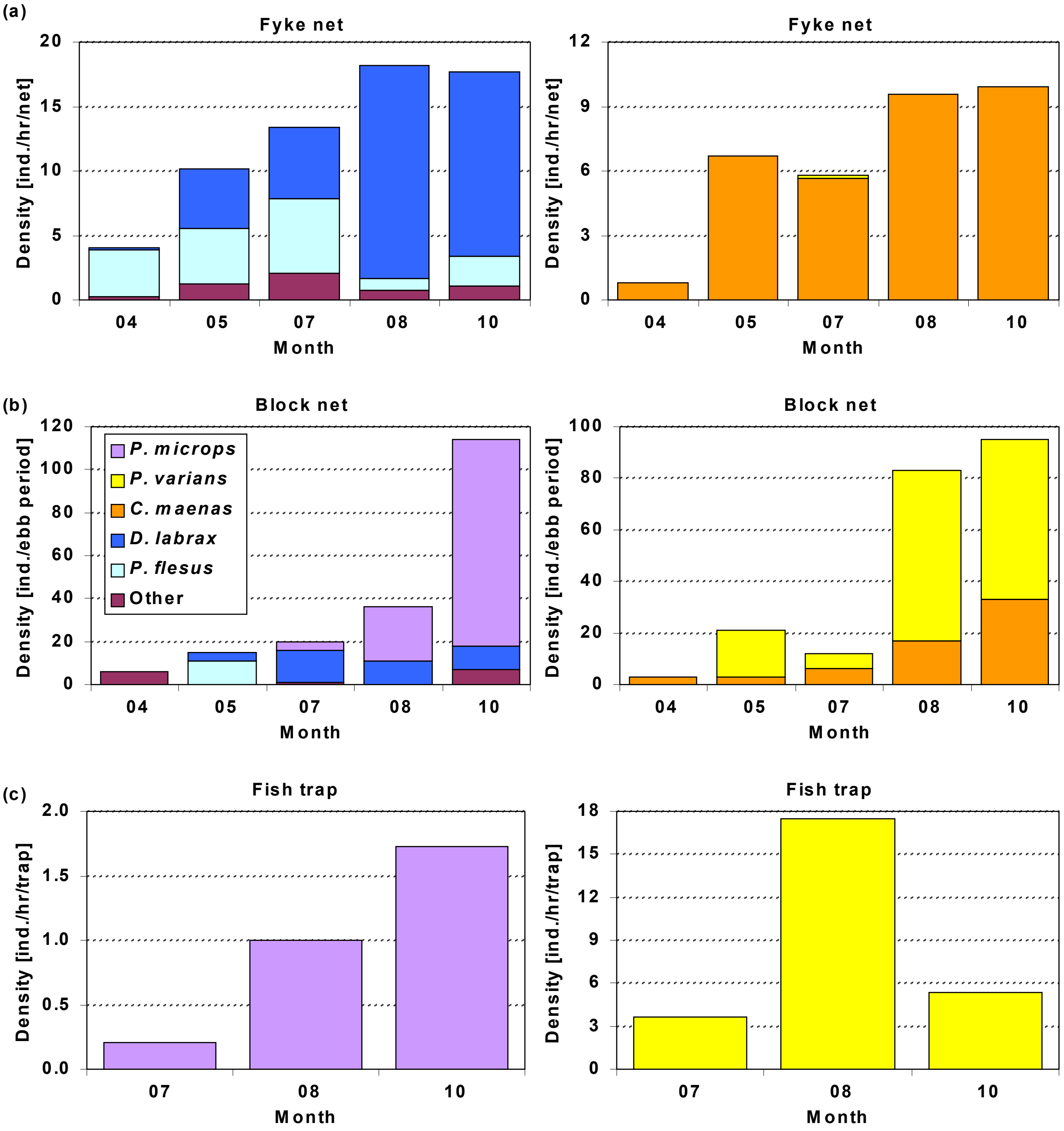

Figure 3. Total number of individuals caught by fyke net (a), block net (b) and fish trap (c) in the five marshes during the sampled months.

4.4.2.2 Intertidal small creeks

The block net catches showed that fish and shrimp visit the small intertidal creeks in large numbers only during late summer and early autumn (Fig. 3b). In spring and summer the block net catches were low. *Pomatoschistus microps* appeared mainly in August and October (25 and 96 ind. per ebb period respectively), which supports the results of Cattrijsse *et al.* (1994). In the subtidal of the Westerschelde estuary, the adult common goby reached the highest density during the winter period from November till March (Hostens, 2003). The seasonal change in abundance of *Carcinus maenas* was also clear from these samples. Increasing number of shore crab utilize the small creeks towards autumn reaching a total of 33 individuals. *Dicentrarchus labrax* was present in the small creeks in low numbers (0-15 ind. per ebb period) during the whole sampling period. *Platichthys flesus* appeared in this habitat only in May.

4.4.2.3 Tidal pond

Fish traps collected maximum numbers (18.3 ind. hour^{-1} trap^{-1}) in August when *Palaemonetes varians* was highly abundant in this marsh habitat (Fig 3c). Frid (1988) also observed high number of *Pomatoschistus* and *Palaemon* species in marsh ponds during summer and autumn in Eastern England. Juvenile common gobies make maximum use of the high marsh pools as nurseries between August and October. These maximum catches in the marsh pools coincided with maximum catches of these species in the block net.

4.4.3 Spatial variation of abundance of nekton species in different marsh habitats

4.4.3.1 Large intertidal channels

The densities of the species in the three habitats of the different marshes are given in Appendix 2.

Fyke net catches in the freshwater marsh were always low and were composed of completely different species than in the other marshes (Fig. 4a). The eel, *Anguilla anguilla* was the dominant species in each sample irrespective of the sampling period. Crucian carp, *Carassius carassius* and schneider, *Alburnoides bipunctatus* were the other species caught. The low catches in the Groot Schoor can partly be attributed to the very high amount of organic material trapped in the fyke net but the fish community of the tidal freshwater part of the estuary is very poor in density and diversity (Maes *et al*., 1997). Based on fyke samples, Maes *et al*. (1997) recorded 7 fish species and one shrimp species on the mudflats of the tidal freshwater part of the estuary. Their catches in the most upstream sampling location consisted of only two species: *A. anguilla* and *Rutilus rutilus*, the later one was recorded only once. Grembergen was even further upstream than this location. Our low catches seem thus to mirror the poor fish fauna of the tidal freshwaters of the Schelde river.

The catches in the other marshes were dominated by the common goby *Pomatoschistus microps*, the flounder *Platichthys flesus,* the seabass *Dicentrarchus labrax* and the shore crab *Carcinus maenas*.

Only the mentioned species seem to be able to use the marsh habitat as nursery or as foraging ground. These fish species together with mullets dominate the European fish fauna of marshes (Frid and James, 1989; Drake and Arias, 1991a; Cattrijsse *et al*., 1994; Costa and Cabral, 1999; Laffaille *et al*., 1998; 2000). Mathieson *et al*. (2000) reported *P. flesus* and *Anguilla anguilla* to be the two most widely recorded species in European estuarine and lower river marsh systems. Mullets were not captured during this study. Cattrijsse *et al*. (1994) observed their occurrence but since the juveniles swim close to the surface they could hardly be caught with the method used. In Saeftinghe and Waarde, *P. flesus* migrated into the creeks until August. Maximum abundance occurred in April in Saeftinghe (2.9 ind. hour^{-1} net^{-1}) and in July in Waarde (3.3 ind. hour^{-1} net^{-1}). In August and October high numbers of *D. labrax* and *Carcinus maenas* were caught. Also in the Zuidgors marsh, *P. flesus* mainly appeared during the first three months with a maximum in July (1.3 ind. hour^{-1} net^{-1}) but here *D. labrax* was more numerous in every month except for October when only *C. maenas* was captured. In the euhaline marsh, Zwin, the only species caught in high numbers was *C. maenas.*

This species is known to avoid low salinities during most of the year (De Veen *et al*., 1979). The low turbidity most likely maximised net avoidance by fish. The absence of flounder in this marsh might derive from the low catching efficiency of the net. Although along the salinity gradient of the Westerschelde estuary, Hostens (2003) reported *P. flesus* as common species and observed that the density of flatfish stayed relatively low in the marine part and increased in the brackish area. The salinity preference of this species might explain better the lack of flounder in the euhaline marsh. Young *Dicentrarchus labrax* were regularly observed swimming in the larger creek but caught only in low numbers. In the small channels seabass was captured with the block net in July and August. Besides the possibility that seabass avoids the net, *D. labrax* was reported mainly from the brackish part of the estuary (Hostens, 2003). In contrast to the marshes, the seabass was classified as species occurring only occasionally in the subtidal of the estuary (Hostens, 2003).

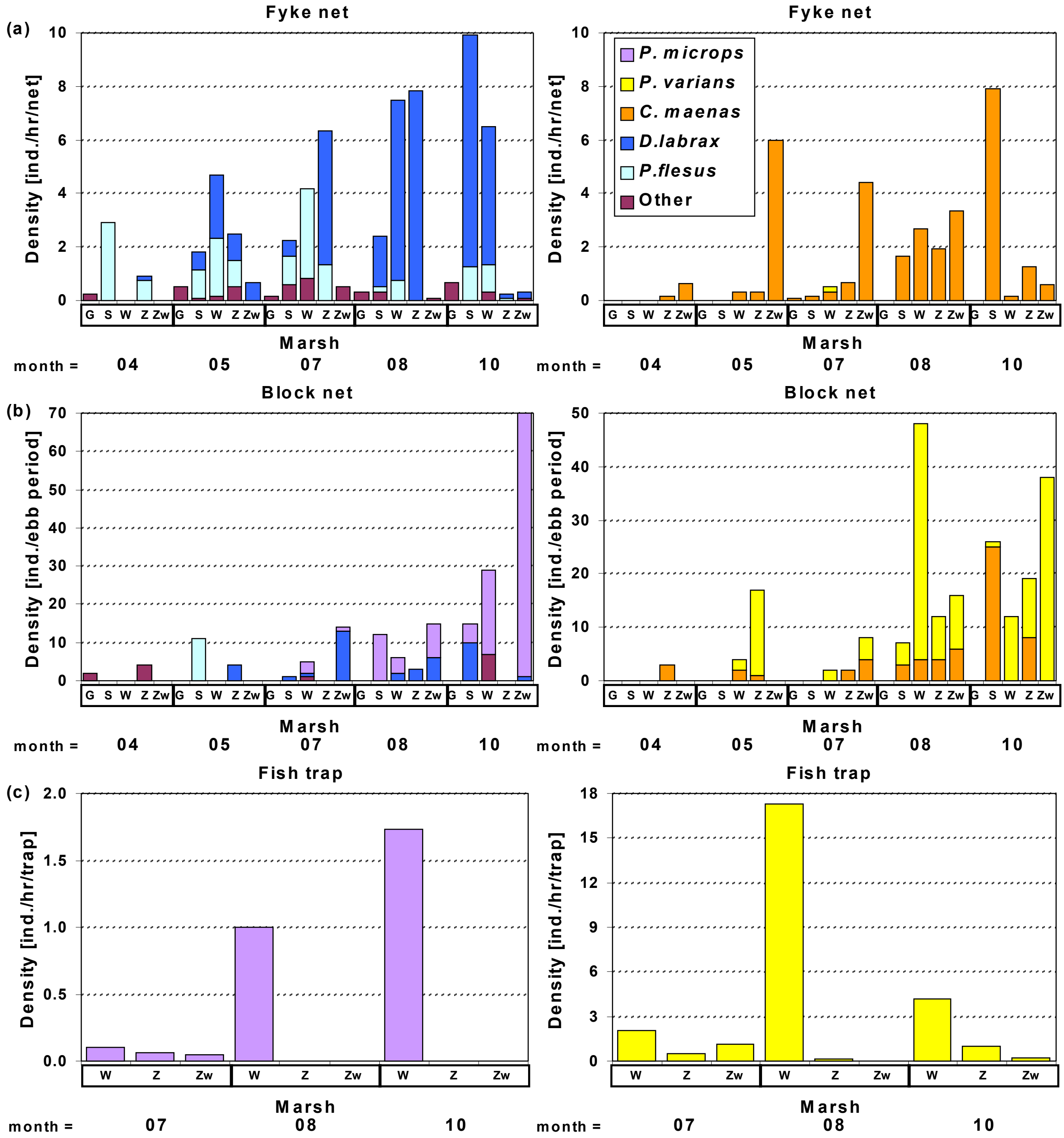

Figure 4. Densities of different fish (left) and macrocrustacean (right) species in the large creeks sampled by fyke net (a), in the small creeks used a block net (b) and in the marsh pond used fish traps (c). Letters are used to label the marshes as indicated in Figure 1.

The result of the TWINSPAN performed on the density data of the five marshes sampled in the large channel is presented in Figure 5a. The first division yielded a cluster of the freshwater marsh in April. This marsh was characterized by the typical freshwater species, *Alburnoides bipunctatus*. At the second division, the freshwater samples were separated from the other marshes. The indicator species for the later group were *Carcinus maenas, Dicentrarchus labrax* and *Platichthys flesus*. Low species densities corresponded to the two clusters of the fresh water marsh samples. The third division resulted a cluster of euhaline marsh samples and a cluster of the other brackish marshes. The indicator species for the later cluster was *Platichthys flesus* (second cut level). For a comparison of the output of cluster analysis, a dendogram derived from group average sorting using Bray-Curtis similarities is presented in Figure 6a. This technique yielded more separation of the euhaline marsh from the other areas indicating a different community structure. Similarly to the result of TWINSPAN, the segregation of the freshwater marsh was clear. Other marshes in the brackish part of the estuary showed strong similarities to each other. This result differed that Hostens (2003) found in the Westerschelde estuary. In the estuary, the mesohaline and the polyhaline areas were characterized by two different epibentic communities.

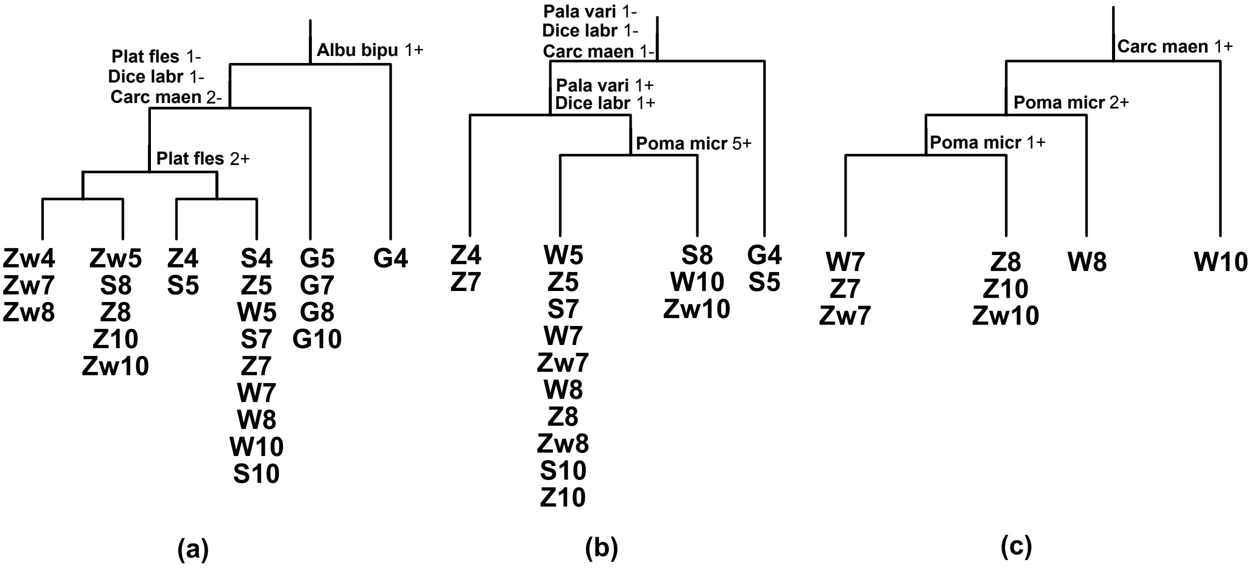

Figure 5. Result of TWINSPAN for density data in the large channel (a), small creek (b) and tidal pond (c). Indicator species are indicated with their cut level.

4.4.3.2 Small intertidal creeks

Only the common goby *Pomatoschistus microps,* the shore crab *Carcinus maenas,* the brackish water shrimp *Palaemonetes varians* and young *Dicentrarchus labrax* were the dominant species in the small creeks (Fig. 4b). Other species like *Platichthys flesus*, *Alburnoides bipunctatus*, *Crangon crangon*, and *Atherina presbiter* and *Clupeidae* species were only a few times captured.

The result of the TWINSPAN performed on the data of the five marshes sampled in the small channel is presented in Figure 5b. The first division yielded one cluster of the freshwater marsh in April and Saeftinghe in May. The indicator species were *D. labrax, P. varians and C. maenas* for the other cluster on the first cut level. TWINSPAN does not show real segregation of the marshes with different salinity.

For a comparison of the output of cluster analysis, a group average sorting using Bray-Curtis similarities is presented in Figure 6b. This technique yielded similar result as TWINSPAN. Community structure in the freshwater marsh in April had high dissimilarity with the epibenthic community in Saeftinghe in May. Other sampling occasions did not segregate from each other but indicating similar community structures.

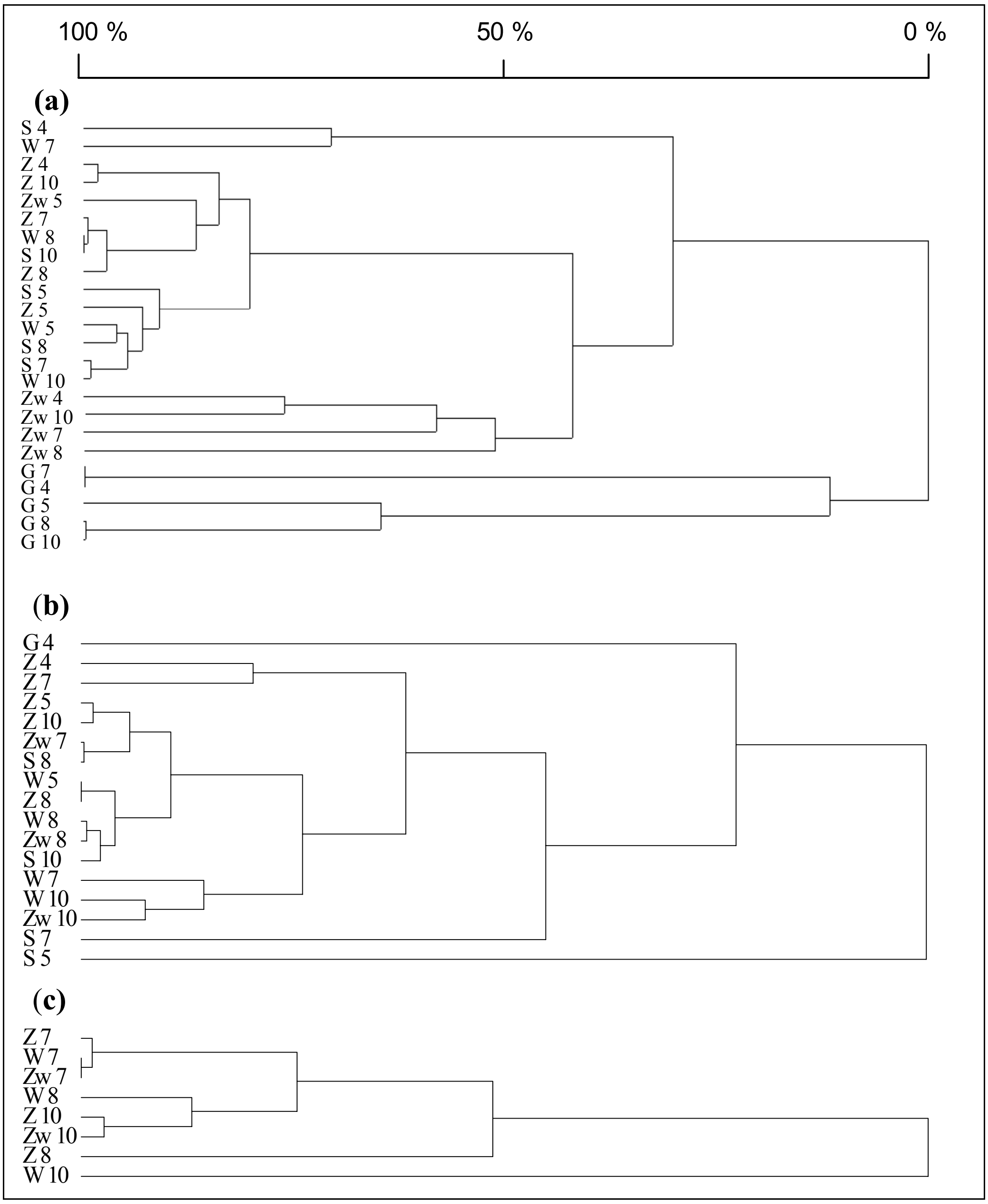

Figure 6. Dendogram for nekton densities in the intertidal channel (a), intertidal creek (b) and tidal pool (c). Horizontal scale represents the relative similarity among sites. Marshes are labeled as indicated in Figure 1. Sampled months were April (4), May (5), July (7) August (8) and October (10) indicated next to the marsh labels.

The difference of salinity in the marshes seemed not to restrict the few species, which are able to utilize the small creek visiting this habitat. Rozas and Odum (1987) observed in a North American freshwater marsh that fish and macroinvertebrates concentrate in the upper reaches of the tidal creeks where the creeks become more shallow and narrow. In addition, our data also showed that not only larvae venture into this habitat. Young flounder was caught in these small channels to feed upon the infauna. Desmond *et al.* (2000) argued that in a salt marsh, situated at the US-Mexico border, the low oxygen environment and the higher temperatures in the smallest intertidal creeks restricted their use by fish. Excessive high temperatures were however never recorded during our study in these small creeks.

4.4.3.3 Tidal ponds

During the sampling campaign, the fish traps captured *Pomatoschistus microps* and *Palaemonetes varians* but large numbers of fish and shrimp were caught only in Waarde (Fig. 4c). *P. varians* was captured in higher numbers in the three marshes. The two classification techniques, TWINSPAN (Figure 5c) and the Group Average Sorting cluster analysis (Figure 6c) revealed the same pattern and showed the close similarities of sampling occasions. Only the sample of Waarde in October segregated from the other sampling occasions indicating a different community structure. Indicator species was *Carcinus maenas* on the first cut level. In Waarde, the pans were close to small creeks so that tides might have regularly well refreshed the water. In Zwin and Zuidgors, the ponds were situated further from the creek and the water entered very slowly to the ponds with the tide and this less intense water supply might explain the lower presence of gobies and shrimp. The physical environment of marsh ponds can be very variable (Bulger, 1984; Cochran and Burnett, 1996) and only a few species have the tolerance to withstand these conditions. The species, which can adapt to the environmental conditions of the marsh ponds, can find a good refuge and foraging area (Kneib, 1997; Talbot and Able 1984; Smith and Able, 1994).

Several authors from North America reported high habitat use of marsh ponds by nekton (Holbrook and Schmitt, 1988; Layman *et al*., 2000; Power, 1984; Werner *et al*., 1983). In Europe, Frid (1988) and Frid and James (1989) reported utilization of tidal ponds by fish and macrocrustaceans like juvenile mullet, small plaice and flounder, gobiid fish and *Palaemon* species. In the marshes of the east coast of US, *Fundulus heteroclitus* is the typical species use intensively the marsh ponds during the whole year (Smith and Able, 1994; Halpin, 2000; Layman *et al*., 2000). This species has a similar ecological role in North American marshes as *Pomatoschistus microps* in the European tidal areas. *F. heteroclitus* found both growth advantages and predator refuge in marsh ponds.

4.5 Conclusions

As hydrology is the most important factor in the development and functioning of wetlands (Reed, 1993), salinity is considered the major influence on the distribution and movements of estuarine nekton (Gunter, 1961, Marshall and Elliott, 1998). Fish and invertebrate assemblages of estuarine salt marshes fluctuate both temporally and spatially (Rakocinski *et al*., 1992).

In North America, researchers argued about the primary factor of large-scale environmental gradients, (salinity, hydrology and current patterns) influencing community structure of estuarine fishes (Ross and Epperly, 1985; Weinstein *et al*., 1980). On the east coast of the US, distributions of estuarine fishes and macroinvertebrates have been shown to directly follow primary salinity gradients in the salt marshes along an estuary (Weinstein *et al.,* 1980). Rakocinski *et al*. (1992) also found that salinity is the primary abiotic factor structuring the fish community in a salt marsh at the east coast of the US. Similar researches are lacking in European intertidal areas. In this study, the nekton fauna of the four saline marshes did not differ significantly. Similar species utilized the eu-, poly-, mesohaline intertidal areas. Among the fish species, dominance of *Dicentrarchus labrax, Platichthys flesus* and *Pomatoschistus microps* was observed. *Anguilla anguilla* was still captured several times however this species was not considered abundant. *Carcinus maenas* and *Palaemonetes varians* were the most abundant macrocrustacean species in every marsh. Only the freshwater marsh had a distinct fish fauna with some typically freshwater species. Additionally, no difference in species composition was observed between large or small intertidal creeks. The main species used tidal marsh creeks as habitats entering both the larger and the smaller channels. Marsh ponds were only utilized by two species, *Pomatoschistus microps* and *Palaemonetes varians*. These pans are shallow and not regularly flooded which might represent a too stressful environment for other species.

The description of the community structure and the abundance of nekton species give an overview about the utilization of the marsh habitats but future research is suggested to focus on the feeding habits of the nekton species on large- and small spatial scale. Investigations about the feeding habits of marsh visiting species would contribute further to assess the value of marsh habitats as feeding ground.

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5 Macrobenthos as a food source for fish species in five marshes situated along the salinity gradient of the Westerschelde estuary

Abstract: *The present study focuses on macrobenthos in tidal marshes as food for fish and macrocrustacean. The study measured the primary community parameters of density and species richness together with the biomass of the four dominant taxa (the amphipod Corophium volutator, the polychaete Nereis diversicolor, the bivalve Macoma baltica and Oligochaeta). In addition, the community diversity was determined at the sampling stations. The study sampled a large intertidal channel and a smaller creek in five marshes along the salinity gradient of the Westerschelde estuary, the Netherlands and Belgium, every six weeks between May and October in 2000. There were two different temporal changes in density observed. In the upstream marshes the density increased towards summer and declined towards October. While in the two more saline marshes the density decreased during the sampling period. The density of the macrofauna fluctuated along the estuary without any identifiable spatial trend due to the abundance of Oligochaeta. In contrast, the total biomass increased towards the euhaline area due to the dominance of N. diversicolor and M. baltica. Also diversity showed a significant positive correlation with salinity. A comparison of the macrofauna on the intertidal flats of the estuary indicated similar trends in density, biomass and diversity along the salinity gradient. Among the main taxa N. diversicolor, Macoma baltica and Oligochaeta had a higher and Corophium volutator a lower density and biomass than that measured on the intertidal flat.*

5.1 Introduction

The macrobenthos of estuarine intertidal areas is exposed to extreme and highly variable environmental conditions. Benthic animals with limited mobility have to cope with a low oxygen concentration in the predominantly fine-grained sediment, fluctuations in salinity, drying and flooding, suspended sediment etc. (McLusky *et al.,* 1993, Ysebaert, 2000). The colonization by macrofauna and the subsequent development and modification of macrobenthic communities therefore depends upon several factors (Elliott *et al.,* 1998). In estuaries, macrobenthos is important in benthic remineralization processes, both directly and indirectly through its process of structuring the sediment (Mazik and Elliott, 2000; Ysebaert, 2000). Macrofauna is also often used in monitoring programmes (e.g. Heip *et al*., 1992) and as an indicator of water and sediment quality (Austen *et al*., 1989; Harrel and Hall, 1991). Macrofauna represents a central element of the estuarine food web, being an important food resource for crustaceans, fish and birds (Day *et al*., 1989). Macrobenthos is an important trophic link between producers and the higher trophic level also in salt marshes (Sarda *et al*., 1995). Several fish species have been reported in the European marshes to prey upon benthos. *Dicentrarchus labrax* (Cabral and Costa, 2001), *Platichthys flesus* (Gardner, 1996), *Pomatoschistus minutus* (Laffaille *et al*., 1999) and *P. microps* (Cattrijsse *et al*., 1994) use intertidal marshes as feeding and nursery grounds. Food availability influences the nursery value of a marsh (Kneib, 1993) therefore it is important to investigate the abundance of macrobenthos in the marsh habitat.

The macrobenthos of the extensive US saltmarshes has been well studied (Rader, 1984; Sheridan, 1992; Sarda *et al*. 1995; Szalay and Resh 1996; Alphin and Posey, 2000; Angradi *et al*., 2001). In Europe, in contrast, investigations of macrofaunal communities in salt marshes are rare. Jackson *et al*. (1985) studied macro-invertebrate populations and production in east England and

Frid and James (1989) investigated the temporal change of macrobenthos of another English salt marsh in North Norfolk. Tagliapietra *et al.* (2000) sampled macrobenthos in a marsh pond in the Venetian Lagoon, Italy. Other studies have focused on one or two macrobenthic species like *Nereis diversicolor* (Emmerson, 2000; François *et al.*, 2002), *N. oligohalina* (Alves and Lana, 2000) or *Corophium volutator* (Essink *et al.* 1989; Hughes and Gerdol, 1997).

The present study was conducted in marshes situated along the Schelde River (The Netherlands and Belgium). The intertidal flat benthic macrofauna along the estuarine gradient of this estuary has been intensively studied by Ysebaert *et al.* (1993) and Ysebaert and Herman (2002). The macrobenthos of intertidal marsh creeks of the Westerschelde has not been previously sampled. The fish community of this estuary has been extensively investigated (Maes *et al.* 1997, 1998; Hostens, 2000). Marsh creeks are important feeding grounds for the seabass *Dicentrarchus labrax*, the flounder *Platichthys flesus* and the common goby *Pomatoschistus microps* (Mathieson *et al.*, 2000, Chapter 3,6). These species occur in the marsh creeks in high abundance between spring and autumn (Cattrijsse *et al.*, 1994) and seabass and flounder also attain feeding maxima during these months (Arntz, 1978; Kelley 1987). Since the main aim of the present study was to determine prey availability for fishes, this period was considered the best time for sampling. Macrobenthic species comprise a large part of the diet of the seabass, flounder and the common goby (Elliott *et al.*, 2002; Chapter 6). For this reason, data on macrobenthos abundance are required to obtain a better understanding of the food potential of marsh creeks.

