33842

CHAPTER 1 INTRODUCTION, OBJECTIVES AND OUTLINE
OF THE THESIS

K. Hostens

Abstract. The thesis focuses on the nursery function of the Westerschelde and Oosterschelde estuaries for demersal fish and macro-invertebrate species. The main aim of the thesis is to provide a baseline about the higher trophic levels for future process studies in the Delta area. More specifically, both structural and functional patterns in several population parameters (density, biomass, growth, biodiversity, food and feeding behaviour) are investigated at community and species levels, and at different temporal (short-, mid- and long-term) and spatial (between and within estuaries) scales. This introductory chapter gives a general description of the epibenthic assemblages and a short overview of the factors on which the nursery function of a system depends. The study area is described and the major engineering works in the Delta area are summarized. An overview of the different sampling methodologies and of the available and used datasets is given. This chapter finishes with the main objectives and an outline of the thesis.

1.1 Introduction

Shallow coastal areas, and especially estuaries, are widely recognized as important nurseries for juvenile fish and macro-crustaceans, feeding areas for adults and migration routes for diadromous species (McHugh 1967, de Sylva 1975, Pihl & Rosenberg 1982, Haedrich 1983, Elliott *et al.* 1990, and Chapter 2-Add.2). Recently, the status of European estuaries and brackish habitats in relation to fish and macro-crustaceans has been thoroughly reviewed in a collaborative work from 18 laboratories across 11 countries, based on data from 26 estuarine systems (Elliott & Hemingway 2002). The contributions concerning the Westerschelde and Oosterschelde estuaries to this review, resulting from a FAIR concerted action (CT96-1634, *Commercial Fish in Estuaries – Priorities for Management and Research*), were partly based on data presented in this thesis.

Estuaries are characterized by a low diversity and dominance of only a few macro-invertebrate and juvenile fish species (McLusky 1989, Wootton 1992). The most abundant fish and macro-invertebrate species in estuaries are eurytopic, euryhaline, and present at high numbers during their early life history for different periods of the year. To assess the nursery function of the Westerschelde and Oosterschelde estuaries, both structural and func-

tional patterns have to be investigated, taking into account density dependent (*e.g.* competition, predation) and independent (environmental) factors (Blaber & Blaber 1980, Elliott & Taylor 1989, Marchand 1993, Gibson 1994). Therefore, information is needed on several biotic and abiotic compartments. The main forcing variables structuring the fish communities are given in Fig. 1.1. The present study is largely rooted in the multidisciplinary research on the Westerschelde and Oosterschelde. Both estuaries, but mainly the Westerschelde, are among the best-studied systems in Europe (and probably in the
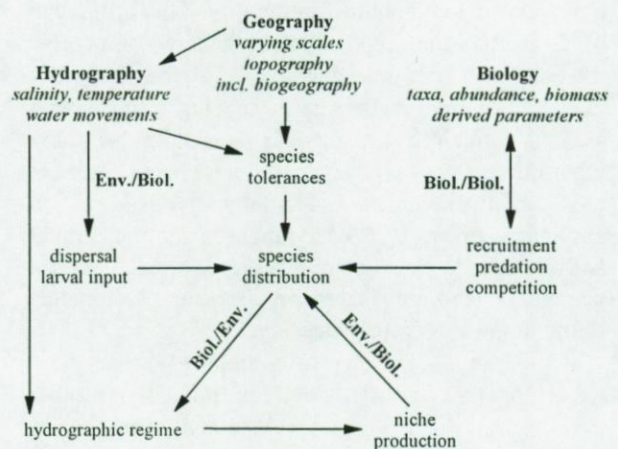

Fig. 1.1 Main forcing variables on structuring fish communities (from Elliott & Hemingway 2002)

world). One of the main reasons is the large anthropogenic pressure on both systems. The Westerschelde and Oosterschelde estuaries are part of the Delta area in the southwest part of the Netherlands. The human impact on this area is quite high: poldering for agriculture and industry, dykes and dams for safety and freshwater hold, dredging for the ever-growing shipping industry, commercial fisheries on demersal fish and shrimps in the Westerschelde and mussels and oysters in the Oosterschelde. All these activities lead to a quantitative loss of habitats for growing juvenile fish and macro-invertebrates. The direct consequences of the human impact, such as untreated organic waste loads, industrial pollution and fresh water and tidal reduction, contribute to the diminishing quality of the Delta area. This introductory chapter gives an overview of the study area and the major engineering works in the Delta area.

In their report on habitat structures and communities, Van Damme *et al.* (1999) described the research effort on fish in the Schelde estuary as fragmented, sampled by means of different methodologies, at different places and times, or only partly reported. Of course, to study the different aspects of a nursery, different sampling periods and methodologies are required. Moreover, long-term records of biological data are necessary to differentiate between natural changes in the ecosystem and those caused by humans (Wolfe *et al.* 1987). An overview is given on the available and (partly) used data, and on the different methodologies to sample different life stages of demersal fish and macro-invertebrates in the different subhabitats of the Westerschelde and Oosterschelde estuaries. Finally, the main objectives and the rationale of the thesis are given.

1.2 Description of the demersal fish and macro-invertebrate assemblages

In earlier studies the demersal fish and macro-invertebrate assemblages have been termed the epibenthos or epibenthic community. This group can be defined as the larger animals that live on or near the bottom to rest, hide, feed or reproduce. Pragmatically, all animals caught with a beam trawl, which are less efficiently caught near the bottom with any other device, are considered to belong to the epibenthos. Mainly juveniles and older individuals of fish and macro-invertebrates are caught in shallow coastal and estuarine areas. Today, we prefer to use the term demersal fish and macro-invertebrate assemblage, living in the epibenthic waterlayer.

Fish species typically belong to the Pleuronectiformes (flatfish), Gobiidae (gobies) and other Perciformes, Clupeiformes (clupeoids), Gadiformes (gadoids), Syngnathiformes (pipefish), Scorpaeniformes, and a number of other taxonomic groups.

Macro-invertebrates are much more abundant than the fish fauna in estuarine and shallow coastal areas (*e.g.* Pihl 1985, Bamber & Henderson 1994, Beyst *et al.* 2002). However, till the 1980s the macro-invertebrates were rarely integrated into fish studies (Chapter 2-Add.2). In earlier studies discussed in this thesis, only the four most conspicuous epibenthic invertebrates were taken into account (i.e. brown shrimp *Crangon crangon*, starfish *Asterias rubens* (only in the Oosterschelde), shore crab *Carcinus maenas*, and swimming or flying crab *Liocarcinus holsatus*). During later surveys, all macro-invertebrates were quantified, comprising different species from the echinoderms, caridean shrimps and prawns, brachyuran and anomuran crabs, and cephalopods.

Other invertebrate species are quite common in the beam trawl samples from the Oosterschelde, but these were not considered as part of the 'epibenthic assemblage', as they are either sessile or planktonic organisms. The following groups were not quantified: tunicates (a.o. *Styela clava, Ciona intestinalis* and *Ascidiella aspersa*), cnidarians (also in the Westerschelde, a.o. *Aurelia aurita, Chrysaora hysoscella* and *Cyanea lamarckii*), sea anemones (a.o. *Actinia equinea*), bivalves (*Mytilus edulis, Ostrea edulis* and *Crassostrea gigas*), gastropods (a.o. *Littorina littorea, Crepidula fornicata* and *Nucella lapillus*), polychaetes (a.o. *Aphroditae* and *Harmothoe* species), and nudibranchs (a.o. *Aeolidia papillosa* and *Elysia viridis*).

Older and/or mature fish only sporadically enter shallow coastal and estuarine areas. The thesis mainly focuses on juvenile fish, i.e. the O- and I-group, and the juvenile and adult stages of the macro-invertebrates. In the final synthesis, the (post)larval stages of the most abundant fish and macro-invertebrate species are taken into account as well, to give a complete overview of the seasonal and spatial distribution of the demersal fish and macro-invertebrate assemblage. Larvae and postlarvae of fish and invertebrates are more effectively caught with a hyperbenthic sledge, and are part of the mero-hyperbenthos. Together with the permanent hyperbenthos (mainly mysids and amphipods), they constitute the hyperbenthos. These small organisms usually live close to the bottom in the hyperbenthic waterlayer, at least during part of the day. See Mees & Jones (1997) for a review, and Beyst *et al.* (1999) for data on post-larval fish in the Dutch Delta.

