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# IS COROPHIUM MULTISETOSUM STOCK, 1952 AN EXOTIC INVASIVE SPECIES IN EUROPE? DISTRIBUTION, HABITAT AND RECENT OBSERVATIONS IN THE NETHERLANDS

BY

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## ABSTRACT

Corophium multisetosum Stock, 1952 has been found in several estuaries and water bodies in Europe ranging from fresh and brackish to salt water. The species appeared to be distributed over a wide geographic range from the Iberian Peninsula to the southern Baltic region and is recently found in the Mediterranean and Gulf of Mexico showing remarkable

differences in ecology between populations. The recorded observations of the species in the Netherlands however remained restricted to a few smaller waters, and were published in grey literature. Recently, the species is observed in a variety of waters in the southwestern part of the Netherlands and appeared to be relatively common. The current study gives an overview of the recordings of C. multisetosum within its geographic range and its habitat preferences. The recent observations on distribution and habitat preferences of C. multisetosum in the Netherlands are compared with the findings in other parts of Europe. Seemingly discontinuities in recorded ecology of the species in the Netherlands and over Europe are discussed. C. multisetosum appears to be very flexible in its behaviour and appears to tolerate a broad range of environmental conditions. Local environmental conditions (e.g. salinity and substrate) and related communities (in the Netherlands particularly the presence of the seemingly competing species Corophium volutator (Pallas, 1766) and Chelicorophium curvispinum (G.O. Sars, 1895)) determine the presence of C. multisetosum and the local behaviour and abundance of the species in the system. As the species shows a typical distribution pattern with many recent recordings, its origin and possible distribution routes are discussed.

# INTRODUCTION

The amphipod Corophium multisetosum Stock, 1952, was described by Stock in 1952 from the North Sea Canal (Noordzeekanaal), a canal connecting the port of Amsterdam with the North Sea forming a brackish water gradient. The species was also recorded from some smaller waters near the Eem (in the Central part of the Netherlands, not to be confused with the Ems or Eems estuary in the North of the Netherlands), where it was found already in the 1920s, and near Wieringen in the 1950s. There it occurred in the less saline waters with salinities below 4 and at depths between 1 and 8 metres on sand and clay bottoms where it builds mud burrows or occasionally builds free tubes upon substratum (Stock, 1952; Mulder & Stock, 1954; Lincoln, 1979). C. multisetosum was found frequently together with Apocorophium lacustre (Vanhöffen, 1911) and occasionally with the closely related Corophium volutator (Pallas, 1766). After the description of C. multisetosum by Stock in 1952, the species could also be recognized in other parts of Europe (mainly the British Isles) where its presence could also be traced back to earlier days (e.g. Hart, 1930; Crawford, 1937; Ingle, 1963). During the 1960s and 70s the species was recorded from Germany and Poland (Schütz, 1969; Jażdżewski, 1976) and France (Cazaux & Labourg, 1973). From the 1990s on, a series of publications mentioning or related to C. multisetosum in Portugal and Spain were launched (e.g. Queiroga, 1990; Cunha & Moreira, 1995; Cunha et al., 1999; Casado-Martínez et al., 2006). The species may have been present there before, but earlier records are lacking. In the same period, the species was also recorded from Ireland (De Grave & Wilkins, 1994). C. multisetosum is nowadays considered an endemic species of the northeast Atlantic region

