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The North-American amphipods, *Melita nitida* Smith, 1873 and *Incisocalliope aestuarius* (Watling and Maurer, 1973) (Crustacea: Amphipoda: Gammaridea), introduced to the Western Scheldt estuary (The Netherlands)

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Abstract

The American amphipod species *Melita nitida* and *Incisocalliope aestuarius* have been found in the Western Scheldt estuary (the Netherlands). This is the first record of these species in the north-east Atlantic. Shipping is the most likely vector of introduction. The distribution of both species is investigated and compared with the distribution and the microhabitat of co-occurring amphipod species. *Melita nitida* is known from both the east and west coast of North America and *I. aestuarius* originates from the east coast of North America. Until now neither has been reported from other parts of the world. In the Netherlands both species are restricted to the mesohaline part of the Western Scheldt. *Melita nitida* occurs predominantly under Pacific oysters at the underside of boulders, mainly sublittorally. *Incisocalliope aestuarius* is associated to hydrozoans. Both microhabitats are hardly utilized by other amphipod species. Therefore, the theory that the existence of many empty niches in north-western European brackish waters make this environment particularly susceptible to invasions of alien species is corroborated. The application of hard substrates in a region originally predominated by soft bottoms moreover facilitates the introduction of exotic species. The species community on hard substrates in the mesohaline part of the Western Scheldt contains a high proportion of introduced species: approximately one third of the macrofauna species is of allochthonous origin.

Introduction

The Western Scheldt is an estuary in the south-western part of the Netherlands. It is a busy shipping route connecting the port of Antwerp and the North Sea. To improve the accessibility of Antwerp for high-tonnage shipping, frequent dredging occurs, especially in the upstream part of the estuary. At some localities deep channels run close to the shoreline. At these sites boulders have been applied to the landward side of the channels in order to prevent erosion. The development of the fauna on these artificial hard substrates has been investigated (van Moorsel and Waardenburg 1999a; van Moorsel 2000). During this investigation two allochthonous gammaridean amphipod species were discovered. Subsequently, the distribution of both species was investigated. They were only found in the eastern part of the Western Scheldt, ranging from Baarland to the Dutch-Belgian border, i.e. approximately 30 to 60 km from the mouth of the estuary.

Materials & methods

Description of the study area. The eastern part of the Western Scheldt has a typical estuarine character, with a lowered and strongly fluctuating salinity, a high turbidity and strong temperature fluctuations. The bottom consists of mainly soft sediments, except near the shore, where dykes, groynes and boulder slopes in near-shore channels protect the coastline. Salinity ranges from approximately 9 to 31‰ near

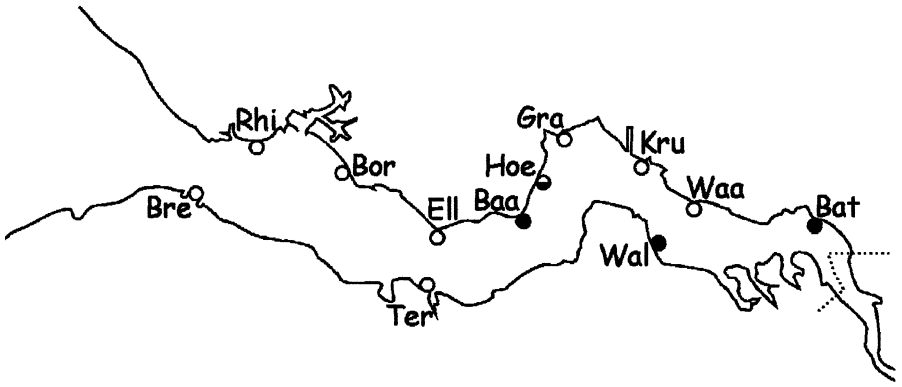

Figure 1. Western Scheldt estuary (The Netherlands) with localities investigated: Bre = Breskens, Rhi = Rhittem, Bor = Borssele, Ter = Terneuzen, Ell = Ellewoutsdijk, Baa = Baarland, Hoe = Hoedekenskerke, Gra ='s Gravenpolder, Kru = Kruiningen, Wal = Walsoorden, Waa = Waarde, Bat = Bath. Closed dots: both *Melita nitida* and *Incisocalliope aestuarius* collected, half-closed dot: *Incisocalliope aestuarius* collected, open dots: neither of these species collected.

