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Early postlarval fish in the hyperbenthos of the Dutch Delta (south-west Netherlands)

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Early (post)larval fish constitute a significant part of the temporary hyperbenthos, i.e. of the fauna living in the lower reaches of the water column close to the substratum. Information on the densities and spatial and temporal variations of these stages, as well as on their lengths at the moment of occurrence, can be an important contribution to the knowledge of their dispersion, migrations and to the identification of possible bottlenecks in their recruitment. Therefore the hyperbenthos of the Voordelta, a shallow coastal zone in front of the Dutch Delta, as well as that of the subtidal channels and the intertidal brackish marsh creeks of the Westerschelde Estuary, was sampled monthly during one year by means of a sledge and a stow net. A total of 37 taxa were recorded from 410 samples. Densities often exceeded 400 ind 1000 m^{-2} in the Voordelta and 300 ind 1000 m^{-2} in the Westerschelde, including the tidal marshes of Waarde and Saeftinghe. The dominant taxa were clupeid larvae (predominantly herring *Clupea harengus* and sprat *Sprattus sprattus*), *Pomatoschistus* spp. (a mixture of sand goby *P. minutus* and Lozano's goby *P. lozanoi*), common goby *Pomatoschistus microps*, *Syngnathus* spp. (probably almost exclusively Nilsson's pipefish *S. rostellatus*), plaice *Pleuronectes platessa*, sole *Solea solea* and flounder *Pleuronectes flesus*. Most species were found at a larger size in the Westerschelde (and in the tidal marshes) suggesting migration from the shallow coastal area into the estuary. Several species utilize the tidal marshes in the brackish reaches of the Westerschelde. The nursery value of these areas however, is restricted to specific early life history stages of a few species, especially flounder, bass *Dicentrarchus labrax* and the common goby. The estuary itself seems to function as a nursery for other species like sole and plaice. The hyperbenthic sledge was found to sample specific life history stages of postlarval flatfish (early settlement stages at the onset of asymmetry), which are not easy to sample with other types of sampling gear.

INTRODUCTION

Shallow coastal areas and estuaries have long been acknowledged as providing nurseries for marine teleosts (e.g. Gunter, 1961; Creutzberg & Fonds, 1971; Blaber, 1987). The distribution of larval fish towards these areas is controlled by both active behaviour and passive transport mechanisms, resulting from a combination of biotic and abiotic factors (Norcross & Shaw, 1984). Variability in abundance of early life stages can have important consequences for the dynamics of nekton populations and communities in estuarine and shallow nearshore environments (Kneib, 1997). Nekton that reside in estuaries and nearshore habitats often produce demersal eggs and young (Haedrich, 1983) that are unlikely to be affected by mortality factors operating within the pelagic environment. Variability during the early life stages of these species however, has not received much attention, particularly in estuaries. Permanent resident species often reside in shallow vegetated habitats, and so they and their young may not be well represented in trawl or plankton samples taken in deeper estuarine waters. As a result, they are often ignored components of the estuarine nekton assemblage (Kneib, 1997).

This study focuses on the distribution and abundance of (post)larval fish in the shallow coastal area in front of the mouth of the rivers Rhine, Meuse and Schelde (the Voordelta) and of the Westerschelde Estuary. Already in the early 1970s, the Westerschelde was, besides the Wadden Sea and some other estuaries, recognized as a nursery area for the North Sea populations of flatfish, clupeids and gadoids (Creutzberg & Fonds, 1971; Zijlstra, 1972). At the end of the seventies, the nursery function for commercially important species such as sole *Solea solea*, dab *Limanda limanda*, plaice *Pleuronectes platessa* and shrimp *Crangon crangon*, was emphasized (De Veen et al., 1979).

More specifically, the focus is on the so-called 'hyperbenthic' phase of fish. The hyperbenthos is a term applied to the association of small animals living in the water layer close to the substratum (Mees & Jones, 1997). Permanently hyperbenthic animals spend variable periods of their adult life in the hyperbenthos, while temporary hyperbenthic species (merohyperbenthos; Hamerlynck & Mees, 1991) spend only part of their early life history in the hyperbenthal. Teleost fish have been found to be a prominent member of the merohyperbenthos (e.g. Hesthagen, 1973; Jahn & Lavenberg, 1986; Hamerlynck & Mees, 1991; Cattrijsse et al., 1994). The hyperbenthos of soft bottoms is usually sampled with sledges. The fish larvae present in such samples are rarely studied as such. Still, since the hyperbenthic sledges seem to sample specific life history stages of postlarval (flat)fish which are not easy to sample with other types of sampling gear (see below), information on the densities and spatial and temporal variations of these stages can be an important contribution to the knowledge of their dispersion, migrations and to the identification of possible bottlenecks in their recruitment. To understand interannual recruitment variability, it is necessary to focus on early life history stages that are subject to intense mortality (Hjort, 1914; May, 1974; Blaxter, 1988; Bailey & Houde, 1989). The importance of mortality occurring in later larval stages and early juveniles has been stressed by several authors (e.g. Sissenwine, 1984; Smith, 1985; Folkvord & Hunter, 1986; Peterman et al., 1988). Larger fish larvae have been shown to be especially abundant in the near-bottom water layers; the fine-scale zonation patterns and depth distribution of fish larvae are discussed in Brewer & Kleppel (1986) and Jahn & Lavenberg (1986).

In order to assess horizontal seasonal migrations and recruitment patterns, the spatial and temporal variability and the length–frequency distributions of the dominant species are investigated. The possible nursery function of the estuary and its tidal marshes is discussed.

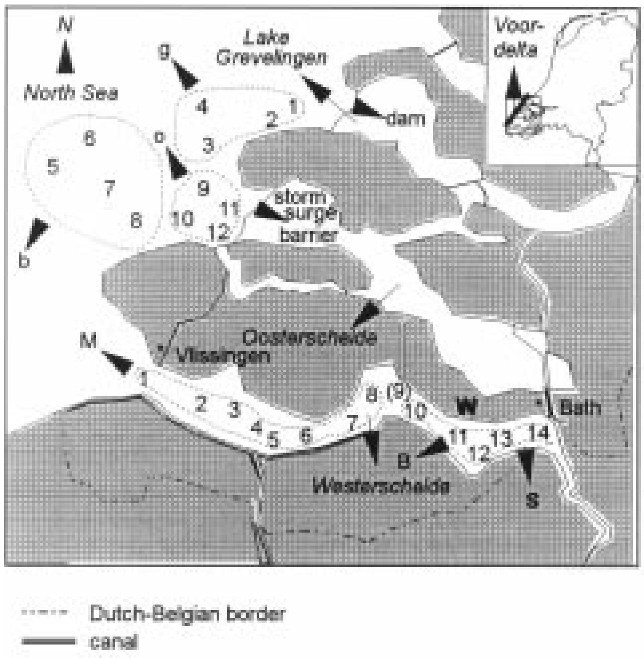

Figure 1. Study area with the sampling localities: g, ebb-tidal delta of the Grevelingen (VD G); o, ebb-tidal delta of the Oosterschelde (VD O); b, Banjaard area (VD B); M, marine part of the Westerschelde (WS M); B, brackish part of the Westerschelde (WS B); W, tidal marsh of Waarde (TM W), S, tidal marsh of Saeftinghe (TM S).

MATERIALS AND METHODS

Study area

The Voordelta is the shallow coastal area that stretches from the Dutch–Belgian border in the south to the Hoek van Holland in the north. Offshore, the area is arbitrarily defined by the mean tidal level (MTL)—15 m depth contour. The study area only covers the central part of the Voordelta at the mouth of the former Grevelingen (closed in 1971) and Oosterschelde estuaries. The Grevelingen now is a closed brackish lake separated by a dam from the open sea, while the Oosterschelde is a marine bay which has an open connection with the Voordelta through a storm surge barrier. The abiotic environment of the Voordelta is discussed in Louters et al. (1991).

The Westerschelde Estuary is the lower seaward part of the River Schelde. The maritime zone of the tidal system is about 70 km long from the North Sea (Vlissingen) to the Dutch–Belgian border near Bath. The Westerschelde is the last remaining true estuary in the Delta area and is characterized by a marked salinity gradient. The abiotic environment is discussed in Van Eck et al. (1991) and Heip (1988, 1989).

Two tidal marshes of the Westerschelde were sampled. The tidal marsh of Waarde (107 ha) is an elongated marsh situated on the right bank of the estuary. It is drained by one major creek that runs parallel to the main channel of the estuary. The tidal marsh of Saeftinghe (2760 ha), situated on the left bank north of the harbour of Antwerp, is one of the largest brackish marshes of

Table 1. *Sampling dates per area (VD, Voordelta; WS, Westerschelde; TM W, tidal marsh of Waarde; TM S, tidal marsh of Saeftinghe).*

Year	Area	J	F	M	A	M	J	J	A	S	O	N	D
1988	VD								*	*		*	*
	WS												
	TM W												
	TM S												
1989	VD	*	*	*	*	*	*	*					
	WS												
	TM W												
	TM S												
1990	VD												
	WS				*	*	*	*	*	*	*	*	*
	TM W		*	*	*	*	*	*	*		*	*	*
	TM S		*	*	*	*	*	*	*		*	*	*
1991	VD												
	WS	*	*	*	*								
	TM W	*	*	*	*	*	*		*				
	TM S	*		*	*	*	*	*	*				

*, sampling.

