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Spatial distribution and general population characteristics of mysid shrimps in the Westerschelde estuary (SW Netherlands)

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ABSTRACT

The distribution and general population characteristics of five mysid shrimps were investigated in the period 2003–2005 in the Westerschelde estuary, a tidal temperate estuary situated along the Dutch–Belgian border. Multivariate analyses revealed that salinity predominantly governs the spatial distribution of *Neomysis integer*, *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Schistomysis spiritus* while temperature, and to a lesser extent turbidity, control the distribution of *Mesopodopsis slabberi*. *N. integer* is a resident species in the mesohaline zone of the estuary, i.e. all life stages of the species are present in the estuary throughout the year. For the first time since decades *N. integer* inhabits the oligohaline zone of the estuary supposedly as a consequence of improved oxygen conditions in the upstream reaches. *M. slabberi*, the most abundant mysid in the Westerschelde, dominates the hyperbenthos of the mesohaline zone of the estuary. The polyhaline zone of the estuary is, most abundantly inhabited by *M. slabberi*, *G. spinifer*, *S. kervillei* and to a lesser extent by *S. spiritus*. The abundance of the latter four species is low in winter, probably due to a migration towards coastal waters to avoid colder temperatures in the estuary combined with an increased mortality after breeding. The sex ratio of all the mysid populations corresponds to the expected 1:1 female:male ratio and no salinity governed segregation is found between the different life stages of each mysid population. A seasonal variation exists in brood size in the *N. integer* population regardless of the body size, with a larger number of broods during winter and spring compared to the summer. In the other mysid populations the brood sizes vary only with the length of the ovigerous females.

Our recent observations underline some general characteristics of mysid populations in the Westerschelde and provide novel insights in their life stage and sex specific population segregation, their brood sizes and the expanding upstream distribution of *N. integer*.

1. Introduction

Estuarine ecosystems rank amongst the most productive biomes of the world and serve as important life-support systems, e.g. by providing nursery and feeding habitats for fish, crustaceans and birds (Day et al., 1989; Costanza et al., 1993; Beck et al., 2001; Elliott et al., 2002). Mysid shrimps (Crustacea: Mysida) are a typical and dominant component of the estuarine hyperbenthos playing a key role in the (estuarine) food web both as consumers and as prey thereby contributing substantially to the nursery function that estuaries provide for many fish species (Mees and Jones, 1997; Hostens and Mees, 1999).

The Westerschelde, the downstream part of the Schelde estuary (Fig. 1), harbours large populations of mysids (Mees et al., 1993a,b). The hyperbenthos of the Westerschelde has been intensively studied in the 1990s revealing a clear spatial pattern, governed by salinity and limited by oxygen, as well as a temporal distribution pattern (Mees and Hamerlynck, 1992; Cattrijsse et al., 1993; Mees et al., 1993a,b, 1994, 1995). During the 1990s mysid shrimps were rarely present in the Zeeschelde, the upstream part of the Schelde estuary where salinities drop below 10. In the Eems, Gironde, Elbe and Guadalquivir, mysid shrimps do occur at these lower salinities (Mees et al., 1995; Köpcke and Kausch, 1996; Drake et al., 2002). In the Zeeschelde hyperbenthic life rapidly declined when oxygen saturation was less than 40% (Mees et al., 1994). However, water purification efforts were intensified and yearly average oxygen concentrations improved slightly by the mid-1990s (Van Damme et al., 2005). It is currently unknown whether these improving oxygen conditions resulted in an upstream mysid shrimp migration in the Zeeschelde.

Despite the well documented spatial and temporal distribution patterns, life history data from the different mysid species in the

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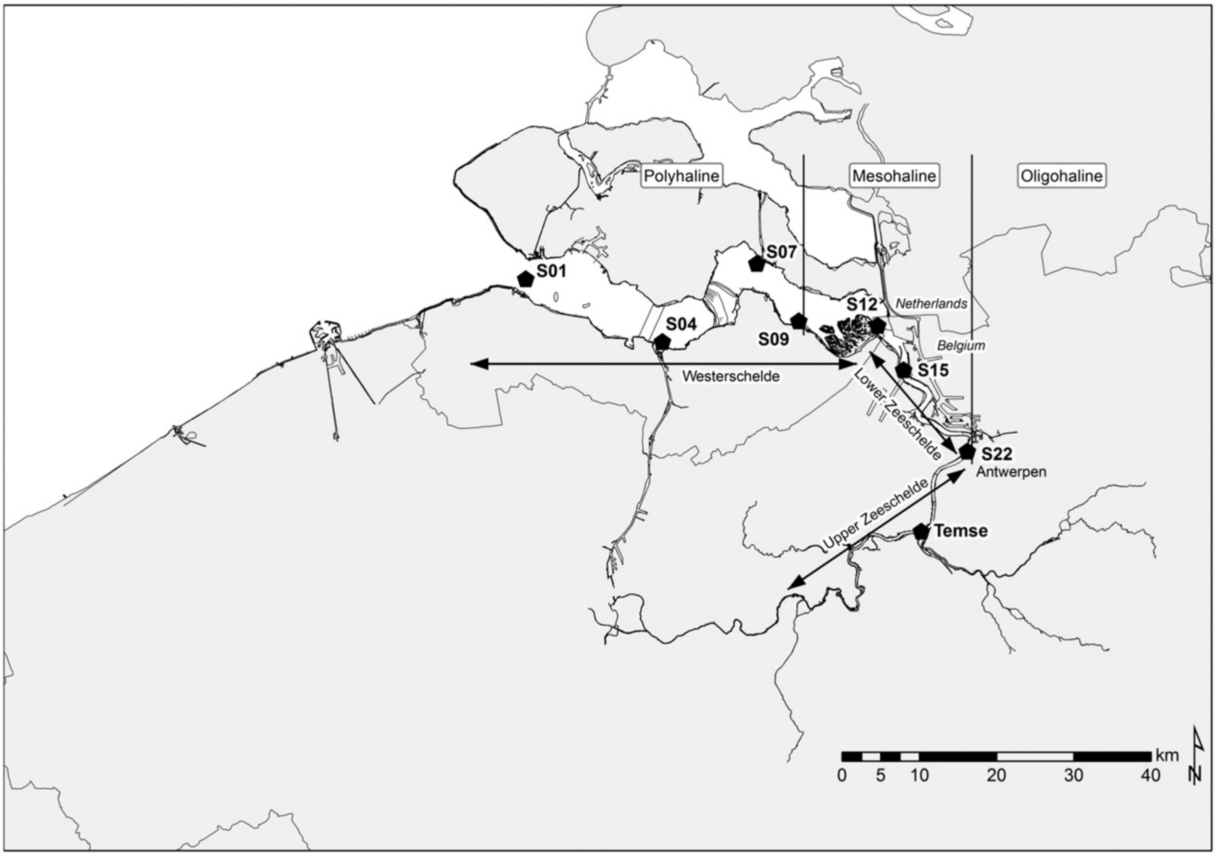

Fig. 1. Map of the Schelde estuary with location of the different sampling stations and indication of the salinity zones.