Baarland and from less than 1 to approximately 13‰ near the Dutch-Belgian border and it is predominantly influenced by river discharge and to a lesser extent by the tides (Wolff 1973; Baeyens et al. 1998). The amount of mud in suspension ranges from approximately 20 to more than 200 $mg.l^{-1}$ (dry weight) (Wolff 1973; Baeyens et al. 1998). Water temperature fluctuates from 0–20 °C (Wolff 1973).

From 1998 to 2000, amphipods were collected at twelve localities in the Western Scheldt (Figure 1). These localities are more or less equally distributed along the length of the estuary. One locality in the mesohaline part of the Nieuwe Waterweg near Rozenburg, some 50 kilometres north of the Western Scheldt, was investigated as well. The Nieuwe Waterweg is a part of the estuary of the rivers Rhine and Meuse, connecting the port of Rotterdam and the North Sea.

At all sites littoral boulders (diameter 10–50 cm) were visually inspected during low tide. Wherever present, boulders were selected in three zones, i.e. high littoral, mediolittoral and lower littoral. Near Bath and near Walsoorden boulders were taken from the sublittoral zone by SCUBA-diving as well (van Moorsel and Waardenburg 1999a; van Moorsel 2000). Living Pacific oysters (*Crassostrea gigas* Thunberg, 1793), and empty valves on boulders were dislodged. All living macrofauna organisms were recorded and samples of amphipods were taken for later identification. Samples were taken of algae and invertebrates (Hydrozoa, Ascidiacea) for later extraction of amphipods. The shallow sublittoral, down to a depth of approximately 1 m below the low water mark, was sampled by scraping with a hand net. No attempts were made to estimate amphipod densities quantitatively.

Results

In the Western Scheldt 18 amphipod species were collected (Table 1). To the knowledge of the authors, two of these 18 species, *viz. Melita nitida* and *Incisocalliope aestuarius*, have not been reported from the north-east Atlantic before. Both species seem to be restricted to the mesohaline part of the Western Scheldt estuary. In the Nieuwe Waterweg, only three amphipod species were collected *viz.* the native species *Apocorophium lacustre* and *Gammarus salinus* and the North-American species *Gammarus tigrinus*. The latter species was first observed in the Netherlands in 1964 and spread rapidly since then (Pinkster et al. 1992).

Melita nitida was first found in the Western Scheldt on 13/10/98 near Bath and has been reported by van Moorsel and Waardenburg (1999a) as *Melita* sp. The species was already abundant near Bath in 1998. In 1999 one specimen was collected near Walsoorden and in 2000 an additional specimen near Baarland.

Melita nitida was collected predominantly under boulders near the low-water mark of spring tides and below. The highest numbers were found in the crevices under oysters at the underside of boulders.

Two free-living amphipod species, *viz. Gammarus salinus* and *Melita palmata*, co-occur with *M. nitida*. *Gammarus salinus* is a more robust species of larger

Table 1. Amphipod species collected in the Western Scheldt and the Nieuwe Waterweg (The Netherlands) in 1998–2000. Abundance classes: +++ abundant, ++ common, + rare. Localities (abbreviations as in Figure 1) arranged from west to east, i.e. according to decreasing salinity. Rozenburg (Roz) is the only locality in the Nieuwe Waterweg. Species tentatively arranged from relatively stenohaline marine species to more euryhaline and brackish water species.

