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CHAPTER 9 THE DEMERSAL FISH AND MACRO-INVERTEBRATE ASSEMBLAGES OF THE WESTERSCHELDE AND OOSTERSCHELDE ESTUARIES: OVERVIEW AND FINAL CONCLUSIONS

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Abstract. An overview on the nursery function of the Westerschelde and the Oosterschelde estuaries for demersal fish and macro-invertebrates is presented, based on all data sets presented in this thesis. The present thesis provides a baseline, and suggests that both the Westerschelde and Oosterschelde estuaries play a significant role as nursery areas for several demersal fish and macro-invertebrate species. The forcing factors for recruitment and the seasonal appearance of (post)larval fish and macro-crustaceans are explained. Biodiversity is related to habitat use and habitat availability. The faunas of the Westerschelde and Oosterschelde are structured by a limited number of environmental variables, and the prediction of species occurrence by means of single-species logistic models is discussed. Spatial, long-term and seasonal patterns in density in relation to the environment are summarized by means of multivariate analyses and graphical representation of trends per species and per taxonomic group. The seasonal appearance of both (post)larval and juvenile fish and macro-crustaceans in the Westerschelde is described. Density of the commonest species is predicted by means of single-species linear regression models. A short description of the human impact on the fish and macro-invertebrate assemblages is given. In the functional part of this overview, a generalized food web for the Westerschelde is presented, and the importance of mysids as prey for several fish and macro-crustaceans in the Westerschelde is discussed. Finally, 10 major conclusions and some remarks are formulated and some recommendations for future research are given.

9.1 Introduction

The thesis focuses on the nursery function of the Westerschelde and Oosterschelde estuaries for demersal fish and macro-invertebrate species. Long-term monitoring in a more or less uniform way has produced a large amount of data on the ecology of the demersal fish and macro-invertebrate fauna in the Dutch Delta area (SW Netherlands), and in the Westerschelde and Oosterschelde estuary in particular. The huge data sets used in the present thesis cover two decades from 1983 through 2001, although a large gap exists from 1993 till 1998 (see Chapter 1).

The bulk of the thesis is based on the 3-m beam trawl surveys in the subtidal, where a total of 2100 samples were taken during diurnal, fortnightly, monthly and/or quarterly surveys (see Table 1.2). From these, 36 % were gathered in the Westerschelde

in the period 1988-1992, and 51 % in the Oosterschelde in the period 1983-1989. Only 5 and 8 % of the subtidal samples were gathered in the period 1999-2001 in the Westerschelde and Oosterschelde, respectively. Data from the ebb-tidal deltas of the Oosterschelde and the Grevelingen (part of the Voordelta, 617 samples) were mainly used in the addenda to several chapters. Data on juvenile fish and macro-invertebrates from the intertidal covered a limited time span, and were only partly used. In the brackish part of the Westerschelde, 139 intertidal samples were gathered in 1992 with a 2-m beam trawl. In the Oosterschelde, the 2-m beam trawl samples (period 1984-'85) were not used; data from 860 fyke samples (period 1979-'88) were used in an addendum. See Fig. 9.1 for a map of the study area. Throughout this synthesis, several paragraphs are based on only part of the data, either for a better representation of the underlying patterns or for comparative reasons.

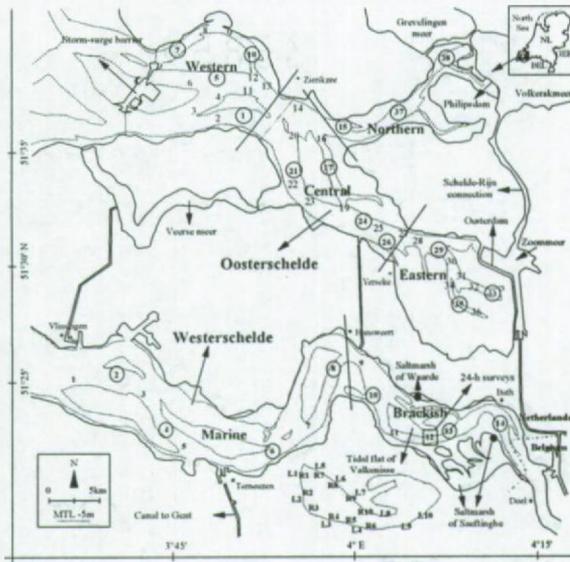


Fig. 9.1 Map of the Westerschelde and Oosterschelde estuary, indicating the sampling locations in the different subhabitats, and the division in different zones

The nursery function of an estuary depends on recruitment of (post)larvae into the system, habitat complexity and availability, environmental properties (hydrographic regime), and prey availability. The environmental/biological and biological/biological interactions act both as extrinsic and intrinsic forcing variables on the structure of the demersal fish and macro-invertebrate assemblages (see Chapter 1). The thesis benefits from the complementary research on other ecosystem components in both estuaries. In this overview, the seasonal appearance or recruitment of (post)larval fish and crustaceans in the hyperbenthal of both estuaries and in the intertidal saltmarsh creeks of the Westerschelde is summarized, and related to the seasonal and spatial distribution patterns of the juvenile fish and (adult) macro-invertebrates in the subtidal and brackish intertidal of the Westerschelde.

The relation between a limited set of environmental variables and the structural patterns in diversity, density, biomass (and growth) of the juvenile fish and macro-invertebrate fauna, either at community or at species level, forms a major component of the present thesis (PART I, Chapters 2 to 6). Both spatial and seasonal patterns at several scales, *i.e.* between and within estuaries and subhabitats, and short-, mid- and long-term changes, are investigated. The results of different graphical and statistical approaches are summarized. In PART II of the thesis (Chapters 7 and 8), the functional patterns in diet and feeding behavior of several fish and macrocrustaceans in the Westerschelde are investigated. The importance of hyperbenthic organisms – and mysids in particular – in the food web of the Westerschelde is emphasized.

Fish and macro-invertebrates are considered to be good biological indicators, although it may be

difficult to differentiate between human induced and natural changes in the communities. The human impact on the structure and functioning of demersal fish and macro-invertebrate assemblages is briefly touched upon in this overview.

9.2 Recruitment

The term recruitment is often been used ambiguously. Fishery biologists are mainly interested in the 'recruitment' of juveniles to the adult exploitable stock (Beverton & Holt 1957). Here, it is preferred to refer to this type of recruitment as 'juvenile production', and to use the term 'recruitment' for larval transport towards and retention within the nursery areas.

9.2.1 Forcing factors

The nursery function of an estuary depends on the supply of (post)larvae to the system, which in turn depends upon (1) the reproductive success of the adults, (2) the distance from the spawning areas, (3) larval survival, (4) efficiency of larval transport, and (5) efficiency of larval retention (Potter *et al.* 1997).

Most of these parameters depend on forcing factors outside the estuary. The reproductive success, for example, is dependent on population viability, genetic structure, size and maturity of the breeding population, and fecundity. These factors themselves may be influenced by overfishing (through resource removal), environmental pollution, geomorphological and hydrographical changes (Daan *et al.* 1990).

For a number of commercial species, the spawning grounds are relatively well-known, *e.g.* plaice *Pleuronectes platessa* spawns in four major areas in the North Sea, mainly in the Southern Bight (Simpson 1959). Several flatfish and gadoid species spawn close to the nursery areas. Still, after more than a century of intensive investigations, the knowledge on the basic breeding biology of most commercial and non-commercial species remains patchy (Daan *et al.* 1990). The majority of marine spawners (including all commercial gadoids, flatfish and several clupeoids) produce large numbers of small pelagic eggs, which are quickly hatched (Costa *et al.* 2002). This is the case for 50 % of the species in the Westerschelde (Cattrijsse & Hampel 2000). Only few species (*e.g.* gobies) spawn or may be able to spawn (large, demersal eggs) in the estuary proper.

Larval survival depends on a whole range of abiotic and biotic parameters. A thorough discussion is given in Costa *et al.* (2002).

Although transport and retention efficiency may be difficult to estimate, it has been shown that larvae of several species are passively transported by means of appropriate currents towards the nurseries

Table 9.1 Seasonal appearance and number of (post)larval fish and macro-crustacean species, with the number of species present with 2 life history stages between brackets

Season	Subtidal Westerschelde		Subtidal Oosterschelde		Intertidal Saeflinghe saltmarsh creek		All areas	
	macro-crust.	fish	macro-crust.	fish	macro-crust.	fish	macro-crust.	fish
	Winter	-	1	-	2	-	-	-
Winter-Spring	-	3	-	-	-	3	-	4
Spring	6 (4)	6	4 (2)	6	-	4	4 (1)	10
Spring-Summer	2	-	2 (1)	-	2 (1)	1	3 (2)	1
Summer	2	2	3 (1)	-	4 (2)	3	5 (1)	4
Autumn	-	-	1	-	-	-	1	-
Total	9 (5)	11	8 (6)	8	5 (2)	9	11 (6)	17

(larval drift) (Miller *et al.* 1988), and/or actively migrate into and within the nursery areas (selective tidal stream transport) (De Veen 1978, Hedvall *et al.* 1998, Jager 1999). In the North Frisian Wadden Sea, (post)larvae of several flatfish species and of brown shrimp *Crangon crangon* are retained in puddles on the tidal flats during low tide (Berghahn 1983). No such data exist for the Delta area, but we know that (post)larvae of 11 macro-crustaceans (of which 6 species with 2 different life stages) and 17 fish species do enter the Westerschelde and/or Oosterschelde estuary (Table 9.1) The diversity will even be higher, as the postlarvae of the different gobiid and clupeoid species were not (or could not be) identified to species level in the different habitats (see also Beyst *et al.* 1999). The (post)larval data presented here, were taken from Mees (1994) and Cattrijsse (1994) for the period August 1990 – May 1991, and from Chavatte (2001) and Hampel *et al.* (in press) for the period August 1999-May 2000.

9.2.2 Seasonal appearance

Larval and early postlarval fish and macro-crustaceans, constitute the major part of the mesohypobenthos, and only appear for a short period, mainly in spring, in the Westerschelde and Oosterschelde estuaries, although several species extend their larval appearance either towards late winter or early summer. A summary on the presence of (post)larval fishes in the Westerschelde and the Voordelta for the period 1988-'91 was given in Beyst *et al.* (1999).

Seasonal appearance may be an important regulating factor, as several species undergo metamorphosis in the nursery areas, and changes in the diet have to match prey availability (Costa *et al.* 2002).

9.2.3 (Post)larval macro-crustaceans

The number of (post)larval macro-crustacean species was lowest intertidally. Highest abundances (maximum 40 ind m⁻³ in June 1990) of postlarval *C. crangon* were recorded in the intertidal saltmarsh creeks (on average 1 to 2 orders of magnitude higher than in the subtidal) (Fig. 9.2a). Zoea larvae of *C. crangon* are rapidly transported from the sea towards these intertidal saltmarsh creeks 50 km upstream in the brackish part of the Westerschelde. This can only be achieved through active and selective tidal transport. In the mean time the larvae undergo metamorphosis to the postlarval stage, as no zoeae were recorded from the marsh creeks. The nursery function of these creeks as refuges and foraging areas for the brown shrimp has been discussed in Cattrijsse *et al.* (1997). Three other caridean (prawn) species were only sporadically caught.

Other important macro-crustaceans were zoea and megalopa larvae of both brachyuran and anomuran crabs. In the intertidal marsh creeks only shore crab (*Carcinus maenas*) larvae were present. Higher densities of *C. maenas*, but also of flying crab *Liocarcinus holsatus*, spider crabs *Macropodia* and both anomuran crabs *Pagurus bernhardus* and *Pisidia longicornis*, were noted in the subtidal Oosterschelde. This is probably related to the habitat complexity and vegetation structure. In a nursery along the Swedish west coast, *C. maenas* megalopae actively selected habitats with filamentous algae, which provide the best refuge from predation (Hedvall *et al.* 1998).

Note the absence in 1999-2000 of all macro-crustacean (post)larvae from the brackish subtidal Westerschelde, of shrimp postlarvae from the north-

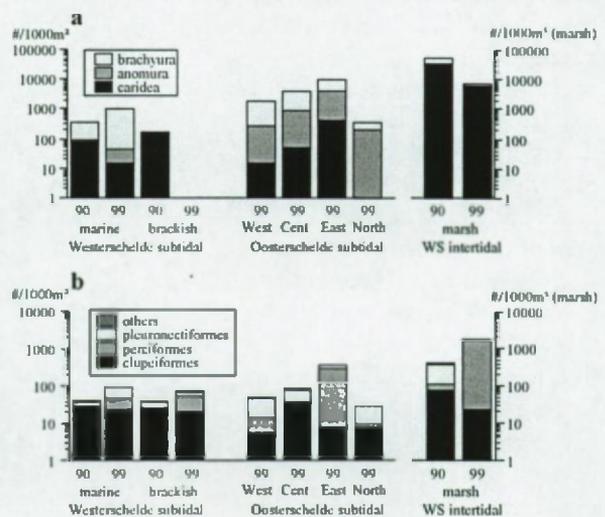


Fig. 9.2 Spatial and long-term patterns in (a) (post)larval macro-invertebrates and (b) fish groups, based on the maximum densities (log-scale) in the subtidal (ind 1000 m⁻³) Westerschelde and Oosterschelde, and in an intertidal creek (ind 1000 m⁻³) in the saltmarsh of Saeflinghe, for the periods 1990-'91 and 1999-2000

ern subtidal Oosterschelde, and of brachyuran larvae from the intertidal saltmarsh. Probably, the short peak abundance was missed due to the quarterly survey design.

9.2.4 (Post)larval fish

The (post)larval fish diversity was comparable in all subhabitats (Table 9.1). Of the 17 postlarval fish species, only 4 (probably 7) species were common in all subhabitats (Fig. 9.2b): clupeoids (sprat *Sprattus sprattus* and herring *Clupea harengus*), gobies (probably 3 species of the genus *Pomatoschistus* in different subhabitats), and flatfish (sole *Solea solea* and flounder *Platichthys flesus* (the latter not in the Oosterschelde)). The other postlarval fish species (6 percids, 2 gadoids, 1 flatfish and 4 others) were only sporadically recorded.

The intertidal creeks also harbored higher densities of postlarval fish, mainly high densities of common goby *Pomatoschistus microps* and seabass *Dicentrarchus labrax* in spring-summer 1999, and flounder *Platichthys flesus* in spring of both periods. Clupeoids were equally abundant in the different subtidal parts of the Westerschelde and Oosterschelde, while gobies were mainly present in the brackish Westerschelde and in the eastern part of the Oosterschelde. A discussion on the presence of the fish larvae in the Dutch Delta area was presented by Beyst *et al.* (1999).

9.3 Biodiversity

9.3.1 Habitat availability

The biodiversity of fish (and macro-invertebrate)

species within an area is a function of habitat diversity, niche availability and area size (Wootton 1992). The reader is referred to Pihl *et al.* (2002) for a thorough discussion on habitat types, habitat extent and habitat use, including the references for the Westerschelde and Oosterschelde (although the values are different, as more data were available for the present study).

Of the nine distinguished estuarine habitat types, subtidal and intertidal soft substratum make up >75 % of the total habitat in both estuaries (Fig. 9.3a & b). This was comparable with other European estuaries in the Boreal/Atlantic region (Pihl *et al.* 2002). The intertidal saltmarsh area in the Westerschelde is largely allocated to the brackish saltmarsh of Saeftinghe, while in the Oosterschelde most saltmarshes disappeared after the major engineering works.

As the data for this paragraph were based on the whole estuarine environment, tidal freshwater and reedbeds were included as habitats, but these are only found in the Zeeschelde, *i.e.* the upstream part of the Schelde estuary (see Chapter 1).

In the Oosterschelde, the intertidal and subtidal habitats are further extended with the presence of biogenic reefs (mainly mussels and oysters) and hard substratum.