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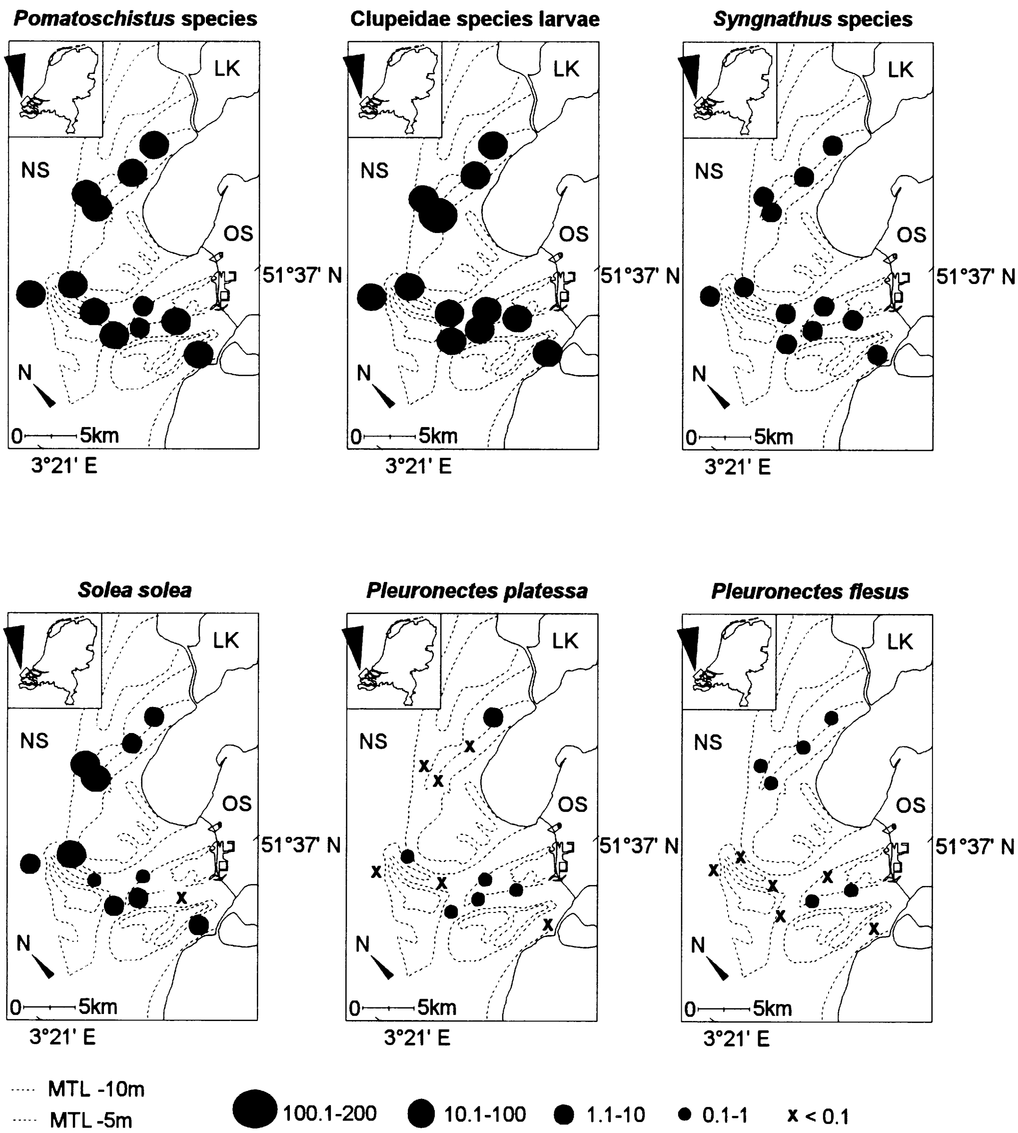

Figure 2. Geographical distribution of the dominant species for the Voordelta (NS, North Sea; LK, Lake Grevelingen; OS, Oosterschelde). Densities are yearly averages of the numbers of individuals caught per trawl (ind 1000 m^{-2}).

Europe. It is drained by several large creeks that run perpendicular to the main estuarine channel.

Sampling sites and sampling regime

Between August 1988 and July 1989, eleven surveys were conducted at approximately monthly intervals in 12 localities in the Voordelta: stations 1–4 in the ebb-tidal delta of the Grevelingen, stations 8–12 in the ebb-tidal delta of the Oosterschelde and stations 5–7 in the more seaward Banjaard area in-between both ebb-tidal deltas (Figure 1). At each station two samples were taken: one in the gully at a depth of about MTL (10 m) and one on the sandbank slope at a depth of about MTL (5 m), thus yielding 24 samples per sampling campaign (Table 1). As no consistent differences were found between these two depth strata, the numbers of individuals caught in both samples were pooled and divided by two for the purpose of this paper. In the Westerschelde 13 surveys were conducted from April 1990 to April 1991. On each occasion 14 stations were sampled along the salinity gradient (Mees et al., 1993a). All samples were taken in the subtidal channels. Where possible, the MTL (10 m) isobath was followed. Besides the subtidal surveys, monthly samples were taken at two intertidal stations in the tidal marshes of Saefthinge and Waarde (S and W in Figure 1) from March 1990 to November 1990. In Waarde, samples were taken in the main creek, while in Saeftinghe the easternmost major creek was selected (Cattrijsse et al., 1994). An overview of all sampling dates is presented in Table 1.

All samples were taken during daytime. The subtidal samples in the Voordelta and the Westerschelde were collected with a hyperbenthic sledge (Hamerlynck & Mees, 1991) according to Mees et al. (1993a). The tidal marsh samples were taken passively with a fyke net according to Cattrijsse et al. (1994). The use of different sampling techniques and the different sampling periods should be kept in mind when comparison between the regions are made.

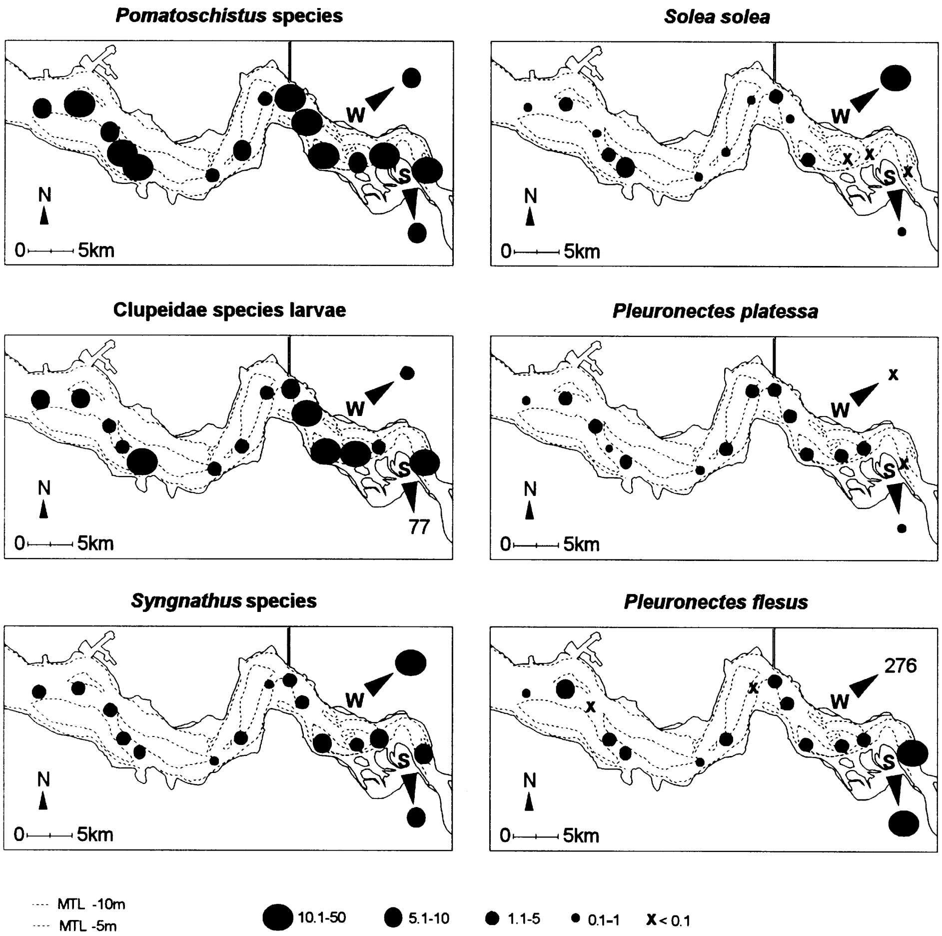

Figure 3. Geographical distribution of the dominant species for the Westerschelde, including tidal marshes of Saeftinghe (S) and Waarde (W). Densities are yearly averages of the numbers of individuals caught per trawl (ind 1000 m^{-2}).

