

CHAPTER 4 THE FISH FAUNA OF THE OOSTERSCHELDE, A DECADE AFTER COMPLETION OF THE ENGINEERING WORKS

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Abstract. *In this study we investigate whether long-term changes in diversity, density and/or biomass of the juvenile fish fauna of the Oosterschelde can be detected. Quarterly beam trawl data from the period 1999-2001 are compared with quarterly data from 1987-89. Also, a brief comparison in frequency of occurrence was made with data from 1960-76. In 1999-2001, a total of 42 fish species was recorded, which is comparable to the period 1960-76. Diadromous species (e.g. *Osmerus eperlanus* and *Anguilla anguilla*) showed a reduced frequency of occurrence. Some species (e.g. *Gobius niger*) still entered the Oosterschelde through sluices, others (e.g. *Gasterosteus aculeatus*) could not withstand the high salinities in the Dutch Delta area. The number of species per season was 21-28 in 1987-89 and 25-34 in 1999-2001, while the number of species per station was 15-22 in 1987-89 and 17-31 in 1999-2001. This increase could mainly be attributed to rare species. The commonest species in both periods were *Pomatoschistus minutus*, *Pleuronectes platessa*, *Limanda limanda* and *Trisopterus luscus*. A 45% increase was noted in total average fish density in 1999-2001, which could mainly be attributed to *P. minutus*. The total average biomass decreased with 35%, but by excluding *P. platessa* and *L. limanda*, the decrease was limited to the eastern part in 1999-2001. Both on temporal and spatial scales, density and biomass were significantly different for more than 10 species. Multivariate analyses revealed seasonal (autumn-winter versus spring-summer) and spatial differences (western-central-eastern subareas), with a separation of both periods. For most species the long-term spatio-temporal differences did not reflect 'real' changes in the nursery function of the Oosterschelde. Either they reflected natural population variability due to a delayed appearance of strong yearclasses after cold winters (e.g. high densities of *P. platessa* and *L. limanda* in 1987), or changes were obscured through sampling bias (e.g. an increased net-efficiency through clogging of the nets for *Syngnathus rostellatus* and *P. minutus* in 1999-2001, or an unexplained reduced efficiency for gobies in 1987-89). For all species with strong yearclasses (also *Myoxocephalus scorpius* in 1987 and *Sprattus sprattus* in 1999), the averaged densities rapidly declined to a 'normal' state of homeostasis within the successive years and seasons of both periods. The highest densities were generally recorded in the western and northern part of the Oosterschelde in both periods. Many species (28) showed an increase in the central part. Still, for most species the loss at one station was compensated with an increase at another station in most subareas. This may be related to the location of food resources (e.g. mussels for flatfish in the western part, shrimps for *Callionymus lyra* in the central part, and high macro- and hyperbenthic biomasses in the northern part). Also, a correlation between substratum type (>50% silt concentration, mainly in the western and northern parts) and high species abundance was observed. For the estuarine resident and marine juvenile species (highest densities of 0- and 1-group individuals in summer and autumn) the Oosterschelde can still be considered to be an important nursery area. For several marine seasonal species the ecosystem is still functioning as an important feeding area. Estuarine ecosystems like the Oosterschelde are able to absorb and adjust to changes, but they can also be very vul-*

nerable. One could speak of 'homeostasis' in the fish population in most parts of the Oosterschelde, except in the eastern part where at least 16 species - and especially all flatfish and gadoid species - drastically declined in 1999-2001.

4.1 Introduction

Long time series of biological data are extremely valuable for documenting ecosystem changes and to distinguish between natural and man-induced changes, but they are reversely uncommon as they are expensive and time-consuming to collect (Wolfe *et al.* 1987). A recent study in the German Wadden Sea revealed that the sampling effort to detect 50 to 20% difference in flatfish assemblages between several surveys was disproportionately high (Berghahn 2001). The cost-benefit analysis is reflected in the timescale and the number of stations or subareas that will be monitored. For example, between 1970 and 1975 the Demersal Young Fish Surveys, which are specifically aimed towards flatfish populations as a whole, were undertaken twice per year in the Dutch shallow coastal areas, but thereafter only during fall (Welleman 2000).

It may be difficult and misleading to interpret short-time variations without knowledge of their periodicity and amplitude (Elliott 2002). Weatherhead (1986) found that only a limited number of ecological long-term studies were determined by some unusual event. Due to the large engineering works in the eighties, the Oosterschelde was converted from a real estuary to a marine bay. The present Oosterschelde could be considered a nature reserve of international value, well-balanced between nature, commercial shellfish culture, recreation, and shipping (Wolff 1997; van Berchum & Wattel 1997). The direct consequences on the functioning of the ecosystem during the first years after the works finished in 1987 were reported as the result of an integrated case-study (Nienhuis & Smaal 1994a). For juvenile fish and macrocrustaceans it could not clearly be stated if the changes were directly related to these barriers. For example, flatfish and gadoid densities increased between 1983 and 1989 while shrimp densities decreased. Possible explanations were lower current velocities and stronger year-classes for the fish species and lower nutrient inputs for shrimp (Chapter 3).

On the other hand, monitoring and the detection of man-induced changes need to take into account a background of natural variability (Elliott 2002). On a mid-term scale, primary production in the period 1990-'95 did not differ from the period directly after closure of the Oosterschelde (Wetsteyn 1997). Macrobenthic biomass was a little lower than before 1990, but only locally and if suspension feeders were not taken into account (Stikvoort 1997).

Also, a study of non-commercial fish species in the Oosterschelde based on yearly surveys between 1987 and 1995, did not reveal large changes in numbers as compared to the period 1970-'86 (de Jong 1997).

In this study we investigated whether long-term changes in diversity, density and/or biomass of the juvenile fish fauna of the Oosterschelde can be detected. Quarterly beam trawl data on juvenile fish from 1999-2001 (post-barrier period) were compared with data from 1987-'89 (upon completion of the major engineering works) and 1960-'76 (pre-barrier period).

4.2 Material and methods

4.2.1 Study area

The Oosterschelde is a mesotidal marine oligotrophic bay in the Southern Bight of the North Sea, with 227 km² subtidal area and a total area of 351 km² (Fig. 4.1). Typical estuarine gradients have disappeared. Through the construction of the storm-surge barrier (1979-'86) the mean tidal volume decreased with 30% to 900 10⁶ m³. Due to several dams (Grevelingendam, closed in 1965; Volkerakdam, closed in 1969; Oesterdam, constructed between 1979-'86; and Philipsdam, constructed between 1977-'87), the mean freshwater load dropped from 70 to less than 20 m³s⁻¹ (Nienhuis & Smaal 1994b; Haas 1998).

The Oosterschelde is characterized by tidal channels, mudflats and large intertidal sandy shoals. Erosion of the intertidal area has been predicted to be an ongoing process with a reduction of 1.5 % per 5 years (van Berchum & Wattel 1997). The intertidal areas are important for the culture of cockles, while

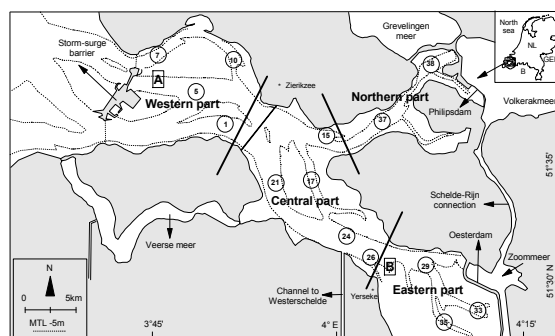


Fig. 4.1 Map of the Oosterschelde with 14 fish sampling locations (circles) in the subtidal area and 2 environmental sampling locations (A and B, from www.waterbase.nl). Note the division in a western, central, eastern and northern part

the shallow subtidal areas are important for the farming of oysters and mussels. There is high shipping and recreational activity in the subtidal area. The Oosterschelde can be divided into four geographical subareas: western (in the mouth), central, eastern (or basin) and northern part (see Fig. 4.1). The ecological and environmental properties of the Oosterschelde are explained in detail in Nienhuis & Smaal (1994a) and van Berchum & Wattel (1997).

4.2.2 Sampling

Juvenile fish and mobile macro-invertebrates have been investigated at the Centre for Estuarine and Marine Ecology (Yerseke, The Netherlands) at several locations during several periods. For the present study, data from 12 subtidal sampling locations (4 in the western, 5 central and 3 in the eastern part) were used from 10 quarterly surveys conducted between August 1987 and November 1989 (directly after the completion of the engineering works) and from 10 quarterly surveys conducted between August 1999 and November 2001 (a decade later) (Fig. 4.1, Table 4.1). Information is further given on the northern subarea, which was only investigated during the latter period (2 stations). Only the data for the fish fauna will be presented in this study, as during the first sampling period only a limited number of invertebrate species were taken into consideration. Primary data on all mobile macro-invertebrates from 1999-2001 will be presented elsewhere (Chapter 5).

Samples were taken with a three-metre beam trawl at an average depth of 13 metres below mean tidal level, operated from the RV Luctor (34 m, 500 Hp) and towed over a distance of 1000 metres at an average speed of 4.5 knots relative to the bottom. For most surveys the beam trawl was equipped with one tickler chain, a chain in the ground-rope and a fine-meshed net (5*5 millimetres in the cod end), except for November 1988 and February 1989 where a net of 10*10 millimetres was used.

To characterize the Oosterschelde environment in both periods averaged data on temperature (°C), salinity (psu), dissolved oxygen (mg.l⁻¹), suspended matter (mg.l⁻¹) and visibility (metres, measured as Secchi depth) were taken from the WaterBase website (Rijkswaterstaat NL, www.waterbase.nl). These were based on surface water analyses from two sampling locations in the western (Roggenplaat West) and eastern (Yerseke verwateringsplaats) subareas for the corresponding 20 months.

The fish species were counted, measured (as total length, TL in millimetres) and wet weighed. Densities were expressed as numbers per 1000 m², taking into account an overall 20% net-efficiency. Biomass was calculated by means of length-weight or number-weight regressions (Table 4.2), and was expressed in gram ashfree dry weight (ADW) per 1000 m². Three-dimensional plots show both temporal and spatial distribution patterns in density and biomass on a long-term scale for the commonest species that were identified during both periods. A Correspondence Analysis (CA) was performed on the averaged density data per station for both periods. A Canonical Correspondence Analysis (CCA) was performed on averaged density data per season for both periods, together with the associated environmental variables (also see §9.6.1). Prior to the multivariate analyses the data were fourth root transformed and reduced by eliminating those species with an average density (1987-2001) of less than 0.5 individuals per 1000m². Simple comparisons in number of species and frequency of occurrence between both periods were made. Mann-Whitney U tests were performed to identify significant differences in species diversity or in density and biomass per species between both periods. The seasonal, spatial and long-term differences in density and biomass for the separate species were presented per taxonomic group.

