Habitat value of a developing estuarine brackish marsh for fish and macrocrustaceans

Henrietta Hampel, Andre Cattrijsse, and Magda Vincx

Marsh creation receives worldwide attention in mitigating loss of coastal wetlands and in management retreat of estuaries. In the Westerschelde, the former Selena Polder, south from the marsh of Saeftinghe, developed into the Sieperda marsh after several dyke breaches. Soon after the tides regained access to the polder, a tidal creek was formed. After 10 years, a developing marsh system was found adjacent to a mature marsh system. This situation offered the opportunity to compare the utilization by nekton species of a natural mature marsh with a recently created developing marsh under similar circumstances.

Between April and October 1999, both the mature Saeftinghe marsh and the developing Sieperda marsh were sampled every 6 weeks on 2 consecutive days. Each sampling occasion covered the whole tidal cycle. The most important environmental parameters (water height, temperature, salinity, turbidity and dissolved oxygen) were similar in both marsh creeks. A distinct difference in nekton community structure between the two marshes was observed. The total biomass and densities of nekton species were higher in Saeftinghe.

In Saeftinghe, a density peak occurred in July and was mainly due to large numbers of the mysid, *Neomysis integer*. In Sieperda, maximum abundance of the mysid, *Mesopodopsis slabberi*, caused the peak density in September. This difference in species dominance was observed in all samples.

Biomass peaked in July in the mature marsh and in October in the developing marsh. Mysid shrimp (*N. integer*) and fish (mainly *Pomatoschistus microps*) were the main contributors to the biomass saeftinghe. Herring, sprat (Clupeidae) and shore crab (*Carcinus maenas*) were more important in Sieperda. For *P. microps*, distinct differences in length–frequency distributions were noted between the marshes.

While creek morphology influences the abundance and species composition of visiting nekton, the age of a marsh and its maturity are believed to be the prime factors in determining the habitat function of creek systems of developing and mature marshes.

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Introduction

Salt marshes fulfil several fundamental ecological functions. They can export nutrients to adjacent waters (Odum, 1968, 1980), act as pollution filters (Adam, 1990), minimize shoreline erosion (Race and Christie, 1982) and serve as nurseries for fish and macrocrustaceans (Boesch and Turner, 1984; Costa *et al.*, 2001). Many fish species depend upon coastal marshes through the provision of food and protection from predators (Minello and Webb, 1997).

In the recent past there has been a strong global interest in the creation and recreation of salt marshes. Marsh restoration is increasingly used to mitigate wetland habitat losses (Zedler, 1996) from agricultural or urban land reclamation and dike constructions (Bakker *et al.*, 1993; Mitsch *et al.*, 1994). Natural and newly created marshes do not always represent similar habitat values for nekton or other estuarine organisms (Moy and Levin, 1991; Minello and Zimmerman, 1992). The time required for a newly created marsh to achieve the same level of ecosystem function as a mature marsh constitutes an important and interesting question.

Sediment (texture, nutrients and organic matter content) characteristics play an important role in the invertebrate distribution in artificial marshes while the development of

the introduced vegetation is vital in offering refuge opportunities for fish (Zedler and Lindig-Cisneros, 2000). The relationship between the vegetation and the infauna seems to depend on the vegetation type and on various predator–prey attributes (Lana and Guiss, 1992). However, Minello and Zimmerman (1992) did not observe a significant relationship between the vegetation structure and the density of infauna, crustaceans or fish in newly created marshes.

Several works have been published on the colonization of restored and artificial salt marshes by fish and macro-crustaceans along the American east Atlantic coast. Most of these, assume that many newly created salt marshes offer similar fish species composition and densities as natural marsh habitats in a relatively short period of time (Williams and Desmond, 2001). Williams and Zedler (1999) found no significant differences in fish species richness between 1 and 12 year old constructed and natural channels. Yet, Scatolini and Zedler (1996) observed similar species composition but lower abundances in a 4 year old constructed marsh in the southeast of the San Diego Bay. Minello and Webb (1997) observed rapid colonization of new marsh habitats (3–15 years) by fish. Dionne *et al.* (1999) also showed that fish visit restored and created marshes in assemblages similar to those found in reference natural marshes.

Management retreat, realignment and set-back have recently become an issue in the management of estuaries. Mainly driven by an increasing need for flood control, Belgian and Dutch authorities began to change policies towards the management of the Schelde estuary. Management retreat, restoring former estuarine areas into tidal marshes, is now under serious consideration.

In this study, we took advantage of a dyke breach that occurred 10 years ago and that was not repaired. The flooded polder slowly developed into an intertidal marsh. The close proximity of an adjacent natural marsh allowed a comparison of the habitat value of the intertidal creeks of the mature and of the developing marsh for fish and macrocrustaceans. Several studies have been carried out on the development of this new marsh but data about the nekton community and its utilization of the marsh area were lacking (van Oevelen *et al.*, 2000). This study represents a comparative assessment of the nursery value of both marsh systems, 10 years after tidal processes have been restored.

Material and methods

Study area

Both the mature marsh 'Het Verdronken Land van Saeftinghe' and the developing marsh Sieperda lie in the oligohaline part of the Westerschelde Estuary, separated by a dyke from each other (Figure 1). Saeftinghe is the largest estuarine brackish marsh left in Western Europe and covers an area of 2800 ha (Dijkema *et al.*, 1984). The formation of Sieperda marsh started after three consecutive dyke breaches

that separated the former polder from the estuary. After the dyke gave away for the third time, Dutch authorities decided not to repair it and the polder evolved into a tidal marsh. This human non-interference with the ecosystem offered an opportunity to compare the functioning of the developing and the adjacent mature marsh as habitats for aquatic organisms.

The intertidal drainage areas of both creeks behind the sampling point were estimated to be around 50 ha (Cattrijsse *et al.*, 1994; van Oevelen *et al.*, 2000). Average tidal volume did not differ significantly between the two creeks during the sampling period (Mann–Whitney U-test, $p = 0.18$). The average tidal volume of the creek in Saeftinghe and Sieperda was, respectively, 70 357 and 86 412 m^3. The tidal elevation of Saeftinghe is 2.95 mNAP (Dutch ground level $\approx$ MTL) (Hemminga *et al.*, 1993) and 2.55 mNAP in Sieperda (van Oevelen *et al.*, 2000).

Median grain size averages 30 µm in Seaftinghe (personal observation) and 67 µm in Sieperda (van Oevelen *et al.*, 2000). The organic matter content of the sediment reaches 1.6% in the developing marsh (van Oevelen *et al.*, 2000) and around 8.5% in Saeftinghe (personal observation).