Localities	Bre	Rhi	Bor	Ter	Ell	Baa	Hoe	Gra	Kru	Wal	Waa	Bat	Roz
Species													
Gammarellus angulosus		+											
Apherusa jurinei		+++											
Dexamine thea		+											
Jassa herdmani	+												
Caprella linearis			+				+						
Jassa marmorata	+					+	+						
Gammarus crinicornis							+						
Hyale nilssoni		+	+										
Melita palmata		++	+	+++	+	++	++	++	+	+++		+++	
Monocorophium insidiosum		+			+		+			+++			
Corophium volutator						+				++		+	
Echinogammarus marinus										++		+++	
Orchestia gammarellus												+	
Gammarus salinus								++		+		+++	++
Incisocalliope aestuarius						++	++			+		+	
Melita nitida						+				+		+++	
Gammarus zaddachi											+		
Gammarus tigrinus													+
Apocorophium lacustre												+	+

size. *Melita palmata* is a native congener of *M. nitida* of similar size and shape.

Incisocalliope aestuarius was first found on 02/09/99, also near Bath, and has been reported by Faasse and van Moorsel (2000) as *Parapleustes* sp. It has been collected at four sites, *viz.* Bath, Walsoorden, Baarland and Hoedekenskerke. During our investigations *Incisocalliope aestuarius* was first found among boulders collected in the sublittoral zone, at a depth of 5.0–9.5 m below the low-water mark (van Moorsel 2000). During the subsequent investigation of the intertidal zone at several localities in the Western Scheldt all *in situ* observations were made in small muddy pools under boulders just above the low-water mark. Here this species was always observed in association with hydrozoans. Collecting hydrozoan colonies near the low-water mark proved to be a successful means of obtaining specimens of *I. aestuarius.* The amphipod was most frequently collected with the hydrozoan *Hartlaubella gelatinosa* (Pallas, 1766). In the eastern part of the Western Scheldt this hydrozoan grows almost exclusively on Pacific oysters. The colour pattern of *I. aestuarius*, which consists of dark brown and creamy light brown streaks and blotches, makes it very difficult to discern the amphipods among the branches of the hydrozoan colonies. The amphipods cling forcefully to the hydrozoan and are reluctant to leave it. Their typical escape reaction is to crawl to the centre of the colony.

Near Walsoorden *Incisocalliope aestuarius* was collected from hydrozoans in a tidal channel, but it was not found on hydrozoans in the harbour.

At Hoedekenskerke a few specimens of the amphipods *Caprella linearis*, *Monocorophium insidiosum* and *Jassa marmorata* and one specimen of *Gammarus crinicornis* were collected together with *I. aestuarius* on the hydrozoan *H. gelatinosa*.

Table 2 lists zones and substrates of all amphipod species collected in the Western Scheldt. *Orchestia gammarellus* was collected only in the upper littoral zone, where *M. nitida* and *I. aestuarius* were never collected. *Corophium volutator* is known as a species of soft substrates. However, when boulders are present on a soft substrate, this species often makes its burrows at the interface of boulders and soft substrate and is thus collected from hard substrates as well. On hydrozoans and ascidians on floats in the

Table 2. Information on the habitat of the amphipod species collected. Data on salinity preference supplemented with data from den Hartog (1963, 1964) and Stock (1952).

Species	Salinity				Zonation				Substrate				
	S	P	M	O	H	M	L	S	B	I	T	A	H
Gammarellus angulosus (Rathke, 1843)	+						+		+			+	
Arherusa jurinei (Milne-Edwards, 1830)	+						+	+	+			+	
Dexamine thea Boeck, 1861	+							+				+	
Jassa herdmani (Walker, 1893)	+							+				+	
Caprella linearis (L., 1767)	+	+						+				+	+
Jassa marmorata Holmes, 1903	+	+						+	+			+	+
Gammarus crinicornis Stock, 1966	+	+						+					+
Hyale nilssoni (Rathke, 1843)	+	+	+		+	+			+			+	
Melita palmata Montagu, 1804	+	+	+		+	+	+	+	+				
Monocorophium insidiosum (Crawford, 1937)	+	+	+					+	+		+		+
Corophium volutator (Pallas, 1766)	+	+	+			+	+			+			
Echinogammarus marinus (Leach, 1815)	+	+	+			+			+				
Orchestia gammarellus (Pallas, 1766)	+	+	+	+	+				+				
Gammarus salinus Spooner, 1947		+	+				+	+	+				
Incisocalliope aestuarius (Watling and Maurer, 1973)			+				+	+					+
Melita nitida Smith, 1873			+				+	+	+				
Gammarus zaddachi Sexton, 1912				+			+		+				
Gammarus tigrinus Sexton, 1939				+			+		+				
Apocorophium lacustre (Vanhöffen, 1911)				+			+	+	+				