1.3 The nursery function

Nurseries are defined as areas where juveniles aggregate, are spatially or temporally separated from the adults, and where their survival is enhanced through better feeding conditions, optimal growth and/or ref-

uge opportunities. Recruitment to the adult or subadult populations follows the emigration from these nurseries after attaining a well-defined length class (Pihl *et al.* 2002).

The nursery function of a system for juvenile fishes and macro-invertebrates is dependent on several factors. Firstly, the nursery function depends on the transport and retention efficiency of (post)larvae and juveniles towards and within the estuary. Larvae and/or postlarvae are attracted to the estuarine system, and either actively or passively find suitable habitats and protection from predators (*e.g.* van der Veer & Bergman 1986, Drake & Arias 1991, Jager 1999). For example, brown shrimp *Crangon crangon* are transported to the Westerschelde as zoea larvae, migrate into the brackish intertidal saltmarsh creeks shortly after metamorphosis to the postlarval stage, and recruit after a few weeks to the deeper regions of the estuary proper as juveniles (Cattrijsse *et al.* 1997).

Secondly, the nursery function is dependent on habitat availability, in relation to diversity, growth and survival of the juveniles. In trying to simplify our understanding of a nursery, the functional guild concept was developed (*e.g.*McHugh 1967, Elliott & Taylor 1989, Whitfield 1999). Fish can be grouped into bottom-dependence and substratum preference guilds, or into reproductive, feeding and ecological guilds, indicating the usage of the estuarine habitats by the fish and the importance of an estuary for fish (Elliott & Dewailly 1995). The different habitats of an estuary (*e.g.* subtidal - intertidal, soft – hard substrate, saltmarsh – seagrass – reed beds, tidal freshwater) are inhabited during different periods by different species and several life stages of fish and macro-invertebrates. Multivariate statistical techniques are widely used to unravel the spatial and temporal patterns in fish and macro-invertebrate assemblages in relation to the environment (*e.g.* Pihl 1986, Marshall & Elliott 1998, and Chapter 2-Add.2). Most studies showed that salinity and substratum/exposure were among the most important variables in structuring the epibenthic assemblages (*e.g.* Henderson 1989). Recently, a number of studies tried to relate single species presence and abundance to changes in environmental parameters (*e.g.* Attrill *et al.* 1999).

Thirdly, the nursery function is largely dependent on food availability. Estuaries are highly productive systems, so juvenile (and adult) fish and macro-invertebrates can find plenty of suitable prey organisms (*e.g.* Henderson *et al.* 1992, Moreira *et al.* 1992, Marshall 1995). In the Westerschelde estuary, two food chains have been demonstrated, a phytoplankton driven food chain in the mouth or marine part and a much more important detritus (and bacterial) based food chain in the brackish part (Hummel *et al.* 1988b, Soetaert & Herman 1995a, also Chapter 8-Add. and Chapter 9). The link between primary

producers and fishes and macro-crustaceans, is composed of the secondary trophic levels. These consist mainly of benthic (in- and epifaunal) and zooplanktonic/hyperbenthic organisms (*e.g.* de Sylva 1975, Hemingway & Elliott 2002).

1.4 Study area

1.4.1 The Dutch Delta

The thesis is mainly based on data from the Westerschelde and the Oosterschelde. Both estuaries are located in the southwest of the Netherlands (51°20'-51°41'N, 3°34' - 4°14'E), and are part of the so-called Dutch Delta area (Fig. 1.2). In this area, three major European rivers, the Rhine, Meuse and Schelde, enter the North Sea. Every chapter includes a short description of the study area, as they will be or have been submitted as such for publication in the international literature. In this introductory chapter, a short overview is given of the major engineering works and the geomorphology (including the more recent evolution) in the Southern Dutch Delta area, with a basic characterisation of the Westerschelde and Oosterschelde estuaries.

A definition of an estuary is given by Day *et al.* (1989): "an estuarine system exists of a coastal embayment, with a narrow connection to the ocean, and at least a temporal free connection with the terrestrial system." They distinguished 3 regions: (1) a turbid coastal area in the mouth of the estuary; (2) a mixed zone (the estuarine proper), characterized by a strong mixing of the water masses and strong gradients in physical, chemical and biotic components; (3) a fluvial zone (freshwater tidal), characterized by the absence of saltwater, but subject to the tides.

According to this definition, the Westerschelde, Oosterschelde and Voordelta area can be seen as estuaries *sensu latu*. However, a distinction between 5 types of 'estuaries' was made, ranging from real and estuarine deltas, over real estuaries, to estuarine and marine lagoons. A definition of an estuary *sensu strictu* was given by Pritchard (1967): "an estuary is a semi-enclosed coastal water body, which has a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage".

The Schelde valley was already colonized around 6000 B.C., but the formation of the Westerschelde only started between 800 and 1000 A.D. (de Mulder & van Strydonck 2000). Landclaim for agricultural reasons started around 1100 A.D. in the Dutch Delta, with a peak of poldering between 1500 and 1600 (Mol 1995). Only since 1870 the Westerschelde and Oosterschelde estuaries got completely separated (Antrop & van der Reest 2001). During the 20th century harbour construction, dyke re-
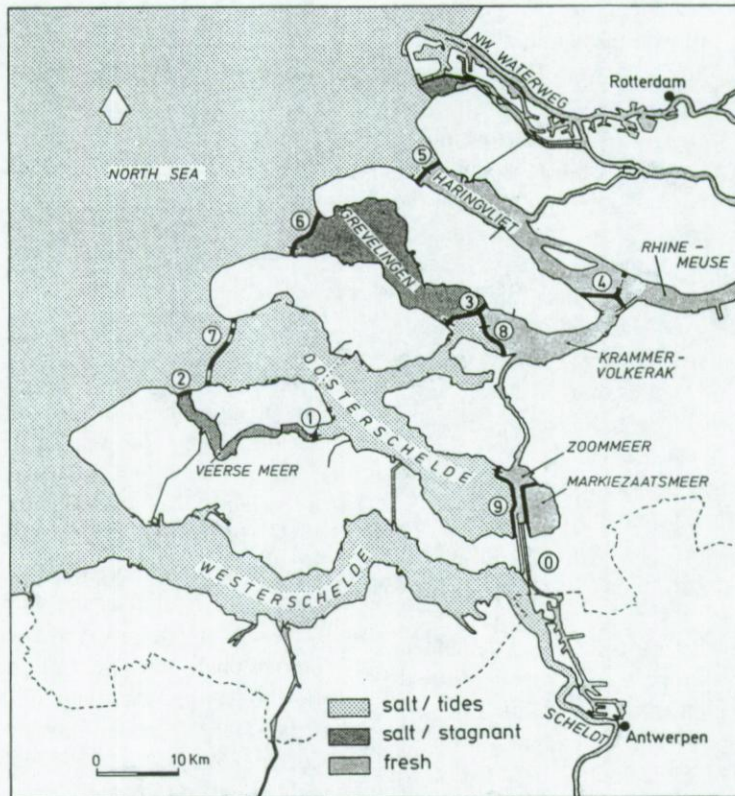
Fig. 1.2 The Dutch Delta area (SW Netherlands), with an indication of the major engineering works. 0 = Kreekrakdam (1867); 1 = Zandkreekdam (1960); 2 = Veersegatdam (1961); 3 = Grevelingendam (1964); 4 = Volkerakdam (1969); 5 = Haringvlietdam (1970); 6 = Brouwersdam (1971); 7 = Oosterschelde storm-surge barrier (1986); 8 = Philipsdam (1987); 9 = Oesterdam (1986). Zoommeer and markiezaatsmeer were separated in 1983 (taken from Nienhuis & Smaal 1994b)

enforcement and poldering were the main causes for landclaim. During the past two centuries 150 km² of marshes and mudflats around the Schelde disappeared (Mol 1995). After the catastrophic storm floods of 1953, the Dutch Delta area in the southwest Netherlands underwent dramatic changes as different sea arms were closed off. This resulted in the creation of freshwater, brackish and salt lakes, marine embayments and tidal deltas.