All samples were immediately preserved in a buffered formaldehyde solution, 7% final concentration. During sampling, temperature and salinity of the water were measured near the bottom. For temperature and salinity values we refer to Hamerlynck & Mees (1991) for the Voordelta, Mees et al. (1993b, in press) for the Westerschelde and Cattrijsse et al. (in press) for the tidal marshes.

Treatment of samples and data analysis

In the laboratory all fish were sorted, identified, counted and measured (standard length (SL): the distance between the tip of the lower jaw and the end of the notochord). Shrinkage caused by formalin preservation was not taken into account, but all samples were preserved for at least 1 y prior to analysis in order to stabilize the shrinkage process. Shrinkage can thus be assumed to be equal for all individuals of the same species. The nomenclature proposed by Wheeler (1992) was followed. Most organisms were identified to species level, except the (post)larvae of Clupeidae (probably a mixture of herring *Clupea harengus* and sprat *Sprattus sprattus*), *Pomatoschistus* spp. (a mixture of sand goby *P. minutus* and Lozano's goby *P. lozanoi*) and *Syngnathus* spp. (probably exclusively Nilsson's pipefish *S. rostellatus*; possibly some greater pipefish *S. acus*). The identification keys of Nichols (1971, 1976), Russell (1976) and Nijssen & De Groot (1987) were used. Gobies were identified according to Hamerlynck (1990). All gobies smaller than 20 mm and all clupeids smaller than 40 mm (metamorphosis of herring takes place around 48–50 mm and that of sprat around 32–41 mm; Russell, 1976) were not identified to species level (except for *Pomatoschistus microps*) and were grouped as 'larvae'. Information available about the species composition of the demersal fish fauna of the Voordelta and the Westerschelde (Hamerlynck et al., 1992, 1993; Hostens & Hamerlynck, 1994; Hostens, in press) facilitated the identification process and allowed for the (hypothetical) characterization of the amalgam 'species groups' described above. Length–frequency distributions are only reported when more than 30 individuals were measured.

Other faunal components of the hyperbenthos included mysids, euphausiids, amphipods, larval decapods, fish eggs, isopods, cumaceans, chaetognaths and a variety of other less abundant groups. For full species lists of the hyperbenthos of the Voordelta, the Westerschelde and the tidal marshes, we refer to Hamerlynck & Mees (1991), Mees & Hamerlynck (1992), Mees et al. (1993b, in press) and Cattrijsse et al. (1994, in press). The distribution patterns of several crustacean groups (Mysidacea, Euphausiacea, Amphipoda and Isopoda) are discussed in detail in Cattrijsse et al. (1993) and Mees et al. (1993a).

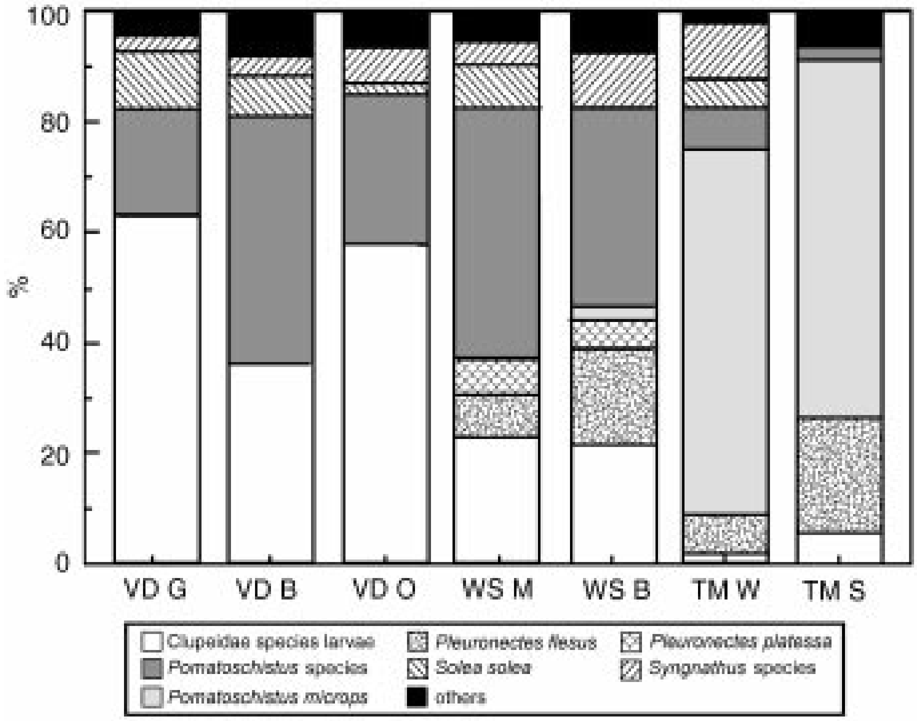

Figure 4. Community composition per subarea (VD G, ebb-tidal delta of the Grevelingen; VD B, Banjaard area; VD O, ebb-tidal delta of the Oosterschelde; WS M, marine part of the Westerschelde; WS B, brackish part of the Westerschelde; TM W, tidal marsh of Waarde; TM S, tidal marsh of Saeftinghe).

Reported densities in each station are the average numbers of individuals per sample taken in that station (ind 1000 m^{-2}) averaged over the whole study period. For the tidal marsh samples, densities were calculated for each hourly sample. Both the cumulative densities of the flood samples and the tidal flood volume were used to estimate an overall abundance present in the marsh at the moment of high water. Applying the same procedure with the ebb samples provided another estimate of the densities present at high water. Both results were subsequently averaged and used as the reported density for a particular sampling date. For more information about hourly temporal trends we refer to Cattrijsse (1994).

The temporal patterns in the densities of the fish populations are presented as the variation of average densities over all stations per area (Voordelta, Westerschelde) per sampling campaign. In order to further describe the migrations and seasonal patterns, both environments are divided into a total of seven regions (three in the coastal marine environment of the Voordelta, two in the estuarine channel environment of the Westerschelde and the two tidal marshes) based on descriptive multivariate community analyses in previous work (both classification and direct ordination techniques: Hamerlynck & Mees, 1991; Mees & Hamerlynck, 1992; Cattrijsse et al., in press; Mees et al., 1993b, in press). The Voordelta is divided into three regions, each comprising four stations: the ebb-tidal delta of the Grevelingen (stations 1–4), the Banjaard area (stations 5–8) and the ebb-tidal delta of the Oosterschelde (stations 9–12). The main channel of the Westerschelde Estuary is divided into a western and eastern part. The marine channel region of the estuary (west) comprises the eight downstream stations and the brackish channel region (east) comprises stations 10–14. Station 9 represents a transitional situation between the two communities and was eliminated for the purpose of this analysis. The seasonal variations in abundance in the tidal marshes of Waarde and Saeftinghe are also presented separately.

RESULTS

Species composition

A total of 37 taxa of teleost fish were recorded from the 410 hyperbenthos samples analysed for this study (Appendix 1). Total densities often exceeded 400 ind 1000 m^{-2} in the Voordelta (maximum of 4430 ind 1000 m^{-2} in station 3 in June) and 300 ind 1000 m^{-2} in the Westerschelde (maximum of 456 ind 1000 m^{-2} in station 14 in April) including the marshes (maximum of 4979 ind 1000 m^{-2} in the marsh of Saeftinghe in April).