(Buckley et al., 2004). It is both referred to as a warm-water species with its northern limit in the Baltic (Schütz, 1969), and as a cold-water species with its southern limit in Portugal (Chainho et al., 2006). The species' salinity range appears to be much wider than initially recorded by Stock (1952) as C. multisetosum is found at salinity values of up to 22.5 (Janta, 1995) or even above 30 in the Canal de Mira in Portugal (Queiroga, 1990). Literature data on C. multisetosum provide a highly variable picture of the habitat of the species within its geographic range. As for other parts of Europe, in the Netherlands there has been no specific attention for the status of the species for decades. However, monitoring intensity increased and from the late 1980s on, monitoring of macrozoobenthic communities in the Netherlands is executed in more standardized ways (e.g. Bij de Vaate et al., 2006; Peeters et al., 2008; Wijnhoven et al., 2010). In the southwestern part of the Netherlands where several waters have been sampled for macrozoobenthos during the 1960s to 1980s (e.g. Wolff, 1973; Nienhuis, 1985; Nienhuis & Smaal, 1994; Wijnhoven et al., 2008), and where an inventory of amphipods in particular has taken place in 1992 (Platvoet & Pinkster, 1995), C. multisetosum was not found until recently. Surprisingly the species seems to be common and present in a variety of waters in the northern part of the so-called delta area, nowadays.

In the present study an overview of the geographic and environmental range of C. multisetosum is presented as basis for further studies on the ecology of the species. Special attention will be given to a series of observations of the species within sampled communities in the Netherlands. The origin and possible routes of dispersion and introduction are discussed.

## MATERIAL AND METHODS

The current study presents an overview of the locations from which Corophium multisetosum Stock, 1952 has been recorded. Recorded habitat and environmental characteristics from the literature will be listed, to come to an ecological profile of the species within its geographic distribution range. Recent observations on the presence of the species in sampled communities, which has been taken as part of some long-term monitoring programmes and shorter-term studies, will be compared to establish the ecological profile of the species as could be derived from the literature. Variation between the habitats and communities in which the species occurred will be discussed. New unpublished records of C. multisetosum from the Netherlands are originating from; (1) Biological monitoring within the framework of the MWTL programme (Monitoring of the Status of Waters of the Netherlands), divided in marine and estuarine water bodies (a) and freshwater bodies (b); (2) Inventory of the biological status of the Dutch riverbanks; (3) Research related to sanitizing the river 'Hollandsche IJssel'; (4) Research to determine chances for tidal freshwater nature development; (5) Inventory of macrobenthic communities of the 'Haringvliet' as part of a planned saltwater inlet; (6) Inventory of the 'Zuidrand' (Nieuwe Merwede, Hollandsch Diep and Dordtsche Biesbosch); (7) Additional sampling to verify earlier observations. All projects are executed by either the Monitor Taskforce of the Netherlands Institute of Ecology (1a,5,7), the research institute Grontmij/Aquasense (1b,2,3,4) or Hydrobiological Advisory Klink bv (6) in cooperation with the Water Directives (Rijkswaterstaat diensten RIKZ and RIZA) of the Directorate General of the Dutch Ministry of Infrastructural Planning and Waterworks. (The data of the studies 1b, 2, 3, 4 and 6 were combined for a project reported by Peeters et al. (2008)). Combining these studies the following basins, roughly situated from north to south and from west to east in the southwestern part of the Netherlands (fig. 2B), are monitored for macrozoobenthos in the years as indicated in table I. In the Grevelingen, Oosterschelde, Veerse Meer and Westerschelde the monitoring involved the soft sediments. In all other

basins both soft sediments and hard substrates had been sampled. General abiotic values and trends, like salinity and temperature for certain basins and periods, when not directly measured during sampling of macrozoobenthos, were extracted from the Waterbase (www.waterbase.nl) of the Dutch Ministry of Infrastructural Planning and Waterworks (Rijkswaterstaat).