9.3.2 Overall fish diversity

Based on all data gathered by different institutes during the last two decades in both estuaries, the total number of fish species amounted to 96, of which 74 species were recorded in the Schelde and 75 species in the Oosterschelde. These values include 15 and 3 additional species to the data given in Pihl *et al.* (2002) for the Schelde and Oosterschelde, respec-

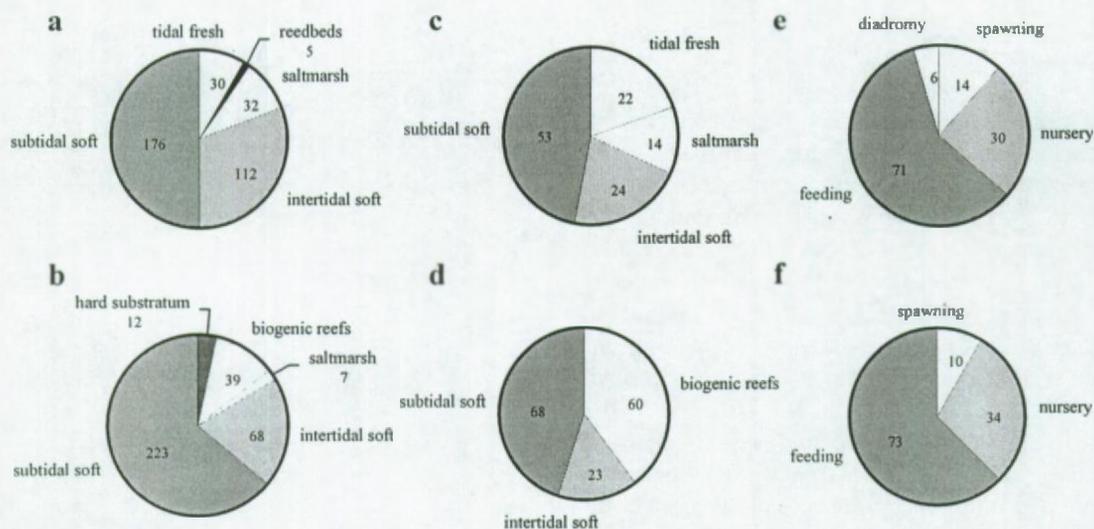


Fig. 9.3 Relative presence of the different habitat types, with the area surface given in km² (a,b), fish diversity in the different habitats (c,d), and number of fish species per habitat use, based on all available data from literature from the last two decades in the Schelde (upper pie charts) and the Oosterschelde (lower pie charts)

tively. This indicates that species richness depends on the extent of the study period and area size (Elliott & Dewailly 1995). However, the total number of species is comparable to that of several estuaries in the NW Atlantic/Boreal region (e.g. the Weser/Elbe, Humber, Seine and Tagus estuaries).

Most of the species were recorded in the subtidal habitats (although no data exist for presence on the hard substratum), while only a limited number of species were recorded in the intertidal (the value for the Oosterschelde given in Pihl *et al.* (2002) is incorrect) (Fig. 9.3c & d). Surprisingly, 22 fish species were recorded from the tidal freshwater part of the Schelde estuary during the 1990s, related to an improved water quality in the upstream part.

9.3.3 Habitat use

In respect to habitat use, 14 (10) species normally should be able to spawn in the estuary proper (Fig. 9.3e & f). However, for most species we believe no spawning activity takes place. Fish eggs (mainly from *Solea solea* and *Pomatoschistus* species) were recorded in the hyperbenthic sledge samples from both estuaries and in the ebb-tidal deltas (Beyst *et al.* 1999). Yet, it cannot be claimed that these originated from local spawning activities (Cattrijsse & Hampel 2000).

Only six diadromous species were recorded in the Westerschelde and none in the Oosterschelde. The physical constructions (e.g. barrages and dams), the absence of suitable habitats at the riverine side, and the relatively bad water quality conditions in the Zeeschelde during most part of the year are the main reasons for the low representation of this ecological guild. The same holds for most European estuaries (Pihl *et al.* 2002).

Most of the marine adventitious, freshwater and marine juvenile species (Elliott & Dewailly 1995) enter the estuary for feeding purposes. Juveniles of ca. 30 marine and estuarine resident species use the Westerschelde and Oosterschelde as nursery areas. These are of main interest in the present thesis and in the rest of this chapter.

9.3.4 Juvenile fish and macro-invertebrate diversity

The following paragraph is based on quarterly subtidal data from both estuaries for the periods February 1988 – November 1989 and February 2000 – November 2001. As the sampling period is much shorter, the number of juvenile fish and macro-invertebrate species is much lower as well, with a total of 32 fish and 6 macro-invertebrate species in the Westerschelde, and 41 fish and 31 macro-invertebrate species in the Oosterschelde (see Chapter 3, Chapter 2, Chapter 5). In comparison, 40 species were listed for the Schelde in the period before the 1940s (Poll 1945, Van Damme *et al.* 1994), and 44 fish species were recorded in the period 1960-'76 in the former open Oosterschelde estuary (Doornbos *et al.* 1981).

On average 16 fish and only 3 macro-invertebrate species were recorded per season in both the marine and brackish parts of the Westerschelde, with a little higher values in spring (Fig. 9.4a-c). The low number of macro-invertebrates (3 brachyuran crabs, 2 caridean prawns and 1 caridean shrimp) is mainly attributed to the fact that only few species can withstand the harsh estuarine conditions, e.g. rather low and largely fluctuating salinities and much higher turbidities (Chapter 5).

In the Oosterschelde the fish diversity was higher in 2000-2001 compared to 1988-89, with on

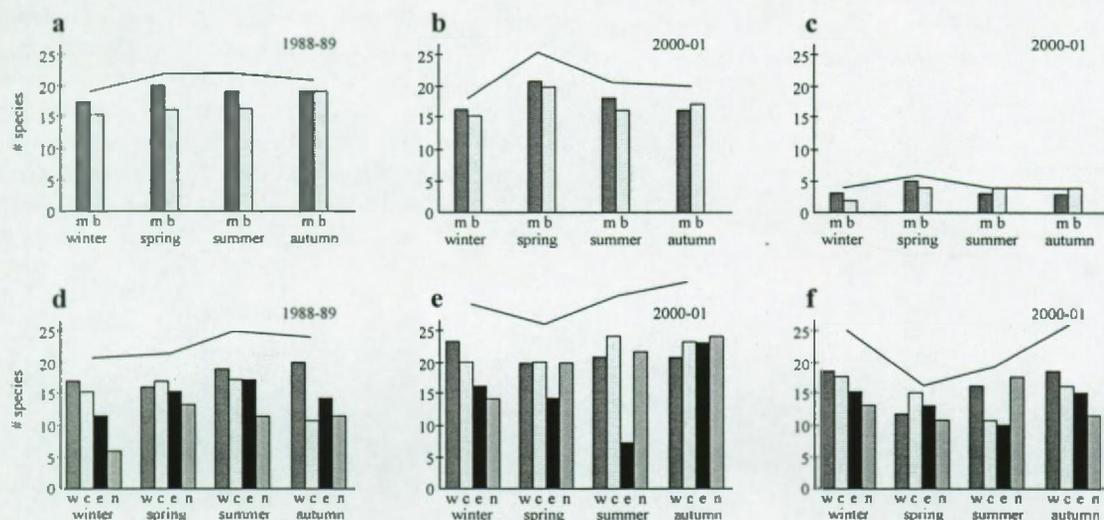


Fig. 9.4 Fish (a-b, d-e) and macro-invertebrate (c, f) diversity in the Westerschelde (a-c) and Oosterschelde (d-f) for the periods 1988-89 and 2000-2001, per season and per subhabitat: marine (m) and brackish (b) parts in the Westerschelde, western (w), central (c), eastern (e) and northern (n) parts in the Oosterschelde

average 7 to 24 species per season (Fig. 9.4d & e). The macro-invertebrate diversity was much higher throughout the Oosterschelde compared to the Westerschelde, with a minimum of 16 species in spring (Fig. 9.4f). The large habitat complexity in the Oosterschelde (soft-hard substrate, mussel beds, macro-algae) seems to favour the occurrence of the macro-invertebrate fauna, constituted of 10 brachyuran crabs, 9 caridean prawns, 5 (6) echinoderms, 3 caridean shrimps, 3 cephalopods and 2 anomuran crabs (Chapter 5).

The juvenile fish species present in the Westerschelde and Oosterschelde (the second values between brackets) belonged to the clupeoids (4, 3), gadoids (3, 4), flatfish (8, 6), gobiids (4, 6), other percids (7, 8), scorpaenids (3, 4), pipefish (1, 3), and several other groups like salmonids, eels, atherinids and sticklebacks (2, 7). Several demersal fish species are eurytopic with a high tolerance towards a broad range of environmental conditions. Still, only few fish and macro-invertebrate species are really common in both estuaries. For example, only 3 fish and 7 macro-invertebrate species occurred in >70 % of the Oosterschelde samples (Chapter 4, Chapter 5). Moreover, in both systems, diversity was only a little higher in the more marine parts, showing a dominance of the seasonal pattern over the spatial pattern.

Diversity (surely of the macro-invertebrates) is influenced by the invasion of so-called alien species, mainly imported by means of anthropogenic transportations (Little 2000). In the Westerschelde, Chinese mitten crab *Eriocheir sinensis* was already imported during the beginning of 20th century. In the lower Zeeschelde, 3 of the 4 recorded crab species were 'exotics' (Maes *et al.* 1998a). In the Oosterschelde, arch-fronted swimming crab *Liocarcinus arcuatus* became the commonest swimming crab since it entered the system in 1982. Common species like *Carcinus maenas* and harbour crab *Liocarcinus depurator* might suffer the aggressive invasion of Japanese brush crab *Hemigrapsus penicillatus*, as has

been shown in the Gulf of Biscay (d'Udekem d'Acoz 1999).

All these data prove that the diversity of the fish and macro-invertebrate assemblage is highly correlated with the occasional immigration of a large number of typical marine species at different times of the year. In conclusion, the main environmental variables influencing the biodiversity patterns were salinity/turbidity, sediment/habitat type and temperature.

9.4 Environmental properties

In temperate areas, the estuarine abiotic environment can be largely characterized by the patterns in salinity, temperature, turbidity, dissolved oxygen concentration, and sediment type. As such, these environmental variables and their combined effects are most likely to be the important controlling factors in the distribution of fish and macro-invertebrate assemblages (Elliott & Hemingway 2002). Patterns in current velocity and degree of exposure might be important characteristics of an estuary, but could not be measured at the sampling locations. The underlying patterns can partly be deduced from the sediment and turbidity characteristics. Several biological factors may be important as well.

The following paragraphs are based on quarterly data from the period 2000-2001, and give a general view of the spatial and seasonal patterns in temperature (°C), salinity (psu), dissolved oxygen concentration (mg l⁻¹) and turbidity (m⁻¹, measured as the reciprocal of secchi depth) in the Westerschelde and Oosterschelde estuaries.

Both on a spatial and seasonal scale, temperature more or less showed an inverse relationship with dissolved oxygen concentration in the Westerschelde, while salinity showed an inverse relationship with turbidity (Fig. 9.5 and Fig. 9.6). A comparable inverse relationship between temperature and dissolved oxygen in the Oosterschelde was only found on a seasonal scale. The figures for salinity clearly show that the Westerschelde is a true estuary, with a marked salinity gradient along the horizontal axis and higher salinities in summer, while the Oosterschelde

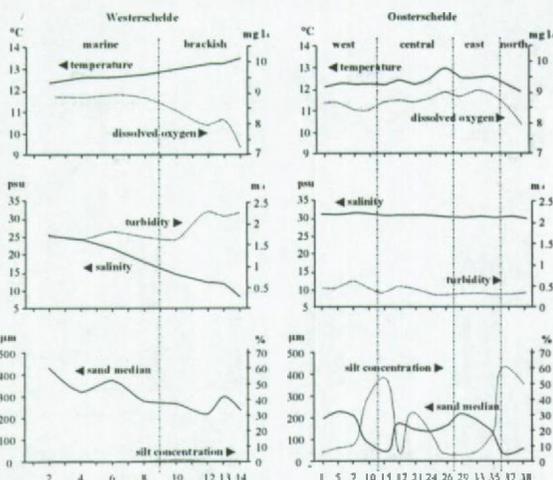


Fig. 9.5 Spatial patterns in six environmental variables in the Westerschelde and Oosterschelde estuaries

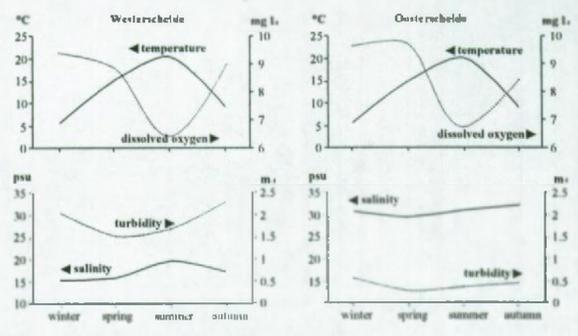


Fig. 9.6 Seasonal patterns in four environmental variables in the Westerschelde and Oosterschelde estuaries

is a marine bay with constant high salinities and low turbidities (5 times lower than in the Westerschelde) in all subareas throughout the year. The higher turbidities (and lower salinities) in the Westerschelde during the colder months are mainly due to higher river runoff (Heip 1989b).

A striking feature was the serious drop in dissolved oxygen concentration in the brackish part of the Westerschelde. The organic enrichment in this area, and the bacterial/microbial respiration related with the decaying processes (Heip *et al.* 1995) are the main reasons for this gradient. Also, the increased turbidity in the brackish part is related with the increased concentration of suspended matter in the water column, as sediment particles are retained for several days within the brackish part of the Westerschelde (Soetaert & Herman 1995b). The observed patterns were comparable with those found for the period 1988-'89 (Chapter 2). Also, in the northern part of the Oosterschelde, dissolved oxygen concentrations were lower, probably related with the currents and the high concentrations of mud in the sediment of this subarea. For most stations in the Oosterschelde the median grain size was below 250 μm , while in the Westerschelde the sand was coarser and gradually decreased from the marine to the brackish part.

9.5 Prediction of occurrence

Alterations in the environmental conditions can lead to changes in the estuarine populations of fish and macro-crustaceans (Chapter 6). A simultaneous examination of several different variables is often required to study ecosystem responses to perturbations (Jassby & Powell 1990). Still, for a sound ecological management, it might be useful to be able to predict the occurrence and distribution of fish and macro-crustacean species in the estuary.

We tried to predict the response of the 15 most common species (12 fish and 3 macro-invertebrate species) to (natural) changes in the environment in the Westerschelde. The probability of occurrence was modelled by means of single and multiple logistic regressions as quadratic functions of only 4 environmental variables (Chapter 6).

9.5.1 Single species response curves

Single species response curves yielded good descriptions of the occurrence of every species along the four environmental gradients (temperature, salinity, turbidity and dissolved oxygen concentration), which was related to the maximum likelihood of presence in the field (Chapter 6).

Several species responded the same way to the four environmental variables, if compared per

ecological guild. For example, several marine juveniles were more likely to be found at higher salinities and lower turbidities (*e.g.* flying crab *Liocarcinus holsatus*) or at higher temperatures (*e.g.* sole *Solea solea*), while the opposite holds for a number of estuarine resident species (*e.g.* common goby *Pomatoschistus microps*).

Salinity is regarded as an extremely important variable for many animals and plants (Attrill *et al.* 1999). This is mainly related to the process of osmoregulation (Little 2000). The presence of several fish and macro-invertebrate species is limited exactly by salinity, and euryhalinity is a precondition for estuarine visitors and inhabitants (Blaber 1997). However, it is unlikely that those euryhaline species will be distributed over the full salinity regime they can tolerate (the potential niche), but rather will be limited to a kind of 'realized' niche (Little 2000). Also, with respect to the other environmental variables, it has been shown that most species are likely to be found within a limited range in the Westerschelde, which does not necessarily mean they are physically limited to these ranges.

In the Thames estuary (UK) it was shown that the combined effect of low salinity and low oxygen levels formed a barrier to migrating brown shrimp *Crangon crangon* (Jones & Wolff 1981). However, fish and macro-invertebrates are highly mobile, and can easily avoid unfavorable conditions (*e.g.* low oxygen concentrations and high turbidity). On the other hand, turbidity may also be important in lowering predation pressure (Blaber & Blaber 1980).