Table 4.1 Overview of the sampling surveys conducted in 1987-'89 (12 stations) and 1999-2001 (14 stations) in the Oosterschelde, with an indication of those stations where the sampling distance was reduced from 1000 to 500 metres or less to prevent clogging or tearing of the net

Season	Surveys during 1987-'89 ¹		Surveys during 1999-2001	
	Date	Reduced	Date	Reduced distance
Winter	5, 8, 11 Feb 1988		7-8 Feb 2000	33, 35, 38
	14-15 Feb 1989		19-20 Feb 2001	33, 35, 38
Spring	13-14 Jul 1988 ²		15-16 May 2000	17, 24, 29, 33, 35, 38
	12-16 May 1989		21-22 May 2001	1, 5, 7, 33, 35, 38
Summer	17-18, 20 Aug 1987		30 Aug - 1 Sep 1999	29, 33, 35, 38
	23, 26 Sep 1988		28-29 Aug 2000	all (except 1 & 21)
	7-8 Aug 1989	29, 33	20-21 Aug 2001	26, 33, 35, 38
Autumn	6, 17-18 Nov 1987		22-24 Nov 1999	15, 35, 38
	14-17 Nov 1988		20-21 Nov 2000	33, 35, 38
	3-6 Nov 1989	1, 21	19-20 Nov 2001	26, 33, 35, 38

¹ No samples in the northern part (37 & 38); ² Delayed due to bad weather conditions

Table 4.2 Species list, ecological guild, frequency of occurrence for 3 periods, range in total length and modal length class (between brackets for 1999-2001 if different from 1987-'89). Logarithmic length (mm) –weight (gram) regressions are given, as well as the slope of the allometric length conversions (in mm) in the formula $TL = x SL$ for a few species. Ashfree dryweight (ADW) is on average 20% of wetweight (WW); TL = total length, SL = standard length

Order – Species	Guild ¹	% frequency of Occurrence ²			Total length (mm)		Length-weight regressions (gram - mm)	Slope
		1960-'76	'87-'89	'99-2001	Range	Mode		
Clupeiformes								
<i>Clupea harengus</i>	MJ	19	28	24	50-310	95	$\ln WW = -13.19 + 3.233 * \ln TL$ (n=119, r ² =0.97)	
<i>Sprattus sprattus</i>	MJ	28	14	27	55-135	75 (65)	$\ln WW = -13.55 + 3.356 * \ln TL$ (n=141, r ² =0.99)	
<i>Alosa fallax</i>	CA	-	-	*	350		idem <i>Clupea harengus</i>	
Gadiformes								
<i>Gadus morhua</i>	MJ	8	18	4	50-590		$\ln WW = -12.326 + 3.139 * \ln TL$ (n=48, r ² =0.99)	
<i>Merlangius merlangus</i>	MJ	22	43	47	40-275	70 (60)	$\ln ADW = -13.35 + 3.066 * \ln SL$ (n=47, r ² =0.98)	1.09
<i>Trisopterus luscus</i>	MJ	14	38	51	30-235	90 (130)	$\ln ADW = -14.1 + 3.293 * \ln SL$ (n=45, r ² =0.97)	1.12
<i>Ciliata mustela</i>	MS	8	8	15	85-225	135 (160)	$\ln WW = -13.063 + 3.260 * \ln TL$ (n=33, r ² =0.98)	
Syngnathiformes								
<i>Entelurus aegoreus</i>	MA	-	1	-	470		idem <i>Syngnathus acus</i>	
<i>Syngnathus acus</i>	ER	1	12	10	95-500	350 (225)	$\ln WW = -16.651 + 3.380 * \ln TL$ (n=75, r ² =0.99)	
<i>Syngnathus rostellatus</i>	ER	17	19	32	55-155	95	$\ln WW = -18.036 + 3.652 * \ln TL$ (n=38, r ² =0.98)	1.05
Scorpaeniformes								
<i>Trigla lucerna</i>	MJ	2	4	9	50-315	120 (160)	$\ln WW = -13.102 + 3.289 * \ln TL$ (n=38, r ² =0.99)	
<i>Myoxocephalus scorpius</i>	ER	33	48	24	65-295	150 (170)	$\ln WW = -11.983 + 3.148 * \ln TL$ (n=180, r ² =0.97)	
<i>Enophrys bubalis</i>	MA	1	°	9	45-115		idem <i>Myoxocephalus scorpius</i>	
<i>Agonus cataphractus</i>	ER	28	16	24	45-155	75	$\ln WW = -11.911 + 3.023 * \ln TL$ (n=153, r ² =0.99)	
<i>Liparis liparis</i>	ER	19	6	8	35-135	120 (60)	$\ln WW = -11.416 + 3.088 * \ln TL$ (n=53, r ² =0.99)	
Perciformes								
<i>Gobius niger</i>	ER	-	-	9	45-125		$\ln WW = -11.867 + 3.144 * \ln TL$ (n=32, r ² =0.98)	
<i>Pomatoschistus microps</i>	ER	12	4	30	20-50	30	$\ln WW = -11.404 + 2.931 * \ln TL$ (n=19, r ² =0.99)	
<i>Pomatoschistus minutus</i>	ER	74	67	92	20-90	65 (55)	$\ln WW = -13.440 + 3.404 * \ln TL$ (n=418, r ² =0.97)	1.16
<i>Pomatoschistus lozanoi</i>	MA	-	7	32	20-70	45	idem <i>Pomatoschistus minutus</i>	
<i>Pomatoschistus pictus</i>	MA	1	-	6	35-50		idem <i>Pomatoschistus minutus</i>	
<i>Aphia minuta</i>	ER	1	°	3	35-60		idem <i>Pomatoschistus minutus</i>	
<i>Dicentrarchus labrax</i>	MJ	2	7	21	50-315	100 (115)	$\ln WW = -11.749 + 3.061 * \ln TL$ (n=66, r ² =0.97)	
<i>Trachurus trachurus</i>	MA	6	5	5	30-105	80	$\ln WW = -11.443 + 2.955 * \ln TL$ (n=130, r ² =0.97)	
<i>Chelon labrosus</i>	MS	-	-	1	35		idem <i>Dicentrarchus labrax</i>	
<i>Crenilabrus melops</i>	ER	-	-	1	85-110		idem <i>Dicentrarchus labrax</i>	
<i>Zoarces viviparus</i>	ER	31	39	34	50-325	105	$\ln WW = -13.1 + 3.167 * \ln TL$ (n=165, r ² =0.96)	
<i>Pholis gunnellus</i>	ER	9	8	30	70-190	155	$\ln WW = -15.501 + 3.590 * \ln TL$ (n=31, r ² =0.98)	
<i>Ammodytes tobianus</i>	MA	16	10	21	80-200	155 (135)	$\ln ADW = -16.737 + 3.551 * \ln TL$ (n=34, r ² =0.97)	1.09
<i>Hyperoplus lanceolatus</i>	MA	3	2	2	160-245		$\ln WW = -13.348 + 3.083 * \ln TL$ (n=22, r ² =0.99)	
<i>Callionymus lyra</i>	MA	14	33	55	50-245	85 (75)	$\ln WW = -10.465 + 2.724 * \ln TL$ (n=110, r ² =0.98)	
Pleuronectiformes								
<i>Scophthalmus rhombus</i>	MJ	4	2	3	170-340		$\ln WW = -12.374 + 3.212 * \ln TL$ (n=49, r ² =0.99)	
<i>Lepidorhombus whiffiagonis</i>	MA	-	-	1	145		idem <i>Limanda limanda</i>	
<i>Pleuronectes platessa</i>	MJ	82	91	86	20-415	90 (70)	$\ln WW = -11.690 + 3.033 * \ln TL$ (n=560, r ² =0.99)	1.22
<i>Limanda limanda</i>	MJ	59	78	74	35-280	60	$\ln WW = -12.330 + 3.161 * \ln TL$ (n=353, r ² =0.99)	1.23
<i>Platichthys flesus</i>	ER	43	24	34	60-400	185 (200)	$\ln WW = -11.051 + 2.926 * \ln TL$ (n=169, r ² =0.98)	
<i>Microstomus kitt</i>	MA	1	4	13	40-235	145 (170)	$\ln WW = -12.188 + 3.168 * \ln TL$ (n=22, r ² =0.99)	
<i>Solea solea</i>	MJ	48	30	36	55-410	90 (80)	$\ln WW = -13.097 + 3.262 * \ln TL$ (n=427, r ² =0.99)	1.13
Other species								
<i>Anguilla anguilla</i>	CA	22	11	5	100-700	500	$\ln WW = -15.245 + 3.326 * \ln TL$ (n=152, r ² =0.97)	
<i>Osmerus eperlanus</i>	CA	22	-	*	85-150		idem <i>Clupea harengus</i>	
<i>Belone belone</i>	MS	-	°	1	150		$\ln WW = -13.701 + 3.020 * \ln TL$ (n=9, r ² =0.99)	
<i>Atherina presbyter</i>	MJ	3	1	8	65-90		$\ln WW = -12.478 + 3.103 * \ln TL$ (n=12, r ² =0.99)	
<i>Gasterosteus aculeatus</i>	CA	7	5	-	30-55		$\ln WW = -11.359 + 2.938 * \ln TL$ (n=41, r ² =0.99)	
Species only recorded in 1960-76		1						
<i>Lampetra fluviatilis, Raja clavata, Dasyatis pastinaca, Engraulis encrasicolus, Pollachius pollachius, Eutrigla gurnardus, Cyclopterus lumpus, Arnoglossus laterna, Scophthalmus maximus, Buglossidium luteum</i>								
Number of species		44	32	38				

¹ estuarine resident (ER), marine juvenile (MJ), marine seasonal (MS), marine adventitious (MA), diadromous (CA)

² ° recorded in 1987-'89 but not in the stations considered in this study; * only caught in the northern part in 1999-2001

Table 4.3 Average density and biomass per species, total average, and number of species per season for 1987-'89 and 1999-2001 (between brackets). Significant differences (Mann-Whitney U-test) between both periods per season and in the overall comparison (middle column) are noted with * ($p < 0.05$) and ** ($p < 0.001$)

Order/species	Density (#/1000m ²)				Overall	Biomass (gADW/1000m ²)			
	Winter	Spring	Summer	Autumn		Winter	Spring	Summer	Autumn
Clupeiformes									
<i>Clupea harengus</i>	9 (4) *	- (2)	1 (3)	12 (14)		30 (6) *	- (0.3)	1 (2)	15 (11)
<i>Sprattus sprattus</i>	6 (10)	- (0.4)	- (0.1)	11 (4)		4 (9)	- (0.5)	- (<0.1)	6 (2)
Gadiformes									
<i>Gadus morhua</i>	0.5 (0.2)	0.5 (-)	0.9 (0.6)	1 (-)		11 (18)	0.4 (-)	3 (2)	26 (-)
<i>Merlangius merlangus</i>	0.3 (0.5)	11 (7)	8 (8)	3 (4)		4 (6)	14 (13)	34 (36)	37 (65)
<i>Trisopterus luscus</i>	1 (3)	50 (8)	23 (50)	5 (5)		17 (43)	90 (1)	103 (256)	75 (67)
<i>Ciliata mustela</i>	- (0.3)	0.2 (0.2)	0.3 (0.5)	0.4 (0.8)		- (3)	2 (1)	<0.1 (1)	2 (4)
Syngnathiformes									
<i>Entelurus aegoreus</i>	-	0.1 (-)	-	-		-	0.8 (-)	-	-
<i>Syngnathus acus</i>	-	0.3 (0.2)	1 (2)	0.2 (0.1)		-	2 (1)	2 (5)	0.6 (0.1)
<i>Syngnathus rostellatus</i>	0.1 (-)	0.2 (1)	3 (7)	1 (6)		<0.1 (-)	<0.1 (0.1)	0.2 (0.4)	0.1 (0.3)
Scorpaeniformes									
<i>Trigla lucerna</i>	-	0.2 (2) *	0.3 (0.1)	0.1 (-)		-	1 (16) *	3 (2)	0.1 (-)
<i>Myoxocephalus scorpius</i>	7 (1) *	4 (2)	5 (1) *	4 (1)	**	71 (34) *	45 (15)	65 (15) *	56 (20)
<i>Enophrys bubalis</i>	- (2)	-	- (1)	- (0.7)		- (3)	-	- (0.6)	- (1)
<i>Agonus cataphractus</i>	0.6 (0.6)	0.3 (1.1)	0.6 (2)	1 (3)		0.7 (0.3)	0.4 (1)	1 (1)	2 (4)
<i>Liparis liparis</i>	- (0.1)	- (0.4)	0.2 (1)	4 (0.2)		- (0.5)	- (0.1)	0.3 (1)	20 (1)
Perciformes									
<i>Gobius niger</i>	- (0.6)	- (0.2)	- (0.5)	- (0.5)		- (2)	- (0.5)	- (1)	- (1)
<i>Pomatoschistus microps</i>	0.2 (20) **	-	0.6 (3)	- (4.1) *	**	<0.1 (2) **	-	0 (0.2)	- (0.4) *
<i>Pomatoschistus minutus</i>	25 (351) **	4 (20) **	21 (304) **	85 (225) **	**	15 (139) **	2 (8) **	6 (68) **	38 (86) **
<i>Pomatoschistus lozanoi</i>	0.1 (1)	0.5 (2)	0.3 (3)	0.3 (2) *	**	<0.1 (0.2)	0.1 (0.3)	0 (0.2)	<0.1 (0.3) *
<i>Pomatoschistus pictus</i>	-	- (0.3)	-	- (13)		-	- (<0.1)	-	- (1)
<i>Aphia minuta</i>	- (0.1)	- (0.2)	-	- (0.1)		- (0)	- (0.1)	-	- (<0.1)
<i>Dicentrarchus labrax</i>	0.5 (10)	-	0.2 (0.1)	5 (14) *	*	1 (52)	-	0.1 (5)	9 (49) *
<i>Trachurus trachurus</i>	-	-	1 (1)	-		-	-	0.7 (1)	-
<i>Chelon labrosus</i>	-	-	-	- (<0.1)		-	-	-	- (<0.1)
<i>Crenilabrus melops</i>	- (0.2)	-	- (0)	- (0.2)		- (0.2)	-	-	- (0.4)
<i>Zoarcetes viviparus</i>	5 (1)	4 (3)	4 (13)	6 (2)		19 (4)	27 (9)	22 (39)	24 (7)
<i>Pholis gunnellus</i>	0.1 (2) *	0.5 (5) *	2 (4)	- (0.5)	**	0.2 (4) *	1 (10) *	4 (7)	- (0.4)
<i>Ammodytes tobianus</i>	0.1 (1) *	0.8 (-)	0.5 (4)	0.3 (0.7)		0.3 (1) *	4 (-)	2 (13)	1 (1)
<i>Hyperoplus lanceolatus</i>	-	-	0.1 (0.1)	0.1 (-)		-	-	0.6 (0.4)	0.1 (-)
<i>Callionymus lyra</i>	0.3 (2)	1 (10)	3 (32)	6 (29) **	**	0.3 (5)	3 (20)	7 (44)	13 (50) **
Pleuronectiformes									
<i>Scophthalmus rhombus</i>	- (0.1)	- (0.1)	- (0.1)	0.1 (0.1)		- (2)	- (1)	- (7)	4 (1)
<i>Lepidorhombus whiffiagonis</i>	-	-	- (0.1)	-		-	-	- (0.6)	-
<i>Pleuronectes platessa</i>	57 (29)	56 (74)	98 (233)	156 (33)	*	435 (112) *	749 (456)	1351 (1358)	1257 (194) *
<i>Limanda limanda</i>	69 (19)	12 (14)	17 (95)	138 (21)		212 (24)	39 (64)	32 (62)	245 (57) *
<i>Platichthys flesus</i>	2 (3)	2 (4)	1 (1)	1 (1)		46 (27)	28 (51)	19 (36)	42 (58)
<i>Microstomus kitt</i>	- (0.1)	0.4 (3)	0.1 (2)	- (0.7)		0 (1)	4 (23)	0.5 (12)	- (5)
<i>Solea solea</i>	12 (1)	4 (6)	5 (23) *	2 (1)		23 (2)	41 (49)	29 (144) *	8 (3)
Other species									
<i>Anguilla anguilla</i>	- (0.1)	1.5 (-)	1 (0.5)	0.1 (-)		- (5)	71 (-)	34 (22)	4 (-)
<i>Belone belone</i>	-	-	- (0.1)	-		-	-	- (<0.1)	<0.1 (-)
<i>Atherina presbyter</i>	-	-	- (0.1)	0.1 (0.7)		-	-	- (<0.1)	<0.1 (0.5)
<i>Gasterosteus aculeatus</i>	1.2 (-)	-	0.7 (-)	-		0.2 (-)	-	0.1 (-)	-
Total average	198 (463)	153 (165)	199 (794) *	444 (389) *	**	892 (506)	1124 (744)	1721 (2139)	1886 (691)
# species	20 (28) *	22 (25)	27 (33)	25 (29) *	**				

