CHAPTER 7

General discussion

7

In this final chapter we summarize the major findings of the previous chapters and formulate our final analysis and conclusions. The aim of this thesis was to describe the habitat use of fishes in the Scheldt estuary on both a local (intertidal mudflat) and regional (estuary) scale. We examined the importance of intertidal migration for fishes and discussed the different factors that affect the intertidal habitat quality (**first part**). Chapter 2 described the migration and zonation patterns of the fish community on a brackish water mudflat. As foraging is one of the main triggers for intertidal migration, the diet and feeding strategy of the intertidal fishes was studied in chapter 3. The high niche overlap among flatfishes observed, suggested that competition might be a structuring force for the intertidal fish community. Competition can only occur when resources are limited, i.e. when the competing predators deplete their prey populations. The effects of epibenthic predators on the macrobenthic community were examined in two exclosure experiments (Chapter 4). In the **second part**, we described the effect of abiotic factors on the use of the Scheldt estuary by European flounder *Platichthys flesus*. In chapter 5 we constructed a bioenergetics model which describes growth of flounder as a function of temperature. This model was further extended with oxygen and salinity dependent functions to estimate the habitat quality for flounder in the Scheldt estuary (Chapter 6). The main results of these chapters can be summarized in six theses:

T. 1 Most estuarine fishes utilize the intertidal area either in an opportunistic (aided by the tidal currents) or compulsory way. Only flatfishes seem to be bounded to intertidal migration to exploit the abundant benthic food resources, whereas piscivorous predation seems not important as a trigger for intertidal migration (Chapter 2 & 3).

T. 2 Zonation of fishes on the studied mudflat, when observed, is mainly the result of species-specific differences in mobility. When fish densities are high, spatial segregation on the mudflat may arise to avoid competition for food (Chapter 2 & 3).

T. 3 The intertidal fish community is characterized by generalist feeders and their diet largely reflects the relative availability of prey species (e.g. *C. volutator*) (Chapter 3).

T. 4 Fishes and birds have a negligible effect on the abundance of their infaunal prey species, but they may affect the prey size spectrum. In the absence of predation, infaunal interactions become more important and may regulate the macrobenthic community structure (Chapter 4).

T. 5 The carrying capacity of the estuary for fishes is probably not reached, but it may happen in years with high fish recruitment (Chapter 3 & 4, this discussion).

T. 6 When food is not limiting, temperature is an important factor determining habitat selection in the estuary. Oxygen depletion limits the use of the available habitats in the freshwater reaches of the Scheldt estuary (Chapter 5 & 6).

These theses will be further developed in the following paragraphs. Given the importance of food availability as a steering factor for intertidal habitat use, we will elaborate on the trophic interactions on the mudflat and their effects on the estuarine fish community. In this respect, we discuss the possibility for the presence of a carrying capacity for fishes in the Scheldt estuary. We also present a generalized food web for the intertidal estuarine zone and quantify the major energy fluxes and compartments of this web.

1. The importance of intertidal migration for fishes

The migration of fishes in and out the intertidal zone has been studied extensively (Gibson, 1969; Gibson, 1993; Horn and Martin, 1999). The vast majority of these studies focused on marine habitats and are limited to rocky (Horn and Martin, 1999) and sandy (Gibson, 1973) shores. In contrast, intertidal migration on estuarine soft sediment habitats is less studied. Although the cues for intertidal migration on estuarine and marine shores are likely to be the same, their relative importance may be somewhat different because of the specific nature of the estuarine system. The increased turbidity and lower abundance of large piscivores in estuaries may reduce the importance of predation as a cue for intertidal migration. Other important differences between marine and estuarine shores that may cause differences in the use of the intertidal zone are the high variability of the abiotic estuarine environment and the structure of the substratum, which generally consists of muddier sediments in estuaries. In addition, the concentration of juvenile fishes in estuarine nurseries may intensify competitive interactions and hence influence the distribution of species. Intertidal fishes on rocky shores generally display a strict zonation, whereas on sandy shores, the whole intertidal is much more uniform and zonation patterns are less clear.

As our samples were representative of the fish community of the Beneden Zeeschelde, our study showed that most estuarine fishes enter the intertidal zone (Chapter 2; Maes *et al.,* 2005b). The fishes migrated onto the mudflat either actively looking for food (flatfishes) or passively transported by the tidal currents (pelagic species). Catches were dominated by flatfishes, which preyed on the dense macrobenthic species. The intertidal area seems vital for food supply (Chapter 3). The (semi-)pelagic species can be considered vagrants on the mudflat. They possibly follow their migrating epibenthic prey (e.g. mysids and shrimps) and may find a valuable supplement to their diet in the infauna that disperses into the water column (e.g. *Corophium volutator*). Feeding seems to be the most likely trigger for intertidal migration. Almost all flatfishes had macrobenthic prey in their stomachs, which are abundant and readily available in the intertidal zone. Two other factors that are known to influence intertidal migration are temperature (growth) and predation (survival). As a result of the well-mixed nature of estuaries, the vertical temperature gradients are either small or negligible. A significant temperature differential between the shallow intertidal and deeper subtidal may only be observed during windless conditions and when the air temperature is clearly different from the water temperature (warm summer or cold winter days). Furthermore, estuarine fishes are generally eurytopic species and adapted to the highly variable environment, so it seems less likely that they gain a substantial (growth) benefit from relatively small temperature increases in the intertidal zone. However, temperature differences may be important for growth along the longitudinal axis of the estuary as was shown in chapter 6.