The objective of the present paper is to investigate temporal and spatial variation of macrobenthos and to compare the marsh and the intertidal part of the estuary especially focusing on a few taxa, which are an important food source for the marsh visiting fish species.

5.2 Materials and Methods

5.2.1 Study Area

In this study, five marshes were chosen along the salinity gradient of the Westerschelde estuary (Fig. 1). In the tidal freshwater part of the Westerschelde one of the largest freshwater marsh is the ‘Groot Schoor’ or the marsh of Grembergen (G). ‘Het Verdronken Land van Saeftinghe’ (S) lies in the mesohaline part of the Westerschelde estuary. The marsh of Waarde (W) also belongs to the mesohaline zone but with a higher salinity than in Saeftinghe. The Zuidgors (Z) marsh situated in the polyhaline zone and Zwin (Zw) at the mouth of the estuary, in the euhaline part.

5.2.2 Sampling

A large intertidal channel and a smaller creek were sampled in each marsh. The dimensions of the larger creeks varied between 10-20 m wide and 3-4 m deep whereas the smaller creeks were generally 2 m wide and 1.5-1.8 m deep. At low tide the water left the channel and 5 replicate plastic cores were used to sample the macrobenthos to a depth of 15 cm from the large and small creek adjacent to the bottom of the channel. The diameter of 6.2 cm was in accordance with other studies (Frid and James, 1989; Ysebaert *et al.*, 1993; Ysebaert and Herman, 2002).

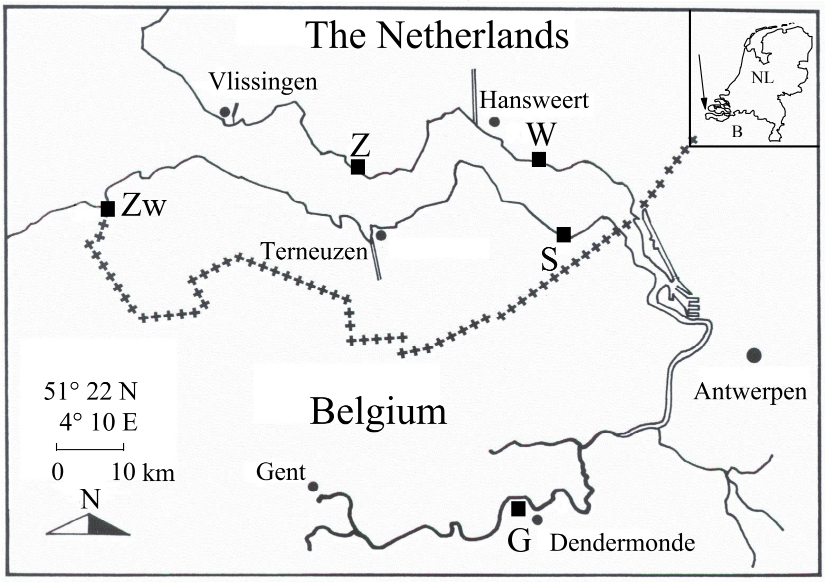

Figure 1. Location of the five marshes sampled along the Schelde River. Marshes labeled by letters: Grembergen (G), Saeftinghe (S), Waarde (W), Zuidgors (Z) and Zwin (Zw). Relative macrobenthic species abundances are indicated next to each marsh.

Samples were collected every six weeks between May and October 2000. This period was considered adequate to indicate the settlement, recruitment, establishment and development of the main species. The five marshes were sampled on consecutive days during spring tide periods. In Grembergen, samples could be taken only from the large channel as the small channel became inaccessible after May due to the dense vegetation.

The environmental parameters of water temperature, salinity and dissolved oxygen were measured in the large and small creeks. Measurements were performed in the water column during the ebb period before the macrobenthic samples were taken in order to indicate the conditions experienced by the macrofauna prior to exposure. In each creek, a sediment core of diameter 6.2 cm was taken for the measurement of the median grain size and organic matter content of the sediment.

In the field, samples were preserved in a brackish water-formalin solution. Samples were washed in the laboratory, sieved on a 1 mm sieve, stained with Rose Bengal and individuals were counted and identified to the lowest possible taxonomic level. The use of a 1 mm sieve after fixing the samples will have taken organisms smaller than the mesh used (pers. obs.). Individuals belonging to the class Oligochaeta were not identified to species level. Since more than 80% in Zwin and more than 90% of the density in the other marshes was composed of Oligochaeta, *Corophium volutator* and *Nereis diversicolor* and because of the high individual biomass of *Macoma baltica*, the biomass estimation focused on these four taxa. Samples of Oligochaeta, *C. volutator* and *N. diversicolor* were dried at 60 °C for 4 days and then 2 hours at 550 °C. Samples were placed in a dessicator for 2 hours to reach room temperature and ash free dry weight (ADW) was determined. To minimise the weighing bias, the 5 replicates from the same creek were measured together. The biomass of *Macoma baltica* was calculated using a regression established in the laboratory.

Total and species density was calculated for each replicate using the number of individuals and the surface area of the sampling cores. The average total macrobenthic density, average species densities, average total biomass and average species biomass were calculated for each sampled station, each month and every marsh.

The values of the environmental parameters in each month were used to calculate the coefficient of variation in each marsh as following: % Coefficient of variation = standard deviation/mean *100 (Jongman *et al.*, 1987).

The Shannon-Wiener function H' (Pielou, 1966) was used as an indicator of the diversity and calculated for each station and for every marsh.

A Spearman-Rank correlation was used to test the relationship between the environmental parameters (salinity, temperature) and the diversity and the abundance and biomass of macrobenthic species.

5.3 Results

5.3.1 Environmental parameters

Only the parameters in the large creeks are presented. The values in the small creeks were identical. Figure 2a indicates that Grembergen is situated within the fresh water part of the river (0.2-0.4 psu). Salinity varied between 8-10.8 psu in Saeftinghe and between 14.8-16.7 psu in Waarde. In Zuidgors salinity recordings ranged around 25 psu while in Zwin the salinity reached maximum values of around 30 psu.

Water temperature (Fig. 2a) generally followed the seasonal pattern in all marshes with lower values in spring and autumn and maxima during summer. Exceptions were Zuidgors and Zwin where a relatively low temperature (16-17 °C) was measured in August. Figure 2b shows that the dissolved oxygen concentration (DO) in the water column was defined both by the position of the marsh in the estuary and by the temperature. Lowest dissolved oxygen concentrations were measured in Grembergen and highest values were detected in Zwin. In Grembergen and Saeftinghe, DO showed similar patterns with low values in the first three months of sampling and increased oxygen concentration in October (7.2 and 7.7 mg l^{-1} respectively). In Waarde and Zuidgors, the dissolved oxygen concentrations slightly decreased towards autumn while it remained around 9 mg l^{-1} in Zwin.

The median grain size of the sediment in the marsh creeks ranged between 10 and 37 μm indicating the silt and clay dominance (Table 1a.). In each marsh, sediments with a smaller grain size were deposited in the small creek in comparison to the larger creek. In Seaftinghe, Waarde and Zuidgors, the organic matter content was higher in the small creeks (11.9, 13.8, 11.9 % respectively) than in the large channel (4.7, 9.6, 9.3 % respectively). In the euhaline area, the organic matter content of the sediment was 5.4 % in both habitats.

The inherent variability within each site and parameter is indicated by the coefficient of variation (%) (Table 1b). The high coefficient of variation for salinity coincided with a high variation in oxygen concentration in Grembergen (salinity: 30.2%; oxygen: 17.4%) and Saeftinghe (salinity: 11.8%; oxygen: 19.0%). In the three downstream marshes (Waarde, Zuidgors and Zwin), the temperature was the most variable environmental parameter (20.3, 15.6, 24 CV% respectively). The coefficient of variation of the grain size in the small creek was 39.0% and in the large creeks was a bit lower, 31.1% (Table 2b). The variability in OM content was 29.8 in the small and 30.6% in the large creek.

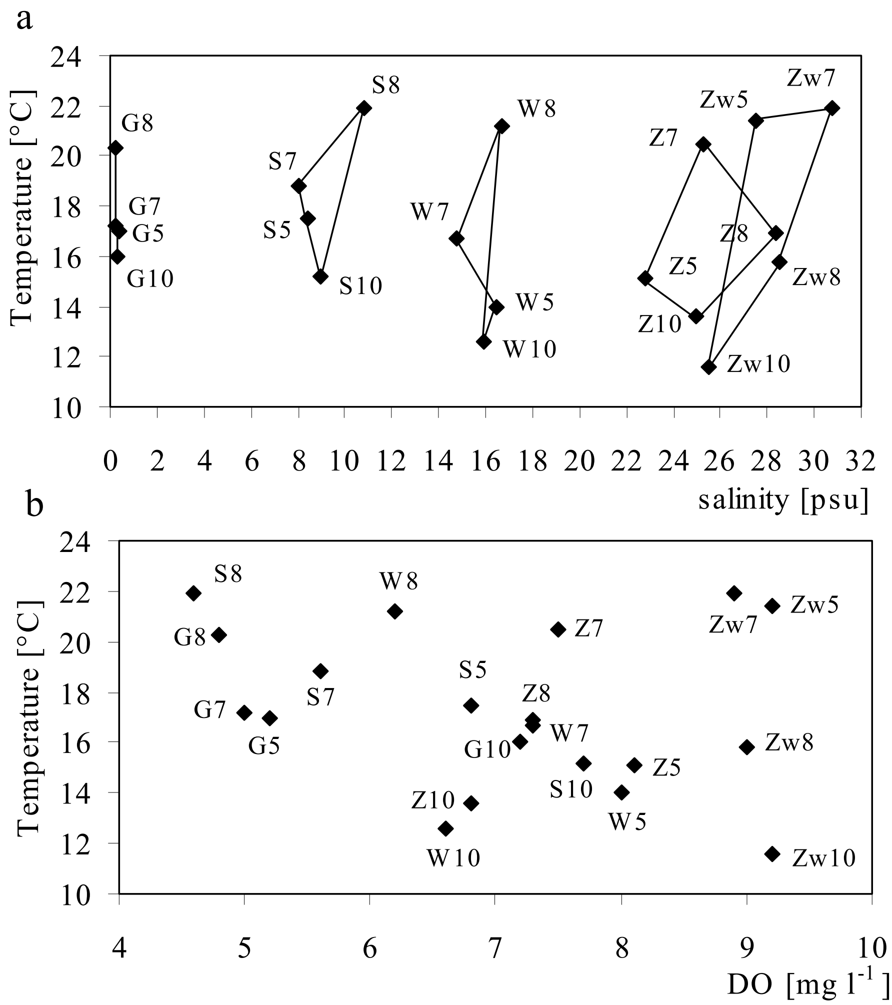

Figure 2a-b. Temperature recordings vs. salinity (a) and versus DO (b) as recorded in the water column of the large marsh creeks. May (5), July (7), August (8) and October (10) are indicated by numbers.

Table 2a-b. The median grain size (µm) and average OM (organic matter) content (%) of the sediment in the small and the large creek. The Coefficient of Variation (CV%) is given for each creek type (a). The Coefficient of Variation (CV%) for each of the parameters is reported for each marsh (b).

(a)

Environmental parameter	*Location*	Creek size	
		Small	Large
Median grain size (µm)	*Grembergen*		27.1
	Saeftinghe	13.3	21.5
	Waarde	10.0	16.5
	Zuidgors	13.3	22.0
	Zwin	26.0	36.6
CV %		*39.0*	*31.1*
OM content (mass %)	*Grembergen*		7.3
	Saeftinghe	11.9	4.8
	Waarde	13.8	9.6
	Zuidgors	11.9	9.3
	Zwin	5.4	5.4
CV%		*29.8*	*30.6*

(b)

Location	Coefficient of variation		
	Salinity	**Temperature**	**DO**
Grembergen	30.2	9.1	17.4
Saeftinghe	11.8	13.2	19.0
Waarde	4.6	20.3	9.8
Zuidgors	7.9	15.6	6.3
Zwin	6.8	24.0	1.4

5.3.2 Species composition

The marsh samples yielded 26 taxa or faunal groups of which some were identified to species but others to a higher taxonomic level (Table 2). Life stages of *Carcinus maenas* were distinguished because of their different ecology. One bivalve, one mysid, 3 decapod, 3 amphipod and 3 isopod and 12 polychaeta taxa were found in the samples. The taxon Oligochaeta probably included the species *Tubificoides benedii*, *Tubifex costatus*, *Tubifex tubifex* and Enchytraeidae (Barnes, 1994).

Table 2. Species found in the five sampled marshes: "j" indicates the juvenile and "m" the megalopa stage of *Carcinus maenas*.

Mysidacea	**Polychaeta**	**Other**
Neomysis integer	*Aonides* sp.	Hirundinea indet.
Caridea	*Cirratulidae* sp.	Nematoda indet.
Crangon crangon	*Eteone longa*	**Isopoda**
Brachyura	*Heteromastus filiformis*	*Cyathura carinata*
Carcinus maenas (m)	*Malacoceros tetraceus*	Isopod indet.
Carcinus maenas (j)	*Nephtys caeca*	*Lekanesphera rugicauda*
Amphipoda	*Nereis diversicolor*	**Oligochaeta**
Corophium volutator	*Polydora ciliata*	Oligochaeta indet.
Gammarus zaddachi	*Pygospio elegans*	
Melitta pellucida	*Scolelepis squamata*	
Bivalva	*Spio filicornis*	
Macoma baltica	*Streblospio benedicti*	

5.3.3 Temporal variation

5.3.3.1 Total and species density

The average density of all the species in each month in every marsh is presented in Figure 2. The patterns indicate that the macrofaunal abundance fluctuated in Grembergen with the highest value in July (38400 ± 10140 ind. m^{-2}). In Saeftinghe and Waarde, the average density was lower at spring and increased to mid summer (maximum 15070 ± 1940 and 22570 ± 2760 ind. m^{-2} respectively) before reducing again in October. The density in both marshes correlated with the measured water temperature (Spearman-Rank correlation, $p=0.04$ and $p<0.001$ respectively). In contrast, at the higher salinity areas (Zuidgors and Zwin) the densities are highest at the beginning of the summer before declining over the sampling period with a minimum in October (min. 26470 ± 5200 and 7500 ± 1020 ind. m^{-2} respectively). Correlation analysis indicated a negative regression of macrobenthic density along the sampling period in Zuidgors ($R^2=0.92$) and Zwin ($R^2=0.83$).

Three taxa (Oligohaeta, *Corophium volutator*, *Nereis diversicolor*) composed the major part of the macrobenthic density during all sampled months. In Grembergen, the density of oligochaetes fluctuated throughout the sampling period and composed 97-99% of the total abundance (21200-38000 ind. m^{-2}) (Figure 2). The relative abundance of oligochaetes was higher during the first part of the year and in Zuidgors and Zwin reached 78% and 55% in May respectively. *Corophium volutator* was present only in the brackish marshes and composed 35-60% of the total abundance in Saeftinghe, 40-67% in Waarde and 7-53% in Zuidgors. This species reached the maximum average abundance in July in Saeftinghe (7000 ind. m^{-2}), in August in Waarde (12500 ind. m^{-2}) and in October in the polyhaline marsh (9600 ind. m^{-2}). The ragworm, *Nereis diversicolor* showed stable densities ranging from 1800 to 5300 ind. m^{-2} during the sampling period. Its relative abundances were similar in the three brackish marshes: 19-26% in Saeftinghe, 13-25% in Waarde and 7-11% in Zuidgors. In the euhaline area, the contribution of *N. diversicolor* increased towards autumn and reached the maximum of 54% in October.

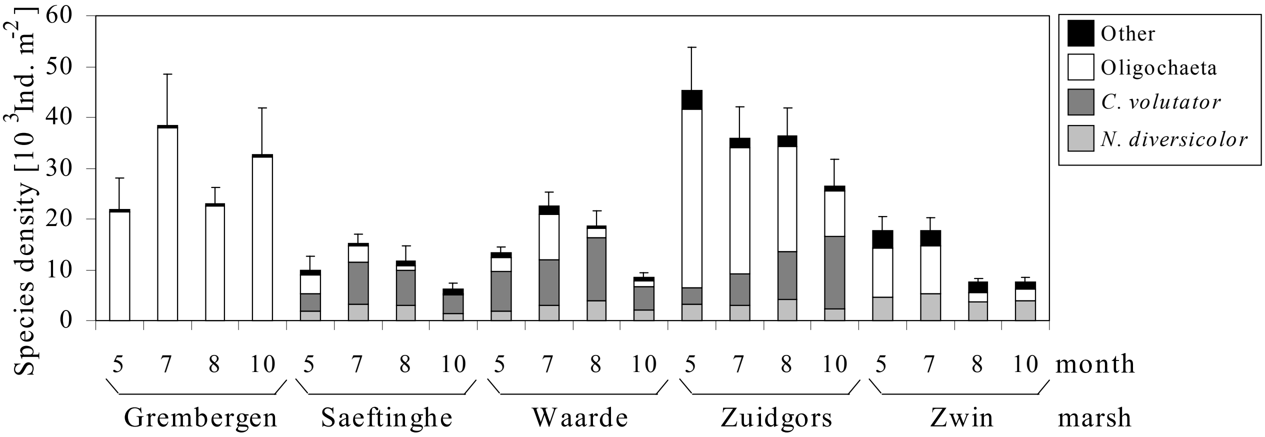

Figure 2. Total and species densities and standard error at the different locations and months. Months are represented by numbers such as May (5), July (7), August (8) and October (10).

5.3.3.2 Total and species biomass

The average biomass of each taxa and the summed biomass of the four taxa in every month are presented in Figure 3. In Grembergen, an increase in the average biomass was observed towards autumn reaching a maximum value in October (1.72 g ADW m^{-2}). In Saeftinghe, the average summed biomass of Oligochaeta, *N. diversicolor*, *C. volutator* and *Macoma baltica* showed a minimum in 2.1 ± 1.23 (g ADW m^{-2}) and correlated negatively with temperature (Spearman-Rank correlation, p=0.04). In the other three marshes, biomass peaked in August although no correlation was found with temperature. In Waarde, the maximum average biomass was 4.95 ± 1.76 g ADW m^{-2}. In Zuidgors, and Zwin the macrobenthic biomass reached 27 ± 5.58 and 23.02 ± 11.86 g ADW m^{-2} respectively.

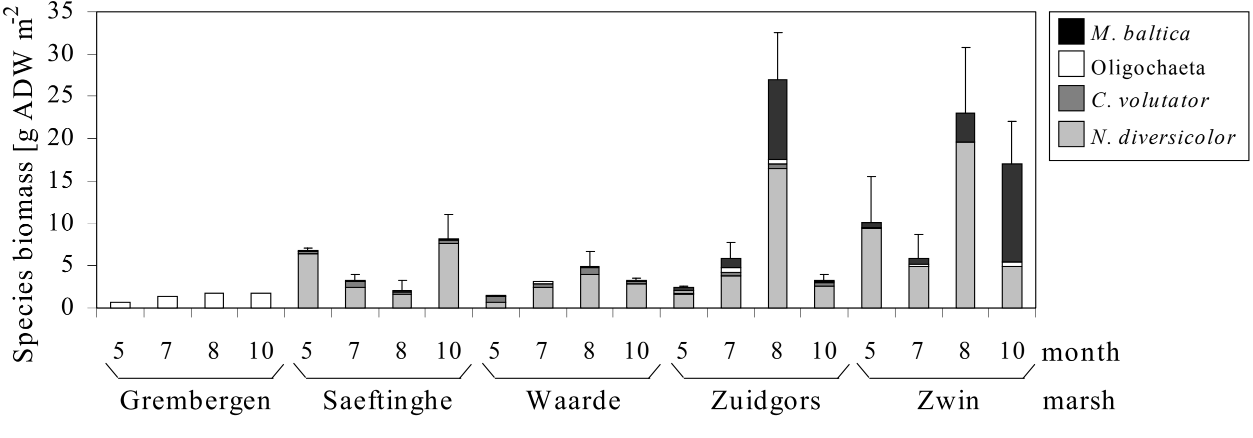

Figure 3. Total and species biomass and standard error at the different locations and months.

In Grembergen, where only oligochaetes were present, biomass increased towards October (Figure 3). In the other marshes, biomass was dominated by *Nereis diversicolor*, and this determined the general biomass pattern during the sampling period. In Saeftinghe the biomass of *N. diversicolor* reached the maximum of 7.7 g ADW m^{-2} in October. In Waarde, Zuidgors and Zwin, the biomass of this species peaked in August with the value of 4.0, 16.5 and 19.5 g ADW m^{-2} respectively. During this period *Macoma baltica* also had the highest biomass in Zuidgors (9.4 g ADW m^{-2}) composing 34.8% of the total biomass. In Zwin, *M. baltica* attained a high biomass in August (3.4 g ADW m^{-2}) and a maximum in October (11.5 g ADW m^{-2}) when it contributed 68.2% to the total value.

5.3.3.3 Diversity

Diversity indices did not show any general seasonal variation (Figure 4). Grembergen had the lowest diversity in every month fluctuating between 0.07 and 0.15. In this marsh oligochaetes were the most abundant but individuals were not identified to species level, which may have affected the calculated diversity index. In Saeftinghe the highest diversity indices occurred in May (1.42) while 1.28 was the highest value in July in Waarde. In Zuidgors and Zwin, the diversity peaked in August (1.17 and 1.62 respectively).

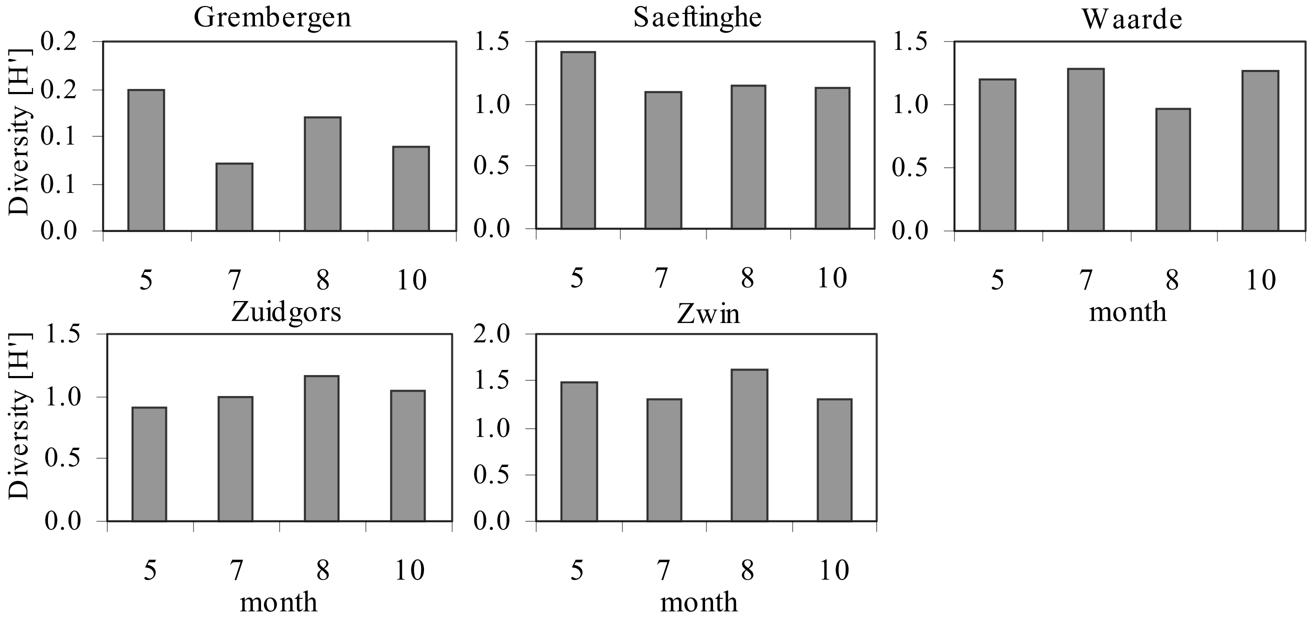

Figure 4. Shannon-Wiener diversity indices (H') calculated for every month in the five marshes.

5.3.4 Geographic variation

5.3.4.1 Density

A Spearman-Rank test did not show a significant correlation (p=0.6) between the salinity and the density of macrofaunal species (Fig. 5). The highest densities were detected in Zuidgors (11060-63300 ind. m^{-2}) and in Grembergen (21800-38400 ind. m^{-2}) due to the high number of Oligochaeta. In Saeftinghe and Zwin, the average density was approximately 10000 ind. m^{-2}. In Waarde an intermediate average density (6260-28700 ind. m^{-2}) was observed.

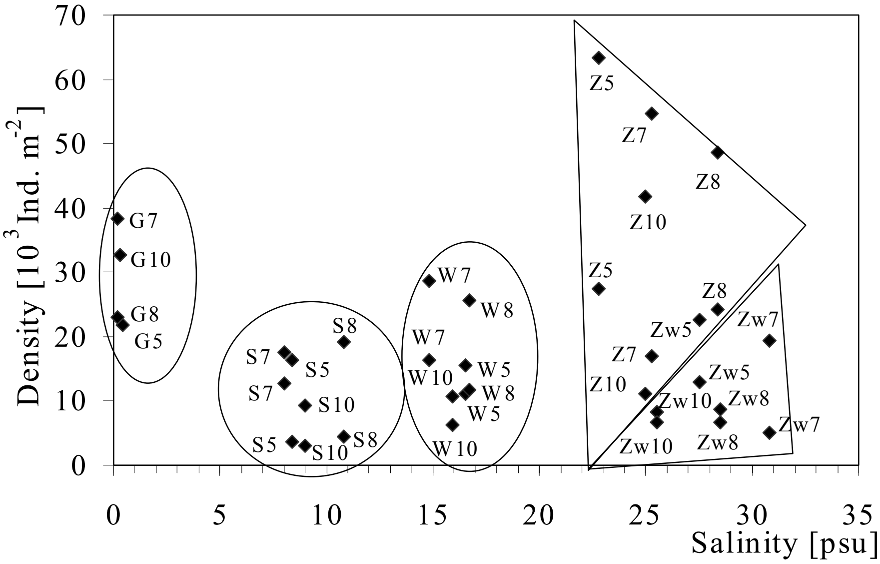

Figure 5. Average macrobenthic densities versus salinity (psu). Marshes are labelled as indicated in Figure 1. Numbers are used to indicate the months.

Macoma baltica generally occurred generally in low densities in every marsh (Figure 6). In Grembergen, this species was absent. The average abundance of *M. baltica* showed an increasing trend towards the euhaline area and reached 0.19 ind. m^{-2} in Zwin. The density of this species is positively correlated with the salinity (Spearman-Rank correlation, p=0.001). Oligochaetes were present in high densities in the freshwater marsh (28500 ± 4160 ind m^{-2}) and in the polyhaline Zuidgors (22480 ± 3410 ind m^{-2}). The other three marshes had similar densities (Saeftinghe, 2020 ± 450, Waarde, 3660 ± 930 and Zwin, 5800 ± 1050 ind. m^{-2}). *Corophium volutator* was present only in the three brackish water marshes where it reached similar average abundances ranging between 5550 and 8440 ind m^{-2}. Neither the density of oligochaetes nor *C. volutator* correlated with salinity in the five marshes. In contrast, densities of *Nereis diversicolor* increased towards the euhaline marsh; from 2400 ind m^{-2} in Saeftinghe to 4370 ind m^{-2} in Zwin and showed a positive correlation with salinity (Spearman-Rank correlation, p <0.001).

5.3.4.2 Biomass

Macrofaunal biomass was positively correlated with salinity (Spearman-Rank correlation, p=0.03). The highest biomass was measured in Zwin (average 13.98 g ADW m^{-2}) and the lowest value was found in Grembergen (average 1.36 g ADW m^{-2}). The three brackish marshes had intermediate biomass; 5.09 in Saeftinghe, 3.17 in Waarde and 9.62 g ADW m^{-2} in Zuidgors (Figure 7).

Figure 8 shows the biomass of the main taxa in the 5 different marshes. *Macoma baltica* had generally low biomass although in Zuidgors and Zwin the average biomass increased to 2.8 and 4.0 g ADW m^{-2} due to the high values in August and in October respectively. The biomass of this species correlated positively with salinity (Spearman-Rank correlation, p<0.001). The average biomass of Oligochaeta was the highest in Grembergen (1.4 g ADW m^{-2}). In the other marshes the average biomass did not exceed 0.5 g ADW m^{-2}. *Corophium volutator* was found only in the three brackish marshes. Waarde had the highest average biomass 0.5 g ADW m^{-2}. In the other two marshes, between 0.3 and 0.4 g ADW m^{-2} *Corophium* was observed. The biomass of oligochaetes and *C. volutator* did not correlate with salinity in the different marshes (Spearman-Rank correlation, p=0.6 and 0.25 respectively). The biomass of *Nereis diversicolor* in Zuidgors and in Zwin increased to 6.11 and 9.7 ind. m^{-2} respectively towards August. In Saeftinghe 4.6 and in Waarde 2.5 g ADW m^{-2} biomass was observed. A Spearman Rank correlation indicated a positive relationship between salinity and the biomass of *N. diversicolor*.