The engineering works in the Delta area started with the construction of compartmentalisation dams to reduce the tidal influence in the region. In 1960-61, the former estuary 'Veerse Gat' was closed (zandkreekdam and Veerse dam) and transformed into a stagnant brackish lake 'Veerse Meer', with a loss of 42 km² of estuarine habitat. The next compartmentalisation dams cut off the riverine influence of the Rhine and Meuse in the former 'Grevelingen' (1964, Grevelingendam) and 'Oosterschelde' (1969, Volkerakdam) estuaries, turning both systems into marine bays. Next, the former estuaries 'Haringvliet' (1970, Haringvlietdam) and 'Grevelingen' (1971, Brouwersdam) were closed off from the sea and transformed into a non-tidal freshwater system and the stagnant salt lake 'Grevelingenmeer' (with an artificial flow regime through sluices), respectively. This resulted in a total loss of 65 and 140 km² estua-

rine habitat (Visser 1995). In 1986, the storm-surge barrier in the mouth of the Oosterschelde reduced the tidal range and tidal volume, with a loss of 75 km² of intertidal habitat (Nienhuis & Smaal 1994b). The last Delta works included the construction of two dams (1986, Philipsdam; 1987, Oesterdam), and the creation of two freshwater lakes ('Volkerak/Zoommeer' and 'Markiezaatsmeer'), with a loss of 83 and 21 km² estuarine habitat, respectively (Wanningen & Boute 1997, Haas 1998). With the reduction of the freshwater input to a minimum, the former Oosterschelde estuary was transformed into a marine bay.

As a result of the Delta works, the tidal currents at the seaward side of the dams were largely reduced. The tidal gullies in front of the former estuaries were filled and new sandbanks were formed, leading to the creation of marine tidal deltas. The formation of the deltas is mainly induced by ebb-tidal currents (Louters *et al.* 1991). This dynamic area is called the 'Voordelta', and stretches from the 'Nieuwe Waterweg' in the north to the mouth of the Westerschelde in the south, with a marine boundary 10 to 15 km seaward from the coastline, arbitrarily defined by the depth contour of 10 m below mean tidal level (MTL, as defined for Amsterdam). As such, the Voordelta is composed of the ebb-tidal deltas of the former Oosterschelde, Grevelingen and
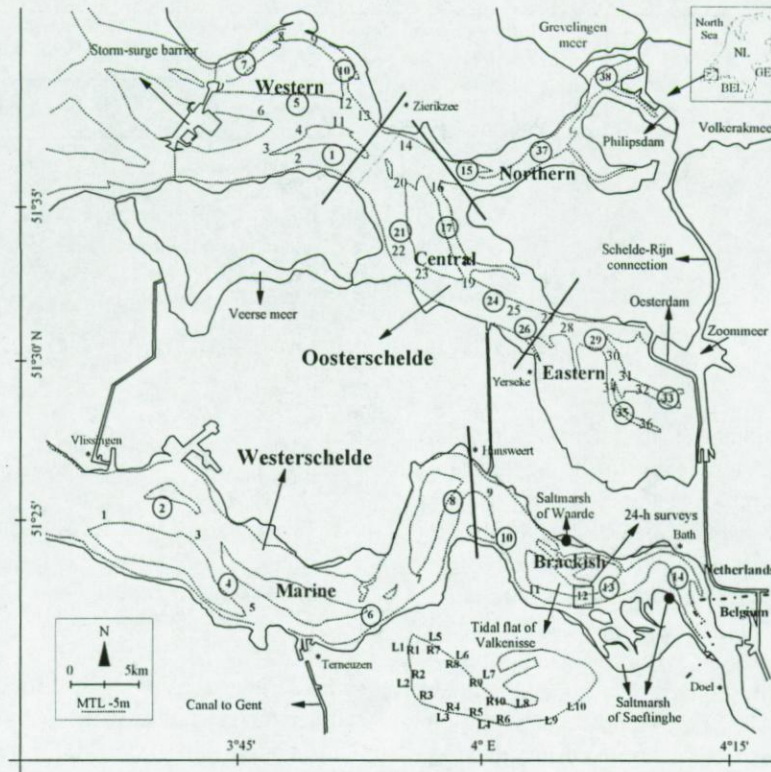
Fig. 1.3 The Westerschelde and Oosterschelde estuaries, with an indication of the sampling locations during the different surveys. See text and Table 1.2 for an explanation

Haringvliet estuaries, which have lost their estuarine 'mouth' character.

The Westerschelde remained open at both the river and sea side, for international shipping purposes (Nienhuis & Smaal 1994a). The complementary Sigma works (started in 1977) in the Schelde estuary, mainly consisted of dyke elevation and reenforcement, and the creation of 13 controlled inundation areas in the upper part of the estuary (the Zeeschelde) and its major tributaries (Rupel, Durme and Dender) (Van Damme & Meire 2001). In 1994, 75 % of the dyke works were completed and most inundation areas were constructed. The consolidation of almost all borders by concrete dykes inhibits the natural processes of erosion and sedimentation, and leads to fixation of the main subtidal channel (Mol 1995). According to both definitions of an estuary, only the Westerschelde can be regarded a true estuary.

1.4.2 The Westerschelde estuary

The Westerschelde consists of the lower and middle parts of the Schelde estuary and covers 310 km² (Fig. 1.3). The Westerschelde stretches along 55 km from the mouth (arbitrarily situated near Vlissingen, 5000 m width) to the Dutch-Belgian border (near Bath, 350 m width), and can be divided into two subareas near Hansweert: the western (marine) and eastern (brackish) part. The tidal zone upstream the border is

called the Zeeschelde (105 km long till Gent and a surface of 44 km²), which can be divided near Antwerp into the 'lower' and 'upper' Zeeschelde.

The Westerschelde is characterized by a marked salinity gradient (range 4-32 psu during the studied period). It is a well-mixed water body, and the residence time of the water is about 120 tidal cycles in the brackish zone and 10 to 15 days in the most seaward region (Soetaert & Herman 1995b). Salinity zones in the estuary remain relatively stable and are maintained in more or less the same position throughout a tidal cycle, but can shift over a few km between seasons (Heip 1989a). River discharge is largely dependent on rainfall, and highest during winter (on average 180 m³ s⁻¹) and lowest in summer (60 m³ s⁻¹) (Baeyens et al. 1998). The Westerschelde is a macrotidal estuary, with an average tidal amplitude of 3.8 m near Vlissingen and 4.9 m near Bath (Claessens 1988). Maximum ebb and flood current velocities vary between 1 and 1.5 m s⁻¹ at average neap and spring tides, respectively (recalculated from Anonymous 1992).

Turbidity is high, with 7.5 10⁵ tonnes yr⁻¹ of fluvial fine sediments and 9 10⁴ tonnes of marine suspended matter entering the system, which accumulate in the maximum turbidity zone in the Lower Zeeschelde (Anonymous 1998, Baeyens et al. 1998). The Westerschelde is a nutrient-rich system. The ongoing discharge of untreated wastewater through the Rupel and the Zenne, is the main source of high organic loads in the Schelde estuary. This leads to
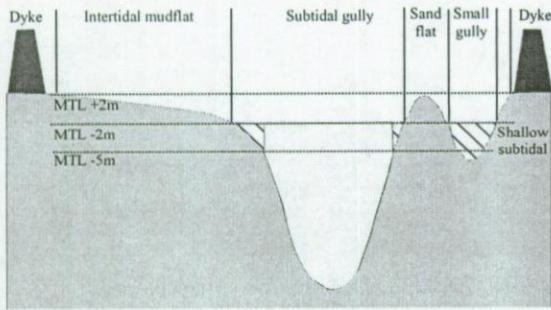
Fig. 1.4 Schematic drawing of the different habitats in an estuary

Table 1.1 Areal extent of the different subhabitats in the Westerschelde and Oosterschelde (km²)

Subhabitat	Westerschelde[a]	Oosterschelde
Tidal freshwater	(30)	
Reed beds	(5)	
Saltmarsh	25	6
Intertidal soft substratum	83	68
Intertidal hard substratum		11
Subtidal soft substratum	170 +32[b]	223
Subtidal hard substratum		1
Subtidal seagrass beds		1
Biogenic reefs		41
Total surface	**310 (+35)**	**351**

[a] values between brackets are part of the Schelde estuary but not of the Westerschelde
[b] + shallow subtidal area

heterotrophic respiration due to intense microbial activities, and oxygen deficiency in the upper estuary, mainly during summer (Heip *et al.* 1995, Van Eck *et al.* 1998). However, in the Westerschelde the water column is relatively well oxygenated, with concentrations of dissolved oxygen seasonally changing between 6 and 10 mg.l^{-1} (Chapter 5). Industrial pollution is still very high in the Schelde estuary. Micropollutants (mainly bound to suspended solids), like heavy metals, PAHs, PCBs and organochlorine pesticides, show a decreasing trend during the last decade, but concentrations are still elevated, both in the water column and in the sediments throughout the estuary (Van Zoest & Van Eck 1990, Anonymous 1998).