Schelde estuary are absent, except for *Neomysis integer* (Mees et al., 1994). As intra-specific distribution pattern of mysids can be linked to salinity tolerance of the respective life stages (Baldó et al., 2001; Vilas et al., 2009; Suzuki et al., 2009), fundamental knowledge is essential to interpret mysid distribution patterns thoroughly. Moreover, such knowledge can provide useful information for e.g. experimental work (Fockedey et al., 2005; Vilas et al., 2006).

In this paper, we analyze the spatial distribution and general population characteristics of the five most abundant mysid species (*Neomysis integer*, *Mesopodopsis slabberi*, *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Schistomysis spiritus*) of the Schelde estuary. Therefore, the following questions were addressed: First, what is the spatial distribution and abundance of the mysid species along the Westerschelde between March 2003 and July 2005 and what environmental factors are steering these patterns? Second, do these distributions differ among different life stages of the mysid species? Third, does the population sex ratio and the brood size of female mysids change in space and/or over time? Finally, we questioned whether improved oxygen conditions, from the mid-90s onwards, are reflected by a change in mysid distribution in the Zeeschelde.

2. Material and methods

2.1. Study area

The river Schelde is a lowland river, which takes rise in the northern part of France (St. Quentin), and flows into the North Sea near Vlissingen (The Netherlands). The middle and lower part of the Schelde estuary are called the Westerschelde. The Westerschelde is situated between the Dutch–Belgian border (km 58) and the mouth at Vlissingen (km 0) and is characterized by a complex morphology with flood and ebb channels surrounding several large intertidal flats and salt marshes (Fig. 1). More upstream, the Schelde estuary situated between the Dutch–Belgian border and Gent (Belgium) (km 160) is called the Zeeschelde; it is characterized by a single ebb/flood channel, bordered by relatively small mudflats and marshes (Meire et al., 2005).

Being a typical rain-fed river, river discharge varies seasonal with maxima during winter and minima during summer (Struyf et al., 2004). The longterm yearly averaged river discharge at Schelle (between Temse and Antwerpen) amounts to 104 m^3/s (Meire et al., 2005). Depending on the river discharge, the residence time of the water ranges between one to three months (Soetaert and Herman, 1995). The estuary is well mixed (except during peak discharges) keeping vertical salinity gradients small to negligible (Meire et al., 2005). The polyhaline zone (salinity of 18–30) ranges from S09 to the river mouth (S01). The oligohaline zone (salinity of 0.5–5) is situated roughly upwards from S22. The mesohaline zone (salinity of 5–18) is highly variable in space and time, stretching over a range of 20–40 km, and shifting according the changes in the oligohaline and the polyhaline zones. In the mesohaline zone, discharge has a maximum effect on salinity (Van Damme et al., 2005). The turbidity maximum zone is situated at about 110 km from the mouth during dry periods and at about 50 km during wet periods (Wollast, 1988). Thanks to wastewater treatment, dissolved oxygen concentrations increased during the eighties, and this improvement continued in the 1990s

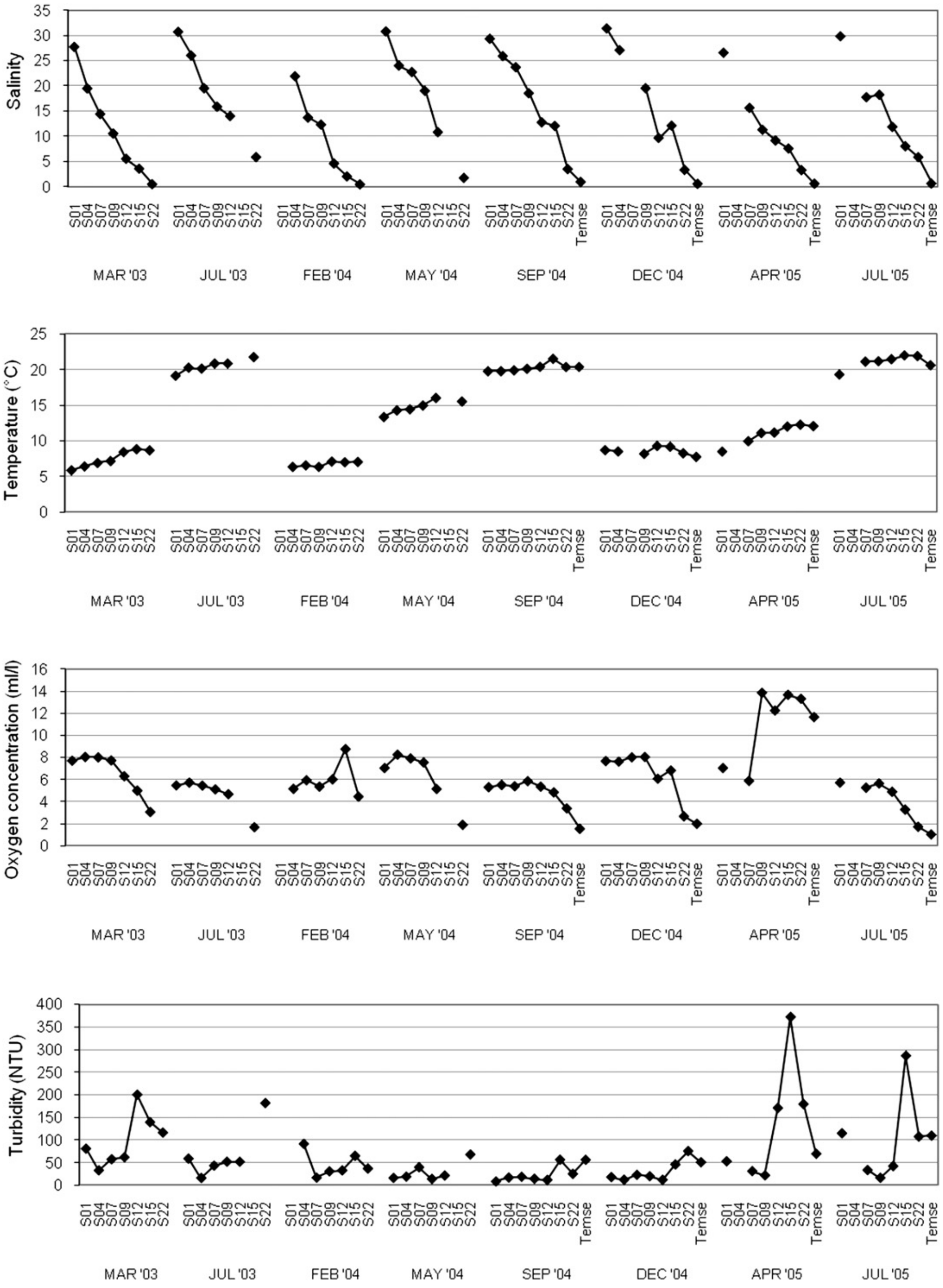

Fig. 2. Temperature (°C), salinity, oxygen concentration (ml/l) and turbidity (NTU) in the Schelde estuary at stations S01–S22 and Temse.