9.5.2 Presence/Absence models

Changes in one variable (*e.g.* salinity) are usually accompanied by changes in several other parameters (*e.g.* current flow, oxygen levels, food supply and so on), which makes it difficult to decide if only one or several factors are important (Little 2000). It is argued that the combined interaction between different environmental variables will be more powerful to predict species occurrence (and density), than the single variables. In the following paragraph best-fitting models were built for the same 15 species, by means of multiple forward stepwise logistic regressions to predict presence/absence.

All response surfaces were highly significant when combining data on temperature, salinity, turbidity, dissolved oxygen concentration and/or their quadratic effects. The addition of other variables, such as current velocity, mysid prey density, chlorophyll a or suspended particulate matter, did not substantially improve the predictions. For most species the prediction of presence/absence was relatively successful, as 60-90 % of the occurrences were correctly predicted (Fig. 9.7). For the eight most common species, sensitivity (% present predicted as pre-

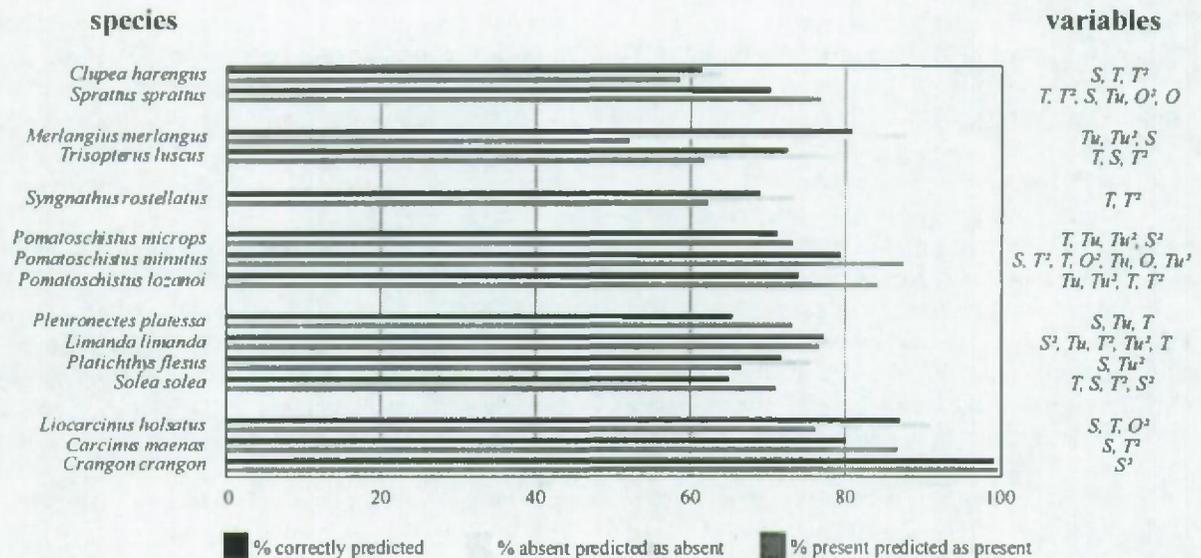


Fig. 9.7 Predictive success (% correct), specificity (% absent predicted as absent) and sensitivity (% present predicted as present) for the 15 presence/absence models, and the selected environmental variables (and/or the quadratic effects) in order of importance per model: temperature (T, T²), salinity (S, S²), dissolved oxygen concentration (O, O²), and turbidity (Tu, Tu²)

sent) was higher than specificity (% absent predicted as absent).

The presence of several fish and macro-crustaceans in the estuary is likely to be triggered by temperature. However, the presence/absence models showed that different environmental variables interact at both temporal and spatial scales. For example, the models for plaice *Pleuronectes platessa* and sand goby *Pomatoschistus minutus* predicted a higher probability of occurrence at lower temperatures (negative sign of the regression coefficient) and higher salinities (positive sign) (Chapter 6). This seemed contradictory to the fact that both species were more common in the 'brackish' part of the Westerschelde. Still, the predictions were in general agreement with the actual presence of plaice and sand goby, as both species were more common during the colder months in this part of the estuary, when the saltwedge penetrates deep into the middle reaches of the estuary. The combined effect of temperature and salinity was more important than the single factors in predicting species occurrence. The same was found in the Severn estuary (UK), where the presence of euryhaline species like whiting, flounder and bass was related with times or areas where salinity was relatively high (Potter *et al.* 1997).

Cross-validation with part of the data sets and with randomly generated values for the 4 environmental variables, proved the models to be accurate and robust (Chapter 6). Also, it was shown that the logistic models that were developed for the Westerschelde were capable of predicting the occurrence (presence/absence) of several demersal fish and macro-crustaceans in the Oosterschelde (see Chapter 6 Addendum). Although for a number of species the absence could not be predicted well, and the pres-

ence/absence models generally failed to predict the absence of species like brown shrimp *Crangon crangon* (also in the Westerschelde) and shore crab *Carcinus maenas*, as these species were present almost everywhere and throughout the year in Oosterschelde.

From the presence/absence models, it can be concluded that, next to species diversity, also species occurrence is dominated by a seasonal rather than a spatial pattern. This might explain why most models could be successfully applied to the Oosterschelde, where no marked salinity/turbidity gradient exists.

9.6 Density patterns

9.6.1 The multivariate (multispecies) approach

The relation between the environmental variables and species abundance at the community level has been tackled since the 1980s by a whole battery of multivariate statistical techniques, either by means of direct or indirect classification or ordination, all with their own pros and cons (James & McCulloch 1990). These techniques created the possibility of summarizing the structural patterns in large multispecies data sets (see Chapter 2-Add.2, Chapter 3-Add.).

In the quantitative description of fish communities, numerical data are most commonly used as abundance measure, and in most situations the choice between numbers and biomass in multivariate analyses matters little (Bianchi & Høisæter 1992). Throughout the different chapters of this thesis on structural patterns (PART I), both density and biomass data were presented and in most cases they yielded the same results when characterizing the

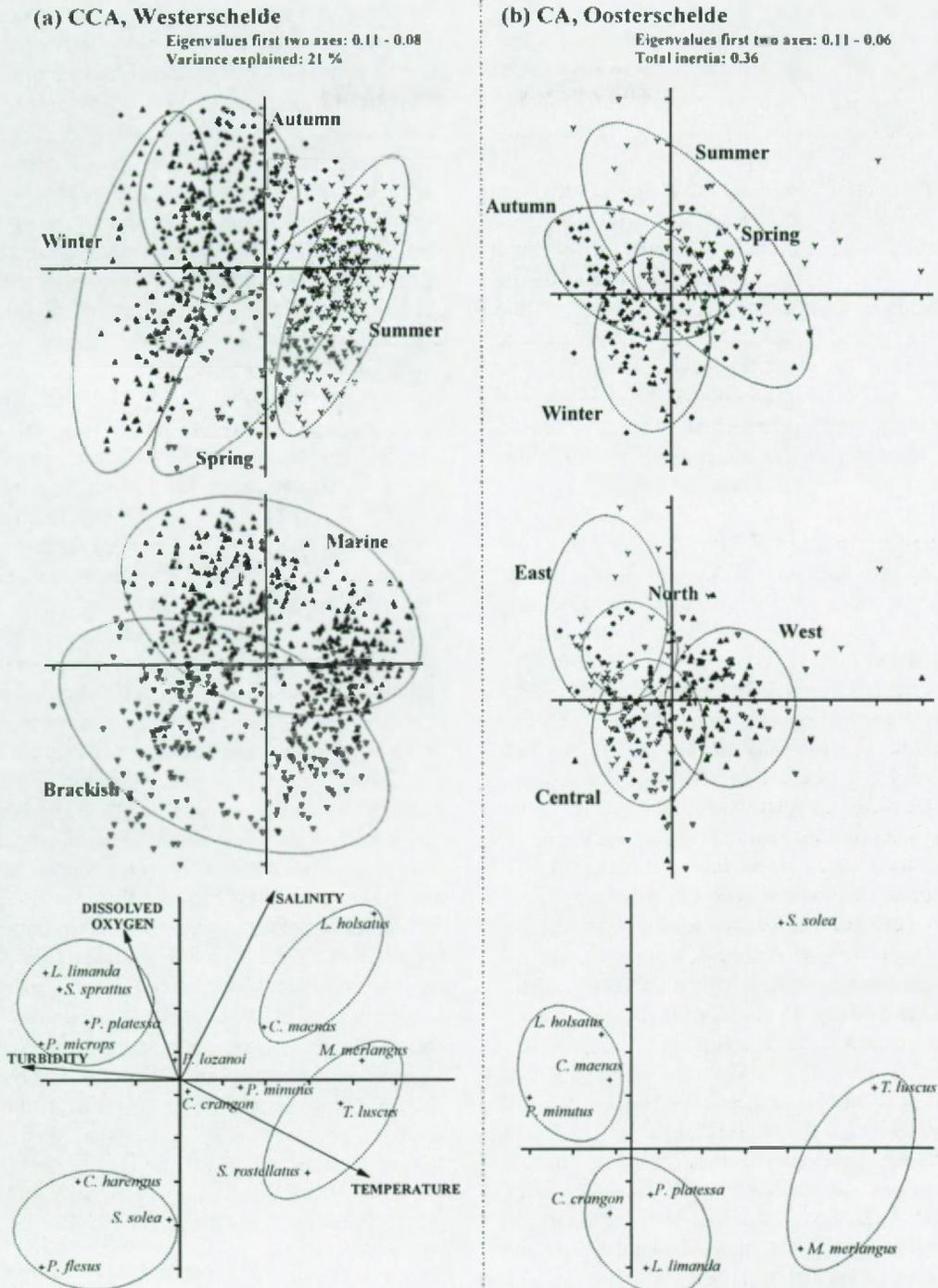


Fig. 9.8 Sample and species(-environmental) scores in the plane of the first two axes, representing seasonal and spatial multi-species responses as a result of (a) Canonical Correspondence Analysis with the Westerschelde data (15 species, 730 sampling points, 4 environmental variables), and (b) Correspondence Analysis with the Oosterschelde data (9 species, 255 sampling points)

demersal fish and macro-invertebrate assemblages. Data reduction through elimination of rare species may alleviate the inordinate amount of zero observations (Field *et al.* 1982).

Canonical Correspondence Analysis (CCA) is now probably the most widely used multivariate direct gradient analysis method in community ecology (Palmer 1993). As the ordination of samples and species is constrained by their relationships to only a

few environmental variables, this type of analysis presumes that meaningful environmental variables are measured. In other words: though a direct gradient analysis facilitates interpretation, the results from the CCA should not deviate much from the pure community gradients shown by CA (Correspondence Analysis) or RA (Redundancy Analysis). Although not always made that clear, many more multivariate analyses were performed for the different studies

than those shown, where the results of different classification and ordination techniques were compared, following the guidelines as indicated in Chapter 2-Add.2. Moreover, multivariate techniques should only be used as descriptive tools in exploratory analyses.

Multivariate analyses on the whole assemblage of the Westerschelde are given in Chapter 2 and Chapter 2-Add.1; on both estuaries in Chapter 3 and Chapter 2-Add.2; on the fish assemblage of the Oosterschelde in Chapter 3-Add. and Chapter 4; and on the macro-invertebrate assemblages in Chapter 5. In this synthesis, the CCA for the Westerschelde was constrained by the 4 environmental variables, and based on 4th-root transformed density data for 15 common species gathered during the monthly surveys in the period 1988-'91 and the quarterly surveys in August 1999- May 2000. As for the Oosterschelde not enough environmental data were gathered, the Correspondence Analysis (CA) was based on the quarterly data for 9 common species, from the periods August 1987 – November 1989 and August 1999 – November 2001.

For the Westerschelde, a seasonal separation in warmer and colder seasons was shown, mainly related to temperature and turbidity, along the first axis (Fig. 9.8a). A spatial segregation between marine and brackish samples (see Fig. 9.1) along the second ordination axis was correlated with salinity and dissolved oxygen. According to their position in the plot of the 2 canonical axes, the species could be classified as typical brackish or marine, typical summer or winter, or indifferent species. Almost the same seasonal patterns were shown in the CA of the Oosterschelde, where the allocation of the species was even more correlated with the corresponding seasonal quadrants (Fig. 9.8b). The aggregation of the sampling points in a western, central, eastern and northern group (cf. Fig. 9.1) was less clear.

As has been shown with the single species response curves and surfaces, the relation with salinity, turbidity, dissolved oxygen concentration and temperature in the Westerschelde seemed quite obvious. The same correlations have been found in many other estuaries (e.g. Henderson 1989, Thiel *et al.* 1995, Cyrus & Blaber 1992, Whitfield 1999). For example, in the Humber estuary (UK), the same correlations were found with temperature, salinity and oxygen, but not with turbidity (Marshall & Elliott 1998). However, Potter *et al.* (1997) concluded that the species composition in the Severn estuary (UK) was not related with either salinity or water temperature. Also, in the Oosterschelde the relation with salinity was probably of less importance.

It was suggested by Maes (2000) that pooling monthly data often produces trivial correlations and that there exists no causal relation between fish distribution and the environment. In the present study, the low eigenvalues and the low percentage of

the variance explained could be partly attributed to the large variation, introduced in the analyses by taking all density values as individual sampling points. Though, the results were in general agreement with previous studies, where data were averaged exactly to reduce this variation (e.g. Chapter 2-Add.2, Chapter 2). Moreover, clear differences in densities were noted within and between the Westerschelde and Oosterschelde estuaries, which is clearly related with the environmental characteristics of the systems. Also, between the Grevelingen and Oosterschelde ebb-tidal deltas differences were found (Chapter 4-Add., Chapter 2-Add.2).

The definition of ecological guilds within the functional guild concept, which was optimized by Elliott & Dewailly (1995), is nowadays widely accepted to describe common patterns of estuarine usage (see Elliott & Hemingway 2002). In Chapter 2, it was shown that species could be further classified dependent on the period of maximum abundance, both on a temporal and spatial scale. For example, some species are typically summer-early autumn species preferring marine waters (e.g. bib *Trisopterus luscus*, whiting *Merlangius merlangus* and flying crab *Liocarcinus holsatus*); others were more or less resident in the Westerschelde, but occurred at higher densities during winter in the brackish reaches (e.g. herring *Clupea harengus*, flounder *Platichthys flesus* and common goby *Pomatoschistus microps*); others were typical winter species which tended to occur at moderate salinities (e.g. plaice *Pleuronectes platessa* and dab *Limanda limanda*). The same patterns were reflected in the multivariate analyses (Fig. 9.8). The most common and estuarine resident species, which occurred almost throughout the estuary (brown shrimp *Crangon crangon*, sand goby *Pomatoschistus minutus* and lozano's goby *Pomatoschistus lozanoi*), were found in the middle of the plots for the Westerschelde. The lack of typical estuarine gradients in salinity and turbidity in the Oosterschelde mainly explains why the seasonal patterns in the fish and macro-crustacean assemblage were clearer than the spatial patterns.

9.6.2 Spatial and long-term patterns

Another way of looking at patterns in community structure is by means of a simple graphical method. The thesis largely benefits from the fact that two different periods with a separation of 10 years could be compared. In the following paragraphs, both spatial and long-term patterns in the overall fish and macro-invertebrate assemblages within and between the Westerschelde and Oosterschelde estuaries are discussed. For comparative reasons, only part of the density data are used, based on the quarterly surveys for the periods February 1988 – November 1989 and February 2000 – November 2001.