The overwhelming presence of juveniles confirms the nursery status of this part of the estuary. Beck *et al*. (2001) defined a nursery as a habitat 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 production from other habitats in which juveniles occur. Several studies showed that survival is enhanced by migration into estuaries (Blaber and Blaber, 1980; Maes *et al.,* 2005a) and into the intertidal zone of marine sandy beaches (Burrows, 1994; Gibson *et al.,* 2002). It is however unclear whether intertidal migration in estuaries directly influences the survival of juvenile fishes by reducing the predation risk. The fishes in our study that actively migrated onto the mudflat were probably too large to be consumed by piscivorous fishes (Chapter 2). Furthermore, it was suggested that the turbidity makes predation unlikely as a strong driving force for intertidal migration in estuaries.

We had expected to find a zonation of fishes on the mudflat, according to their size or to species-specific habitat use. However, clear patterns were absent, probably because of the homogenous nature of the intertidal zone (prey distribution, abiotic conditions, absence of predation). Mobility may limit the intertidal distribution of some species, as was shown for the less mobile gobies, which were restricted to the lower and middle shore. We did find (weak) evidence for density-dependent zonation in flatfishes. In the year with high fish density, *Platichthys flesus* moved up higher on the mudflat. This might suggest that interspecific competition (in this case with *Solea solea*) can regulate the vertical distribution of fishes, especially when food is limiting. This kind of spatial resource separation was also suggested for *Pleuronectes platessa* in the Wadden Sea, which move onshore when there is competition for food (Berghahn, 1987).

2. Muddy trophic interactions

The possible structuring effect of trophic competition was further examined in a diet study of the intertidal fish community, in which we combined prey availability with prey consumption (Chapter 3). This study showed that all fish species on the mudflat, without exception, fed to a more or lesser extent on *Corophium volutator*. The importance of prey species in the diet of fishes reflected the prey availability in the field, confirming the generalist and opportunistic feeding nature of estuarine fishes. The analysis of niche overlap indicated that there was a significant dietary overlap between the two flatfish species flounder and sole. This suggests possible competition between these two species. Competition is only likely if food resources are limiting, which implies that fish predators can deplete their prey populations. In our study, the macrobenthic prey community was sampled simultaneously with the intertidal fish community (Chapter 3 and 4). The analysis of the macrobenthic samples showed that in a year with a high fish abundance (2001), the density of *C. volutator* had dropped significantly from August to October on the lower and middle shore, but not on the higher shore. This was not the case in the following year (2002), when fish abundance on the mudflat was four times lower. As the lower parts on the shore are inundated for longer periods, the macrobenthos will be more exposed to fish predation, which could explain the observed decrease in that part of the intertidal zone in the high fish density year.

We examined the effect of epibenthic predation on the infaunal community by exclosure experiments in which both fish and birds were excluded. Birds were also taken into account because they can have significant effects on the macrobenthic community (Daborn *et al.,* 1993; Goss-Custard *et al.,* 2001). Fish and bird predation did not have a significant direct effect on the abundance of macrobenthic species. Both predators select the larger size classes of the macrobenthic species, but only birds influence the size distribution of their prey. Our results also suggest that in the absence of predation, infaunal interactions like competition could become more important and can regulate the benthic community structure. From the exclosure experiments, it was found that fish predation was relatively unimportant as a structuring factor for the macrobenthic prey community. However, the fish density during those experiments was lower than in 2001 (see previous paragraph). The high interannual variation in fish recruitment makes it difficult to predict the outcome of fish exclosure studies. Probably, fishes significantly affect the prey abundance only when their population is close to the carrying capacity of the system.

The lack of clear direct effects of predation on the abundance of organisms at the lower trophic levels, suggests that the interaction strength in the benthic food web is rather weak. The strength of the interaction between two consecutive trophic levels determines the food web stability, with weak links generally supporting food web stability (Woodward *et al.,* 2005). Most well studied food webs show only a few strong interactions in a matrix of weak interactions, making the effect of trophic cascades unlikely (Raffaelli and Hall, 1992; Neutel *et al.,* 2002; Bascompte *et al.,* 2005). What determines the strength of these interactions? Emmerson and Raffaelli (2004) showed that the *per capita* effect of predators on their prey scales with **predator–prey body size ratio**, with an exponent of around 0.6. This indicates that the size of predators relative to their prey determines the strength of trophic interactions (Shurin and Seabloom, 2005). This might partly explain why the effect of shorebird predation on benthic food webs is generally more pronounced than the effect of fish predation (Quammen, 1984; Daborn *et al.,* 1993; Wootton, 1997; Hamilton, 2000; Goss-Custard *et al.,* 2001). The effect of predation is affected by the **availability of the prey** organisms. The vulnerability of prey depends on the possibility to hide in the sediment or between the vegetation (Barnes and Hughes, 1999). Organisms that burry in the sediment are often consumed only partly (e.g. tail tips of polychaetes and siphons of bivalves) by the predators that move over the surface of the sediment. The three-dimensional structure of soft sediments may also reduce the intensity of infaunal competition.

It is believed that soft sediment habitats generally **lack keystone predators** (Raffaelli and Hawkins, 1996). The attribute 'keystone' refers to the effect the predator has on a competitive superior prey species, which in the absence of predation may become dominant. As a result of the lack of strong competitive interactions, direct effects of keystone predators may be less obvious in soft sediments. Effects of predation in soft sediments may be further dampened by the complexity of the benthic food web. This complexity may, at least partly, be the result of the generalist and omnivorous diet of many of the species. It is suggested that **omnivory** dampens top-down control by predators and that greater omnivory leads to weaker trophic cascades (Shurin *et al.,* 2006; Vandermeer, 2006). Omnivory is widespread in the intertidal food web of our study (Figure 7.1). Most fishes feed on primary consumers (*C. volutator*) as well as on secondary consumers (*C. crangon*). Omnivory was also observed for fish feeding on gobies and for *N. diversicolor* feeding on *C. volutator*. The latter link was not examined in our study, but *N. diversicolor* is known to be omnivorous and feeding on *C. volutator* (Commito and Ambrose, 1985; Ölaffson and Persson, 1986).