1. Salinity preference: S = seawater, P = polyhalinicum, M = mesohalinicum, O = oligohalinicum.
2. Vertical zonation: H = high littoral, M = mediolittoral, L = lower littoral, S = sublittoral.
3. Substrates: B = boulders, I = interface boulders-soft substrate, T = Tunicata, A = algae, H = Hydrozoa.

harbour of Walsoorden, *Monocorophium insidiosum* was the only amphipod species collected.

During this and other investigations we observed several other invasive invertebrate species in the mesohaline part of the Western Scheldt: the hydrozoan *Garveia franciscana* (Torrey, 1902), the mussel *Mytilopsis leucophaeata* (Conrad, 1831), the Pacific oyster *Crassostrea gigas*, the acorn barnacle *Balanus improvisus*, the amphipod *Gammarus tigrinus* and the mud crab *Rhithropanopeus harrisii* (Maitland, 1874) (van Moorsel (2000); Faasse, unpublished observations).

Discussion

Melita nitida (Figure 2)

Identification

A useful guide to the pertinent literature is the publication of Jarrett and Bousfield (1996), which also provides a world list of species in the genus *Melita* s.s. Mills (1964) redescribed *M. nitida*, because the original description is very brief and moreover became unsatisfactory following the description of many related species. *Melita setiflagella* Yamato (1988) is morphologically very similar to *M. nitida*, even more than the three American species of the *M. nitida*-group described by Sheridan (1979) and the one described by Shoemaker (1935). Only a notch in the antennal sinus and the different setation on the fifth peduncle article of the second antenna separate the two species (Yamato 1988). However, Chapman (1988) reported variable setation patterns on the second antenna of *M. nitida* on the west coast of North America. Jarrett and Bousfield (1996) placed *M. setiflagella* with a question mark in the synonymy of *M. nitida*. *Melita setiflagella* has been reported from Japan (Yamato 1988) and Korea (Kim et al. 1992). The latter authors mention some minor morphological differences with the original description, such as spines on the inner margin of the telson lobes and only two dorsolateral spines on the second urosome segment.

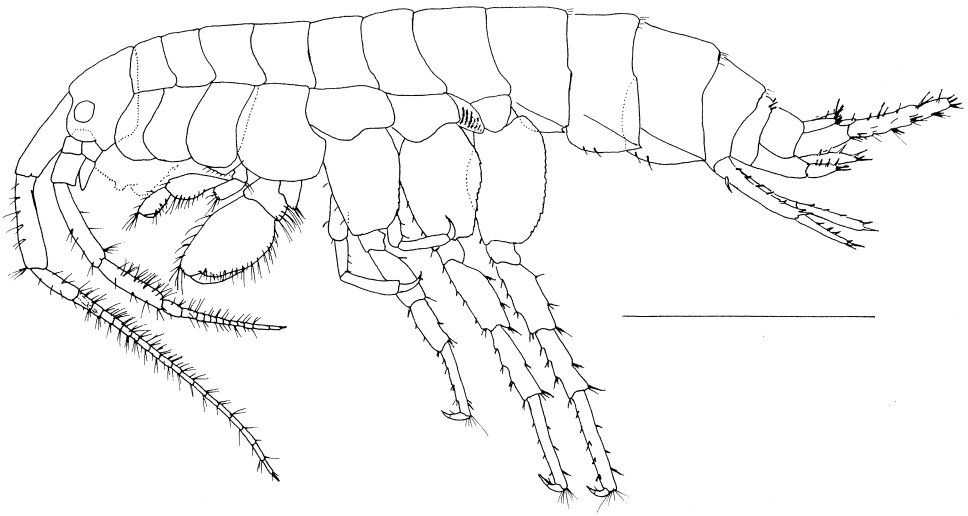

Figure 2. Melita nitida Smith, 1874, male, 10/03/99, Bath. Scale bar = 2 mm.