To investigate possible real long-term changes in the Oosterschelde (including the northern part), the number of species and the frequency of occurrence in 1999-2001 were compared with 1960-

'76, where fish were investigated on basis of a similar sampling methodology (Doornbos *et al.* 1981).

Table 4.4 Average density and biomass per species, total average, and number of species per subarea for 1987-'89 and 1999-2001 (between brackets). Significant differences (Mann-Whitney U-test) between both periods are noted with * ($p < 0.05$) and ** ($p < 0.001$)

Order/species	Density (#/1000m ²)				Biomass (gADW/1000m ²)			
	Western	Central	Eastern	Northern	Western	Central	Eastern	Northern
Clupeiformes								
<i>Clupea harengus</i>	3 (4)	5 (4)	11 (13)	(79)	5 (2)	4 (4)	30 (11)	(43)
<i>Sprattus sprattus</i>	2 (4)	1 (4)	13 (3)	(117)	2 (3)	1 (3)	6 (2)	(31)
<i>Alosa fallax</i>	-	-	-	(0.1)	-	-	-	(0.1)
Gadiformes								
<i>Gadus morhua</i>	2 (1)	0.4 (<0.1)	0.3 (-)	(0.1)	29 (12)	2 (<0.1)	2 (-)	(0.5)
<i>Merlangius merlangus</i>	12 (8)	3 (5) *	1 (0.5)	(5)	55 (69)	14 (23) *	4 (2)	(9)
<i>Trisopterus luscus</i>	21 (35)	13 (16)	24 (1)	(3)	131 (216)	21 (80)	90 (3)	(13)
<i>Ciliata mustela</i>	0.2 (1)	0.2 (0.5)	0.4 (-)	(-)	1 (3)	0.2 (3)	2 (-)	(-)
Syngnathiformes								
<i>Entelurus aegoreus</i>	-	<0.1 (-)	-	(-)	-	0.4 (-)	-	(-)
<i>Syngnathus acus</i>	0.2 (0.1)	0.5 (1)	0.3 (1)	(0.5)	1 (0.1)	1 (3)	2 (1)	(0.4)
<i>Syngnathus rostellatus</i>	0.6 (3)	2 (4)	1 (6) *	(16)	<0.1 (0.2)	0.1 (0.2)	<0.1 (0.3) *	(1)
Scorpaeniformes								
<i>Trigla lucerna</i>	0.2 (1)	0.1 (0.5)	-	(0.1)	3 (5)	1 (6)	-	(1)
<i>Myoxocephalus scorpius</i>	4 (1)	7 (1) **	4 (1) *	(2)	55 (21)	71 (22) **	47 (17) *	(17)
<i>Enophris bubalis</i>	-	-(1)	-(1)	(0.5)	-	-(1.2)	-(2)	(1)
<i>Agonus cataphractus</i>	1 (4)	0.7 (1)	0.1 (0.2)	(-)	2 (4)	1 (1)	0.1 (0.3)	(-)
<i>Liparis liparis</i>	3 (1)	0.3 (0.3)	0.2 (0.1)	(0.1)	16 (1)	1 (1)	1 (0.1)	(0.1)
Perciformes								
<i>Gobius niger</i>	-	-(0.2)	-(1)	(3)	-	-(0.9)	-(3)	(6)
<i>Pomatoschistus microps</i>	<0.1 (4)	-(3)	1 (16) **	(3)	<0.1 (0.4)	-(0.3)	<0.1 (2) **	(0.3)
<i>Pomatoschistus minutus</i>	17 (133) **	17 (235) **	100 (364) *	(1126)	8 (41) **	9 (76) **	41 (121) *	(301)
<i>Pomatoschistus lozanoi</i>	1 (4) *	-(2) *	2 (0.1)	(-)	0.1 (0.4) *	-(0.2) *	-(<0.1)	(-)
<i>Pomatoschistus pictus</i>	-	-(10)	-(0.2)	(1)	-	-(0.6)	-(<0.1)	(<0.1)
<i>Aphia minuta</i>	-(0.1)	-(0.1)	-(0.1)	(-)	-(<0.1)	-(<0.1)	-	(-)
<i>Dicentrarchus labrax</i>	-(4)	0.3 (3)	6 (15)	(35)	-(23)	0.4 (19)	12 (47)	(123)
<i>Trachurus trachurus</i>	-(0.4)	1 (0.5)	0.1 (0.1)	(-)	-(0.3)	0.5 (0.4)	<0.1 (0.2)	(-)
<i>Chelon labrosus</i>	-(<0.1)	-	-	(-)	-(<0.1)	-	-	(-)
<i>Crenilabrus melops</i>	-	-	-(0.4)	(-)	-	-	-(0.7)	(-)
<i>Zoarces viviparus</i>	8 (8)	5 (6)	0.5 (0.4)	(27)	33 (23)	26 (20)	4 (0.3)	(61)
<i>Pholis gunnellus</i>	-(3) **	1 (3)	0.5 (2)	(10)	-(6) **	3 (5)	1 (3)	(12)
<i>Ammodytes tobianus</i>	1 (0.4)	0.2 (4) *	0.2 (0.1)	(-)	4 (1)	1 (11) *	1 (0.2)	(-)
<i>Hyperoplus lanceolatus</i>	<0.1 (<0.1)	0.1 (<0.1)	-	(-)	0.1 (0.2)	0.4 (0.1)	-	(-)
<i>Callionymus lyra</i>	5 (14) **	3 (36) **	1 (3)	(19)	10 (32) **	6 (49) **	2 (8)	(30)
Pleuronectiformes								
<i>Scophthalmus rhombus</i>	-	-(0.1)	0.1 (0.1)	(-)	-	-(6)	5 (1)	(-)
<i>Lepidorhombus whiffiagonis</i>	-	-(<0.1)	-	(-)	-	-(0.4)	-	(-)
<i>Pleuronectes platessa</i>	211 (230)	49 (52)	33 (9) **	(186)	2330 (1340)	353 (254)	382 (111) **	(297)
<i>Limanda limanda</i>	127 (84)	40 (31)	14 (3) **	(20)	240 (96)	90 (47)	62 (7) **	(23)
<i>Platichthys flesus</i>	2 (4)	0.4 (1)	2 (1)	(2)	47 (88)	8 (17)	55 (30)	(40)
<i>Microstomus kitt</i>	-(1)	0.3 (2)	-	(0.4)	-(9)	2 (17)	-	(0.2)
<i>Solea solea</i>	12 (20)	1 (4)	3 (1)	(17)	38 (86)	6 (60)	34 (4)	(48)
Other species								
<i>Anguilla anguilla</i>	1 (0.1)	0.2 (0.3)	1 (-)	(0.2)	40 (6)	8 (14)	36 (0)	(8)
<i>Osmerus eperlanus</i>	-	-	-	(1)	-	-	-	(2)
<i>Belone belone</i>	-	-(<0.1)	-	(-)	-	-(<0.1)	-	(-)
<i>Atherina presbyter</i>	<0.1 (0.1)	-(0.4)	-(0.2)	(0.1)	<0.1 (0.1)	-(0.3)	-(0.1)	(<0.1)
<i>Gasterosteus aculeatus</i>	0.6 (-)	0.5 (-)	0.2 (-)	(-)	0.1 (-)	0.1 (-)	<0.1 (-)	(-)
Total average	434 (570)	153 (432) **	221 (442)	(1671)	3050 (2089)	633 (745)	822 (376) **	(1066)
# species	25 (31) **	28 (36) **	27 (28)	(28)				

4.3 Results

4.3.1 Species richness and frequency of occurrence

A total of 42 fish species were caught in the Oosterschelde (Table 4.2). For the comparison between both periods all averages were calculated for 12 stations, excluding the northern part. In 1987-'89 an

average of 21 species were noted in winter (February) and spring (May) and 26 species in summer (August) and autumn (November). In 1999-2001 5 fish species more were caught on average, which was significantly different for autumn and winter and in the overall comparison (Table 4.3). The number of species per station averaged around 20 in 1987-'89, while a significantly higher number was noted in the western and central parts in 1999-2001 (Table 4.4).

In the northern part 28 species were recorded during 1999-2001.

Only 3 species were recorded in more than 75% of all samples (Table 4.2). Most species were less common: 50-25% (9 species), 25-10% (10 species), 10-1% (13 species). The other 5 species were caught only once or occurred in less than 1% of the samples. More than 70% of the 40 species that were caught in the Oosterschelde excluding the northern part, showed an increased occurrence in 1999-2001 (>20% for 3 *Pomatoschistus* species, butterfish *Pholis gunnellus* and dragonet *Callionymus lyra*); 10 species were found in fewer samples during 1999-2001 (>20% difference for bull-rout *Myoxocephalus scorpius*).