(Van Damme et al., 1995; Soetaert et al., 2006). However, oxygen conditions are still low in the Zeeschelde, especially during summer (Van Damme et al., 2005). Along the longitudinal axis, oxygen conditions improved considerably towards the Dutch–Belgian border, and in the Westerschelde the water column became fully oxygenated. Till 2006 an important source of pollution remained, as the city of Brussels discharged untreated wastewater through the Zenne and the Rupel in the Schelde estuary. Since 2000, a small wastewater treatment plant became operational and since 2006 a bigger one (Meire et al., 2005).

2.2. Sampling

Samples were taken at eight stations (Fig. 1) along the salinity gradient in March and July 2003, February, May, September and December 2004 and April and July 2005. Sampling was done from the RV 'Belgica' with a hyperbenthic sledge (Sorbe, 1983). All samples were taken during daytime, when hyperbenthic mysids are known to concentrate near the bottom (Mauchline, 1980). Quantitative sledge samples were taken at the stations S01, S04, S07, S09 and S12, trawling was performed in the main channel,

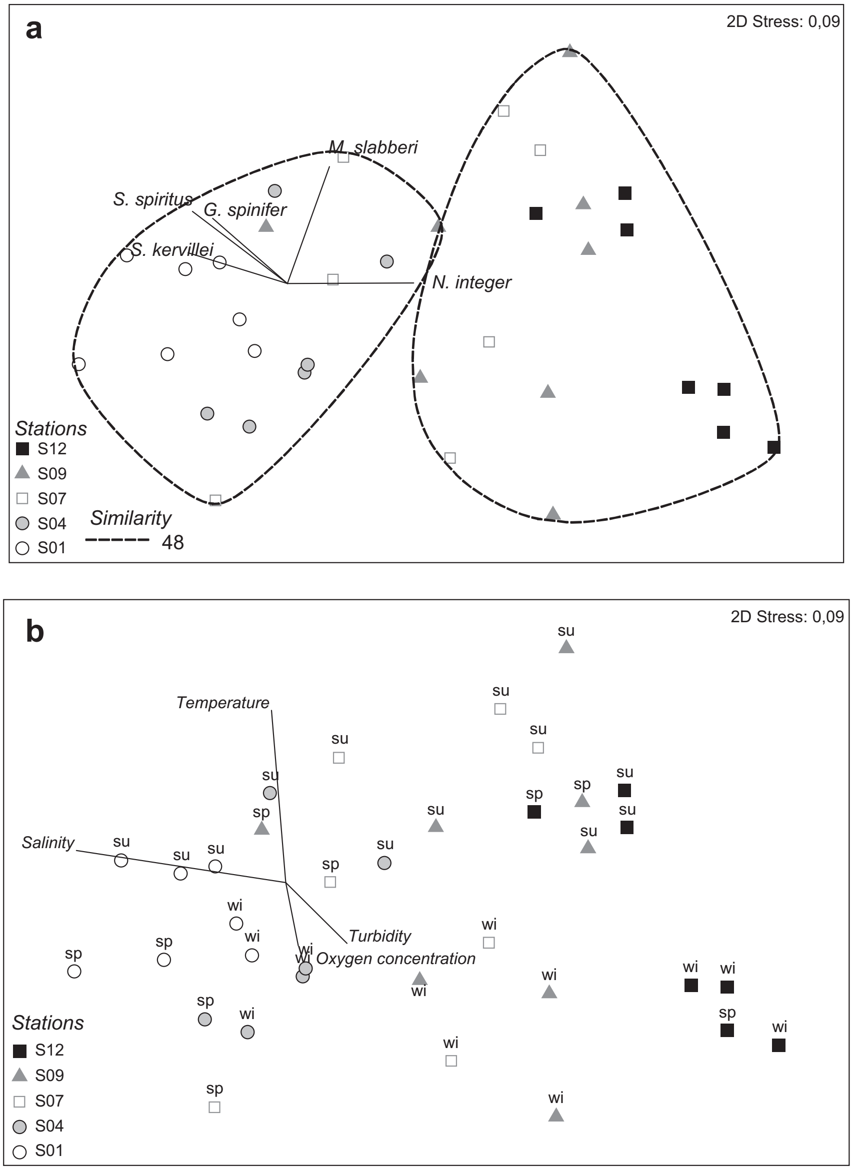

Fig. 3. Multidimensional scaling (MDS) ordination plot of the mysid species spatial (S01–S12) and temporal (spring, summer, winter) distribution, based on Bray–Curtis similarity for log $(x + 1)$ transformed mysid densities. A similarity cluster (55%) (a) and correlation vectors of temperature, oxygen concentration, turbidity and salinity are superimposed (b).

with the current over an average distance of 1000 m at an average ship speed of 4.5 knots. On the stations S15, S22 and Temse only stationary qualitative sampling was performed, as the soft mud bottom did not allow towing of the sledge. For the qualitative sampling the hyperbenthic sledge was lowered to the bottom collecting a passive sample during approximately 15 min. The samples were preserved in a buffered formaldehyde solution, 8% final concentration. At the end of each haul temperature (°C), salinity (Practical Salinity Scale), turbidity (NTU) and dissolved oxygen concentration (ml/l) were recorded 1 m above the bottom using a CTD SBE19.

2.3. Laboratory procedures

In the laboratory all mysid shrimps were sorted out, identified to species level and counted. For each sample a maximum of 1000 individuals per species were randomly selected, sexed and categorized into six life cycle stages according to Mauchline (1980): adult males, adult females, subadult males, subadult females, juveniles and gravid females.

Embryo counts (i.e. brood sizes) were made on all gravid females with a completely full marsupium, present in the subsample. The standard length (the distance from the base of the eye stalk to the end of the last abdominal segment) of gravid females was measured using a calibrated binocular microscope with drawing mirror using image software (Image J 1.42q) on resulting drawings.

2.4. Data analysis

Based on the densities of the quantitatively sampled stations, multivariate techniques were applied to assess the relationship between the environmental variables and the mysid spatial distributions (PRIMER, Clarke and Gorley, 2006). Sample groups were distinguished based on a hierarchical CLUSTER and SIMPROF analysis ($p < 0.05$) and visualized by non-metric multidimensional scaling (MDS). A factor station (S01–S12) and a factor season (spring: May ′04 & April ′05; summer: July ′03, September ′04 & July ′05; winter: December ′04, March ′03 & February ′04) were a priori defined. Environmental variables were superimposed on MDS ordination diagrams using correlation vectors in order to allow a better visualization of the relation between species densities and the environment. In addition, the relationship between mysid densities and environmental variables was investigated using the BIO-ENV procedure (BEST, Clarke and Gorley, 2006). This analysis identifies what combination of environmental factors correlates best with the observed densities. This is achieved by comparing the biotic (Bray–Curtis) similarity matrix and the Euclidian distance environmental matrix using Spearman's rank correlation coefficient (ρ). Mysid densities were fourth root transformed prior to analysis while environmental variables were square root transformed and normalized.