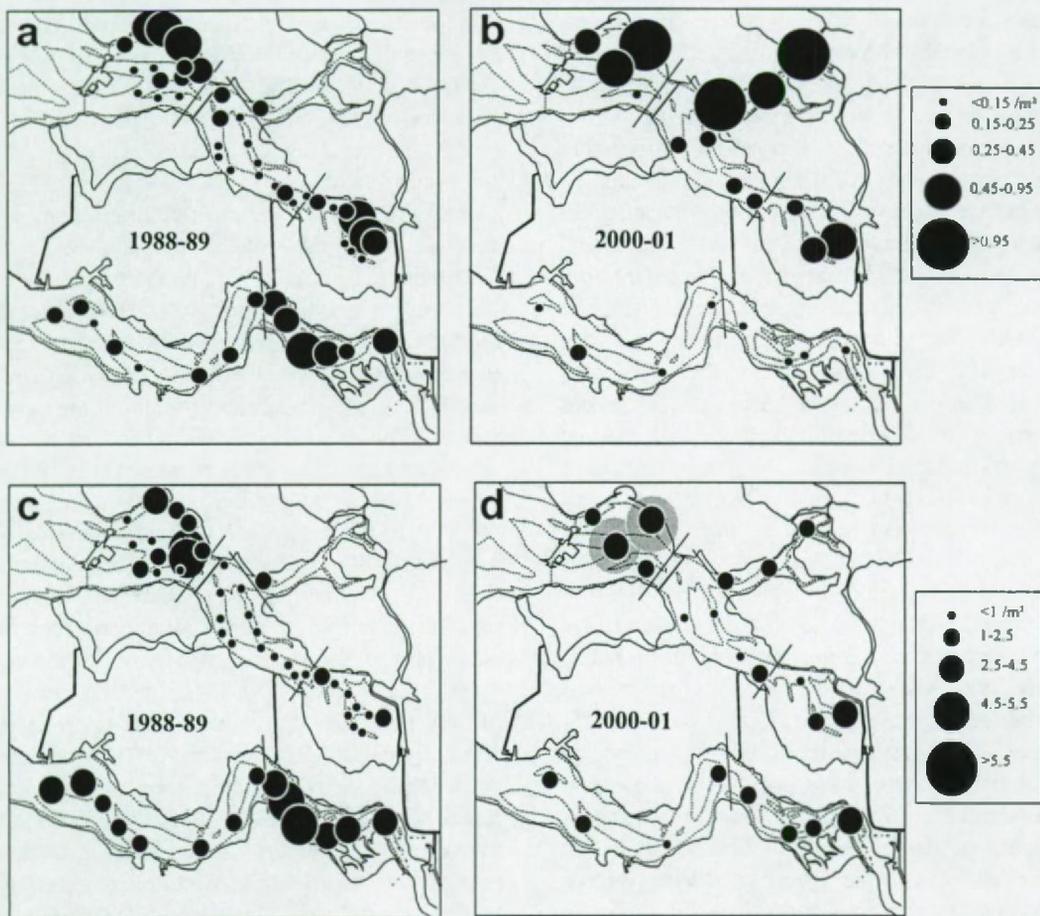


Fig. 9.9 Spatial and long-term patterns in total average densities for the fish (a,b) and macro-invertebrate (c,d) communities in the periods 1988-'89 and 2000-'01 in the Westerschelde and Oosterschelde estuaries. Note the different scales for fish and macro-invertebrates. The grey circles include average densities for ophiroids, which were not investigated during the first period

At the end of the 1980s, total average densities were higher in the brackish part of the Westerschelde, both for the fish (on average 0.4 ind m^{-2}) and macro-invertebrates (on average 4 ind m^{-2}) (Fig. 9.9). The overall dominance of a few macro-invertebrate species (an order of magnitude higher than all fish species together) has been noted for most, if not all, shallow estuarine and coastal areas (overview in Elliott & Hemingway 2002).

At the beginning of 2000, average densities were much lower for both fish (on average 0.1 ind m^{-2}) and macro-invertebrates (1.6 ind m^{-2}), and more or less comparable between the two zones in the Westerschelde estuary. In the Oosterschelde, average fish densities were lowest in the central part (on average 0.4 and 0.9 ind m^{-2}) in both periods, and higher in all subareas in 2000-'01 (on average 1.9 ind m^{-2} in the western, eastern and northern part). Macro-invertebrates densities were a little higher throughout the Oosterschelde in 2000-'01, and were highest in the western part (on average 1.9 and 3.5 ind m^{-2}) in both periods. Total average fish and macro-invertebrate densities were comparable in several subareas between both estuaries in 1988-'89, while this was only the case for macro-invertebrates in

2000-'01. Average fish densities were almost an order of magnitude higher in the latter period in the Oosterschelde compared to the Westerschelde.

From these graphs one might conclude that fish and macro-invertebrates are doing relatively well in the Oosterschelde, while the role of the Westerschelde as a nursery has decreased at the beginning of the 21st century. In the Tagus estuary (Portugal), a decreased abundance of many juvenile fish species (e.g. *Trisopterus luscus*, rockling *Ciliata mustela*, and flounder *Platichthys flesus*) was noted from 1978-'80 towards 1994-'96, which was mainly attributed to pollution, fishery regulation and water-flow control (Costa & Cabral 1999).

Next to the extraction of sand (yearly $3 \cdot 10^6 \text{ m}^3$), dredging the main shipping channel and dumping of the dredged material in the Westerschelde has continuously increased during the past 40 years from 2 to $10 \cdot 10^6 \text{ m}^3$ per year, and mainly takes place in the brackish part (Mol *et al.* 1997). For the recent deepening 48'/43', even $>16 \cdot 10^6 \text{ m}^3$ per year was (and will be) dredged (Anonymous 1998). Both activities lead to a reduction of the shallow subtidal and intertidal habitats (erosion of the flats and filling of the marsh creeks), which are necessary foraging areas

and refuges for juvenile fish and macro-crustaceans. Independent of habitat loss, changed sediment characteristics (coarser sand and more shell fragments) and disturbance due to the increased dredging activities during recent years, may also have contributed to the lower densities in 2000-'01 in the Westerschelde.

On the other hand, the high densities in 2000-'01 in the Oosterschelde may partly be related to net efficiency and conversion problems. During several surveys in this latter period, the net was clogged with macrophytes, which may have increased the net efficiency for smaller organisms (Chapter 4). These allochthonous algal mats also seem to be of major concern for the harvesting of mussels in the Oosterschelde. To reduce the risk of tearing or losing the net (due to high amounts of oysters, mud, macrophytes, tunicates) mainly in the eastern and northern part of the Oosterschelde, the sampling distance was reduced from 1000 to 500 m and sometimes to 300 m during most surveys in 2000-'01 (see Chapter 5). The conversion to a standard unit surface, will surely have led to overestimations of the real densities present in these subareas. Moreover, natural inter-annual variability partly obscures long-term changes in fish density. Additionally, the protection of the Oosterschelde as nature reserve and the complete banning of fishing activities (except shell and recreational fishery) in the Oosterschelde may have created favorable conditions for growing up juvenile fishes.

9.6.3 Seasonal patterns per taxonomic group

While Chapters 2 and 3 mainly focused on the 1980s, the comparison between seasonal, spatial and long-term patterns in density, biomass and growth for the different taxonomic groups at the end of the 1980s and 1990s, has been extensively discussed in Chapters 4 and 5.

As the ecological guild concept is used to describe the seasonal patterns, it may be necessary to explain the terms used: ER - estuarine resident species, which spend their entire lives in the estuary; MJ - marine juvenile migrant species, which use the estuary as a nursery and spend the rest of their life at sea; MS - marine seasonal migrants species, which regularly visit the estuary as adults; MA - marine adventitious visitors or stragglers, which can appear in the estuary, with no apparent estuarine requirements; CA - catadromous/anadromous migrant species, which pass through the estuary between their spawning and feeding areas; FW - freshwater adventitious species, which occasionally enter the estuary (Elliott & Dewailly 1995).

The following paragraphs are again based on the quarterly density data from the periods 1988-'89 and 2000-'01. Although, Fig. 9.10 and Fig. 9.11 contain a lot of information on spatial and long-term patterns as well, mainly the seasonal patterns for the

commonest species within the different taxonomic groups will be discussed here. The possible reasons for the higher densities in 2000-'01 for most groups have been given in the previous paragraph.

Gobiidae

Gobies are amongst the most common fish species in coastal and estuarine habitats (Miller 1986, Hamerlynck 1990). In the Westerschelde, three gobiid species Lozano's goby *Pomatoschistus lozanoi* (MA), sand goby *Pomatoschistus minutus* (ER), and to a lesser extent common goby *Pomatoschistus microps* (ER), were common throughout the year, but at lower densities in spring when the first two species are located in deeper water to spawn (Fig. 9.10a).

Although six gobiid species were recorded in the Oosterschelde, only *P. minutus* was really common during the same seasons as in the Westerschelde (Fig. 9.11a). Also, in other European estuaries *P. lozanoi* seemed to be only sporadically recorded and was therefore categorized as MA (e.g. Pomfret *et al.* 1991, Thiel *et al.* 1995). Probably, the low densities of mysids (Chavatte 2001), its preferred prey (Hamerlynck & Cattijssse 1994, Chapter 7) and the predation by visual predators such as bib *Trisopterus luscus* (Chapter 7-Add.) due to the high water transparency in the Oosterschelde, are the main reasons why this species is not able to establish itself in the Oosterschelde (Chapter 2-Add.2).

Pleuronectiformes

Estuaries are important nurseries for flatfish (e.g. van der Veer *et al.* 1990b, Henderson & Seaby 1994). In terms of biomass they are the most important group of fishes (Chapter 3, Chapter 4). Of the eight species, three species are common in both estuaries, all with higher densities in the brackish part of the Westerschelde, and in the western and northern part of the Oosterschelde (Fig. 9.10b). Dab *Limanda limanda* (MJ) was the commonest species in the Westerschelde, but only present in autumn-winter. Also, plaice *Pleuronectes platessa* (MJ) was mainly recorded in autumn-winter.

In the Oosterschelde, plaice was the commonest species, and both plaice and dab were abundant throughout the year (Fig. 9.11b). In the period 1969-'78, before the engineering works in the Oosterschelde, dab showed more or less the same density pattern as in the Westerschelde (De Veen *et al.* 1979). As the Oosterschelde was altered from a real estuary into a marine bay, dab (and plaice) densities in 1988-'89 and 2000-'01 resembled a coastal pattern, comparable to that in the shallow ebb-tidal delta of the Grevelingen (Chapter 4-Add.). In shallow subtidal coastal areas, small juveniles arrive earlier at higher densities and especially larger individuals (1 and 2 group) stay longer in the ecosystem during springtime (Chapter 4-Add.). In winter two cohorts of *L. limanda* and *P. platessa* could be detected,

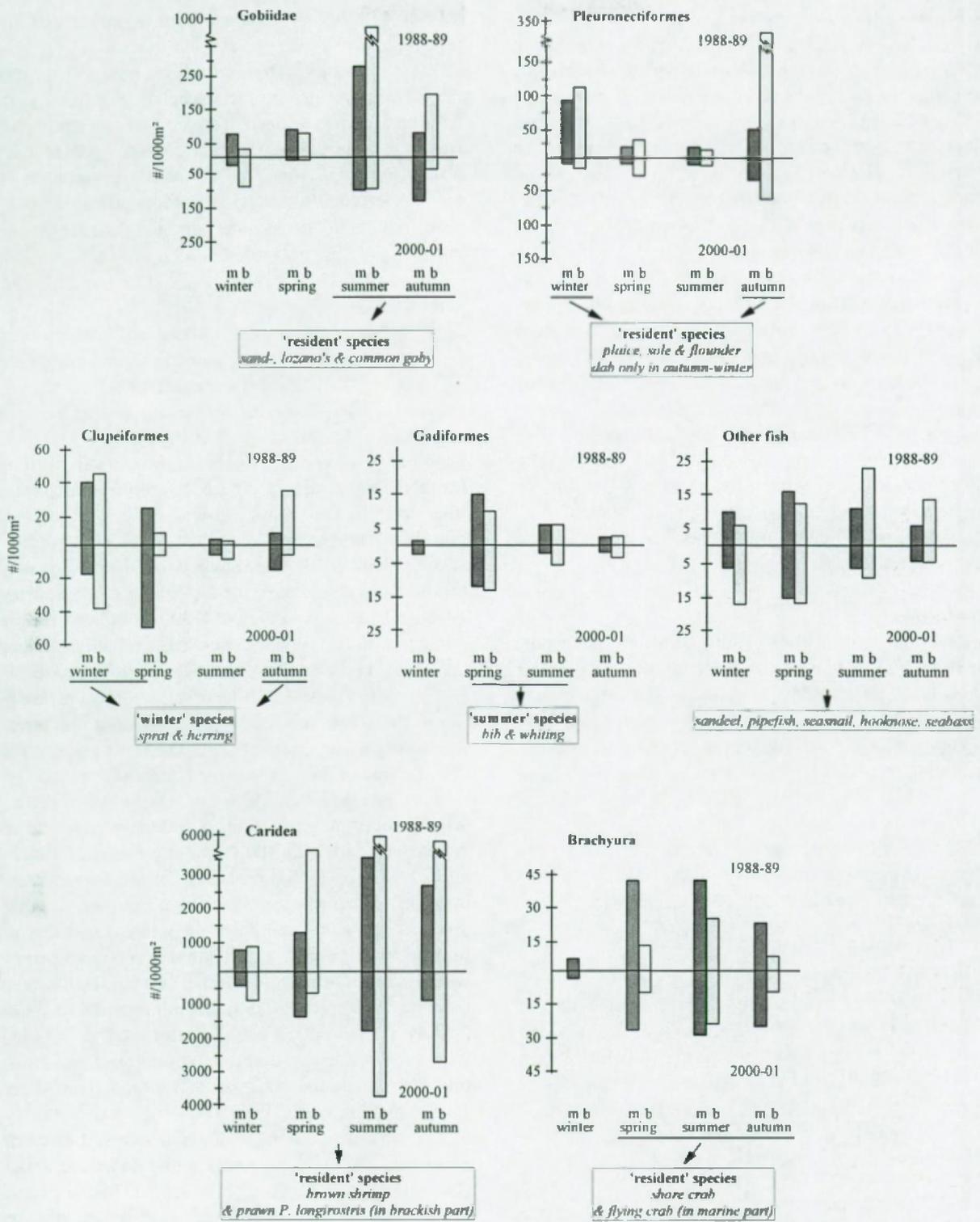


Fig. 9.10 Seasonal, spatial and long-term patterns in average densities per taxonomic group in the periods 1988-'89 (upper part of the graphs) and 2000-'01 (lower part) in the Westerschelde estuary; subareas: marine (m) and brackish (b). An indication of the main species is given

which was in accordance with observations in the estuaries on the west coast of Scotland as well as in the Wadden Sea (Elliott *et al.* 1990).

Although, 22 % of the juvenile sole *Solea solea* (MJ) population in the Dutch coastal waters are located in the Delta area, this species was recorded in lower numbers in both estuaries, compared to plaice

and dab. As *S. solea* prefers muddy substrates (*e.g.* Marchand 1988), a 3-m beam trawl with only 1 tickler chain, may not be efficient enough to catch this species. Flounder *Platichthys flesus* (ER/CA) was present throughout the year in lower numbers in both estuaries.

Clupeiformes

Of the 4 clupeoid species only 2 species are really common in both estuaries, with sprat *Sprattus sprattus* (MS) mainly present in autumn and winter (Fig. 9.10c and Fig. 9.11c). Herring *Clupea harengus* (MJ) was more common than sprat (except for the period 1988-'89 in the Westerschelde), also occurring mainly in the colder months in the Oosterschelde, but with a shift towards winter and early-spring in the Westerschelde.

In the Thames estuary (UK) peak abundances of herring and sprat were found in December-March, which was correlated with high dissolved oxygen concentrations and low temperatures (Power *et al.* 2000a). Gobies, nilsson's pipefish *Syngnathus rostellatus*, and clupeoids were the only important groups in the Zeeschelde (Belgium), where pipefish arrived in summer, gobies in late fall and juvenile clupeoids in early winter (Maes *et al.* 1998a). No explanation was found for the high density peak of *C. harengus* in summer in the northern part of the Oosterschelde.

Gadiformes

Of the four gadoid species, only 2 species are common in both estuaries, with bib *Trisopterus luscus* (MJ) twice as abundant as whiting *Merlangius merlangus* (MJ). They are typical 'summer' species, with 0-group whiting mainly present in spring, and bib extending its occurrence till summer (Fig. 9.10d and Fig. 9.11d). Although 1+ individuals were recorded in low numbers throughout the year.

Both gadoid species are an important ecological component of shallow coastal waters and estuaries (Claridge & Potter 1984), and were extensively studied in many areas (Chapter 7-Add.).

Other fish species

Most other fish species are less common, with the exception of nine species (5 in each estuary) which are almost all classified as estuarine resident species (Fig. 9.10e and Fig. 9.11e). Nilsson's pipefish *Syngnathus rostellatus* (ER) was mainly found in spring-summer, mainly in the brackish part of the Westerschelde and not from the western part of the Oosterschelde.