The vegetation is dominated by *Scirpus maritimus*, *Triglochin maritima*, *Elymus athericus*, *Phragmites australis* and *Atriplex hastata* in Saeftinghe (Hemminga *et al.*, 1993). *Puccinellia maritima*, *Aster tripolium*, *Juncus gerardi* and *Salicornia* sp. are the dominant marsh plants growing in Sieperda (Stikvoor and de Winder, 1998). *Puccinellia* and *Salicornia* are pioneer species (Beeftink, 1977) while *Elymus* is more typical for mature areas (de Jong, pers. comm.). Eighty-seven percent of the total vegetated surface of Saeftinghe and 94% of the marsh surface of Sieperda are covered 80 100% by vegetation (Koppejan, 1998).

Some differences were observed concerning the shape of the creeks in the mature and developing marsh. Both creeks were 4 m deep at the sampling point but in Saeftinghe the creek was 35 m wide whilst in Sieperda it measured only 25 m. While the creek in Saeftinghe showed a typical natural sigmoid shape, the Sieperda creek was partly man-made and linear. The creek was dredged, narrowed and channelled over a short distance. Our sampling point was by necessity positioned in that artificial section. Upstream and downstream of the sampling point in Sieperda large pools, several meters wide and long and more than 50 cm deep, were formed. Such large intertidal pools were absent in the mature marsh.

The whole tidal cycle lasts for 6 h in Saeftinghe and 5 h in Sieperda. Water starts entering the mature marsh 3 h before high water and leaves the creek within 3 h. In Sieperda flood takes around 2 h and drainage is completed in 3 h.

Sampling

In both marshes, sampling took place from a bridge spanning the creek. A stow net with a 1 mm mesh size, a
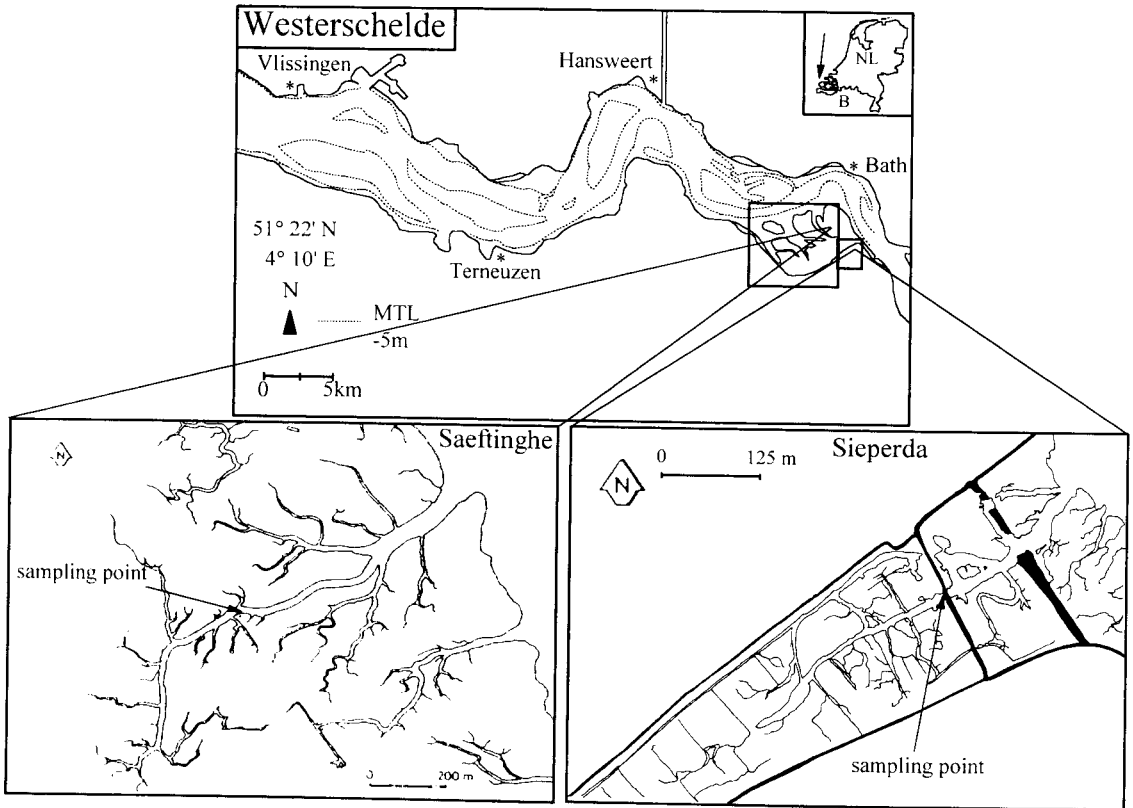
Figure 1. Location of Saeftinghe (mature marsh) and Sieperda (developing marsh) in the Westerschelde. Map of Saeftinghe is after Hemminga *et al.* (1993).

1 m² opening and a length of 5 m was placed on the bottom of the creek and used to sample the migrating nekton. The net was mounted on an iron frame. Two weights attached to the sides of the frame prevented the net from being lifted by the currents, while ropes kept the net in place during sampling. The opening size of the net, the mesh size and the diameter of the fibre were used to calculate the necessary length of the net in order to keep the pressure inside the net under all current conditions (Tranter, 1979). This reduced the probability that animals avoided the net. Since the banks of the creek are symmetrical, we assumed that the migrating fauna was evenly distributed over the lower water column (McIvor and Odum, 1988). The focus was to sample hyperbenthic and epibenthic species in the lower 1 m of the creek.

The net fished for 1 h was rinsed and then replaced in the same position. After high water the net was turned around to sample the ebb current until all water had left the creek. Sampling lasted a complete tidal cycle yielding three flood and three ebb samples in Saeftinghe, and two flood and three ebb samples in Sieperda during every sampling period.

Samples were preserved in a 10% formalin solution. When large amounts of plant material were caught in the net, volumetric subsamples were taken. In the laboratory, all samples were sorted and the species were identified to the lowest possible taxonomic level. When species had very high abundances, volumetric subsamples were taken for that specific species. The organic material trapped in the net was oven dried at 60 °C for 2 days and weighed.

Samples were collected every 6 weeks from April until October 1999. Sampled months were April (code as 04), June (06), July (07), September (09) and October (10). The two marshes were sampled on 2 consecutive days. During sampling, water temperature, salinity, turbidity and dissolved oxygen concentration were measured every hour. Water speed and water height were measured every 15 min. Current speed was measured with a current meter, placed about 20 cm above the bottom next to the net. The water height was measured with a ruled stake placed next to the net in the deepest part of the creek.