4.3.2 Total average density and biomass

Sand goby *Pomatoschistus minutus* and plaice *Pleuronectes platessa* showed average densities of 135 and 100 ind/1000m² respectively, and only 3 species had average densities between 50-10 ind/1000m². More than 85% of the species were less abundant: 10-0.1/1000m² (15 species), 1-0.1/1000m² (14 species), and < 0.1/1000m² (6 species). 28 species showed an increased average density in 1999-2001 (largest difference for sand goby, but also significantly higher for dragonet, two other gobiid species and butterfish (Table 4.3). On the other hand, 9 species had decreased densities, with the largest (but not significant) difference for dab *Limanda limanda*. Only in terms of density, a significant increase was noted for summer and for the overall comparison between 1987-89 and 1999-2001, and a significant decrease for autumn. The total average density per season was 150 in spring, 200 in winter-summer, and 440 ind/1000m² in autumn in 1987-89, and 160 in spring, 390 in autumn, 460 in winter, and 790 ind/1000m² in summer in 1999-2001 (Table 4.3). The average density was significantly higher in the central part in 1999-2001 (Table 4.4). The average density varied between 150 (central), 220 (eastern) and 430 (western) ind/1000m² in 1987-89 and between 430 (central), 440 (eastern), 570 (western) and 1670 (northern) ind/1000m² in 1999-2001.

In terms of biomass, highest average values were found for plaice (800 gADW/1000m²). The further distribution in biomass classes was comparable with the density data: 100-50 gADW/1000m² (2 species), 50-10 gADW/1000m² (9 species), 10-1 gADW/1000m² (12 species), 1-0.1 gADW/1000m² (9 species), and <0.1 gADW/1000m² (7 species). In 1999-2001 26 species showed an increased biomass, which was significant for the same species as with the density data, supplemented with seabass *Dicentrarchus labrax*, but also a non-significant increase for bib *Trisopterus luscus*, whiting *Merlangius merlangus* and lemon sole *Microstomus kitt* was noted (Table 4.3). For the other 14 species, the average

biomass decreased (significantly for plaice and bull-rout, and a large but not significant decrease for dab). The total average biomass varied per season between 890-1890 gADW/1000m² in 1987-'89 and between 510-2140 gADW/1000m² in 1999-2001. The total average biomass was significantly lower in the eastern part. Per subarea the values varied between 630 (central), 820 (eastern) and 3050 (western) gADW/1000m² in 1987-89 and between 380 (eastern), 750 (central), 2090 (western) and 1070 (northern) gADW/1000m² in 1999-2001.

4.3.3 Community analyses

Total inertia of the Correspondence Analysis based on the average density per station and per period of 23 species amounted to 0.29 (Fig. 4.3). The eigenvalues of the first two ordination axes were 0.08 and 0.05, respectively. The stations were found together more or less in a western, central and eastern group for both periods, corresponding with the geographical subareas. Canonical Correspondence Analysis clearly divided autumn and winter from spring and summer along the first ordination axis (Fig. 4.2). Winter was characterized by very high concentrations of suspended matter (15 mg.l⁻¹) as opposed to an average concentration of 5.5 mg.l⁻¹ for the other seasons, which was comparable for both periods (Table 4.5). Typical species for autumn were herring *Clupea harengus* and sprat *Sprattus sprattus* for both periods, and seabass and common goby *Pomatoschistus microps* for winter in the period 1999-2001. Spring and summer were characterized by higher temperatures (13.5 and 19 °C, respectively). Most species were found in these seasons. A further arrangement of seasons and periods could be seen along the second ordination axis. The period 1987-'89 was characterized by a higher visibility of the water, with high values for spring (up to 3.5 m) and summer (2.8 m). Typical species were cod *Gadus morhua*, whiting and bull-rout in 1987-'89, while sea-snail *Liparis liparis*, lozano's goby *Pomatoschistus lozanoi* and lemon sole were characteristic for 1999-2001. The total variance explained by the first two ordination axes amounted to 29 and 9 % respectively. Except for autumn, the first period showed somewhat higher dissolved oxygen concentrations, varying between 7

Table 4.5 Averaged environmental data per season for 1987-'89 and 1999-2001 (between brackets), recalculated from www.waterbase.nl (Rijkswaterstaat, the Netherlands)

Variable	Winter	Spring	Summer	Autumn
Salinity (psu)	30.3 (30.3)	30.2 (29.0)	30.8 (31.5)	31.1 (31)
Temperature (°C)	5.5 (5.5)	13.2 (14.0)	18.4 (20.1)	10.3 (8.9)
Secchi depth (m)	1.6 (1.0)	3.5 (1.8)	2.8 (2.1)	2.6 (1.9)
Dissolved oxygen (mg.l ⁻¹)	10.6 (10.2)	10.4 (9.5)	8.3 (7.4)	8.7 (9.3)
Suspended matter (mg.l ⁻¹)	15.3 (14.6)	6.3 (5.6)	5.1 (4.0)	5.9 (6.0)

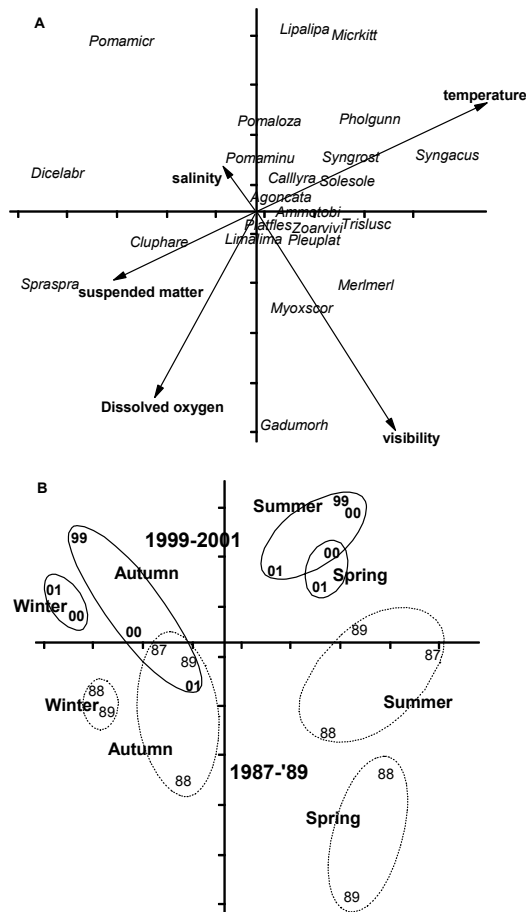


Fig. 4.2 Species (A) and sample-environmental (B) plots as a result of the Canonical Correspondence Analysis in the plane of the first two ordination axes. Surveys grouped per season and per period

and 11 mg.l⁻¹. Salinity did not vary much between both (30.5 psu) (Table 4.5).

4.3.4 Comparison 1960-76 with 1999-2001

In 1960-76 a total of 44 fish species were recorded in the Oosterschelde (including the northern part), of which 12 and 11 species were not found in 1987-'89 and 1999-2001, respectively (Table 4.2). During the latter period 40 fish species were recorded, with 6 species that were not found in 1960-76. In both cases these were mainly species that were only recorded once. Three species were most common in both periods: sand goby, plaice and dab. Five species had an increased frequency of occurrence >20% (dragonet, bib, butterfish, whiting and seabass), 7 species between 20-10 %, 7 species between 10-5%, 3 species between 5-1%, and 6 species <1%. Three species had a decreased frequency of occurrence between 20-10% (smelt *Osmerus eperlanus*, eel *Anguilla anguilla* and sea-snail), 5 species between 10-5%, 4 species between 5-1%, and 10 species <1%.

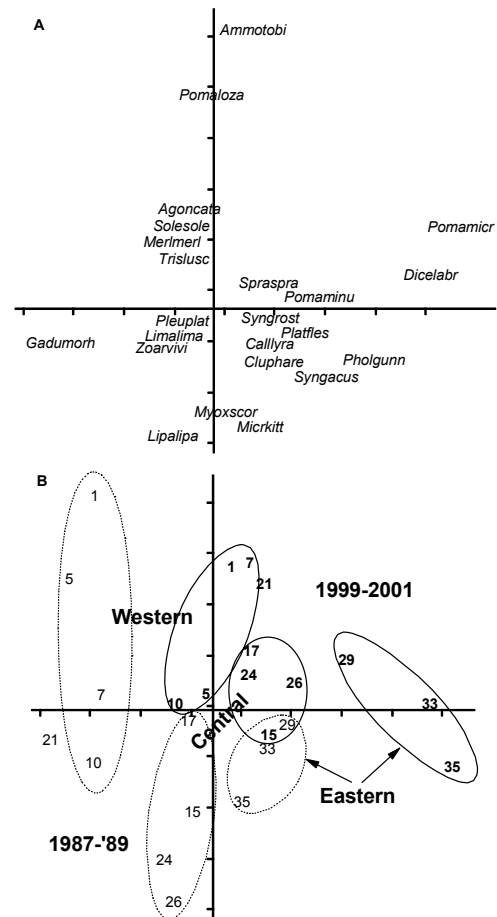


Fig. 4.3 Species (A) and sample (B) plots as a result of the Correspondence Analysis in the plane of the first two ordination axes. Stations grouped per subarea and per period

4.3.5 Spatio-temporal patterns in density, biomass and growth

The average density and biomass per season and per station for both periods is given in Fig. 4.4. The spatio-temporal distribution patterns of the 4 commonest species were comparable in terms of biomass as the ones presented for density (Fig. 4.5). The length-frequency distributions per season for both periods for 12 common species were given in Fig. 4.6. The total length range and modal lengthclasses were given in Table 4.2. Average densities and biomasses per period, with a note on the significant differences for individual species, were given in Table 4.3 per season and in Table 4.4 per subarea.

Clupeiformes

Three clupeoid species were recorded in the Oosterschelde. Twaite shad *Alosa fallax* was caught only once at station 37 in November 1999. The two other species, herring *Clupea harengus* and sprat *Sprattus sprattus*, were mainly present in autumn and winter during both periods, and completely absent in spring and summer in 1987-'89.

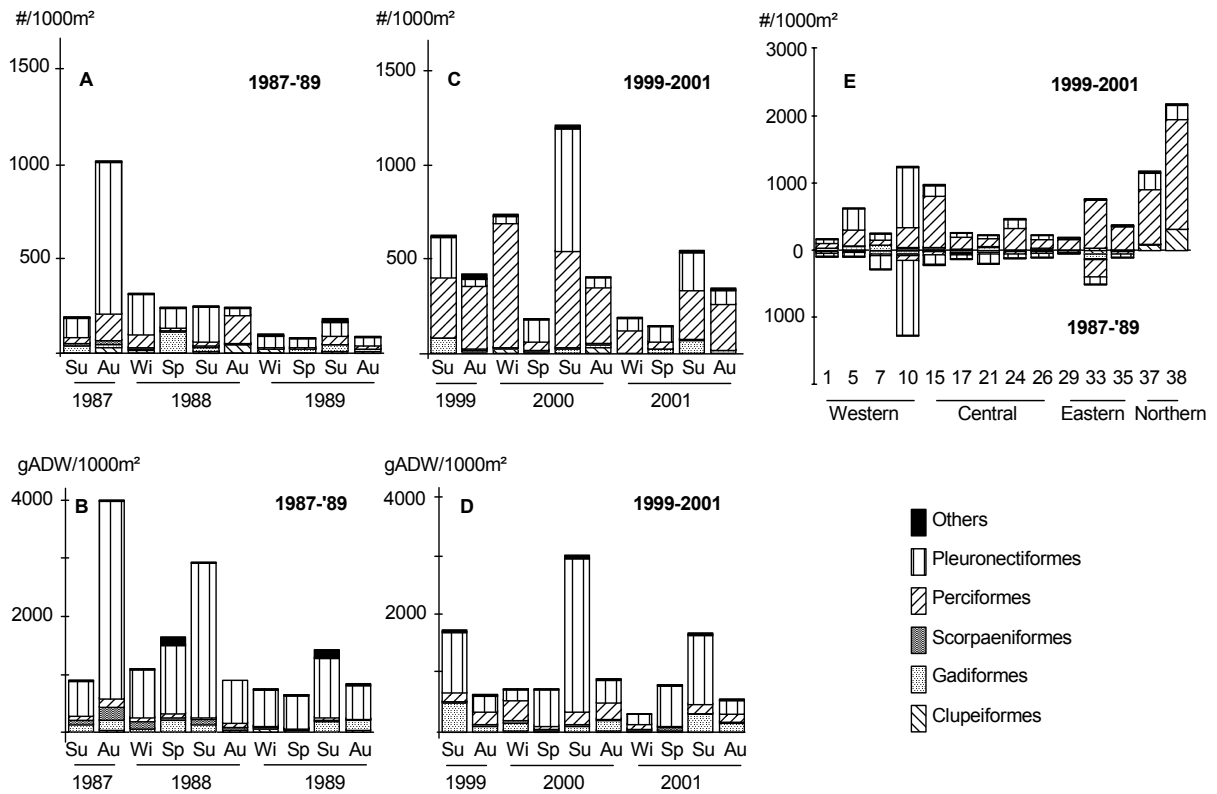


Fig. 4.4 Average density (A & C) and biomass (B & D) per seasonal survey (starting in summer 1987 and summer 1999, respectively), and average density per station (E) per taxonomic group for the periods 1987-'89 and 1999-2001

No significant differences were found for either species between both periods, nor per season or per station. Autumn was the richest season for *C. harengus* in both periods in numbers (on average 13 ind/1000m²); average biomass was highest in winter for 1987-'89 (30 gADW/1000m²) and in autumn for 1999-2001 (11 gADW/1000m²). This was mainly due to a number of large herring (>200 mm TL) that were caught during the first period, while in the latter period herring never exceeded a length of 150 mm. For *S. sprattus*, maximal density and biomass was recorded in autumn in 1987-'89 (11 ind/1000m² and 6 gADW/1000m²) and in winter in 1999-2001 (10 ind/1000m² and 9 gADW/1000m²).