Dragonet *Trigla lucerna* (MJ), viviparous blenny *Zoarces viviparus* (ER) and butterfish *Pholis gunnellus* (ER) were mainly recorded from the Oosterschelde, throughout the year, with dragonet mainly in summer-autumn, viviparous blenny almost not in the eastern part, and butterfish almost not in the western part.

Sandeel *Ammodytes tobianus* (ER) and seasnail *Liparis liparis* (ER) were mainly recorded from the Westerschelde. Sandeel was found throughout the year, but more in winter in 1988-'89 and more in the marine part in 2000-'01. Seasnail is a typical bimodal

species with higher densities both in spring and autumn (Chapter 2).

Bull-rout *Myoxocephalus scorpius* (ER) was more common in the Oosterschelde, but less in autumn and with a decreased density in 2000-'01. Hooknose *Agonus cataphractus* (ER) and seabass *Dicentrarchus labrax* (MJ) were more common in the Westerschelde during the colder months, hooknose mainly in the marine part and seabass in the brackish part, but not in 1988-'89.

Caridea

Three caridean shrimps were recorded of which only 1 in the Westerschelde. Brown shrimp *Crangon crangon* (ER) is the most common macro-crustacean species in both estuaries, occurring throughout the year at high densities (Fig. 9.10f and Fig. 9.11f). It is commercially fished on the North Sea coasts, with an average annual landing of 2.6 10⁴ tonnes (consumption shrimps) between 1995 and 2000 (Anonymous 2001). Although, the contribution of the Westerschelde to the exploitable stock of the North Sea may be rather low compared to the Dutch coast and the Wadden Sea (Anonymous 2001), the juvenile population in the Westerschelde is probably a major contributor to the adult stocks in the Belgian coast.

The lower densities of *C. crangon* in 1988-'89 in the Oosterschelde were related to a temporarily disturbed distribution during the 1980s, due to the construction of the storm-surge barrier (Chapter 5).

The nine caridean prawns in the Oosterschelde were mainly found in autumn-winter and in the eastern part, with the commonest species *Palaemon adspersus* (MS), probably related to the presence of green macro-algae and seagrasses (Pihl 1986). This 'alien' species clearly took the niche of other prawn species, as till the 1980s *P. adspersus* was almost not caught in the Dutch Delta area (Adema 1988). Also, *Pandalus montagui* (MS), *Palaemon elegans* (MS) and *Palaemon serratus* (MS) were of some importance in the Oosterschelde, also related to sediment and vegetation type (Heerebout 1974, Smaldon *et al.* 1993). Probably, the abundance of the caridean prawns will be underestimated, as these species are more likely to be found on other than soft substrates.

In the Westerschelde, 2 caridean prawns were recorded, but only white shrimp *Palaemon longirostris* (MS) was of some importance, mainly in spring-summer and in the brackish part. This species was probably not present in 1988-'89 (Mees *et al.* 1995). The re-occurrence of *P. longirostris* in the Westerschelde is probably related to an improved water quality. In the lower Zeeschelde (Belgium) this species was replaced by *Palaemonetes varians*, which together with *C. crangon*, were the only macro-invertebrates of importance in the upper part of the Schelde estuary (Maes *et al.* 1998a).

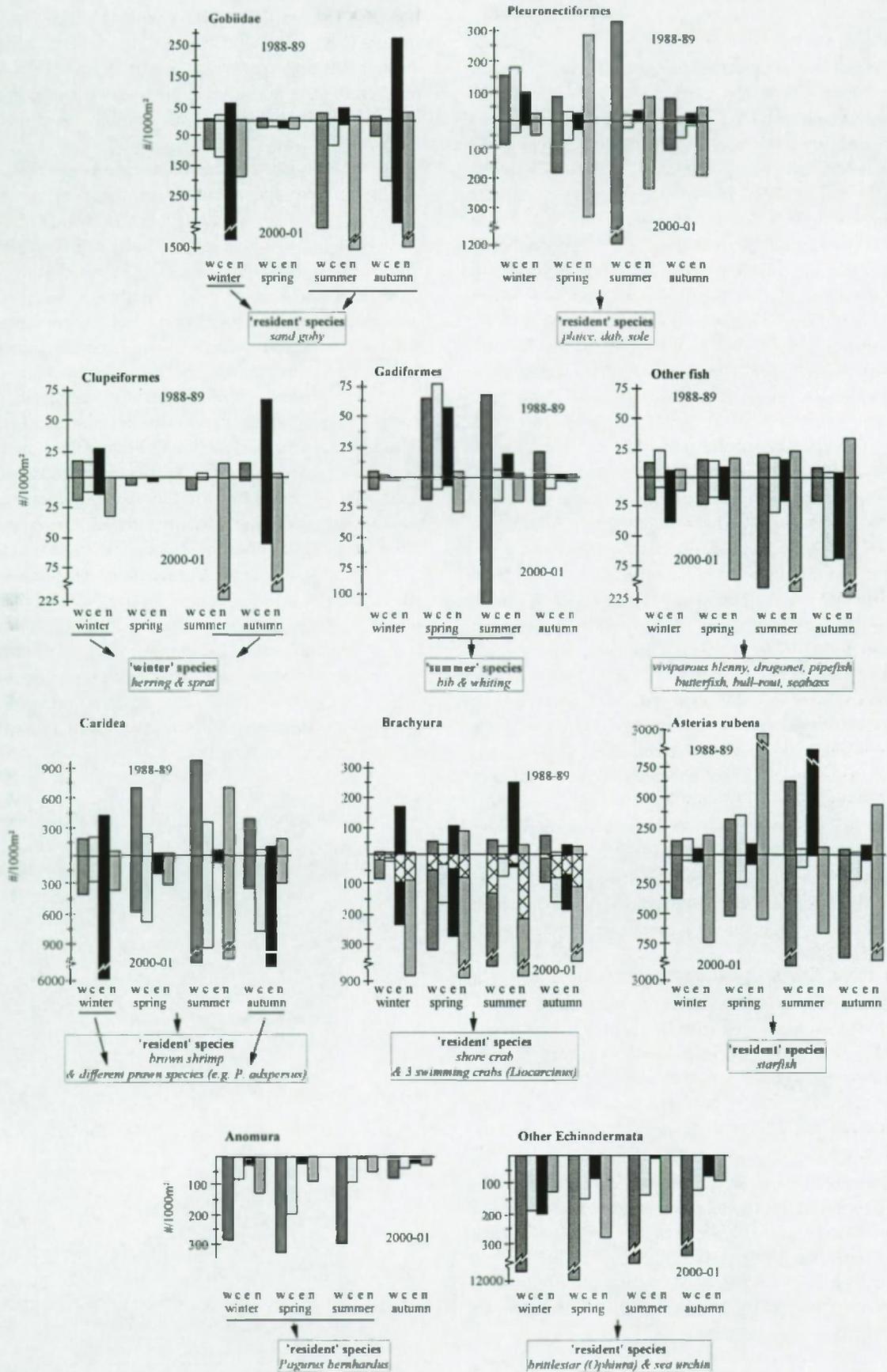


Fig. 9.11 Seasonal, spatial and long-term patterns in average densities per taxonomic group in the periods 1988-'89 (upper part of the graphs) and 2000-'01 (lower part) in the Oosterschelde estuary; subareas: western (w), central (c), eastern (e) and northern (n). An indication of the main species is given. Hatched bars for the Brachyura include crab species, which were not investigated during the first period

Brachyura

Of the 10 brachyuran species, only 3 species were recorded in the Westerschelde and 9 species in the Oosterschelde, with an overall dominance of shore crab *Carcinus maenas* (ER) throughout the year. *C. maenas* has been found to be common in other estuaries as well, related to substratum type, e.g. higher production in areas with musselbeds on the Swedish west coast (Pihl & Rosenberg 1982). This species is well adapted to adjust its apparent water permeability in response to decreased salinities (Rainbow & Black 2001), which explains why this species is also found in high numbers in the brackish part of the Westerschelde (Fig. 9.10g). The presence of berried females of *C. maenas* throughout the year (but mainly in spring), was in agreement with the presence of different brood waves in the shallow coastal waters in Sweden (Pihl & Rosenberg 1982).

Flying crab *Liocarcinus holsatus* (MJ/ER) was mainly present in spring-summer in the marine part of the Westerschelde, while together with arch-fronted swimming crab *Liocarcinus arcuatus* (ER) and harbour crab *Liocarcinus depurator* (ER), these swimming crabs are found throughout the year in the Oosterschelde (Fig. 9.11g). However, *L. holsatus* reached highest densities in the western part, while *L. depurator* was mainly recorded from the northern part. The latter species only started to colonize the Oosterschelde since 1990 (Adema 1991b). This spatial separation was probably related to their sediment preferences. The successful invasion of *L. arcuatus* since 1982 may be related to its herbivorous feeding habits (Adema 1991a). Moreover it is the only crab species with a changed sex ratio from 1:1 to 3:1 females over males during the colder seasons, which could be advantageous for a rapid population growth (Chapter 5).

The spider crab *Macropodia rostrata* (MS) was of some importance in the Oosterschelde, mainly in summer, but the densities are probably underestimated, as this species prefers rough substrates (Wolff & Sandee 1971).

Anomura

Two species of hermit crabs were recorded in the Oosterschelde, with only *Pagurus bernhardus* (ER) being common throughout the year, but mainly found in the western part (Fig. 9.11i). This group was only investigated in 2000-'01. The absence of hermit crabs from the Westerschelde is probably related to the lack of suitable gastropod shells, rather than to salinity preferences (Chapter 5).

Echinodermata

Most echinoderms prefer higher salinities, which probably explains the absence of this group in the Westerschelde (Wolff 1968). Six species of echinoderms were found in the Oosterschelde, but only star-

fish *Asterias rubens* (ER) and brittlestar *Ophiura* species (ER) (*O. ophiura* and *O. albida*) are abundant throughout the year (Fig. 9.11h & j). *A. rubens* reached highest densities in the western and northern part, while *Ophiura* were only common in the western part.

The high densities of *A. rubens* are probably correlated with the abundant presence of its main food source, blue mussel *Mytilus edulis* in the Oosterschelde (Guillou 1996, Smaal & Lucas 2000). The absence of starfish in the Westerschelde may also be related to industrial pollution with polychlorinated biphenyls (PCB) and heavy metals (Cadmium), which seem to affect their reproduction (den Besten 1991, Chapter 2-Add.2).

O. ophiura prefers soft sediments and has been found in thick layers in several areas (e.g. Wolff 1968, Aronson 1989). The success of the brittlestars is probably related to a series of successive mild winters at the end of the 1990s, which has a positive effect on the high interannual variability of these species (Leewis *et al.* 1994).

The other echinoderms *Echinocardium cordatum*, *Psammechinus miliaris* and *Ophiothrix fragilis* were only of limited importance. *E. cordatum* was mainly present in spring-summer in the western part. The other two were recorded throughout the year, with *P. miliaris* mainly in the western and northern part, and *O. fragilis* mainly in the eastern and northern part of the Oosterschelde.

9.6.4 Seasonal patterns throughout the early history

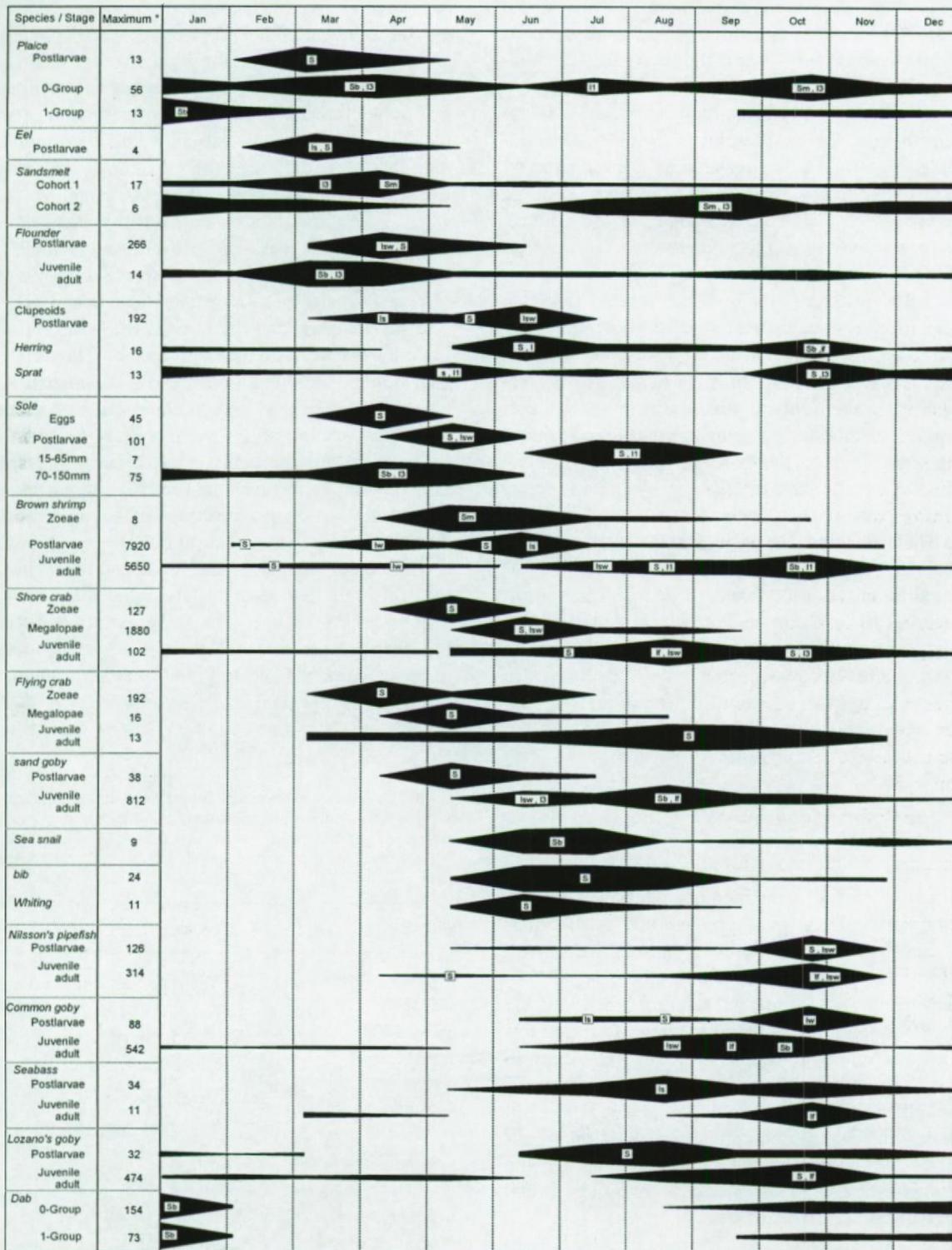
In conclusion of the previous paragraph, it has been shown that estuarine residents (ER) and marine juveniles (MJ) are the commonest species in both estuaries, sometimes with a preference for a certain part of the estuaries. Also, only few species are really abundant as well in the Westerschelde as in the Oosterschelde. Many marine seasonal or adventitious species (MS/MA) increased the biodiversity of the fish and macro-invertebrate assemblages, but these are usually found in low numbers during different part of the year, and mostly in the higher salinity reaches. Only one freshwater (FW) species and only six catadromous species (CA) were recorded in the Westerschelde during the study period described in these paragraphs. More or less the same conclusions were drawn for several other European estuaries (see Elliott & Hemingway 2002).

Moreover, not only the subtidal, but also the other subhabitats of an estuary are inhabited during different periods, by different species and several life stages of fish and macro-invertebrates. In the following paragraphs, a combination of the (post)larval appearance and the juvenile/adult life stages of 17 common species, is presented for the Westerschelde estuary. This summarizing graph (Fig. 9.12) is based on subtidal data from the marine and brackish zones

gathered between 1988-'91, intertidal data gathered in 1992 at 2 different depths (MTL -1 m and -3 m) on the brackish intertidal flat of Valkenisse-Walsoorden, and intertidal data gathered in 1990-'91 in two brackish saltmarsh creeks (Saefinghe and Waarde) (see Chapter 1, and Fig. 9.1). More details are given in Hostens *et al.* (1996) and in Chapter 2.