The Westerschelde is characterized by multiple channels (average depth 15-20 m below MTL) surrounding large intertidal flats, bordered by mudflats and saltmarshes (Van Maldegem *et al.* 1993). A schematic drawing of the different habitats in an estuary is given in Fig. 1.4. The division between the subtidal gullies and intertidal flats and marshes lies around mean low water (MLW or MTL –2 m). The transition zone from subtidal to intertidal can further be divided into 'shallow' (MTL –5 m to –2 m) and 'intertidal' (MTL –2 m to +2 m) water masses (Mol *et al.* 1997). The saltmarshes are intersected by several intertidal creeks of different sizes. The main shipping channel actually exists of successive ebb-dominated gullies, while the smaller side channels are flood-dominated.

The Westerschelde forms an important connection between the North Sea and 4 major harbours: Vlissingen, Terneuzen, Antwerpen en Gent (5-8 10⁴ ship movements per year). To maintain (and deepen) the main channel, the dredging intensity is very high, up to 8 10⁶ m³ per year (Vroon *et al.* 1997). Due to this continuous dredging, shallow subtidal areas and intertidal mudflats (mainly in the brackish part) disappear, while the extent of deep subtidal areas and high sandflats increases (Mol 1995). Moreover, about 100 10⁶ m³ of sand has been extracted from the Westerschelde since 1950, which may play a determining role in the morphological development of the estuary on a long time scale (100 years) (Vroon *et al.* 1997). Disposal of the dredged material leads to a

gradual increase in tidal elevation of flats and saltmarsh creeks, also with a subsequent loss of intertidal habitat. Pihl *et al.* (2002) defined 9 subhabitats of importance for estuarine fish. The areal extent of the different habitats in the Westerschelde is given in Table 1.1. The subtidal surface area amounts to 130 km² in the marine part and 40 km² in the brackish part. The subtidal is characterized by sandy sediments: median grain size 330 ± 97 μm in the marine part and 240 ± 55 μm in the brackish part (Chapter 5). The intertidal covers 35% of the total surface area, with 49 km² sandflats and 33 km² mudflats (Anonymous 1998). Another 32 km² is allocated to shallow subtidal water. Several smaller sandflats got aggregated to larger entities, and have steeper borders than during the 1960s (Mol *et al.* 1997). The lower parts of the intertidal are mostly poor in silt concentration, while the upper parts are characterized by high silt concentrations. The high intertidal part of the brackish sandflat of Valkenisse had a mixed sand-silt sediment, with a median grain size 168 ± 40 μm and an average concentration of 10 % silt (Chapter 8). Most of the saltmarsh surface area is part of one of the largest European saltmarshes 'Verdronken Land van Saeftinghe' (25 km²).

Primary production is partly derived from phytoplankton (*e.g.* diatoms, dinoflagellates) and microphytobenthos (mainly intertidal benthic diatoms), although annual gross bacterial production exceeds the net primary production, even in the marine part (Goosen *et al.* 1997). Zooplankton (mainly copepods) and hyperbenthic organisms (mainly mysids and amphipods) are present in high numbers in the subtidal (*e.g.* Mees *et al.* 1993b, Soetaert & Van Rijswijk 1993). Meiobenthic (nematodes) and macrobenthic organisms (mainly bivalves, polychaetes and amphipods) are abundant in the intertidal (*e.g.* Ysebaert *et al.* 1993, Steyaert *et al.* 2001). The

whole estuary is of international importance for several life stages of different bird species (*e.g.* Ysebaert 2000). Recently, the number of sea mammals (mainly seals) increased again to some 20 individuals (Witte *et al.* 1998). At several places in the Westerschelde commercial fisheries exist, mainly on sole and plaice in the delta (Vlakte van de Raan), on shrimp in the subtidal and on cockles on the intertidal flats throughout the Westerschelde. Also, a small-scale fishery on eel and sprat exists in the Zeeschelde. Recreational shipping and fishing are of minor importance, and mainly take place in the mouth near Vlissingen (Anonymous 1998).

More details on the morphological, physical, chemical and ecological properties of the Westerschelde estuary are given in Hummel *et al.* (1988a), Meire & Vincx (1993), Heip & Herman (1995), Anonymous (1998), and Van Damme *et al.* (1999).

1.4.3 The Oosterschelde estuary

The Oosterschelde is a marine bay with a total surface area of 350 km² (Fig. 1.3). The Oosterschelde is directly connected with the Westerschelde through a channel between Hansweert and Yerseke, and indirectly through sluices in the Zoommeer. The distance form the storm-surge barrier in the mouth to the Oesterdam in the east and to the Philipsdam in the north equals 40 km. The Oosterschelde can be divided into four subareas: the western part in the mouth, downstream from the Zeeland Bridge, the central and eastern (or basin) parts divided near Yerseke, and the northern part covering the Keeten-Mastgat area (or Noordelijke Tak).

After the engineering works, typical estuarine gradients have disappeared. The mean freshwater load dropped from 70 to <20 m³ s⁻¹, leading to a high and stable salinity of 30-34 psu (Haas 1998). The mean tidal volume decreased with 30% to 900 10^6 m³, the tidal amplitude near Yerseke is 3.3 m, and the maximum current velocity is 1 m s⁻¹ (Oosterlaan & Zagers 1996). The residence time of the water is 10-100 days, leading to high sedimentation of organic matter and high water transparency (Nienhuis & Smaal 1994b). The Oosterschelde is a nutrient-poor (oligotrophic) system. Concentrations of micropollutants in the water column are generally low, and polluted sediments of the harbours have largely been treated (van Berchum & Wattel 1997). Dissolved oxygen concentrations range between 7 mg l⁻¹ in summer and 10 mg l⁻¹ in winter-spring (Chapter 5).

The Oosterschelde is characterized by multiple tidal channels, mudflats and large intertidal sandy shoals. Due to a reduced tidal volume, the Oosterschelde changed from a sand-exporting to a fine sediment-importing system (ten Brinke *et al.* 1994). No dredging is necessary, although there is a high commercial shipping activity (5 10^4 ship movements

per year) mainly on the north-south connection through the Oosterschelde. The subtidal channel has a so-called 'sediment hunger', i.e. the need of 500 10^6 m³ of sand to adjust the channel surface to the reduced current velocities. Erosion of the intertidal area has been predicted to be an ongoing process with a reduction of 1.5 % per 5 years (van Berchum & Wattel 1997). The subtidal surface area amounts to 223 km² of soft sediments and only 1 km² of subtidal seagrass beds and hard substratum each (Pihl *et al.* 2002, Table 1.1). The subtidal sediment mainly consists of sand with a median grain size of 187 ± 37 μm (and on average 12 ± 9 % silt), except in the northern part where the sediment is much finer (median 45 ± 14 μm and silt concentration 57 ± 7 %) (Chapter 5). The intertidal area covers 118 km² with 58 % soft sediments, 33 % biogenic reefs and 9 % hard substratum. The latter is mainly covered by brittlestars, ascidians and sponges (Leewis *et al.* 1994). Saltmarshes suffered most from the engineering works, with the total surface area being reduced from 17 to 6 km² (Nienhuis & Smaal 1994b).