In order to identify the spatial variation in life stages of each mysid species, the salinity (S) value at which the population centre of mass (CM) was located was expressed according to González-Ortégon et al. (2006): $S_{CM} = \sum p_i S_i$ (p_i is the proportion of individuals collected at sampling i; S_i is the salinity at which each sample was taken). Inter-specific salinity related segregation between all the mysid species was tested by the Kruskal–Wallis test and a comparison between the species by means of the Mann–Whitney *U*-test. The overall intra-specific segregation of life stages within a mysid species was tested using the Kruskal–Wallis test. A life stage to life stage comparison was made by the Mann–Whitney *U*-test. Spearman Rank correlations were used to control whether mysid density is related to individual environmental variables (temperature, salinity, turbidity and oxygen concentration).

In addition, the sex ratio (i.e. female density/total (female + male) density) was determined and a chi-squared test was used to determine if the overall observed ratios differed from the expected 0.5 ratio. A Spearman Rank correlation was performed to verify whether sex ratio variability was related to the salinity gradient of the Westerschelde estuary.

In order to identify the relations between the brood sizes, the standard lengths of gravid females and the environmental data different analyses were performed. The mean brood size and the mean female length of each mysid species were calculated per season as well as the overall maximum recorded brood size. A Pearson R correlation coefficient was determined between brood size and salinity and between brood size and female length. To determine whether brood size varies amongst seasons, linear regressions were compared using female length as covariate. A linear regression model was only determined when the assumptions of linear regression were met: linearity, normality (Shapiro-Wilk test), homoscedasticity and independence of the errors. A large sample size allowed the statistics to follow a normal distribution (Central Limit Theorem) (Sokal and Rohlf, 1981).

3. Results

3.1. Environmental variables

Water temperature ranges from 6 °C in wintertime to 22 °C in summertime. Temperature is slightly higher towards the inner part of the estuary. Salinity increases throughout the estuary from 0.45 in the oligohaline zone (Temse) to 31.35 at the mouth (S01). Turbidity is on average 65.77 NTU with a peak of 371 NTU at S15 in April 2005. The region upstream of S12 is characterized by a higher turbidity. The dissolved oxygen concentration is on average 6.17 ml/l, with a minimum concentration of 1.05 ml/l at Temse in July 2005 and a maximum concentration of 13.86 ml/l at S09 in April 2005. In general, oxygen concentration declines from the polyhaline zone towards the oligohaline zone (Fig. 2).

3.2. Mysid communities in the Westerschelde

Neomysis integer, *Mesopodopsis slabberi*, *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Schistomysis spiritus* are the most abundant mysid species in the Westerschelde. *Praunus flexuosus* was found occasionally in the polyhaline zone in densities negligible to the abundance of the other mysids. Two individuals of *Hemimysis anomala* were encountered at S12 in February ′04. These two mysid species were not taken in account for further analyses.

Hierarchical clustering accompanied by SIMPROF analysis distinguishes two sample groups, in the distribution of mysid species along the Westerschelde, with a similarity of 48%; i.e. an S01–S04 group and an S09–S12 group, with station S07 intermediate. *Neomysis integer* is mainly distributed upstream the Westerschelde, while *Schistomysis spiritus*, *Schistomysis kervillei* and *Gastrosaccus spinifer* are found downstream. The abundance of *Mesopodopsis slabberi* is intermediate between the two groups (Fig. 3a). The superimposed environmental vectors indicate a spatial separation between the groups related to changes in salinity. Changes in temperature, oxygen concentrations and turbidity show an overall seasonal trend and determine the distribution of *M. slabberi* (Fig. 3b). The BIO-ENV procedure confirms that salinity best explains the biotic assemblage structure ($\rho = 0.67$).

The salinity at which the populations occur differs significantly among the five mysid species (Kruskal–Wallis test $p < 0.05$) (Fig. 4). The *Neomysis integer* population lives in the mesohaline zone. The *Mesopodopsis slabberi* population lives in between the mesohaline and the polyhaline zone. The salinity-based centre of mass of both populations is segregated (Mann–Whitney *U*-test $p < 0.05$) from each other and from the *Schistomysis spiritus*, *Schistomysis kervillei* and *Gastrosaccus spinifer* populations, who all occur strictly in the polyhaline zone (Mann–Whitney *U*-test $p > 0.6$). No intra-specific segregation patterns between different life stages of *N. integer*, *M. slabberi*, *S. kervillei* and *S. spiritus* are seen (Kruskal–Wallis test $p > 0.5$). In the *G. spinifer* population however, the juveniles occur in a more upstream region compared to the rest of the population (Mann–Whitney *U*-test $p < 0.05$).

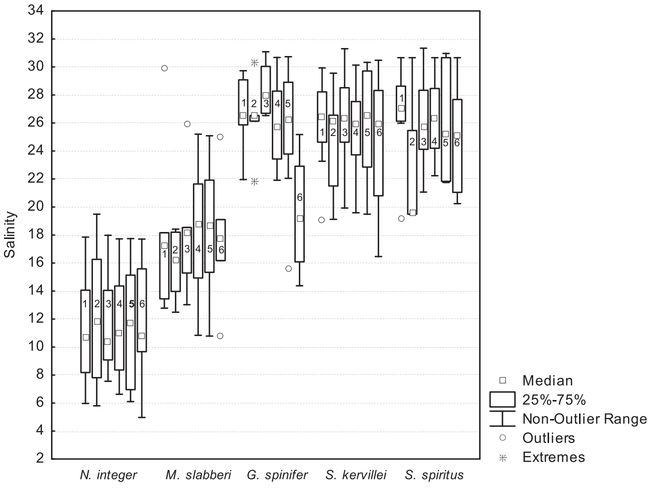

Fig. 4. Salinity values of the Westerschelde (stations S01–S12) where the centre of mass (S_{CM}) of the life stages (1: female adult, 2: female gravid, 3: male adult, 4: female subadult, 5: male subadult and 6: juvenile) of *N. integer*, *M. slabberi*, *G. spinifer*, *S. spiritus* and *S. kervillei* is situated.