Several species were restricted to one or more subarea(s) (Appendices 1 & 2). Of the species that were only found in the Westerschelde (including the marshes), thick-lipped grey mullet *Chelon labrosus*, zander *Stizostedion lucioperca*, nine-spined stickleback *Pungitius pungitius* and bleak *Alburnus alburnus* were restricted to the tidal marsh of Saeftinghe (*C. labrosus* also occurred in the marsh of Waarde). Of the species that occurred in the Westerschelde, lampern *Lampetra fluviatilis*, cod *Gadus morhua*, bib *Trisopterus luscus*, bull-rout *Myoxocephalus scorpius*, sea-snail *Liparis liparis*, butterfish *Pholis gunnellus*, *Hyperoplus lanceolatus*, dragonet *Callionymus lyra* and dab *Limanda limanda*

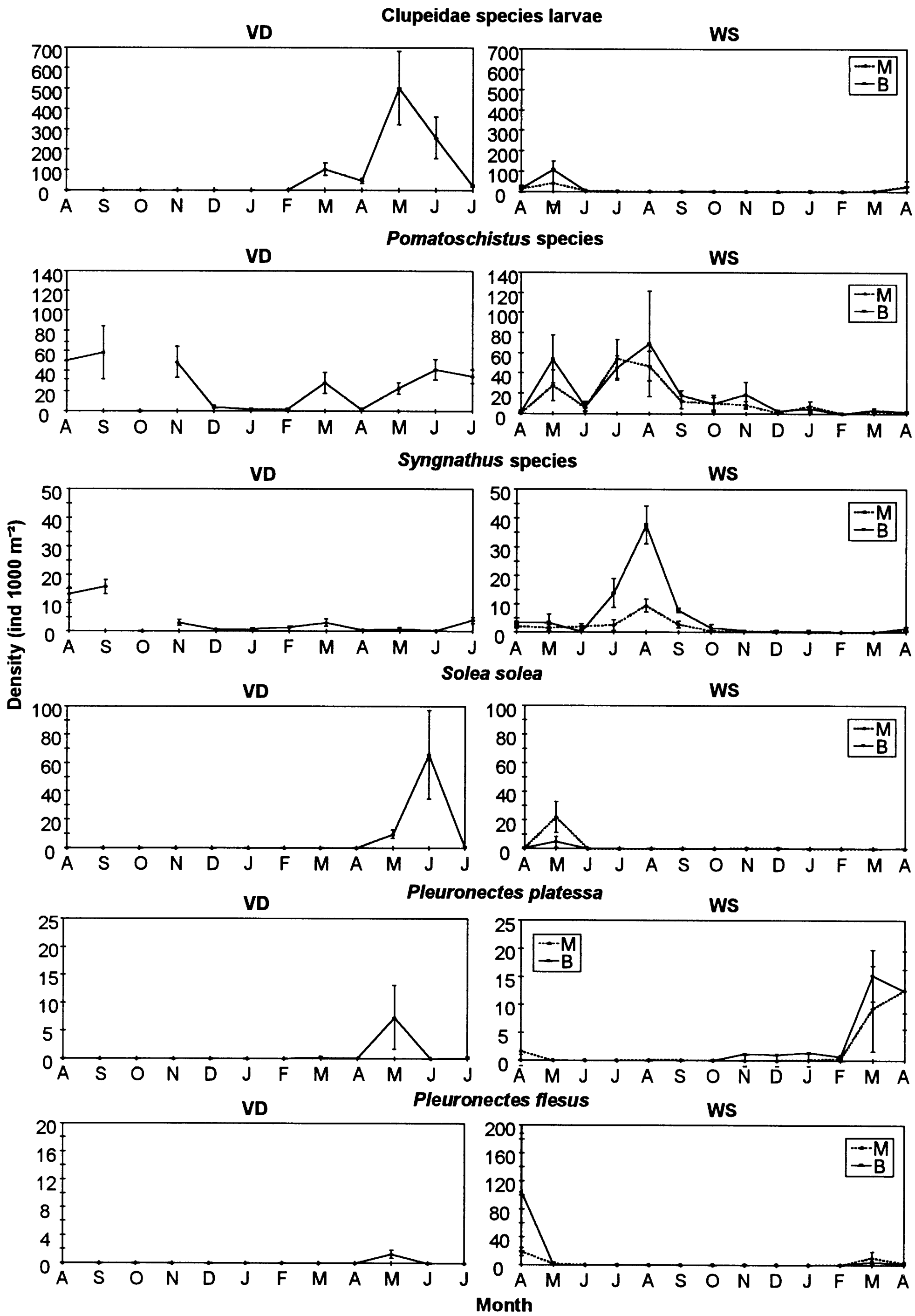

Figure 5. Seasonal variation of the numbers of individuals (average ±SE over all stations per month) of the dominant species for the Voordelta (VD) and the Westerschelde (WS) (M, marine part of the Westerschelde; B, brackish part of the Westerschelde).

were never recorded from the marshes. The bulk of the species however occurred in every region, although most were only present in certain seasons or showed clear preferences for specific regions.

The dominant taxa (mean densities >5% of the total community in one or several of the regions) were: (1) Clupeidae spp. larvae; (2) *Pomatoschistus* spp. larvae; (3) *Syngnathus* spp.; (4) common goby *P. microps* and the flatfish (5) sole *Solea solea*; (6) plaice *Pleuronectes platessa* and (7) flounder *Pleuronectes flesus*. Only these species will be discussed further (data of the common goby are not figured).

Geographical distribution and abundance

The geographical distribution and densities of the dominant species are presented separately for the Voordelta (Figure 2) and the Westerschelde (Figure 3), the community composition of each region (yearly averages) in Figure 4.

In the Voordelta (Figures 2 & 4), total average densities per station were never higher than 400 ind $1000\,m^{-2}$. Densities were significantly higher in the more sheltered area of the ebb-tidal delta of the Grevelingen and lower in the more dynamic ebb-tidal delta of the Oosterschelde

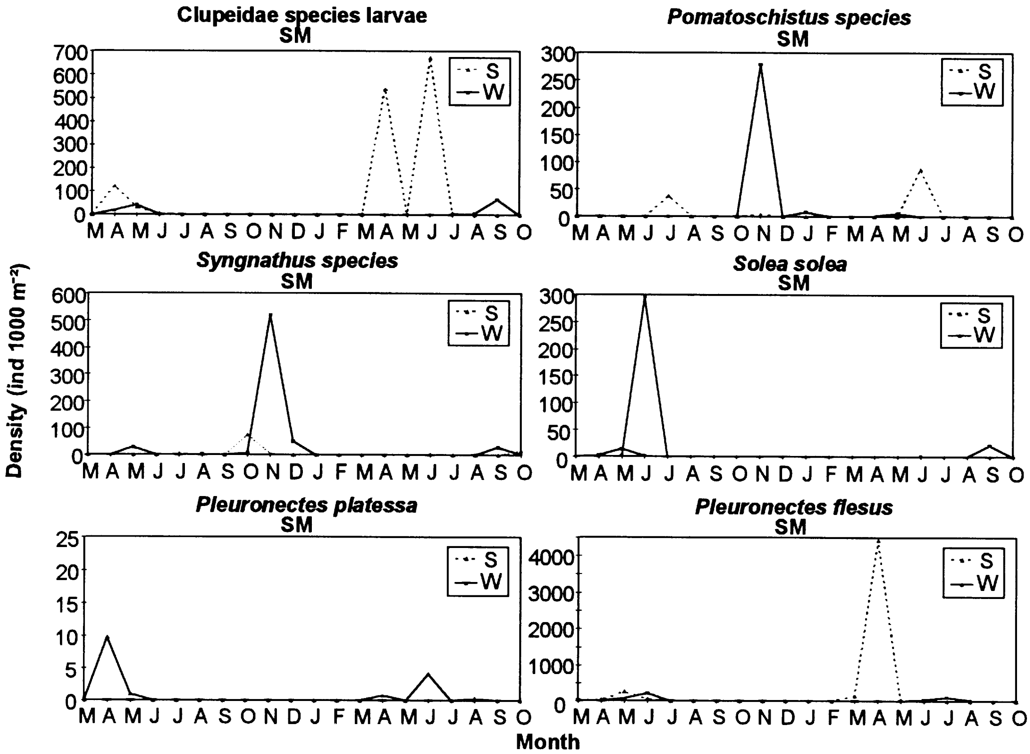

Figure 6. Seasonal variation of the numbers of individuals (monthly average of the estimated numbers present at ebb and flood tide, see also material and methods) of the dominant species for the tidal marshes. SM, salt marsh; S, marsh of Saeftinghe; W, marsh of Waarde.

(Appendix 2). Since the data were not normally distributed, testing for differences between total average densities was done with a Kruskal–Wallis Test ($P<0.05$), and subsequent multiple comparison tests according to Conover (1980) (without accumulation of α-error). The Banjaard stations were characterized by intermediate densities. Clupeid larvae was the most abundant taxon (45 ±13 ind 1000 m^{-2}), followed by *Pomatoschistus* spp. (21 ±3 ind 1000 m^{-2}) and sole (7 ±4 ind 1000 m^{-2}). The three taxa had overlapping geographical distributions. The common goby did not occur in the Voordelta. In all three regions of the Voordelta (Figure 4), clupeid larvae and *Pomatoschistus* spp. represented >80% of the fish communities.

Total average densities per station of the Westerschelde were never higher than 150 ind 1000 m^{-2}. In the five most downstream stations (marine channel region) and in the six most upstream stations (brackish channel region) of the estuary, total densities were on average higher than in the three remaining stations in the middle reaches. *Pomatoschistus* spp. and clupeid larvae were the most important organisms (densities of 15 ±3 and 9 ±2 ind 1000 m^{-2}, respectively) (Figures 3 & 4). They had comparable geographical distributions: high densities were recorded in the marine channel region and in the brackish channel region, while in stations 6–8 densities were much lower. *Syngnathus* spp. and the common goby seemed to prefer the more brackish part of the Westerschelde, while sole was more abundant in the marine reaches. In both the marine and brackish parts of the Westerschelde (Figure 4), *Pomatoschistus* spp. dominated the community (45.1% in the marine part and 32.5% in the brackish part), followed by clupeid larvae (23.2 and 20.3% respectively).