## RESULTS AND DISCUSSION

### Geographic distribution

An overview of C. multisetosum records in the literature in time was made (table IV). The list does not start with Stock (1952), as C. multisetosum was recognized in earlier samples. Besides the year of observation also the country and location are indicated. The locations are indicated in fig. 1. C. multisetosum was described in 1952, but appeared to be collected in the Netherlands already in 1921 (Stock, 1952). Also in England especially in the southern and southeastern part, C. multisetosum appeared to be collected already in the 1920s and 1930s (Hart, 1930; Ingle, 1963), or even before the 1920s (De Grave & Wilkins, 1994). Therefore the species is considered to be native to the area. The status of the species in other parts of Europe might however be less clear. For Germany there are records from the 1950s (Schütz, 1969), and also from Poland the species is known for quite some time (Jażdżewski, 1976). Now, the species also appears to be abundant in Denmark, at least in the Randers Fjord as indicated by an inventory in 2002 (Det Digitale Randers, 2006). In Denmark C. multisetosum is indicated as typical for river mouths (Århus Amt, 2007). Recently, C. multisetosum was also recorded for the southern Lithuanian coastal region (Raudonikis et al., 2009); it is unclear whether the species is common and if the species is permanently

established there. The locations bordering the Baltic Sea, the locations from the English east coast and those from the Danish coast, seem to form the most northern distribution of C. multisetosum. It seems that the species is present at least in Poland and Germany already for a long time and might as well be native in this region, although more recent settling and range extensions (due to changing conditions) have been observed (Bäthe, 2007). However, there is one remarkable northern observation for the Frisian front, which is in contrast to the other locations, from full salinity (34.2) waters (Dewicke et al., 2002). This observation should be confirmed by re-examination of the collected specimens. The recordings furthest northwest are from Ireland where the species is only recently found (De Grave & Wilkins, 1994; Cott et al., 2007). This can mean that it has been introduced there, but might as well be the result of just not having been noticed before.

For France and also for the Spanish Atlantic coast the species was unknown for a long time, except for a basin near Arcachon (Cazaux & Labourg, 1973) where C. multisetosum might have been introduced with or as fish food or with pond weeds. However, since the 80's, C. multisetosum appears to be present abundantly along the Spanish and Portuguese Atlantic coast (e.g. Altuna et al., 1983; Junoy & Viéitez, 1990; Queiroga, 1990; Cunha & Moreira, 1995). Observations soon covered the whole Iberian Atlantic coast, which also described the species' most southern and western border of distribution. But now, there appears to be another southern observation, namely from Menorca (Lucena-Moya et al., 2010). This is of special interest as this is the first observation from the Mediterranean.

At its southern border of geographic distribution, in Portugal and Spain, the species can completely dominate the communities. This is more often observed for several species of Corophiidae (Gerdol & Hughes, 1993; Kevrekidis et al., 2005; Van Riel et al., 2006; Pérez et al., 2007), but was not known for C. multisetosum from other places where the species can be found. The species appears to be common in the region at least since the early 1980s when

specific macrozoobenthic research started in the Iberian estuaries. Whether the species is native to this region is unclear.

In the Portuguese estuaries, but also near Arcachon (France), C. multisetosum is the dominant macrozoobenthic species in at least certain parts of the systems (Queiroga, 1990; Cunha & Moreira, 1995; Cunha et al., 2000a; 2000b; Chainho et al., 2006). At several sites near Eem and in the North Sea Canal, the Netherlands (Stock, 1952), in the river Stour, England (Ingle, 1963), and in the river Suir, Ireland (De Grave & Wilkins, 1994), C. multisetosum was found in large numbers. At Whitby harbour, the river Stour and West of Calstock, England (Hart, 1930; Ingle, 1963) and Martwa Wisla, Poland (Jaždžewski, 1967), also several specimens of C. multisetosum could be collected. But in several other Dutch samples near Eem and of the North Sea Canal (Stock, 1952) and the rivers Adur, Bure and Yare, all in England (Ingle, 1963), not more than 1 specimen per sample was found, which means that the species was present in low densities at the time of sampling.

Even more out of range is the recording from coastal sites in the Gulf of Mexico, more specifically near Progreso (Yucatán; Mexico) where the species appears to be present very abundantly (Ardisson & Castillo-Fernández, 2004).