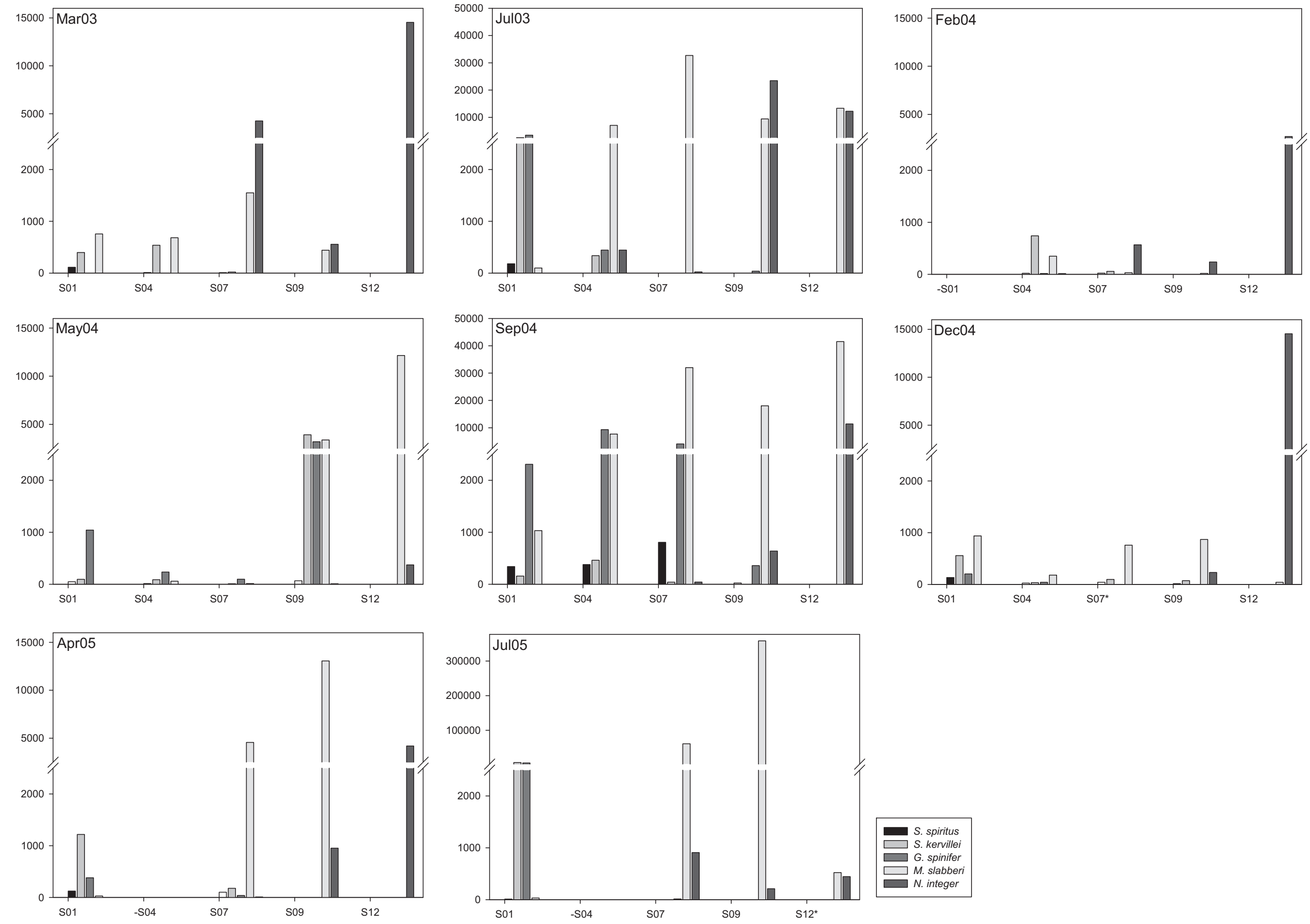

Fig. 5. Density distribution of *N. integer*, *M. slabberi*, *G. spinifer*, *S. spiritus* and *S. kervillei* along the Westerschelde estuary for each sampling date.

In general, mysid densities decrease towards the polyhaline zone (Fig. 5). *Neomysis integer* is present in the mesohaline zone of the Westerschelde throughout the year, with higher abundances in the upstream region and increasing species abundance with decreasing salinity ($R = -0.85$, $p < 0.05$). A maximum abundance of 23 432 *N. integer*/1000 m^2 was recorded in July ′03 at station S09. Occasionally quantitative samplings showed that *N. integer* reached high densities (>9000 ind/1000 m^2) at station S15 (Table 1). During additional qualitative samplings in the Zeeschelde at S15 and S22 high amounts of *N. integer* were encountered. Even in the most upstream station Temse, some individuals of *N. integer* were found (up to 28 individuals in December ′04).

Table 1
Additional quantitative and qualitative sampling for *N. integer* and *M. slabberi* at the stations S15, S22 and Temse. Not sampled is indicated by ns. As no standardized densities could be determined (except for S15 in March ′03 and February ′04) presence (+) or absence (0) are presented.

	S15		S22		Temse	
	N. integer	*M. slabberi*	*N. integer*	*M. slabberi*	*N. integer*	*M. slabberi*
Mar ′03	9209 ind/1000 m^2	0	ns	ns	ns	ns
Jul ′03	ns	ns	+	0	ns	ns
Feb ′04	11 877 ind/1000 m^2	0	0	0	ns	ns
May ′04	ns	ns	+	0	ns	ns
Sep ′04	+	+	+	0	+	0
Dec ′04	+	0	+	0	+	0
Apr ′05	+	+	+	0	0	0
Jul ′05	+	0	+	0	0	0

Mesopodopsis slabberi is present along the whole Westerschelde with higher abundances during spring and summer, especially in the mesohaline stations. A strong positive relation exists between *M. slabberi* density and temperature ($R = 0.66$; $p < 0.05$). While less strong correlations exist with turbidity and oxygen (resp. $R = -0.36$, $R = -0.42$; $p < 0.05$). A maximum of 358 122 *M. slabberi*/1000 m^2 was recorded in July ′05 at S09. During additional qualitative samplings in the Zeeschelde *M. slabberi* was only recorded twice at station S15; in September ′04 in a high amount while in April ′05 only a few specimens were found.

Gastrosaccus spinifer has a preference for the most polyhaline stations (i.e. stations S01 and S04) and reaches high densities during summer (maximum of 9344 ind/1000 m^2 at S04 in September ′04). *Schistomysis kervillei* occurs in the polyhaline zone with higher abundances during summer (maximum of 7035 ind/1000 m^2 in July ′05). Densities of *Schistomysis spiritus* are low throughout the year in the polyhaline zone except for an abundance peak in September ′04 of 806 ind/1000 m^2 at S07. The densities of *G. spinifer*, *S. kervillei* and *S. spiritus* are all positively correlated with salinity (resp. $R = 0.77$, $R = 0.77$, $R = 0.83$; $p < 0.05$).

3.3. Mysid sex ratio and brood sizes

An equilibrium exists between the number of females and males in all the mysid populations as the female/(female + male) sex ratio

Table 2
Female/(female + male) sex ratios for *N. integer*, *M. slabberi*, *G. spinifer*, *S. spiritus* and *S. kervillei* with chi-squared test values, non significant (ns) if $p > 0.05$.