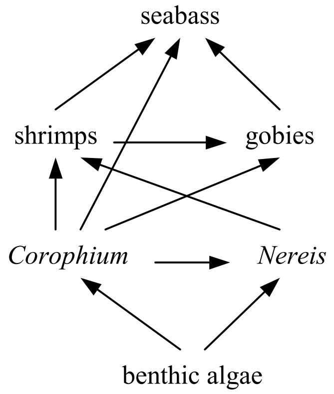


Figure 7.1. *Example of omnivory in the benthic food web of the Scheldt mudflats. Four omnivorous loops can be observed:*

1 – Benthic algae → Corophium → Nereis
2 – Corophium → Nereis → *shrimps*
3 – Corophium → *shrimps* → *gobies/seabass*
4 – Corophium → *gobies* → *seabass*

In order to estimate the efficiency of the energy transfer through the intertidal food web, we quantified the energy fluxes on the mudflat. The aims of this exercise were to obtain a first idea of the importance of the different components in the benthic food web and to estimate the amount of energy available to the higher trophic levels. Because of the illustrative nature of this exercise, the calculations were confined to only six compartments: organic matter, benthic algae, macrobenthos, shrimps, fishes and shorebirds. Where appropriate, we calculated for each component the biomass (standing stock), production (growth), consumption, respiration and metabolic losses (faeces and excretes). All the calculations, except for the fish compartment, are taken from Wilson and Parkes (1998) and adapted to the situation of the mudflat we studied, in the brackish zone of the Scheldt estuary. Details of the calculations are available in Appendix 1-3. Input data for the equations were obtained from our own study or from published studies on mudflats in the mesohaline zone of the Scheldt estuary. For the fish compartment, we applied the Wisconsin bioenergetics model (Hanson *et al.,* 1997). For *P. flesus*, this model was parameterised in chapter 4. The same model was applied to common sole (*Solea solea*), but the temperature-dependence functions of consumption and respiration were adapted to the specific nature of sole. For herring (*Clupea harengus*) we used the model of Rudstam (1988).

The parameters for the allometric functions for the seabass (*Dicentrarchus labrax*) model were taken from the striped bass model (*Morone saxatilis*; Hartman and Brandt, 1995) and the temperature-dependence functions were parameterised with data from literature (Appendix 7.3). The relative importance of the different prey categories in the diet of these four species was estimated from appendix 3.1 in chapter 3. The three prey categories included were macrobenthos, shrimps and other prey (zooplankton, mysids). All the estimates of fluxes and stocks were converted to kJ m^{-2}.