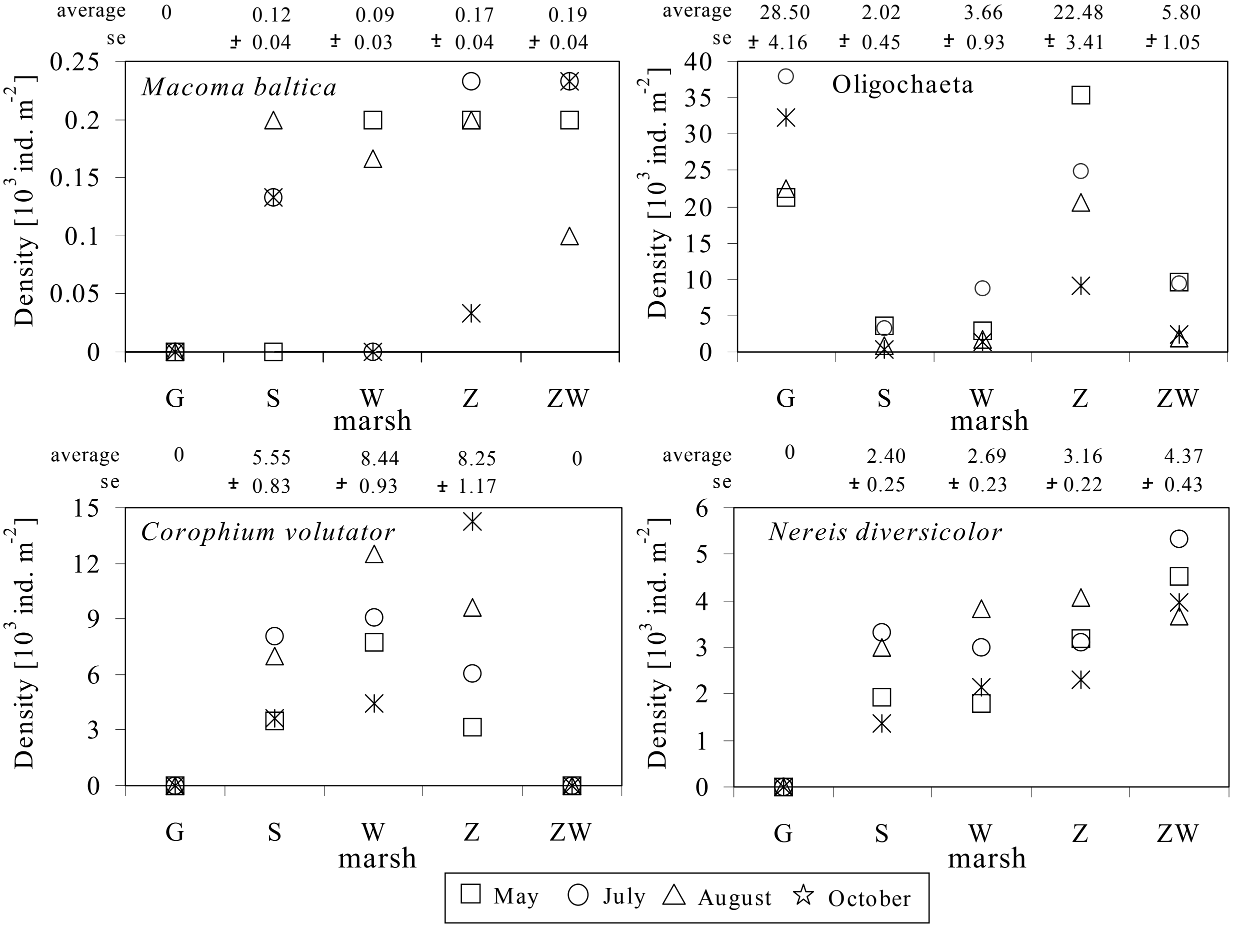

Figure 6. Density of the main macrobenthic species in the five marshes during the sampling period. Average density and standard error are indicated above the graphs.

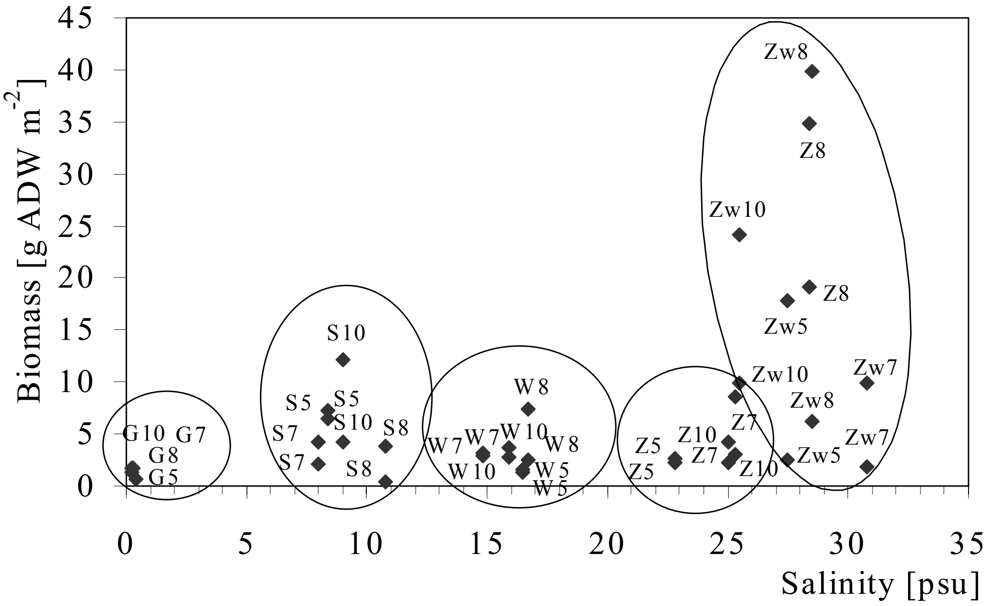

Figure 7. Average macrobenthic biomass versus salinity (psu).

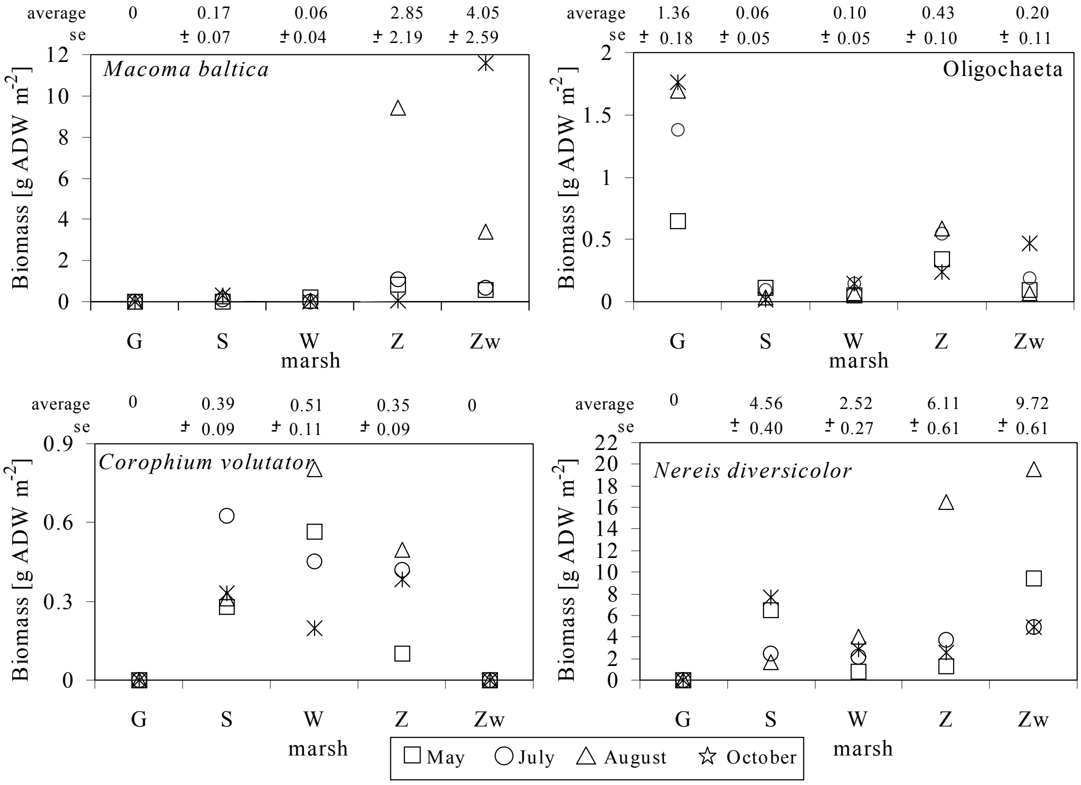

Figure 8. Biomass of the main macrobenthic species in the five marshes during the sampling period. Average biomass and standard error are indicated above the graphs.

5.3.4.3 Diversity

The number of taxa found in the replicates of Grembergen ranged between 4 and 6. In Saeftinghe 4-7, Waarde 6-8, Zuidgors 6-14 and Zwin 7-15 taxa were sampled. The Spearman-Rank correlation indicated a positive correlation between salinity and the number of taxa ($p<0.001$). The locations were also separated from each other in diversity (H') and the index values of the different marshes were significantly correlated with salinity (Spearman-Rank test, $p<0.001$) (Fig. 9). The Shannon-Wiener index values were lowest in the freshwater marsh (0.07-0.14). Zwin had the highest Shannon-Wiener indices (0.99-1.63) but the diversity showed similar values in the three remaining brackish marshes: in Zuidgors between 0.58 and 1.41, in Waarde 0.77-1.23 and in Saeftinghe 0.76-1.77. The individuals from the Oligochaeta taxa were not identified to species level, which might affect the calculated diversity index. In the freshwater marsh the 98% of the sampled individuals belonged to the Oligochaeta therefore the lack of identification of this taxa may have the greatest effect on the diversity index in this marsh.

5.4 Discussion

Along an estuary the source of spatial variability of macrofaunal composition lies within a marsh (e.g. different habitats), between marshes (e.g. situation along the salinity gradient), between months and between habitats (e.g. mudflats vs. salt marsh) (e.g. McLusky *et al.*, 1993). That spatial variability is the result of environmental gradients, patchiness over the scales and faunal interactions. Estuarine and marine communities are formed under the influence of a combination of physico-chemical parameters which, given an organism's tolerances, produce the fundamental niche for settlement and colonisation (e.g. McLusky 1981; Costa *et al.*, 2002). The high variability of environmental parameters always indicates increased stress for any organisms inhabiting the area. Recruitment and the further development of a community are dependent not only upon those physico-chemical characteristics but also upon the biological inter-relationships like predator-prey cycles, food and space availability (Costa *et al*., 2002). Due to the mentioned complexity of the system and the limited observations, the present study does not attempt giving a general overview about community structures in the different marshes or extrapolating the results for the complete systems. The main aim of the study was to give an overview about the availability of macrobenthic species and their temporal changes and spatial changes in the marshes with different salinities. Since these areas are used as feeding ground for several fish species a comparison with intertidal flats can further evaluate the foraging potential of the marsh creeks.

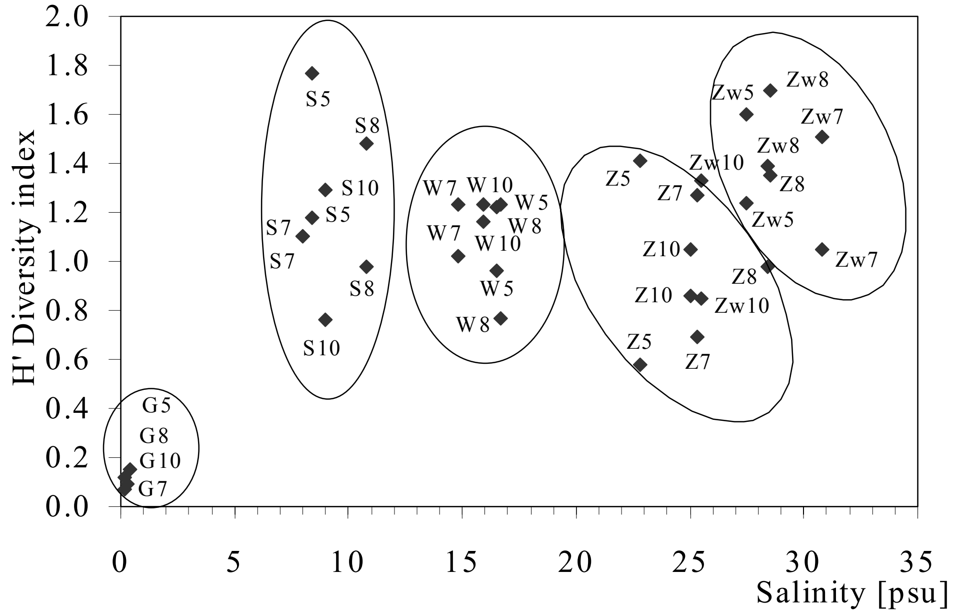

Figure 9. Shannon-Wiener diversity indices versus salinity (psu).

5.4.1 Temporal pattern

In the Westerschelde marshes, the general temporal pattern showed a higher density at the first part of the sampling period and a decrease towards autumn. Although in the five marshes there were two different temporal patterns of the macrobenthic density observed. In the more upstream marshes, density peaked in the summer months (July, August). Such a peak may be the net result of recruitment in early summer and growth. In the downstream marshes, density decreased towards the autumn, which does not support the observations of other studies indicating a summer or autumn peak. In these marshes the temperature decreased in August, which might contribute to the explanation of the decreasing density. Sarda *et al*. (1995) found high macroinfaunal densities in muddy sediments in June-July and October-November in the Great Sippewissett marsh in the USA. Jackson *et al.* (1985) also found two different patterns in a *Spartina anglica* marsh in the UK. One year the density peaked in July while the following year a spring and an autumn peak were observed. Wiltse *et al*. (1984) recorded a summer decrease in macrofaunal abundance and attributed this pattern to the intense predation. Cattrijsse *et al*. (1994) observed a decrease in the infaunal population (e.g. *Corophium volutator*, *Nereis diversicolor*) in a marsh creek at the end of the summer although they stated that predation by epibenthos did not solely cause this decrease. Reise (1978) found that the high abundance of predators especially young *Pomatoschistus microps*, *Dicentrarchus labrax*, *Crangon crangon* and *Carcinus maenas* would nevertheless affect the abundance of benthic communities. In this study, the temporal change in the whole community abundance was mainly influenced by the seasonal dynamics of the most important taxa. Jackson *et al*. (1985) also reported a maximum abundance of the Oligochaeta (*Peloscolex (Tubificoides) benedini* and *Tubifex costatus*) in the summer months in a *Spartina* marsh. In contrast, Frid and James (1989) found high Oligochaeta densities in March, September and November in a marsh in eastern England.

The macrofaunal biomass was generally lower in the first part of the sampling period and dominated by oligochaetes, which had a low contribution to the biomass. The highest biomass at the end of August coincided with the high biomass of *Macoma baltica* in Zuidgors and Zwin, of *Nereis diversicolor* in Waarde, Zuidgors and Zwin and with the high biomass in May and October in Saeftinghe. Alves and Lana (2000) observed a biomass peak of *Nereis oligohalina* in June, September and January, which lagged 2-3 months behind the peak densities (May-June and October-November) similar to our observation when density peaked 1-2 months before the biomass maximum.

5.4.2 Spatial pattern

In contrast to estuaries as a whole, scientific investigations examining the macrobenthic species density and biomass in intertidal marshes with different salinity are lacking. The number of taxa found in the marsh creeks showed a decrease with the declining salinity although species belonging to the dominated taxa (Oligochaeta) were not identified which might influence the pattern of the number of species and also the calculated diversity indices. The found pattern contradicts the general estuarine pattern where the number of species decreases with a progression upstream towards the tidal brackishwater area and then increases with a movement into freshwater areas. The brackish part of the estuary was indicated as the most species poor area (Remane, 1934; McLusky, 1981).

In the present study, the total population density did not show any trend along the salinity gradient. Oligochaeta dominated the total abundance of macrobenthos. The density fluctuation of this taxon contributed to the observed pattern. Frid and James (1989) reported a much lower mean density of oligochaetes (2100 ind m^{-2}) in a brackish marsh in the UK than in the Westerschelde marshes (average 9400 ± 3000 ind m^{-2}). Although similar sampling methods were used, the mesh size of the present study was larger than that of Frid and James (1989) hence the latter possibly sampled marsh habitats with different sediment and vegetation characteristics. The lack of correlation between total density and salinity is also caused by *Corophium volutator*, which appeared in high densities in the creeks of the three brackish marshes but was almost absent in the euhaline and freshwater marshes. Jackson *et al*. (1985) also found *C. volutator* as one of the main species contributing to the total density in a *Spartina anglica* marsh in the UK. The density of *Nereis diversicolor* positively correlated with salinity. Lerberg *et al*. (2000) found a similar density pattern in the tidal creeks located in Charleston Harbor where the relative abundance and the total number of polychaetes was positively associated with salinity. The abundance of *Macoma baltica* also showed a positive correlation with salinity. This result does not support Hiddink *et al*. (2002) who found that *N. diversicolor* has a negative effect on the abundance of *Macoma baltica* in field and laboratory experiments.

In contrast to the density fluctuation, the mean total biomass and the macrobenthic diversity of the sampled stations showed a clear decrease towards the freshwater area. This phenomenon is explained by the decrease of the biomass of *Macoma baltica* and *Nereis diversicolor* who had the largest contribution to the biomass and correlated positively with the salinity. *Macoma* was not present and *N. diversicolor* was captured only occasionally in the freshwater area but had a high biomass in the poly- and euhaline marshes.

5.4.3 Habitat differences (marsh – intertidal flat)

Saltmarshes are well known to serve as important feeding grounds for several fish species (Minello and Webb, 1997; Craig and Crowder, 2000; Mathieson *et al*., 2000). The macrobenthos comprises a significant part of the diet of some species like the seabass *Dicentrarchus labrax* and the flounder *Platichthys flesus*, which use the European saltmarshes (Gardner, 1996). Hence our comparison of the macrobenthic availability focused on the main prey species of these fish. Comparing their abundance in the marsh creeks with that on the adjacent intertidal area of the estuary will provide further information about the potential of marshes as fish feeding grounds.

A similar mesh size and method was used for sampling the marsh creeks as the estuarine intertidal (Ysebaert *et al*., 1993) thus making the results comparable. The total community density along the salinity gradient did not show any trend, thus agreeing with the observation of Ysebaert *et al*. (1993) who sampled intertidal areas in the Schelde estuary and found high and low macrofaunal abundance distributed randomly along the estuarine gradient. Similarly Mannino and Montagna (1997) did not find significant differences on macrobenthic abundance among salinity regions of the Nueces Estuary.

The average abundance of the macrobenthic species in the marsh creeks in the early autumn was lower (10218 ± 2524 ind. m^{-2}) than the values reported by Ysebaert *et al*. (1993) from the intertidal of the Westerschelde estuary (21000 ± 4600 ind. m^{-2}) and Ysebaert and Herman (2002) (20000-25000 ind. m^{-2}). However, lower values (6378-16682 ind. m^{-2}) were found on the intertidal areas analysing a dataset from 1978 to 1997 (Ysebaert, 2000) where samples were collected in September-October and March-April.

Among the main macrobenthic species and taxa (*Nereis diversicolor*, *Corophium volutator*, Oligochaeta) consumed by fish, the measured density of *N. diversicolor* (3083 ± 303 ind. m^{-2}) was higher in the early autumn in the marsh creeks than on the intertidal flats (200-550 ind. m^{-2}) (Ysebaert and Herman, 2002). Other studies reported a max. of 6000 ind. m^{-2} on mudflats of the Danish Wadden Sea (Jensen and Andre, 1993). Ysebaert *et al*. (1993) detected a lower density of *N. diversicolor* in the marine zone of the Westerschelde estuary than in the brackish part. In contrast, our study showed generally a higher density and biomass of *N. diversicolor* in the euhaline than in the brackish marsh creeks. This species contributed highly to the biomass in the intertidal marsh creeks (7.4 ± 2.0 g ADW m^{-2}) in early autumn exceeding the biomass of this species on the intertidal flat (1.1-1.4 g ADW m^{-2}) (Ysebaert and Herman, 2002).

In the present study, the abundance of *Corophium volutator* ranged around 6741 ± 1613 ind. m^{-2} in the brackish marsh creeks in early autumn. Cattrijsse (1994) reported average densities of 6597 and 1839 ind. m^{-2} from two mesohaline marsh creeks. Ysebaert *et al*. (1993) also observed arthropod species mainly in the brackish part of the estuary where *C. volutator* composed 90% of this taxa with densities between 3000 and 10000 ind. m^{-2}. In the year 2000, density of *C. volutator* reached a high peak comparing with the earlier years and ranged between 10000-12000 ind. m^{-2} (Ysebaert and Herman, 2002). Hughes and Gerdol (1997) reported the opposite pattern with a mean of 6077 ind. m^{-2} from marsh creeks and only 3181 ind. m^{-2} from mudflats in south-east England. The biomass of *C. volutator* in the brackish marsh creeks during the early autumn was also lower (0.4 ± 0.1 g ADW m^{-2}) as measured on the intertidal flat (around 2.1 g ADW m^{-2}).

The mean density of Oligochaeta in the freshwater marsh creek was 27366 ± 4710 ind. m^{-2} in the early autumn. Ysebaert *et al*., (1993) reported approximately 11700 ind. m^{-2} for the intertidal flats of the freshwater part of the estuary although one station had an extreme high density, which increased the mean abundance up to 26000 ind. m^{-2}. In the euhaline and oligohaline areas of the estuary respectively approximately 5000 and 2000 ind. m^{-2} were detected by Ysebaert and Herman (2002). In the oligohaline marsh stations, the density of oligochaetes in the early autumn was much lower (580 ± 167 ind. m^{-2}) as on the intertidal flat while in the euhaline marsh creek the density value was comparable (2100 ± 600 ind. m^{-2}) with the estuary intertidal flat.

The present study showed a decrease of the mean total biomass in the marshes towards the freshwater area, a feature present in estuarine areas (Meire *et al.*, 1991; Schaffner, 1987, Ysebaert *et al.*, 1993, Ysebaert *et al.*, 1998). The main contributors to the biomass are the polychaetes and molluscs in the marsh creeks. It is notable that in the intertidal marsh creeks, the gastropod, *Hydrobia ulva* was lacking. The tellinid bivalves, *Macoma baltica* reached higher densities (1616 ± 701 ind m^{-2}) and biomass (3.1 ± 1.7 g ADW m^{-2}) in early autumn in the Westerchelde marsh creeks than on the intertidal flat (average 550 ind m^{-2} and 2.5 g ADW m^{-2}) (Ysebaert and Herman, 2002). *Macoma baltica* has a wide tolerance for environmental variables. Water current velocity above 0.4 m s^{-1} restricts the occurrence of *M. baltica* (Ysebaert pers.comm.) although in the marsh creeks average velocity was around 0.1-0.2 m s^{-1}, which is favorable for this species.

The total number of taxa found in the marshes (26) was lower than on the estuarine intertidal flats (35). The number of replicates taken in the estuary was higher and since the number of species correlates with sampling size (Magurran, 1987), it may result these differences. Diversity (H') of the sampled marsh creek stations showed a positive and significant correlation with the salinity similarly to the Westerschelde intertidal flats (Ysebaert *et al.*, 1993) and other estuaries (Dittmer, 1983; Michaelis, 1983; Mannino and Montagna, 1997). The sampled stations in the marshes along the Westerschelde had higher Shannon-Wiener index values than in the estuary. This is in contrast to other observations where the sampled marsh creeks tended to harbor a lower diversity relative to comparable estuarine habitats (Engle *et al.*, 1994). Lerberg *et al.* (2000) found that tidal creeks were numerically dominated by a few species of stress tolerant oligochaetes and polychaetes. In the Westerschelde, the upper part of the estuary is anoxic during much of the year (Van Eck *et al.*, 1991). This forms the main reason for the exclusive occurrence of organic-tolerant oligochaetes in the fresh water part of the estuary (Ysebaert *et al.*, 1993). In contrast, Rhode (1982) reported other species (e.g. freshwater gastropods, gammarids, insect larvae) living in the upper part of the Ems estuary reflecting the downstream migration of the freshwater fauna. As indicated by the present study, other species (e.g. insect larvae, freshwater isopods) also inhabited the sampled fresh water marsh station of the Schelde. The presence of these species may be supported by the less anoxic/hypoxic conditions in the marsh creeks.

Nowadays several factors threaten the existence of the estuarine marshes. Salt marshes have been filled, diked and impounded for purposes of agricultural or urban land reclamation (Bakker *et al.*, 1993; Mitsch *et al.*, 1994). On a global level, relative sea-level change influenced by an array of anthropogenic factors affect the coastal wetlands (Kennish, 2001). The calculation of the total stock of macrobenthos in the whole intertidal flat of the Westerschelde estuary vs. the intertidal marsh areas would give a good indicator about the importance of the marshes as feeding ground for fish or birds, which could be a topic for further research.

This study indicated the importance of salinity influencing the macrobenthic species distribution in the marshes. Density of the sampled stations fluctuated along the salinity gradient without any trend but biomass and diversity were positively correlated with salinity. A comparison of marsh creeks stations with the intertidal flat part of the estuary indicated similar density, biomass and diversity patterns along the salinity gradient. The most available important prey items for marsh visiting species, *Corophium volutator*, occurred in higher abundance and biomass on the intertidal flats which indicates that fish may forage better there, on the intertidal flats although other prey species *Nereis diversicolor* and *Macoma baltica* had higher densities and biomass in the sampled marshes which contradicts this view. The food availability (density and biomass of prey species) influences the nursery value of a marsh (Kneib, 1993) for fish and macrocrustaceans but other factors like temperature (Elliott *et al*., 2002), tidal change (Chapter 3), salinity (Armstrong, 1997) and dissolved oxygen (Pihl, 1994) influence the feeding behaviour of fish. Biological factors like life stages (Elliott *et al*., 2002), sex (Lozan, 1992) and behaviour also control the utilization of the feeding ground. The food availability is an important indicator for the potential of an area as feeding ground but the exploitation of the marsh creek by fish species is still influenced by several other factors.

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6 Feeding habit of young predator fishes in marsh creeks situated along the salinity gradient of the Westerschelde

Abstract: *To investigate the importance of marsh creeks as foraging grounds for larger fish species, fish and macrobenthos were sampled in five different marshes along the salinity gradient of the Schelde River. Total density and biomass of the main macrobenthic taxa, Corophium volutator, Nereis diversicolor, Oligochaeta and Macoma baltica was calculated using core sampling in a small and a large creek. Several fish species were captured but only the feeding habit of large predators (Platichthys flesus, Dicentrarchus labrax and Anguilla anguilla) was investigated. Block nets were set in smaller intertidal creeks while in the larger channels fyke nets were deployed to capture the fish leaving the marsh at ebb. Qualitative and quantitative stomach analyses included the calculation of the frequency of occurrence, the numerical and the gravimetric diet composition, the mean food index, the diet diversity using Shannon-Wiener diversity index and the fullness index. These analyses showed that the two most important benthic prey items for Platichthys flesus were Corophium volutator and Nereis diversicolor. Dicentrarchus labrax preyed upon on wider range of species including C. volutator, N. diversicolor Crangon crangon, Carcinus maenas and Orchestia species. The stomach diversity of D. labrax and P. flesus showed differences between the marshes but no typical change in diet composition could be attributed. The observed fullness indices of both flounder and seabass did not differ significantly between the marshes along the salinity gradient. The estimated minimum consumption of these predators showed that these fish do not control the macrobenthic community. The prey availability will not restrict the utilization of marsh creeks by these larger fish. The salt marsh creeks seem to offer sufficient food for the visiting fish species. The benthic prey was present in very high abundances, which contribute to the fact that the typical nursery species like Crangon crangon, Carcinus maenas, early juveniles of P. flesus, D. labrax and Pomatoschistus microps were not preyed upon significantly. This indicates that salt marsh creeks represent good refuge areas against predation of larger fish for the latter nursery species.*

6.1 Introduction

It is well demonstrated that juveniles of several species use coastal environments and that the life cycles of these species are closely associated with estuaries, lagoons, tidal flats and salt marshes (Cattijsse *et al*., 1994; Kneib, 1997; Feuteun *et al*., 1999; Hostens and Mees, 1999; Laffaille *et al*., 2001b).

Fish have been reported in several parts of the US (Weinstein *et al*., 1980; Rountree and Able, 1992; Dionne *et al*., 1999; Rozas and Zimmerman, 2000) and also in Europe (Drake and Arias, 1991; Cattrijsse *et al*., 1994; Lefeuvre *et al*., 2000; Costa *et al*., 2001) to utilise salt marshes as nurseries. Nursery areas offer good protection (Whitfield, 1998; Halpin, 2000; Paterson and Whitfield, 2000) and food (Rozas and Odum, 1988) for the visiting species. Several species perform tidal feeding migrations from the estuary into the tidal marsh creeks where they find high numbers of a range of possible prey items (Raffaelli *et al*., 1990; Elliott *et al*., 2002). The energy expenditure involved in these movements is assumed to be compensated by the high abundance and biomass of the available invertebrate prey (Wolff *et al*., 1981). Gibson (1994) suggested that food is probably the major factor determining habitat quality.

In predator-prey relationships, the abundance of predator and prey can be regulated by top-down or bottom-up control. In the subtidal area, studies have reported reduced densities of benthic invertebrates when nekton become seasonally abundant (Wiltse *et al*., 1984). In the tidal marshes, the foraging time is limited by tidal inundation but marsh nekton may still affect the abundance of invertebrates (Kneib, 1984, 1995), the dynamics of individual prey populations (Joyce and Weisberg, 1986) and the community composition of both benthic (Frid and James, 1988) and epibenthic prey (Walters *et al*., 1996). In contrast, prey densities may restrict the abundance of predators in a habitat.

The density of juveniles present in a habitat reflects recruitment, mortality and emigration and can thus be an important indicator of nursery value of that habitat (Minello *et al*., 2003). Cattrijsse *et al*. (1994) showed the importance of tidal marshes in the Westerschelde estuary as nurseries for estuarine fish species. Chapter 4 focused on the fish communities in marshes along the salinity gradient of this estuary. Two predatory fish, the flounder *Platichthys flesus* and the seabass *Dicentrarchus labrax*, occur in the salt marsh creeks in high numbers. These species are completely absent from the freshwater marsh where the European eel *Anguilla anguilla* is present as the sole large predator fish. The occurrence of larger predators in the marsh creeks questions the refuge function of this habitat.

In order to interpret the functioning of an estuarine habitat and to create food webs, it is also necessary to consider prey availability (Elliott *et al*., 2002). Food availability varies with many factors, both environmental and physical, including tidal inundation thus highlighting the complexity of food webs, even in species poor areas (Gorman and Raffaelli, 1993). Since macrobenthos contribute significantly to the diet of the flounder, seabass and the European eel (Arntz, 1978; Doornbos and Twisk, 1984; Costa *et al*., 1992; Laffaille *et al*., 2001a) the value of macrobenthic communities as potential food source for these species was addressed in Chapter 5. Feeding habit and diet composition of young flounder, seabass and European eel in the estuary or coastal water were reported in several studies (Ferrari and Chieregato, 1981; Aprahamian and Barr, 1985; Costa *et al*., 1992; Aarnio *et al*., 1996; Aarnio and Bonsdorff, 1997) but only a few researches have been done in the salt marshes (Laffaille *et al*., 2000, 2001b).

This study examines the feeding habit of the main predator fish species through qualitative stomach analysis in different salt marshes situated along the salinity gradient of the Westerschelde estuary. The final objectives were to assess the importance of marsh creeks as feeding grounds for larger seabass and flounder and to define the relative importance and impact of *Platichthys flesus* and *Dicentrarchus labrax* as predators on the infauna and the nursery/refuge function of the creeks for juvenile fish and crustaceans.

6.2 Material and Methods

6.2.1 Study area

Four marshes were chosen along the salinity gradient of the Westerschelde estuary and one marsh from the freshwater part (Zeeschelde) to investigate the feeding habit of young predator fish species (Fig. 1).