	Sex ratio ± SE	χ^2	p
N. integer	0.47 ± 0.05	3.08	ns
M. slabberi	0.56 ± 0.02	1.30	ns
G. spinifer	0.59 ± 0.05	2.24	ns
S. kervillei	0.62 ± 0.04	2.07	ns
S. spiritus	0.54 ± 0.05	2.01	ns

does not differ significantly from the expected 0.5 ratio (Table 2). A shift in sex ratio along the salinity gradient of the Westerschelde estuary is not observed in the populations of *Neomysis integer*, *Mesopodopsis slabberi*, *Gastrosaccus spinifer* and *Schistomysis spiritus* (Spearman rank correlation $p > 0.05$). The *Schistomysis kervillei* population tends to have a decreasing proportion of females with increasing salinity (Spearman Rank correlation $R = -0.67$, $p < 0.05$), although no significant differences are seen in the salinity related distribution of the separated life stages (Fig. 4).

Table 3 shows a conspicuous seasonal variation in the mean brood sizes and the mean female lengths for all mysid species. Gravid *Neomysis integer*, *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Schistomysis spiritus* are smaller and attain a smaller brood size during summer compared to spring and/or winter. In contrary, gravid *Mesopodopsis slabberi* attain, on average, the smallest brood size during winter. Overall, a significant strong correlation exists between brood size and female length for all mysid species (Pearson's R: 0.58–0.83, $p < 0.05$). Linear regressions indicate significant relationships between brood size and female length in all seasons for *N. integer*, in spring and summer for *M. slabberi* and *S. kervillei* and only in summer for *G. spinifer* and *S. spiritus*. The only significant seasonal variation in brood sizes is recorded for *N. integer* with smaller brood sizes in summer compared to spring and winter. The brood sizes of *N. integer* and *S. kervillei* are negatively correlated with salinity (Pearson's R -0.41 and -0.20, $p < 0.05$). No significant correlation exists for the other mysid species (Fig. 6).

4. Discussion

4.1. Spatial distribution of mysid species and their life stages

Neomysis integer, an euryhaline and eurythermic brackish water mysid (Tattersall and Tattersall, 1951), is a resident species of the Schelde estuary. It is present in the estuary throughout the year at salinities ranging from 0.6 to 27, with the majority of the population in the mesohaline part (at salinities below 16). This distribution corresponds with the salinity range (3–32) at which adult *N. integer* have a strong osmoregulatory capability (Vilas et al., 2006). The presence of *N. integer* in the oligohaline zone is remarkable. Particular the occurrence at Temse in September 2004 at a salinity of 0.95 constitutes the most upstream recording since decades in the Zeeschelde. Leloup and Konietzko (1956) described that *N. integer* occurred until S22. In contrast, the lacustrine limit of the *N. integer* population was in the 1990s only a few kilometres upstream situated from S12 (Mees et al., 1993a). The absence of mysids upstream the Dutch–Belgian border resulted from a very poor water quality. High allochtonous organic matter and nutrient inputs in the upper estuary enhanced microbial respiration and associated oxygen depletion (Baeyens et al., 1998). This study shows that the zone of oxygen depletion moved 20 km upstream; i.e. oxygen concentrations below 4 ml/l and oxygen concentrations around 30% are now found at S22 and Temse. *N. integer* thus appears to be quite tolerant to low oxygen concentrations. Moreover, the current distribution of *N. integer* in the Schelde estuary is no longer determined by dissolved oxygen concentration (Mees et al., 1995), but primarily related to changes in salinity. This distribution of *N. integer* towards the oligohaline zone corroborates the generally described salinity occurrence of *N. integer*, in nearly freshwater (Elbe estuary: Bernát et al., 1994; Köpcke and Kausch, 1996; Gironde estuary: Castel, 1993; David et al., 2005; Guadalquivir estuary: Vilas et al., 2009). Depending on the estuary, various environmental factors govern the abundance of *N. integer*. In the Elbe estuary suspended particulate matter (SPM) and to a lesser extend salinity (Bernát et al., 1994) or current velocity and SPM (Köpcke and Kausch, 1996) determine the abundance, in the Gironde estuary abundance of prey was found most important (Castel, 1993; David et al., 2005). A similar shift, towards more saline waters, was observed for *N. integer* in the Guadalquivir estuary during unusual high and persistent turbidity events. This salinity related shift was not accompanied by a reduction in density (González-Ortégon et al., 2010).

The *Neomysis integer* densities recorded in this study are lower than those recorded by Mees et al. (1994, 1995) in the mesohaline zone of the Westerschelde in spring and summer of 1991 (>100 000 ind/1000 m^2). These high densities were possibly caused by a spatial compression of the population between critically low oxygen concentrations and competition with species typical for higher salinities on the seaward side. Since the oxygen rich zone has nowadays expanded, the absence of such spatial compression may explain the lower *N. integer* densities observed, as is also the case for its prey *Eurytemora affinis* (Appeltans et al., 2003). Nonetheless, variability, due to the swarming behaviour of mysids might bias our findings.

The life stages or sexes of *Neomysis integer* do not live segregated along the Westerschelde. This corroborates Mauchline (1971) and Vilas et al. (2009) who also described an equilibrium between the number of males and females in a *N. integer* population. However, Vilas et al. (2009) reported a life stage dependent spatial pattern for this species in the Guadalquivir estuary. Adult *N. integer* moved together with the water mass along the estuary to remain in a constant salinity zone, while juveniles (subadults and juveniles) maintained their position in the same part of the estuary. Hough and Naylor (1992) on the other hand reported ovigerous *N. integer* to occur further up an estuary compared to other adults.

Mesopodopsis slabberi, an euryhaline species (Tattersall and Tattersall, 1951), is nowadays the most abundant mysid of the Westerschelde. It is distributed between salinities of 8 and 31 and

Table 3
Seasonal difference in average body length and brood size of ovigerous females for all mysid shrimps along the Schelde estuary (S01 – Temse).