## General type of water, current and depth

C. multisetosum was found in canals, channels, river arms, creeks, streams and ditches. Thus the species can occur in a range of biotopes, but larger open standing waters seemed to be avoided (Stock, 1952). Van der Molen & Pot (2007) call the species an indicator for small brackish to salt waters. Depths recorded are largely shallow (between 0 and 3 metres), with an exception for the recorded depths in the Noordzeekanaal (North Sea Canal) in the Netherlands where the species could be found at depths up to 8 metres (Stock, 1952).

For England and Portugal observations are also from shallow areas, although Chainho et al. (2006) recorded the species from depths up to 6 metres in the Mondego estuary. Observations of C. multisetosum in these countries are typically from banks, mud flats and obstacles at which it is attached in shallow water. The species was found at slow water current or in calm water (Schütz, 1969; Jaždżewski, 1976; Bäthe, 2007). Cunha & Moreira (1995) defined the distribution range in Canal de Mira at flow velocities between 0 and 0.45 m $s^{-1}$. Cunha et al. (2000b) mentioned that C. multisetosum avoids low flow areas, which can also be the reason why according to Schütz (1969) the species avoids open water. Verdonschot et al. (2003) characterized the species as an indicator for tidal surface waters, but mentioned that the species is very sensitive to hydrological disturbance. The oxygen status is more or less connected to the flow conditions. Schütz (1969) recorded that the species can stand low oxygen conditions, which is agreed by the wide range from 2 - 18 mg $l^{-1}$ (15 - 200 % saturation) found by Cunha & Moreira (1995) and the observation that the species can occur in reduced sand (Stock, 1952). Cunha et al. (2000b) found a negative correlation of the densities of C. multisetosum with oxygen saturation at low water. Other mentioned water characteristics of the environment for C. multisetosum, however only recorded by a few studies, are tidal range and pH. The tidal range in canal de Mira (Portugal) varied between 0.6 and 1.2 metres in the area where C. multisetosum was found (Cunha & Moreira, 1995), but is probably larger at the British estuarine sites. The pH of the Teich fishponds near Arcachon (France) where C. multisetosum flourished, varied between 6.0 and 7.6 (Cazaux & Labourg, 1973), but for instance in southern Spain the species is also found by a pH of 8 (Sánches-Moyano & García-Asencio, 2010).

## Substrate

C. multisetosum is recorded from a variety of substrates including soft sediments (muddy, clayish and reduced sand) and hard substrates (Stock, 1952). The species is found to burrow in soft sediments but can make tubes on hard surfaces. In its geographic distribution area, the species is actually recorded from the whole range from mud to coarse sediments. Most often the species is found on mud (Crawford, 1937; Jaždżewski, 1967, De Grave & Wilkins, 1994) on medium sands (Queiroga, 1990; Taylor, 1994; Janta, 1995; Cunha et al., 1999, 2000b; Casado-Martínez et al., 2006), or on both (Schütz, 1969; Jaždżewski, 1976; Cunha & Moreira, 1995). Chainho et al. (2006) and Sánches-Moyano & García-Asencio (2010) recorded the species however from coarse-medium and coarse sands and Cott et al. (2007) recorded C. multisetosum on coarse gravel with soft mud. Where Ré et al. (2007) records the species to be less abundant at high levels of particles < 125 μm, the survival or development of C. multisetosum was not diminished in such an environment (Castro et al., 2006). The reason may be the sensitivity of very young specimens to sediments with high fine contents (Quintino et al., 2000). Tubes are found on a variety of hard substrates, like cables, stones, poles, algae and stolons of the hydroid Cordylophora caspia (Pallas, 1771) (Crawford, 1937; Stock, 1952; Schütz, 1969; Taylor, 1994) but surprisingly no observations of tube building on hard substrates are present from the southwestern European countries.