The Zwin (Zw) is situated at the mouth of the estuary, in the euhaline zone and has a total surface area of 125 ha. The Zuidgors (Z) marsh belongs to the polyhaline zone of the estuary and the marsh of Waarde (W) to the mesohaline part. The total surface area of these two marshes are 50 ha and 107 ha respectively. 'Het Verdronken Land van Saeftinghe' (S) (2078 ha) also lies in the mesohaline part of the Westerschelde estuary but has lower salinity than Waarde. In the tidal freshwater part of the Schelde small reed and willow marshes are still present. One of the largest tidal freshwater marshes (8.77 ha) is the 'Groot Schoor' or the marsh of Grembergen (G).

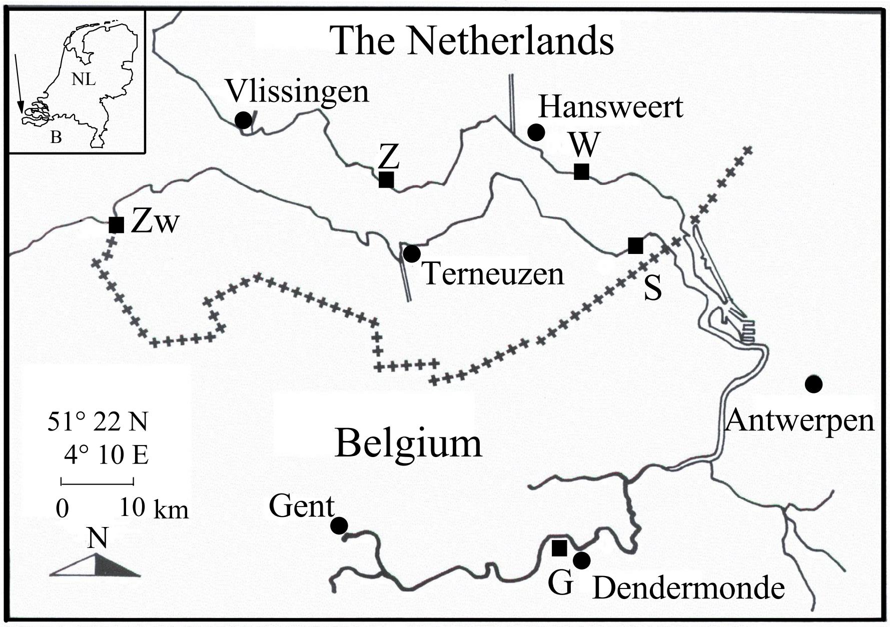

Figure 1. Location of the five marshes sampled along the Schelde river. Letters indicate the marshes Grembergen (G), Saeftinghe (S), Waarde (W), Zuidgors (Z) and Zwin (Zw).

6.2.2 Sampling of fish

The marshes were sampled on five consecutive days during spring tide period between April and October 2000 for fish and between May and October 2000 for macrobenthos. Samples were taken every six weeks. In Waarde, no sampling was done in April.

In each marsh, two channels were sampled for fish. Large intertidal channels were sampled with fyke nets to capture larger fish species. The dimensions of the larger creeks varied between 10-20 m wide and 3-4 m deep. The fyke nets had an opening of 1 m and a mesh size of 15x15 mm. The nets were 5 m long and contained 6 parlours. At the mouth 3 m long wings enlarged the sampling area of each net. The fyke nets were set before water entered the system and faced the outgoing ebb currents to sample fish leaving the creek with ebb. Collections were made after the water receded.

Smaller intertidal creeks higher up the marsh were sampled with a block net. These smaller creeks were generally 2 m wide and 1.5-1.8 m deep and opened into the larger creeks. The block net was constructed of 5 mm gauze and had two lateral wings of 2 m and a central bag. The whole net was 2 m height and the topline was provided with float. The ground rope was fitted with a heavy chain. The block net was set at high water near the mouth of the creek. The chain in the ground rope was manually placed on the bottom of the creek and sticks kept the net and ground rope in place. After all water had left the creek the net was emptied.

Description of the fish communities in the five sampled marshes is presented in Chapter 4. Catches were counted and expressed as numbers caught during the ebb period. *Platichthys flesus* and *Dicentrarchus labrax* were the two main predator fish occurring in relative high numbers in the creeks. *Anguilla anguilla* was also present but always in very low numbers therefore only qualitative stomach analyses (numerical and gravimetric percentage) were performed.

In the field, all the fishes were anaesthetised in a benzocaine (Ethyl amino-4-benzoate)-water solution to prevent regurgitation of the stomach contents and preserved in formaline solution. In the laboratory, for each captured fish the total length of each individual was recorded. All prey items in the stomachs encountered were counted, identified, if possible to species level, and length of each individual was measured. The biomass (mg ADW m^{-3}) of each prey item present in the stomachs was computed with length-ADW regressions established formerly in the laboratory by Hamerlynck and Cattrijsse (1994) and Beyst *et al.* (1999). Stomach contents were placed in pre-weighed aluminium foil cups, dried at 110 °C for 5 hours and cooled to room temperature in a dessicator for 2 hours before weighing.

6.2.3 Stomach content analysis

6.2.3.1 Quantitative stomach analysis

For the quantitative analysis of the stomach contents, the fullness index (FI), was used:

$$\mathrm{FI} = \frac{S_i}{W_i} \times 100 \tag{1}$$

where S_i is the ash-free dry weight (ADW) of the stomach content in milligram (mg) and W_i is the ash-free dry weight of the fish in mg.

6.2.3.2 Qualitative stomach analysis

Shannon-Wiener index (H') of the stomach contents of *Platichthys flesus* and *Dicentrarchus labrax* was calculated for every marsh and each month to assess the niche breadth:

$$\mathrm{H'} = -\sum \mathrm{p_i} \times \ln \mathrm{p_i} \tag{2}$$

where p_i is the proportion of the individuals found in the 'i'th species.

Three percentages (frequency of occurrence, numerical and gravimetric percentages) were calculated to characterise the stomach content of the fish. Each of the three indices has their own meaning and limits (Hyslop, 1980). The frequency of occurrence (FO%) calculates the percentage of the total number of stomachs in which the specific prey species occur:

$$\mathrm{FO\%} = \frac{\mathrm{FO_i}}{\mathrm{FO_t}} \times 100 \tag{3}$$

where FO_i is the number of stomachs in which the 'i' species occur and FO_t is the total number of stomachs analysed (Hyslop, 1980).

The diet composition was also expressed as a numerical percentage (N%):

$$\mathrm{N\%} = \frac{\text{Number of individuals of prey type}_\mathrm{i}}{\text{Total number of the prey items ingested}} \times 100 \tag{4}$$

and as a gravimetric percentage (G%) (Hyslop 1980):

$$G\% = \frac{\text{ADW of prey type}_i}{\text{Total ADW of the ingested food}} \times 100 \tag{5}$$

Following Zander (1982) and Laffaille *et al*. (2001b), the three indices were synthesised as the Main Food Index (MFI) which was calculated for each food item i, as:

$$\text{MFI}_i = \sqrt{\frac{G_i\% \times (N_i\% + FO_i\%)}{2}} \tag{6}$$

The MFI_i was expressed as a percentage of the total MFI. Species, which had MFI higher than 10% were considered an important prey item.

6.2.4 Macrobenthic sampling

Five replicate plastic cores (diameter 6.2 cm) were used to sample the macrobenthos to a depth of 15 cm from the large and small creek bed. The description of macrobenthic communities focused on the main prey species in the marsh creeks has been presented in Chapter 5. Since more than 80% of the sampled macrobenthic density in Zwin and more than 90% in the other marshes were composed of Oligochaeta, the amphipod *Corophium volutator*, the polychaeta *Nereis diversicolor* and the bivalve *Macoma baltica* and because these species were present in the stomach of the fish, the average total macrobenthic densities (ind. m^{-2}) and biomass (ADW) of these taxa were estimated for each month and marsh.

The surface area of the sampled creek was estimated from topographic maps (scale 1:10.000). The surface area of each creek and the average macrobenthic density and biomass of the four taxa in each month were used to estimate the macrobenthic standing stock and biomass stock in the creek which was available for fish to prey upon.

6.2.5 Statistical analysis

Analysis of Variance (ANOVA) was not applicable to test differences between fullness indices of *Platichthys flesus* and *Dicentrarchus labrax* in the different marshes due to the lack of normality and homogeneity therefore a non-parametric Kruskal-Wallis test was used. The diet diversity indices were tested for normality and homogeneity of the variances. Homogeneity was verified by the Bartlett test (Sokal and Rohlf, 1981). Diet diversity of the two fish species in the different marshes then were subjected to a single classification ANOVA. A Spearman-Rank correlation tested the relation between the numbers of fish captured and the macrobenthic density and biomass in the marsh creeks.

The total minimum consumption of the three predatory fish (*Platichthys flesus*, *Dicentrarchus labrax* and *Anguilla anguilla*) was estimated from the available standing stock (#%) and biomass stock (ADW%) of macrobenthos.

$$\#\% = \frac{\text{total number of macrobenthic prey in all the analysed stomachs of the three fish species}}{\text{total number of macrobenthos in the creek}} \times 100 \tag{7}$$

$$\text{ADW}\% = \frac{\text{total biomass of macrobenthic prey in all the analysed stomachs of the three fish species}}{\text{total biomass of macrobenthos in the creek}} \times 100 \tag{8}$$

6.3 Results

6.3.1 Number and average length of *Platichthys flesus* and *Dicentrarchus labrax*

Platichthys flesus did not inhabit the freshwater marsh and was also not found in the euhaline marsh Zwin. The total number of *P. flesus* captured during ebb in the marsh creeks of Saeftinghe ranged from 2 to 35. In Waarde, 9 to 40 individuals were caught while, in the Zuidgors marsh, between 2 and 16 flounders were found in the nets (Fig. 2). Higher numbers were caught during the first part of the sampling period. Highest numbers were observed in April in Saeftinghe and in July in Waarde and Zuidgors.

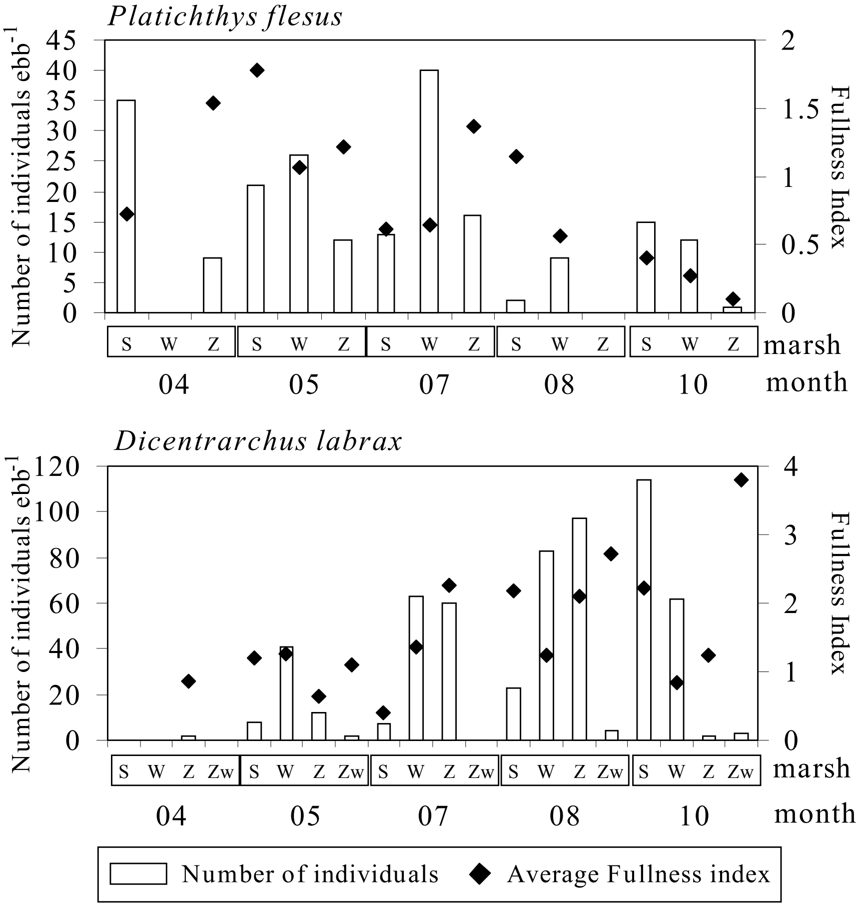

Figure 2. Total number (left y-axis) and average stomach fullness (right y-axis) of Platichthys flesus and Dicentrarchus labrax in Saeftinghe (S), Waarde (W), Zuidgors (Z) and Zwin (Zw) caught with fyke and block nets. There was no sampling in April in Waarde.

Dicentrarchus labrax was not present in the freshwater marsh, Grembergen. The number of seabass captured in Saeftinghe ranged between 8 and 114, in Waarde between 41 and 83, in Zuidgors between 1 and 97 and in Zwin only between 0 and 4 individuals. The highest values were counted in October in Saeftinghe and in August in Waarde, Zuidgors and Zwin.

In Saeftinghe the average total length of flounder increased from 152 to 234 mm till October (Fig 3). In Waarde and Zuidgors, the average total length ranged between 163-235 and 199-239 mm respectively. These individuals generally belonged to the 1+ or 2+ year class.

In Saeftinghe, *Dicentrarchus labrax* had the smallest length, 108 mm TL, in October and reached a maximum size of 135 mm TL in July. In Waarde the average total length of seabass ranged between 108-171 and 113-167 mm in Zuidgors. The smallest individuals (55-116 mm TL) were measured in Zwin. The fish caught mainly belonged to 1+ year class.

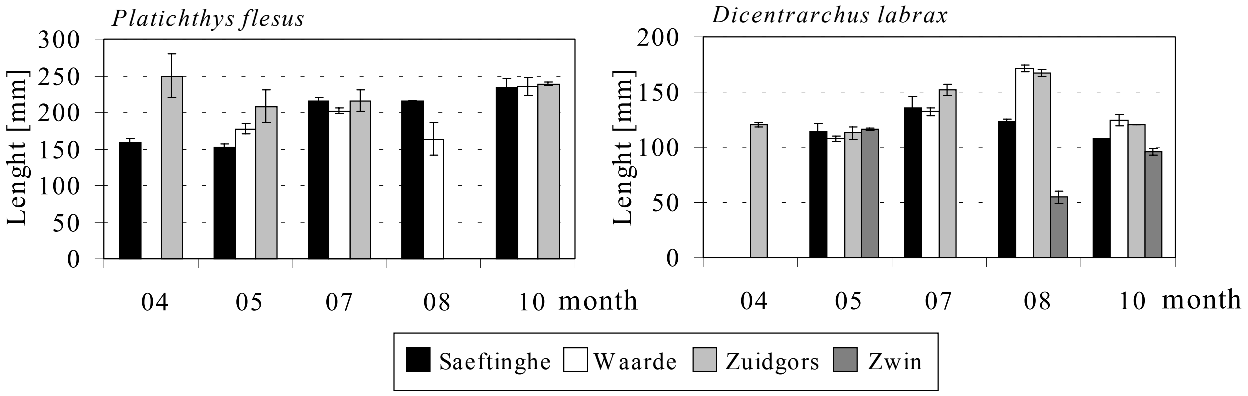

Figure 3. Average total length and standard error of Platichthys flesus and Dicentrarchus labrax caught in the marsh creeks with fyke and block nets.

6.3.2 Fullness index and diet diversity

The average fullness index of *Platichthys flesus* in Saeftinghe ranged between 0.4 in October and 1.77 in May (Figure 2). In Waarde, the highest average fullness index (1.06) was recorded in May and the lowest (0.27) in October. In Zuidgors, the fullness index reached 1.53 in April and decreased to 0.01 in October.

In Saeftinghe, average stomach fullness of *Dicentrarchus labrax* in Saeftinghe reached the maximum (2.21) in October and minimum (0.41) in July. The FI was 1.36 and 2.26 in July and 0.84 and 0.65 in October in Waarde and Zuidgors respectively. Only 2-4 seabass were captured in Zwin and their fullness index was high with a maximum 3.8 in October.

The Shannon-Wiener diversity index of the stomach contents of *Platichthys flesus* was generally low (Fig. 4). Higher indices were calculated in Saeftinghe in May and August (0.85 and 0.64 respectively) and in Zuidgors in May (1.15). Diet diversity of *Dicentrarchus labrax* was generally higher than *P. flesus*, indicating a wider prey spectrum (1.07-1.81). The exceptions occurred in May in Zwin (0.34) and in October in Zuidgors and Zwin (0.12 and 0.58 respectively) but these figures were based on only 1-3 fish stomachs.

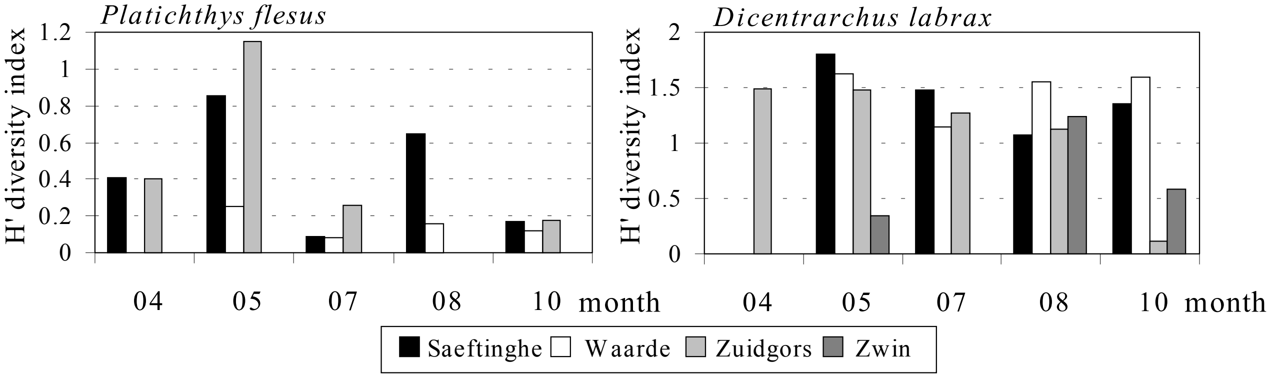

Figure 4. Shannon-Wiener diversity index (H') of the diet of Platichthys flesus and Dicentrarchus labrax during the sampling period.

A Kruskal-Wallis test did not reveal significant differences between the fullness indices of *Platichthys flesus* (p=0.13) caught in Saeftinghe, Waarde and Zuidgors (Table 1a). Similarly there were no significant differences in the fullness indices of *Dicentrarchus labrax* (p=0.07) caught in the four marshes of Saeftinghe, Waarde, Zuidgors and Zwin (Table 1a). These results indicated that fish foraged similar amount of food in every marsh. Marshes represented similar foraging grounds for flounder and seabass.

One-way ANOVA was used to test differences between the diet diversity of *Platichthys flesus.* A significant difference was found between Saeftinghe and Waarde (p<0.001) and between Zuidgors and Waarde (p<0.001) (Table 1b). In every month the diversity index of the stomach content of flounder was lower in Waarde indicating a narrow niche breadth. *P. flesus* had the highest stomach content diversity at Saeftinghe in May and August and at Zuidgors in May. The wider niche breadth in these months resulted in the significant difference in diet diversity between Saeftinghe and Waarde, and Zuidgors and Waarde.

ANOVA indicated a significant difference in the diet diversity of seabass between Waarde and Zuidgors (p=0.002) (Table 1b) probable due to the very low diversity index in October in Zuidgors. Similar niche breadth was observed in the other marshes showing that *Dicentrarchus labrax* foraged on similar range of prey items in these creeks.

Table 1a-b. P values of pair wise comparisons of the fullness indices (FI) (a) and the Shannon-Wiener diversity indices (H') (b) of the stomach content of *Platichthys flesus* and *Dicentrarchus labrax* as reported by Kruskal-Wallis tests and ANOVA's respectively.

(a) **FI**

Fish species	Marsh	p-value
Platichthys flesus	Saeftinghe-Waarde-Zuidgors	0.13
Dicentrarchus labrax	Saeftinghe-Waarde-Zuidgors-Zwin	0.07

(b) **H' diversity index**

Platichthys flesus

marsh	Saeftinghe	Waarde
Waarde	<0.001	-
Zuidgors	0.70	<0.001

Dicentrarchus labrax

marsh	Saeftinghe	Waarde	Zuidgors
Waarde	0.41	-	
Zuidgors	0.15	0.002	-
Zwin	0.14	0.79	0.31

6.3.3 Qualitative stomach analysis

6.3.3.1 Platichthys flesus

Frequency of occurrence of the species (FO%), which occurred in the stomach of *Platichthys flesus* is listed in Table 2. *Corophium volutator* was present in at least 90 % of the stomachs of flounders (Table 2). *Nereis diversicolor* was the second most abundant prey reaching a frequency of occurrence between 44 and 100%. The isopod, *Cyathura carinata* was consumed by flounder only in Saeftinghe and its occurrence reached a maximum of 50%. In Seaftinghe and Zuidgors, flounder also consumed the other isopod species, *Lekanesphera rugicauda*. The maximum frequency of occurrence of *Macoma baltica* was reached in October in Zuidgors with 31%.

Table 2. Occurrence frequency (FO%) of all the taxa found in the stomach of *Platichthys flesus* during the sampling period. Marshes are labelled as indicated in Figure 1.

FO%	*April*		*May*			*July*			*August*		*October*	
Marsh	**S**	**Z**	**S**	**W**	**Z**	**S**	**W**	**Z**	**S**	**W**	**S**	**W**
Carcinus maenas	0	44.4	0	0	25	0	20	68.7	50	0	0	8.3
Clupeidae spp.	0	0	0	3.8	8.3	0	0	0	0	0	0	8.3
Corophium volutator	100	100	100	100	91.7	100	100	100	100	88.9	100	100
Crangon crangon	0	0	4.2	3.8	0	0	2.5	6.3	0	11.1	6.7	8.3
Cyathura carinata	8.6	0	45.8	0	0	23.1	0	0	50	0	53.3	0
Decapoda megalopa	0	0	0	7.7	8.3	0	0	0	0	0	0	0
Gammarus zaddachi	0	0	4.2	3.8	0	0	0	0	0	0	0	0
Insect	0	0	12.5	0	0	0	0	6.2	0	0	0	0
Lekanesphera rugicauda	11.4	33.3	50	7.7	41.6	7.7	5	0	100	0	33.3	0
Macoma baltica	2.8	0	0	15.4	0	0	12.5	31.2	0	11.1	13.3	16.7
Melita pellucida	2.8	0	0	0	8.3	0	0	0	0	0	0	0
Mesopodopsis slabberi	0	11.1	0	0	0	0	0	6.2	0	22.2	0	0
Nematoda spp.	0	11.1	0	0	0	0	0	0	0	0	0	0
Neomysis integer	0	0	0	7.7	0	0	2.5	0	0	0	0	0
Nereis diversicolor	80	88.9	95.8	50	91.7	53.8	65	68.7	100	44.4	100	91.7
Oligochaeta	2.9	0	0	0	0	0	0	6.2	0	0	0	8.3
Orchestia spp.	0	0	12.5	0	0	0	0	6.2		0	0	0
Paragnatia formica	0	0	0	0	0	0	0	0	0	11.1	0	0
Syphon of bivalve	0	0	0	0	16.7	0	2.5	18.7	0	0	0	0

In Saeftinghe the numerical index indicated that 89% of the diet of *Platichthys flesus* was dominated by *Corophium volutator* (Fig 5). In Waarde flounder almost exclusively preyed upon this amphipod. Also in Zuidgors *C. volutator* was numerically the most important prey (89%). In Saeftinghe and Zuigors the ragworm, *Nereis diversicolor* reached a numerical percentage around 8.4%.

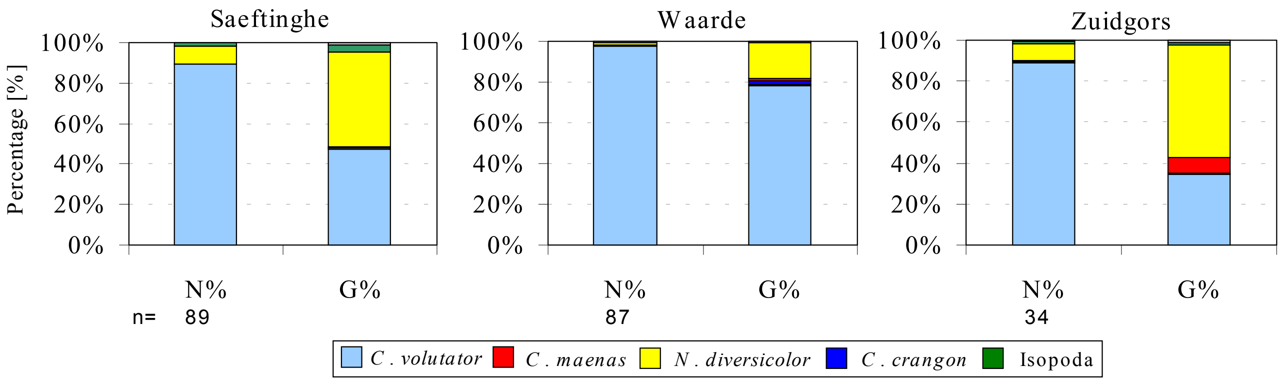

Figure 5. Numerical (N%) and gravimetric (G%) percentage derived from the stomach analysis of Platichthys flesus in the marshes of Saeftinghe, Waarde and Zuidgors in all sampled months. Number of stomachs analysed (n) is indicated below each graph.

The gravimetric composition of the stomach content also showed the high dominance of these two species. In Saeftinghe and Zuidgors, *Nereis diversicolor* figured very important in the diet (46.5 and 54.6% respectively), while in Waarde *Corophium volutator* was also in terms of biomass the most important species (78.5%). In Saeftinghe and Zuidgors isopods still contributed with 3.9% and 1.5% to the gravimetric percentage. In Zuidgors, next to the two dominant species, *Carcinus maenas* (8%) figured a relatively high gravimetric percentage in the diet of flounder.

Table 3 also lists the Mean Food Index (MFI) of all the species found in the stomachs of flounder. The MFI showed the exclusive dominance of *Corophium volutator* and *Nereis diversicolor* in the three marshes. The MFI's of *C. volutator* ranged between 18 and 83. This value was due to the high frequency of occurrence and the numerical dominance of this species. The MFI of *N. diversicolor* reached a maximum of 64% because of its high contribution to the weight of the stomach content in every marsh.

Table 3. Mean Food Index of the taxa (MFI) found in the stomach of *Platichthys flesus.* Marshes are labelled as indicated in Figure 1.

MFI	*April*		*May*			*July*			*August*		*October*	
Marsh	**S**	**Z**	**S**	**W**	**Z**	**S**	**W**	**Z**	**S**	**W**	**S**	**W**
Carcinus maenas	0	17	0	0	1.7	0	3.0	5.0	12.8	0	0	3.5
Clupeidae spp.	0	0	0	0.4	1.4	0	0	0	0	0	0	2.1
Corophium volutator	67.4	41.9	34.4	69.6	18.4	82.4	81.8	56	18.9	83.1	53.7	57.2
Crangon crangon	0	0	0.1	0.3	0	0	0	1.4	0	1.0	0.3	6.6
Cyathura carinata	0.7	0	5.3	0	0	1.7	0	0	4.4	0	5.6	0
Decapoda megalopa	0	0	0	0.2	0.2	0	0	0	0	0	0	0
Gammarus zaddachi	0	0	0.3	0.3	0	0	0	0	0	0	0	0
Insect	0	0	2.4	0	0	0	0	0.1	0	0	0	0
Lekanesphera rugicauda	2.3	1.5	7.8	0.7	11.2	1.2	0.4	0	13.4	0	3.1	0
Macoma baltica	1.0	0	0	0.9	0	0	1.3	3.6	0	0.7	0.6	1.4
Melita pellucida	0.2	0	0	0	0.7	0	0	0	0	0	0	0
Mesopodopsis slabberi	0	0.6	0	0	0	0	0	0.2	0	9.0	0	0
Neomysis integer	0	0	0	0.9	0	0	0.3	0	0	0	0	0
Nereis diversicolor	28.4	39.0	47.4	26.7	64.3	14.6	13.1	31.4	50.4	5.9	36.6	28.6
Oligochaeta	0	0	0	0	0	0	0	0.1	0	0	0	0.7
Orchestia spp.	0	0	2.2	0	0	0	0	0	0	0	0	0
Paragnatia formica	0	0	0	0	0	0	0	0	0	0.1	0	0
Syphon of bivalve	0	0	0	0	1.9	0	0	1.4	0	0	0	0

6.3.3.2 Dicentrarchus labrax

Table 4 shows the frequency of occurrence of all the prey species in the stomachs of *Dicentrarchus labrax*. Seabass preyed upon a wide range of species (Table 4). *Corophium volutator*, *Crangon crangon, Lekanesphera rugicauda, Nereis diversicolor* and different *Orchestia* species occurred most frequently in the stomachs of the seabass. Juveniles of *Carcinus maenas* were not preyed upon by *D. labrax* at the beginning and at the end of the sampling campaign while between May and August it was intensively consumed (18-67%).

In the three brackish marshes *Corophium volutator* and isopods numerically dominated the diet of seabass. In Saeftinge, the numerical importance of *Corophium volutator* and isopods reached 43% and 40% respectively. *Orchestia* species still contributed 13% to the number of prey consumed in Saeftinghe. The numerical percentage also showed the importance of *C. volutator* and isopods in Waarde (41 and 29% respectively) and in Zuidgors (59 and 20% respectively). In Zwin, the typical prey items in term of numbers were *C. maenas* (77%) and *Orchestia* spp. (13%).

Table 4. Frequency of occurrence (FO%) of all the taxa found in the stomach of *Dicentrarchus labrax* during the sampling period. Marshes are labelled as indicated in Figure 1.