Both species reached high densities in the eastern part (station 33) in 1987-'89, while this was only the case for herring in 1999-2001. Also, at station 15 high densities were recorded for herring in both periods, while this was only the case in 1999-2001 for sprat. For both species, highest average densities were recorded in the northern part during the latter period, with on average 120 and 200 ind/1000m² at station 38 for herring and sprat respectively. In this subarea herring and sprat were mainly present in summer and autumn.

Small juveniles (<60 mm) of *C. harengus* were only caught in spring. The bulk varied between 85 and 100 mm in length in autumn, while in February mainly larger individuals of 105-115 mm were present. For *S. sprattus* the modal length was 75 mm

TL in 1987-'89, and a little bit smaller in 1999-2001 (65 mm). For both periods, the larger individuals (up to 130 mm) were only caught in winter.

Gadiformes

Four species were caught in the Oosterschelde. Poor cod *Trisopterus minutus* was recorded sporadically in 1987-'89 at other locations than the ones considered here. The most abundant species were bib *Trisopterus luscus* and whiting *Merlangius merlangus*, which mainly occurred in spring and summer. No significant differences were found between both periods for both species, but *T. luscus* was more abundant in spring of 1987-'89 (on average 50 ind/1000m², 90 gADW/1000m²), and in summer of 1999-2001 (on average 50 ind/1000m², 260 gADW/1000m²). The density and biomass for whiting were comparable per season between both periods, except in spring when highest densities were recorded (11 and 7 ind/1000m²) and in autumn when highest biomasses were found (40 and 65 gADW/1000m², respectively for both periods).

Both bib and whiting were found throughout the Oosterschelde, but whiting preferred the western part in both periods. Densities of bib were higher at most stations in 1999-2001, although this difference was only significant in terms of biomass for station 5 (40 gADW/1000m² in 1987-'89 against 260 gADW/1000m² in 1999-2001). In the eastern part *T. luscus* was more abundant in 1987-'89, which was

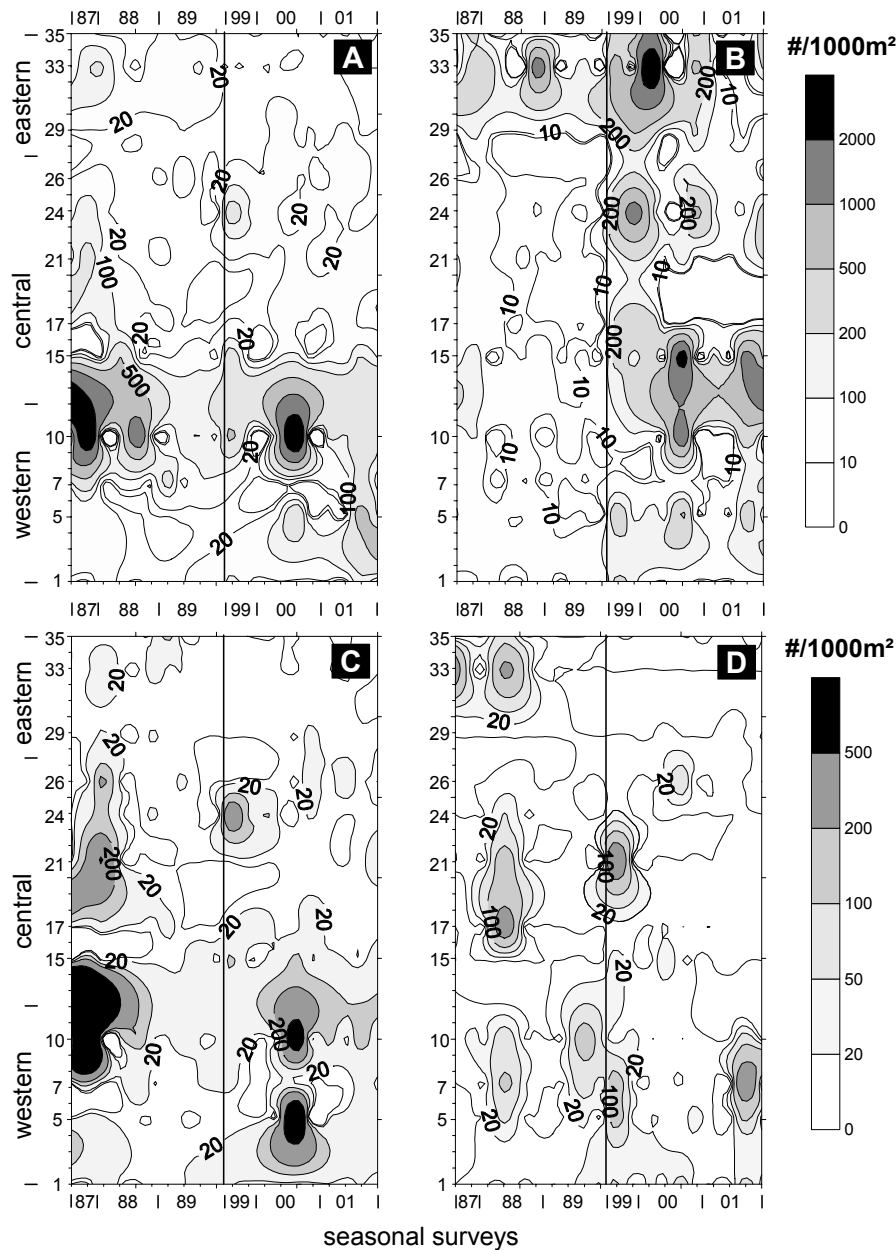


Fig. 4.5 Surface plots showing the spatio-temporal density patterns for *Pleuronectes platessa* (A) and *Pomatoschistus minutus* (B) (upper scale bar), and for *Limanda limanda* (C) and *Trisopterus luscus* (D) (lower scale bar). Seasonal surveys were successively ordered from August 1987 till November 1989 and from August 1999 till November 2001. Station numbers as in Fig. 4.1

mainly attributable to peak densities in summer 1987 and spring 1988. There was a clear growth observed from season to season for bib and whiting, with the smallest individuals found in spring (between 30–45 mm TL in 1999–2001 and 65–100 mm in 1987–‘89 for bib, and between 40–90 mm TL for whiting). This was followed by the modal length classes 90 and 130 mm in both periods for bib and the length classes 115–165 mm for whiting in summer, and by a few larger individuals (up to 235 mm for bib and 275 mm for whiting) in autumn and winter.

Cod *Gadus morhua* and five-bearded rockling *Ciliata mustela* were much less common, and mainly elder individuals were caught. *C. mustela* was found in somewhat higher densities in 1999–2001

(0.5 ind/1000m²), and *G. morhua* was almost not found during this period (on average 0.8 and 0.2 ind/1000m² in 1987–‘89 and 1999–2001 respectively). Both species were present at several stations in the Oosterschelde, but they were absent from the eastern part in 1999–2001. Bib, whiting and cod were also caught in the northern part at station 37, but never at station 38.

Syngnathiformes

Three pipefish species were recorded. Snake pipefish *Entelurus aequoreus* was only caught once in July 1988 at station 26. Nilsson’s pipefish *Syngnathus rostellatus* was the most abundant species in the whole Oosterschelde, with a preference for the cen-

tral part (on average 4 and 12 ind/1000m² at station 15 in 1987-'89 and 1999-2001, respectively). The highest densities occurred in summer for both periods, and all length classes (55-155 mm TL) were present with a modal length class of 95 mm. In autumn of 1999-2001 *S. rostellatus* was also abundant in the length range 60-90 mm. The average density was twice as high in the latter period during summer and six times as high during spring and autumn, as compared to 1987-'89. *S. rostellatus* was also recorded in the northern part, with a peak abundance of 240 ind/1000m² in August 2000 in station 37.

Greater pipefish *Syngnathus acus* was not recorded in winter, and was present in most stations in low densities in spring and autumn (on average 0.2 ind/1000m²). The maximum average density in summer was twice as high in 1999-2001 (2 ind/1000m²). The length range of *S. acus* varied between 95 and 500 mm TL in 1987-'89 and between 125-405 mm in 1999-2001.

Scorpaeniformes

In this order 5 species were recorded. The most common species was bull-rout *Myoxocephalus scorpius*, followed by hooknose *Agonus cataphractus*, and sea-snail *Liparis liparis*, sea scorpion *Enophrys bubalis* and tub gurnard *Trigla lucerna*.

For *M. scorpius*, average densities were 3 to 5 times lower every season of 1999-2001, which was significantly different for winter (7 against 1 ind/1000m²) and summer (5 against 1 ind/1000m² in 1987-'89 and 1999-2001, respectively). In 1989 densities were much lower than in 1987 or 1988. The average biomass was 2 to 3 times higher in 1999-2001, with a maximum in winter (70 against 35 gADW/1000m²). Bull-rout was found throughout the Oosterschelde with higher densities at stations 10 and 26 in 1987-'89 and at stations 5 and 17 in 1999-2001 (significantly different in the central and eastern parts). Most length classes (65-295 mm TL) were present throughout the year, but three cohorts could be distinguished: a small cohort between 65 and 100 mm in winter (which was almost absent in 1999-2001), the commonest cohort between 100 and 175 mm, and elder species from 170 mm onwards.

A. cataphractus occurred at most stations with low densities, with a preference for the western part. During most seasons (except winter) this species was twice as abundant in 1987-'89. Higher average densities were recorded in autumn during all years (3 and 1.5 ind/1000m² in 1987-'89 and 1999-2001 respectively). Two successive cohorts could be seen, starting in summer with the commonest cohort between 45 and 95 mm TL, and a second year class between 90 and 155 mm.

L. liparis was found sporadically at several stations during 1999-2001. This species was almost absent in 1987-'89, except for a few records in autumn and summer, and an exceptionally high density

in November 1987 at station 10 (120 ind/1000m²). In 1999-2001, the smallest individuals (35 mm TL) entered the Oosterschelde in February, and grew to a size of 135 mm in November. *E. bubalis* was only recorded in 1999-2001 (average density <1 ind/1000m²), although it was registered a few times in autumn and winter of 1987-'89 at locations not considered in this study. Sea scorpion did not occur in spring, nor in the western part. *T. lucerna* was only found in spring and summer, with significantly higher densities in May 2000 and 2001. Tub gurnard mainly occurred in the western part in 1987-'89, but also in the central part in 1999-2001. Length varied between 50 and 315 mm TL, with smallest and biggest individuals being recorded in summer, and the modal length classes in both periods (120, 160 mm) in spring. Most scorpaenid species, except hooknose, were also recorded in the northern part, but only *M. scorpius* was present in autumn throughout the whole period 1999-2001. *T. lucerna*, *L. liparis* and *E. bubalis* were recorded once in this subarea in spring, summer and autumn of 2001, respectively.