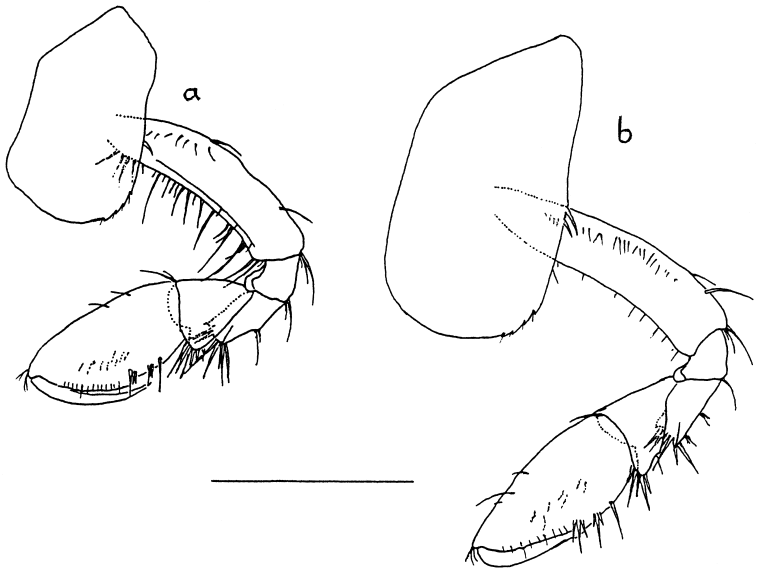

Figure 3. Incisocalliope aestuarius (Watling and Maurer, 1973), ovigerous female, 03/07/00, Hoedekenskerke, a: gnathopod 1, b: gnathopod 2. Scale bar = 0.5 mm.

Melita nitida can be distinguished from all other north-east Atlantic *Melita* species by the dorsolateral spine group on each side of the hind margin of the second urosome segment (Figure 2), this spine group being the only ornamentation of the urosome.

Ecology

Melita nitida lives in muddy bottom-areas, in mesohaline regions of estuaries, in salinities of 3 to 20‰, occasionally up to 30‰ (Bousfield 1973). This species originates from North America. Its distributional area ranges from the south-western Gulf of St. Lawrence (Canada) to Yucatan (Mexico) on the Atlantic coast (Bousfield 1973; Sheridan 1979) and from the Strait of Georgia (British Columbia, Canada) to Elkhorn Slough (California) on the Pacific coast (Chapman 1988). This indicates a tolerance for low as well as high temperatures. *Melita nitida* is found in waters with temperatures up to 32 °C (Sheridan 1979). A tolerance for muddy environments and wide salinity and temperature ranges makes *M. nitida* a potential invader of estuaries in other parts of the

world. Indeed, Chapman (1988) argued that its occurrence on the west coast of North America must be due to introduction by man, in this case as a result of the massive importations of Atlantic oysters, *Crassostrea virginica* (Gmelin, 1791). If the above-mentioned *M. setiflagella* would prove to be a junior synonym of *M. nitida*, then *M. nitida* may have been introduced to Japan and Korea as well. *Melita nitida* is recorded regularly from fouling of floats and pilings (Chapman 1988; LeCroy 2000). This facilitates transport in ballast-water tanks or in the fouling on ship's hulls.

Melita nitida seems to utilize a niche not occupied formerly. The only nestling amphipod species collected together with *M. nitida* were *Gammarus salinus* and *M. palmata* (Tables 1 and 2). *Gammarus salinus* does not occur in the tiny crevices under oysters where *M. nitida* is most frequently collected. *Melita palmata* frequently occurs together with *M. nitida*. However, *M. palmata* occurs mainly higher, in the mediolittoral zone, and furthermore this species is not rectricted to the mesohaline part of the estuary (Table 2).