Primary production in the Oosterschelde is primarily derived from phytoplankton (including *Phaeocystis* blooms) subtidally and microphytobenthos intertidally (Wetsteyn & Kromkamp 1994, de Jong *et al.* 1994b). Meiobenthic nematodes are mainly present intertidally, meiobenthic and zooplanktonic copepods subtidally (Smol *et al.* 1994, Bakker & van Rijswijk 1994). Hyperbenthic organisms (mainly ctenophores and crab larvae) are abundant in the subtidal (Chavatte 2001). Macrobenthic densities (mainly gastropods, oligochaetes and polychaetes) are highest intertidally, macrobenthic biomasses (mainly oysters and mussels) are highest in the shallow subtidal (Stikvoort 1997). Macrophytes (mainly green macro-algae) are found both intertidally and subtidally (van Berchum & Wattel 1997). The Oosterschelde is one of the most important bird sites within the Delta area (Meininger *et al.* 1997). A small number of seals (20 individuals) is found mainly on the intertidal flats in the western part (van Berchum & Wattel 1997). The extensive flats and the surrounding shallow subtidal areas in the Oosterschelde are especially used for shellfish farming. The intertidal areas are important for the exploitation of cockles, while after the engineering works the shallow subtidal areas became important for the farming of oysters and mussels. The high densities of these macrobenthic suspension feeders and their feeding activity, result in a dominant and potentially controlling role in the main nutrient fluxes in the Oosterschelde (*e.g.* Herman & Scholten 1990). Recreational shipping and scuba-diving are largely extended. The commercial (fish) fishery is limited, and recreational fishing seems to decrease (van Berchum & Wattel 1997).

More details on the morphological, physical, chemical and ecological properties of the Ooster-

schelde estuary are given in Nienhuis & Smaal (1994a) and van Berchum & Wattel (1997).

1.5 sampling methodology

The sampling strategy depends on the survey objectives, the logistics and restrictions, substratum and habitat type, the hydrodynamic regime, the spatial and temporal coverage, and the life stage and distribution in the water column of the biota, all interrelated with net efficiency (Hemingway & Elliott 2002). Several authors have summarized the methods required for sampling fish assemblages or the associated factors required to interpret fish data. A complete overview of 'all' sampling techniques for different life stages and different estuarine habitats, is given in Hemingway & Elliott (2002).

Most of the thesis is based on data gathered in the subtidal with a 3-m beam trawl, equipped with a fine-meshed net (5x5 mm). Again, as most chapters will be published in international journals, a 'material and method' chapter is included in every chapter, although the information on sampling is mostly limited. Moreover, in the last chapter some extra material has been used from other studies (*e.g.* research on hyperbenthos and saltmarshes). Therefore, a complete overview of the sampling methodologies used (biotic and abiotic) and a short discussion on net efficiency is given in this introductory chapter.

1.5.1 Subtidal sampling

Demersal fishes and mobile macro-invertebrates are usually caught with a beam trawl, both for commercial and scientific purposes. The net mouth is kept open by a beam, carried by two triangular 'shoes', which run over the seabed. For catching the juvenile fauna a 3-m beam trawl was used (Fig. 1.5). One tickler chain and a chain in the ground rope of the net are attached between the runners to enlarge the net efficiency (see further). In most cases the beam trawl was equipped with a 6-m long small-meshed net, i.e. mesh-sizes of 5x5 mm (10 mm stretched) or 6x6 mm in the cod-end (the last 2 m of the net). During the earliest surveys (mainly in the Oosterschelde before 1986), a mesh-size of 10x10 mm has been used, as well.

Many sledge types have been designed to sample the larger 'planktonic' organisms immediately above the bottom. The post(larval) stages of both fishes and macrocrustaceans (together with the preferred prey of the juveniles), which live in the lowest metre of the water column, are most efficiently sampled with a hyperbenthic sledge. In the Westerschelde and Oosterschelde a simple device was used (Fig. 1.6), consisting of a metal frame (1 m width), mounted on gliders, with 2 fine-meshed nets
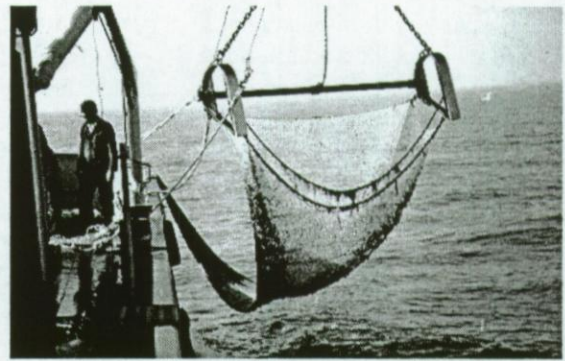

Fig. 1.5 A 3-m beam trawl with a small-meshed net, operated from the R.V. Luctor

(length 4 m, mesh 1x1 mm, total opening 0.8 m²). More details on this sampling methodology and the hyperbenthic communities of the Westerschelde are given in Mees (1994).

The beam trawl and hyperbenthic sledge were operated from the RV Luctor (34 m, 500 Hp) from the Centre for Estuarine and Marine Ecology (CEME, Yerseke, NL). All samples in the subtidal habitat of the Westerschelde and Oosterschelde were taken at the border of the main channel at an average depth of 13 ($\pm$ 3) m (range 7-21 m) below mean tidal level. Sampling was done with (in front of) the tidal currents, at a towing speed of approximately 2.3 m s^{-1} (4.5 knots) and over a distance of 1000 m per sample. Sometimes the distance was less to prevent clogging or tearing of the nets by storm-torn macrophytes, oysters or mud in the Oosterschelde, and mud or stones in the Westerschelde. All samples were taken during daytime except for the 24-hour cycle.

For completeness, it should be stated that several trials were made to sample upstream the Dutch-Belgian border with the beam trawl, but gear loss was so frequent (due to rubbish and ship wrecks) that no results can be reported. However, several researchers from the Laboratory for Aquatic Ecology (Catholic University Leuven) have been collecting fish and macro-crustaceans from the filtration devices in the cooling water intakes of several powerstations in the upper part of the estuary. More details on this sampling methodology and the fish community of the Zeeschelde are given in Maes (2000).
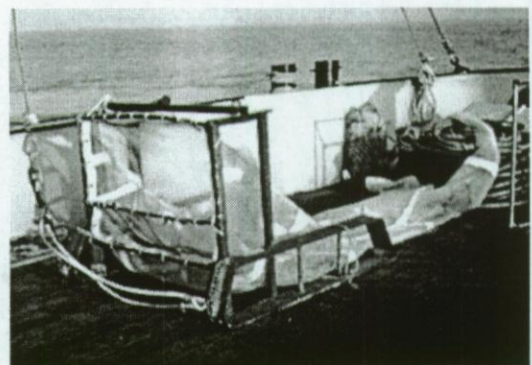

Fig. 1.6 A simple hyperbenthic sledge with two 1 mm² nets

1.5.2 Intertidal sampling

In the Westerschelde, the brackish intertidal sandflat of the Valkenisse-Ossenisse complex has been investigated by means of 2-m beam trawls. The lower intertidal (on average MTL –3 m) was sampled with the same 3-m beam trawl in the same way as in the subtidal. In the upper part of the intertidal (on average MTL –1 m), the fish and macro-crustaceans were sampled with a 2-m beam trawl, equipped with a small-meshed net (length 4m, mesh 5x5 mm) and 1 tickler chain. This sampling device was operated from the dinghy Riekus (7 m, CEME) at an average speed of 0.8 m s^{-1} (1.5 knots), over a distance of 800 m per sample. Sampling was limited to a 4-hour period around high tide.

On four intertidal flats in the Oosterschelde, samples were taken with a 2-m beam trawl. As these data were mainly used in a report so far (Hostens *et al.* 1994), no further details are given here.

The intertidal fish fauna from the Oosterschelde has been monitored for a number of years by means of 3 fyke nets (close to the dykes) and a weir or trap (near an intertidal flat). These are passive sampling techniques, where fykes are conical-shaped small-meshed nets, with a number of chambered one-way funnels, mounted on metal rings (Fig. 1.7). Traps work more or less the same way, but consist of a long 'leader' net (>100 m long) mounted on stakes, which guide the fish into one or two larger, fyke-like chambers. These samples were gathered by commercial fishermen, and initially worked out by Bureau Waardenburg (Culemborg, NL) (Meyer 1989).