Perciformes

With 15 species, this order contained the highest number of fish species in the Oosterschelde. Sand goby *Pomatoschistus minutus* was the commonest species, followed by dragonet *Callionymus lyra*, viviparous blenny *Zoarcetes viviparus* and seabass *Dicentrarchus labrax*.

P. minutus occurred at all stations throughout the year, but density and biomass were significantly higher in 1999-2001 for all seasons and almost all stations (on average 40 and 230 ind/1000m² and 15 and 75 gADW/1000m² for 1987-'89 and 1999-2001 respectively). In both periods, density was lowest in spring and reached about the same value in the other seasons. Average density was highest in the eastern part at station 33 for both periods. This could mainly be attributed to very high densities in November 1988 (1600 ind/1000m²) and February 2000 (4700 ind/1000m²). This was also the main reason why the maximum average density and biomass had shifted from autumn in 1987-'89 to winter in 1999-2001. For the latter period, the average density was even higher in the northern part, with a peak density of 4140 ind/1000m² at station 38 in November 2001. In several other seasons the highest density was found at station 15 (on average 30 and 580 ind/1000m² in 1987-'89 and 1999-2001, respectively). The modal length classes (55, 65 mm TL) were present throughout the year. Still, growth could be seen through the seasons with the new recruits (20-40 mm) occurring in summer and autumn in the Oosterschelde, and larger individuals (up to 95 mm) found in autumn and winter of the succeeding year.

The four other gobiid species were much less common. In 1987-'89 common goby *Pomatoschistus microps* was only recorded in the eastern part in Feb-

ruary 1988 and in August 1989. The difference in density and biomass was significant for winter (on average 0.2 versus 20 ind/1000m²) and for autumn (0 versus 4 ind/1000m² in 1987-'89 and 1999-2001 respectively). In 1999-2001 *P. microps* was not found in spring, but during the other seasons it was found throughout the Oosterschelde, mainly in the eastern part (up to 20 ind/1000m² at station 33) and with a modal length of 30 mm TL. In the northern part average densities of 3 ind/1000m² were recorded. In 1987-'89 lozano's goby *Pomatoschistus lozanoi* was sporadically recorded in the western and eastern part and in 1999-2001 also in the central part. The length range varied between 20 and 70 mm. During all seasons density and biomass were higher in 1999-2001, although this was only significant for autumn and for station 7 (1 versus 6 ind/1000m²) and station 21 (0 versus 5 ind/1000m² for 1987-'89 and 1999-2001, respectively). Painted goby *Pomatoschistus pictus* was not recorded in 1987-'89. In February 2001 a few individuals were recorded. In November 2001 exceptionally high densities were found at station 15 (370 ind/1000m²) and at station 17 (100 ind/1000m²). In 1987-'89 black goby *Gobius niger* was caught at a station not considered in February 1989, while in 1999-2001 it was mainly found at station 35, with an average of 0.5 ind/1000m² for every season. Together with the previous species, *G. niger* was also found in the northern part, but never in the western part. Transparent goby *Aphia minuta* was sporadically recorded in 1999 and 2000, within a length range of 35-60 mm TL. It was caught a few times in July 1988 in the western part, but at stations not taken into consideration.

The density and biomass of *Callionymus lyra* were on average 5 to 10 times higher in 1999-2001, with a significant difference in autumn when the highest values were recorded (6 versus 29 ind/1000m² and 13 versus 50 gADW/1000m² in 1987-'89 and 1999-2001, respectively). Densities were lowest in winter. *C. lyra* preferred the western part, but in 1999-2001 also the central part with highest densities at station 15 (on average 110 ind/1000m²). Relatively high densities were recorded in summer and autumn in the northern part (on average 30 ind/1000m², 48 gADW/1000m² in 1999-2001). Two cohorts could be distinguished. The commonest year class entered the Oosterschelde in summer at 50 mm TL and grew till 130 mm in spring, followed by a second year class between 130 and 240 mm from summer onwards.

Zoarces viviparus was almost absent in 1989. Still, equal average densities and biomasses per season were recorded in both periods (5 ind/1000m², 21 gADW/1000m²). In 1999-2001, this species was mainly present in summer (on average 13 ind/1000m²), and this was the only season with higher densities than in 1987-'89. During both periods higher densities were recorded at station 10, and

the species was sporadically caught in the eastern part. In 1999-2001 *Z. viviparus* was most abundant in the northern part (and at station 15), especially during spring and summer, with a maximum of 120 ind/1000m² at station 37 in summer 2000. At least two cohorts could be distinguished in both periods, with the smallest individuals (65 mm TL) of the commonest cohort starting in spring and growing till 145 mm in winter, followed by another cohort in spring which grew to 220 mm. Most probably the few bigger individuals belonged to other yearclasses.

Seabass *Dicentrarchus labrax* was not recorded in spring during both periods. For the period 1987-'89 it was found occasionally at stations 15 and 33 in summer 1987, winter 1988 and winter 1989, with an exceptionally high density at station 33 in November 1987 (170 ind/1000m²). In 1999-2001 *D. labrax* was a little bit more common at several stations in autumn (significantly different from 1987-'89) and winter (on average 14 and 10 ind/1000m² with 50 gADW/1000m² in both seasons). In comparison, high densities were recorded at station 37, but only in autumn 1999 and 2000 (130 and 530 ind/1000m²). In 1999-2001 the modal length class was 115 mm (100 mm in 1987-'89), and only a few larger individuals (up to 315 mm) were recorded.

Butterfish *Pholis gunnellus* was mainly found in the central and eastern parts at low densities in spring and summer in 1987-'89 (on average 1 ind/1000m²). In 1999-2001 *P. gunnellus* was more common throughout the Oosterschelde, also in the northern part (on average 10 ind/1000m²). The average density was significantly higher in spring and winter in 1999-2001 (resp. 5 and 2 ind/1000m²) and in the western part at station 5. The length range varied between 70 and 190 mm TL, with the smallest individuals occurring in summer.

Also sandeel *Ammodytes tobianus* was a little bit more common in 1999-2001 (on average 0.5 versus 2 ind/1000m² in 1987-'89 and 1999-2001 respectively), but the difference was only significant for winter and at station 21 in the central part. The highest average density and biomass was found in summer (5 ind/1000m², 13 gADW/1000m²), with a clear preference for station 17. *A. tobianus* was not found in the northern part. The modal length varied between 155 and 135 mm TL.

The other percid species were only sporadically recorded, and were not found in the northern part. The greater sandeel *Hyperoplus lanceolatus* was caught a few times in autumn 1987, summer 1988 and summer 1999. Scad *Trachurus trachurus* was found every year at several stations in summer with comparable densities and biomasses in both periods (on average 1 ind/1000m² and 1 gADW/1000m²), and within a length range of 30-105 mm TL. Thick-lipped mullet *Chelon labrosus* was caught once at station 1 in November 2001. Corkwing wrasse *Crenilabrus melops* was recorded a few times in the

beam trawl samples from the eastern part in February 2000 and November 2001.

Pleuronectiformes

Seven flatfish species were recorded in the Oosterschelde. Megrim *Lepidorhombus whiffiagonis* was only caught once at station 15 in August 1999. The most common species were plaice *Pleuronectes platessa* and dab *Limanda limanda*. For both species average density and biomass were much higher in 1987-'89 during autumn and winter, although this was only significant in terms of biomass (on average 1260 versus 190 and 440 versus 110 gADW/1000m² for plaice, 250 versus 60 and 210 versus 25 gADW/1000m² for dab). On the other hand, densities were much higher in 1999-2001 during summer and comparable (per species) between both periods in spring. Both plaice and dab were present throughout the Oosterschelde, but in most cases highest densities were recorded at station 10 (on average 670 versus 680 ind/1000m² for plaice, and 440 versus 160 ind/1000m² for dab in 1987-'89 and 1999-2001, respectively). Significantly higher density and biomass were recorded at station 7 in 1987-'89 for plaice and at station 5 in 1999-2001 for dab, although this was not clear from the averages per subarea. For both species densities became significantly lower in the eastern part in 1999-2001, where they almost disappeared (a decrease from 70 to 2 ind/1000m² for plaice, and from 20 to 2 ind/1000m² for dab at station 33). In the northern part high densities were recorded for plaice (on average 190 ind/1000m²) and to a lesser extent for dab (on average 20 ind/1000m²) during the latter period.

All length classes of *P. platessa* were present throughout the year in both periods, except the smallest individuals (20-50 mm TL). These were only found in 1999-2001 in spring, and were followed by the commonest length classes (60-80 mm) in summer. In 1987-'89 the bigger modal length class (90 mm) was found in autumn. In February of both years a second cohort started with a length varying between 55 and 135 mm. This second year class was also more common in summer of 1999-2001 and in autumn of 1987-'89. By next winter the biggest individuals of this cohort had reached a length of 230 mm. Bigger and elder individuals (up to 415 mm) were only sporadically caught in both periods. The sex ratio for plaice was approximately 65% males and 35% females for all length classes, while for dab the sex ratio was 1:1. *L. limanda* entered the Oosterschelde in summer at a length of 35 mm TL in both periods. In 1999-2001 the commonest length ranged from 50 to 75 mm in summer, while in 1987-'89 the commonest length classes were found in autumn (50-100 mm). As with plaice, relatively high densities of small dab (40-90 mm) were recorded in winter of both periods. By the following summer the bigger individuals of this cohort had reached a length of 120

mm. The second cohort and elder individuals (up to 280 mm) were only sporadically caught in the Oosterschelde.

For sole *Solea solea* highest average densities were recorded in winter in 1987-'89. This could mainly be attributed to higher densities in February 1988 (25 ind/1000m²). Significantly higher densities and biomasses were found in summer in 1999-2001 (5 versus 25 ind/1000m² and 30 versus 145 gADW/1000m² in 1987-'89 and 1999-2001, respectively). *S. solea* preferred the western part in both periods, but high densities were also recorded in the northern part in 1999-2001 (on average 17 ind/1000m²). The new recruits (55 mm TL) entered the Oosterschelde in summer in both periods, and by next summer they had reached a length of 150 mm. For 1999-2001 a clear succession could be seen, while for 1987-'89 the commonest length classes were found in winter. Bigger and elder individuals (up to 410 mm) were sporadically caught in spring and summer of both periods.

The other 3 flatfish species were less common. The average density of flounder *Platichthys flesus* was a little higher for all seasons in 1999-2001 (on average 1.5 versus 2 ind/1000m² and 35 versus 45 gADW/1000m² in 1987-'89 and 1999-2001, respectively). The average density and biomass were a little higher in winter and spring for both periods. They were caught at several stations, but more in the western and eastern parts. Significant differences were found for station 10 (higher in 1999-2001) and for station 33 (lower in 1999-2001). *P. flesus* was also recorded in the northern part (on average 2 ind/1000m² in 1999-2001). The length varied from 60 to 400 mm TL, with the smallest individuals occurring in winter and a clear increase towards autumn and the following winter in both periods.

Lemon sole *Microstomus kitt* was caught a few times in the central part in July 1988 and August 1989. In 1999-2001 it mainly occurred in spring and summer with on average 2 ind/1000m², which was 10 times higher than in 1987-'89. In 1999-2001 *M. kitt* was mainly found in the central part, although a significant difference was noted for station 5. The species was never caught in the eastern part, and only occurred at station 37 in May 2000. Three distinct cohorts could be seen in 1999-2001, all starting in spring and ending in autumn with lengths between 40-110 mm, 120-190 mm, and 190-235 mm.

Brill *Scophthalmus rhombus* was caught a few times in autumn at stations 29 and 35 in 1987-'89, and a few times more in different seasons (on average 0.1 ind/1000m² every season) at stations 29 and 21 in 1999-2001. Mainly elder individuals were caught, with lengths varying between 170 and 340 mm TL.