FO%	*April*	*May*				*July*			*August*				*October*		
Marsh	**Z**	**S**	**W**	**Z**	**Zw**	**S**	**W**	**Z**	**S**	**W**	**Z**	**Zw**	**S**	**W**	**Zw**
Carcinus maenas	0	0	0	66.7	50	33.3	44	75.6	18.2	46.1	58.1	25	2	6.4	0
Clupeidae spp.	0	0	0	0	0	0	0	10.8	0	0	2.1	0	1	1.6	0
Corophium volutator	50	75	60	100	50	100	74	86.5	77.3	28.2	79.6	25	74	85.5	0
Crangon crangon	100	50	40	91.7	100	66.7	46	67.6	59.1	46.1	55.9	25	24	40.3	0
Cumacea spp.	0	0	0	0	0	0	0	0	0	0	2.1	0	0	0	0
Cyathura carinata	0	12.5	0	0	0	0	2	2.7	0	0	0	0	0	0	0
Decapoda megalopa	0	0	3.3	8.3	50	0	0	5.4	0	2.6	2.1	75	0	0	0
Orchestia spp.	0	25	41.4	16.7	50	66.7	22.4	20	31.8	24.3	40.8	75	76.2	50	66.7
Eurydice pulchra	0	0	0	0	0	0	4	0	0	2.6	0	0	3	37.1	0
Gammarus salinus	0	0	3.3	0	0	0	0	0	0	0	0	0	0	0	0
Gammarus zaddachi	0	0	6.7	0	0	0	0	0	0	0	0	0	0	0	0
Idotea spp.	0	0	0	0	0	0	0	0	0	0	1.1	0	0	0	0
Insect	0	0	6.7	0	0	0	0	0	0	0	2.1	0	3	12.9	0
Lekanesphera rugicauda	100	12.5	3.3	8.3	0	100	38	8.1	68.2	38.5	78.5	75	82	62.9	50
Melita pellucida	0	0	0	0	0	0	0	0	0	0	0	0	0	1.6	0
Mesopodopsis slabberi	0	0	0	0	0	0	2	2.7	4.5	35.9	1.1	0	0	0	0
Nematoda spp.	0	0	0	0	0	0	0	0	0	1.3	0	0	0	0	0
Neomysis integer	100	37.5	3.3	0	0	33.3	0	2.7	0	0	0	0	3	1.6	0
Nereis diversicolor	100	75	36.7	50	0	33.3	14	21.6	22.7	5.17	6.5	50	7	3.2	0
Oligochaeta	100	0	10	0	0	0	0	0	0	0	1.1	0	0	0	0
Paragnatia formica	0	12.5	0	0	0	0	0	0	0	2.6	0	0	4	0	0
Platichthys flesus	0	0	0	0	0	0	0	2.7	0	0	0	0	1	1.6	0
Pomatoschistus microps	0	0	0	0	0	0	4	0	0	0	1.1	0	4	3.2	0
Schistomysis kervillei	0	0	0	0	0	0	0	40.5	0	0	31.2	0	0	1.6	0
Syphon of bivalve	0	0	0	41.7	0	0	2	14	0	1.3	0	15	0	1.6	0

Gravimetrically *Carcinus maenas*, *Crangon crangon* and *Orchestia* species were important in the diet of seabass. In Saeftinghe, 27, 18, 28, in Waarde, 57, 20, 4, in Zuidgors, 45, 25, 3 and in Zwin 9, 32, 55 gravimetric percentages of these taxa were calculated respectively (Figure 6). In Saeftinghe the biomass of *Nereis diversicolor* was still important in the diet of the seabass (11%) while in Zuidgors, Mysidacea represented 9% of the biomass of the stomach content.

The MFI of the prey species of *Dicentrarchus labrax* indicated that *Corophium volutator*, *Crangon crangon* and *Nereis diversicolor* were the most important prey items in Saeftinghe, Waarde and Zuidgors (Table 5).

The MFI of *C. volutator* was always higher than 10% because of its high N% and FO%. The only exception was May and August in Waarde. *N. diversicolor* was important in Saeftinghe from May till August, while in Waarde and Zuidgors the MFI was higher than 10% only in May. This pattern was due to the high gravimetric percentage of *N. diversicolor* in these months and also to the lower frequency of occurrence at the end of the sampling period. *C. crangon* was an important food item in Saeftinghe and Waarde except in August when due to the lower numerical percentage in Saeftinghe and lower FO% in Waarde, the MFI did not reach the 10%. In Zuidgors, brown shrimp reached the 10% in every month.

Table 5. Mean Food Index of the taxa (MFI) found in the stomach of *Dicentrarchus labrax.* Marshes are labelled as indicated in Figure 1.

MFI	*April*	May				*July*			*August*				*October*		
Marsh	**Z**	**S**	**W**	**Z**	**Zw**	**S**	**W**	**Z**	**S**	**W**	**Z**	**Zw**	**S**	**W**	**Zw**
Carcinus maenas	0	0	0	3.8	4.1	14.1	21.1	28.3	24.3	56.8	31.7	9.2	3.3	4.0	0
Clupeidae spp.	0	0	0	0	0	0	0	1.2	0	0	0.5	0	0.7	0.3	0
Corophium volutator	12.7	11.5	13.9	11.4	3.0	11.3	19.6	16.8	13.8	1.9	18.0	1.4	18.6	14.5	0
Crangon crangon	11.1	25.9	25.2	35.5	58.2	2.9	35.8	26.4	21.4	21.5	18.5	6.0	14.2	20.1	0
Cyathura carinata	0	2.4	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0
Decapoda megalopa	0	0	0.1	0.3	30.6	0	0	0.1	0	0	0	23.2	0	0	0
Eurydice pulchra	0	0	0	0	0	0	0.1	0	0	0	0	0	0.3	3.3	0
Gammarus zaddachi	0	0	0.8	0	0	0	0	0	0	0	0	0	0	0	0
Idotea spp.	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0
Insect	0	0	0.4	0	0	0	0	0	0	0	0	0	0.8	4.18	0
Lekanesphera rugicauda	8.9	2.8	0	0	0	11.1	8.2	0.7	16.9	8.9	15.6	11.0	18.9	12.9	3.5
Mesopodopsis slabberi	0	0	0	0	0	0	0.1	0	0.4	4.9	0	0	0	0	0
Neomysis integer	38.4	10.6	1.9	0	0	0.6	0	0.3	0	0	0	0	1.1	0.1	0
Nereis diversicolor	13.4	34.2	20.8	42.9	0	57.4	7.4	2.4	9.7	0.9	0.7	19.9	1.8	0.3	0
Oligochaeta	15.4	0	1.4	0	0	0	0	0	0	0	0.3	0	0	0	0
Orchestia spp.	0	12.4	35.3	1.8	4.0	2.6	4.9	1.7	13.4	4.9	8.5	26.7	37.8	23.4	96.5
Schistomysis kervillei	0	0	0	0	0	0	0	18.8	0	0	5.9	0	0	1.7	0
Paragnatia formica	0	0.2	0	0	0	0	0	0	0	0	0	0	0.1	0	0
Platichthys flesus	0	0	0	0	0	0	0	1.3	0	0	0	0	0	0.6	0
Pomatoschistus microps	0	0	0	0	0	0	2.4	0	0	0	0.1	0	2.5	13.9	0
Syphon of bivalve	0	0	0	4.1	0	0	0.1	1.8	0	0.1	0	2.4	0	0.4	0

The MFI of *Carcinus maenas* indicated the importance of this species in July and August in Saeftinghe, Waarde and Zuidgors due to its high G% and relatively high frequency of occurrence. *Lekanesphera rugicauda* was important in the diet of the seabass during the second part of the sampling period (11-15 % MFI) in Saeftinghe, Waarde and Zuidgors. *Orchestia* species had higher MFI in May in Waarde and in October in Saeftinghe and Waarde. In Zwin, *C. crangon*, *C. volutator*, *Carcinus maenas*, decapod megalopa larvae and *Orchestia* species reached an MFI higher than 10. The low number of fish analyzed here cautions for interpretation of these figures.

6.3.3.3 Anguilla anguilla

Figure 7 shows the numerical and gravimetric percentage of the stomach content of *Anguilla anguilla*. The number of the stomachs analysed was not sufficient to describe differences among areas and the result is only indicative for the general diet of the European eel in the marshes. Numerical percentages showed that this species consumes insects, oligochaetes, *Carcinus maenas*, *Nereis diversicolor* and *Orchestia* spp. Other less numerous prey items were fish eggs, *Neomysis integer, Lekanesphera rugicauda* and *Crangon crangon*. Gravimetric percentages indicated the dominance of *Carcinus maenas* and *N. diversicolor*.

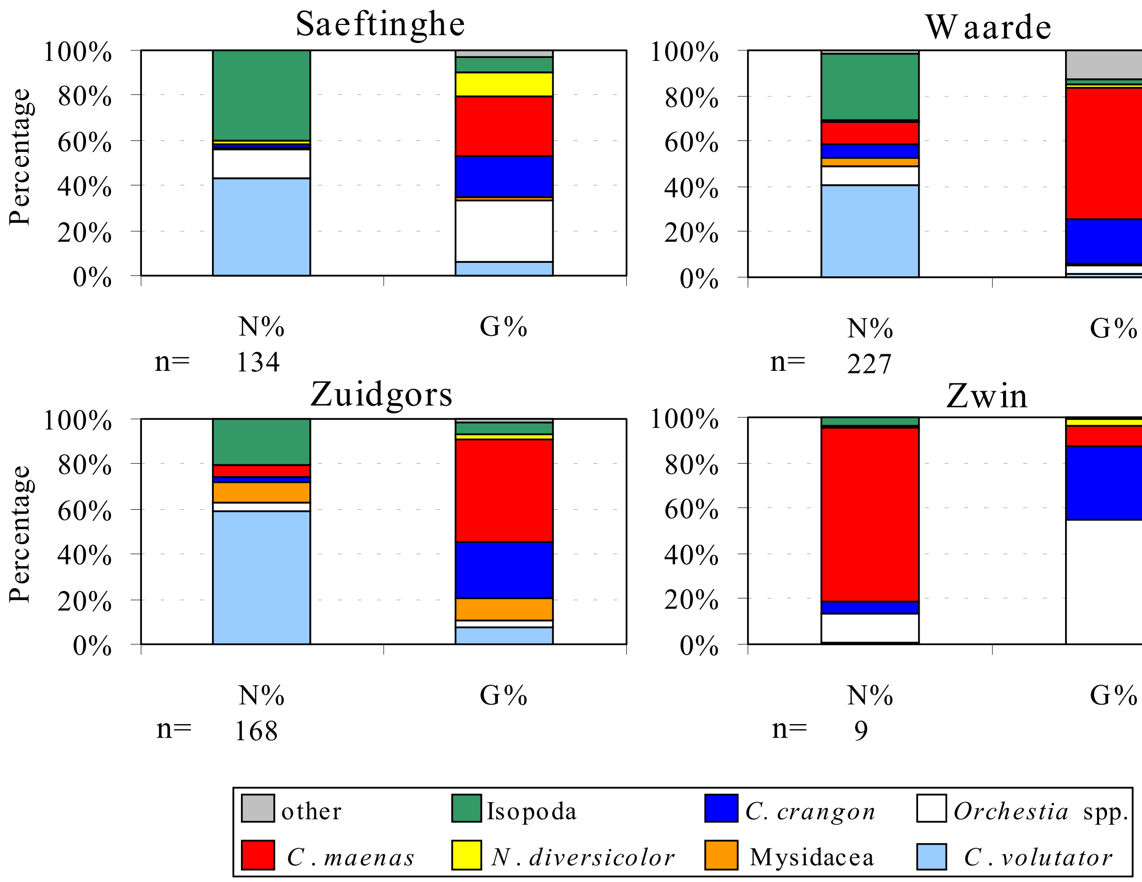

Figure 6. Numerical (N%) and gravimetric (G%) percentage derived from the stomach analysis of Dicentrarchus labrax in the marshes of Saeftinghe, Waarde, Zuidgors and Zwin in all sampled months. Number of stomachs analysed (n) is indicated below each graph.

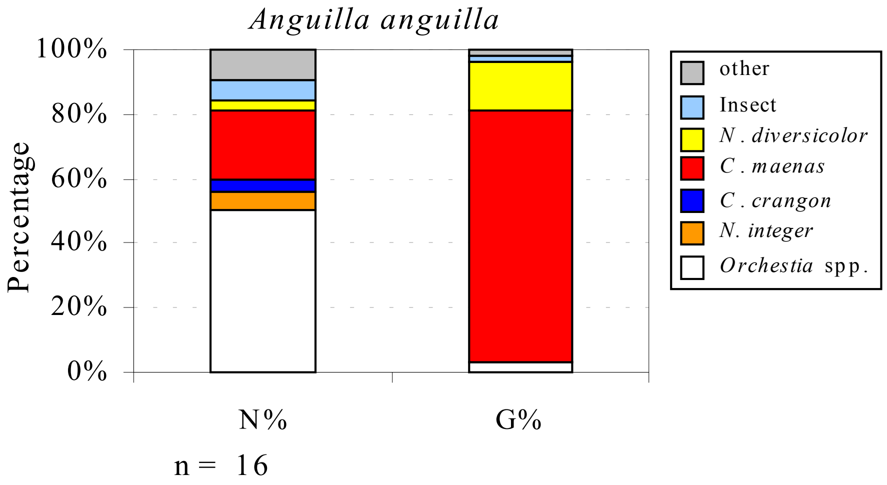

Figure 7. Numerical (N%) and gravimetric (G%) food composition of Anguilla anguilla. Number of stomachs analysed (n) is indicated below the figure.

6.3.4 Infaunal densities of the two main prey species in the marsh creeks

Corophium volutator and *Nereis diversicolor* were the two most important prey items and found very frequently in the stomachs of *Platichthys flesus* and *Dicentrarchus labrax* in all marshes therefore their macrobenthic densities in the marsh creeks were presented in Figure 8.

In the freshwater marsh, *Corophium volutator* was not present and *Nereis diversicolor* was sampled only occasionally. In Saeftinghe, the average density of *C. volutator* reached a maximum of 8100 ind. m^{-2} in July and a minimum in May of 3467 ind. m^{-2}. In Waarde, *C. volutator* had the highest density in August and in Zuidgors the maximum density occurred in October (12500 and 14233 ind. m^{-2} respectively).

Nereis diversicolor was observed in the highest density in Zwin with a peak in July of 5330 ind m^{-2}. The highest abundance in Saeftinghe (3300 ind. m^{-2}) was observed in July and in Waarde (3833) and in Zuidgors (4066 ind. m^{-2}) in August.

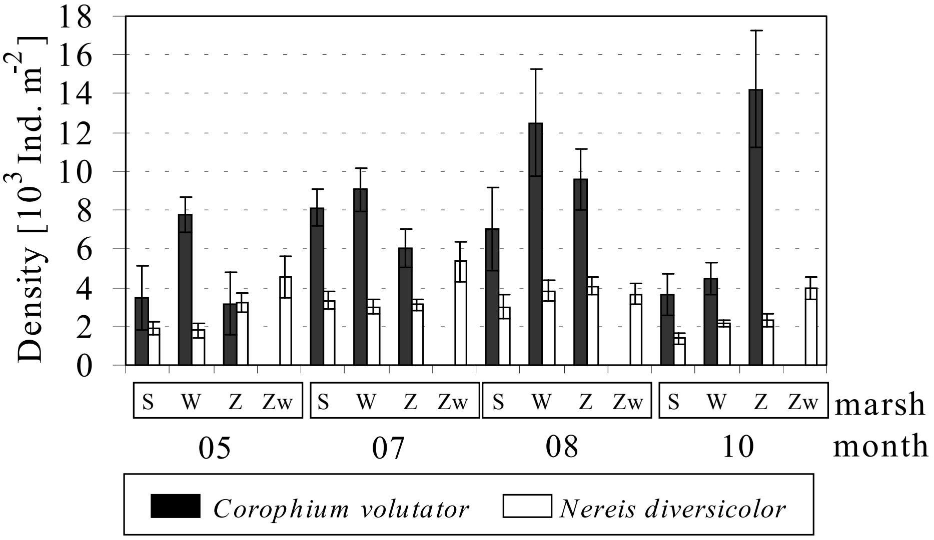

Figure 8. Average infauna density and standard error of Corophium volutator and Nereis diversicolor in the marsh creeks. Marshes are labelled as in Figure 1.

A Spearman Rank test did not indicate a correlation between the average density and biomass of *Corophium volutator* and the total number of *Platichthys flesus* in the three brackish marshes (p=0.2 and 0.8). Neither was a correlation found between the average density and biomass of *C. volutator* and the total number of *Dicentrarchus labrax* in Saeftinghe, Waarde, Zuidgors and Zwin (p=0.4 and 0.6). A similarly lack of correlation was observed between the average density and biomass of *Nereis diversicolor* and the total number of flounder (p=0.8 and 0.6 respectively) and the total number of seabass (p=0.4 and 0.2 respectively) in the saltmarshes.

A Spearman Rank test did not show a correlation between the average number and biomass of *Corophium volutator* in the marsh creeks of Saeftinghe, Waarde and Zuidgors and in the stomach of *Platichthys flesus* (p=0.4 and p=0.6 respectively) or *Dicentrarchus labrax* (p=0.6 and p=0.6 respectively). There was also no correlation between the average number and biomass of *Nereis diversicolor* in the marsh creeks of Saeftinghe, Waarde, Zuidgors and Zwin and the number and biomass of these species found in the stomach of flounder (p=0.2 and p=0.6) and seabass (p=0.4 and p=0.2).

6.3.5 Benthic stock (number and biomass) in the marsh creeks and minimum consumption of fish

The surface area of the marsh creeks was used to calculate the macrobenthic stocks of the four most important prey species in the marsh channels. The surface area was estimated to be 6400 m^2 in Grembergen, 17600 m^2 in Saeftinghe, 10000 m^2 in Waarde, 10500 m^2 in Zuidgors and 9000 m^2 in

Zwin. Table 6 shows the total numbers and the total biomass of these four main taxa (Oligochaeta, *Corophium volutator*, *Nereis diversicolor, Macoma baltica*) in the five different marsh creeks for each month. In the three more upstream marshes the marcrobenthos had highest stock in July reaching 2.46 x 10^8 individuals in Grembergen, 2.63 x 10^8 individuals in Saeftinghe and 2.26 x 10^8 individuals in Waarde. In Zuidgors and Zwin, the macrobenthic stock was maximal in May bearing 4.75 x 10^8 and 1.17 x 10^8 individuals respectively (Table 6).

The infaunal biomass stock estimated to reach highest values in October in Saeftinghe (14.1 x 10^4 g ADW) and in August in the other four marshes (Grembergen: 1.09 x 10^4, Waarde: 4.89 x 10^4, Zuidgors: 18.5 x 10^4, Zwin: 17.7 x 10^4 g ADW).

Table 6. Total number (#) of individuals and total biomass (g ADW) of four macrobenthic taxa (Oligochaeta, *Corophium volutator*, *Nereis diversicolor, Macoma baltica*) in the marsh creeks.

Marsh	**Grembergen**		**Saeftinghe**		**Waarde**		**Zuidgors**		**Zwin**	
Month	# x 10^8	g ADW x 10^4	# x 10^8	g ADW x 10^4	# x 10^8	g ADW x 10^4	# x 10^8	g ADW x 10^4	# x 10^8	g ADW x 10^4
05	1.40	0.41	1.74	12.1	1.31	1.36	4.75	2.15	1.17	8.59
07	2.46	0.88	2.63	5.59	2.26	3.07	3.73	4.95	1.09	4.63
08	1.47	1.09	2.04	3.47	1.86	4.89	3.80	18.5	0.68	17.7
10	2.09	1.01	1.06	14.1	0.84	3.21	2.78	3.33	0.65	4.85

Due to the very low number of fish caught in the fresh water marsh their total consumption from the infauna was completely negligible (Table 7). In the other marshes the minimum consumption of the available stock was still very low.

The consumption of macrobenthos by *Platichthys flesus*, *Dicentrarchus labrax* and *Anguilla anguilla* was estimated to be maximal in October in Saeftinghe, Waarde and Zwin (with respectively 0.035%, 0.015% and 0.0009% of the present stock) and in August in Zuidgors (0.011% of the available numbers) (Table 7).

From the available total biomass of Oligochaeta, *Corophium volutator*, *Nereis diversicolor* and *Macoma baltica* fish consumed the most in August in Saeftinghe and Waarde (0.014% and 0.041% respectively) and in July in Zuidgors (0.021%). In Zwin, fish had the highest consumption of the macrobenthic biomass in October with 0.0003%.

Table 7. The minimum number (#%) and the minimum biomass of (ADW%) of Oligochaeta, *Corophium volutator*, *Nereis diversicolor* and *Macoma baltica* consumed by seabass, flounder and European eel from the available stock in five marsh creeks over the sampling period.

Marsh	**Grembergen**		**Saeftinghe**		**Waarde**		**Zuidgors**		**Zwin**	
Month	# %	ADW%	# %	ADW%	# %	ADW%	# %	ADW%	# %	ADW%
05	0.000	0.000	0.0056	0.0053	0.0071	0.0182	0.0004	0.0076	0.0004	0.0002
07	0.000	0.0001	0.0046	0.0050	0.0128	0.0266	0.0067	0.0215	0.0000	0.0000
08	0.000	0.0001	0.0035	0.0142	0.0053	0.0412	0.0115	0.0072	0.0008	0.0001
10	0.000	0.000	0.0351	0.0074	0.0154	0.0176	0.0003	0.0001	0.0009	0.0003
average	*0.000*	*0.000*	*0.0122*	*0.0080*	*0.0101*	*0.0259*	*0.0047*	*0.0091*	*0.0005*	*0.0001*

6.4 Discussion

Several studies focused on the feeding habit of juvenile flounder in coastal or estuarine waters (Pihl, 1982; Aarnio *et al*., 1996; Aarnio and Bonsdorff, 1997; Mattila and Bonsdorff, 1998). Juveniles were reported to switch from copepods to amphipods at the size of 11-15 mm standard length while flounder larger than 25 mm consumed almost entirely Amphipoda. *Crangon crangon* are not preyed upon in the size classes below 16 mm (Venema, 1998). From the Ythan estuary in Scotland, Summers (1980) reported that flounder living on mud flats mainly consumed *Corophium volutator* and *Nereis diversicolor* and when living in areas with *Mytilus edulis* beds they ate *N. diversicolor* and *Carcinus maenas*. In the Grevelingen Lake, The Netherlands, adult flounder was reported to consume mainly *Arenicola marina*, *Nereis virens* and *Nephtys hombergii*. *Crangon crangon* and small *Carcinus maenas* were particularly preferred. *Pomatoschistus* species were consumed as well (Doornbos and Twisk, 1984). Hostens and Mees (1999) reported the importance of mysids in the diet of the flounder caught in the subtidal of the Westerschelde estuary.

The gut evacuation time of the stomach of *Platichthys flesus* was estimated to be 6 to 17 hours at 17°C (Arndt and Nehls, 1964; de Groot, 1971). This suggests that the majority of the prey items found in the stomachs of flounder in the Westerschelde marshes originated from the tidal creek and represented the available macrobenthic species in this habitat. *Corophium volutator* and *Nereis diversicolor* were definitely the most important prey for flounder foraging in the marsh creeks of the Westerschelde estuary. Occasionally other items like isopods, crab or shrimp were of minor importance. Molluscs were also present in this study but their occurrence in the stomachs was too low to be of significance. Doornbos and Twisk (1984) also found that molluscs were hardly eaten by flounder in the Grevelingen Lake, The Netherlands. Although other observation reported that high density of mussels resulted the shift of the diet of young flounder from polychaetes towards bivalves in a shallow bay of Sweden (Pihl, 1982). More than 80% in Zwin and more than 90% of the density in the other marshes was composed of Oligochaeta, *Corophium volutator* and *Nereis diversicolor*. The high density of *C. volutator* and *N. diversicolor* in the marsh creeks (in relation to other macrobenthic organisms would have caused the low diet diversity of flounder foraging in marsh areas. In other estuarine habitats flounder foraged upon a wider range of prey.

The food intake of juvenile seabass was reported to decrease rapidly at the temperature <10°C and stops at temperatures <7°C (Lancaster, 1991; Russell *et al*., 1996). The sampling campaign was considered appropriate to cover the period when temperature does not restrict the foraging activity of seabass. Several scientists reported on the feeding habit of juvenile *Dicentrarchus labrax* in estuarine habitats (Roblin and Suslé, 1984; Aprahamian and Barr, 1985; Kelley, 1986; Hostens and Mees, 1999; Cabral and Costa, 2001). Only a few studies deal with the feeding habit of seabass in salt marshes. Laffaille *et al*., (2000, 2001b) found that *Neomysis integer* and *Orchestia gamarellus* were the two major preys for seabass in the salt marsh of Mont Saint Michel Bay. Gardner (1996) reported the presence of *Crangon crangon, Nereis diversicolor, N. integer* and *Sprattus sprattus* in the their diet in a salt marsh of the Humber estuary. In the salt marshes of the Westerschelde, one of the main food items of seabass was *Corophium volutator*. This species is easily available for predators since it reaches very high abundances in the brackish part of the estuary (Hughes, 1988; Ysebaert and Herman, 2002). Although *C. volutator* is considered as a benthic species it exhibits an intense swimming behaviour (Essink *et al*., 1989; Hughes, 1988, Hughes and Horsfall, 1990), which makes it more vulnerable for predation by *D. labrax*. *Crangon crangon* is also an important prey species in the estuary (Costa, 1988; Cabral and Costa, 2001) and in the intertidal marsh (Cattrijsse *et al*., 1997; Laffaille *et al*., 2001a). *Crangon crangon* reaches the highest abundance in the Westerschelde marshes between April and July (Cattrijsse *et al*., 1997; Chapter 7). This coincided with the period when higher numbers of shrimp were found in the stomach of seabass, indicating a preference for shrimp. The shore crab also was an important prey. Higher densities of *Carcinus maenas* were reported from a marsh creek of the Westeschelde between June and December (Cattrijsse *et al.*, 1994; Chapter 7). Seabass seems to exploit the juvenile shore crab population since it migrates in higher numbers into the creeks when *C. maenas* is the most abundant. *Crangon crangon* and *C. maenas* became especially important in the euhaline area where *C. volutator* is largely absent.

The density of young individuals (Minello *et al.*, 2003) and their feeding habit (Rozas and LaSalle, 1990; Moy and Levin, 1991) are both good indicators of the nursery value of a biotope. The potential of an area as a nursery partly depends upon the foraging opportunities the habitat offers (Rozas and LaSalle, 1990; Rountree and Able, 1992; Craig and Crowder, 2000). In the marsh creeks similar densities of *Corophium volutator* and higher densities of *Nereis diversicolor* and *Crangon crangon* (Ysebaert *et al.,* 1993; Ysebaert and Herman, 2002; Cattrijsse *et al.*, 1997) were found as in the estuarine intertidal or subtidal. The macrobenthos is very abundant in the marsh creeks and the availability of potential prey will not restrict the utilization of marsh creeks by fish. The minimum consumption of the larger predatory fish from the available stock was very low indicating the high food excess in the marsh creeks. Marsh creeks seem to offer good foraging opportunities for 1+ and older flounder and seabass and indicate the value of this habitat as a feeding ground. Apart from the predation by these larger fish, gobies, small seabass and young shrimp will add to the predation on the macrobenthos when the creeks are flooded.

In the Westerschelde marshes, the high densities and biomass of *Corophium volutator volutator* and *Nereis diversicolor* might influence the number of the flounder migrating into the creek, however no correlation was found. This might be explained by the huge excess of macrobenthic prey but also the few sampling occasions weakened the statistical test.

Spatial variations in the diet of estuarine fish may be induced by the salinity gradient (Elliott *et al.*, 2002). In the Loire estuary, Masson (1987) showed that feeding of flounder exhibited a progressive transition in the diet from the euhaline to the oligohaline areas. Spionidae, Corophiidae and molluscs were dominant in the euhaline and polyhaline areas, while in the mesohaline zone the proportion of crustaceans increased and in the freshwater part copepods and chironomid larvae were abundant. In the present study, the diet diversity of *Platichthys flesus* and *Dicentrarchus labrax* also showed differences between the different marshes but these differences could not be attributed to the salinity gradient. No clear change in diet composition along the estuary was found. The generally limited range of prey excluded the existence of estuarine gradient related changes in diet.

The observed fullness indices of flounder and seabass in the marshes did not show differences either along the salinity gradient. The potential marsh creeks as feeding grounds seem similar along the whole estuary.

Predator-prey interactions may influence both predator and prey densities (Taylor, 1984). Murdoch and Oaten (1975) reported that predators could stabilize the population size of its prey by switching between different prey items. In the present study, the benthic food items were present in very high abundances and the consumption of the studied predators was too low to have a significant effect on the macrobenthic community. Ward and Fitzgerald (1983) also concluded that fish predation played an insignificant role in structuring the invertebrate community in salt marsh pools, in Canada. Frid and James (1988) found in a salt marsh of UK that epibenthic predators had a minimal effect on most of the infaunal species. Reise (1978) however showed that in most soft sediments, epibenthic predators are important in determining the infaunal community structure. In this context Joyce and Weisberg (1986) reported that *Fundulus heteroclitus* influenced the distribution of the marsh snail, *Melampus bidentatus*.

The nursery value of a marsh depends partly on the refuges it provides against predation (Whitfield, 1998; Halpin, 2000; Paterson and Whitfield, 2000). The stomach content of *Platichthys flesus* showed that flounder hardly consumed *Crangon crangon, Carcinus maenas* or *Pomatoschistus microps*. Similarly the common goby was found only occasionally in the diet of seabass, although *P. microps* reach peak densities in the marsh creeks in the same season as

Dicentrarchus labrax (Cattrijsse *et al*., 1994). These species use the marshes as nursery during their early lifestages. The stomach analyses performed here indicate that the larger predator fishes that use the marsh habitat as foraging grounds do not prey predominantly upon these juveniles. This strongly suggests that the marsh creeks indeed offer a refuge for young of the year shrimp, crab and gobies.

Dicentrarchus labrax was generally more abundant during the second part of the sampling in August and October. Postlarvae of this species migrate into the marsh creeks in high abundances in June and July (Cattrijsse *et al*. 1994; Chapter 7). A temporal segregation of the utilization of the marsh creeks by postlarvae and 1+ juveniles lowers the predation risk of the younger individuals. Cattrijsse *et al*. (1997) reported that *Crangon crangon* reaches the highest densities in the marsh creeks between May and June. During this period 1+ *D. labrax* were present in the creeks in lowest abundances. Again such a temporal segregation could increase the survival of *C. crangon* in the marsh creeks. The consumed number of shore crab did not exceed the 20 % of the total number of prey, which indicates that although *C. maenas* is a preferred prey, seabass cannot affect their survival seriously.

The value of the habitat as a nursery depends on the refuge function and the potential of the area as feeding ground for larvae or juveniles. The investigated marsh creeks surely act as nurseries for specific lifestages of several estuarine species (Cattrijsse *et al*. 1994). The present study showed that marshes also offer abundant food for larger predatory fish. The presence of these larger fish does not restrict the utilisation of the marsh creeks as a nursery by other species of younger conspecifics. Also due to the abundance of the macrobenthic prey, predator fish have no significant impact on the macrobenthos or on the nursery species.