Until now (July 2001) *M. nitida* seems to have a very limited range in the Western Scheldt. As the first record from the Western Scheldt is just four years old, only future investigations may reveal whether its distributional range is expanding and/or population numbers are increasing in this estuary and whether significant competition with *M. palmata* will occur.

Incisocalliope aestuarius (Figure 3)

Identification

Bousfield and Hendrycks (1995) revived the genus *Incisocalliope* to accomodate several species formerly in the genus *Parapleustes* s.l. This publication is a useful guide to the pertinent literature. Until now *Incisocalliope* was not known to occur in the north-east Atlantic. Barnard and Karaman (1991) mentioned five species of *Parapleustes* s.l. from the north-east Atlantic. *Parapleustes* sp. (Hamond, 1965) has a middorsal tooth on the second pleosome segment and *P. mielcki* (Sokolowsky, 1925) has middorsal teeth on the first two pleosome segments. Probably both should be considered synonyms of *P. bicuspis*. The other three *viz. P. assimilis* (Sars, 1882) *P. bicuspis* (Kröyer, 1838) and *P. gracilis* (Buchholz, 1874) are valid species, which are also mentioned in the checklist of gammaridean amphipods of the north-east Atlantic and Norwegian Arctic by Palerud and Vader (1991). None of these species belongs to the genus *Incisocalliope*. The *Incisocalliope* species from the Western Scheldt is therefore most likely a recent introduction to the Western Scheldt.

We compared some of our specimens with *I. derzhavini* (Gurjanova, 1938), the only known invasive *Incisocalliope* species. Material of *I. derzhavini* from the west coast of North America differs in the distally widening coxal plate 1, particularly long and thick anterodistal setae on the basis of pereiopod 1 and other characters. The *Incisocalliope* species from the Western Scheldt is most similar to *I. aestuarius* (Watling and Maurer, 1973) and *I. filialis* (Hirayama 1988), these two species being the only *Incisocalliope* species having more than 20 setae on the anterior margin of the basis of the first gnathopod. *Incisocalliope aestuarius* is the only North Atlantic *Incisocalliope* species described to date and *I. filialis* is described from Japan. Our material from the Western Scheldt differs from *I. filialis* in the posterior lobe of pereiopod 7 not extending beyond the ischium, the higher number of posterodistal cusps on coxal plates 1–3 and non-setose lateral sides of coxal plates 1–4. Our specimens were more similar to *I. aestuarius*. The anterodistal lobe of the bases of pereiopod 5–7 in the drawing of Watling and Maurer (1973) seems to us to be present only at the medial side. We found the outer ramus of uropod 2 to be 30% shorter than the inner, whereas the difference is 18% in the drawing of Watling and Maurer (1973). We do not think this single character suffices to erect a new species.

Incisocalliope aestuarius has been collected in the Western Scheldt before, but it was not properly identified. Cattrijsse et al. (1993), using the monograph on British gammaridean amphipods by Lincoln (1979), reported *Pleusymtes glaber* (Boeck, 1861) from the eastern part of the Western Scheldt in saltmarsh gullies and deep channels in the main estuary. Taking into consideration the geographical and ecological distribution of this species in Europe (Lincoln 1979), the presence of *P. glaber* in the mesohaline part of the Western Scheldt seems highly unlikely. Bousfield (1973) mentioned a variant of *P. glaber* "in summer-warm and more brackish waters" on the east coast of North America. However, this variant turned out to be the species *I. aestuarius*, the true *P. glaber* being confined to more northerly, open rocky coasts (E.L. Bousfield, pers. comm.). The material of Cattrijsse et al. (1993) probably no longer exists. Ysebaert et al. (2000) mentioned *P. glaber* from the Belgian part of the estuary. We got the opportunity to study material collected by these authors in 1996 near the Dutch-

Belgian border, which proved to belong to *I. aestuarius.* Brummelhuis et al. (1997) recorded *Parapleustes assimilis* from the eastern part of the Western Scheldt from 1991 onwards. Just as is the case with *P. glaber*, the geographical distribution and ecology of *P. assimilis* (see Lincoln (1979)) make its presence in the mesohaline part of the Western Scheldt highly improbable. We got the opportunity to study some preserved specimens identified as *P. assimilis* and they indeed proved to belong to *I. aestuarius* as well. Consequently, the introduction of *I. aestuarius* to the Western Scheldt must have occurred in or prior to 1991.