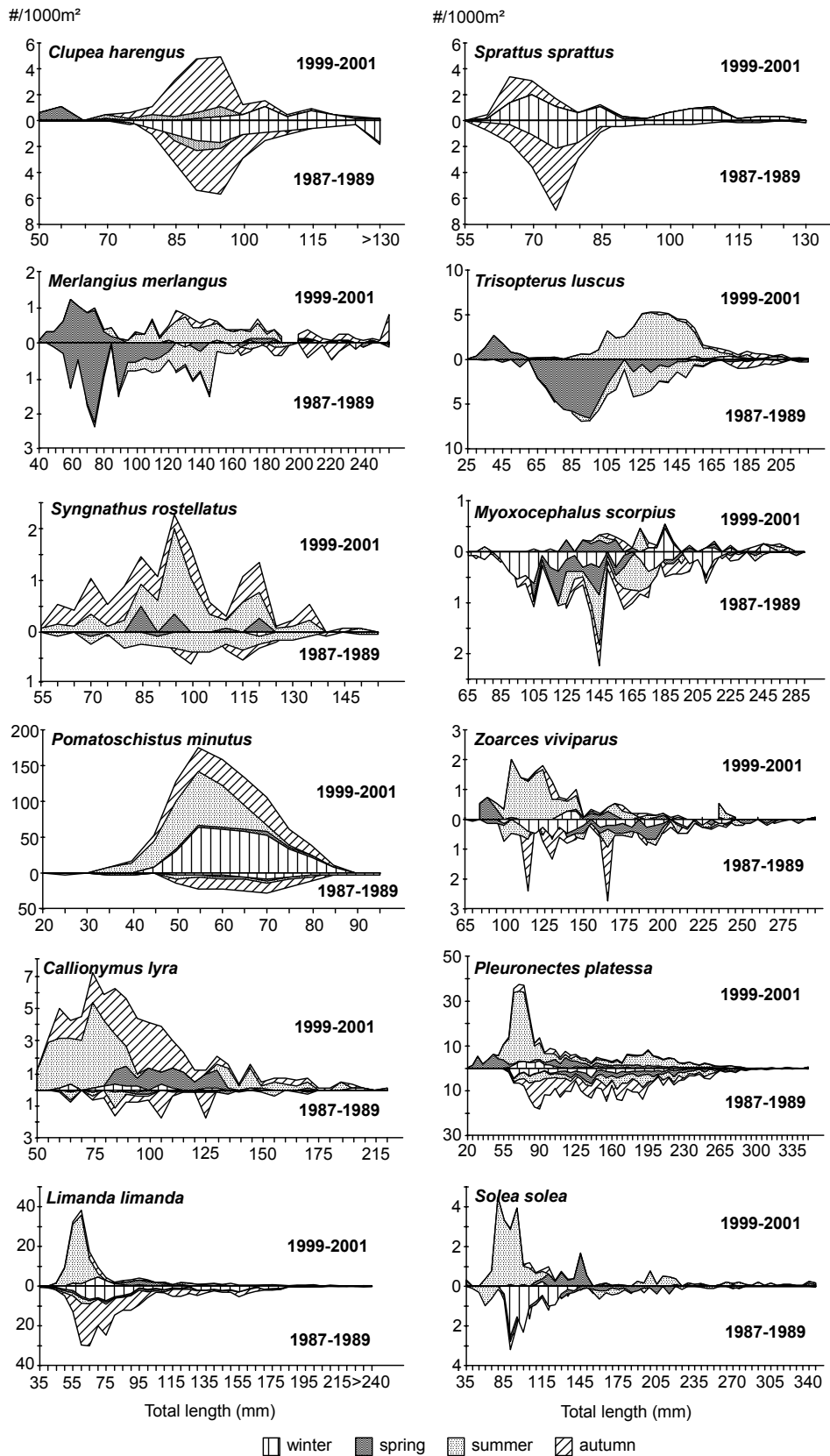


Fig. 4.6 Length-frequency distributions for 12 relevant species divided per season and compared between the two periods (1987-'89 and 1999-2001). Note the different scale bars

Other fish species

Six more species belonging to different taxonomic entities were occasionally recorded in the Ooster-

schelde. The average density and biomass of eel *Anguilla anguilla* was a little higher in 1987-'89 (0.7 ind/1000m² and 25 gADW/1000m² versus 0.2

ind/1000m² and 8 gADW/1000m²). In 1987-‘89 it was caught mainly in spring and summer and in 1999-2001 mainly in summer, both at several stations. The length range varied between 100 and 700 mm TL, with the smallest individuals occurring in spring and mostly individuals >300 mm caught. *A. anguilla* was caught once at station 37 in August 2001.

Smelt *Osmerus eperlanus* was caught three times in the northern part in May 2000 and 2001 and in August 2001. Garfish *Belone belone*, although recorded once in July 1988 at a station not considered here, was caught once at station 21 (150 mm TL) in August 1999.

Sand-smelt *Atherina presbyter* was recorded once at station 7 in November 1989 and a few times at several stations in autumn and summer of 1999-2001. The length varied between 65 and 90 mm TL. *A. presbyter* was also found at station 37 in November 1999. Three-spined stickleback *Gasterosteus aculeatus* was caught a few times at several stations in winter and summer of 1987-‘89 (on average 1 ind/1000m²). It was never recorded in 1999-2001. The length varied between 30 and 55 mm TL.

4.4 Discussion

4.4.1 Long-term overall differences

It seems difficult to find correlations between large-scale artificial changes to an ecosystem and changes in fish parameters. For example, no immediate changes in the fish fauna could be attributed to the building of the storm-surge barrier in the mouth of the Oosterschelde (Chapter 3; Chapter 3-Add.). Fish species are not only dependent on the Oosterschelde, but are influenced by recruitment to the adult North Sea stocks, yearclass strength, commercial fisheries (and bycatch), spawning possibilities, and larval movement. For example, in the Tagus estuary (Portugal) it was difficult to assess the relative importance of anthropogenic versus naturally induced fluctuations, due to the masking effect of a range of natural short-term variations (Cabral *et al.* 2001). The Oosterschelde is still changing: during the nineties the mussel farming practices have changed which resulted in an increased harvest (Smaal & Lucas 2000), commercial fisheries other than shellfisheries were banned due to the status of nature reserve (Wolff 1997), total cargo capacity and recreational activities have increased (van Berchum & Wattel 1997), and the option to partly restore the estuarine character of the Oosterschelde has been taken under consideration (Haas 1998). It is quite difficult to judge the influence of all these changes upon the fish fauna.

Inherent to the large spatial and temporal variability in fish populations within an estuary, is the ability of both the population and the environment to absorb and adjust to changes, where the population size can be regulated according to the available resources and the environment still can function normally. This was termed ‘population and environmental homeostasis’ (Elliott 2002). For example, by means of a partial Principal Component Analysis (with elimination of the temperature effect), it was shown that changes in the fish communities of the Oosterschelde in 1989 retrospectively evolved towards a state more or less comparable with the period 1983-‘85 (Hostens *et al.* 1993).

In this study we investigated whether important changes had occurred in the fish fauna of the Oosterschelde, or if there was a kind of ‘population homeostasis’ over a ten years period after the major engineering works were completed. For this comparison, a reduction of the existing data had to be made (from 36 stations sampled between 1983-‘89 to 12 stations between 1987-‘89). The inevitable consequence was that a number of (mainly rare) species caught in 1987-‘89 were lacking in the data set used, *e.g.* pollack *Pollachius pollachius* (Feb. 1987), tadpole fish *Raniceps raninus* (May 1989) and lump-sucker *Cyclopterus lumpus* (Nov. 1988). In the last decades, a total of 73 fish species have been caught in the Oosterschelde with several sampling devices (Elliott & Hemingway 2002). Maandag (1999) calculated that an average reduction of 4 species could be expected if 12 instead of 36 stations were taken into account. However, species richness was between 15 and 20% higher in 1999-2001. Actually, four species (except painted goby) that were only present in 1999-2001 were also recorded in 1987-‘89 at stations not considered in the present study (garfish, sea scorpion, transparent goby and black goby). Most species that were only caught once or a few times in any period have a real pelagic life style, *e.g.* wrasses, mullets, scads, garfish, smelts and sand-smelts (Froese & Pauly 2002).

In comparison with 1960-‘76 (Doornbos *et al.* 1981) 12 species occurred in fewer samples in 1999-2001. A number of the ‘decreasing’ species on this longer time scale (*e.g.* hooknose and brill) were also found to have a decreased frequency of occurrence based on fyke catches between 1979 and 1988 (Chapter 3-Add.). On the other hand, several species that showed a decrease in the period 1979-‘88 (*e.g.* sand goby and five-bearded rockling) seemed to have increased when a comparison is made between 1960-‘76 and 1999-2001. In total 23 species, amongst which abundant species like plaice, dab and sand goby, showed an increased frequency of occurrence from 1960-‘76 as compared to 1999-2001. Frequency of occurrence is not the best indicator of change (Chapter 3-Add.), but at this time it was the only useful measurement. No comparison could be made in

terms of density since the 1960-'76 sampling was not always done during the same season or month, and only averaged data were given per 100 minutes sampling, which by conversion to a surface unit (1000m²) gave doubtful densities an order of magnitude lower than in 1999-2001. This could be related to the fact that for 1960-'76 the averages were calculated over a total of 356 samples from 43 surveys, while the averages for 1999-2001 were only based on 140 samples from 10 surveys. Nevertheless, two or three decades later the number of species caught with a beam trawl was still comparable.

On a shorter time scale (from 1987-'89 towards 1999-2001), 28 of the 40 species showed an increased frequency of occurrence after the engineering works were completed, and the most abundant species were abundant in both periods. Sand goby and dragonet were mainly responsible for the increase in total average densities with 45% from 260 to 480 ind/1000m². Without sand goby, the total average densities were comparable between both periods. The average biomass of all fish species together decreased with 35% from 1500 gADW/1000m² in 1987-'89 to 1100 gADW/1000m² in 1999-2001. This was mainly due to a reduced average weight of 2 flatfish species, namely plaice and dab, which was not reflected in terms of density. If those two species were excluded, the average biomass increased in the central and western part, and only decreased in the eastern part.

4.4.2 Long-term seasonal differences

On a temporal scale higher average densities were recorded for 3 seasons in 1999-2001, except in autumn. This was reflected in the Canonical Correspondence Analysis, where all seasons were separated per period while the autumn surveys overlapped each other. In winter and spring twice as many species showed an increased average density and biomass in the period 1999-2001. On average 23 species increased and 10 species decreased. In summer even 26 against 7 species increased. The difference was significant for 13 species within several seasons, but mainly in autumn (5 species increased, 2 species decreased significantly) and in winter (4 increased and 4 decreased). If data from the same periods and seasons were compared from the neighbouring Westerschelde estuary, most fish species showed a decreasing density (Chapter 9). Comparably, in the Tagus estuary (Portugal) a decreased abundance of many juvenile fish species (*e.g.* bib, rockling, and flounder) was noted from 1978-'80 towards 1994-'96, which was mainly attributed to pollution, fishery regulation and waterflow control (Costa & Cabral 1999).

Six species showed an increased density and biomass throughout the whole period in all seasons. Lemon sole was only caught in 1999-2001, which was reflected in the Canonical Correspondence

Analysis. According to the results of the Demersal Young Fish Surveys, the Oosterschelde was the only ecosystem along the Dutch coast where the O-group of this species was caught (Welleman *et al.* 2000). The large discrepancy between both periods for sand goby (on average 40 ind/1000m² for 1987-'89 and 230 ind/1000m² for 1999-2001) - as well as for the other *Pomatoschistus* species - could not easily be explained. The low density in 1987-'89 could be partly due to a reduced net efficiency for these small species as a bigger mesh size was used in November 1988 and February 1989. However, this does not explain why the density was equally low for example in November 1987 or 1989. On the other hand, data from a fortnightly study between 1987-'89 at 4 sampling points in the western and central Oosterschelde (Hostens & Hamerlynck 1993), showed that the average density for sand goby in summer and autumn (*resp.* 230 and 170 ind/1000m²) was in the same order of magnitude as was found for 1999-2001 in the present study. Most probably the low densities in 1987-'89 that were recorded in the present study were not really representative due to an unknown sampling error for these small gobiid species.