More or less the same patterns were found for the fish and macro-invertebrate assemblages in the Oosterschelde (see Chapter 4, Chapter 5).

First of all, a clear succession of the different life stages per species can be seen, from egg or larvae, over postlarvae to juvenile 0-group and juvenile 1-group individuals (Fig. 9.12). Secondly, a seasonal



* (The largest width of the kites agrees with the given maximum density (#/1000m²) per species, averaged per month (1988-1992) for all subhabitats) Subtidal (S) marine (Sm) and brackish (Sb), Intertidal (I) flat (If) -3m stratum (I3) and -1m stratum (I1), intertidal saltmarsh creek Saefinghe (Is) and Waarde (Iw).

Fig. 9.12 Summarizing scheme on the seasonal appearance of different early-life history stages of 17 common species in different subhabitats of the Westerschelde, with an indication of the subhabitats where the life stages were recorded with the highest densities

succession of different species is shown, where post-larvae of plaice *Pleuronectes platessa* and eel *Anguilla anguilla* and the smallest juveniles of sandeel *Ammodytes tobianus* already appear in February (late-winter) in the Westerschelde. Most of the species appear in early-spring, like brown shrimp *Crangon crangon*, shore crab *Carcinus maenas*, swimming crab *Liocarcinus holsatus*, flounder *Platichthys flesus*, herring *Clupea harengus*, sprat *Sprattus sprattus*, sole *Solea solea* and sand goby *Pomatoschistus minutus*. Others appear for the first time in late-spring, like seasnail *Liparis liparis*, bib *Trisopterus luscus*, whiting *Merlangius merlangus*, seabass *Dicentrarchus labrax* and lozano's goby *Pomatoschistus lozanoi*. These species then are followed by a number of species, which appear in summer in the Westerschelde, like nilsson's pipefish *Syngnathus rostellatus*, common goby *Pomatoschistus microps* and dab *Limanda limanda*.

Highest densities of (post)larvae for brown shrimp, flounder, clupeoids, pipefish, common goby and seabass are recorded from the intertidal saltmarsh creeks. Highest densities of most juveniles were recorded from the subtidal and/or the intertidal flat. Although, estuarine resident species are present throughout the year, several species show a preference for either the warmer (summer-resident species) or colder seasons (winter-resident species). Most of the marine juvenile species appeared at varying times (summer, winter or bimodal), but most of the O-group cohorts reach their highest densities in spring-summer and often remain for only a short time. A number of species are more common in summer-autumn, while dab, plaice, sole and sandeel, are also represented by a 1+ cohort during winter-spring. Older individuals are only occasionally noted in the estuary.

9.6.5 Prediction of abundance

Clear seasonal and/or spatial patterns in density (and biomass) of the different demersal fish and macro-invertebrate species were pointed out. Also, long-term density patterns in both estuaries were shown. Single-species models can contribute to reveal important species-environmental relationships (Attrill *et al.* 1999). In addition to the prediction of occurrence, it was also tried to predict patterns (changes) in abundance of 15 common species. This was done by means of single species multiple linear regression models, with 4 environmental variables and their quadratic derivations as the forcing effects, and the log-transformed (ln+1) density data from the subtidal Westerschelde (Chapter 6).

Although most density models agreed with the actual distribution of the species, these models generally failed to predict extreme peaks and troughs, which is not uncommon to data series that fluctuate through several orders of magnitude (Nisbet & Gur-

ney 1982). In accordance with the presence/absence models, both temporal and spatial patterns were predicted, but the different models could only explain between 20-55 % of the variance (Table 9.2).

Best models were built for those species that were present in the estuary for a longer period, but with only one clear density peak in either a cold or a warmer season (see previous paragraph). In decreasing order of variance explained, these were the models for *Limanda limanda*, *Pomatoschistus microps*, *Carcinus maenas*, *Liocarcinus holsatus*, *Platichthys flesus*, *Sprattus sprattus* and *Pomatoschistus minutus*. It is concluded that the combined interaction between the four environmental variables was the main forcing factor structuring the temporal and spatial distribution of these seven species (Chapter 6).

The least models concerned species belonging to the ecological guild of 'marine juveniles', i.e. species that either were present in the estuary during only a short period (*Trisopterus luscus* and *Merlangius merlangus*), or to species with higher densities in both a warmer and a colder season (*Clupea harengus*, *Solea solea* and *Pleuronectes platessa*). Also, the density models for *Syngnathus rostellatus*, *Pomatoschistus lozanoi* and *Crangon crangon* were less successful. Most probably, the temporal and spatial distribution of the latter eight species was more governed by the proper appearance of suitable food resources (Hemingway & Elliott 2002).

In a next step, the six best-fitting models were applied to a data set from the Oosterschelde (Chapter 6 Addendum). These were mainly successful when temperature was the main forcing variable (e.g. for *Sprattus sprattus* and *Pomatoschistus microps*). The constant high salinity in the Oosterschelde is a favorable condition for *Carcinus maenas*

Table 9.2 Variance explained (R^2) for the 15 density models, and the selected environmental variables (and/or the quadratic effects) in order of importance per model: temperature (T, T^2), salinity (S, S^2), dissolved oxygen concentration (O, O^2), and turbidity (Tu, Tu^2)

Species	R^2	Variables
<i>Clupea harengus</i>	0.33	S, S^2 , Tu^2 , T
<i>Sprattus sprattus</i>	0.50	T, T^2 , O^2 , O, S, Tu
<i>Merlangius merlangus</i>	0.32	Tu, Tu^2
<i>Trisopterus luscus</i>	0.28	T, S^2
<i>Syngnathus rostellatus</i>	0.30	S^2 , T, S
<i>Pomatoschistus microps</i>	0.55	T, T^2 , Tu, O^2
<i>Pomatoschistus minutus</i>	0.45	O^2 , O, T^2 , T, Tu, Tu^2 , S
<i>Pomatoschistus lozanoi</i>	0.22	S, T, T^2 , S^2
<i>Pleuronectes platessa</i>	0.27	Tu, S, T^2
<i>Limanda limanda</i>	0.58	T^2 , O^2 , T, O, Tu, S, Tu^2 , S^2
<i>Platichthys flesus</i>	0.51	S, O, O^2 , S^2 , T
<i>Solea solea</i>	0.37	S, S^2 , T, T^2
<i>Liocarcinus holsatus</i>	0.54	S^2 , S, T^2 , O^2
<i>Carcinus maenas</i>	0.54	S, T, Tu
<i>Crangon crangon</i>	0.22	O^2 , O, T

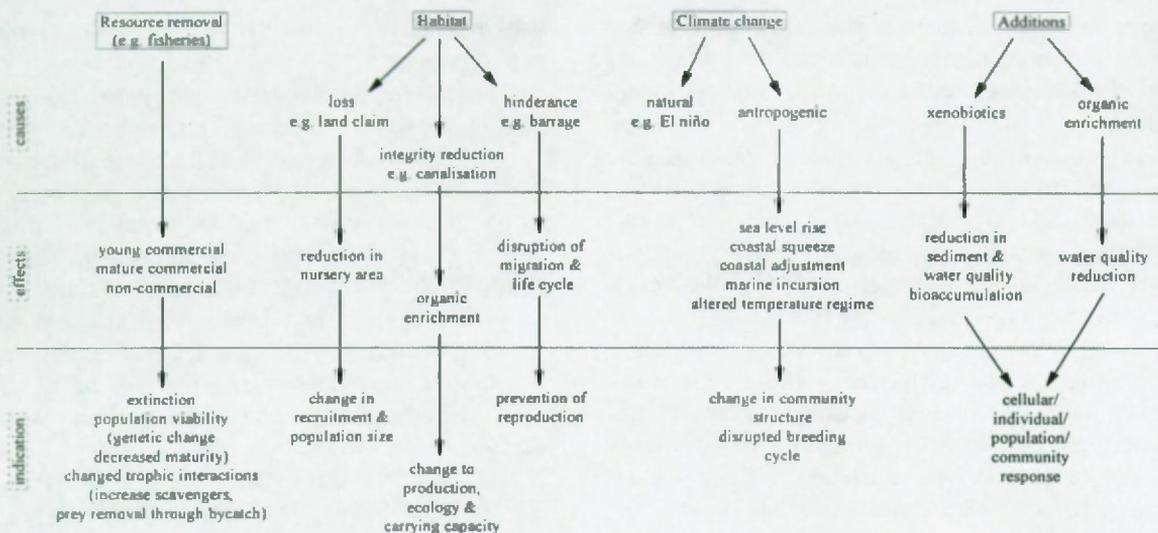


Fig. 9.13 Schematic overview of human impact on environmental changes and on the fish and macro-invertebrate assemblages (after Elliott 2002)

and *Liocarcinus holsatus*, partially repressing the effect of the other environmental variables in these models. *Limanda limanda* and *Pomatoschistus minutus* showed a different seasonal distribution pattern in the Oosterschelde, which could not be predicted by the Westerschelde models. Perhaps for *L. limanda* a distinction should be made between the different cohorts (0- and 1+ groups). Also, it could be that the Westerschelde models are less useful in the Oosterschelde, as some of the environmental variables found in the Oosterschelde are at the limit (even outside the limits for turbidity) from the ranges found in the Westerschelde.

There has been much discussion about the relative importance of environmental and biological factors in regulating natural populations, where environmental variables are associated with stochastic fluctuations, and biological ones with deterministic regulation (Sugihara *et al.* 1990). Probably other variables are needed to improve the prediction of density in both systems.

9.7 Human impact

Up till now we have tried to relate structural patterns in biodiversity, occurrence and density to the environment. Throughout this overview we briefly touched upon the impact of human activities on the integrity of the demersal fish and macro-invertebrate assemblage and on the estuarine environment in both estuaries.

Human impact can be grouped in general terms as additions (of pollutants, diseases, structures) or as removals (of space as area or volume, and of physical or biological components) (Elliott 2002). Hence, the major threats to estuarine fish and macro-

invertebrates can be summarized as follows: (1) overfishing and the ecosystem effects of fisheries; (2) modifications to the habitat and the effects of climate change; (3) the repercussions of polluting inputs, including chemical, biological and physical inputs to the system (Fig. 9.13).

Resource removal through overfishing usually takes place outside the estuary, and may lead to a reduced population viability and changed trophic interactions, leading to a decreased input of juveniles into the estuarine nurseries. Habitat reduction and disturbance may decrease the carrying capacity of a system. Most probably, the dredging activities in the Westerschelde contributed to the decreased densities in 2000-'01. Hinderance mainly leads to a decrease in diadromous species (Maes 2000), but is of less importance in the Westerschelde. Also, the engineering works in the Oosterschelde may have led to temporarily changes, but a decade later the fish and macro-invertebrate populations reverted to pre-barrier densities (Hostens *et al.* 1993, Chapter 4).

Additions of alien species may have a negative impact on the native populations, as is the case in the Oosterschelde for a number of crab species (Chapter 5). Organic enrichment and the subsequent oxygen depletion are known problems in the upper part of the Schelde estuary, but this will probably only have a minor effect on the fish and macro-invertebrate distribution in the Westerschelde, as dissolved oxygen concentrations rarely dropped below 5 mg l^{-1} throughout the whole study period of the present thesis in this part of the estuary (Chapter 6). Moreover, the water quality in the upper part of the Schelde has improved during the past decade through waste water treatment and the reduction of nutrient inputs (Van Damme *et al.* 1999).

Problems with chemical pollution may be more of concern in the near future, linked to an im-

proved oxygen balance in the upper part of the Schelde estuary. Although, little is known about the fate of this type of pollution in the estuary, except that they are bound to fine sediments (Van Eck *et al.* 1998). As such, they are not directly dangerous for fishes and macro-invertebrates. Still, there is a general lack of basic understanding about the various toxic substances, *e.g.* the complexes of heavy metals and micropollutants that may be formed due to increased oxygen levels (Little 2000).

Human impact surely has contributed to the diminishing quality of the Dutch Delta area. However, it is difficult to make a distinction between human impact and natural population variability. It is still not known how and at which life stage population regulation works (Rijnsdorp *et al.* 1991). Most probably, long-term and expensive data monitoring are needed to fully understand this problem.

9.8 A generalised food web of the Westerschelde

Next to the structural forcing environmental variables, the nursery function is largely dependent on food availability. In an early assessment, it was noted that generalised estuarine food chains are basically fuelled by either phytoplankton or detritus as a source of energy (de Sylva 1975). Recent studies proved that microphytobenthos, dissolved organic matter, bacteria and microfauna (the so-called microbial loop) are likely to be the starting point of the food chains, especially in turbid estuarine environments (Billen *et al.* 1990, Heip *et al.* 1995). However, it is as yet not clear which factor really contrib-

utes most to the rest of the food chain (P. Herman, pers. comm.).

Several studies have constructed food webs of fish assemblages in estuarine systems, all of them showing a high complexity (overview in Elliott *et al.* 2002). The generalized food web presented here, has by no means the intention to be 'complete'. Building food webs is time consuming and labour intensive (Little 2000). Surely, not all biological components are studied or taken into account, and links are partly based on literature. The present thesis largely benefits from complementary research on other biotic compartments in the very well studied Westerschelde.

Still, the relative importance of each component and the energy flow between them is not included (*e.g.* Baird & Ulanowicz 1993). Either the data on production/consumption do not exist, or those data largely suffer from conversion problems at several steps of the calculations (see Gerking 1994). First, there is the problem of net-efficiency in the calculation of densities and growth (see Chapter 1), and the gravimetric conversion to biomass/production units. Secondly, there is the problem of consumption calculations by means of experiments on gut-passage time, daily rations, and the gravimetric conversion of food-items. Thirdly, there are problems of upscaling from experiments to the field, from small areas to large areas, and even from one area to another. All these factors make it almost impossible to calculate appropriate energy budgets. Several attempts led to enormous discrepancies (see Chapter 7-Add., Chapter 8)

The food web is based on that of Henderson *et al.* (1992), presenting the trophic levels from primary producers to primary, secondary and higher

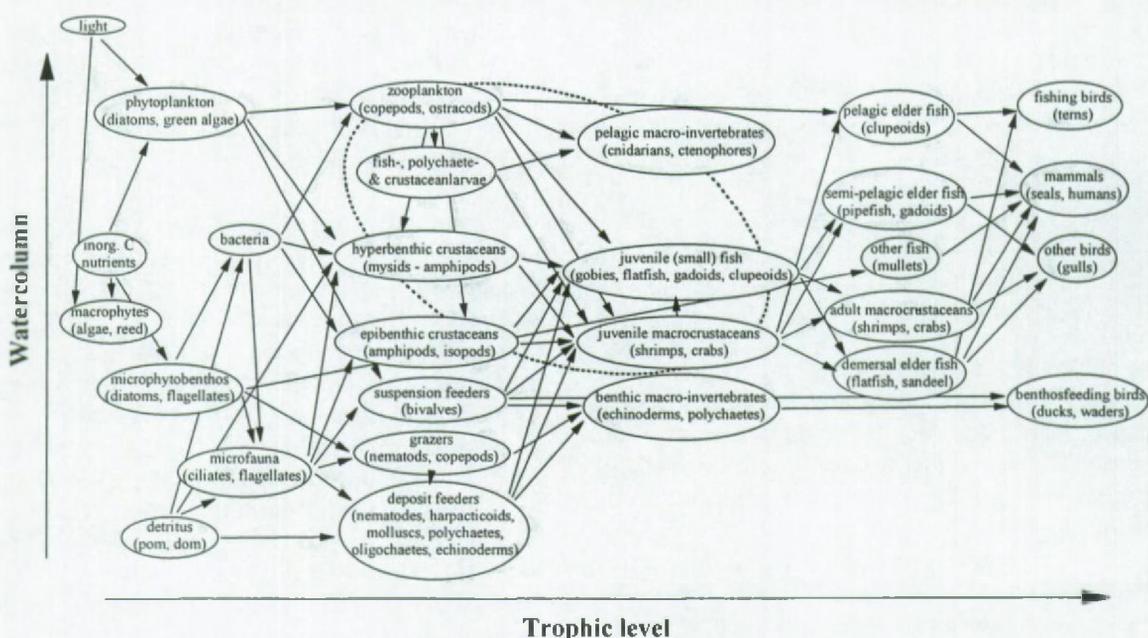


Fig. 9.14 A generalized food web for the Westerschelde estuary presenting the trophic levels along the horizontal axis, and the distribution in the watercolumn along the vertical axis. The arrows towards detritus have not been drawn for simplicity

consumers along the horizontal axis, and the distribution from benthic to pelagic in the water column along the vertical axis (Fig. 9.14). Two food webs are known to exist in the Westerschelde: an autotrophic food web in the marine part and a heterotrophic food web in the brackish part (e.g. Chapter 8-Add., Hummel *et al.* 1988b, Goosen *et al.* 1997). As already explained, the main source of energy in the Westerschelde is detritus (either particulate or dissolved organic carbon, Soetaert & Herman 1995a) and the bacteria/microfauna associated with it (Billen *et al.* 1990, Heip & Herman 1995, Hamels *et al.* 1998), next to micro-phytobenthos (Underwood & Kromkamp 1999, mainly in the intertidal) and phytoplankton (van Spaendonk *et al.* 1993, mainly in the marine subtidal, as this source of primary production is being suppressed due to water turbidity). The benthic primary production forms the main food source for macrobenthic (Herman *et al.* 2000) and meiobenthic (Moens & Vincx 1997) organisms intertidally, while copepods (Tackx *et al.* 1995) and mysids (Fockedeij & Mees 1999) mainly use the pelagic component (subtidally). The following trophic level consists of the demersal (small) fish and macrocrustaceans (the present study), next to the benthic and pelagic macro-invertebrates. At the following level larger demersal fish and macro-invertebrates and pelagic fish are found, while the top level exists

of birds (Ysebaert 2000) and mammals (including man).