Incisocalliope aestuarius is most easily distinguished from from *Pleusymtes glaber* and *Parapleustes assimilis* by the ornamentation of the posterodistal margin of the coxal plates 1–3: this margin is provided with a number of weak cusps in *I. aestuarius*, however with a single distinct tooth in both other species mentioned. *Pleusymtes glaber* furthermore differs in the mandibular molar being strongly triturative. *Parapleustes assimilis* furthermore differs in the carpus of the first gnathopod being almost as long as the propodus. In *I. aestuarius* the carpus of the first gnathopod is approximately half as long as the propodus (Figure 3).

Ecology

Incisocalliope aestuarius is known from estuaries on the east coast of North America. Temperatures recorded at the type locality, the Broadkill River in Delaware, range from −2–29 °C and salinities from 10–33‰. Its distributional area ranges from Delaware Bay to Sapelo Island, Georgia (Watling and Maurer 1973). The specimens studied by Watling and Maurer (1973) were collected from the bases of hydroids attached to oysters. The congener *Incisocalliope derzhavini* is known to be a hydrozoan associate as well (Chapman 1988). Its nontriturative mandibular molar, a character shared by all *Incisocalliope* species, suggests it is an ectoparasite (Chapman 1988). Association with hydroids facilitates transport in fouling on ship's hulls. Wide temperature and salinity ranges enhance the success of *I. aestuarius* as an invader.

The absence of *I. aestuarius* from hydrozoans in the harbour of Walsoorden, in contrast with its presence in the nearby tidal channel, suggests a preference for strong currents. However, other unfavourable harbour conditions cannot be ruled out.

No co-occurring amphipod species with a similar niche can be indicated (Table 2). The only hydrozoan associates among amphipods in the Western Scheldt are *Photis reinhardi* Kröyer, 1842 and *Stenothoe* species (see Faasse and van Moorsel (2000)). These species do not penetrate into mesohaline waters. The amphipod species collected together with *I. aestuarius* on the hydrozoan *H. gelatinosa,* cannot be regarded as typical hydrozoan associates and certainly not as ectoparasites. *Caprella linearis*, *M. insidiosum* and *J. marmorata* usually live in dense aggregations. *Caprella linearis* was never recorded this far upstream the Western Scheldt (Hummel et al. 1985) as was *J. marmorata* (see Faasse and van Moorsel (2000)), and *G. crinicornis* only once (den Hartog 1964; Cattrijsse et al. 1993). Apparently they encounter a suboptimal part of their habitat here.

As *I. aestuarius* has been introduced to the Western Scheldt at least eleven years ago, it is assumed that it will not extend its present range in this estuary significantly. Its known range extends from Doel in Belgium (Ysebaert et al. (2000); as *Pleusymtes glaber*) to Baarland.

General discussion

Melita nitida and *I. aestuarius* were only collected in the mesohaline part of the Western Scheldt (Figure 1). Both species were never encountered elsewhere in the Delta-area in the south-west Netherlands during our investigations: the BIOMON monitoring scheme for the Ministry of Transport, Public Works and Water Management by Bureau Waardenburg bv (van Moorsel and Waardenburg 1999b) and extensive collections by the first author (M.F.) (Faasse and van Moorsel 2000).