Data processing and analyses

The volume of water filtered by the net and passing through the whole creek was calculated every 15 min in order to quantify the catches and to estimate the tidal volume. At the sampling point, the cross-sectional area of the creek for every possible water height was measured. Water height, current, and the cross-section allowed calculation of the flow (m³ s⁻¹) at the sampling point.

Table 1. Average measured environmental variables (salinity, temperature, dissolved oxygen) and standard error, maximum water height, current and turbidity and the amount of detritus available at the moment of the high water in the two sampled marshes. Saeftinghe (Sae) and Sieperda (Sie). Sampling months are labelled by numbers such as April (04), June (06), July (07), September (09) and October (10).

	Sae 04	Sie 04	Sae 06	Sie 06	Sae 07	Sie 07	Sae 09	Sie 09	Sae 10	Sie 10
Salinity (psu)	5.4±0.2	5.1±0.2	9.9±0.2	9.0±0.2	9.4±0.04	8.9±0	14±0.2	13.8±0.4	13.1±0.1	13.2±0
Temperature (°C)	14.4±0.3	14.3±0.4	21.5±0.6	19.9±0.2	19.9±0.3	20.7±0.2	22.3±0.3	21.3±0.03	10.1±0.4	11.2±0.4
Oxygen (mg l^{-1})	6.5±0.3	5.9±0.3	7.2±0.1	5.7±0.2	8.7±0.5	8.5±0.5	5.9±0.2	6.3±0.07	8.1±0.2	6.5±0.2
Water height (cm)	320	270	260	270	240	255	250	250	160	175
Current speed (m s^{-1})	0.2	0.7	0.1	0.4	0.1	0.6	0.2	0.6	0.1	0.70
Turbidity (cm^{-1})	0.025	0.025	0.025	0.016	0.016	0.016	0.013	0.014	0.028	0.018
Detritus (g m^{-3})	0.06±0.02	0.006±0	0.06±0.01	0.01±0.005	0.007±0.002	0.001±0	0.03±0.02	0.009±0.005	0.15±0.005	0.005±0.002

The amount of detritus was measured and the number of individuals that passed the sampling point during each sampling hour was counted for each species. The sum of the flood samples (total number of individuals entering the creek) and the total volume of water that passed at the sampling point during flood yielded an estimate of density in the lower 1 m of the creek at high water. A similar high water density estimate was made based upon the total number of individuals and volume of water that left the creek system during ebb. The average of the flood and ebb estimates was used as an estimate of the abundance at the moment of high water. The same procedure was used to calculate the biomass (mg ADW m^{-3}), which was computed with length–ADW regressions found in literature (Hamerlynck *et al.*, 1990) or established in the laboratory (A. Cattrijsse, K. Hostens and J. Mees, unpublished data).

All individuals were identified to the possible lowest taxonomic level. Larval stages were treated as separate species because of their different ecologies. Decapods were considered as postlarvae if they were under 10 mm standard length (SL). Clupeidae species were grouped as postlarvae under 40 mm SL. Syngnathidae less than 70 mm were also considered postlarvae, while a 20 mm SL was used to classify the other fish species (*Pomatoschistus microps, Dicentrarchus labrax, Pleuronectes flesus* and *Pleuronectes platessa, Solea solea* and *Liza ramada*).

Due to the low number of samples and the lack of normal distribution, Mann Whitney U-test was used to test the differences between environmental variables and densities and biomass of species in the mature and developing marsh.

One species density and one species biomass matrix were constructed. Similar data matrices were constructed for the environmental variables. Species appearing twice or less in the samples were removed from the analyses. Density and biomass data were fourth root transformed to approximate normal distribution prior to the multivariate analysis. Following Field *et al.* (1982) different techniques were used to characterize the communities. Cluster analysis based upon Bray Curtis similarities using group average sorting were used to detect differences in the nekton community structure between the two marshes. The PC ORD version 4 software package (McCune and Mefford, 1999) was used to perform CCA. Ter Braak (1987) was followed to decide between PCA or CCA to investigate the relationship between communities and environmental factors.

Results

Environmental variables

Except for the water current and the detritus, all abiotic parameters were similar in both marshes and fluctuated similarly during the sampling period (Table 1). Average salinity was lowest in April (around 5 psu) and increased over the sampling period to 14 psu in September in both marshes. Average temperature showed the same seasonal

change in both marshes with maximum values in September (21–22 °C) and minima in October (10–11 °C). Apart from the observation in October, dissolved oxygen concentrations were also similar in both creeks and peaked in July, with values of $8.5 \, \mathrm{mg\,l^{-1}}$.

Maximum water height decreased towards autumn in the natural as well as in the developing marsh to 160 cm in Saeftinghe and to 95 cm in Sieperda.

Turbidity showed similar values and fluctuations in both marshes. Highest turbidity recordings (around $0.014 \, \mathrm{cm^{-1}}$) were observed in September and lowest readings (0.03–$0.025 \, \mathrm{cm^{-1}}$) occurred in April and October in both marshes.

The total amount of detritus caught in the net was significantly higher in Saeftinghe (0.007–$0.15 \, \mathrm{g\,m^{-3}}$) than in Sieperda ($0.006$–$0.01 \, \mathrm{g\,m^{-3}}$) (Mann–Whitney U-test, $p < 0.01$). The lowest amount of detritus was caught in July and the highest in October in both marshes. The water current at the sampling point was significantly higher (Mann–Whitney U-test, $p < 0.01$) in Sieperda. While in Saeftinghe maximum current speed varied between 0.1 and $0.2 \, \mathrm{m\,s^{-1}}$, maxima in Sieperda ranged between 0.4 and $0.7 \, \mathrm{m\,s^{-1}}$.

Species occurrence

In total, nine amphipod, nine decapod, three mysid, four isopod, one polychaete, one jellyfish, one cladoceran and 22 fish morphotypes were found. Table 2 lists all 50 morphotypes which include 36 species. In the developing marsh, 49 species were collected while in the mature marsh only 42 were caught. No clear differences in species composition were observed between the two marshes.

Typical marsh nekton species occurred in both creeks. These included the mysids *Neomysis integer* and *Mesopodopsis slabberi*, the amphipods *Corophium volutator* and *Gammarus zaddachi*, the brown shrimp *Crangon crangon* and the brackish water shrimp *Palaemonetes varians*, the shore crab *Carcinus maenas*, the common goby *P. microps* and seabass *D. labrax*. Among the main marsh nekton species, only adult flounder (*P. flesus*) were found exclusively in Saeftinghe.