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7 Habitat value of a developing estuarine brackish marsh for fish and macrocrustaceans

***Abstract**: Marsh creation receives world-wide attention in mitigating loss of coastal wetlands and in management retreat of estuaries. In the Westerschelde, the former Selena Polder, south from the marsh of Saeftinghe, developed into the Sieperda marsh after several dyke breaches. Soon after the tides regained access to the polder, a tidal creek was formed. After ten years, a developing marsh system was found adjacent to a mature marsh system. This situation offered the opportunity to compare the utilisation of a mature marsh by nekton species with a recently created developing marsh under similar circumstances. Between April and October 1999, both the mature Saeftinghe marsh and the developing Sieperda marsh were sampled every six weeks on two consecutive days. Each sampling occasion covered the whole tidal cycle. Most environmental parameters (water height, temperature, salinity, turbidity and dissolved oxygen) were similar in both marsh creeks. A distinct difference in nekton community structure between the two marshes was observed. The total biomass and densities of nekton species were higher in Saeftinghe. In Saeftinghe, a density peak occurred in July and was mainly due to large numbers of the mysid, Neomysis integer. In Sieperda, maximum abundance of the mysid, Mesopodopsis slabberi, caused the peak density in September. This difference in species dominance was observed in all samples. Biomass peaked in July in the mature marsh and in October in the developing marsh. Mysid shrimp (Neomysis integer) and fish (mainly Pomatoschistus microps) were the main contributors to the biomass in Saeftinghe. Herring, sprat (Clupeidae) and shore crab (Carcinus maenas) were more important in Sieperda. For P. microps, distinct differences in length-frequency distributions were noted between the two marshes. While creek morphology influences the abundance and species composition of visiting nekton, the age of a marsh and its maturity is believed to be a prime factor in determining the habitat function of creek systems in the developing and mature marshes.*

7.1 Introduction

Salt marshes fulfil several fundamental ecological functions. They can export nutrients to adjacent waters (Odum, 1968; 1980), act as pollution filters (Adam, 1990), minimise shoreline erosion (Race and Christie, 1982) and serve as nurseries for fish and macrocrustaceans (Boesch and Turner, 1984; Costa *et al*., 2001). Many fish species depend upon coastal marshes through the provision of food and protection from predators (Minello and Webb, 1997).

In the recent past there has been a strong global interest in the creation and recreation of salt marshes. Marsh restoration is increasingly used to mitigate wetland habitat losses (Zedler, 1996) from agricultural or urban land reclamation and dike constructions (Bakker *et al*., 1993; Mitsch *et al*., 1994). Natural and newly created marshes do not always represent similar habitat values for nekton or other estuarine organisms (Moy and Levin, 1991; Minello and Zimmerman, 1992). The time required for a newly created marsh to achieve the same level of ecosystem function as a mature marsh constitutes an important and interesting question.

Sediment characteristics play an important role in the invertebrate distribution in artificial marshes while the development of the introduced vegetation is vital in offering refuge opportunities for fish (Zedler and Lindig-Cisneros, 2000). The relationship between the vegetation and the infauna seems to depend on the vegetation type and on various predator-prey attributes (Lana and Guiss, 1992). However, Minello and Zimmerman (1992) did not observe a significant relationship between the vegetation structure and the density of infauna, crustaceans or fish in newly created marshes.

Several works have been published on the colonization of restored and artificial salt marshes by fish and macrocrustaceans along the American east Atlantic coast. Most of these assume that many newly created salt marshes offer similar fish species composition and densities as natural marsh habitats in a relatively short period of time (Williams and Desmond, 2001). Williams and Zedler (1999) found no significant differences in fish species richness between 1-12 year-old constructed and natural channels. Yet, Scatolini and Zedler (1996) observed similar species composition but lower abundances in a 4 year-old constructed marsh in the southeast of the San Diego Bay. Minello and Webb (1997) reported rapid colonisation of new marsh habitats (3-15yr) by fish. Dionne *et al.* (1999) also showed that fish visit restored and created marshes in assemblages similar to those found in reference natural marshes.

Managed retreat, realignment and set-back have recently become an issue in the management of estuaries. Mainly driven by an increasing need for flood control, Belgian and Dutch authorities began to change policies towards the management of the Schelde estuary. Managed retreat, restoring former estuarine areas into tidal marshes, is now under serious consideration.

This study took advantage of a dyke breach that occurred ten years ago and that was not repaired. The flooded polder slowly developed into an intertidal marsh. The close proximity of an adjacent natural marsh allowed a comparison of the habitat value of the intertidal creeks of the mature and of the developing marsh for fish and macrocrustaceans. Several studies have been carried out on the development of this new marsh but data about the nekton community and its utilization of the marsh area were lacking (van Oevelen *et al.*, 2000). This study represents a comparative assessment of the habitat value of both marsh systems for fish and macrocrustaceans, ten years after tidal processes have been restored.

7.2 Material and methods

7.2.1 Study area

Both the mature marsh ‘Het Verdronken Land van Saeftinghe’ and the developing marsh Sieperda lie in the mesohaline part of the Westerschelde estuary, separated by a dyke from each other (Fig. 1).

Saeftinghe is the largest estuarine brackish marsh left in Western-Europe and covers an area of 2800 ha (Dijkema *et al.,* 1984). The formation of Sieperda marsh started after three consecutive dyke breaches that separated the former polder from the estuary. After the dyke gave away for the third time, Dutch authorities decided not to repair it and the polder evolved into a tidal marsh. This human non-interference with the ecosystem offered an opportunity to compare the functioning of the developing and the adjacent mature marsh as habitats for aquatic organisms.

The intertidal drainage areas of both creeks behind the sampling point were estimated to be around 50 ha (Cattrijsse *et al.*, 1994; Van Oevelen *et al.*, 2000). Average tidal volume did not differ significantly between the two creeks during the sampling period (Mann-Whitney U test, p= 0.18). The average tidal volume of the creek in Saeftinghe and Sieperda was respectively 70357 m^3 and 86412 m^3. The tidal elevation of Saeftinghe is 2.95 mNAP (Dutch ground level ≈ MTL) (Hemminga *et al.*, 1993) and 2.55 mNAP is in Sieperda (van Oevelen *et al.* 2000).

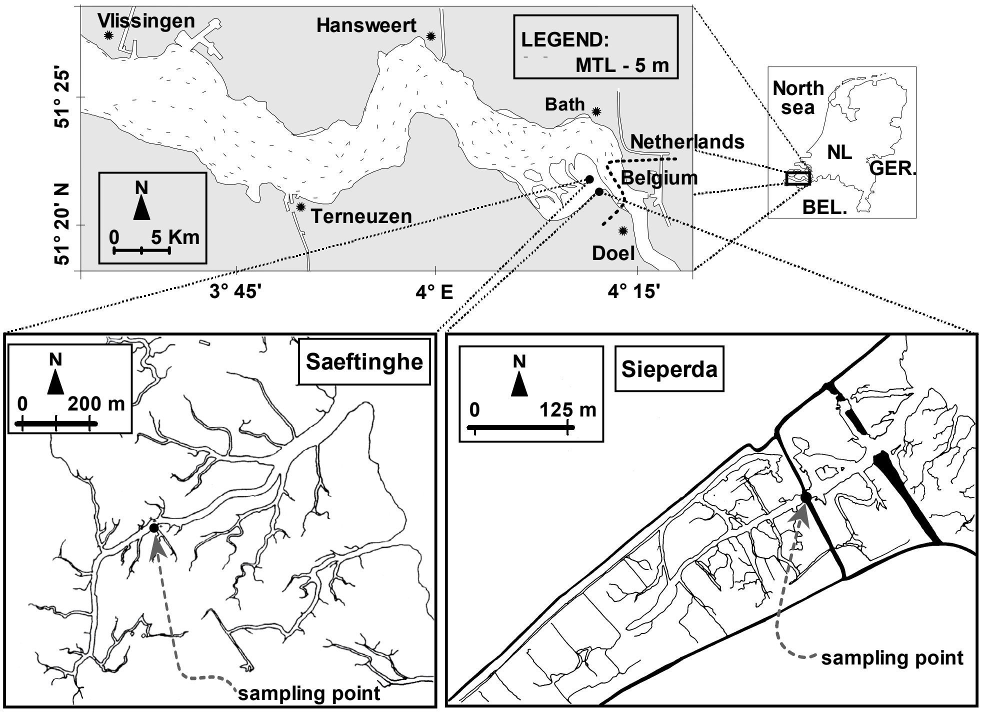

Figure 1. Location of Saeftinghe (mature marsh) and Sieperda (developing marsh) in the Westerschelde and detailed of the creeks sampled in each marsh. Map of Saeftinghe is after Hemminga et al. (1993).

Medium grain size averages 30 µm in Saeftinghe (pers. obs.) and 67 µm in Sieperda (van Oevelen *et al*. 2000). The organic matter content of the sediment reaches 1.6% in the developing marsh (van Oevelen *et al*. 2000) and around 8.5% in Saeftinghe (pers. obs.).

The vegetation is dominated by *Scirpus maritimus*, *Triglochin maritima*, *Elymus athericus*, *Phragmites australis* and *Atriplex hastata* in Saeftinghe (Hemminga *et al*., 1993). *Puccinellia maritima*, *Aster tripolium*, *Juncus gerardi*, *Salicornia* sp. are the dominant marsh plants growing in Sieperda (Stikvoor and Winder, 1998). *Puccinellia* and *Salicornia* are pioneer species (Beeftink, 1977) while *Elymus* is more typical for mature areas (de Jong pers. comm.). 87% of the total vegetated surface of Saeftinghe and 94% of the marsh surface of Sieperda is covered 80-100% by vegetation (Koppejan, 1998).

Some differences were observed concerning the shape of the creeks in the mature and developing marsh. Both creeks were 4 m deep but in Saeftinghe the creek was 35 m wide whilst in Sieperda it measured only 25 m. While the creek in Saeftinghe showed a typical natural sigmoid shape, the Sieperda creek was partly man made and linear at the sampling point. The creek was dredged, narrowed and channelled over a short distance. Our sampling point was by necessity positioned in that artificial section. Upstream and downstream of the sampling point in Sieperda large pools, several meters wide and long and more than 50 cm deep, were formed. Such large intertidal pools were absent in the mature marsh.

The whole tidal cycle lasts for 6 hours in Saeftinghe and 5 hours in Sieperda. Water starts entering the mature marsh 3 hours before high water and leaves the creek within 3 hours. In Sieperda flood takes around 2 hours and drainage is completed in 3 hours.

7.2.2 Sampling

Sampling took place from a bridge spanning the creek. A stow net with a 1 mm x 1 mm mesh size, an opening of 1 m x 1 m and a length of 5 m was used to sample the migrating nekton. The net was placed on the bottom and mounted on an iron frame. Two weights attached to the sides of the frame prevented the net from being lifted by the currents while ropes kept the net in place during sampling. The opening size of the net, the mesh size and the thickness of the fibre were used to calculate the necessary length of the net in order to keep the pressure inside the net under all current conditions (Tranter, 1979). This reduced the probability that animals avoided the net. The net fished for one hour, was rinsed and then replaced in the same position. After high water the net was turned to sample the ebb current until all water had left the creek.

Marsh creeks were sampled every six weeks from April till October in 1999. Cattrijsse *et al.* (1994) showed that most marsh visiting species reached the peak density and biomass between April and October therefore the sampling campaign of the present study was planned to cover this period. The two creeks were sampled on consecutive days during spring tide to minimise the variation of the environment conditions.

7.2.3 Data processing and analyses

The volume of water filtered by the net and passing through the whole creek was calculated every 15 minutes in order to quantify the catches and to estimate the tidal volume. At the sampling point, the cross sectional area of the creek for every possible water height was measured. Water height, current, and the cross section allowed calculating the flow ($m^3 s^{-1}$) at the sampling point.

Detritus was weighted and the number of individuals that passed the sampling point during each sampling hour was counted for each species. Using the total number of individuals and the total volume of water passing through the net during one hour, the density was estimated in the lower metre of the water column. The densities of the 3 flood samples were summed which yielded an estimate at high water. Densities were also calculated for every ebb hour also using the total number of individuals and volume of water leaving the creek. The sum of these four densities also yielded an estimate at high water. The abundance of the species at the moment of high water of each tidal cycle was calculated by averaging the flood and the ebb estimate. The same procedure was used to calculate the biomass (mg ADW m^{-3}), which was computed with length-ADW regressions (Appendix 3).

In the laboratory individuals were sorted and identified to the possible lowest taxonomic level. Larval stages were treated separately because of their different ecology. Decapods were considered as postlarvae if they were less than 10 mm standard length (SL). *Clupeidae* species were grouped as postlarvae under 40 mm standard length. *Syngnathidae* less than 70 mm were also considered postlarvae, while a 20 mm standard length was used to classify the other fish species (*Pomatoschistus microps, Dicentrarchus labrax, Platichthys flesus* and *Pleuronectes platessa, Solea solea* and *Liza ramada*).

Due to the low number of samples and the lack of normal distribution non-parametric test was chosen. Wilcoxon matched pairs test was used to test the differences between environmental variables, densities and biomass of species in the mature and developing marsh.[1]

One species-density and one species-biomass matrix was constructed. Similar data matrices were constructed for the environmental variables. Species appearing twice or less in the samples were removed from the analyses. Density and biomass data were fourth root transformed to approximate normal distribution prior to the multivariate analysis. Following Field *et al.* (1982) different techniques were used to characterise the communities. Cluster analysis based upon Bray-Curtis similarities using group average sorting was used to detect differences in the nekton community structure between the two marshes. Ter Braak (1987b) was followed to decide between

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[1] Wilcoxon matched pairs test was used instead of the Mann-Whitney U test originally included in Hampel et al. (2003).

linear and unimodal response model. Data were subjected to ordination techniques from the CANOCO package (Ter Braak, 1987a). Firstly, Principal Component Analysis was performed using only the species density and biomass data of the two marshes. Then environmental variables were incorporated into the analysis and the canonical form of PCA (RDA) was run. The two analyses revealed similar distribution of the sampling stations therefore RDA was used to explain the observed pattern in the community structures.

7.3 Results

7.3.1 Environmental parameters

Except for the water current and the detritus, all abiotic parameters were similar in both marshes and fluctuated similarly during the sampling period (Table 1). Average salinity was lowest in April (around 5 psu) and increased over the sampling period to 14 psu in September in both marshes. Average temperature showed the same seasonal change in both marshes with maximum values in September (21-22°C) and minima in October (10-11°C). Apart from the observation in October, dissolved oxygen concentrations were also similar in both creeks and peaked in July, with values of 8.5-8.7 mg l^{-1}.

Maximum water height decreased towards autumn in the natural as well as in the developing marsh by 160 cm in Saeftinghe and by 95 cm in Sieperda. The water current at the sampling point was significantly higher in Sieperda (Wilcoxon test, p=0.04). While in Saeftinghe maximum current speed varied between 0.1 and 0.2 m s^{-1}, maxima in Sieperda ranged between 0.5-0.7 m s^{-1}.

Table 1. Average measured salinity (psu), temperature (°C), dissolved oxygen (mg l^{-1}) and calculated standard error, maximum water height (cm), current (m s^{-1}) and turbidity (m^{-1}) and the amount of detritus (g m^{-3}) available at the moment of the high water in the two sampled marshes, Saeftinghe and Sieperda. Sampling months are labelled by numbers such as April (04), June (06), July (07), September (09) and October (10).

Variable	Marsh	*Month*				
		04	*06*	*07*	*09*	*10*
Salinity (psu)	Saeftinghe	5.4 ± 0.2	9.9 ± 0.2	9.4 ± 0.0	14.0 ± 0.2	13.1 ± 0.1
	Sieperda	5.1 ± 0.2	9.0 ± 0.2	8.9 ± 0.0	13.8 ± 0.4	13.2 ± 0.0
Temperature (°C)	Saeftinghe	14.4 ± 0.3	21.5 ± 0.6	19.9 ± 0.3	22.3 ± 0.3	10.1 ± 0.4
	Sieperda	14.3 ± 0.4	19.9 ± 0.2	20.7 ± 0.2	21.3 ± 0.0	11.2 ± 0.4
Dissolved oxygen (mg l^{-1})	Saeftinghe	6.5 ± 0.3	7.2 ± 0.1	8.7 ± 0.5	5.9 ± 0.2	8.1 ± 0.2
	Sieperda	5.9 ± 0.3	5.7 ± 0.2	8.5 ± 0.5	6.3 ± 0.1	6.5 ± 0.2
Water height (cm)	Saeftinghe	320	260	240	250	160
	Sieperda	270	270	255	250	175
Water current (m s^{-1})	Saeftinghe	0.2	0.1	0.1	0.2	0.1
	Sieperda	0.7	0.4	0.6	0.6	0.7
Turbidity (m^{-1})	Saeftinghe	2.5	2.5	1.6	1.3	2.8
	Sieperda	2.5	1.6	1.6	1.4	1.8
Detritus (g m^{-3})	Saeftinghe	0.06	0.06	0.007	0.03	0.15
	Sieperda	0.006	0.01	0.001	0.009	0.005

Turbidity showed similar values and fluctuations in both marshes. Highest turbidity recordings (around 1.4 m^{-1}) were observed in September and lowest readings (2.8 to 2.5 m^{-1}) occurred in April and October in both marshes.

The total amount of detritus caught in the net was significantly higher in Saeftinghe (0.007-0.15 g m^{-3}) than in Sieperda (0.001-0.01 g m^{-3})(Wilcoxon test, p=0.04). The lowest amount of detritus was caught in July and the highest in October in both marshes.

7.3.2 Species

In total, 8 amphipod, 9 decapod, 3 mysid, 4 isopod, 1 polychaete, 1 jellyfish, 1 cladoceran and 22 fish ecotypes were found. Table 2 lists all 49 ecotypes, which included 35 species that were collected during sampling. In the developing marsh, 47 ecotypes were collected while in the mature marsh only 40 were caught.

Typical marsh nekton species occurred in both creeks. These included the amphipods *Corophium volutator* and *Gammarus zaddachi*, the brown shrimp *Crangon crangon* and the brackish water shrimp *Palaemonetes varians*, the shore crab *Carcinus maenas*, mysids *Neomysis integer* and *Mesopodopsis slabberi*, the common goby *Pomatoschistus microps* and seabass *Dicentrarchus labrax.* Among the main marsh nekton species, only adult flounder (*Platichthys flesus*) were found exclusively in Saeftinghe.

Table 2. Nekton species occurring in the mature (Sae) and developing (Sie) marsh. Adult (a), postlarvae (pl), juvenile (j), megalopa (m), zoea (z) are used to indicate the life stages.

Taxon-Species	**Marsh**		**Life stage**	**Taxon-Species**	**Marsh**		**Life stage**
	Sae	**Sie**			**Sae**	**Sie**	
Amphipoda				**Teleostei**			
Bathyporeia pilosa	•			*Allosa fallax*		•	
Corophium volutator	•	•		*Anguilla anguilla*	•	•	
Corophium arenarium		•		*Atherina presbiter*		•	
Gammarus zaddachi	•	•		*Clupea harengus*	•	•	a
Gammarus salinus	•	•		*Clupea harengus*	•	•	pl
Melita pellucida	•	•		*Dicentrarchus labrax*	•	•	a
Orchestia gammarellus		•		*Dicentrarchus labrax*	•	•	pl
Orchestia mediterranea		•		*Gasterosteus aculeatus*	•	•	
Caridea				*Liza ramada*		•	a
Crangon crangon	•	•	a	*Liza ramada*	•	•	pl
Crangon crangon	•	•	pl	*Osmerus eperlanus*		•	
Palaemonetes varians	•	•	a	*Platichthys flesus*	•		a
Palaemonetes varians	•	•	pl	*Platichthys flesus*	•	•	pl
Brachyura				*Pleuronectes platessa*	•	•	pl
Carcinus maenas	•	•	a	*Pomatoschistus microps*	•	•	a
Carcinus maenas	•	•	j	*Pomatoschistus microps*	•	•	pl
Carcinus maenas	•	•	m	*Pomatoshistus minutus*		•	
Carcinus maenas	•	•	z	*Sprattus sprattus*		•	a
Mysidacea				*Sprattus sprattus*	•	•	pl
Gastrosaccus spinifer	•	•		*Solea solea*	•	•	pl
Mesopodopsis slabberi	•	•		*Syngnathus rostellatus*	•	•	a
Neomysis integer	•	•		*Syngnathus rostellatus*	•	•	pl
Isopoda				**Other**			
Cyathura carinata	•	•		*Daphnia magna*	•	•	
Eurydice pulchra	•	•		Decapoda larvae	•	•	
Lekanesphaera rugicauda	•	•		Jelly fish	•	•	
Paragnathia formica	•	•		*Nereis diversicolor*	•	•	

7.3.3 Density

Except in October, the total species density was different between the two marshes (Fig. 2) although no significant density difference was found during the sampling period (Wilcoxon test, p=0.22). Several species were recorded in significant higher abundance in Saeftinghe like *Crangon crangon* (p=0.04), *Corophium volutator* (p=0.04), *Neomysis integer* (p=0.04), *Pomatoschistus microps* (p=0.04) and *Dicentrarchus labrax* (p=0.04). In Sieperda only *Mesopodopsis slabberi* (p=0.04) occurred in significant higher densities. All other important species did not show significant different densities.

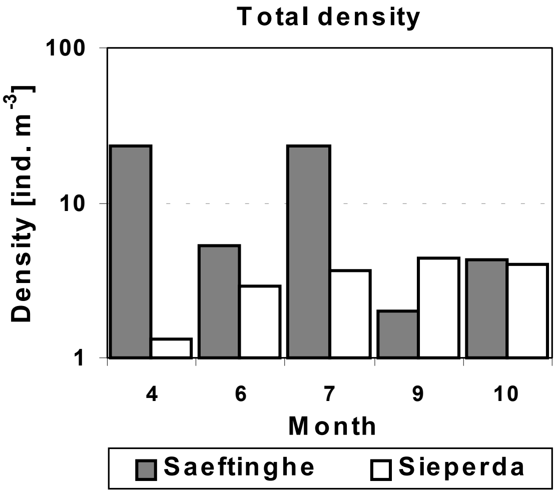

Figure 2. The total density of nekton species on a logarithmic scale in the mature and the developing marsh.

Figure 3 shows the density of nekton species in the two marshes. Mysids numerically dominated all catches in both marshes, accounting for 90% of the total density in some cases. *Neomysis integer* strongly influenced the total density pattern in Saeftinghe, whereas in Sieperda, total nekton density was influenced by the abundance of *Mesopodopsis slabberi*. Mysid densities fluctuated strongly in Saeftinghe. In Sieperda the abundance of *N. integer* decreased during the summer and reached minimum values in autumn, while an opposite trend was observed for *M. slabberi*. *Neomysis* was always present in higher densities in Saeftinghe. The maximum density of *M. slabberi* observed in September (4.3 ind m^{-3}) caused a higher total density in the developing marsh than in the mature marsh.

Brown shrimp *Crangon crangon* reached a peak density in April in both marshes: 6.8 ind m^{-3} in Saeftinghe, 0.3 ind m^{-3} in Sieperda. In Saeftinghe young shrimp were present until September, while in Sieperda they were already absent by the end of April.

In Saeftinghe, juvenile *Carcinus maenas* attained maximum densities of 0.2 ind m^{-3} in June. Later, densities decreased towards autumn, reaching similar values as in Sieperda in September where densities never exceeded 0.02 ind m^{-3}. Zoea larvae of *C. maenas* showed similar temporal changes in abundance in both marshes but in July they reached densities almost 10 times as high in Sieperda.

Pomatoschistus microps was most abundant in July in both marshes, but densities were higher in Saeftinghe during the whole sampling period. In the mature marsh, higher numbers of the common goby were still caught in September (1.2 ind m^{-3}), while by the same time in Sieperda abundances had fallen below 0.02 ind m^{-3}.

Dicentrarchus labrax showed a density peak in June, with higher densities in Saeftinghe (0.8 ind m^{-3}) than in the developing marsh (0.02 ind m^{-3}). The seasonal fluctuations in abundance were similar in both marshes.

The abundance of *Clupeidae* species peaked in June (0.026 ind m^{-3} in Saeftinghe, 0.178 ind m^{-3} in Sieperda) and decreased to October. Thereafter *Clupeidae* disappeared in July from the mature marsh, while they were still present in the developing marsh during this month (0.036 ind m^{-3}).

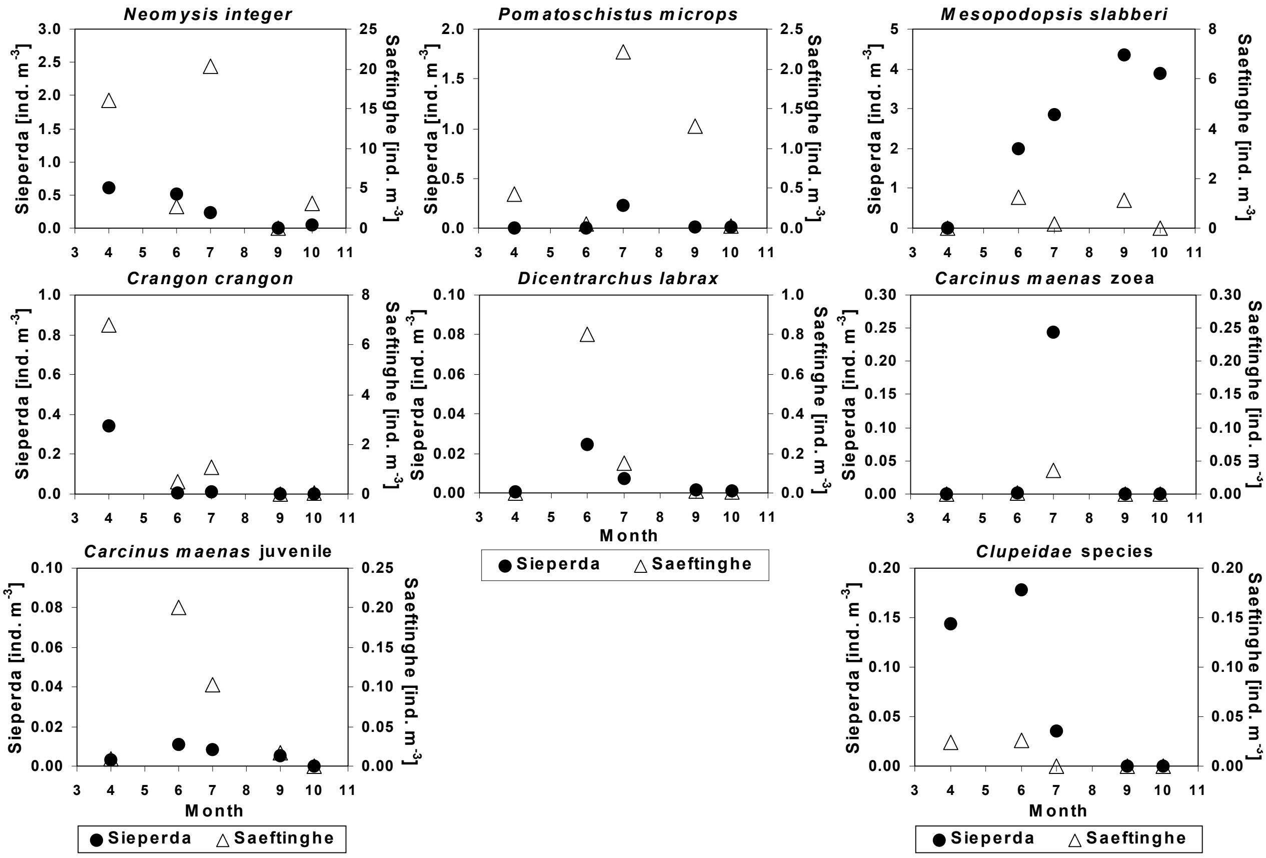

Figure 3. Density of the main species occurring in the mature (Saeftinghe) and the developing marsh (Sieperda).

7.3.4 Biomass

Throughout the study period total biomass was significantly higher in the mature marsh, Saeftinghe (Fig 4) (Wilcoxon test, p=0.04). *Neomysis integer* (p=0.04), *Corophium volutator* (p=0.04), *Crangon crangon* (p=0.04), *Pomatoschistus microps* (p=0.04), and *Dicentrarchus labrax* (p=0.04) attained significantly higher biomass in Saeftinghe (Fig 5). In the mature marsh, *N. integer* was the main contributor to the biomass in April (445 mg ADW m^{-3}), July (501 mg ADW m^{-3}) and October (71 mg ADW m^{-3}). The three most important fish species, *D. labrax, P. microps* and *Platichthys flesus*, reached a maximum biomass in June, respectively, 84.3, 8.8 and 10 mg ADW m^{-3}. In September, 94% of the total biomass was due to *D. labrax* (15 mg ADW m^{-3}) and *P. microps* (137.7 mg ADW m^{-3}).

In Sieperda, the main contributors to the biomass were fish, accounting for 76% of the total biomass in June. Highest biomass levels were associated with Clupeidae species (6.7 mg ADW m^{-3}) and the mysid, *Neomysis integer* (2.9 mg ADW m^{-3}) in April, in June with Clupeidae (26.3 mg ADW m^{-3}) and *Dicentrarchus labrax* (2.0 mg ADW m $^{-3}$) and in July again with Clupeidae (1.7 mg ADW m^{-3}), *D. labrax* (2.1 mg ADW m^{-3}) and *Mesopodopsis slabberi* (3.3 mg ADW m^{-3}). In September and in October, adult *Carcinus maenas* constituted the main portion of the biomass in Sieperda with 4.9 and 55 mg ADW m^{-3}.

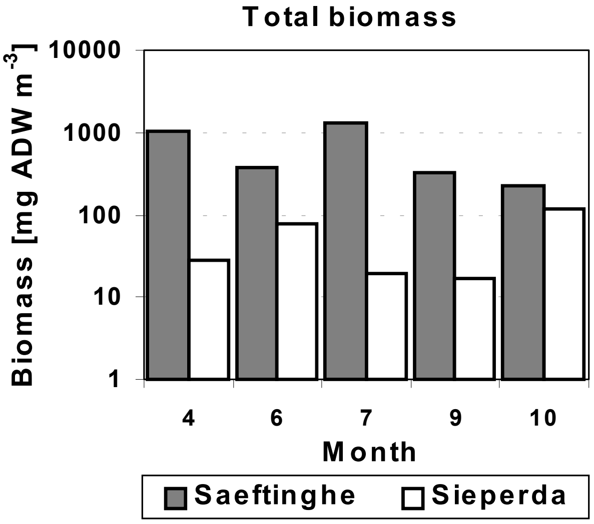

Figure 4. Total biomass of nekton species on a logarithmic scale in the mature and the developing marsh.