A small stow net (length 5 m, opening 1 m², mesh 1 mm²) mounted on a metal frame, has been operated from a bridge in several intertidal saltmarsh creeks in the brackish part of the Westerschelde (Fig. 1.8). This technique is comparable with fyke nets. The net was placed on the creek bottom against the tide to catch the migrating nekton fauna, and emptied every hour as long as water was present in the creeks. More details on this sampling device and the nursery/refuge function of the intertidal saltmarsh creeks are given in Cattrijsse (1994).
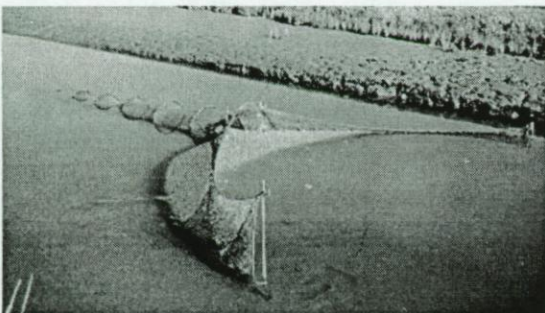

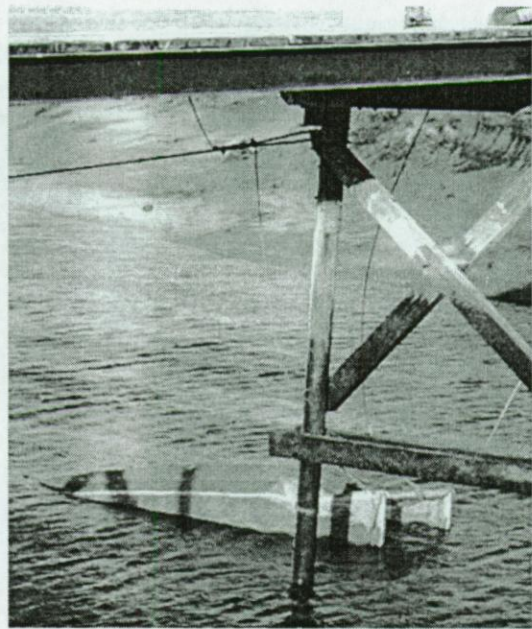Fig. 1.7 A fyke net, used in the intertidal

Fig. 1.8 A modified stow net, operated from a bridge in an intertidal saltmarsh creek

1.5.3 Net efficiency

The estimates of all population parameters are subject to various sources of bias. Net efficiency, or the proportion of fish caught in relation to the total available fish that can be caught, is a major source of uncertainty (Kjelson & Colby 1976). Few studies have assessed net efficiency thoroughly, as catch efficiency is dependent on the biotic component aimed at, the size and morphology of the target species, gear and habitat type, environmental conditions, manipulation of the sampling device, etc. (Hemingway & Elliott 2002). For most sampling devices net efficiency has never been investigated. Therefore, a net efficiency of 100 % is assumed for both the hyperbenthic sledge and the stow net (see Mees & Jones 1997 and Cattrijsse 1994 for more details).

On the other hand, beam trawls seem to have a low and variable net efficiency (Rozas & Minello 1997). Beam trawls are generally accepted to catch 20 to 33 % of the available fauna (Kuipers 1975, Elliott & Taylor 1989). Fish can escape from a beam trawl in four ways: through the meshes, underneath the ground rope, over the beam, and sideways (Kuipers 1975). Escapement through the meshes will be lower for larger individuals and for species with ornamental projections or spines (like most macro-crustaceans). On sandy bottoms, escapement under the gear can be limited by using one or more tickler chains. The tickler chain and the ground rope are longer than the beam to disturb the fishes and invertebrates before being covered by the net. Fast swimmers and larger fish can be expected to be able to avoid a small beam trawl by moving up or sideways (see Chapter 7-Add.).

In a number of surveys presented in this thesis, several parallel hauls were taken per sampling point (see further). Multivariate analyses always showed a high similarity between the 'replicate' samples, as they always clustered together (*e.g.* Hostens *et al.* 1993, Hostens *et al.* 1994, Verbeke 1994). This partly shows that the efficiency of a beam trawl does not vary much on sandy bottoms.

In conclusion, it is either impossible or too labour-intensive to calculate actual densities for every size of every species in every sample. The densities reported in this study are therefore to be considered as rough estimates. Although, a net efficiency of 20 % for all size classes of all fish and macro-invertebrates caught with a 3-m beam trawl, may be something of a wild guess, it is believed that it will give better population estimates, than assuming 100 % efficiency.

1.5.4 Environmental variables

Environmental information is important to explain the structure and function of biotic assemblages. Of course, the collection of a whole range of environmental data is expensive and time consuming. Salinity (psu), temperature (°C), dissolved oxygen (mg l^{-1}) and turbidity (m^{-1}) are believed to be the master controlling factors for fish assemblages (see Hemingway & Elliott 2002). The first 3 variables were measured approximately 1 m above the sea bottom with a CTD-sampler (Conductivity, Temperature, Depth). Turbidity was calculated as the reciprocal of secchi disc depth (light extinction). Moreover, sediment samples have been taken a few times in the different systems with a van Veen grab. The median grain size and silt concentration were measured with a Coulter LS Particle Size Analyser.

1.6 Overview of the available data and surveys

The present study is based on different large datasets, and several people have been working on part of the data. Table 1.2 gives an overview on all available data, though not all of them were used for the thesis. Some data were only published in reports, others were only used in the papers given as addenda. Most of the data have been used for several poster and oral presentations at international symposia and workshops. For completeness, information is given on the sampling of (post)larval fish and macro-crustaceans, and on the availability of environmental data. Most data were gathered by the Marine Biology Section of Ghent University (Belgium; before 1990 by O. Hamerlynck, after 1990 by K. Hostens for the 'epibenthic' data), in close cooperation with and with the logistic support of the Centre for Estuarine and

Marine Ecology (CEME, Yerseke, the Netherlands), except the quarterly subtidal and the intertidal data of the Oosterschelde (gathered by CEME, NL; before 1990 under direction of R.H.D. Lambeck, after 1998 under direction of H. Hummel) and the fyke catches in the Oosterschelde (data gathered by Bureau Waardenburg, NL, and now property of CEME). Part of the 'epibenthic' data have been (re-)entered in the huge benthos database of the CEME. The length-frequency, density and biomass data on the demersal fish and macro-invertebrates, and the environmental data will be attached as a CD-rom.

At a number of occasions no samples could be taken, mostly due to bad weather conditions, sometimes due to logistic problems. As several people and institutes were involved in the numerous sampling campaigns, a few samples inevitably got lost, either completely or partly. Only a limited part of the epibenthic (sub)samples was taken to the lab (and is still available) for further analyses and/or determination. Computerization of the data was sometimes difficult, as surely for the earlier surveys (prior to 1989), only the notes taken aboard of the ship were available, which were not always accurate (*e.g.* subsampling conversions, mesh-size, identification uncertainties). See Fig. 1.3 for the different sampling locations.

1.6.1 Westerschelde

Subtidal beam trawl samples were taken during the following surveys:
1. monthly surveys were conducted along the salinity gradient at 14 subtidal locations between January 1988 and December 1991. Basic data were reported in Hostens *et al.* (1996) and partly in Puturuhu (1994)
2. this monitoring was repeated on a quarterly basis at the same 14 subtidal locations between September 1999 and May 2000. The number of sampling points was reduced to 8 for the period August 2000 - November 2001
3. a third series was limited to the brackish part of the Westerschelde, where two-monthly surveys at 4 subtidal locations (and some extra) were conducted in the period January - December 1990 (with 3 parallel hauls per location), and monthly surveys at the same 4 stations (but single hauls) in the period January - December 1991. Basic data were derived from Verbeke (1994)
4. a 24-hour cycle (actually 26 hours) has been carried out at subtidal station 12 on 18-19 September 1991, with samples taken every 2 hours. Basic data were derived from Muhando (1992).