Density

In April and July, total species density was different between the two marshes (Figure 2) although no significant density difference was found during the sampling period (Mann–Whitney U-test, $p = 0.15$). Only *Crangon crangon* ($p = 0.04$) and *C. volutator* ($p = 0.04$) were recorded in significantly higher abundance in Saeftinghe. In Sieperda, only *M. slabberi* ($p = 0.03$) occurred in significant higher densities. All other important species did not show significant different densities.

Table 2. Nekton species occurring in the mature (Sae) and developing (Sie) marsh labelled by a black dot. Adult (a), postlarvae (pl). juvenile (j), megalopa (m), and zoea (z) are used to indicate the life stages.

| Species names	Sae	Sie	Life stage	Species names	Sae	Sie	Life stage
Amphipod				**Other**			
Corophium volutator	●	●		Jelly fish	●	●	
Corophium arenarium		●		Daphnia magna	●	●	
Gammarus zaddachi	●	●		Nereis diversicolor	●	●	
Gammarus salinus	●	●		**Fish**			
Orchestia cavimana	●	●		Clupea harengus	●	●	a
Orchestia gammarellus		●		Clupea harengus	●	●	pl
Orchestia mediterranea		●		Sprattus sprattus		●	a
Melita pelludica	●	●		Sprattus sprattus	●	●	pl
Bathyporeia pilosa	●			Syngnathus rostellatus	●	●	a
Decapod				Syngnathus rostellatus	●	●	pl
Palaemonetes varians	●	●	a	Anguilla anguilla	●	●	
Palaemonetes varians	●	●	pl	Dicentrarchus labrax	●	●	a
Crangon crangon	●	●	a	Dicentrarchus labrax	●	●	pl
Crangon crangon	●	●	pl	Gasterosteus aculeatus	●	●	
Carcinus maenas	●	●	a	Pomatoschistus microps	●	●	a
Carcinus maenas	●	●	j	Pomatoschistus microps	●	●	pl
Carcinus maenas	●	●	m	Pomatoshistus minutus	●	●	
Carcinus maenas	●	●	z	Pleuronectes flesus	●		a
Decapoda larvae	●	●		Pleuronectes flesus	●	●	pl
Mysis				Pleuronectes platessa	●	●	pl
Neomysis integer	●	●		Solea solea	●	●	pl
Gastrosaccus spinifer	●	●		Liza ramada		●	a
Mesopodopsis slabberi	●	●		Liza ramada	●	●	pl
Isopod				Atherina presbiter		●	
Lekanesphaera rugicauda	●	●		Osmerus eperlanus		●	
Eurydice pulchra	●	●		Allosa fallax		●	
Paragnathia formica	●	●					
Cyathura carinata	●	●					
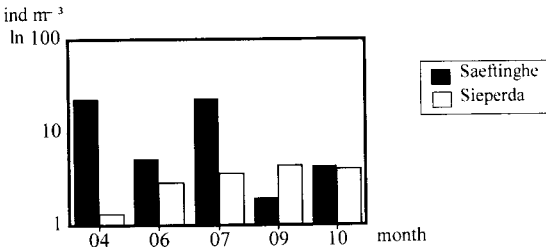
Figure 2. The total density of nekton species on a logarithmic scale in the mature and the developing marsh.

Figure 3 shows the density of nekton species in the two marshes. Mysids numerically dominated all catches in both marshes, accounting for 90% of the total density in some cases. *N. integer* strongly influenced the total density pattern in Saeftinghe, whereas in Sieperda, total nekton density was strongly influenced by the abundance of *M. slabberi*. Mysid densities fluctuated in Saeftinghe. In Sieperda, the abundance of *N. integer* decreased during the summer and reached minimum values in autumn, while an opposite trend was observed for *M. slabberi*. *Neomysis* was always present in higher densities in Saeftinghe. The maximum density of *M. slabberi* observed in September (4.3 ind. m^{-3}) caused a higher total density in the developing marsh than in the mature marsh.

Brown shrimp *Crangon crangon* reached a peak density in April in both marshes: 6.8 ind. m^{-3} in Saeftinghe and 0.3 ind. m^{-3} in Sieperda. In Saeftinghe young shrimp were

present until September, whereas in Sieperda they were already absent by the end of April.

In Saeftinghe, juvenile *C. maenas* attained maximum densities of 2.2 ind. m^{-3} in June. Later, densities decreased towards autumn, reaching similar values as in Sieperda in September where densities never exceeded 0.5 ind. m^{-3}. Zoea larvae of *C. maenas* showed similar temporal changes in abundance in both marshes but in July they reached densities almost 10 times as high in Sieperda. *P. microps* was most abundant in July in both marshes, but densities were higher in Saeftinghe during the whole sampling period. In the mature marsh, higher numbers of the common goby were still caught in October (1.4 ind. m^{-3}), while by the same time in Sieperda abundances had fallen below 1 ind. m^{-3}. *D. labrax* showed a density peak in June, with higher densities in Saeftinghe (4.1 ind. m^{-3}) than in the developing marsh (1 ind. m^{-3}). The seasonal fluctuations in abundance were similar in both marshes. The abundance of Clupeidae species (postlarvae, adult) peaked in June (0.6 ind. m^{-3} in Saeftinghe and 2.8 ind. m^{-3} in Sieperda) and decreased in October. Thereafter, Clupeidae disappeared in July from the mature marsh, while they were still present in the developing marsh during this month (0.7 ind. m^{-3}).