In the following paragraphs it is tried to prove that the major energy flow between the secondary trophic level and the demersal fish and macrocrustaceans in the subtidal Westerschelde, passes through the pelagic rather than the benthic food chain.

9.9 The paradigm of the mysids in the Westerschelde

9.9.1 Foraging strategies

The diet of most estuarine fish species is more or less restricted to part of the total available prey spectrum as dictated by their capability to capture and ingest specific prey species. Most dietary shifts (ontogenetic, seasonal, or shifts towards the most profitable prey) are related to e.g. the trophic adaptability of the fish species, food partitioning and/or seasonality in prey availability (Gerking 1994).

Several studies on trophic relationships have shown that estuarine fish are primarily feeding near the bottom, mainly on small epibenthic crustaceans and benthic organisms (see Elliott *et al.* 2002). In the

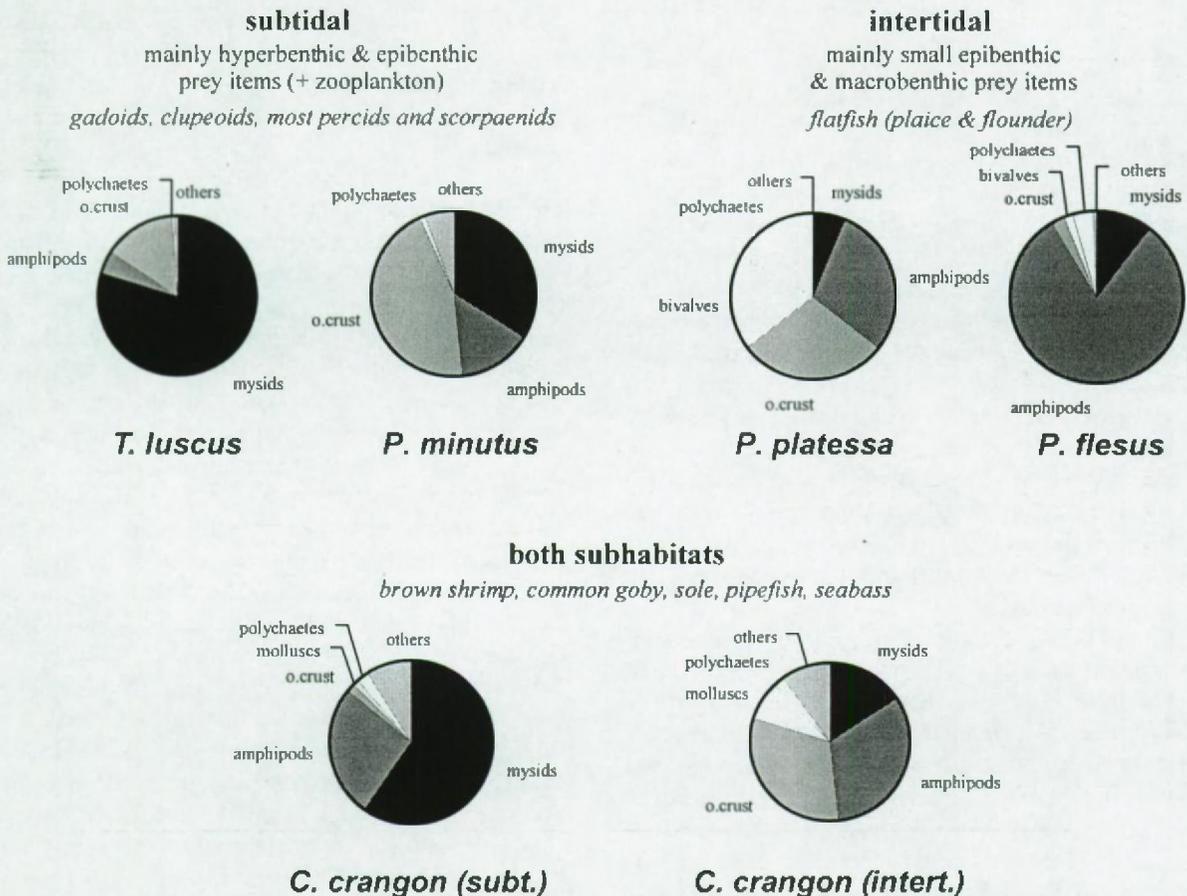


Fig. 9.15 Numerical diet composition for a number of representative species divided into three groups, based on their foraging strategies

Forth (UK) and the Tagus (Portugal) estuaries, fish feeding in the subtidal habitats were highly dependent on small crustaceans, especially shrimps and crabs (Costa & Elliott 1991). Only few studies mention mysids as important prey items for both fish and macro-crustaceans (Moreira *et al.* 1992, Marshall 1995, Oh *et al.* 2001).

The presence of an estuarine mysid-feeding guild was investigated by means of stomach content analyses on *ca.* 1500 stomachs of 25 fish species and 750 stomachs of brown shrimp *Crangon crangon*, taken from both the subtidal and intertidal habitats in several seasons (Chapter 7, Chapter 8, and K. Hostens unpubl. data). Only the main foraging patterns are presented in this overview.

The demersal fish and macro-crustacean assemblage of the Westerschelde could be divided into 3 main groups, according to their foraging strategy. A first group foraged subtidally on fast-moving hyperbenthic and epibenthic prey items (and zooplankton). Members of this group belong to the gadoids, clupeoids, most percids and scorpaenids. For example, bib *Trisopterus luscus*, got most of its energy from mysids (mainly *Neomysis integer* in the brackish zone and *Gastrosaccus spinifer* in the marine zone) and other small crustaceans. Sand goby *Pomatoschistus minutus* took 90 % crustaceans, of which almost half were mysids (mainly *N. integer* and *Mesopodopsis slabberi*) (Fig. 9.15).

A second group foraged on slow-moving epibenthic crustaceans and macro-endobenthic organisms, mainly in intertidal areas. This group mainly consisted of two flatfish species. Plaice *Pleuronectes platessa* took 70 % small crustaceans (*N. integer* and *Corophium volutator*), next to bivalves (mainly siphons of *Macoma balthica*) and polychaetes (mainly tail-ends, mostly *Heteromastus filiformes*). Flounder *Platichthys flesus* even took 90 % crustaceans (mainly *C. volutator*).

A third group showed no clear preference, feeding in both subtidal and intertidal areas. Species like common goby *P. microps*, brown shrimp *Crangon crangon*, sole *Solea solea*, pipefish and seabass, belong to this group. For example, *C. crangon* mainly preyed upon mysids (*N. integer* and *M. slabberi*) and amphipods (*Corophium* and *Bathyporeia* species) in the subtidal, and on the same prey groups but in different proportions in the intertidal, supplied with some molluscs.

The same partitioning in subtidal-intertidal feeding groups has been found in other systems, like the Medway (UK) (van den Broek 1978) or the western Irish Sea (McDermott & Fives 1995). Other studies also showed that mainly plaice and flounder used the intertidal areas to forage on amphipods, bivalves and polychaetes, while sole and dab *Limanda limanda* fed in the subtidal (McLusky 1989). However, in the Westerschelde, stomachs of *L. limanda* were always empty in the subtidal, and the intertidal

sampling period was too short to figure out if dab makes use of the intertidal.

9.9.2 Resource overlap

Demersal fish and macro-crustaceans clearly use the same sources of energy both in the subtidal and intertidal, comparable with other studies (Hall & Raffaelli 1991, Marshall 1995). The term 'opportunistic feeders' is often used for many fish and macro-invertebrate species. The same can be said for most species in the Dutch Delta area.

For example, the fish and macro-crustacean assemblage was comparable between the Westerschelde and the Oosterschelde estuary. However, the Oosterschelde ecosystem is basically thriven on macrobenthic filter feeding organisms, which take away most of the primary production (*e.g.* Herman & Scholten 1990). This might explain the low densities of permanent hyperbenthos in the Oosterschelde (Mees & Hamerlynck 1992, Chavatte 2001). As hyperbenthic crustaceans were very important in the diet of most fish and macro-crustaceans in the Westerschelde, the same species will probably feed on other organisms in the Oosterschelde.

Moreover, different fish and macro-crustacean species forage both in the subtidal and intertidal areas on partly different prey items (Chapter 7, Chapter 8). As such, they may be termed opportunistic feeders. However, the present study proves that, although they may be opportunistic, feeding on whatever passes by, they are also selective, clearly preying upon the most energetic prey that pass by.

Generalized graphs like those presented in Fig. 9.15 obscure the presence of a number of prey items. Seasonal and ontogenetic shifts, mostly related with growth of the predators are not captured here (Chapter 7, Chapter 8). As the fish grows other organisms are preyed upon, mostly starting with copepods, changing to mysids, shrimp and fish (*e.g.* Chapter 7-Add.). Differences between size classes and subareas have been shown for flounder in the Seine estuary (France), where small flounder mainly preyed upon copepods and mysids in the subtidal, and on *corophium* and endobenthic organisms in the intertidal mudflats, while large flounder mainly preyed upon shrimps and crabs subtidally, and on larger bivalves and polychaetes intertidally (Bessineton *et al.* 1998). Also, common goby *Pomatoschistus microps* showed a seasonal partitioning of food resources by changing from an intertidal to a subtidal foraging behaviour (Rogers 1988). In the Westerschelde smaller common gobies mainly foraged in the intertidal saltmarsh creeks (Cattrijsse 1994), while bigger ones were mainly foraging subtidally (Chapter 7). The present thesis also showed ontogenetic shifts for sand goby *Pomatoschistus minutus* and bib *Trisopterus luscus* (Chapter 7).

9.9.3 The mysid-feeding guild

Mysids (and copepods) are a major food source for many juvenile fish and for brown shrimp *Crangon crangon* in the subtidal Westerschelde. Also, the small epibenthic crustaceans that were preyed upon in the intertidal (mainly amphipods like *Corophium* and *Bathyporeia* species) are more vulnerable to fish predation during their temporal excursions into the hyperbenthic water layer. This proves that the 'pelagic' part of the food chain is more important than the 'benthic' one, at least in the subtidal part of the Westerschelde.

Also other studies have appointed mysid-feeding guilds in the demersal fish assemblages (see Mees & Jones 1997). In the Humber estuary (UK), the food web was dominated by mysids and gammarid amphipods, with only larger flatfish feeding on polychaetes (Marshall 1995). In a Brazilian estuary, four feeding groups were distinguished, one group feeding mainly on suprabenthic mysids and copepods (Ribeiro *et al.* 1997). In a review, it was shown that 51 fish species from the North-east Atlantic preyed upon mysids (Mauchline 1980). In the Baltic ecosystem, herring and other semi-pelagic fish species also preyed upon mysids and zooplankton (Rudstam *et al.* 1992).

As already pointed out, the nursery function of a system is dependent on prey availability. Many species prey upon the same organisms. However, no food limitation could be detected. In the subtidal zone of the Westerschelde, copepods (Soetaert & Van Rijswijk 1993), mysids (Mees *et al.* 1993a), amphipods (Cattrijsse *et al.* 1993) and shrimps (Chapter 2) are very abundant. Epibenthic crustaceans and endobenthic organisms like bivalves and polychaetes are very abundant intertidally (Ysebaert 2000), and almost absent from the subtidal (Mees & Jones 1997).

From recalculations on the number of mysid in the diet and number of mysids available in the subtidal, it was shown that only a small fraction (1% and between 10 and 35%) of the standing stock of the mysid populations, was removed per day by the local fish and shrimp populations, respectively. This indicates that there is no top-down control on the invertebrate populations in the Westerschelde.

9.10 Final conclusions

The present thesis provides a baseline on the fish and macro-invertebrate assemblages in the Westerschelde and Oosterschelde. The thesis suggests that both estuaries play a significant role as nursery areas for several demersal fish and macro-invertebrate species. The analysis of the structure and functioning of the

demersal fish and macro-invertebrate assemblages in the Westerschelde and Oosterschelde estuaries, at several spatial and temporal scales has yielded the following conclusions:

1 (Post)larvae of 17 fish and 11 macro-crustaceans enter the Westerschelde and/or Oosterschelde, mainly in spring. Only a few species were represented by high densities of (post)larvae: sprat, herring, 3 gobiid species, sole and flounder in all subhabitats (the latter not in the Oosterschelde); brown shrimp, shore crab and flying crab in both estuaries (the latter not in the marsh creeks); and also spider crab and anomuran crabs in the Oosterschelde. The intertidal saltmarsh creeks proved to be very important for the postlarvae of brown shrimp, clupeoids, gobies and flounder. As yet, the importance of intertidal mudflats and puddles on the sandflats for post-larvae is unknown

2 In total 96 fish species have been recorded during the last two decades, 75 species in the Oosterschelde and 74 in the Schelde estuary (including the tidal zone upstream of the Westerschelde). On a shorter time scale, only 32 fish and 6 macro-invertebrate species were recorded in the Westerschelde, with on average 16 fish and 3 macro-crustacean species per season. In the Oosterschelde, diversity was higher (41 fish and 31 macro-invertebrates). This was probably related with a higher habitat-complexity. Diversity is highly influenced by the occasional immigration of a large number of typical marine seasonal or adventitious species in different seasons. Salinity/turbidity, sediment/habitat type and temperature are the main structuring environmental variables

3 The maximum likelihood of occurrence (presence/absence) of 15 common species could be predicted fairly well by means of single species (multiple) logistic regression models, using only 4 environmental variables in both estuaries (temperature, salinity, dissolved oxygen concentration and turbidity, and/or their quadratic effects). The combined interaction of the different environmental variables is more powerful than the single variables to predict species occurrence, with a dominance of a seasonal rather than a spatial pattern

4 The multivariate (multispecies) approach has been shown to be a very efficient and powerful technique to summarize structural patterns in large multispecies data sets, either based on pooled or individual sampling points. In the Westerschelde, a clear spatial separation between the marine and brackish parts was found, correlated with salinity/turbidity gradients. In both estuaries, the seasonal patterns in the fish and macro-invertebrate assemblages were correlated with temperature/dissolved oxygen concentration gradients

5 The average densities in the brackish part of the Westerschelde were higher at the end of the 1980s, but decreased overall at the beginning of the 21st century. This was probably related to dredging and dumping activities, and the subsequent quantitative and qualitative reduction of intertidal (and subtidal) habitats. In the Oosterschelde estuary, long-term differences were less obvious and probably obscured by sampling bias. Fish and macro-invertebrate densities were relatively high in the Oosterschelde (except in the central part) both at the end of the 1980s and at the beginning of 2000

6 Only few species, mainly marine juvenile and estuarine resident species, were really common in both estuaries, with the macro-invertebrates largely outnumbering the fish fauna. The main fish species belong to gobiids, flatfish, clupeoids and gadoids; the main macro-invertebrate species belong to caridean shrimp and brachyuran crabs, supplemented with echinoderms and anomuran crabs in the Oosterschelde. Spatial differences within and between both estuaries were apparent for several species

7 A clear seasonal succession of different life history stages (postlarva – juvenile – immature – adult) of different species in different subhabitats (intertidal marsh creeks – intertidal flats – subtidal) has been shown. Several estuarine resident species showed a preference for the warmer (summer-resident species) or colder seasons (winter-resident species). Most of the marine juvenile species appeared at varying times (summer, winter or bimodal species), and stayed only for a short period in the estuaries, mostly with peak densities in spring-summer

8 Prediction of single species abundance, by means of multiple linear regressions constrained by four characteristic environmental variables (temperature, salinity, dissolved oxygen concentration and turbidity) was partly successful. Best models were built for 7 species that were present in the estuary for a longer period, but with only one clear density peak. Densities of these species were mainly structured by environmental patterns. Applicability of the best-fitting models to the Oosterschelde (a system without a marked salinity gradient) was limited

9 In the subtidal food webs of the Westerschelde, the major energy flow between the secondary trophic level and the demersal fish and macro-crustaceans, passes through the pelagic food-chain. Small crustaceans (copepods, mysids, amphipods) constituted the main diet component, with an overall dominance of mysids. There is no top-down control on the mysid populations

10 The demersal fish and macro-crustacean species showed different foraging strategies. Two flatfish species (plaice and flounder) mainly foraged in the intertidal on amphipods, bivalves and polychaetes. In the subtidal, most juvenile fish species (all gadoids, clupeoids, scorpaenids, percids, and other flatfish species) and brown shrimp mainly preyed upon mysids, amphipods and copepods. Some of these (e.g. sole, common goby, seabass, pipefish and brown shrimp) also foraged in the intertidal, mainly on amphipods. There is a large resource overlap, but also ontogenetic and seasonal shifts in the diet were observed, related with growth of the species, migration between the different subhabitats, and prey availability.