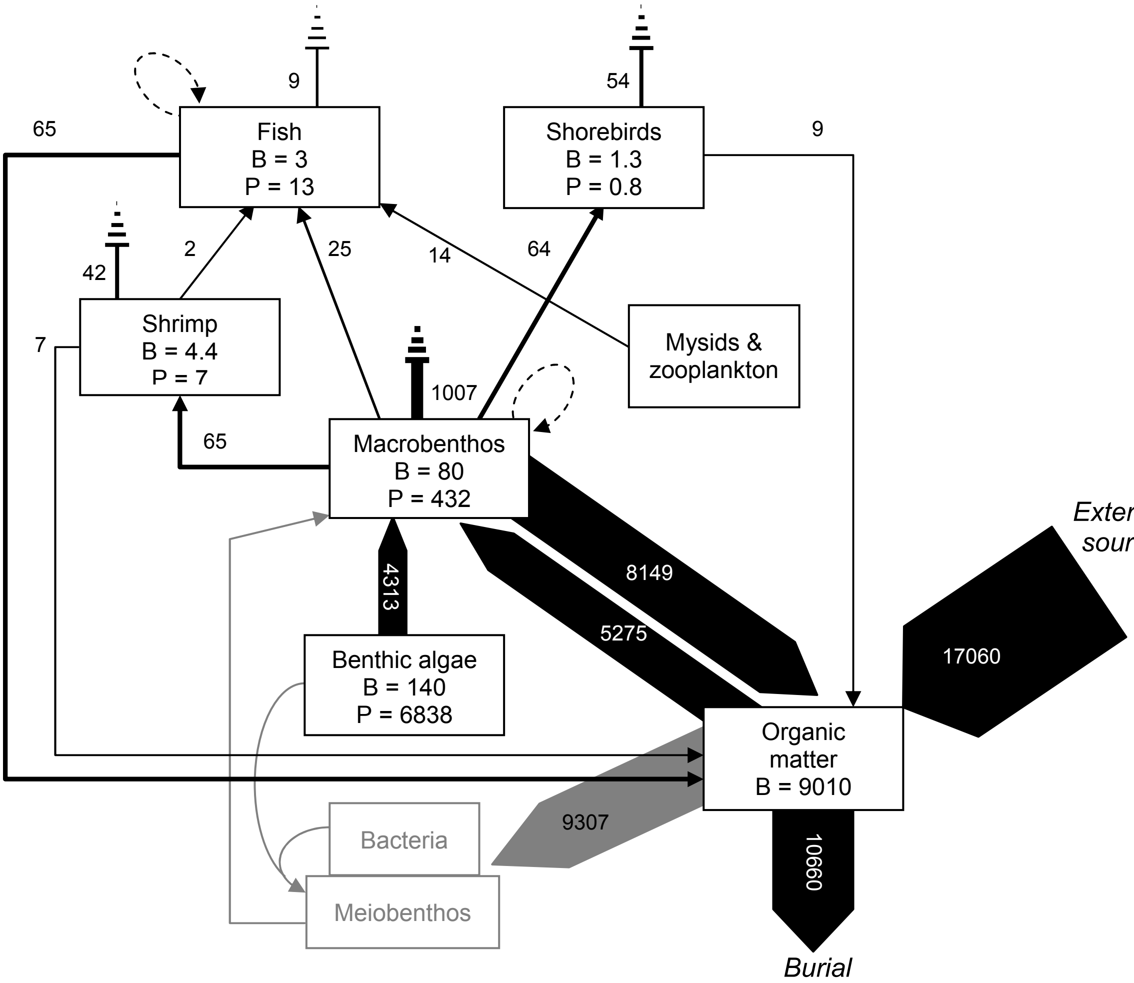


***Figure 7.2**. Food web of an intertidal mudflat in the mesohaline zone of the Scheldt estuary. The values represent the energy in biomass (*B*) (kJ m^{-2}), production (*P*) (kJ m^{-2} year^{-1}) and major fluxes in the web. Respiration is symbolized by an upward broken arrow. Loops (dashed line) represent intra-compartment predation (e.g. piscivorous fish). The compartments and fluxes that were not calculated are in grey. Arrows are proportional to the energy flux they represent. See appendix 7.1-7.3 for details about the calculation of the different components of the food web.*

The food web presented in figure 7.2 only deals with the organisms that contribute directly to the higher trophic levels. Bacteria and meiobenthos are important components of the benthic food web and process a large amount of energy, either between them or transferred to the macrobenthos (Heip *et al.,* 1995). In our food web, the energy consumed by macrobenthic deposit feeders (5275 kJ m^{-2} year^{-1}) is directed immediately from the organic matter pool. However, it should be clear that a substantial part of this energy channels through the meiobenthos and bacteria compartments. We did not quantify this loop in order to limit the complexity of the web. Figure 7.2 shows that a large part of the total production of benthic algae (microphytobenthos; MFB) is consumed by macrobenthic grazers. Although there is substantial evidence that benthic diatoms are the primary food resource of *C. volutator*, this crustacean also feeds on other microbenthic items and detritus (Gerdol and Hughes, 1994a). Consequently, the contribution of MFB to the food of macrobenthos in our web may be somewhat overestimated. However, as also meiobenthos grazers consume a significant proportion of the algae (Heip *et al.,* 1995), microphytobenthos might be top-down controlled. The reduction of the microalgae populations destabilizes the sediment and might stimulate the erosion of the mudflat (Daborn *et al.,* 1993; Hughes and Gerdol, 1997). Roughly one third of the annual macrobenthic production is consumed by the higher trophic levels. *C. volutator* accounts for about 30 % of the macrobenthic production on our mudflat, which corresponds to 130 kJ m^{-2} $year^{-1}$. If the predators (shrimps, fishes and birds) would obtain only half of their energy from *C. volutator*, they would consume about 60 % of the annual *C. volutator* production. Pihl (1985) showed that up to 98 % of the annual production of *C. volutator* in a Swedish estuary is consumed by shrimps, crabs and fish. Although the values we calculate are first approximations and the uncertainty in the calculation of the predator density is substantial, the order of magnitude of the presented fluxes is probably correct. Our calculations suggest that epibenthic predation by birds, fishes and shrimps can have significant effects on the abundance of the most available macrobenthic species on the mudflat.

3. Is prey limiting? The carrying capacity of the intertidal zone

The idea that predators can deplete their prey is closely linked to the existence of a carrying capacity for the system. The carrying capacity is usually defined as the population density of a habitat at which the *per capita* population growth rate is zero (van der Veer *et al.,* 2000a). When the carrying capacity is reached, competition becomes more intense and may result in density-dependent growth and population regulation. Density-dependent processes in the fish nurseries are thought to dampen the recruitment variability of marine fish populations (Beverton, 1995; van der Veer *et al.,* 2000b). Rijnsdorp *et al.* (1992) found a positive relationship between relative recruitment and nursery size, which raises the question whether nursery areas ever become saturated with settling larvae and reach their carrying capacity. At least for zooplanktivorous fishes in estuaries there is some evidence that their consumption may exceed prey production (Mehner and Thiel, 1999; Luo *et al.,* 2001; Maes *et al.,* 2005c). It was also shown for striped bass (*Morone saxatilis*) that its population decline in San Francisco Estuary was partly caused by a decline of the carrying capacity, following a decrease in the abundance of hyperbenthic mysids, its main prey (Kimmerer *et al.,* 2000). With regard to flatfishes, the general idea seems to be that food in nurseries is seldom limiting and that saturation of nursery grounds is rare or non-existent (Gibson, 1994; van der Veer, 2000b). Our data suggest that in years with high fish recruitment (e.g. 2001), the macrobenthic prey populations can be depleted by predation and that under those conditions, the benthic system is close to its carrying capacity. However, this conclusion is based on the assumption that the decrease of the *C. volutator* abundance can be largely attributed to (fish) predation. Furthermore, our exclosure experiments didn't show any effect of predation on the abundance of the macrobenthos. It seems therefore delicate to jump to conclusions about the carrying capacity of the estuary for benthic fish, based on our preliminary results. There are reasons to accept that intertidally foraging fishes can't fully exploit the available prey populations and hence are more likely to be food limited. At least three reasons can be given why only a fraction of the intertidal prey energy is available to benthivorous fishes:

1. The tide constraints the feeding possibilities of intertidal foraging fishes. The macrobenthic prey species are only accessible when the flats are covered by water. Pelagic feeding fishes, on the other hand, do not have this limitation and can feed continuously on zooplankton in the water column (till satiation).

2. Most of the macrobenthic species are buried in the sediment and as such reduce their vulnerability for epibenthic predators. Only a fraction of the prey population is available to the fishes, when they disperse into the water column or when they occupy in the top layer of the sediment.

3. Fishes that feed on the intertidal infauna have to share their prey with shorebirds, shrimps and, in the case of commercially harvested shellfish, also with men. This means that a substantial fraction of the total amount of energy in the intertidal food web is directed to birds and crustaceans and as such is not available for fish.