Biomass

Throughout the study period total biomass was significantly higher in the mature marsh Saeftinghe (Figure 4) (Mann-Whitney U-test, p = 0.01). *N. integer* (p = 0.04),
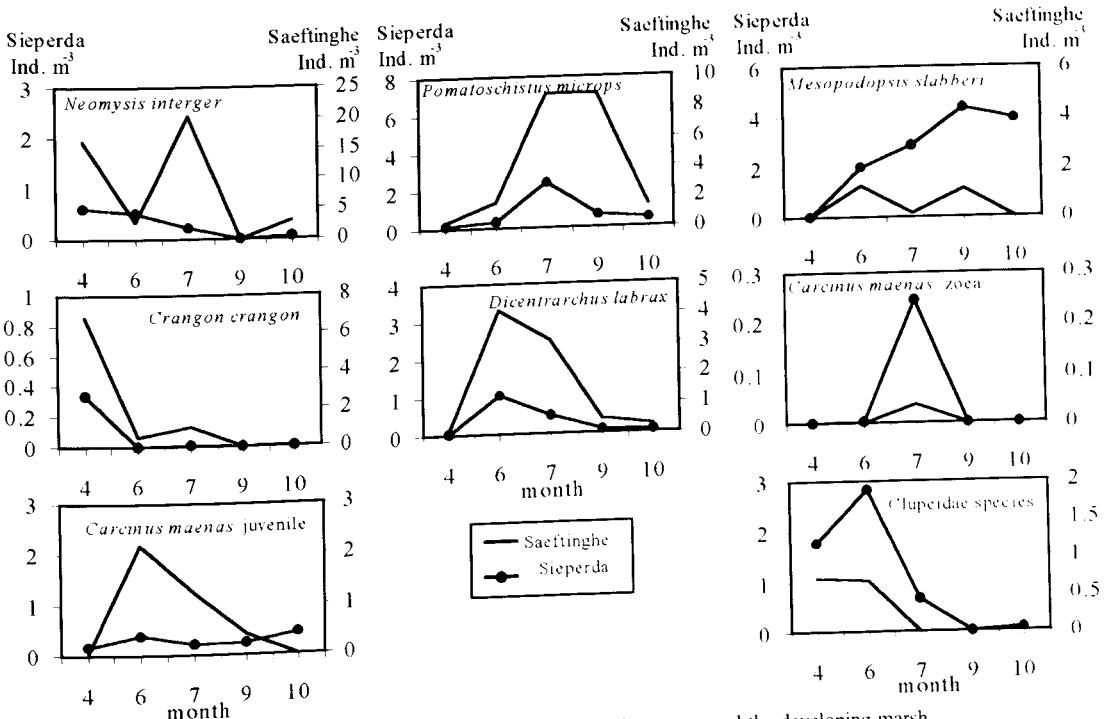

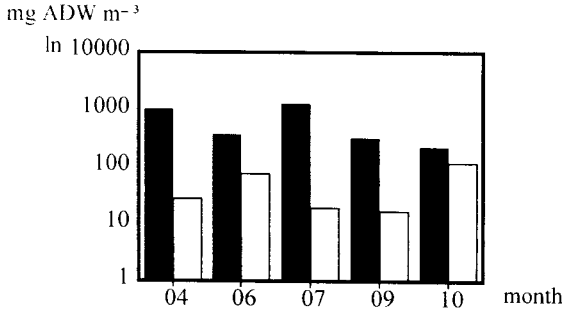Figure 3. Density of the main species occurring in the mature and the developing marsh.

mg ADW m⁻³

Figure 4. Total biomass of nekton species on a logarithmic scale in the mature (black bar) and the developing marsh (white bar).

C. volutator (p = 0.03), *Crangon crangon* (Mann–Whitney U-test, p = 0.03), *P. microps* (p = 0.01), and *D. labrax* (p = 0.01) attained significantly higher biomass in Saeftinghe (Figure 5). In the mature marsh, *N. integer* was the main contributor to the biomass in April (445 mg ADW m⁻³), July (501 mg ADW m⁻³) and October (71 mg ADW m⁻³). The three most important fish species, *D. labrax*, *P. microps* and *P. flesus*, had biomass in June, respectively, 84.3, 8.8 and 10 mg ADW m⁻³. In September, 94% of the total biomass was due to *D. labrax* (15 mg ADW m⁻³) and *P. microps* (108 mg ADW m⁻³).

In Sieperda, the main contributors to the biomass were fish, accounting for 76% of the total biomass in June. Highest biomass levels were associated with Clupeidae species (6.7 mg ADW m⁻³) and the mysid, *N. integer* (2.9 mg ADW m⁻³) in April, in June with Clupeidae

(26.3 mg ADW m⁻³) and *D. labrax* (2.02 mg ADW m⁻³) and in July again with Clupeidae (1.7 mg ADW m⁻³), *D. labrax* (2.1 mg ADW m⁻³) and *M. slabberi* (3.3 mg ADW m⁻³). In September and in October, juvenile *C. maenas* constituted the main portion of the biomass in Sieperda with 4.9 and 55 mg ADW m⁻³.

Length–frequency distribution

The length–frequency distribution of *P. microps* in both marshes is shown in Figure 6. In April, larger individuals migrated to the creeks of Saeftinghe. The larvae appeared in June in Saeftinghe and July in Sieperda. After July the size of the gobies remained around 9–13 cm SL in the developing marsh. In Saeftinghe the individuals grew in autumn, reaching 19–27 cm SL in October. The length–frequency distributions of the other two main fish species, *D. labrax* and Clupeidae spp., did not show different length–frequency distributions between the two marshes.

Species composition

Cluster analyses using Bray-Curtis similarities showed similar seasonal community structures in both marshes (Figure 7a). According to the density data, temporal changes influence the community structure more than the spatial differences between the two marshes. The first division separated the spring communities from the nekton community of the other months, the exception being the October sample in Saeftinghe, which resembled the two April samples. The second division yielded two other clusters.
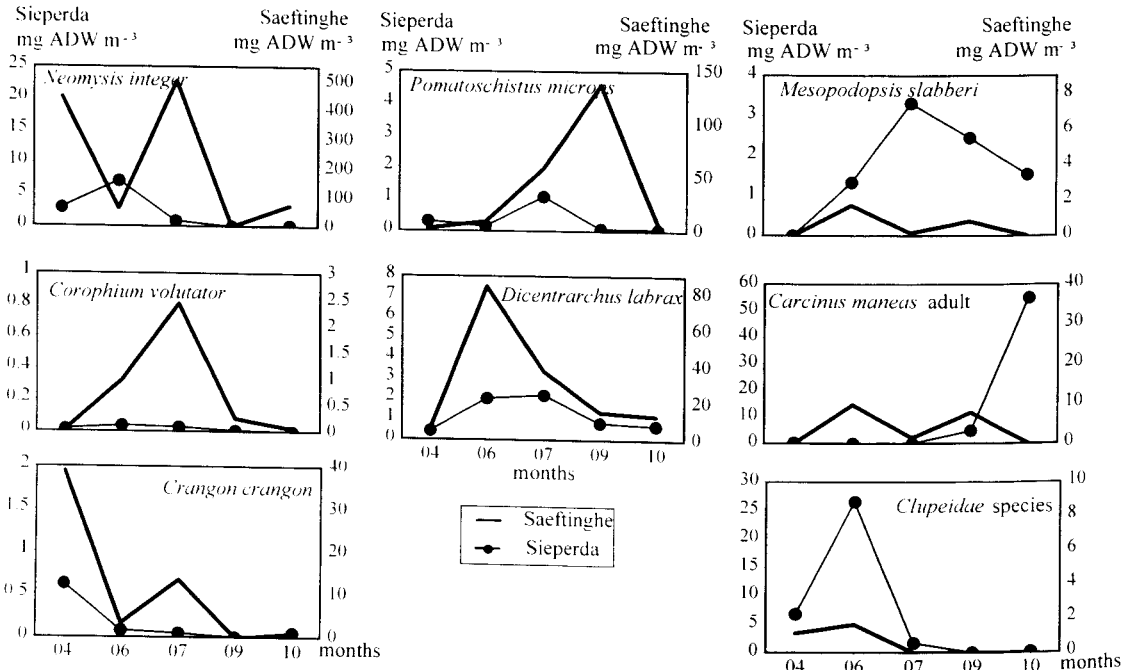