	Spring		Summer		Winter		Brood size
	Brood size ± SE	Fem. length ± SE	Brood size ± SE	Fem. length ± SE	Brood size ± SE	Fem. length ± SE	Max
N. integer	44.37 ± 1.25	14.28 ± 0.13	13.03 ± 0.31	9.99 ± 0.07	35.10 ± 0.85	14.77 ± 0.10	88
M. slabberi	13.34 ± 0.43	10.74 ± 0.07	8.53 ± 0.18	8.40 ± 0.06	5.57 ± 0.64	8.39 ± 0.14	29
G. spinifer	96.45 ± 5.93	16.67 ± 0.31	42.65 ± 1.43	11.57 ± 0.12	–	–	162
S. kervillei	25.45 ± 1.00	12.52 ± 0.14	16.04 ± 0.06	9.99 ± 0.09	19.12 ± 2.11	11.71 ± 0.24	44
S. spiritus	17.38 ± 2.84	12.24 ± 0.45	6.09 ± 0.35	8.79 ± 0.16	–	–	34

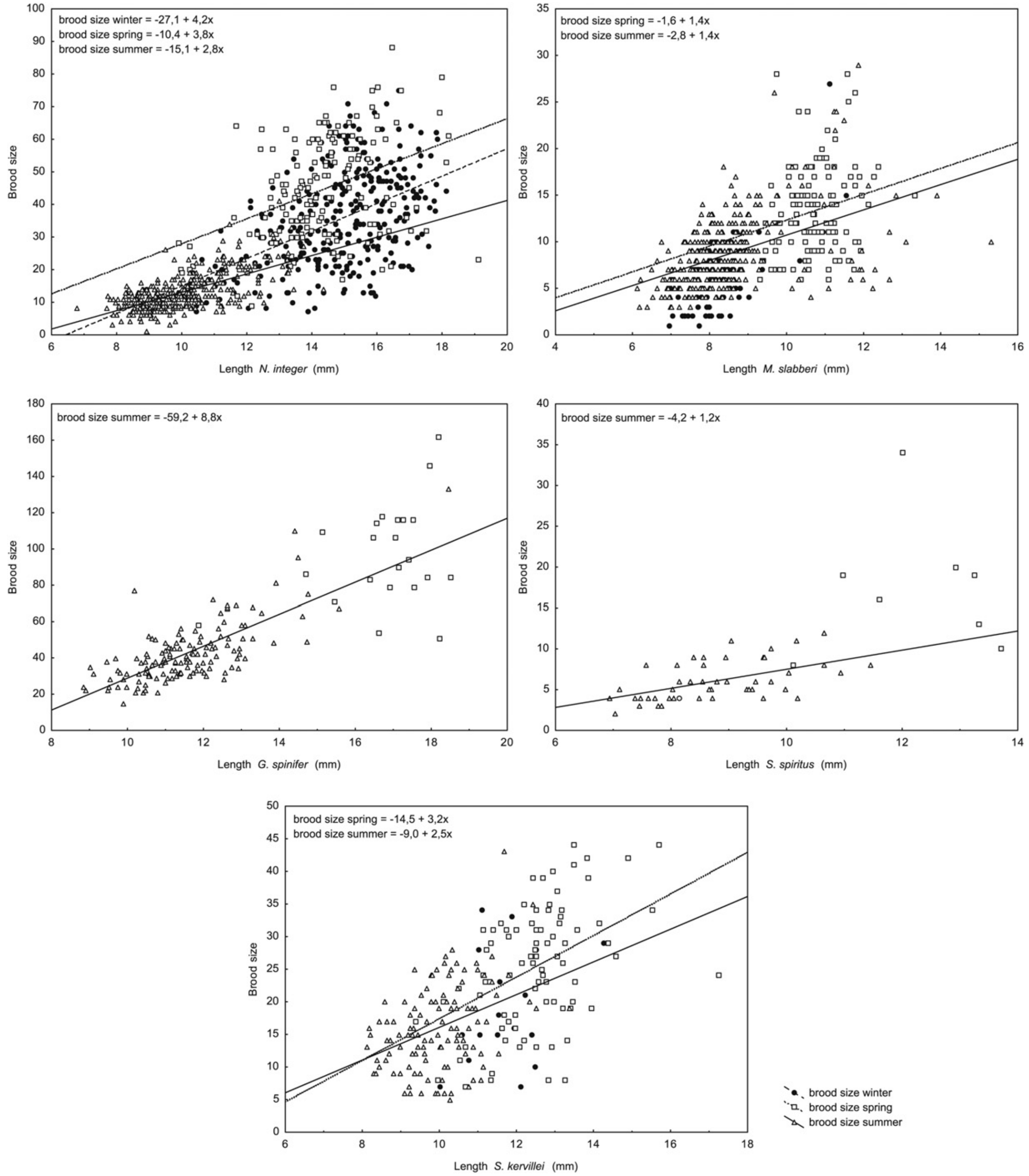

Fig. 6. The brood size of five mysid species in relation to the standard length (mm) of the gravid female; Schelde estuary (S01-Temse).

most ubiquitous in the mesohaline zone. The species is not observed upstream S15, whereas Leloup and Konietzko (1956) recorded *M. slabberi* up to S22. In the Guadalquivir estuary *M. slabberi* was found in a salinity range determined by their osmoregulation capabilities. Adults are strong hyper and hypo-regulators at salinities between 7 and 29 and show higher oxygen consumptions at the low salinity of 6 (Vilas et al., 2006). The abundance of *M. slabberi* along the Westerschelde is primarily positively correlated with temperature, probably due to the temporal distribution pattern. Secondary turbidity negatively steers the *M. slabberi* abundances, although no extreme high turbidity values were recorded. González-Ortégon et al. (2010) found in the Guadalquivir a significant decrease in the number of *M. slabberi* during high and persistent turbidity events (up to 713 NTU) whereas under normal conditions the distribution was primarily determined by salinity (Fernández-Delgado et al., 2007). In the Gironde salinity determines the distribution of *M. slabberi* (Castel, 1993; David et al., 2005).

No intra-specific differences in distribution of life stages along a salinity gradient are found for *Mesopodopsis slabberi* and females do not outnumber males along the salinity gradient. Vilas et al. (2006, 2009) neither found a significant difference between sexes along resp. their spatial distribution or the salinity gradient. They did observe that as salinity increased individuals moved upstream to maintain their positions along the salinity gradient. Contrary, in the Tamar estuary adult *M. slabberi* preferred salinities below

10 whereas juveniles and subadults occurred in a wider area with a higher salinity (Moffat and Jones, 1993).

Though *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Schistomysis spiritus* are defined as euryhaline and eurythermic species (Tattersall and Tattersall, 1951) their distribution along the Schelde estuary is restricted to the polyhaline zone. Their abundance in the Westerschelde is governed by salinity. The *Mesopodopsis slabberi*, *G. spinifer*, *S. kervillei* and *S. spiritus* populations all attain low densities during winter, while their densities increase from spring onwards to reach highest values in summer. The seasonal abundances appear to be controlled by changes in water temperature. The low numbers of mysids found in winter are often attributed to a migration from shallow coastal to deeper offshore waters to avoid colder temperatures (Beyst et al., 2001). Van Der Baan and Holthuis (1971) suggested this migration behaviour for *M. slabberi*, *G. spinifer* and *S. kervillei* since these species displayed winter maxima in their offshore sampling station in the southern North Sea. Mees et al. (1993a) claimed that the winter minimum in *M. slabberi* abundance is probably a combination of natural mortality and active emigration and that the summer–autumn maxima of *M. slabberi* in the eastern part of the estuary are due to the combined effect of active immigration into the estuary and reproduction. Collins and Williams (1982) described this pattern as well as they considered *M. slabberi* and *S. spiritus* to belong to a more euryhaline-marine community in winter and to an estuarine-marine community in summer. Mauchline (1967) mentioned for *S. spiritus* lower winter–early spring densities and allocated it as well to an emigration to deeper water during winter.