9.11 Remarks on the thesis and recommendations for future research

The papers presented in this thesis span a period of 13 years. This probably makes the thesis less coherent than if it would have been written in a much shorter period. Also our understanding of the functioning of estuaries, and of the demersal fish and macro-invertebrate assemblages in estuaries, improved during that 13-year period. Most of the research on fish and macro-crustaceans in European estuarine environments have been compiled and reviewed in the book 'Fishes in Estuaries' (Elliott & Hemingway 2002), in which I also made a contribution to several chapters. Indisputably, this has influenced the writing of the latter papers and of this final chapter.

On the other hand, the thesis benefits from the fact that three adjacent and different water bodies, a true estuary (the Westerschelde), a marine bay (the Oosterschelde) and an ebb-tidal area (the so-called Voordelta), could be compared. Additionally, at least two distinct periods (spanning more than a decade) could be compared for the Westerschelde and Oosterschelde estuaries, but unfortunately with a large gap during the 1990s.

During the 1980s (and before) much attention was given to the Oosterschelde and the Voordelta, where several research groups investigated the effects of the major engineering works (the so-called Delta plan) in an interdisciplinary approach (Nienhuis & Smaal 1994a). By the end of the 1980s most 'scientific eyes' got focused on the Schelde estuary (Westerschelde and Zeeschelde). Throughout the study period and to date, it is generally accepted that the Schelde estuary harbors a cocktail of pollutants and that the system suffers from high organic loads mainly upstream the Westerschelde (Baeyens 1998). For many system components baseline information was needed. Additionally, the importance of habitat complexity (subtidal, intertidal, saltmarsh

creeks) for the functioning of the Westerschelde as a nursery for demersal fish and macro-invertebrate species got more attention. During the mid-1990s most of the fish research in the (Dutch part of the) Delta area ceased.

Only at the end of the 1990s (after 'alarming' news from local fishermen about 'strong' decreases in fish and shrimp populations in both systems) the monitoring was repeated both in the Oosterschelde and Westerschelde. From the previous studies we knew that macro-invertebrate species were very important in these shallow areas. An increased interest in the biodiversity of the whole demersal fish and macro-invertebrate assemblages, led to the fact that since the late 1990s all macro-invertebrates (sampled with a beam trawl) have been taken into account, while during the earlier sampling periods mainly the fish and only the most conspicuous macro-invertebrates have been investigated.

Recommendation 1: future beam trawl campaigns should always concern the whole demersal fish and macro-invertebrate assemblages.

Although the different data sets were gathered through different monitoring studies (partly collected before the start of this study, but largely analyzed during the study period), they all suit the same purpose: increasing our knowledge on the nursery function of the Delta area. Of course, the constraints on the sampling (e.g. quarterly sampling, not all groups investigated, limited set of environmental variables, unknown net-efficiencies of the different gear types) and the continuous human impact on the systems, often make it not possible to reach firm conclusions.

A large part of the thesis is spent on providing descriptive baseline information, giving an idea about species composition, diversity, density and biomass of the demersal fish and macro-invertebrate assemblages, and the relation with the environment at different scales in time and space. Multivariate statistical techniques have proved to be very successful to explore and summarize that information. During the progress of the study we moved from pure descriptive ecology towards more predictive ecology, and single-species correlative models on the occurrence and density of the common species were developed. Perhaps, more progress in process studies could have been made if the descriptive study (one of the initial aims of this thesis) had been finished earlier.

Still, the major conceptual limitation of all regression techniques (either in a single or multi-species approach) is that one can only ascertain relationships (or correlations), but never be sure about underlying causal mechanisms. A number of authors find seasonality (independent of temperature or salinity) to be the main forcing factor in the distribution of migratory species (like fish and macro-invertebrates)

(see Maes 2000). Still, in my opinion, the environmental conditions are of primary importance for the distribution of a number of these mobile organisms (mainly the estuarine residents). The effects of temperature on optimal growth, the avoidance of unfavorable salinities and temperatures, the effect of salinity on osmoregulation, etc., have been described by several authors (see Elliott & Hemingway 2002). The need for dissolved oxygen to survive seems obvious. Moreover, combined interactions between the environmental variables are known to influence recruitment and the migrating behavior of several fish and macro-invertebrates, and the environmental interactions can affect both prey and predator distributions.

To increase the predictive success of the density models (and the prove of causal relationships) it might be necessary to include biological factors (such as prey availability as a measure for habitat quality) or other environmental parameters (such as habitat complexity). However, it will make the models less useful, as it will be too time and money consuming to gather all necessary data. As stated in several chapters in the thesis, not many studies exist where prey abundance of several groups (hyperbenthos, zooplankton, macrobenthos) have been gathered simultaneously with epibenthic data. Moreover, the link between intertidal macrobenthos and subtidal fish data will be difficult to model directly. Also, only slightly more variance got explained by the inclusion of hyperbenthic data, mainly due to a reduction in number of sampling points that could be used. It might be interesting to try to model presence/absence and/or density of the prey organisms, and use these as predictor variables in the fish models. On the other hand, this and other studies showed that food supply is never (or seldom) a limiting factor for fish and macro-invertebrates in estuarine environments. Still, more and better multidisciplinary research is needed.

*Recommendation 2: the future mainly lies in extending and fine-tuning predictive process studies. A target species might be dab *Limanda limanda* as this species shows different distribution patterns in the Westerschelde and the Oosterschelde, the latter system lacking typical-estuarine gradients.*

A major remark may be that the papers presented in this study mainly focus on the estuarine area, with less attention for what is happening both up- and downstream the systems. Of course, the distribution of fish and macro-invertebrate assemblages does not stop at geographical borders. As has been indicated in Chapter 1, we unsuccessfully tried to sample with a beam trawl upstream the Dutch-Belgian border. Although, since the 1990s data have been gathered from the upstream part of the Schelde estuary, these were taken by different sampling tech-

niques, which make these data difficult to compare with our beam trawl data from the Westerschelde. The studies from the Zeeschelde have shown an improvement in the occurrence of fish and macrocrustaceans in the upper estuary (mainly gobies, clupeoids, pipefish, brown shrimp *Crangon crangon* and prawn shrimp *Palaemonetes varians* subtidally, and sole *Solea solea*, plaice *Pleuronectes platessa* and eel *Anguilla anguilla* intertidally), but only in the Beneden Zeeschelde. The Boven Zeeschelde is still almost void of 'epibenthic' life (Peeters *et al.* 1999, Maes 2000). Also, preliminary comparisons indicate that densities upstream the Dutch-Belgian border are still much lower than in the brackish part of the Westerschelde (K. Hostens, unpubl. data).

Recommendation 3: in the future it is necessary to monitor the whole estuarine part of Schelde (and even the riverine part for diadromous species). For both systems, but especially the Oosterschelde, it might be of interest to investigate the status of fishes and macro-invertebrates in the adjacent waterbodies and upstream the rivers, in case it is decided to re-establish an estuarine gradient (from fresh to marine) in the system.

The human impact clearly diminished the quality of the Delta area, but it is difficult to judge how large the human impact really is (see §9.7). Climatological variation, year-class strength and human impact on a larger scale, largely mask the possible anthropogenic effects in the estuaries themselves. Moreover, basic knowledge on the physics (i.e. hydrodynamics and geomorphology) of the system is needed in order to interpret the biology.

Inter-annual variability in population densities forms a major constraint in establishing causal relationships. The relation between (post)larval recruitment from the spawning areas, juvenile densities in the nurseries (like the Delta area) and the adult populations (or year-class strength) in the North Sea is not yet fully understood to date. The same holds for the effects of overfishing (and/or pollution) in the North Sea on year-class strength. Yearclass data only exist for commercial species (e.g. cod *Gadus morhua*, herring *Clupea harengus*, or plaice *Pleuronectes platessa*) and are biased by several assumptions as well. Most probably yearclass strength is correlated with climatological changes, rather than with human impact, although the impact of overfishing on changes in the food web, and the subsequent decrease in viability of the target organisms, may not be underestimated. As can be seen from reports by the DYFS (RIVO, NL), the Wadden Sea and the Dutch coast are much larger and as such harbor much higher densities of juvenile fish. Still, it is argued that the Delta area delivers an important contribution to the North Sea stocks for a number of species living in the vicinity of the Delta area.

Recommendation 4: continuous long-term monitoring of both biological and environmental components is necessary, and full-drawn (field)-experiments are needed to assess the problems related to human versus natural changes. Especially, increasing our knowledge on net-efficiency would largely improve the interpretation of the data.

In this study, the effects of chemical (in)organic micro-pollution (mainly in the Westerschelde) on fish and macro-invertebrates are considered to be of minor importance (as these substances are now 'safely' bound to small particles). However, the (near) absence of a number of species (e.g. viviparous blenny *Zoarces viviparus*, starfish *Asterias rubens* and crustacean parasites of shore crab *Carcinus maenas*) seemed to be correlated with several kinds of industrial pollution. Although, the industrial and agricultural input of several pollutants has been reduced substantially during the past 30 years, in the near future more problems might arise (through bio-availability and bio-accumulation) from micro-pollutants. These may form suspended complexes due to increased dissolved oxygen levels (through reduced organic input and hence reduced bacterial productivity) and mixing of the water column (due to stronger currents as a result of the deepening of the shipping channel). Recently, an OSTC-project of the Belgian Federal Science Policy (ENDIS/RISKS) investigates the effects of endocrine disturbance in several organisms of the secondary trophic level (including shrimps and gobies) in the Schelde estuary.

Recommendation 5: comparison between individuals from the 'pristine' Oosterschelde and the 'polluted' Westerschelde might shed a light on the effects of industrial and agricultural pollution.

Another problem is the quantification of the carrying capacity of a system, i.e. how many resources (both food and space) are available and how many of these resources are used by the demersal fish and macro-invertebrate assemblages. As stated several times, intertidal habitats (saltmarsh creeks, sand or mud flats) are crucial for the presence of both demersal fish and macro-invertebrates, mainly as foraging and refuge areas. Moreover, it has been shown that 14 fish species might spawn in the Westerschelde, although no hard information exists for most of them. It would be interesting to have better information on (post)larval entrance and the use they make of the intertidal sand- or mudflats.

Recently a long-term vision on the Schelde estuary has been created by the Dutch and Flemish governments (Resource Analysis 2001). A major topic is 'naturalness', with the preservation of morphology and habitat complexity as the main aim. Throughout the thesis, it has been shown that the

areal extent of intertidal habitat decreases both in the Westerschelde and Oosterschelde estuaries. Moreover, (almost) nothing is known on the usage of the large intertidal mudflats throughout the systems or the sandflats in the marine part of the Westerschelde. Also, no recent intertidal data from the Oosterschelde exist. It would be interesting to know how the controlled inundation areas in the upper part of the Schelde estuary will get populated by the fish and macro-invertebrate assemblages.

Recommendation 6: the study of the nursery function would largely benefit from an increased understanding of the early life history stages of both fish and macro-invertebrates. The functioning of the intertidal habitats for fish and macro-invertebrates should be investigated in more detail, both on a macro- and microscale (e.g. extent, 'distance' from the subtidal, current regime, sediment characteristics, shape of the slopes). This might help to generate better estimates of the carrying capacity of the different systems.

Moreover, not only the quantity but also habitat quality is important. During the three last sampling campaigns in the Westerschelde (May, August and November 2001) the subtidal sediment seemed to be coarser throughout the system (although this was not confirmed by analyses), where in previous campaigns shell fragments (and peat) used to be limited to a small part of the Westerschelde. A possible correlation between coarse sediments and decreased densities in the demersal fish and macro-invertebrate assemblages at the beginning of the 21st century can be made. However, it remains unclear if this coarser sediment was only a temporarily phenomenon. A link with the excessive dredging (partly due to the extra deepening of the navigation channel) seems obvious, but should be explored further.

Decreasing fish densities in the eastern part of the Oosterschelde in 2000-'01 were attributed to a reduced habitat quality, due to more wild oysters (reducing the areal extent of soft sediments) and the increased presence of (drifting) macrophytes. A link with the engineering works (and the reduced freshwater input, next to lower current velocities) seems obvious. Also, several so-called alien species invade the coastal and estuarine waters. It might be interesting to look at the effect of global warming on habitat quality and on changes in the geographical distribution of 'new', 'sporadic' and 'common' species.

Recommendation 7: in the future, it might be worth to found the possible correlations between habitat quality and global warming and demersal fish and macro-invertebrate densities.

Since the 1980s progress has been made in the elucidation of food webs, in estuaries and the

Westerschelde in particular, through this and other studies. The basic idea of two food chains in the Westerschelde (autotrophic in the marine part and heterotrophic in the brackish part) established by Hummel *et al.* (1988b), remains valid to date. Although, the importance of detritus as the main food source for the lower trophic levels in the heterotrophic food-chain seems to be smaller than previously thought.

The functional part of this thesis mainly tackles the identification of the main food sources and foraging strategies. Food availability and feeding ecology have always been central themes in the Marine Biology research group at Ghent University. At the end of the 1980s mysids were 'discovered' as a very important food source for fish in the Delta area. Many studies and projects have been developed to unravel that part of the food-chain.

The seasonal appearance of different species might lead to a fully realized carrying capacity throughout the year. However, most of the food resources seem to be not used (e.g. only 30 % of the mysid standing stocks is consumed per day) and almost nothing is known of predation impact by fish on macrobenthic organisms in the Delta area. Most probably, the carrying capacity of the system is not optimized, but as yet unknown. Because of limited information (and lots of assumptions) on gastric evacuation rates, daily rations, secondary production, P/B and P/C ratios, also the production and consumption estimates reported in the different chapters of the thesis are preliminary and should only serve as baseline information for the area concerned. Large discrepancies are found between consumption values based on stomach content analyses and real calorific needs of the demersal fish and macro-invertebrates.

Recommendation 8: more detailed investigation of the diet of different macro-invertebrate and fish species in the Westerschelde and the Oosterschelde should be encouraged. The latter system seems to be completely dominated by the benthic food-chain where the secondary production is mainly delivered by bivalves and polychaetes intertidally. This is in contrast to the Westerschelde, where the pelagic food-chain (secondary production mainly delivered by copepods and mysids subtidally and amphipods intertidally) is very important, as has been shown in this thesis. Estimating reliable consumption rates for the investigated species will require further validation with extensive sets of experimental data.

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