Figure 5. Biomass of the main species occurring in the mature and the developing marsh.
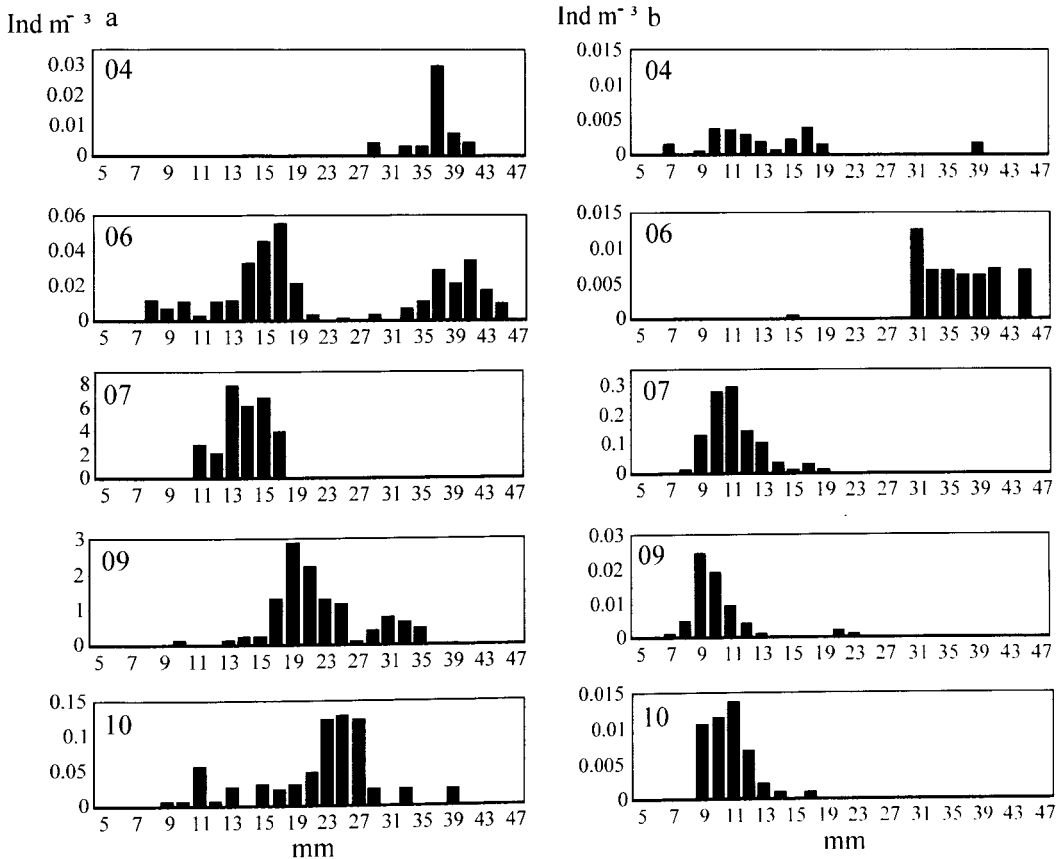
Figure 6. Length–frequency distribution of *Pomatoschistus microps* in Saeftinghe (a) and Sieperda (b). Sampling months are labelled by numbers such as April (04), June (06), July (07), September (09) and October (10).

One grouped the summer (June and July) and the other the autumn (September and October) samples. The seasonal structure in the density data of both marshes was shown in the CCA analysis (Figures 8a). The eigenvalues of the first and the second axes in the CCA were 0.275 and 0.155 and the ordinations explained 49.1% of the observed variance.

In CCA the ordination axes are, by definition, derived as linear functions of the environmental variables. Turbidity and salinity seemed to explain the observed variance the most. The vectors representing these parameters were quite long and correlated well with the first axis. Detritus almost coincided with the first axis but its vector is short. Also, the vector representing the temperature changes is representative for the observed seasonal changes. The other parameters gave large vectors but their correlation with the axes was weak. The temporal variation is clearly shown as samples taken in the same months plot in each others' vicinity in the ordination plane.

The cluster dendogram using biomass data (Figure 7b) showed a complete segregation between the two marshes. Here, the samples of the mature and the developing marsh grouped together. Only the second division revealed a

seasonal pattern. The same spatial difference in community structure was confirmed by the CCA using the biomass data (Figure 8b). The eigenvalues of the first and the second axes were, respectively, 0.251 and 0.196. The amount of explained variance in this ordination was 46.8%. In this ordination, the samples from both marshes were clearly separated in the ordination plane. The vector of the water current best indicates the segregation of the Sieperda and Saeftinghe samples in the ordination plane. Also, detritus seemed to explain the observed segregation but its vector was small. Salinity, water current, water height and turbidity had the largest vectors but only salinity, turbidity and water height correlated well with the first axis and indicated the seasonal changes.

Discussion

The nekton assemblages of the mature and the developing marsh showed similarities with one another and to the assemblages found earlier in that part of the estuary (Cattrijsse *et al.*, 1994). Clear differences were found regarding species abundance and biomass, and in the length
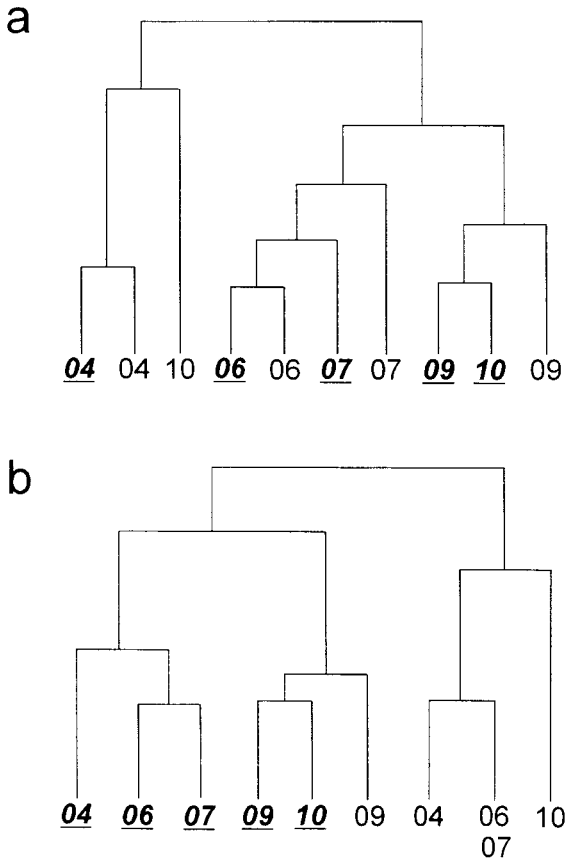
a