The temporal pattern and the recorded densities of *Mesopodopsis slabberi* are in close accordance with the observations of Mees et al. (1993a,b) for the Westerschelde and of Moffat and Jones (1993) for the Tamar estuary. Azeiteiro et al. (1999) on the other hand found in the Mondego estuary that *M. slabberi* was absent during winter and summer, but peaking in autumn and in spring.

The *Gastrosaccus spinifer* densities, found in this study, are comparable to the maximal densities reported by Mees et al. (1995) in the Westerschelde. On the other hand Mees et al. (1993a) found a lower average number, i.e. <100 ind/1000 m^2. The burying character of *G. spinifer* may cause this variability in densities since the species is known to bury itself in the sediment during daylight and to emerge at night into the pelagic environment. This makes a quantitative sampling of *G. spinifer* quiet difficult during daylight (Mauchline, 1980). Mees et al. (1993a) also report the year round presence of *Schistomysis kervillei* in the western part of the estuary, but in low densities during summer and with peak abundances of 650 ind/1000 m^2 in January and early March. In the same study Mees et al. (1993a) recorded the absence of *Schistomysis spiritus* from the estuary during the summer months. The species enters the polyhaline zone again in low numbers in the winter period to reach maximal abundance in spring. The temporal pattern of *S. kervillei* and *S. spiritus* recorded in this study are opposite to the observation of Mees et al. (1993a). The overall low densities found for *S. spiritus* are probably due to its rather marine than estuarine character. Dewicke et al. (2003) and Beyst et al. (2001) confirm this suggestion as they found that *S. spiritus* and *S. kervillei* are the dominant mysids in the hyperbenthos of the Belgian coastal and sandy beach surf zone, respectively.

No intra-specific differences in distribution of life stages along a salinity gradient are found for *Schistomysis kervillei* and *Schistomysis spiritus*. In the *Gastrosaccus spinifer* population, the juveniles occur at lower salinities compared to the other life stages. This is probably due to a coincidental higher input of juveniles at moments of higher river discharge and thus decreased salinities. Mauchline (1980) mentions that sex ratios within mysid populations are variable and that females frequently outnumber males. The ratio found in this study varies slightly between samples and seasons, but overall all mysid populations in the Schelde estuary correspond to the supposed 1:1 ratio. An equilibrium is not found in all mysid populations, e.g. in the Guadalquivir estuary a partial segregation by sex along the salinity gradient exists in the *Rhopalophthalmus mediterraneus* population (Baldó et al., 2001); while in a tropical mangrove estuary, female *Mesopodopsis orientalis* predominate the males (Hanamura et al., 2008).

4.2. Brood size

The brood sizes found in this study are similar to field observations described in literature (*Neomysis integer*: Mauchline, 1973; Mees et al., 1994; *Mesopodopsis slabberi*: Macquart-Moulin, 1965; Delgado et al., 1997; *Gastrosaccus spinifer*: Mauchline, 1973, *Schistomysis kervillei*: Mauchline, 1973; San Vicente and Sorbe, 1990; *Schistomysis spiritus*: Mauchline, 1973; San Vicente and Sorbe, 1995) and the recorded strong positive correlation between the length of gravid females and their brood size is a general mysid characteristic (Mauchline, 1980). Looking at seasonal differences between brood size and female length, firm conclusions can only be made for *N. integer*. Regardless of the body size, gravid *N. integer* have a larger brood size during winter and spring as compared to summer. This contradicts previous research (Mees et al., 1994) which demonstrated that the reproduction of *N. integer* halted completely at temperatures below 10 °C. In this study gravid *N. integer* are recorded throughout winter even at temperatures below 10 °C which illustrates that *N. integer* is a resident species of the estuary. In contrast, gravid females of the other mysid species are less abundant (*M. slabberi*, *S. kervillei*) or absent (*G. spinifer*, *S. spiritus*) from the estuary during winter, probably because of the assumed migration towards deeper coastal waters where temperature is more favorable or the mortality after breeding.

The winter brood sizes of *Mesopodopsis slabberi*, all recorded by the end of the season (March 2003), are relative small. As adult individuals are virtually absent from the winter population, the recorded brood sizes probably derived from female subadults who just transformed into gravid females which explains the small brood size.

In laboratory experiments, Fockedey et al. (2005, 2006) assessed that sexual maturation of *Neomysis integer* is only possible between a salinity of 5–15 and a temperature of 15–25 °C while the optimal salinity for in vitro embryonic/larval development is 14–17 under low temperature (<15 °C). Consequently, living at lower or higher salinities implies suboptimal conditions for the juvenile recruitment to the *N. integer* population. This study shows that gravid *N. integer* are most abundantly present at salinities between 2 and 16; i.e. in the zone of optimal maturation. However, this study also shows that gravid females occur in the field from 7 °C onwards, which is a suboptimal temperature for maturation according to Fockedey et al. (2005). Moreover, in this study a negative correlation is shown between salinity and brood size, demonstrated by larger brood sizes at salinities below 12; i.e. according to the lab experiment a suboptimal condition for in vitro embryonic development according to Fockedey et al. (2006). These results suggest that gravid *N. integer* in the field are more tolerant to varying salinities and temperatures than in lab conditions or that others factors play a role such as competition, food availability, turbidity, etc.

5. Conclusions

Salinity primarily determines the spatial distribution of *Neomysis integer*, *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Schistomysis* *spiritus* along the Westerschelde estuary. The spatial distribution of *Mesopodopsis slabberi* is determined by temperature and turbidity. In the past the spatial distribution of *N. integer* in the upstream reaches was determined by limited oxygen concentrations (Mees et al., 1995). Today, however, the population occurs again in the oligohaline zone, an indication of a better oxygenation in this region.

Mesopodopsis slabberi outnumbers *Neomysis integer* in the Westerschelde estuary but *N. integer* is the only resident mysid species. The more marine populations of *M. slabberi*, *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Schistomysis spiritus* attain lower densities during winter probably due to a migration towards deeper coastal waters where temperature is more favorable, while from spring onwards their densities in the estuary increase. Within the mysid populations of the Westerschelde a female–male balance exists and no apparent life stage segregation occurs. The resident mysid *N. integer* reproduces throughout the year. Female *N. integer* produce, at the same body size, during winter and spring a higher number of larvae per brood than during summer. The other mysid species exhibit a simple correlation between body size and brood size, no seasonal effects are measured. No aberrant brood sizes are found.

This study supplies some general characteristics of the mysid populations of the Westerschelde and shows that characteristics of mysid populations of different estuaries might vary and can be influenced by various environmental variables. The continuation of mysid population research in the Schelde estuary is necessary to follow their responses to the improving oxygen condition as well as to the presence of pollutants.

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