Simultaneously, hyperbenthic sledge samples were taken in the subtidal. Several theses and papers on the hyperbenthic fauna from the Wester-

Table 1.2 Overview of the different available and used datasets and surveys

System Subhabitat/campaign	sampling device	period	frequency	# surveys	# locations	# samples	remarks	env. var.	Chapter
Westerschelde									
subtidal 'gradient'	3-m beam trawl	Jan88-Dec91	monthly	47	14	647		yes	all, except 4, 4add, 7add, 8
	hyperbenthic sledge	idem					larvae, prey		7, 8add, 9
subtidal 'brackish'	3-m beam trawl	Jan90-Dec90	2-monthly	5	4	60	3 hauls/loc	yes	7, 9
		Jan91-Dec91	monthly	11	4	44		yes	7, 9
subtidal '24h'	3-m beam trawl	Sep91	2-hourly	1	1	13		yes	8
	hyperbenthic sledge	idem					larvae, prey		8
subtidal 'gradient 2'	3-m beam trawl	Sep99-May00	quarterly	4	14	56		yes	5, 6, 8, 9
	hyperbenthic sledge	idem					larvae, prey		8
	3-m beam trawl	Aug00-Nov01	quarterly	6	8	47		yes	5
	hyperbenthic sledge	idem							
intertidal flat	3-m beam trawl	Mar92-Oct92	monthly	8	10	80	Valkenisse	yes	7, 9
	2-m beam trawl	idem		7	10	59	+Ossenisse	no	8, 9
intertidal saltmarsh	stow net	Mar90-Oct91	monthly	18	1		Saeftinghe	yes	9
		Apr99-Oct99		5	1		Idem	yes	9
		Mar90-Augt91		18	1		Waarde	yes	9
Oosterschelde									
subtidal 'whole'	3-m beam trawl	Jun83	once	1	36	29		no	9
		May84-Oct86	±quarterly	9	36	321	no winter	no	3, 9
		Feb87-Nov89	quarterly	12	36	430		no	3, 4, 5, 9
subtidal 'selected'	3-m beam trawl	Oct87-Nov88	fortnightly	26	3	229	3 hauls/loc	no	3, 9
		Nov88-Dec89	monthly	14	4	56	3 hauls/loc	limit	3add, 9
	hyperbenthic sledge	Dec88	once	1	4	4			
subtidal 'whole 2'	3-m beam trawl	Aug99-Nov01	quarterly	12	14	167	sedim. Feb00	yes	4, 5, 6add, 9
	hyperbenthic sledge	Idem					Postlarvae		9
Intertidal active	2-m beam trawl	Apr84-Nov84	fortnightly	13	4	489	10 hauls/loc	no	9
		May85-Oct85	fortnightly	10	3	273	10 hauls/loc	no	9
Intertidal passive	Fyke net + weir	79-88	fortnightly	216	4	860		no	3add, 9
Voordelta									
Subtidal 'whole'	3-m beam trawl	May88-Dec89	monthly	20	24	457	2 depths	yes	3, 3add, 4add, 7add
	hyperbenthic sledge	idem					Postlarvae		
Subtidal 'grevelingen'	3-m beam trawl	Oct92-Jul94	monthly	20	8	160	2 depths	yes	
	hyperbenthic sledge	idem							

schelde have been published (*e.g.* Mees *et al.* 1993a, Mees *et al.* 1993b, Mees *et al.* 1994, Mees & Jones 1997, Fockedey & Mees 1999). A paper on the post-larval fish from the Dutch Delta area was published by Beyst *et al.* (1999). The data on (post)larval fish and macro-invertebrates were derived from Mees (1994) and Chavatte (2001).

Intertidally, two different beam trawl surveys were performed on a large brackish sandflat. No hyperbenthic samples were taken here. Basic data were reported in Hostens *et al.* (1996):

1. monthly surveys were carried out between March and October 1992 at 10 locations in the lower intertidal with a 3-m beam trawl. Basic data were partly derived from Sas (1993)

2. simultaneously, the upper intertidal was sampled at 10 (and several extra) locations with a 2-m beam trawl.

In the intertidal saltmarsh creeks, monthly samples have been gathered with a stow net, during the periods March 1990 - October 1991 and April - October 1999 in the brackish saltmarsh 'Het Verdronken Land van Saeftinghe', and during the period March 1990 - August 1991 in the much smaller brackish saltmarsh 'Schor van Waarde'. Several theses and papers on the nekton fauna from intertidal saltmarsh have been published (*e.g.* Cattrijsse *et al.* 1994, Cattrijsse *et al.* 1997). The data on postlarval fish and macrocrustaceans were derived from Cattrijsse (1994) and Hampel *et al.* (in press).

1.6.2 Oosterschelde

Subtidally, the following beam trawl surveys have been conducted in the Oosterschelde:

1. more or less quarterly throughout the Oosterschelde (except the northern part) at 36 locations between June 1983 and November 1989. Basic data were reported in Hostens *et al.* (1993)
2. the monitoring was repeated on a quarterly basis, but limited to 12 locations, with additionally 2 locations in the northern part during the period August 1999 - November 2001. During these surveys, the hyperbenthic sledge was used simultaneously. Postlarval data were derived from Chavatte (2001)
3. fortnightly surveys were conducted between October 1987 and November 1988 at 3 locations, and at 4 locations (1 extra) from November 1988 to December 1989 on a monthly basis. The stations were located in the western and central part, with 3 parallel tows per station. Basic data were reported in Hostens & Hamerlynck (1993)

Intertidally, a 2-m beam trawl was used on 4 intertidal flats during fortnightly surveys in the period April - November 1984, and on 3 locations in the period May – October 1985. On each location 10 replicate hauls were taken. These data were reworked in Hostens *et al.* (1994).

Fyke catches in the Oosterschelde were taken on a fortnightly basis between 1979 and 1988 at 4 intertidal locations. These data have been reworked in Hamerlynck & Hostens (1991) and are presented in Chapter 3-Add.

1.6.3 Voordelta

In the Voordelta, 24 stations were sampled both with a 3-m beam trawl and a hyperbenthic sledge, covering two depth strata (MTL -5 m and MTL –10 m) at 12 localities in the ebb-tidal deltas of the Oosterschelde and the Grevelingen and in the more seaward area inbetween both deltas. The sampling was carried out on a monthly basis during the period May 1988 - December 1989. These data were partly gathered in order of Rijkswaterstaat (Ministry of public transport, NL), and have been reported in several reports, theses and papers. They formed the main basis of several papers given as addenda (Chapter 4-Add., Chapter 7-Add., Chapter 2-Add.2).

The surveys in the Grevelingen ebb-tidal delta (4 stations, 2 depths) were repeated during the period September 1992 – July 1994. These data were partly published in Arellano (1995) and Arellano *et al.* (1995), but were not used in the present thesis.

The papers included in the present thesis have been written over a timespan of 13 years. Several chapters only use part of the available data. Either the other data were not yet computerized at the moment of writing the specific chapter, or only shorter but similar sampling periods were investigated for comparative reasons. As shown in Table 1.2 the bulk of the thesis is based on the subtidal monitoring surveys in both the Westerschelde and the Oosterschelde during the periods 1988-'89 and 1999-2001. Most of the other sub- and intertidal surveys have been used in the papers on feeding ecology and in the final chapter.

1.7 Objectives of the thesis

The main aim of this study is to provide a baseline for future functional and process studies on the fish and macro-invertebrates of the Delta area, and of the Westerschelde and Oosterschelde estuaries in particular. The Westerschelde estuary is affected by high organic waste loads and by industrial pollution (Baeyens *et al.* 1998, Van Damme *et al.* 1999) the Oosterschelde by major engineering works during the past decades (Nienhuis & Smaal 1994b). To comply with international standards, a massive reduction of the pollution load of the Westerschelde will have to be achieved in the (near) future. Most probably, the Oosterschelde will be subject to hydraulic engineering interventions (*e.g.* freshwater input) in the future, as well. The impact assessment of these changes will hopefully be monitored. A baseline study is a prerequisite for such a monitoring program.

Although the different data sets were gathered through different projects - partly before the start of the thesis, others specifically designed for it - they all suit the same purpose: enlarging our knowledge on the nursery function of the Delta area for demersal fish and macro-invertebrate species. Estuaries, and more specifically fish and macro-invertebrates within these estuaries, have received considerable international attention during the last decades (see Elliott & Hemingway 2002). The thesis fits within several national and European projects on biology and ecology of 'benthic' organisms. Most of the work has been carried out at the Marine Biology Laboratory (UGent), but the thesis would not have been possible without the logistic support from, and scientific cooperation with the Centre of Estuarine and Marine Ecology (CEME, Yerseke, the Netherlands).