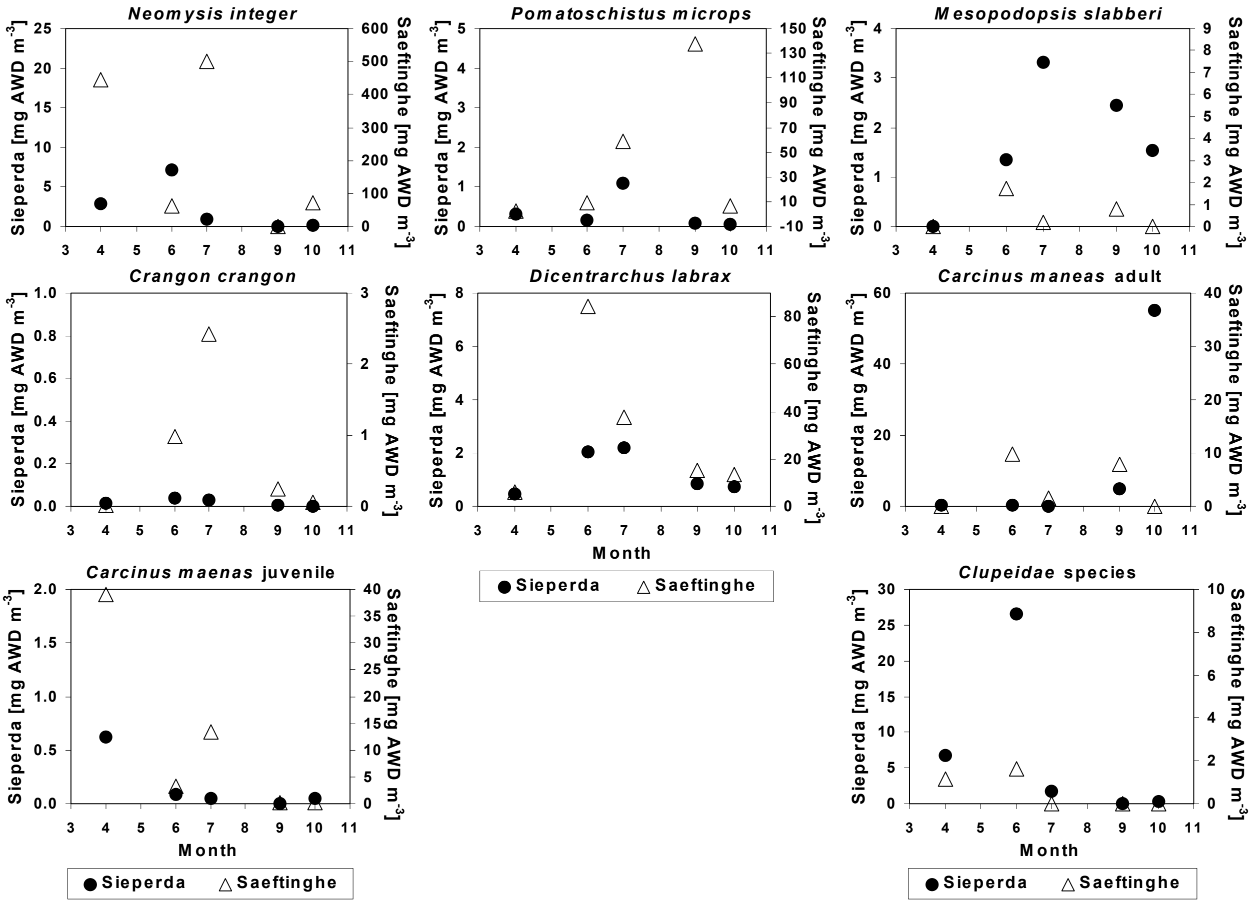

Figure 5. Biomass of the main species occurring in the mature and the developing marsh.

7.3.5 Length-frequency distribution of *Pomatoschistus microps*

The length-frequency distribution of *Pomatoschistus microps* in both marshes is shown in Figure 6.

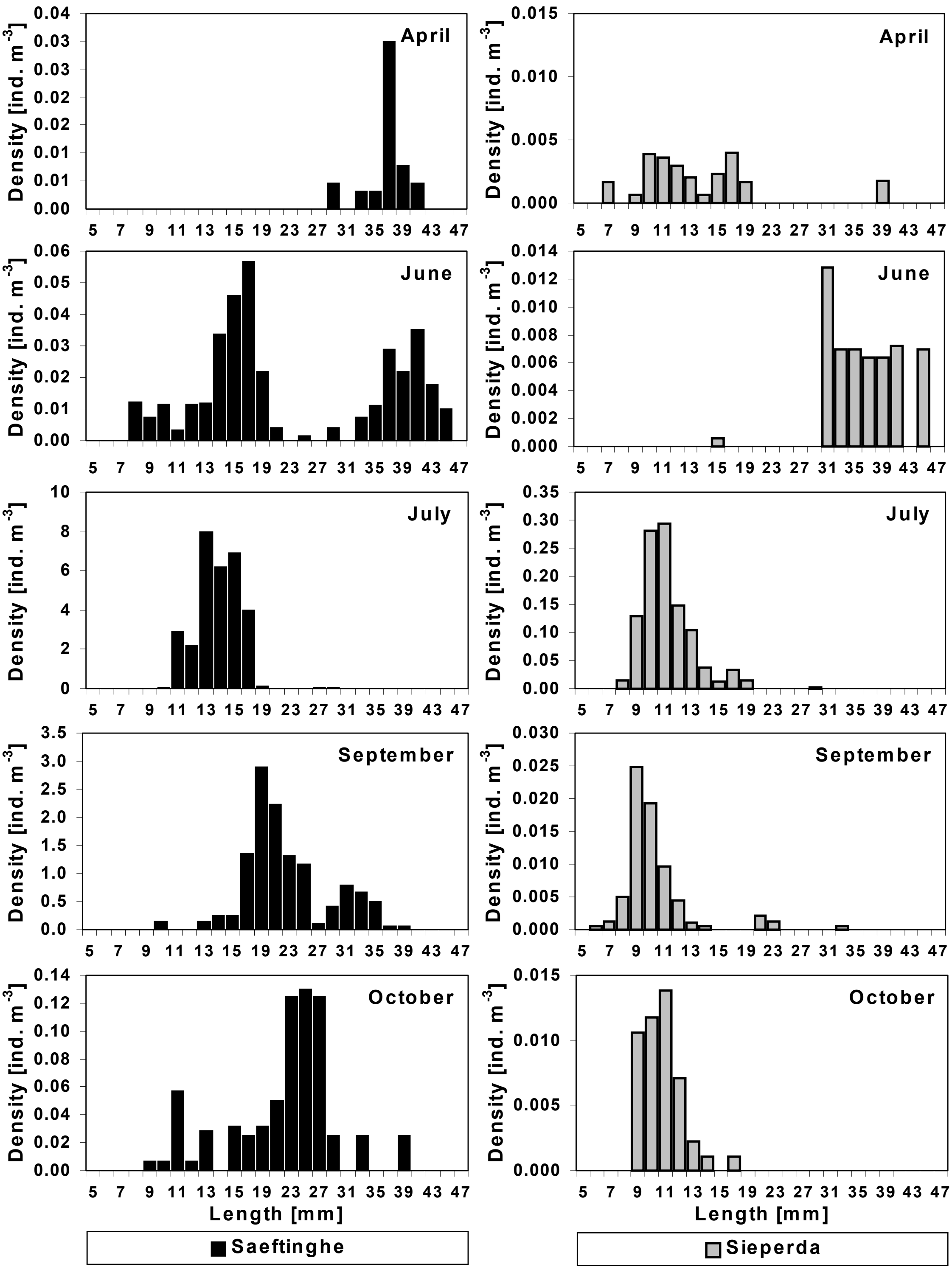

Figure 6. Length-frequency distribution of Pomatoschistus microps in Saeftinghe (left) and Sieperda (right) during the sampling period.

In April, larger individuals migrated to the creeks of Saeftinghe. The larvae appeared in June in Saeftinghe and in July in Sieperda. After July the size of the gobies remained around 9-13 cm SL in the developing marsh. In Saeftinghe the individuals grew in autumn, reaching 19-27 cm SL in October.

The length-frequency distributions of the other two main fish species, *Dicentrarchus labrax* and *Clupeidae* spp., did not show differences between the mature and the developing marshes.

7.3.6 Community structure

Cluster analyses using Bray-Curtis similarities showed similar seasonal community structures in both marshes (Fig 7a). According to the density data temporal changes influence the community structure more than the spatial differences between the two marshes. The first division separated the spring communities from the nekton community of the other months. The exception was the October sample in Saeftinghe, which resembled the two April samples. The second division yielded two other clusters. One grouped the summer (June and July) and the other the autumn (September, October) samples.

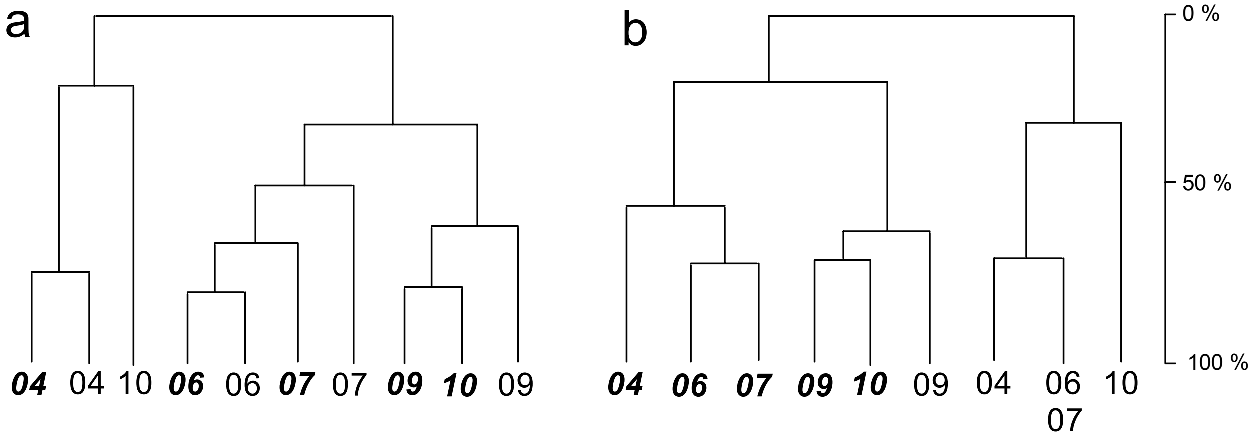

Figure 7. Result of the Group Average Sorting using Bray-Curtis similarities. Cluster dendogram using density (a) and biomass (b) data. Sieperda samples are labelled as bold italic numbers. The vertical scale represents the relative similarity. Numbers indicate the months of the sampling period (04-April, 06-June, 07-July, 09-September, 10-October).

The seasonal structure in the density data of both marshes was shown in the plot resulted from the Redundancy Analysis (RDA) (Fig. 8a). The eigenvalues of the first and the second axes in the RDA were 0.51 and 0.18. In RDA the ordination axes are, by definition, derived as linear functions of the environmental variables. Temperature seemed to explain the observed variance the most and it is representative for the observed seasonal changes. The vector representing this parameter was quite long and correlated well with the first axis. Water current had large vector but correlated less with the axes. The other environmental variables gave large vectors but their correlation with the axes was weak. Several species plotted to the vicinity of sampling days where they occurred as typical species. *Neomysis integer* and *Crangon crangon* characterised the April, *Carcinus maenas* juvenile the sampling months of June and *N. integer* was typical in July in the mature marsh. *Clupeidae* species plotted close to the sampling days of Sieperda in June.

The cluster dendogram using biomass data (Fig. 7b) showed a complete segregation between the two marshes. Here the samples of the mature and the developing marsh grouped together. Only the second division revealed a seasonal pattern. The same spatial difference in community structure was confirmed by the RDA using the biomass data (Fig. 8b). The eigenvalues of the first and the second axis were respectively 0.42 and 0.17. In this ordination the samples from both marshes were clearly separated. The vector of the water current best indicates the segregation of the Sieperda and Saeftinghe samples in the ordination plane. Water current vector points towards the samples of Sieperda indicating positive correlation while Saeftinghe samples are inferred to be positively correlated with the detritus. Species plot indicated that Saeftinghe samples were characterised by *Neomysis integer*, *Crangon crangon*, *Dicentrarchus labrax* and *Pomatoschistus microps*. These species situated in the vicinity of the sampling days of Saeftinghe. Less obvious but *Mesopodopsis slabberi*, *Carcinus maenas* adult and Clupeidea species are plotted closer to the sampling days of

Sieperda. These species were more typical for the developing marsh where they occurred in higher biomass.

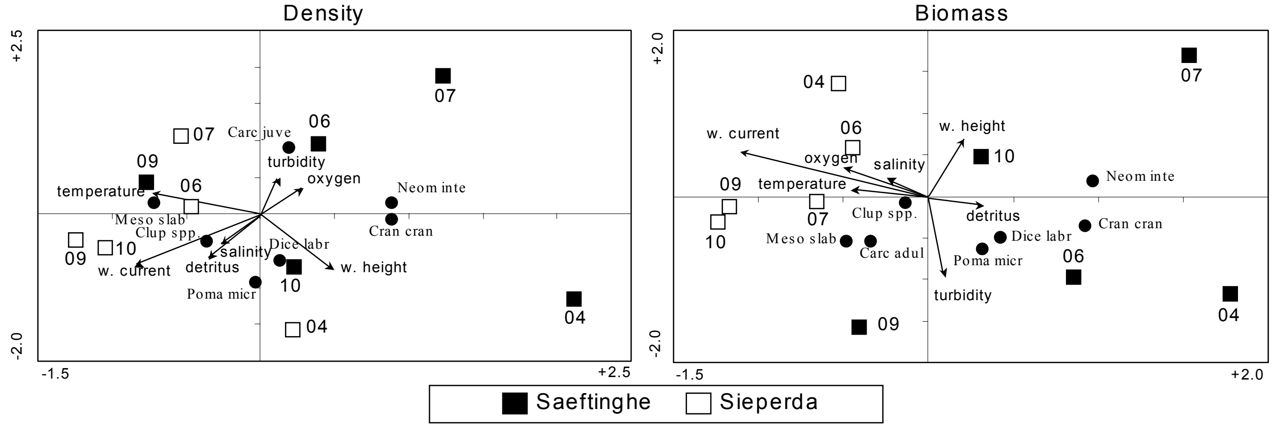

Figure 8. Sample-environmental biplot as the result of Redundancy Analysis (RDA) in the plane of the two ordination axes using density (a) and biomass (b) data. Samples of Saeftinghe are labelled with black rectangles while Sieperda is indicated with white colour. Numbers indicate the months of the sampling period (04-April, 06-June, 07-July, 09-September, 10-October). Abbreviations are used to label the species like Neomysis integer (Neom inte), Crangon crangon (Cran cran), Carcinus maenas juvenile (Carc juve), Carcinus maenas adult (Carc adul), Mesopodopsis slabberi (Meso slab), juvenile Pomatoschistus microps (Poma micr), juvenile Dicentrarchus labrax (Dice labr), Clupeidae species (Clup spp.). [2]

7.4 Discussion

The nekton assemblages of the mature and the developing marsh showed similarities with one another and to the assemblages found earlier in that part of the estuary (Cattrijsse *et al.*, 1994). Clear differences were found regarding species abundance and biomass, and in the length frequency distribution of the common goby, the resident species in the estuarine salt marshes of the Westerschelde. These dissimilarities between the two sites suggest a different use of the marsh creek habitat by the estuarine nekton. Several factors can cause the observed differences between the mature and the developing marsh.

Tidal marshes function as nurseries for juvenile fish and macrocrustaceans, providing better growth conditions through improved predation refuge and/or abundant food resources (Bozeman and Dean, 1980; Boesch and Turner, 1984; Minello *et al.* 1989; Minello and Webb, 1997; Zimmerman *et al.*, 2000). The vegetation in North American Atlantic salt marshes does not occur below Mean Tidal Level (Reimold, 1977). As a consequence these marshes are regularly flooded and refuge is offered by submerged vascular plants for nekton (Minello and Zimmerman, 1983; Rozas and Odum, 1988). Mean High Water Neap tide borders the low marsh (Beeftink, 1977) in Europe and the vegetated surface is only flooded occasionally for short periods. As a consequence, the refuge offered by submerged vascular plants is minimal or non-existent. Fish and crustaceans are restricted to the intertidal creeks. In the present study sites, no marsh pools were present adjacent to the creeks. Considering this, the intertidal channels are the true nursery areas providing food and refuge from a high turbidity. If density and biomass of nekton species in the two systems differs, the main reason should be found in the environmental conditions factors of the tidal channels. Our measurements indicate that the environments of both creeks were very similar and that they differed only in two aspects: the current regime and the amount of organic material.

The different hydrological and geomorphological characteristics of both creek systems will inevitably influence the nekton species composition. During the sampling campaign we observed

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[2] After Hampel et al. (2003).

fivefold higher water currents in the developing marsh than in the mature marsh. Strong water currents might restrict the occurrence of species that avoid such stressful conditions. The differences in density and biomass observed in the 2 marshes can however not be fully explained by the different current regimes, since currents are even stronger (0.05-1.35 m s^{-1}) in the estuarine subtidal (Stroomatlas, 1992), where all the recorded animals occur as well (Mees *et al*., 1993). Rather than the strength of the tidal currents, the shape of the creek partly being altered and channelled by man may have had its influence on the species composition of Sieperda. In southern California, native fishes do not appear to discriminate between natural and constructed wetlands channels. There, the composition of fish assemblages is closely related to channel morphology and hydrology rather than to type (natural vs. constructed) (Zedler *et al*., 1997; Williams and Zedler, 1999). According to these authors the channel's physical properties (water depth, temperature, dissolved oxygen, channel width, presence of small creeks, salinity) were more important in determining fish use than its restoration status. These physical characteristics of the creek in Saeftinghe and Sieperda show a high similarity. The difference in channel width may thus partly explain the observed differences. Predation refuge plays a role in marsh creek utilisation of nekton species (Cattrijsse *et al.,* 1997), but the characteristics of both marsh creeks are very similar. Minello and Zimmerman (1992) argued that the protective habitat of created marshes may reach equivalency with natural marshes after 1 or 2 growing seasons. In contrast to the North-American marshes, in Europe the vegetated surface of marshes is hardly used by nekton species (Cattrijsse *et al*., 1994). The vegetation almost completely covers the marsh surface, leaving ample space for fish or shrimp to move between the stems of the halophyte vegetation. All fish, shrimp and crabs remain in the intertidal creek where no vegetation occurs. Refuge from predation (e.g. adult *Platichthys flesus* and *Dicentrarchus labrax*) results from the shallowness of the habitat and especially from the highly turbid waters. Turbidity in the marsh creeks varied between 2.8-1.3 m^{-1} while in the estuary turbidity ranges around 0.007 (Hostens pers. comm.). The higher turbidity in the intertidal creeks is likely to provide better refuge for nekton than the subtidal area. Since similar water depths and turbidities were measured in both marshes, the refuge potential of both areas will be likewise.

Food availability may also cause the observed biomass and density difference between the natural and developing marsh. Craft *et al.* (1988) examined the amount of the macro organic matter (MOM) derived mainly from *Spartina alterniflora* and *Juncus* sp. in the upper layer of the soil in natural and transplanted marshes and found significantly less MOM in the transplanted marshes. In accordance with these results, Minello and Webb (1997) documented a positive but weak relationship between sediment MOM and marsh age. Minello and Zimmerman (1992) also proved that MOM was significantly higher in natural marshes and that the macro organic matter of the sediment correlated positively with the density of infauna and decapod crustaceans. According to Zedler *et al.* (1997) marsh detritus ends up into the tidal channels where it fuels the detritivore food chain. This finally leads to fish moving into the salt marsh to feed on marsh invertebrates. Even though Saeftinghe does not export organic material to the estuary (Hemminga *et al*. 1993), MOM gets washed into the studied creeks. Higher amounts of MOM were present in the creek of the mature marsh, which may provide more food resources for detritivore benthic animals like *Corophium volutator* and this will in turn influence the occurrence and density of species in higher trophic levels.

Minello and Zimmerman (1992) found that the mean densities of amphipods were consistently lower in a transplanted marsh. *Corophium volutator*, a ubiquitous detritivore infauna organism in the salt marsh creeks of the Westerschelde (Cattrijsse *et al.* 1994), occurred at lower densities in the developing marsh. A lower amount of organic matter may thus influence the occurrence of infaunal species in Sieperda.

The same mechanism can explain the higher abundance of brown shrimp in the mature marsh. Brown shrimps are omnivores feeding on detritus, plant material and animal food (Plagmann, 1939). In Saeftinghe they were found to prey predominantly upon organic material and infauna organisms, like *Corophium volutator* and the polychaete *Heteromastus filiformis* (Cattrijsse *et al*., 1997).

Fish density in the developing marsh exceeded the fish density in the mature marsh in April and October. During the other three months, fish densities were higher in the mature marsh. Talley (2000) reported higher fish abundance in the natural marsh but similar species richness in the natural and created systems. Minello and Webb (1997) also found that overall fish densities were significantly higher in natural marshes, but in contrast to our results, that difference was more pronounced in spring and autumn.

Clupeidae species (*Clupea harengus* and *Sprattus sprattus*) reached peak densities in both marshes in April and June, with higher densities recorded in the developing marsh. Havens *et al.* (1995) hypothesized that the zooplankton population of a newly-created marsh was higher than in a natural marsh because the creek did not dry completely, i.e. resident zooplankton did not leave. The resident zooplankton population may encourage greater use of the developing marsh by plankton feeders like the Clupeids. A similar situation may exist in the Sieperda creek, since large deep pools have been formed behind and in front of the sampling point. In this study the density of zooplankton was not measured but it may have influenced the abundance of *Clupeidae* species.

The common goby *Pomatoschistus microps* is a typical intertidal species and possibly plays a similar role in European marsh ecosystems to that played by *Fundulus* spp. the North American marshes. Williams and Zedler (1999) found highest mean density of *Fundulus parvipinnis* in constructed channels, while Moy and Levin (1991) observed that planted marshes appear to support considerably less juvenile *Fundulus heteroclitus* than natural marshes. Size structure of *Fundulus parvipinnis* differed between the created and the natural creeks in a California marsh, with the created marsh population being skewed towards larger size. However these size differences were believed to arise from difference in creek morphology (Talley, 2000). During our sampling campaign, gobies occurred in higher densities and had a longer residence time in the mature marsh. The length-frequency distribution of *Pomatoschistus microps* shows clear differences between the two marshes. Individuals increased in size from July onwards in the mature marsh, while growth was not observed in the developing marsh where all individuals remained between 9 and 13mm SL during the whole growing season. Gobies were reported to feed predominantly on the amphipod *Corophium volutator* (Magnhagen, 1986). This may further support the hypothesis that abundance of food is the prime factor causing the observed differences between the two marshes.

The size and density differences of the nekton species may be due to inadequate food resources in created marshes (Moy and Levin, 1991). Minello and Zimmerman (1992) suggested that transplanted marshes could function as natural marshes if just given enough time. Protection from predators in transplanted marshes may reach equivalency with natural marshes after 1 or 2 growing seasons. However the development of man-made marshes as foraging area is probably slower. Minello and Webb (1997) expected to see a general pattern of increased nekton use with marsh age. However there were no obvious relationships found. Their data indicate that the time required to reach functional equivalency is very long, and trends were not be observed within 15 years. In the literature, there is no evidence of a relationship between fish densities and the age of created marshes. Simenstad and Thom (1996) observed in the created Gog-Le-Hi-Te estuarine wetland that fish species richness and density approached asymptotes within 3-5 years. From the study of Dionne *et al*. (1999) in the Gulf of Maine, it appears that both created and restored marshes can be visited by fish assemblages comparable to those found in reference marshes over 1-5 year periods. Thus, rapid colonization of a new marsh habitat in high numbers seems the rule, but fish assemblages do not develop in a linear fashion through time (Williams and Zedler, 1999).

According to this study, this newly-restored estuarine marsh developed some functions of a typical marsh (e.g. refuge) for estuarine nekton relatively quickly but full functional development may require more than 10 years. Creating new marshes in West-Europe would allow nekton species to rapidly colonise the system regardless of the lowered potential as a feeding ground and thus as a nursery area. It seems that the creation of new marshes will only be as beneficial as a mature marsh system to the fish and crustacean populations in the medium to long term.

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Main findings

In conclusion, the present work shows that the life of the nekton species, which use the marsh creeks as nursery or as a foraging area, is strongly influenced by short-term temporal variation (1). The importance of the marsh creek for nekton is reflected in the migration pattern of several species, which tend to utilise the marsh creeks for the longest period possible. Feeding is one of the main reasons why species migrate to the marsh creeks as was proven by the tidal foraging pattern of *Pomatoschistus microps* feeding more while entering the marsh. Diel variation also influences the utilisation of the marsh creek. Species migrate to the creek in different abundances at night due to their activity differences or the better protection from predators. This last assumption was supported by the activity of *P. microps*, which migrated in higher abundance to the creek at night but generally foraged less. There were diel differences in the utilisation of the marsh creek although feeding habit of the common goby indicated that the influence of the tidal cycle is superior over diel variation. Spring tide brings more organisms into the marsh creek and fish feed more, which exemplifies the more intense usage of the area during spring tide. In order to maximise the utilisation of the marsh habitat, species have to adapt to the constant change of the environment and the combined effect of the short-term temporal cycles. Because of the rapid changes of the environment and the complexity of the system the response of the nekton species is not always clear to explain. As an example the combined effect of the semi-lunar and the diel cycle on the feeding habit of the common goby requires further studies.

(2) Only a few larger fish species are able to utilise the intertidal marshes. The same species use the brackish marshes from the polyhaline up to the mesohaline area. The freshwater marsh had a distinct community structure. The absence of *Platichthys flesus* in the euhaline area also contributed to a slightly different community. The main species use both large and smaller creek. Marsh ponds represent a stressful environment that only a few species are able to tolerate. Fish using the marsh creeks along the salinity gradient adapt their prey spectra to the available prey items although the main prey species were similar in every saltmarsh. The high macrobenthic stock in the marsh creeks creates a similar potential of the areas as feeding ground and results in the lack of top-down control by the three main predatory fish species (*Platichthys flesus*, *Dicentrarchus labrax* and *Anguilla anguilla*). The high abundance of the macrobenthic prey species will also contribute to the fact that juveniles of nursery species are not preyed upon significantly by *P. flesus* and *D. labrax*. Besides the high macrobenthos density and biomass also the temporal or spatial segregation from the large predator fish increases the survival of the nursery species. The refuge in the marsh creek from predator fish indicates good nursery conditions.

(3) After ten years of re-establishing a marsh system nekton species intensively utilise the creek habitat. Although in comparison with a mature marsh this usage is less intense. The lower density and the significantly lower biomass of the marsh visiting species indicate the preference of nekton for a mature area. The better nursery conditions are also reflected in the increasing length of the common goby in the mature marsh creek. The developing marsh is quickly invaded by nekton species but for a full functional development probably a longer period is necessary.

Final conclusions

Nowadays intertidal marshes are world-wide recognised as fundamental elements of the estuarine ecosystems. The Ramsar Convention (1971, Iran) was the first international agreement acknowledging the importance of wetlands. This convention encouraged states to designate wetlands for inclusion in the List of Wetlands of International Importance and to promote their conservation, including, where appropriate, its sustainable use. Selection for the Ramsar List is based on the wetland's significance in terms of ecology, botany, zoology, limnology, or hydrology. States have also undertaken to establish nature reserves in wetlands and they are also expected to promote training in the fields of wetland research and management. Among the marshes chosen as sampling locations during this study both Saeftinghe and Zwin are designated as Ramsar sites and as such considered especially important for conservation.

There is a general agreement that marshes are important to the health of the estuarine or coastal ecosystem although the precise manner in which salt marshes affect offshore systems is not known (Nixon, 1980; Adam, 1990). Marshes fulfil several functions in the estuarine ecosystems. Man has always utilised marshes as grazing ground for cattle (Bakker *et al.*, 1993) and as fields for exploiting different resources (Adam, 1990). Saltmarshes are natural sediment sinks, which increase their capability to function as pollution filters (Hazelden and Boorman, 1999). Intertidal marshes also serve as a buffer during flood events and prevent erosion at the coast line or along the estuarine border.

Salt marshes are among the most productive ecosystems in the world (Mitsch and Gosselink, 1993). They can export nutrients and organic matter to the adjacent coastal environment (Teal, 1962; Lefeuvre and Dame, 1994). Marshes are considered as nursery grounds of young individuals visiting the marsh habitat (Boesch and Turner, 1984; Davis, 1988, Cattrijsse *et al.*, 1994; Costa *et al.*, 1994; Dionne *et al.*, 1999). Beck *et al.* (2001) suggested that a habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than the production from other habitats in which juveniles occur. They recognise that the production reaching adult population is dependent on a combination of successful recruitment to juvenile habitats, adequate growth in these habitats and adequate survival both within juvenile habitats and during migration to adult habitats. The adequate growth and survival of juveniles in the nursery area (e.g. marsh habitat) requires good foraging potential (Rozas and Odum, 1988; Craig and Crowder, 2000; Laffaille *et al.*, 2002) and protection against predation (Paterson and Whitfield, 1996; Halpin, 2000, Costa *et al.*, 2001). The value of the marsh habitat (the habitat value) for young marsh visiting individuals is therefore reflected in the capacities of the intertidal marsh to offer food and refuge. Measuring and describing the habitat value different indicators can be used. The density of juveniles reflects recruitment, mortality and emigration, thus density can be an important indicator of nursery habitat value (Minello, 1999). Relative nursery value also can be obtained from analysis of diet (Moy and Levin, 1991), bioenergetics (Madon *et al.*, 2001) ecophysiological responses (Miller *et al.*, 2000), stable isotopes (Weinstien *et al.*, 2000), otolith microchemistry (Gillanders and Kingsford, 2000) and trace elements in body tissues (Courtney *et al.*, 1994). Food is probably the major factor determining the habitat quality (Gibson, 1994). Most investigations have used one or two indicators from the above mentioned to describe the marsh habitat value for nursery species and to observe changes in the potential of marsh habitats as nursery grounds. **The present thesis combined the measurement of different indicators. Density and biomass of marsh visiting species, growth of the common goby *Pomatoschistus microps* were measured and macrobenthic food availability was assessed.** Salt marshes are ecotones lying at the border of two ecosystems which results in the complexity of the marsh ecosystem. This necessitates more than one indicator in order to obtain an understanding of the habitat value and its change under the influence of different environmental parameters.