04 04 10 06 06 07 07 09 10 09

b

04 06 07 09 10 09 04 06 10
                          07

Figure 7. Cluster dendogram using density (a) and biomass (b) data. Sieperda samples are labelled as bold underlined numbers.

frequency distribution of the common goby, the resident species in the estuarine salt marshes of the Westerschelde. These dissimilarities between the two sites suggest a different use of the marsh creek habitat by the estuarine nekton. Several factors can cause the observed differences between the mature and the developing marsh.

Tidal marshes function as nurseries for juvenile fish and macrocrustaceans, providing better growth conditions through improved predation refuge and/or abundant food resources (Bozeman and Dean, 1980; Boesch and Turner, 1984; Minello *et al.*, 1989; Minello and Webb, 1997; Zimmerman *et al.*, 2000). The vegetation in North American Atlantic salt marshes does not occur below Mean Tidal Level (Reimold, 1977). As a consequence these marshes are regularly flooded and refuge is offered by submerged vascular plants for nekton (Minello and Zimmerman, 1983; Rozas and Odum, 1988). Mean High Water Neap tide borders the low marsh (Beeftink, 1977) in Europe and the vegetated surface is only flooded for a short period during spring tide. As a consequence, the refuge offered by submerged vascular plants is minimal or non-existent. Fish and crustaceans are restricted to the intertidal creeks. In our

study sites, no marsh pools were present adjacent to the creeks. Considering this, the intertidal channels are the true nursery areas providing food and refuge from a high turbidity. If density and biomass of nekton species in the two systems differ, the main reason should be found in the environmental conditions of the tidal channels. Our measurements indicate that the environments of both creeks were very similar and that they differed only in two aspects: the current regime and the amount of organic material.

The different hydrological and geomorphological characteristics of both creek systems will inevitably influence the nekton species composition. During the sampling campaign, we observed fivefold higher water currents in the developing marsh than in the mature marsh. Strong water currents might restrict the occurrence of species that avoid such stressful conditions. The differences in density and biomass observed in the two marshes can, however, not be fully explained by the different current regimes, since currents are even stronger (0.05–$1.35\,\mathrm{m\,s^{-1}}$) in the estuarine subtidal (Stroomatlas, 1992), where all the recorded animals occur as well (Mees *et al.*, 1993). Rather than the strength of the tidal currents, the shape of the creek partly being altered and channelled by man may have had its influence on the species composition of Sieperda. In southern California, native fishes do not appear to discriminate between natural and constructed wetlands channels. There, the composition of fish assemblages is closely related to channel morphology and hydrology rather than to type (natural vs. constructed) (Zedler *et al.*, 1997; Williams and Zedler, 1999). According to these authors channel's physical properties (water depth, temperature, dissolved oxygen, channel width, presence of small creeks, salinity) were more important in determining fish use than its restoration status. These physical characteristics of the creek in Saeftinghe and Sieperda show a high similarity. The difference in channel width may thus partly explain the observed differences. Predation refuge plays a role in marsh creek utilization of nekton species (Cattrijsse *et al.*, 1997), but the characteristics of both marsh creeks are very similar. Minello and Zimmerman (1992) argued that the protective habitat of created marshes may reach equivalency with natural marshes after one or two growing seasons. In contrast to the North-American marshes, in Europe the vegetated surface of marshes is hardly used by nekton species (Cattrijsse *et al.*, 1994). The vegetation almost completely covers the marsh surface, leaving ample space for fish or shrimp to move between the stems of the halophyte vegetation. All fish, shrimp and crabs remain in the intertidal creek where no vegetation occurs. Refuge from predation (e.g. adult *P. flesus* and *D. labrax*) results from the shallowness of the habitat and especially from the highly turbid waters. Turbidity in the marsh creeks varied between 0.03 and $0.014\,\mathrm{cm^{-1}}$ while in the estuary turbidity varies around 0.007 (Hostens, personal communication). The higher turbidity in the intertidal creeks is likely to provide better refuge for nekton than the subtidal area. Since
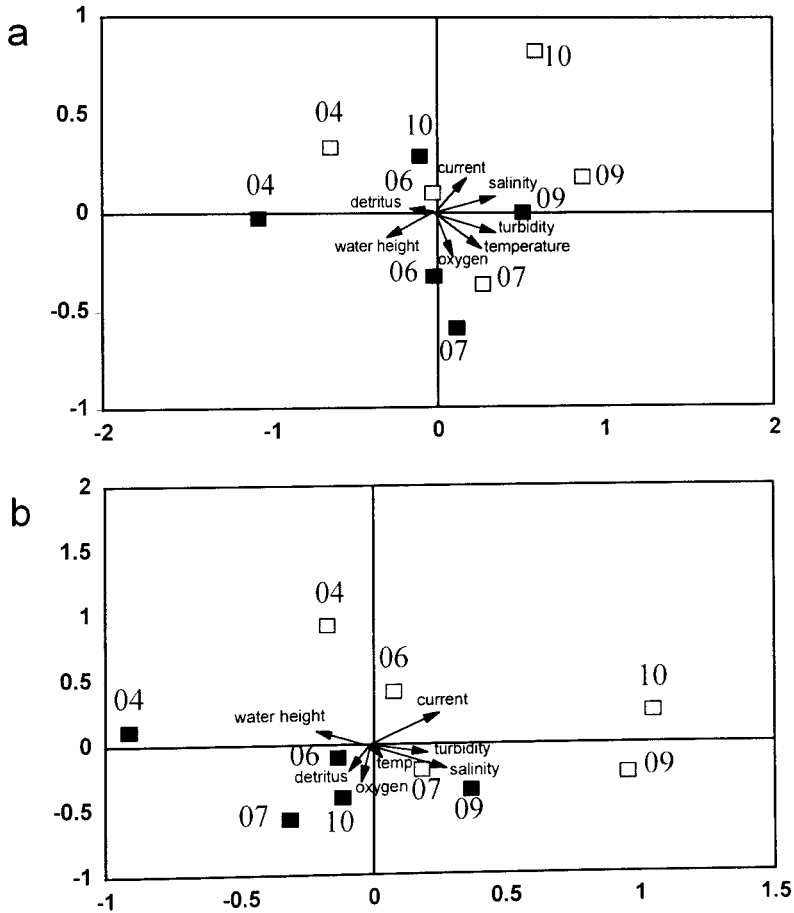
Figure 8. CCA plot using density (a) and biomass (b) data. Samples of Saeftinghe are labelled with black rectangles while those of Sieperda are indicated by grey colour.

we measured similar water depths and turbidities in both marshes, the refuge potential of both areas will be likewise.