The fact that benthic prey could be limiting does not mean that a carrying capacity exists for demersal fishes in the estuary. It was shown from the diet analysis in our study (Chapter 3) that omnivory is prevalent in the estuarine food web. Consequently, fishes are flexible to switch between prey species (infaunal, epibenthic, hyperbenthic or pelagic), according to the relative availability of prey in the field.

If intertidal benthic prey is limiting for fishes, it should also be so for shorebirds and crustaceans. While food limitation for crustaceans in estuaries is less well documented, there is a body of literature available on the carrying capacity of benthic systems for shorebirds. Given the amount of published studies on this topic, one could conclude that the carrying capacity of a system is reached more frequently for birds than for fish. The research effort on this topic may be somewhat biased towards birds because of their high visibility, charismatic status and the competition of some birds (e.g. eiders, *Somateria mollissima* and oystercatchers, *Haematopus ostralegus*) with the shellfish industry (Goss-Custard *et al.,* 2004). Several studies indicate that shorebirds are able to deplete their prey to the extent that the remaining prey may become insufficient to support the population, resulting in the emigration or death of at least part of the population (Camphuysen *et al.,* 2002; Atkinson *et al.,* 2003). The effect of shorebirds on the macrobenthos may be temperature-driven. Most shorebirds arrive in the estuarine feeding areas in late autumn, when the environmental temperature is low and benthic production is dropping. The birds maintain a higher body temperature than the environment and have to build up a reserve for winter. As a result, these birds have a higher mass-specific energy demand than poikilothermic fishes. Furthermore, most of the studies that report on prey limitation for birds deal with large bivalves (mussels and cockles) as prey. These bivalves are also harvested by man and commercial shellfishery is shown to decrease the carrying capacity of the system for wintering oystercatchers (Goss-Custard *et al.,* 2004).

It may be clear from the shorebirds, that temperature and body weight are important determinants of the carrying capacity of an ecosystem. The idea that the carrying capacity of nursery areas is never reached for 0-group flatfishes (van der Veer *et al.,* 2000a), stems from the lack of evidence for density-dependent growth. This lack of evidence may be due to the inability to incorporate the effect of ambient temperatures on field estimates of growth rate (van der Veer *et al.,* 2000a). Bioenergetics modelling (Chapter 5) could offer a solution, but these models are time-consuming to construct and highly species-specific. Recently, Brown and co-workers (West *et al.,* 1997; Gillooly *et al.,* 2001; Brown *et al.,* 2004; Savage *et al.,* 2004) presented a metabolic theory of ecology (MTE) in which they describe how the metabolic rate (I) of an organism scales with body size and temperature:

$$I = i_0 M^{3/4} e^{-E/kT}$$

where i_0 is a normalization constant (varies with the organism, biological traits and environment), E is the activation energy (estimated as ≈ 0.63 eV; Gillooly *et al.,* 2001), k is Boltzmann's constant, M is the body mass and T is the absolute temperature in K.

This macro-ecological theory and derived models offer a framework to explore food web stability, patterning of energy fluxes and responses to perturbation. The model predicts that metabolic rate constrains biological processes at all levels of organization like population and community dynamics and ecosystem processes (Brown *et al.,* 2004). The carrying capacity (K; expressed as number of individuals) of a system is predicted to vary as

$$K \propto [R] M^{-3/4} e^{E/kT}$$

linearly with the supply rate or concentration of the limiting resource (R), as a power function of body mass and exponential with temperature (Savage *et al.,* 2004). This means that the carrying capacity of a system decreases with increasing temperature (body temperature in homoiotherms or environmental temperature in poikilotherms) and body size. This may be the reason why the carrying capacity for warm-blooded birds in winter is smaller than for cold-blooded fishes. The theory is still at its initial stage and the fit contains several sources of variance, which make its predictions for the present unreliable for individual-based modelling. However, it offers a consistent framework for ecosystem wide predictions and provides insight into the regulation of food web processes.

From the previous paragraphs, it is clear that a fixed estimate for a species-based carrying capacity in a highly variable environment like an estuary is unrealistic. Further steps taken to determine the carrying capacity for demersal fishes in estuaries should account for body size, ambient temperature, possible competitors (e.g. shorebirds and crustaceans) and feeding strategy of the target species. In particular, the relation between benthic prey density and prey availability needs more attention in order to construct a realistic foraging model as available for pelagic zooplanktivorous species (e.g. Maes *et al.,* 2005a).

4. How important are abiotic factors as estimators of the habitat quality of an estuary?

The availability of suitable prey items is probably one of the two most important factors determining habitat quality for juvenile fishes, the other factor being predation risk (Gibson, 1994). The size classes of flounder we modelled probably reached a size refuge for predation and consequently, habitat selection should be mainly determined by food availability and abiotic factors. If food is not limiting, which is thought to be the rule in estuarine nurseries, then abiotic factors determine the habitat selection of fishes. The predominance of temperature as a regulator of growth and hence habitat quality was demonstrated in chapter 5, where we were able to describe the growth of flounder in an estuarine environment, solely based on temperature. The growth of flounder in the Ythan estuary (Scotland) was modelled using temperature measurements of a single location in the estuary. We assumed that the population was resident and didn't migrate between the sea and the estuary or between different habitats in the estuary. One may question whether this is realistic for a facultative catadromous species like flounder. A large part of the flounder population moves into deeper coastal waters during winter and 0-group flounder are known to migrate into the freshwater reaches of estuaries (Summers, 1979; Kerstan, 1991). In both situations, they experience different temperature regimes, which probably influence their growth rate. It would therefore be more appropriate to use a dynamic state-variable model (Clark and Mangel, 2000). In dynamic modelling, the fish are allowed to respond to changes in their environment in order to maximize their fitness. In the majority of current applications of bioenergetics models it is assumed that fish choose habitats based on maximization of energy gain. However, the growth rate potential of an environment based on bioenergetics estimates does not always effectively predict fish growth and distribution (Tyler and Brandt, 2001). The authors attribute this discrepancy between predicted and observed patterns to the lack of appropriate habitat selection submodels in individual-based spatially-explicit models. If fish choose habitats based on a hierarchy of variables (e.g. temperature over food) then the application of bioenergetics models without allowing for such a hierarchy of choice can lead to erroneous conclusions (Wildhaber and lamberson, 2004).