Wolff (1973) stated a relatively high number of empty niches to exist in the brackish waters of northwestern Europe. He assumes that this is the main reason why these waters are particularly susceptible to invasions by species from brackish waters in other parts of the world. For a number of well-investigated taxonomic groups of macrobenthos of brackish waters in the Netherlands as a whole, Wolff (1999) calculated that about twenty percent of the species has been introduced by man. The proportion of exotic species among macrofauna organisms on sublittoral hard substrates near Bath and Walsoorden amounts to 35% (calculated from van Moorsel (2000)). Some groups such as hydrozoans were not studied in detail, but it is clear that the percentage alien species is considerable. Our observations suggest that *M. nitida* and

I. aestuarius indeed occupy niches formerly barely utilized. Their microhabitats are, however, created by man. Originally, boulders were almost absent in estuaries along the southern coasts of the North Sea. Application of artificial hard substrates may have facilitated introduction of certain exotic species such as the Pacific oyster, which in turn promote the establishment of other invaders. The native oyster (*Ostrea edulis*, Linnaeus, 1758) did not penetrate into the Western Scheldt as far as the Pacific oyster.

Conlan (1994) listed as possible vectors of introductions of amphipods: range expansion along modified water courses, introduction as fish food, transport amongst other organisms such as algae or shellfish and transport in fouling on ship's hulls or in ballast water. In this case only the latter vectors deserve consideration. Shellfish cultures do not exist in the Western Scheldt. Shipping, however, is very busy on this only route to the port of Antwerp. The fouling on ship's hulls (Carlton 1985; Gollasch 1999) and ballast water are both important sources of alien species. Carlton (1985) presented an overview of the dispersal process by transport in ballast water tanks. He states that the spread of invasive aquatic species has accelerated for several reasons. First, pollution reduction favoured diversity and abundance of the biota in harbour regions and estuaries. Ballast-water biota may have changed accordingly. Second, survival during transport has increased as a result of reduced transport time. Time elapsed between ports has decreased last century because of the opening of the Suez and Panama Canal, reduced time in port and higher speed of ships, which more than doubled since World War II. Third, the practice of using tanks alternately for ballast water and, for example, petroleum products is in decline. This constitutes another reason for enhanced survival.

Apart from data in literature, the occurrence of *M. nitida* and *I. aestuarius* in the mesohaline part of the Western Scheldt *per se* clearly indicates a high euryhalinity and eurythermy in these amphipod species. These characteristics make them potential invaders of other European estuaries. They may have invaded already a number of other European estuaries without having been noticed, due to their absence from local identification keys. As a pelagic larval stage is lacking in amphipods, their dispersal to other brackish water regions depends on transport by chance. Therefore, their distribution patterns may remain patchy. Until now there are no indications for *M. nitida* and *I. aestuarius* to have reached the Nieuwe Waterweg, only some 50 kilometres to the north. Chapman (1988) used a restricted or disjunct distribution of amphipod species as evidence for introduction by man in estuaries on the Pacific coast of North America. In Europe, *Grandidierella japonica* Stephensen, 1938 is another introduced amphipod species known from only a single estuary, *viz.* Southampton Water in southern England (Smith et al. 1999). *Monocorophium sextonae* Crawford, 1937, supposedly native to New Zealand (Hurley 1954), was recorded from Plymouth as early as the 1930s (Crawford 1937), but it took the species more than 20 years to reach the Netherlands (Stock 1952) and forty to fifty years to establish itself in Ireland (Costello 1993).

Conclusions

The amphipod species *Melita nitida* and *Incisocalliope aestuarius* have been introduced to the mesohaline part of the Western Scheldt (the Netherlands), presumably by shipping. They occupy niches barely utilized before their introduction. This corroborates the theory that a high number of empty niches makes western European brackish waters particularly susceptible to invasions of alien species. The application of hard substrates in estuaries originally predominated by soft bottoms may have facilitated the introduction of alien species as well. The proportion of alien macrofauna species in the sublittoral hard substrate community of the mesohaline part of the Western Scheldt is approximately one third. In due course of time *M. nitida* and *I. aestuarius* will probably invade other estuaries in the north-east Atlantic as well. However, as a dispersive larval phase is absent in amphipods, their distribution may remain patchy.

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