Food availability may also cause the observed biomass and density difference between the natural and developing marsh. Craft *et al.* (1988) examined the amount of the macroorganic matter (MOM) derived mainly from *Spartina alterniflora* and *Juncus* sp. in the upper layer of the soil in natural and transplanted marshes and found significantly less MOM in the transplanted marshes. In accordance with these results, Minello and Webb (1997) documented a positive but weak relationship between sediment MOM and marsh age. Minello and Zimmerman (1992) also proved that MOM was significantly higher in natural marshes and that the MOM of the sediment correlated positively with the density of infauna and decapod crustaceans. According to Zedler *et al.* (1997) marsh detritus ends up into the tidal channels where it fuels the detritivore food chain. This finally leads to fish moving into the salt marsh to feed on marsh invertebrates. Even though Saeftinghe does not export organic material to the estuary (Hemminga *et al.*,

1993), MOM gets washed into the studied creeks. Higher amounts of MOM were present in the creek of the mature marsh, which may provide more food resources for detritivore benthic animals like *C. volutator* and this will in turn influence the occurrence and density of species in higher trophic levels.

Minello and Zimmerman (1992) found that the mean densities of amphipods were consistently lower in a transplanted marsh. *C. volutator*, a ubiquitous detritivore infauna organism in the salt marsh creeks of the Westerschelde (Cattrijsse *et al.*, 1993), occurred at lower densities in the developing marsh. A lower amount of organic matter may thus influence the occurrence of macrobenthic species in Sieperda. In September 1995 and 1996 the macrobenthos of the creek of Sieperda reached densities up to 10 400 ind. m^{-2} (Stikvoor and de Winder, 1998), which are average for intertidal areas in the Westerschelde. The macrobenthos of the creek of Saeftinghe can reach much higher densities of up to 40 000 ind. m^{-2} (Cattrijsse *et al.*, 1994).

The same mechanism can explain the higher abundance of brown shrimp in the mature marsh. Brown shrimps are

omnivores feeding on detritus, plant material and animal food (Plagmann, 1939). In Saeftinghe, they were found to prey predominantly upon organic material and infauna organisms, like *C. volutator* and the polychaete *Heteromastus filiformis* (Cattrijsse *et al.*, 1997).

Fish density in the developing marsh exceeded the fish density in the mature marsh in April and October. During the other 3 months, fish densities were higher in the mature marsh. Talley (2000) reported higher fish abundance in the natural marsh but similar species richness in the natural and created systems. Minello and Webb (1997) also found that overall fish densities were significantly higher in natural marshes, but in contrast to our results, that difference was more pronounced in spring and autumn.

Clupeidae species (*Clupea harengus* and *Sprattus sprattus*) reached peak densities in both marshes in April and June, with higher densities recorded in the developing marsh. Havens *et al.* (1995) hypothesized that the zooplankton population of a newly created marsh was higher than in a natural marsh because the creek did not dry completely, i.e. resident zooplankton did not leave. The resident zooplankton population may encourage greater use of the developing marsh by plankton feeders like the Clupeids. A similar situation may exist in the Sieperda creek, since large deep pools have been formed behind and in front of the sampling point. In this study the density of zooplankton was not measured but it may have influenced the abundance of Clupeidae larvae.

The common goby *P. microps* is a typical intertidal species and possibly plays a similar role in European marsh ecosystems to that played by *Fundulus* spp. in North American marshes. Williams and Zedler (1999) found highest mean density of *Fundulus parvipinnis* in constructed channels, while Moy and Levin (1991) observed that planted marshes appear to support considerably less juvenile *Fundulus heteroclitus* than natural marshes. Size structure of *Fundulus parvipinnis* differed between the created and the natural creeks in a California marsh, with the created marsh population being skewed towards larger size. However, these size differences were believed to arise from difference in creek morphology (Talley, 2000). During our sampling campaign, gobies occurred in higher densities and had a longer residence time in the mature marsh. The length–frequency distribution of *P. microps* shows clear differences between the two marshes. Individuals increased in size from July onwards in the mature marsh, while growth was not observed in the developing marsh where all individuals remained between 9 and 13 mm SL during the whole growing season. In European salt marshes, gobies feed predominantly on the amphipod *C. volutator* (personal observation). This may further support the hypothesis that abundance of food is the prime factor causing the observed differences between the two marshes.

The size and density differences of the nekton species may be due to inadequate food resources in created marshes (Moy and Levin, 1991). Minello and Zimmerman (1992)

suggested that transplanted marshes could function as natural marshes if just given enough time. Protection from predators in transplanted marshes may reach equivalency with natural marshes after one or two growing seasons. However, the development of man-made marshes as foraging area is probably slower. Minello and Webb (1997) expected to see a general pattern of increased nekton use with marsh age. However, there were no obvious relationships found. Their data indicate that the time required to reach functional equivalency is very long, and trends were not be observed within 15 years. In the literature, there is no evidence of a relationship between fish densities and the age of created marshes. Simenstad and Thom (1996) observed in the created Gog-Le-Hi-Te estuarine wetland that fish species richness and density approached asymptotes within 3–5 years. From the study of Dionne *et al.* (1999) in the Gulf of Maine, it appears that both created and restored marshes can be visited by fish assemblages comparable with those found in reference marshes over 1–5 year periods. Thus, rapid colonization of a new marsh habitat in high numbers seems the rule, but fish assemblages do not develop in a linear fashion through time (Williams and Zedler, 1999).

According to this study, this newly restored estuarine marsh developed some functions of a typical marsh (e.g. refuge) for estuarine nekton relatively quickly but full functional development may require more than 10 years. Creating new marshes in West Europe would allow nekton species to rapidly colonize the system regardless of the lowered potential as a feeding ground and thus as a nursery area. It seems that the creation of new marshes will only be as beneficial as a mature marsh system to the fish and crustacean populations in the medium to long term.

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