In the tidal marshes (Figures 3 & 4) the common goby was the most abundant species (533±17 ind 1000 m^{-2}), followed by flounder (151 ±17 ind 1000 m^{-2}). *Pomatoschistus* spp., *Syngnathus* spp. and sole occurred in higher densities in the tidal marsh of Waarde than in the marsh of Saefthinghe, while this was the opposite for the other species. Plaice were absent from the marsh of Waarde and only occurred in low densities in the marsh of Saeftinghe (0.89 ind 1000 m^{-2}). The communities of both marshes were dominated by the common goby (±65% of the community) (Figure 4).

Temporal distribution patterns

In spring, plaice appeared first, with maximal densities in March in the Westerschelde and in May in the Voordelta (Figures 5 & 6). Then flounder was recorded with a peak in April (Westerschelde), followed by sole and clupeid larvae, with maximal abundances in May in the Westerschelde and in June in the Voordelta. *Syngnathus* spp. had their peak of abundance in August in the Westerschelde and in August–September in the Voordelta. Two peaks were observed for *Pomatoschistus* spp.: one (smaller) peak in May and one in June–August.

Length–frequency distributions

With a few exceptions, all flatfish caught were early (post)larval stages (Figure 7). Individuals just before or at the onset of asymmetry were clearly dominant. Hardly any planktonic yolk-sac larvae nor post-settlement demersal stages were caught. Monthly length–frequency distribution patterns of *Pomatoschistus* spp. revealed two peaks (not figured): one in May/July and one in August/October

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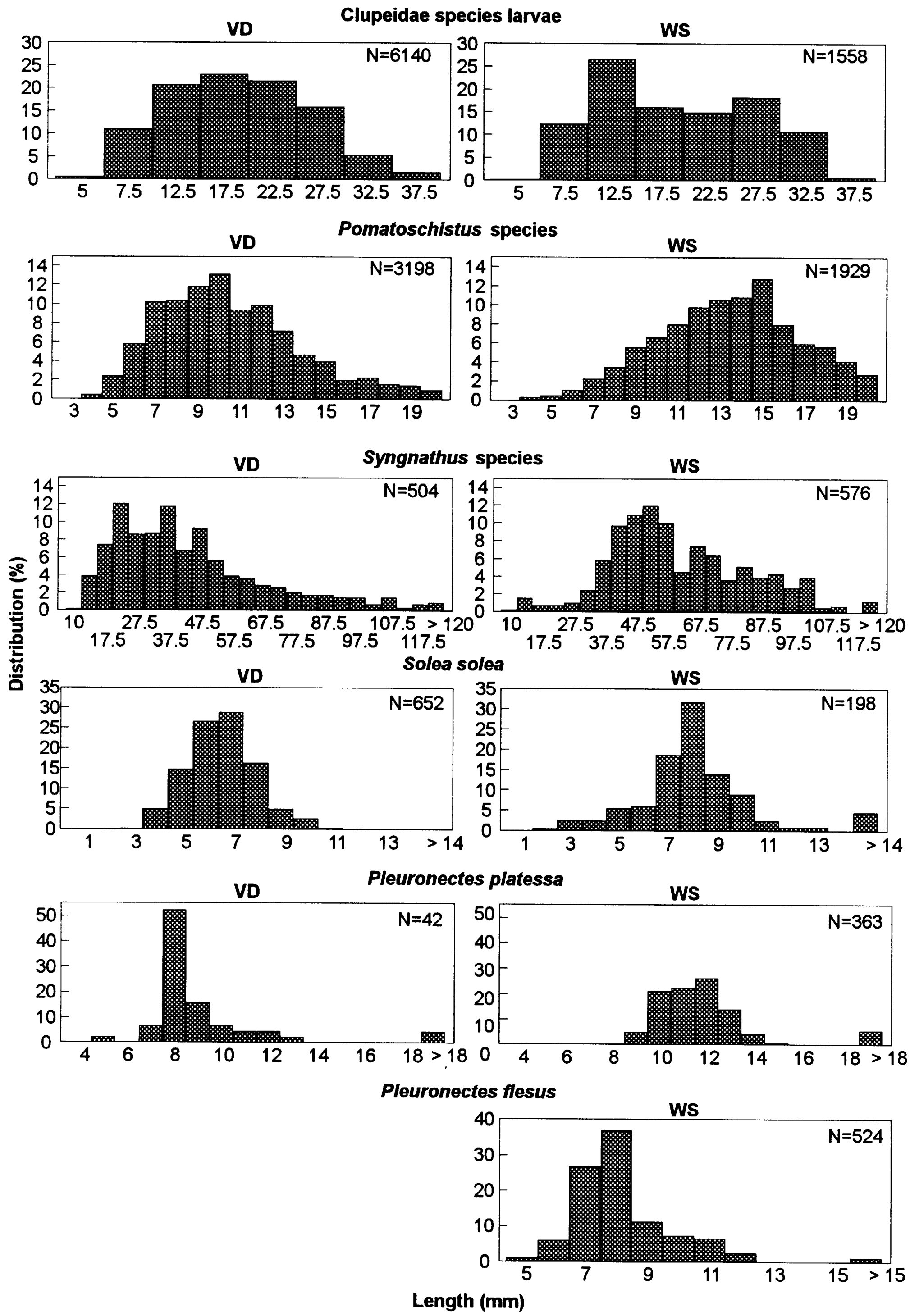

Figure 7. Length–frequency distributions of the dominant species for the Voordelta (VD) and the Westerschelde (WS) (N, total number of individuals measured).

(both around 10 mm SL in the Voordelta, while in the Westerschelde the modal length-class in May/July was 14 mm SL and in August/October two modal length classes were observed of respectively 15 mm SL and 18 mm SL). Monthly length–frequency distributions of *Syngnathus* spp. (not figured) revealed that from May through July individuals measured 22.5 mm in the Voordelta and 42.5 in the Westerschelde. During August/October the length–frequency distributions showed bimodal patterns: modal length-classes were found at 37.5 and 47.5 mm respectively in the Voordelta, while in the Westerschelde the modal length was 55 mm SL and a large number of individuals measured between 65 and 105 mm SL. In general, larger individuals were captured in the tidal marshes (Figure 8).

Mean lengths per month

Monthly length–frequency distributions were very narrow for most species, especially for the flatfish species sole, plaice and flounder (Appendix 3). Clear differences between months could be observed. Mean lengths of clupeid larvae revealed two possible recruitment peaks:

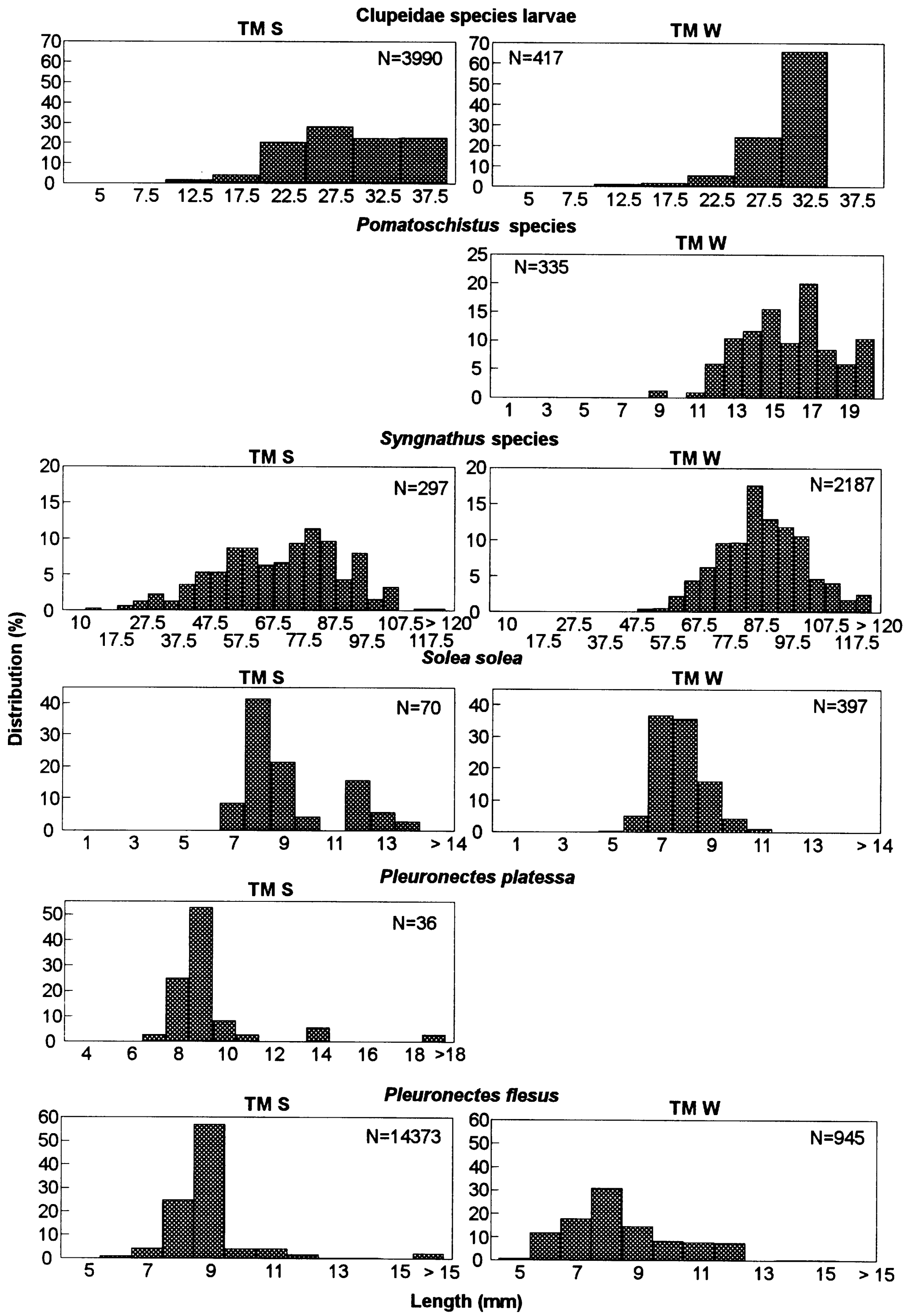

Figure 8. Length–frequency distributions of the dominant species for the tidal marshes (TM S, tidal marsh of Saeftinghe; TM W, tidal marsh of Waarde) (N, total number of individuals measured).

one before March and one in May (Westerschelde) and June (Voordelta) (14.13±0.15 and 13.67±0.09 mm SL, respectively). The same pattern was found for *Syngnathus* species: a first recruitment peak was observed before February and a second one in July (53.28±1.62 mm SL in the Westerschelde and 24.32±0.86 mm SL in the Voordelta). For most species, mean lengths were somewhat greater in the Westerschelde than in the Voordelta.

DISCUSSION

Spatial patterns

In general, average densities were higher in the shallow coastal environment than in the estuary, but also within these areas differences could be found. In the Voordelta, densities were significantly higher in the sheltered region (ebb-tidal delta of the Grevelingen) and lower in the dynamic ebb-tidal delta of the Oosterschelde. The

Banjaard stations were characterized by intermediate densities. These higher densities in the ebb-tidal delta of the Grevelingen can be explained by local current patterns and the higher primary production in this area (Hamerlynck & Mees, 1991). The area seems to act as a sink for passively transported material, e.g. silt, decaying phytoplankton, macrobenthic larvae and fish eggs with near neutral buoyancy. This creates a rich and varied benthic life that sustains high densities of demersal fish. Fish larvae and postlarvae may actively migrate to the area to profit from the high abundance of food (Creutzberg et al., 1978). Although the Banjaard has a rich epibenthic fauna, wave conditions there prevent sedimentation and preclude the establishment of rich macrobenthic communities. Despite being sheltered from the wave action, the ebb-tidal delta of the Oosterschelde has a poorer hyperbenthic fauna than the Grevelingen. The richer water masses of the Banjaard (and offshore) do not reach the area because they are flushed outwards at low tide by the relatively oligotrophic water from the Oosterschelde. Moreover, the high current velocities as attested by high seston loads, prevent sedimentation in the ebb-tidal delta of the Oosterschelde (Hamerlynck & Mees, 1991).

In the Westerschelde, densities were on average lower in the middle reaches than either downstream (marine) or upstream (brackish). This bimodal density pattern was also reported for a wide variety of ecosystem compartments and processes (primary production, zooplankton, macrobenthos, hyperbenthos and epibenthos; e.g. Hamerlynck et al., 1993; Soetaert et al., 1994). In the brackish part, the food web depends on the input of large amounts of organic matter from the land side (heterotrophic food chain), while the area close to the mouth of the estuary is characterized by a food chain based on local primary production (photoautotrophic food chain) (Hummel et al., 1988). Both subsystems also seem to support high densities at the higher trophic levels. The middle reaches of the estuary have been described as a 'nutrient rich desert', where most functional units display low biomass levels. The same (largely unexplained) pattern was observed for the fish larvae in this study (Hamerlynck et al., 1993).

Densities of several fish species were seasonally higher in the tidal marshes than in the main estuarine channel. Two hypotheses are commonly used to explain the high densities of species in tidal marshes: (1) the marsh creeks are used as foraging areas; and (2) function as predator refugia (Boesch & Turner, 1984). The exact reasons why metamorphosing stages of flatfish use the marshes as a nursery still remain unclear.

Most demersal fish species that are common in the adjacent reaches of the Westerschelde are absent from the marshes (Hostens, in press). The common goby spends the major part of its life cycle in the tidal creeks. Bass *Dicentrarchus labrax* and flounder were very abundant in the marshes and seem to utilize these habitats as a nursery (Cattrijsse, 1994). Of all other species recorded from the Westerschelde, only few were occasionally recorded in Waarde or Saeftinghe. The dominance of a small number of generalist species is a common feature of the fish fauna of tidal marshes (e.g. Cain & Dean, 1976; Haedrich, 1983; Weinstein & Brooks, 1983; Kneib, 1987; Sogard & Able, 1991).

The composition of the fish fauna of the tidal marsh of Waarde was quite different from that of Saeftinghe. In Waarde, 13 taxa were recorded. The common goby, *Syngnathus* spp., *Pomatoschistus* spp., flounder and sole dominated the fauna (>5%). In Saeftinge, 20 taxa were recorded. The common goby, flounder and clupeid larvae were the dominant taxa. When salinities increase in summer, typical marine species migrate into the estuary (Mees et al., 1993b). These species were hardly ever recorded from the tidal marsh of Saeftinghe, but some of them were present (sometimes even in high numbers) in the tidal marsh of Waarde (e.g. sole). Except for the obvious difference in salinity (salinity ranged between 15.5 and 26.1 psu in Waarde and between 3.4 and 16.1 psu in Saeftinghe), the different distance of both marshes to the main channel of the estuary can determine the accessibility for certain species (Figure 1). There seems to be a maximal distance that some species are willing to bridge to enter the marsh from the subtidal areas (Rozas, 1993). Good swimmers such as bass can probably resist the strong currents in the subtidal channel—which is very close to the marsh of Saeftinghe—and enter the creeks. In contrast, the presence of an extensive sandbank in front of the marsh of Waarde can give better possibilities to enter the marsh for species that prefer shallow and calmer waters (Cattrijsse, 1994).

Temporal patterns

In all regions, marked seasonal patterns were observed in the densities of the most common species: maximal numbers were recorded in spring and minimal numbers from late summer until late winter. Exceptions were *Syngnathus* (peak in late summer) and *Pomatoschistus* spp. (two peaks: one in spring and one in summer). The low numbers observed from summer onwards are probably mainly due to the absence of the specific life history stages that are sampled efficiently by the sledge and the fyke net: as the fish grow, their swimming capacities improve and they either migrate out of the area or recruit to the demersal, benthic or pelagic stocks.

Our results are in general agreement with current knowledge about the biology of the North Sea populations of the dominant species. Plaice is a winter spawner: eggs and larvae appear from December until March with peaks in January and early February. Postlarvae can generally be found until May (Russell, 1976). Still, some postlarvae were observed in June (Saeftinghe) and July (Voordelta). Flounder spawns from mid January until April in the southern parts of the North Sea and until July in the northern parts (Simpson, 1949). Off Plymouth, spawning took place from February until April (Clark, 1920) and postlarvae occurred from March to June (especially in April and May) (Clark, 1914; Russell, 1935). Spawning of sole occurs in the North Sea between April and August, especially in May (Russell, 1976). Postlarvae off Plymouth appeared in March to June with maxima in April and with the earliest observation in February (Russell, 1940). The clupeid larvae recorded in this study are probably a mixture of herring *Clupea harengus* and sprat *Sprattus sprattus*. The time of year at which postlarval herring are most abundant depends on whether the local stocks are spring or autumn spawners. In northern areas,

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the number of postlarvae generally increases in late spring and summer, while more to the south they mainly occur during late winter and early spring. The main spawning period of sprat occurs earlier in the south than in the north. Eggs have been recorded from January to July (Russell, 1976). De Silva (1973), in a study of the reproductive biology of the sprat on the west coast of Scotland, found that spawning lasted for five to six months starting in February to March. Most *Syngnathus* spp. recorded in this study are probably Nilsson's pipefish *S. rostellatus*. The eggs of greater pipefish *S. acus* appear from May until July, those of Nilsson's pipefish from June to August. The young of greater pipefish take immediately to a bottom life upon release from the parent, while those of Nilsson's pipefish are pelagic for a short period (a few weeks) (Russell, 1976), increasing their catchability with a sledge type gear. *Pomatoschistus* spp. are a mixture of sand goby *P. minutus* and Lozano's goby *P. lozanoi*, both of which are very abundant in the study area (Hamerlynck et al., 1993). The different recruitment periods of sand and Lozano's goby can largely explain the rather erratic abundance pattern observed in the Voordelta and the Westerschelde. In the Belgian coastal area, spawning periods are spring (March to June) and mid-summer (June to August) (Fonds, 1973; Hamerlynck et al., 1986), for sand and Lozano's goby respectively. Juveniles of both species are common in estuaries, even occurring at salinities as low as 5 psu (O. Hamerlynck, unpublished data) and only migrating to the sea in winter when temperatures drop below 2.5°C. If temperatures rise again above 3°C, they return to the estuary (Fonds, 1973). This might explain the low numbers observed in February in the Westerschelde.