Because of the specific nature of estuaries, other abiotic factors like oxygen concentration and salinity also contribute significantly to the quality of fish habitats. The salinity gradient and the fluctuating oxygen levels constitute a major challenge for the species that have to cope with these conditions. While salinity variation mainly determines the distribution of stenohaline species, euryhaline species like flounder are probably less affected. Furthermore, habitats that are characterized by high fluctuating salinities may even yield some advantage to tolerant species by excluding competitive interactions with less tolerant species. A factor that is usually not taken into account when evaluating the habitat quality for fishes is the distribution of parasites. The parasite community of flounder is known to change along a salinity gradient (Schmidt *et al.,* 2003). Möller

(1978) considered stenohalinity of parasites and their hosts as the main reason for a natural reduction in the parasitic fauna in brackish water. Ectoparasites are directly affected by low salinities, whereas in digeneans it is the lack of molluscs that serve as intermediate hosts. Although further information is lacking, migration into freshwater may be an adaptation to reduce parasite load and optimize associated fitness traits.

In highly urbanised estuaries, the combination of high nutrient loads from untreated sewage effluents and low river runoff in summer may seasonally cause hypoxic or even anoxic conditions. The recent history of the Scheldt estuary is characterized by pollution and eutrophication. Particularly in the Zeeschelde anoxic conditions were regularly observed in the seventies. The situation improved noticeably due to wastewater treatment, but low oxygen concentrations still persist around the mouth of the Rupel. The results of our spatially-explicit habitat model (Chapter 6) show that the low oxygen concentrations limit the migration opportunities of flounder in the estuary. In summer, hypoxic conditions prevent the upstream migration to the freshwater reaches, where the model predicts optimal growth conditions. The model further suggests that flounder may use the freshwater zone to optimise their growth rate, as a result of the higher ambient temperatures. However, if temperature would be the dominant trigger for upstream migration, it remains unclear why flounder is the only flatfish adapted to use the freshwater reaches. Beaumont and Mann (1984) suggested that competition for food and space might be a possible stimulus for flounder to move upstream. Before we answer this question, we should extend the model with a foraging compartment to account for food availability and do the same exercise for possible competing species.

The model makes predictions about the habitat selection of flounder in the entire estuary. However, we were not able to reliably falsify our results with field data on the distribution of flounder in the estuary. The lack of a consistent monitoring programme for the entire estuary makes it very difficult to give a well-founded management advice concerning conservation programmes for migrating species. Scientifically, the fish compartment of the Scheldt estuary is running (far) behind the microbial, planktonic, macrobenthic and bird compartments of the estuarine food web. To catch up, cross-border cooperation is needed and sampling programmes have to be coordinated. In addition, the sampling effort in the freshwater zone should be extended spatially as well as temporally if we want to scientifically guide the restoration of the fish community in the Zeeschelde now that the increased capacity for sewage treatment is available in the Brussels region.

Appendix 7.1 - Details of the calculation of the fluxes and compartments in the intertidal food web. For conversion from carbon to energy, the values 1 g C = 12 kcal = 50.28 kJ were used. Unless mentioned differently, all formulas are taken from Wilson and Parkes (1998).

Compartment	**Biomass**	**Consumption**	**Respiration**	**Production/input**	**Metabolic wastes**
Organic carbon (OC)	Herman *et al.* (2000): Weight % OC in top 1 cm = 0.64 % sediment gravity = 2.8 g cm^{-3}	/	Heip *et al.* (1995): Mineralization = 290 gCm^{-2} year^{-1}	Heip *et al.* (1995): Influx = 503 gCm^{-2} year^{-1}	Heip *et al.* (1995): Burial = 212 gCm^{-2} year^{-1}
Benthic algae (MFB)	Biomass (mg C) = 24.3 * Chl a (mg) + 29.3 Heip *et al.* (1995): 113 mg chlorophyll a m^{-2}	/	/	Heip *et al.* (1995): Production = 136 gC m^{-2} year^{-1}	/
Macrobenthos	Biomass of *N. diversicolor* (Nd) and *C. volutator* (Cv) calculated from Length-weight relationships (Zwarts and Wanink, 1993) Length data from chapter 4 Biomass (gAFDW m^{-2}) for Oligochaetes (Oli), *H. filiformis* (Hf) and *M. baltica* (Mb) from Seys *et al.* (1999) Energy values (cal gAFDW^{-1}) from Chambers and Milne (1979)	Respired energy (*R*) = 0.7 * assimilated energy (*A*) $A = 0.15$ * consumed energy (*C*) % dependence of MFB as food (rest = POC) Nd: 50 % Cv: 100 % Mb: 50 % Oli and Hf: 0 %	Respired energy (*R*) $\text{Log}_{10} R$ $= 0.367 + \log_{10} P$	Production (*P*) = mean energy content (kJ m^{-2}) of each species multiplied by *P:B* ratio $P{:}B = 0.525 * W^{-0.304}$	Faeces (*F*) $F = C - A$
Shrimps	Intertidal densities of *C. crangon* from Hostens, 2003 The components of the energy budget (C, R and F) were calculated for a shrimp of 30 mm	Consumed energy (*C*) $= R + G + U$ Assimilation efficiency = 85 %	Respiration (*R*) calculated from equation 8 in Taylor and Peck (2004)	Growth (*G*) calculated from data in appendix 1 from Taylor and Peck (2004): $0.572 * W(\text{g})^{0.56} * T$ (°C)	Excretion (*U*) calculated from Taylor and Peck (2004) $U = 20.9Jg^{-1} * R_{Ti} * R_{18°}^{-1}$
Fish	Fish densities on the mudflat were calculated from fyke catches in 2002-2004 (chapter 4) (Appendix 7.2)	The components of the energy budget were calculated using a bioenergetics equation. The mean length of each species in the catches is given between brackets. *P. flesus* (12 cm): Stevens *et al.* (2006) (Chapter 5) *S. solea* (8.5 cm): appendix 7.3 *C. harengus* (8 cm): Rudstam (1988) *D. labrax* (9.5 cm): appendix 7.3			
Birds	Monthly mean numbers of shorebirds on the mudflat of Groot Buitenschoor (1997-2003) provided by Natuurpunt (http://www.schorrenwerkgroep.be) Bird weights were obtained from http://www.bto.org/ Energy density: 6.5 kJ g^{-1}	Assimilated energy (*A*) (kcal bird^{-1} day^{-1}): $\text{Log}_{10} A$ $= 1.89 + 0.72 * \log_{10} W$ W = weight (kg) Assimilation efficiency = 85 %	Respired energy (*R*) (kcal bird^{-1} day^{-1}): $R = 0.5244\ W^{0.7347}$ W = weight (g)	$P = 0.79 * R - 1.055$ P = production ($\log_{10}$cal m^{-2} year^{-1}) R = respiration ($\log_{10}$cal m^{-2} year^{-1})	Faeces (*F*) $F = C - A$