Respectively 13 and 14 species showed an increased density or biomass in 3 seasons. In some cases this was related to logistical sampling limits. The discrepancy in density and biomass for bib in spring was mainly due to the fact that in 1988 the spring survey was conducted in July, while all others were taken in May. Bib is a species with a typical seasonal occurrence, with the new recruits only starting to immigrate in May, while in July most juveniles already had arrived in the Oosterschelde. This resulted in a 'misleading' higher average density in spring of 1987-'89. For all other seasons the average density was higher in 1999-2001. On the other hand the appearance of the species themselves can be delayed. For example, herring and sprat reached highest average densities in autumn in both periods, except for 1999 and 1988 when the maximum density for sprat (*respectively* herring) was shifted from autumn to winter. This mainly explained why in the CCA most autumn surveys, except that of 1999 and 1988, were found close to each other. 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). Common goby and seabass were characteristic for winter in 1999-2001 in the ordination plot of the CCA. Both species showed a significant increase in the latter period in autumn and winter. Together with a few others (*e.g.* bib), these were the only species that showed an increased density in 1999-2001 in the Westerschelde as well (Chapter 9).

For 9 species a decrease in density and biomass was noted in 2 seasons, *e.g.* in autumn and winter for sole, plaice and dab. In contrast with the den-

sity values, the total average biomass decreased for every season in 1999-2001, except for summer. This could mainly be attributed to a similar discrepancy between both periods as was shown above, due to a delayed appearance of plaice and dab. The higher average densities in autumn and winter for the period 1987-'89 were mainly due to the fact that in 1987 the mass immigration of juvenile flatfish only started in autumn (which was still visible in winter 1988), while for the other years in both periods the highest densities of plaice and dab were always recorded in summer. No differences could be detected if only the total average density per period were compared (on average 100 ind/1000m² for plaice and 50 ind/1000m² for dab in both periods). The yearclass of 1987 appeared to be very strong, with high densities of plaice and dab present in the Oosterschelde. In the western Wadden Sea strong year classes for plaice were characterized by a delayed larval immigration of about 1 month, as eggs were only hatched in February-March after a cold winter (van der Veer *et al.* 2000). Moreover, within both periods the average densities of plaice and dab decreased from 1987 towards 1989 and from 2000 towards 2001. Also in the Thames estuary (UK) a successive decrease was recorded from 1987 towards 1989 for plaice, sand goby and flounder (Araujo *et al.* 2000).

Six species showed a decreased density in 3 seasons (*e.g.* eel and viviparous blenny). Only cod and bull-rout decreased throughout the whole period 1999-2001. The probability to meet a bull-rout as a diver was calculated to be around 25% between 1997 and 2001, mainly in the central part of the Oosterschelde (A. Gmelig, www.anemoon.org). In a previous study based on data from 1983 till 1989, bull-rout was characteristic for the transitional period 1986-'87 (upon completion of the storm surge barrier in the mouth of the Oosterschelde), but declined towards 1989 (Hostens *et al.* 1993). A similar decreasing trend was seen in the German coastal zone of the North Sea (Tiews 1990). Perhaps, the cold winters of 1985-'87 were favourable to produce higher densities of bull-rout during that period, and in 1999-2001 (without preceding cold winters in the nineties, www.waterbase.nl) a population homeostasis similar to other periods and places was noted.

The length-frequency distributions showed that most seasons in both periods were characterized by juveniles, mainly O-group and to a lesser extent 1-group for a number of species. Based on the ecological guild concept (Elliott & Dewailly 1995), 13 species could be classified as estuarine resident and 11 species as marine juveniles, while 4 species were classified as catadromous and 14 species as marine seasonal or adventitious species. This proved the importance of the Oosterschelde both as a nursery and feeding area. More than half of the species reached their highest abundance in summer or autumn (respectively 7 and 14 species in 1987-'89, 17

and 7 species in 1999-2001), which was also clear from the Canonical Correspondence Analysis. Similar results were recorded within the Demersal Young Fish Surveys, with an overall dominance of O-group (and 1-group) and the most abundant species in fall being plaice, dab, sole and herring between 1970-1999 (Welleman *et al.* 2000). For several species the bigger individuals emigrated in winter or showed a growth stop from autumn to winter. For plaice and dab this resulted in a 'negative' growth. According to Welleman *et al.* (2000) the modal length was 90 mm TL in September and 100 mm in March for plaice, and 50 and 60 mm respectively for dab. In the present study the modal length classes for plaice were 75 mm TL in autumn and 90 mm in winter for 1999-2001, and 90 respectively 80 mm for 1987-'89 in autumn and winter. For dab the modal length classes in both periods were 60-65 and 70-75 mm in autumn, which closer resembled the results of Wheeler (1969).

4.4.3 Long-term spatial differences

From the Correspondence Analysis it was clear that the stations were arranged together more or less in geographical entities per period, and that the similarity between both periods per subarea was larger than the difference between the subareas. In a previous study based on data from 1988-'89, the western part was divided in two subareas (Chapter 3), but for 1999-2001 this distinction was not appropriate anymore. Apparently, some spatial differences were noted between both periods in terms of density and biomass. Six species showed an increased abundance in at least 10 stations (excluding the northern part), while another 9 species increased in more than half of the stations. The main species that increased in almost the whole Oosterschelde in 1999-2001 were 3 *Pomatoschistus* species, seabass, nilsson's pipefish and dragonet. In a comparative study with neighbouring areas, the latter species was found to be an indicator species for the Oosterschelde (Chapter 3). On the other hand, 4 species had decreased in >50% of the stations, with lower average densities for bull-rout recorded at 10 stations in 1999-2001. For 11 species the difference was significant in at least one subarea, with a significant difference for 6 species at station 5, and between 2 and 4 species at the other stations, except for station 1.

In the western part 8 species showed a decreased density and 20 species increased. The decrease in whiting densities in the western part in 1999-2001 was of minor importance, as the average density was in the same order of magnitude per station. In terms of biomass an increase was noted in the western part for most gadoid species. Several species that showed an increase in the western part also increased in the rest of the Oosterschelde, while for other species the decrease at one station was com-

compensated with an increase at another station. For example, both plaice and dab showed a decrease at stations 7 and 10, which was attributed to the strong yearclass of 1987. But this was partly compensated with higher densities and biomasses at station 5, which was probably related with an increased food resource. The western part of the Oosterschelde has become extremely important for the sublittoral farming of mussels, as >40% of all landings in 1996 were derived from the upper western part (van Berchum & Wattel 1997). For sole the difference in the western part was merely due to a shift from station 7 in 1987-'89 towards station 10 in 1999-2001. However, also in the western Wadden Sea an increased abundance of sole, flounder and herring was found in fyke catches taken between 1972 and 1994 (Philippart *et al.* 1996).

In the central part 7 species showed a decrease in density and biomass. Mainly species like herring, cod, viviparous blenny and 3-spined stickleback decreased in all stations of the central part in 1999-2001. Most probably, the latter species disappeared because it is more a fresh water species. In the Humber estuary (UK) 3-spined stickleback was mainly correlated with low salinities (Marshall & Elliott 1998), and in the Thames (UK) it was mainly found upstream (Araujo *et al.* 1999). This makes clear that 3-spined stickleback cannot tolerate the overall salinity of 30 psu in the Oosterschelde. But also in the adjacent Westerschelde estuary, no sticklebacks were caught in 1999-2001 (Chapter 9). In the Elbe estuary (Germany) the anadromous fish species (*e.g.* ruffe, flounder, stickleback, eel and twaite shad) were the commonest species in 1989-'92 (Thiel *et al.* 1995). The few individuals of 3-spined stickleback that were caught in 1987-'89 (mainly in the western part) could be seen as relicts from the former estuarine populations. Most other anadromous species already had disappeared from the Oosterschelde before or during the engineering works (Doornbos *et al.* 1981, Chapter 3-Add.). Similarly, the freshwater dams could be the main reason for the decrease in adult eels.

In the central part 28 species increased. In contrast with the other subareas, 16 species showed an increased density at 4 or all 5 stations in this subarea in 1999-2001. For example, the six-fold increase in density of dragonet was noted both in the central and western part. Dragonet is known to be correlated with sandy bottoms (Froese & Pauly 2002), which was the case at most stations in the Oosterschelde (Chapter 5). But the highest densities were recorded at station 15 every year between 1999 and 2001, where the deposition of fine sediments (<50 µm) increased substantially after the construction of the storm-surge barrier (ten Brinke *et al.* 1994). In February 2000 the silt concentration even exceeded 50% at station 15 (Chapter 5). Between 1970 and 1986 this species was recorded as common

during several years in the Oosterschelde (van Beek & Rink 1987), but the densities were not as high as in 1999-2001. Probably, juvenile dragonet could profit of the increase in its main food source, namely shrimps (and polychaetes) in this subarea (Chapter 5). The 'sudden' appearance of painted goby in November 2001 cannot easily be explained. Normally they prefer rocky bottoms in open coastal waters. According to divers, painted goby is not so uncommon in the Oosterschelde (P. van Bragt, www.anemoon.org). The higher densities of both nilsson's pipefish and greater pipefish at stations 15 and 21 could be related with the *Zostera* beds, which were still present in the central part (van Berchum & Wattel 1997). But nilsson's pipefish showed an increase in summer and autumn throughout the Oosterschelde in 1999-2001, which was most probably attributed to an increased net-efficiency. Mainly during these seasons a huge amount of allochthonous macrophytes (*Ulva* and *Chaetomorpha* species) came off the sublittoral mussel plots and clogged the nets, which prevented the pipefish from escaping.

In the eastern part 14 species showed an increased density and biomass and 5 species increased at all 3 eastern stations in 1999-2001. The changed net-efficiency and a sometimes excessive subsampling were probably the main reasons for the increased density of gobies and pipefish. On the other hand, 14 species had decreased in the eastern part. To reduce the risk of tearing the nets due to the presence of oysters or clogging of the nets with macrophytes, the beam trawl was usually swept over a distance <500 metres in this subarea. Both factors could have lead to a conversion discrepancy towards larger fish, but most probably the overwhelming presence of drifting algae and oysters in 1999-2001 reduced the habitat quality. This resulted in a substantial decrease both in density and biomass of all flatfish and gadoid species in the eastern part.

Also, at station 38 in the northern part the trawled distance was reduced to 500m, due to oysters or mud accumulation in the net. The silt concentration amounted to 50-65% in the northern area in 2000 (Chapter 5). With the exception of 12 uncommon species, most species that were found in the rest of the Oosterschelde also occurred in the northern part at comparable densities. For several species peak densities were recorded in the northern part, *e.g.* herring and sprat at station 38, and sole, seabass, butterfish and viviparous blenny at station 37. Conversion discrepancies can only partly explain the higher densities. It is a pity the northern part was not sampled in the eighties in a comparable standardized way. However, this subarea was found to be important between 1960 and 1986 as well (Doornbos *et al.* 1981; van Beek & Rink 1987). The high densities in the northern part were probably related to a high food supply. On the large intertidal mudflat and sandbank in this area high biomasses were recorded for several mac-

robenthic organisms during the eighties (Seys *et al.* 1994). Also, the average density of hyperbenthic organisms in the subtidal station 38 was comparable with other subareas in 2000 (Chavatte 2001). Still, it is interesting to note that at several occasions the highest densities or biomasses of most fish species were recorded at those stations with a higher concentration of fine sediments ($<53 \mu\text{m}$), i.e. station 10 in the western part, station 21 near the closed Veerse Meer in the central part, station 15 towards and stations 37 and 38 in the northern part. This result again proved the importance of sediment or substratum type (Chapter 2-Add.2) in the spatial distribution of fish assemblages. On the other hand, the appearance of black goby in the eastern and northern part of the Oosterschelde was possibly due to a colonisation through sluices from the adjacent lakes. This was most probably also the case for the few recordings of smelt and twaite shad, which were only recorded from the northern part.

4.5 Final conclusion

From this study it was not possible to say what happened in between the periods 1987-'89 and 1999-

2001, nor to say anything about a possible decrease in elder individuals or about pelagic and other species, which are difficult to catch with a 3-metre beam trawl. But, this study made clear that the Oosterschelde still harbours a species-rich fish fauna, with a spatio-temporal increase in density and biomass in most parts of the Oosterschelde for several juvenile fish species. This only had a minor influence on the nursery and feeding function of the ecosystem, except for the eastern part, where the fish fauna probably will not return to a better state of homeostasis in the near future as a consequence of man-induced, but also non-irreversible, changes.

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