To assess the nursery function, information is needed on (changes in) larval and postlarval recruitment, habitat complexity and availability, environmental properties and prey availability. The thesis benefits from complementary research on other biotic and abiotic compartments in the Delta area. Geomorphology, physics, chemistry, organic material, bacteria, phytoplankton, zooplankton, hyperbenthos, mi-

crophytobenthos, meiobenthos, macrobenthos, and birds were studied in detail, both in the Westerschelde and the Oosterschelde. In the Marine Biology Section of Ghent University, the hyperbenthos of the Westerschelde has been thoroughly studied by Mees (1994), and more recently of the Oosterschelde by Chavatte (2001), while the nekton from intertidal saltmarsh creeks was studied by Cattrijsse (1994). General reviews on the environmental and ecological properties are given in Meire & Vincx (1993), Heip & Herman (1995), and Van Damme *et al.* (1999) for the Westerschelde, and in Nienhuis & Smaal (1994a) and van Berchum & Wattel (1997) for the Oosterschelde.

Some of the advantages of using fish and macro-invertebrates as biological indicators are: (1) they can easily be identified in the field; (2) they have a well-known biology and ecology; (3) they may indicate changes in other ecosystem compartments, as they are major contributors in the trophic food chain (Marchand *et al.* 2002). Still, it may be difficult to differentiate natural changes (mainly yearly variability) from those caused by humans (Wolfe *et al.* 1987). Estuaries are complex ecosystems with many natural disturbances, induced by hydroclimatic changes. On the other hand, estuaries have been under human pressure during their whole evolution, and ecological studies suffer from the fact that data from pristine times are almost non-existent (Marchand *et al.* 2002).

To provide a baseline for the understanding of the nursery function, both structural and functional patterns have to be investigated. The specific objectives of this thesis are:

1. to describe the spatial and temporal patterns in diversity, density, biomass and growth of the demersal fish and macro-invertebrates in the Westerschelde and Oosterschelde estuaries, and to evaluate the relation with the major structuring environmental variables

2. to describe the structural patterns at several temporal scales, i.e. short-, mid-, and long-term changes, and at several spatial scales, i.e. within and between estuaries and subhabitats in these estuaries

3. to evaluate the abiotic and biotic influences (including human impact) at the community level, and to predict distribution patterns at the species level, in both estuaries

4. to study the temporal and spatial differences in trophic niche and feeding patterns of several fish and macro-invertebrates in the Westerschelde estuary

5. to evaluate the importance of hyperbenthic organisms, and in particular mysids, in the food web of the Westerschelde estuary.

1.8 Outline of the thesis

In this ecological thesis, the aim is to understand the interaction between the organisms and between the organisms and their environment. Most chapters have been or will be published as such in the international literature. Rather for completeness than as part of the thesis, most chapters are supplemented with an addendum, i.e. papers with complementary information to the Westerschelde and Oosterschelde estuaries that were published as such. My contributions to the papers where I am not the first author are computerization of the data from the field data sheets, data analysis and stomach content analysis.

The **structural patterns** in the fish and macro-invertebrate assemblages, both in space and in time, are described in **PART I** (chapters 2 through 6). The spatial and short-term temporal patterns along the salinity gradient in the subtidal Westerschelde are described in **chapter 2** based on the monthly data of 1988-'89, and in an addendum based on the monthly data of 1990. In a second addendum, an important paper on the strength of multivariate techniques is given, based on monthly data from 1989 from the Oosterschelde, the Westerschelde and the Voordelta:

Hostens K (2000) Spatial patterns and seasonality in the epibenthic communities of the Westerschelde (Southern Bight of the North Sea). J Mar Biol Ass UK 80: 27-36

Hostens K (1996) Spatial and temporal patterns in the epibenthos of the Westerschelde. Prog Belg Oceanog Res 107-110

Hamerlynck O, Hostens K, Arellano RV, Mees J, van Damme PA (1993) The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands): spatial structure. Neth J Aquat Ecol 27(2-4): 343-358

In **chapter 3** the spatial and mid-term patterns in the fish assemblages of the Oosterschelde are based on the subtidal data, sampled fortnightly in 1988 (in comparison to the Westerschelde and Voordelta), and on quarterly samples in the periods 1988-'89 and 1984-'85. Its twin paper, based on intertidal data gathered with fykes between 1979-1988, is given in an addendum:

Hostens K, Hamerlynck O (1994) The mobile epifauna of soft bottoms in the subtidal Ooster-

schelde estuary: structure, function and impact of the storm-surge barrier. Hydrobiologia 282/283: 479-496

*Hamerlynck O, **Hostens K** (1994) Changes in the fish fauna of the Oosterschelde - a ten year time series of fyke catches. Hydrobiologia 282/283: 497-507*

In **Chapter 4** long-term patterns in the fish fauna of the Oosterschelde are presented, based on quarterly data from 1987-'89 and 1999-2001. This chapter deals with the possible effects of the Delta-works in the Oosterschelde. In an addendum, the consequences of the civil engineering works in the ebb-tidal Delta of the Grevelingen were evaluated:

***Hostens K**, Hummel H, Mees J, Vincx M, Heip CH (submitted a) The fish fauna of the Oosterschelde, a decade after completion of the engineering works. J Sea Res*

*Hamerlynck O, **Hostens K**, Mees J, Arellano RV, Cattrijsse A, van de Vyver P, Craeymeersch JA (1992) The ebb-tidal delta of the Grevelingen: a man-made nursery for flatfish? Neth J Sea Res 30: 191-200*

Chapter 5 gives detailed short- and long-term patterns for several macro-invertebrates in a comparison between the two estuaries, based on quarterly data from 1988-'89 and 1999-2001:

***Hostens K**, Mees J, Hummel H (submitted b) The mobile macro-invertebrate fauna of the Oosterschelde and the Westerschelde (SW Netherlands). J Mar Biol Ass UK*

In **Chapter 6** it is tried to predict both fish and macro-crustacean presence and density in relation to the Westerschelde environment at the species level. Most data from the subtidal 'gradient' surveys (1988-'91 and 1999-2001) are used. In the addendum, these models were applied to a limited dataset from the Oosterschelde:

***Hostens K** (submitted) Fish and macro-crustacean response surfaces to environmental gradients in the Westerschelde estuary. Mar Ecol Prog Ser*

***Hostens K** (unpubl. data) Application of the Westerschelde response models to fish and macro-crustacean data from the Oosterschelde*

The **functioning** of the different habitats in the Dutch Delta area as nurseries for juvenile fish and macro-crustaceans is evaluated in **PART II** (chapters 7 and 8). Data from different sub- and intertidal surveys were used. Both chapters are mainly focused on the Westerschelde, and emphasize the (underesti-

mated) role of hyperbenthic prey – and particular mysids – for the higher trophic levels of the estuarine food web.

In **Chapter 7** the importance of mysids in the diet of several fish species in the Westerschelde is shown. A paper on the feeding ecology of two gadoid species in the Voordelta is given as addendum:

***Hostens K**, Mees J (1999) The mysid-feeding guild of demersal fishes in the brackish zone of the Westerschelde estuary. J Fish Biol 55: 704-719*

*Hamerlynck O, **Hostens K** (1993) Growth, feeding, production and consumption in O-group bib Trisopterus luscus L. and whiting Merlangius merlangus L. in a shallow coastal area of the SW Netherlands. ICES J Mar Sci 50: 81-91*

Diurnal, seasonal and spatial patterns in the diet of the brown shrimp in the Westerschelde are discussed in **Chapter 8**. In an addendum, a basic paper on the food webs of the Westerschelde is included:

***Hostens K**, Mees J (submitted) The diet of brown shrimp Crangon crangon (L.) in the Westerschelde estuary. Mar Biol*

*Hamerlynck O, Mees J, Craeymeersch JA, Soetaert K, **Hostens K**, Cattrijsse A, van Damme PA (1993) The Westerschelde estuary: two food webs and a nutrient rich desert. Prog Belg Oceanog Res 217-234*

Finally, in **Chapter 9** an overview is given on the nursery function of both the Westerschelde and the Oosterschelde estuaries. All sub- and intertidal datasets on the juvenile and postlarval life stages are used. The demersal fish and macro-invertebrate species are categorised by means of different functional ecotrophic guilds. This forms the basis of a two-dimensional foodweb in the Westerschelde:

***Hostens K** The demersal fish and macro-invertebrate assemblages of the Westerschelde and Oosterschelde estuaries: overview and final conclusions.*