It is striking that maximal abundance peaks always occurred earlier in the Westerschelde than in the Voordelta, except for clupeids. This is probably due to the fact that the two environments were sampled in different years (interannual variability).

Length–frequency distributions

For most species, individuals were smaller in the subtidal of the Voordelta than in the Westerschelde, suggesting either migrations from the coastal marine environment to the estuary, where the marshes and other intertidal areas are probably chosen as a habitat before recruiting to the subtidal population, or slower growth. For several species (e.g. clupeid larvae, *Pomatoschistus* and *Syngnathus* spp.), individuals were larger in the tidal marshes than in the other regions.

The hyperbenthic sledge and the fyke net obviously sampled predominantly specific pre-settlement stages of all three flatfish species: individuals just before or at the onset of asymmetry are clearly over-represented in the hyperbenthos. Recent evidence suggests that metamorphosis may play a significant role in modifying recruitment potential for some marine fish. In numerous fish species and especially flatfish, this period of metamorphosis may be characterized by extensive morphological, physiological, ecological and behavioural changes (Youson, 1988). There also appears to be a period of intense mortality associated with the completion of metamorphosis and settlement in several species of marine fish. Metamorphosis represents thus an important period with respect to recruitment (Keefe & Able, 1993).

The mean length of young flounders was larger in March (10–11 mm) than in April and May (around 8 mm) which suggests prolonged recruitment. Monthly length–frequency distributions of clupeid larvae were quite irregular. This may also result from several or prolonged recruitment periods and/or from the fact that we are dealing with a mixture of several species. Only one peak was observed in the Voordelta (June) at a mean length of about 14 mm. This was also reflected in the unimodal length–frequency distribution pattern of the pooled data (Figure 7). In contrast, two peaks were visible in the Westerschelde: one before March and one in May, which was again reflected in the pooled length–frequency distributions. In the Voordelta, two clear recruitment periods of *Pomatoschistus* species were revealed: one around June and one in August–September. This probably reflects the different spawning periods of sand and Lozano's goby. In the Westerschelde, this pattern is less obvious because of the smaller differences in mean length per month. Most of the smallest pipefish measured between 10 and 15 mm. Since greater and Nilsson's pipefish hatch at lengths of respectively 25–35 mm and 13–14 mm (Russel, 1976), this again confirms that they were most likely larvae of Nilsson's pipefish. The rather erratic patterns of the length–frequency distributions can again be due to the fact that more than one species was sampled. Further, it should be mentioned that—in contrast to most other species treated in this study—not only 'early postlarvae' of *Syngnathus* spp. were sampled: the length–frequency distributions show that a significant part of the population consisted of subadult (and even some adult) individuals.

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Appendix 1. *List of species recorded, with indication of their distribution and average density in the different subareas and seasons (see also text).*

Order	Species and stage	Area	Month	Density	Remarks
Petromyzontiformes	*Lampetra fluviatilis* (Linnaeus, 1758)	WSB	Mar	—	
Anguilliformes	*Anguilla anguilla* (Linnaeus, 1758)	VDO/WSM, WSB/TMW, TMS	Feb/occ/all	—/—/—	peak in spring
Clupeiformes	*Clupeidae* spp. larvae	VDG > VDB, VDO/WSM < WSB/TMW < TMS	Mar–Jul	***/*/***	peaks in May/June
	Clupea harengus (Linnaeus, 1758)	WSM < WSB/TMW ≪ TMS	all	—/**	
	Sprattus sprattus (Linnaeus, 1758)	WSM < WSB/TMS	all	+/**	
Cypriniformes	*Alburnus alburnus* (Linnaeus, 1758)	TMS	Mar	—	freshwater species
Gadiformes	*Ciliata mustela* (Linnaeus, 1758)	VDB	Jul	—	
	Gadus morhua (Linnaeus, 1758)	WSM < WSB	May	—	
	Merlangius merlangus (Linnaeus, 1758)	VDG, VDB, VDO/WSM/TMS	Apr–Jul	—/—/—	
	Pollachius pollachius (Linnaeus, 1758)	VDG	May	—	
	Trisopterus luscus (Linnaeus, 1758)	VDG > VDB, VDO/WSM, WSB	May–Jul/occ	—/—	peak in June
	Trisopterus minutus (Linnaeus, 1758)	VDB	May	—	
Atheriniformes	*Atherina presbyter* (Cuvier, 1829)	VDG/WSB/TMW, TMS	Sep–Nov	—/—/—	
Gasterosteiformes	*Gasterosteus aculeatus* (Linnaeus, 1758)	VDO/WSM,WSB/TMW > TMS	Jul/occ/all	—/—/+	
	Pungitius pungitius (Linnaeus, 1758)	TMS	occ	—	freshwater species

(*Continued*).

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Appendix 1. *(Continued)*.

Order	Species and stage	Area	Month	Density	Remarks
Syngnathiformes	*Syngnathus* spp.	VDG > VDB, VDO/ WSM < WSB/ TMW > TMS	all	+/+/***	peak in Aug/Sep (Nov in marshes)
Scorpaeniformes	*Myoxocephalus scorpius* (Linnaeus, 1758)	VDG, VDO/WSB	Mar–May	—/—	
	Agonus cataphractus (Linnaeus, 1758)	VDG, VDO	May–Sep	—	
	Liparis liparis (Linnaeus, 1766)	VDG, VDB/WSM, WSB	Apr–Jun	—/—	
Perciformes	*Dicentrarchus labrax* (Linnaeus, 1758)	WSM < WSB/TMW ≪ TMS	occ/all	—/*	
	Stizostedion lucioperca (Linnaeus, 1758)	TMS	occ	—	freshwater species
	Trachurus trachurus (Linnaeus, 1758)	VDG, VDB, VDO	Jul–Aug	—	peak in July
	Chelon labrosus (Risso, 1826)	TMW, TMS	Oct–Dec	—	
	Liza ramada (Risso, 1826)	WSM, WSB/TMW, TMS	occ	—/—	
	Pholis gunnellus (Linnaeus, 1758)	VDO/WSM	Feb/Apr	—/—	
	Echiichthys vipera (Cuvier, 1829)	VDB	Jul	—	
	Ammodytes tobianus (Linnaeus, 1758)	VDG, VDB, VDO/WSM, WSB/ TMS	occ	—/—/—	
	Hyperoplus lanceolatus (Le Sauvage, 1824)	WSM, WSB	occ	—	
	Callionymus lyra (Linnaeus, 1758)	VDG > VDB > VDO/WSM	Jun–Jul/May	+/—	peak in June
	Aphia minuta (Risso, 1810)	VDG > VDB > VDO	Nov–May	—	
	Pomatoschistus microps (Kröyer, 1838)	WSM < WSB/TMW < TMS	all	—/533	
	Pomatoschistus spp. Larvae (comprising *P. minutus* and *P. lozanoi*)	all	all	***/**/***	peaks in May and June/August (November in marshes)
Pleuronectiformes	*Scophthalmus rhombus* (Linnaeus, 1758)	VDG, VDO	Jun–Jul	—	
	Limanda limanda (Linnaeus, 1758)	VDG > VDB > VDO/ WSM < WSB	occ	—/—	
	Pleuronectes flesus (Linnaeus, 1758)	VDG > VDB, VDO/ WSM < WSB/TMW < TMS	Mar–Jun	—/+/150	peak in June (Voordelta and marshes) and May (estuary)
	Pleuronectes platessa (Linnaeus, 1758)	VDG > VDB, VDO/WSM, WSB/TMS	Mar–Jul/ Nov–Apr/Apr	—/+/—	peak in April in marshes
	Solea solea (Linnaeus, 1758)	VDG > VDB > VDO/ WSM > WSB/TMW > TMS	May–Jun/ Apr–Jun/Apr	*/+/*	peaks in March/ April in the estuary and in May in the Voordelta

VDG, ebb-tidal delta of the Grevelingen; VDB, Banjaard area; VDO, ebb-tidal delta of the Oosterschelde; WSM, marine region of the Westerschelde; WSB, brackish region of the Westerschelde; TMW tidal marsh of Waarde; TMS, tidal marsh of Saeftinghe; occ, occasionally; –, 0–1 ind 1000 m^{-2}; +, 1.1–5 ind 1000 m^{-2}; *, 5.1–10 ind 1000 m^{-2}; **, 10.1–20 ind 1000 m^{-2}; ***, 20.1–50 ind 1000 m^{-2}.