Appendix 7.2 - Calculation of the fish density (# m^{-2}) from fyke catches on a mudflat.

Basic principle: We assumed that fishes are equally distributed in the water column on the mudflat and that their abundance in the fyke nets is proportional to the volume of water that flows through the fyke nets. In order to calculate the fish density on the mudflat, we have to multiply the abundance of fishes in the fyke with the volume of water passing through the net.

The total volume of water on the mudflat in front of the fyke net is divided in three compartments A, B and C (see bottom figure). When the water retreats from the mudflat during ebb, it passes through the vertical surface *Hm***Wf*. The fraction that goes through the fyke net is proportional to the height of the fyke net, relative to the height of the water column above the net, which changes during ebb. When the water level is equal to the height of the fyke net, all the remaining water (volume A) passes through the fyke net. In order to calculate the total volume of water filtered by the net, we have to add volume A and the fraction of B+C that passes through the fyke net.

The total volume of water on the mudflat in front of the fyke net decreases per second according to

$$Volume\ decrease\ (m^3\ \sec^{-1}) = \left\{\frac{Wf \times vebv \times vebh}{2} + Wf \times vebv \times Lm\right\} - \{Wf \times vebv \times vebh\} \times T = a_1 + b_1 \times T$$

Of this volume, only a fraction passes through the fyke net. The rest passes through the surface above the fyke net (*Hv***Wf*). The fraction (of B+C) passing through the fyke changes during ebb and is calculated as

$$Fraction = \frac{Hf}{Hm - vebv \times T}$$

This fraction is used to calculate the volume that is filtered through the fyke net:

$$Filtered\ volume = \int_0^T \frac{Hf \times (a_1 + b_1 \times T)}{Hm - vebv \times T}\, dT$$

which is integrated over the time *T* (sec) it takes for the water level to drop from high water (*Hm*) to the height of the fyke (*Hf*).

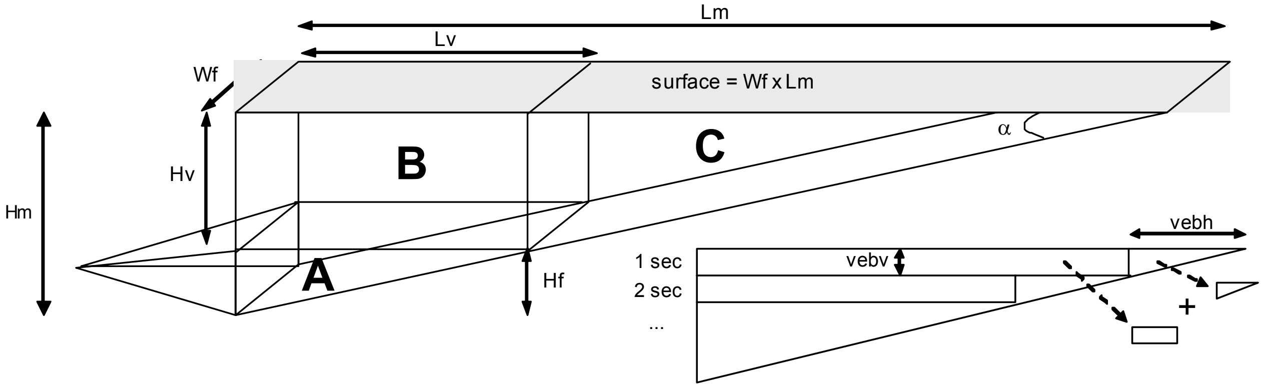
$$Filtered\ volume = \left| (b_2 \times T \times vebv - \log(Hm - vebv \times T)) \times a_2 \times vebv + \frac{\log(Hm - vebv \times T) \times Hm \times b_2}{vebv^2} \right|_0^T$$

with $a_2 = Hf * a_1$ and $b_2 = Hf * b_1$

The sum of this filtered volume and A, gives the total amount of water (m³) passing through the fyke net.