In the last few decades estuaries changed completely due to anthropogenic influences. Some of these activities, like land reclamation or construction of dikes (Mitsch *et al.*, 1994) destroyed vast areas of intertidal wetlands, others changed the functioning of the estuary. Habitat loss through the removal of habitat, the deterioration in its quality or the prevention of its use by faunal species, is a serious threat along estuaries (Elliott, 2002). Along the salinity gradient of the Schelde River intertidal marshes are still present although their areas decreased significantly in the last decades (Meininger and Snoek, 1992). The marshes in the SW Netherlands have diminished and less than 30% of what was present in 1950, remains today (Haperen, 1989). The disappearance of the intertidal marshes in this area was mainly the result of the Delta Project, which treated the estuary from the single point of view of safety and flood control. Over the last 25 years of the Delta Project the delta was being divided and many parts have been closed off (Bijlsma and Kuipers, 1989) resulting in the drastic change of tidal regime. While direct destruction of intertidal marshes is nowadays under very strong restrictions, the alteration of the estuary still continues in the form of the deepening of the shipping channel. This activity has resulted in the increase of the tidal volume, in the increase in tidal height and in a greater deposition of silt on the mudflat and salt marshes. Since hydrology is possible the most important factor regulating wetland processes (Mitsch and Gosselink, 1993) and driving several wetland functions including exchange of nutrients, sediments, organic materials and biota between the marsh and the rest of the estuary (Rozas, 1995) the change of the tidal regime will cause significant effects in the intertidal marsh functioning.

The hierarchical model of the estuarine ecosystem in the SW Netherlands (Figure 1) shows that outer compartments like the water system dominates the inner ones like vegetation and fauna (Haperen, 1989). Changes in the water system will effect the vegetation and the life of the species inhabiting the marsh. This study indicated that short term temporal variation of hydrology has a strong influence on the life of species utilising the marsh habitat. The sensitive equilibrium between the flood and ebb, and the neap and spring tide cycles defines the accessibility of the marsh and the time period of its utilisation.

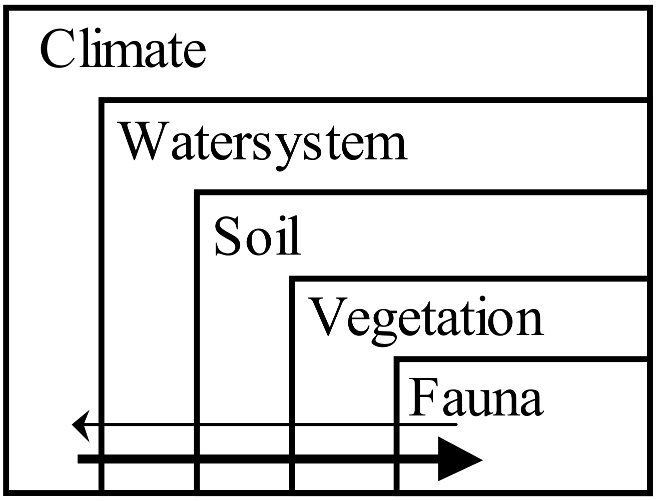

Figure 1. Hierarchical model of the estuarine ecosystems in the South West Netherlands (Haperen, 1989).

This study indicated that most species migrate at the edge of the tidal cycle to maximise the time spent in the marsh creek. The migration is partly driven by the search for food, which was reflected in the feeding habit of juvenile gobies. This species starts to feed intensively as they enter to the marsh showing the importance of this habitat as feeding ground. During the lunar cycle species like *Carcinus maenes*, *Palaemonetes varians*, *Dicentrarchus labrax* and mysids prefer migrating to the marsh with the greater tidal volume at spring tide. Other species like *Pomatoschistus microps* reach higher densities at neap tide. The feeding activity of species visiting the marsh is also influence by the tidal volume. The common goby feeds more during spring tide than neap tide although diel variation still modified this rhythm. The change in tidal volume due to dredging activities can thus influence the migration and feeding habit of marsh visiting species. **The occurrence of some species in the marsh creek, which migrate favourably during low tide and neap tide (e.g. *Pomatoschistus microps*), might be inhibited with the increasing tidal volume.** In contrast, the increase of tidal volume and higher current speed can favour other species utilizing the marsh creek by providing more intense support for migration and possible more food. Although after a certain threshold environmental conditions can become too stressful and inhibit the exploitation of the marsh habitat.

The deepening and canalisation of the estuarine channel may also result in the change of the salinity gradient due to the increase in tidal volume and the penetration of the tides into more upstream regions. Salinity changes may affect the epibenthic species composition of the estuarine subtidal as poly- and mesohaline areas are characterised by distinct community structures (Hostens, 2003). **The results of this thesis indicated that intertidal marshes have similar epibenthic communities from the polyhaline up to the lower salinity mesohaline zone.** The most common epibenthic species were *Dicentrarchus labrax*, *Platichthys flesus*, *Pomatoschistus microps*, *Carcinus maenas* and *Palaemonetes varians*. The freshwater marsh had a distinct epibenthic community and flounder was absent in the euhaline marsh creeks. Like in most highly variable system faunal species diversity is low but species utilising salt marshes, have a wide tolerance to changesin environmental variables and occur in high numbers (Nixon and Oviatt, 1973). Moderate salinity changes would thus not directly influence the fundamental marsh epibenthic communities in the poly- and mesohanile zone. Although some species like *Platichthys flesus*, which avoids the euhaline zone in the estuary (Hostens, 2003) and is absent from the euhaline marsh may shift its position to the more upstream marshes. A **salinity change may effect the macrobenthic food availability for fish.** This study showed that *Corophium volutator* occur only in the brackish marshes and with the increasing salinity this species would shift its position more upstream. This can influence the occurrence of epibenthic species since *Corophium* is a basic prey item for several fish (flounder, seabass, common goby). The density of *Nereis diversicolor* and *Macoma baltica* would increase in the marsh creeks with increasing salinity but most probably this change would not influence the feeding habit of marsh visiting species.

Nowadays the actual loss of the salt marshes in the Westerschelde is unlikely to occur through direct anthropogenic influences due to the conservation status given to them. However, a significant threat to the salt marsh habitat is sea level rise. The Intergovernmental Panel On Climate Change predicted a 65 cm rise by the year of 2100 (Doorncamp, 1990). This would have a significant effect on the marshes as they become inundated by every tide. Normally salt marshes are able to adapt to sea-level rise by shifting their position to higher elevations. The construction of dikes and sea defence walls however prevents the natural regeneration of intertidal marshes (Davidson *et al.*, 1991). Sea level rise may result in the loss of intertidal marshes. Marsh habitats offer significant amount of macrobenthic prey for marsh visiting fish species. **For young predator fish like seabass and flounder, the carrying capacity of marsh creeks along the salinity gradient of the Westerschelde estuary is very high ranging from 58 till 490 ind. m^{-2}. This represents a huge capacity as a foraging ground, which loss would affect the whole estuarine system.** The estuary has large mudflats so the loss of the area of salt marsh to species like flounder would probably not have a large effect. The main prey item of this species is *Corophium volutator*, which reaches very high densities and biomass on the estuarine intertidal flats (Ysebaert and Herman, 2002). Flounder has been shown to be highly adaptive and switching prey items upon depending the availability (Miller and Dunn, 1980). Probably the loss of salt marsh would have a greater impact on the postlarvae and juvenile seabass, which would influence its fishery in the long term. Besides the effect on commercially important fish like *Dicentrarchus labrax* the loss of salt marsh habitat would have a greater impact on smaller fish species like Clupeidae, sticklebacks, gobies and on crustaceans like shore crab and brown shrimp which intensively utilise the marshes (Cattrijsse *et al.*, 1994, 1997). Theses species are important prey items for birds and links to higher trophic level. The loss of marsh areas would result in a decrease in the density of these species affecting the whole estuarine food web.

The way to allow salt marsh adapt to sealevel rise is through managed retreat and set back. Other solution of the management of estuaries often involves re/creation of intertidal marshes (Broome and Craft, 2000; Streever, 2000). This management tool is often used in the US.

Investigations in the North American marshes indicated that restoration sites need to incorporate greater complexity by increasing topographic heterogeneity and habitat linkages on multiple scales (Zedler *et al.*, 1997). The connectivity and proximity of heterogeneous habitats influence species composition, fitness and movement. Zedler *et al.* (1997) found that the biggest difference between the natural and created marshes was the absence of small tidal creek which affected the fish species composition. **The present study indicated the importance of the marsh habitats on a small-scale. In the case of marsh reconstruction attention should be paid to create creek network system with different stream order creeks. Species like seabass, flounder, common goby and shore crab intensively use the small creeks seeking refuge and food indicating the importance of creeks with lower stream order. Fish and crustacean species (*Pomatoschistus microps*, *Palaemonetes varians*) were shown to intensively utilise also the ponds situated on the surface of the marsh. The establishment of different habitats like large creeks, small channels or marsh pond would assist the colonisation of a newly created area by nektonic species.**

The managed retreat and set back involves allowing the degradation of current sea defences or dikes and moving them further inland. Removal of the defences may also be necessary to allow the spread of the salt marsh inland. The extension of salt marshes would buffer the large amount of water during floods and reduce the power of waves before they reach coastal defences (Curry and Pepper, 1991). Areas of land given back to the estuary and evolving into salt marshes will pay themselves in the reduced cost of later flood and sea defence schemes. Besides the benefit for human use the maintenance and possible expansion of a rare and important habitat can be considered as a significant profit. The present study indicated that marshes developed from the former polder area are colonised quickly by marsh visiting species. Other studies also reported quick utilisation of the restored area by fish (Simenstad and Thom, 1996; Williams and Zedler, 1999) and macrocrustacean (Scatolini and Zedler, 1996). Mobile species use immediately the available habitats in a young marsh but their density and biomass are generally stays lower than in the mature marshes for several years (Minello and Zimmerman, 1992; Minello and Webb, 1997). The present study showed that most species used the new marsh in lower density. Biomass of nektonic species was also significantly lower on the developing area. The most common fish species in the marsh, *Pomatoschistus microps* showed increasing length during the year while in the developing area the individuals stayed small. This observation also supported the fact that n**ewly developed marshes probably become fully beneficial for faunal species in the long-term therefore first and foremost conservation should be the highest concern and precede other management strategies**.

The future of the saltmarshes is still uncertain. Perhaps sea-level rise will destroy salt marshes. In addition, technology now exists for modifying coastal environments on a vast scale. The future lies in the sustainable use of the salt marshes and in good management. Management, which includes conservation, mitigation strategies, marsh restoration and managed retreat, is essential to keep a healthy estuarine ecosystem and face to the threat of marsh habitat disappearance.

Remarks on the study

Besides the weather conditions salt marshes have several structural features (e.g. soft sediment, tides, dense creek system, dense vegetation) to tackle with during sampling. The sampling stations are often situated deep inside the marsh making their access sometimes very difficult. These circumstances make sampling often very hard and physically demanding.

The choice of the sampling site faces several difficulties too. Due to the marsh structural features, sampling stations are sometimes situated on a certain point by necessity (e.g. accessibility, presence of a bridge etc). Because of the heterogeneity within a marsh area, it is difficult to find identical sampling stations in different marshes to ensure identical sampling conditions. Moreover, marshes sometimes do not possess all the different habitats therefore sampling had to be restricted to the available ones.

To compare the nekton community structure in the mature and developing marsh a sampling campaign was planned to minimise the influence of the environmental parameters. Samplings were carried out on consecutive days during spring tide period and creeks with similar size were chosen. Predicted water heights were checked to define the sampling days. Despite of the careful planning, of the sampling meteorological conditions modified the water height on same of the sampling days, which was not foreseen and might have influenced the observed pattern.

Cattrijsse (1994) described the seasonal pattern of nekton communities in the marsh creeks therefore there was no need to redo the seasonal sampling covering the whole year. From his study the period between April and October was defined to be the most appropriate to sample the marsh nekton. In these months nekton species were the most abundant.

The use of the appropriate sampling methods is crucial to understand the functional role of nekton in tidal marshes. However collecting mobile aquatic organisms in this environment presents a unique set of methodological challenges. Shallow water, soft sediments and the many structural features of marsh habitats such as undercut creekbanks, dense vegetation, fallen trees in the freshwater marshes, all make it difficult to use most conventional methods (e.g. trawls, seines) (Kneib, 1997). Nearly continuous changes in water depth, current speed and flow directions are characteristics of intertidal environments, adding to the practical problems of sampling in tidal marshes. To overcome these problems several modified conventional gears and unique techniques have been developed which can yield difficulties to compare the result with other studies. Each sampling methodology (e.g. active, passive, quantitative, qualitative samplers) has its own drawback therefore selecting a device is one of the most important steps in planning a study. The construction or the choice of the sampling device has to consider several aspects like the gear efficiency, the ease of standardisation, the area sampled and the target organism (Rozas and Minello, 1997). Most sampling methodology used to sample in marshes does not yield replicates. In this study the lack of replicates resulted a relatively low number of observations.

During the present study different passive sampling strategies were used according to the aim of the investigation. A stow net (Fig. 1) was designed by Cattrijsse *et al.* (1994) and used in the studies where sampling hyperbenthic and epibenthic species in the lower 1 m of the creek was the aim. Since the focus was on these target groups, avoidance above the net therefore was not considered. The aim was to sample species moving close to the bottom of the creek, a net opening of 1 m x 1 m was used and 1 mm x 1 mm mesh size. The opening size of the net, the mesh size and the thickness of the fibre were used to calculate the necessary length of the net in order to keep the pressure inside the net under all current conditions (Tranter, 1979). This reduced the probability that animals detect the net. Since the banks of the sampled creeks were symmetrical the migrating fauna was evenly distributed over the lower water column. The net was placed on the bottom, always at the same spot during the campaign, and mounted an iron frame. Two weights attached to the sides of the frame prevented the net from being lifted by the currents while ropes kept the net in place during sampling. A rope tided the tale of the net making easy to empty the net. Considering the target animals, the construction of the net, the position of the net in the channel and the physical characteristics of the creek this sampling method provided representative samples about the hyper- and epibenthic community structure of the sampled area. The drawback of this sampling method is the lack of replicates, which could be solved to use another net in an adjacent marsh creek during the same period.

Marsh habitats were sampled with different sampling methods. The target animals and the physical characteristics of the habitat were considered to choose the most effective sampling methodology. Large intertidal channels were sampled with fyke nets. These fyke nets had an opening of 1 m and a mesh size of 15x15 mm. The nets were 5 m long and contained 6 trouths. At the mouth 3 m long wings enlarged the sampling area of each net. Metal poles helped to keep the net stretched and in position. Regarding the topography, the nets were always placed to the same site between the bottom and the edge of the creek alternating the two nets in order to reach higher fishing efficiency. The fyke nets were set before water entered the system and faced the outgoing ebb currents to sample fish and macrocrustaceans leaving the creek with ebb. Individuals were captured during the ebb, which lasted 3-4 hours in all marsh creeks. The short period what fish spent in the net prevented the digestion of prey. Hence the type and the amount of prey found in the stomachs gave a good estimate about the feeding habit of fish utilising the large creek habitat. To increase the catching efficiency more and larger nets may be more efficient in future research.

The smaller intertidal creeks were sampled with a block net. This net was constructed of 5 mm gauze and had two lateral wings of 2 m and a central bag. The whole net was 2 m height and the topline was provided with floaters. The ground rope was fitted with a heavy chain. The block net was set at high water near the mouth of the creek. The chain in the ground rope was manually placed on the bottom of the creek and sticks kept the net and ground rope in place. All water had left the creek when net was emptied therefore all individuals were captured which used the creek behind the net. The mesh size of the net ensured that smaller individuals, which may preferable use the small marsh creeks, would be efficiently captured with this method.

Fish traps were selected to passively catch small fish or macrocrustaceans inhabiting tidal pools. The traps were placed at the edge of the pools before the tide started to enter and collected after the ebb. Bait was not placed inside the trap. Fish traps were made of transparent plastic bottles. The neck of the bottle was cut off and inserted backwards into the bottle. The bottom was also opened to insert another neck. This created a trap with two openings of 25 mm, a diameter of 75 mm and a total length of 250 mm. To minimize the sampling bias all the traps were uniform. Soak time was defined around 5 hours. Traps were placed before the flood and collected after the tide receded. The number of the traps placed in the pond was estimated to the size of the pool. Traps were placed at the edge of the pond approximately 5 m from each other. Layman and Smith (2001) discussed the drawbacks of using fish traps in the marsh habitats and suggested a careful choice of sampling method in accordance with the aim of the study. Fish traps give a qualitative description about the species composition of a habitat. Since the aim of the present study was a qualitative sampling this method was considered appropriate. Stomach analysis was not planned to perform because individuals did not forage in the trap and during the 5 hours of soaking time the stomach content could be digested.

The used methods were appropriate to sample hyper- and epibenthos and provide a study about the community structure and its changes due to environmental variables. Although to understand better how marshes function for fish and macrocrustacean (e.g. calculating carrying capacity and Production/Biomass ratio, describe food web) additional study should sample the possible prey species like macrobenthos and zooplankton and the calculation of the growth of individuals during long term would be necessary.

Gobies whose stomach contents were analysed during the semi-lunar cycle were between 20-30 mm standard length. The limited number of *Pomatoschistus microps* during the semi-lunar cycle prevented to define more cohorts of fish length although it may have provided additional information about the feeding habit of the common goby.

The present study benefits from the fact that fish and macrocrustaceans communities in the intertidal marshes in general and along the Westerschelde estuary in particular is little studied. Any information about the habitat value of marshes for aquatic organisms will be beneficial for the better understanding of the intertidal marshes functioning.

Recommendations for future research

** Macrobenthos seems to be very abundant from the perspective of fishes. A calculation should be carried out to evaluate the number of fish, which are able to feed on the available number of Corophium volutator and Nereis diversicolor. An assessment of the quantitative potential of one unit area of the marsh creek can be made. This potential should be compared between marshes with different salinity.*

** In the present study macrobenthos was sampled to indicate the food availability for fish in the marshes along the salinity gradient of the Schelde River. Because of the aim of the study and the limited capacity for working out the samples sampling campaign was limited and focused mainly on the four main prey taxa. It might be worthwhile to investigate the macrobenthic community structure and its spatial variability between the different habitats and between marshes with different salinity.*

Functioning of marsh creek habitat

** To extend the investigation in the mature and developing marsh future work should be carried out to compare the feeding habit of the main fish species in these areas.*

The habitat value of the marsh can differ in the protective function and in the potential to offer food for the marsh visiting species. Besides measuring the density and the biomass of juveniles a future study is suggested to investigate the feeding habit of the main fish species in the mature and developing marsh creeks. Macrobenthos composes the large part of the diet of the marsh visiting fish species. Besides the sampling of fish for stomach analysis, macrobenthic samples should be also taken to indicate the food availability in the mature and developing areas. This study would provide further details about the utilisation of the areas with different age by nekton species.

** A future sampling is suggested to further evaluate the utilisation of the marsh creeks by Pomatoschistus microps.*

The sampling methodology used in the present study was appropriate to indicate the utilisation of the creek habitat by marsh visiting species measuring the species densities but it did not provide information about the utilisation of the area by the individuals. An intense sampling is suggested to collect common gobies from the marsh creeks by fish traps during a tidal cycle. The captured individuals should be labelled and released back to the creek. For recapturing the tagged individuals traps should be placed in the same creek and further in other marsh channels. The result of recapturing of the tagged individuals would indicate whether gobies keep returning to the same creek or they utilise larger areas in the marsh.

Functioning of marsh pond habitat

** To evaluate the importance of the marsh ponds an artificial pan should be created and the utilisation of this habitat by fish and shrimp should be monitored on long term.*

Change of food availability (e.g. sampling zooplankton and macrobenthos) and the change of the density and biomass of the visiting fish and macrocrustaceans should be monitored. The period could be assessed when the created pond can function as the natural one. Parallel monitoring should be carry out in the natural pond to make the result comparable with the artificial pan.

** Further sampling is suggested to study the utilisation of the marsh ponds by visiting species.*

A habitat should be chosen with a single connection to the adjacent marsh creek. The water entering the pond with the coming tide should be sampled. The fish captured should be tagged and realised back to the pond. During the ebb fish should be sampled again in the water leaving the pond. This sampling would indicate how much time fish spend in the marsh pond, whether they grow there and which are the environmental conditions fish can still tolerate in this habitat.

** A comparison should be carried out about the utilisation of marsh ponds situated in different distances from the marsh creek.*

Species utilise the marsh pond generally have wide environmental tolerance. To assess the importance of marsh ponds for fish and macrocrustaceans it is important to know how far these species can venture leaving the marsh creek to seek for refuge or food.

Comparison of marsh and intertidal flat habitat

** A future study is suggested comparing the foraging potential of a marsh creek and the intertidal flat.*

An experiment is suggested to carry out. Cages should be placed in a marsh creek where water is always present even at low tide and other enclosures should be situated on the intertidal flat. Caging would exclude the predation pressure and the growth of the individuals would indicate the foraging potential of the area.

** Comparing the growth of the common goby (Pomatoschistus microps) in the part of the estuary where marshes are present and where this habitat is lacking should be carried out in a future investigation.*

Marshes act as nursery providing protection and food, which enhance the survival of juveniles. To investigate the importance of marshes a growth rate of fish species should be compared in a marsh creek and on the intertidal flat of the estuary where fish cannot utilise marsh habitats.

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Appendix 1

Definitions of ecological terms

Community: A group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and identifiable by means of ecological survey from other groups (Hiscock *et al.*, 1999).

Classification of estuarine divisions according to salinity (McLusky, 1993).

Tidal freshwater reaches: salinity < 0.5

Oligohaline reaches: salinity 0.5 and 5

Mesohaline reaches: salinity 5 and 18

Polyhaline reaches: salinity 18 and 30

Euhaline reaches: salinity > 30

Benthos: those organisms attached to, living on, in or near the seabed, river bed or lake floor (Lincoln *et al.*, 1998).

Brackish: Referring to mixtures of fresh and seawater. Usually regarded as between 0.5 and 30 psu (McLusky, 1993).

Ecosystem: A community of organisms and their physical environment interacting as a ecological unit (Lincoln *et al.*, 1998).

Environment: The complex of biotic climatic, edaphic and other conditions which comprise the immediate habitat of an organism; the physical, chemical and biological surroundings of an organism at any given time (Lincoln *et al.*, 1998).

Epibenthos: All organisms living on the surface of the sea or river bed (Hiscock *et al.*, 1999).

Estuary: Semi-enclosed coastal water, open to the sea, having high fresh water drainage and with marked fluctuations in salinity (Lincoln *et al.*, 1998).

Habitat: The habitat of a species is the place where a population of that species (or life stage) lives at any particular time (Odum, 1971).

Hyperbenthos: Small animals, which spend part or all their lives in the water layer close to the bottom (Mees and Jones (1997).

Intertidal zone: The zone between tide marks, i. e. between high-tide and low-tide level (Baretta-Bekker *et al*., 1998).

Microhabitat: A small part of the habitat, which has distinct physical conditions (Hiscock *et al*., 1999).

Neap tide: Seven days after the spring tide, tides occurring at first and third moon quarters, where the range between high tide and low tide is smallest (Adam, 1990).

Nekton: Animals that live in the water and capable of sustained self-propulsion through that medium in a horizontal direction, usually beyond the capability of individuals <20 mm in size (Aleyev, 1977).

Spring-tide: The larger tidal forces experienced when sun, moon and earth are aligned, which occurs one and a half days after new and full moons and produces tides of large amplitude (Adam, 1990).

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Appendix 2.

Density of nekton species (ind. $hour^{-1}$ net^{-1}) captured by fyke net in the five different marshes during the sampling campaign. Marshes are indicated as following: Grembergen (G), Saeftinghe (S), Waarde (W), Zuidgors (Z), Zwin (Zw).

Month	*April*				*May*					*July*					*August*					*October*				
Location	**G**	**S**	**Z**	**Zw**	**G**	**S**	**W**	**Z**	**Zw**	**G**	**S**	**W**	**Z**	**Zw**	**G**	**S**	**W**	**Z**	**Zw**	**G**	**S**	**W**	**Z**	**Zw**
Alburnoides bipunctatus	1.7																							
Anguilla anguilla					0.3	0.1	0.1	0.3		1.7	1.7				0.2	0.3			0.1	0.3		0.1		
Carassius carassius	0.1				0.3																			
Clupeidae spp.											0.4	0.8										0.3		
Dicentrarchus labrax			0.2			0.7	2.3	1.0	0.7		0.6		5.0			1.9	6.8	7.8			8.7	5.2	0.2	0.3
Gasterosteus aculeatus							0.1																	
Liza spp.														0.5										
Platichthys flesus		2.9	0.8			1.1	2.2	1.0			1.1	0.3	1.3			0.2	0.8				1.3	1.0	0.1	
Pleuronectes platessa								0.1																
Pomatoschistus microps																								0.1
Syngnathus rostellatus								1.7																
Carcinus maenas			0.2	0.6			0.3	0.3	6.0	0.1	0.4	0.3	0.7	4.4		1.7	2.7	1.9	3.3		7.9	0.2	1.3	0.6
Eriocheir sinensis															0.1					0.3				
Palaemonetes varians												1.7												

Number of individuals caught by blocknet during one ebb period. Marshes are indicated as following: Grembergen (G), Saeftinghe (S), Waarde (W), Zuidgors (Z), Zwin (Zw).

Month	*April*				*May*				*July*				*August*				*October*			
Location	**G**	**S**	**Z**	**Zw**	**S**	**W**	**Z**	**Zw**	**S**	**W**	**Z**	**Zw**	**S**	**W**	**Z**	**Zw**	**S**	**W**	**Z**	**Zw**
Alburnoides bipunctatus	2																			
Atherina presbiter			1																	
Clupeidae spp.			3							1										
Dicentrarchus labrax						4			1	1		13		2	3	6	10			
Platichthys flesus					11															
Pomatoschistus microps										3		1	12	4		9	5	22		69
Carcinus maenas			3			1	2				2	4	3	4	4	6	25		8	
Crangon crangon																		7		
Palaemonetes varians						16	2			2		4	4	44	8	10	1	12	11	21

Density of species (ind. $hour^{-1}$ net^{-1}) in the marsh ponds captured by fish traps. Marshes are indicated as following: Grembergen (G), Saeftinghe (S), Waarde (W), Zuidgors (Z), Zwin (Zw).

Month	*July*			*August*			*October*		
Location	**W**	**Z**	**Zw**	**W**	**Z**	**Zw**	**W**	**Z**	**Zw**
Gasterosteus aculeatus							0.03		
Pomatoschistus microps	0.1	0.06	0.05	1.0			1.73		
Carcinus maenas							0.03		
Crangon crangon							0.03		
Palaemonetes varians	2.03	0.48	1.15	17.3	0.15		4.13	1.0	0.2

Appendix 3

List of the assigned values, the length-Ash Free Dry Weight (ADW) and the length-Wet Weight (WW) regressions. All lengths (L), standard length (SL), total length (TL) and carapace widths (CB) are in millimetres, all weights (ADW and WW) are in milligrams and assigned values are in milligram ADW. Adults (a) and postlarval (pl) stages are indicated.

Amphipoda	ln ADW= -5.857+2.863 ln SL	**Teleostei**	
Bathyporeia pilosa		*Allosa fallax*	ln WW= -13.19+3.233 ln TL
Corophium volutator		*Anguilla anguilla*	ln WW= -15.245+3.326 ln TL
Corophium arenarium		*Atherina presbiter*	ln WW= -12.478+3.103 ln TL
Gammarus zaddachi		*Clupea harengus (*pl)	ln ADW= -10.2+3.816 ln SL
Gammarus salinus		*Clupea harengus (*a)	ln WW= -13.19+3.233 ln TL
Melita pellucida		*Dicentrarchus labrax*	ln WW= -11.749+3.061 ln TL
Orchestia gammarellus		*Gasterosteus aculeatus*	ln WW= -11.359+2.938 ln TL
Orchestia mediterranea		*Liza ramada*	ln ADW=-7.851+3.46 ln SL
Caridea	ln ADW= -5.379+2.903 ln SL	*Osmerus eperlanus*	ln WW= -11.749+3.061 ln TL
Crangon crangon		*Platichthys flesus (*pl)	lnADW= -6.427+3.08 ln SL
Palaemonetes varians		*Platichthys flesus* (a)	ln WW= -11.051+2.926 ln TL
Brachyura		*Pleuronectes platessa (*pl)	lnADW= -6.427+3.080 ln SL
Carcinus maenas juvenile	ln ADW= -3.967+3.164 ln CB	*Pleuronectes platessa* (a)	ln WW= -11.690+3.033 ln TL
Mysidacea		*Pomatoschistus microps* (pl)	
Gastrosaccus spinifer	ln ADW= -5.896+2.873 ln SL	8-10 mm	0.9549
Mesopodopsis slabberi	ln ADW= -6.107+2.867 ln SL	10-12 mm	1.8063
Neomysis integer	ln ADW= -4.103+2.294 ln SL	12-14 mm	2.8319
Schistomysis kervillei	ln ADW= -5.898 +2.931 ln SL	14-16 mm	5.2772
Isopoda	ln ADW= -5.910+2.807 ln SL	16-18 mm	8.0867
Cyathura carinata		18-20 mm	13.9485
Eurydice pulchra		*Pomatoschistus microps* (a)	ln ADW= -7.851+3.46 ln SL
Lekanesphaera rugicauda		*Pomatoshistus minutus* (a)	ln ADW= -7.851+3.46 ln SL
Paragnathia formica		*Sprattus sprattus* (pl)	ln ADW= -10.2+3.816 ln SL
Bivalva		*Sprattus sprattus* (a)	ln WW= -13.55+3.356 ln TL
Macoma baltica	ln ADW= -4.249+2.909ln L	*Solea solea (*pl)	
Cumacea		8-10 mm	0.7424
Cumacea spp.	ln ADW= -5.775+2.870 ln SL	10-12 mm	1.3825
Nematoda		12-14 mm	2.4687
Nematoda spp.	0.003	14-16 mm	3.5046
Other		16-18 mm	5.7571
Decapoda larvae	0.081	18-20 mm	8.7922
Polychaeta		*Syngnathus rostellatus* (pl)	ln ADW=-10.42+3.139 ln SL
Nereis diversicolor	ln ADW= -7.139+2.489 ln SL	*Syngnathus rostellatus* (a)	ln WW= -18.036+3.652 ln TL