Appendix 2. *Mean ±SE densities (ind 1000 m^{-2}) per subarea for each 'species'.*

	Mean ±SE						
	VDG	VDB	VDO	WSM	WSB	TMW	TMS
Lampetra fluviatilis	—	—	—	—	0.06 ±0.05	—	—
Anguilla anguilla	—	—	0.01 ±0.01	0.02 ±0.02	0.27 ±0.11	—	0.06 ±0.02
Anguilla juveniles						2.95 ±0.40	1.48 ±0.29
Clupea harengus	—	—	—	0.02 ±0.03	0.31 ±0.10	0.08	33.54 ±6.41
Sprattus sprattus	—	—	—	0.53 ±0.16	2.08 ±0.64	—	25.14 ±3.13
Clupeidae spp. larvae	86.02 ±33.48	19.82 ±4.84	23.43 ±4.87	4.18 ±2.02	11.23 ±3.44	7.21 ±1.09	76.64 ±9.66
Alburnus alburnus	—	—	—	—	—	—	0.02 ±0.00
Ciliata mustela	—	0.01 ±0.01	—	—	—	—	—
Gadus morhua	—	—	—	0.00 ±0.02	0.06 ±0.06	—	—
Merangius merlangus	0.02 ±0.02	0.04 ±0.02	0.08 ±0.04	0.00 ±0.05	—	—	0.02
Pollachius pollachius	0.01 ±0.01	—	—	—	—	—	—
Trisopterus luscus	0.83 ±0.46	0.23 ±0.13	0.16 ±0.08	0.02 ±0.04	0.03 ±0.03	—	—
Trisopterus minutus	—	0.01 ±0.01	—	—	—	—	—
Atherina presbyter	0.01 ±0.01	—	—	—	0.03 ±0.03	0.14 ±0.02	0.12 ±0.07
Gasterosteus aculeatus	—	—	0.01 ±0.01	0.02 ±0.02	0.02 ±0.02	2.53 ±0.18	0.43 ±0.02
Pungitius pungitius	—	—	—	—	—	—	0.04
Syngnathus spp.	4.10 ±0.69	1.88 ±0.56	2.69 ±0.87	0.85 ±0.35	5.61 ±1.46	35.92 ±5.08	6.06 ±0.66
Myoxocephalus scorpius	0.01 ±0.01	0.00 ±0.00	0.01 ±0.01	—	0.03 ±0.03	—	—
Agonus cataphractus	0.01 ±0.01	—	0.05 ±0.03	—	—	—	—
Liparis liparis	0.08 ±0.03	0.08 ±0.05	0.00 ±0.00	0.02 ±0.04	0.03 ±0.03	—	—
Dicentrarchus labrax	—	—	—	0.00 ±0.02	0.02 ±0.02	0.03	11.09 ±0.31
Stizostedion lucioperca	—	—	—	—	—	—	0.03 ±0.01
Trachurus trachurus	0.72 ±0.47	1.01 ±0.67	1.29 ±0.74	—	—	—	—
Chelon labrosus	—	—	—	—	—	0.80	0.69 ±0.10
Liza ramada	—	—	—	0.01 ±0.02	0.06 ±0.05	0.55 ±0.39	0.05 ±0.02
Pholis gunnellus	—	—	0.01 ±0.01	0.01 ±0.01	—	—	—
Echiichthys vipera	—	0.89 ±0.66	—	—	—	—	—
Ammodytes tobianus	0.14 ±0.08	0.09 ±0.05	0.10 ±0.04	0.15 ±0.12	0.50 ±0.18	—	0.23 ±0.17
Hyperoplus lanceolatus	—	—	—	0.02 ±0.02	0.03 ±0.03	—	—
Calionymus lyra	3.33 ±1.50	1.84 ±0.73	1.03 ±0.35	0.04 ±0.11	—	—	—
Aphia minuta	0.48 ±0.18	0.14 ±0.06	0.02 ±0.01	—	—	—	—
Pomatoschistus spp.	26.22 ±5.28	23.93 ±7.55	10.95 ±1.99	8.14 ±2.59	17.97 ±5.14	26.58 ±1.65	35.53 ±3.26
Pomatoschistus microps	—	—	—	0.10 ±0.07	1.32 ±0.46	229.78 ±9.68	836.27 ±31.23
Scophthalmus rhombus	0.01 ±0.01	—	0.01 ±0.01	—	—	—	—
Limanda limanda	0.57 ±0.21	0.22 ±0.11	0.023 ±0.02	0.07 ±0.06	0.21 ±0.10	—	—
Pleuronectes flesus	0.05 ±0.03	0.01 ±0.01	0.01 ±0.01	1.41 ±0.94	9.13 ±7.11	25.57 ±2.33	276.22 ±48.66
Pleuronectes platessa	0.31 ±0.31	0.09 ±0.06	0.11 ±0.07	1.00 ±0.55	2.57 ±1.00	—	0.89 ±0.18
Solea solea	14.65 ±9.39	3.73 ±2.18	0.70 ±0.27	1.45 ±1.00	0.37 ±0.26	17.78 ±9.48	1.21 ±0.25

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Appendix 3. *Mean ±SE lengths per months (in mm) of the dominant species for the Voordelta (A), the Westerschelde (B) and the tidal marshes of Waarde (C) and Saeftinghe (D). For sampling dates per study area, see Table 1.*

A. Voordelta	A	S	O	N	D	J	F	M	A	M	J	J								
Clupeidae spp. larvae								27.1 ±0.2	28.7 ±0.1	21.9 ±0.1	13.7 ±0.1	15.7 ±0.2								
Pomatoschistus spp.	9.4 ±0.1	9.8 ±0.2			14.7 ±0.3					12.0 ±0.2	7.4 ±0.1	9.1 ±0.1								
Syngnathus spp.	33.7 ±0.7	40.3 ±1.3	81.4 ±2.7				67.7 ±2.7	77.1 ±3.4				24.3 ±0.9								
Solea solea										7.6 ±0.2	6.2 ±0.1									
Pleuronectes platessa										8.1 ±0.2										
B. Westerschelde	A	M	J	J	A	S	O	N	D	J	F	M	A							
Clupeidae spp.	28.7 ±0.3	14.1 ±0.1	15.1 ±0.6									24.1 ±1.5	27.9 ±0.2							
Pomatoschistus spp.		14.0 ±0.1	11.7 ±0.2	12.6 ±0.2	13.9 ±0.2	13.3 ±0.5														
Syngnathus spp.				53.3 ±1.6	61.7 ±1.1	73.1 ±3.1														
Solea solea	8.1 ±0.2	7.4 ±0.2																		
Pleuronectes platessa												10.6 ±0.1	12.0 ±0.1							
Pleuronectus flesus	7.6 ±0.0											10.5 ±0.1	7.6 ±0.2							
C. Tidal marsh of Waarde	M	A	A	M	J	J	A	S	O	O	N	D	J	F	M	A	M	J	J	A
Clupeidae spp. larvae		28.4 ±0.4	28.7 ±0.4																34.0 ±0.3	
Pomatoschistus spp.				14.6 ±0.1	18.2 ±0.2													17.3 ±0.2		
Syngnathus spp.			99.4 ±2.0			109.0 ±3.1			90.6 ±0.4	94.3 ±1.5								90.7 ±1.0		
Solea solea				7.8 ±0.1														7.7 ±0.1		
Pleuronectes platessa																				
Pleuronectes flesus			8.0 ±0.1	8.1 ±0.1											10.8 ±0.1	8.1 ±0.1				
D. Tidal marsh of Saeftinghe	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O
Clupeidae spp. larvae		30.7 ±0.1	30.5 ±0.7											34.9 ±0.1		24.2 ±0.1				
Syngnathus spp.								76.7 ±1.1												
Solea solea			9.0 ±0.2																	
Pleuronectes platessa		11.7 ±0.1																		
Pleuronectes flesus	11.7 ±0.2	8.2 ±0.1	8.9 ±0.0	21.5 ±0.2									11.0 ±0.0	8.7 ±0.1	8.4 ±0.2	10.8 ±0.2				