***Table A7.1**. Measurements and parameters used to calculate the volume passing through the fyke net (m^3 day^{-1}). The measurements are represented on the figure below.*

Width mudflat (*Lm*)	400 m	Volume B (*Lv***Hv***Wf*)	1171 m³
Tidal height at high water (*Hm*)	5.4 m	Volume C (*Hm***Lm***Wf*/2-A-B)	1391 m³
Height fyke net (*Hf*)	1.6 m	Time from high water (*Hm*) to low water in seconds (*T*)	6h 30min = 23400sec
Width fyke net (*Wf*)	2.6 m	Horizontal displacement of the tide on the mudflat in 1 sec (*vebh*)	$vebh = Lm\ T^{-1} = 0.017$ m
Height of the water column above the fyke net at high water (*Hv*)	3.8 m	Vertical displacement of the tide on the mudflat in 1 sec (*vebv*)	$vebv = Hm\ T^{-1} = 23 \cdot 10^{-5}$ m
Volume A (*Wf***Hf***Lv*/2)	247 m³	Total volume through fyke net (day^{-1})	2835 m^3



Appendix 7.3a - Parameters from the bioenergetics equations used to calculate the different components of the energy budget of fishes in the mudflat food web (for equation see appendix 7.3b). The activity multiplier (ACT) for seabass was calculated from the swimming speed function (equation 2) for striped bass (*Morone saxatilis*; Hartman and Brandt, 1995).

	flounder[1]	**herring**[2]	**sole**[1,3,4]	**Seabass**[5-9]
Consumption	*Eq.1*	*Eq. 1*	*Eq. 1*	*Eq. 1*
CA	0.186	0.642	0.186	0.302
CB	-0.202	-0.256	-0.202	-0.252
CQ	2	1	5	6
CTO	20	15	23	24
CTM	21	17	24	27
CTL	27	25	27.2	31
CK1	0.05	0.1	0.01	0.01
CK4	0.01	0.01	0.01	0.01
Respiration	*Eq. 3*	*Eq. 2*	*Eq. 3*	*Eq. 3*
RA	0.0178	0.0033	0.0178	0.0028
RB	-0.218	-0.227	-0.218	-0.218
RQ	2.5	0.0548	3	2
RTO	21	0.03	19.7	27
RTM	27	0	27.2	32
RK1		15		
RK4		0.13		
SDA	0.19	0.175	0.19	0.175
ACT	1.1	3.9	1.1	1.6
FA	0.17	0.16	0.17	0.15
UA	0.1	0.1	0.1	0.1
F+U+SDA (C)	0.443	0.419	0.443	0.41

[1] Stevens *et al.,* 2006
[2] Rudstam, 1988
[3] Lefrançois and Claireaux, 2003
[4] Sims *et al.,* 2005
[5] Hartman and Brandt, 1995
[6] Claireaux and Lagardère, 1999
[7] Jobling, 1994
[8] Person-Le Ruyet, 2004
[9] Pickett and Pawson, 1994

Appendix 7.3b – Abbreviations and equations used in the bioenergetics models for the fish compartment of the mudflat food web. The equations for the temperature dependence functions (1-3) were taken from the manual of *Fish bioenergetics 3.0* (Hanson *et al.,* 1997). Growth was calculated as: $G = C - (R + S + F + U)$. Further information about the different components of a bioenergetics model is given in chapter 5.

- **Consumption**

$$C = C_{\max} \cdot p \cdot f(T) \qquad C_{\max} = CA \cdot W^{CB}$$

where	C	specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$)
	C_{max}	maximum specific feeding rate ($g \cdot g^{-1} \cdot d^{-1}$)
	p	proportion of maximum consumption
	f(T)	temperature dependence function
	T	water temperature (°C)
	W	fish mass (g)
	CA	intercept of the allometric mass function ($g \cdot g^{-1} \cdot d^{-1}$)
	CB	slope of the allometric mass function (dimensionless)

Equation 1

$$f(T) = K_A \cdot K_B$$

$$K_A = (CK1 \cdot L1)/(1 + CK1 \cdot (L1 - 1)) \qquad K_B = (CK4 \cdot L2)/(1 + CK4 \cdot (L2 - 1))$$

$$L1 = e^{(G1 \cdot (T - CQ))} \qquad L2 = e^{(G2 \cdot (CTL - T))}$$

$$G1 = (1/(CTO - CQ)) \cdot \ln((0.98 \cdot (1 - CK1))/CK1 \cdot 0.02))$$

$$G2 = (1/(CTL - CTM)) \cdot \ln((0.98 \cdot (1 - CK4))/CK4 \cdot 0.02))$$

- **Respiration**

$$R = RA \cdot W^{RB} \cdot f(T) \cdot ACT \qquad S = SDA \cdot (C - F)$$

where	R	specific rate of respiration ($g \cdot g^{-1} \cdot d^{-1}$)
	W	fish mass (g)
	RA	intercept of the allometric mass function ($g \cdot g^{-1} \cdot d^{-1}$)
	RB	slope of the allometric mass function (dimensionless)
	f(T)	temperature dependence function
	T	water temperature (°C)
	ACT	activity multiplier (dimensionless)
	S	proportion of assimilated energy lost to SDA
	SDA	Specific Dynamic Action
	C	specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$)
	F	specific egestion rate ($g \cdot g^{-1} \cdot d^{-1}$)

Equation 2

$$f(T) = e^{(RQ \cdot T)}$$

$$ACT = e^{(RTO \cdot VEL)}$$

$$VEL = RK1 \cdot W^{RK4}$$

Equation 3

$$f(T) = V^X \cdot e^{(X \cdot (1 - V))}$$

$ACT =$ multiplier

$$V = (RTM - T)/(RTM - RTO)$$

$$X = (Z^2 \cdot (1 + (1 + 40/Y)^{0.5})^2)/400$$

$$Z = LN(RQ) \cdot (RTM - RTO)$$

$$Y = LN(RQ) \cdot (RTM - RTO + 2)$$

- **Egestion (F) and excretion (U)**

$$F = FA \cdot C$$

$$UA = UA \cdot (C - F)$$