As mentioned before, C. multisetosum can be found in a variety of types of waters. Besides that the species is often found on bare substrates, it is also recorded from vegetated areas, from extensive and luxuriant submersed macrophyte vegetation (Myriophyllum spp. and/or Potamogeton spp.) in particular (Cunha & Moreira, 1995; Cunha et al., 2000b) at the Ria de Aveiro, Portugal. In England the species is also recorded from reed beds according to Ingle (1963), but Taylor (1994) mentioned the species from other parts particularly lacking in reed.

## Salinity

C. multisetosum was first mainly recorded from oligohaline waters with some additional observations from mesohaline water. In the Netherlands the salinity of the water bodies in which C. multisetosum lives did not exceed 6 (Practical Salinity Scale) (Stock, 1952; Mulder & Stock, 1954). Observations in Germany and Poland show a wider range of 0 – 8.5 (Schütz, 1969; Jaždżewski, 1976; Grzelak & Kuklinski, 2010). Stock (1952) already mentioned that the morphological variations on C. volutator as found by Hart (1930) might be in fact C. multisetosum. If that is the case, C. multisetosum has been observed in England at salinities of generally more than 20. This is in line with later records from other countries. In France the recorded salinity range of C. multisetosum was 4.5 – 22.5, and in Portugal 0.0 to 31.6 (e.g. Queiroga, 1990; Chainho et al., 2006). These high salinities are extremes and are no year round salinities, but the species at least can cope with such conditions temporarily. Cunha et al. (2000b) summed up the preferential salinities found by other authors, and concluded that those are generally below 20, and finds mortality and much lower fecundity when salinities approach 0.0. Cunha et al. (2000c) adds to this that the species produces no offspring at salinities above 25. Cunha et al. (2000a) recorded a highest fecundity at a salinity of 3.5 (in combination with a temperature of 18 °C) and shows that the species breeds in the laboratory at a salinity range from 2 to 18. Provincie Noord Holland (2006) and Van der Molen & Pot (2007) mention C. multisetosum a good quality indicator species for slightly brackish and smaller brackish to salt waters in the Netherlands.

## Temperature

In accordance with the geographic distribution, the temperature tolerance of C. multisetosum is high. An average temperature of 17.0 °C is given for the Kentish Stour Estuary (England) at the locality and month of observation of C. multisetosum (Buckley et al., 2004). In the southwestern European systems the species has to cope with an annual temperature range from 8 to 25 °C measured in the water column and in the sediment (Queiroga, 1990; Cunha & Moreira, 1995; Cunha et al., 2000a). Cunha et al. (2000c) recorded an optimal breeding temperature of 18 °C. Cunha et al. (2000a) mentioned that breeding is more intense between 15 and 20 °C (in combination with a salinity >1). Ré et al. (2007) mentioned that a new generation is produced in 28 days at 22 °C, but that this will take twice the time at 15 °C. Schütz (1969) reasons that the species must be sensitive to cold temperatures as the records from Germany are from the northern border of its geographic distribution range.

## Nutrients and pollutants

The organic matter content of the sediment is often relatively low in the areas where C. multisetosum is found. The values recorded by Cunha & Moreira (1995) and Cunha et al. (1999) are in the range of 0.2 to 6 % dry weight of organic matter (OM), or are characterized as OM poor (Queiroga, 1990). Also Ré et al. (2007) recorded that the species is less abundant on sediments rich in OM. Chaino et al. (2006) recorded a range from 6.4 to 9.6 mg $l^{-1}$ dissolved organic matter, and Buckley et al. (2004), 53.1 mg ± 36.5 mg $l^{-1}$ of suspended solids of which 22.1 % is OM, which is more nutrient rich than for the Portuguese situation. Cunha & Moreira (1995) also recorded the range of chlorophyll a concentrations for the area of distribution of C. multisetosum in Canal de Mira, viz. 5 – 120 mg $m^{-3}$. In the classification of marine species to Biotic Groups for the AMBI evaluation system to evaluate the

environmental stress which is basically a combination of eutrophication and pollutants in this classification (Borja et al., 2000), C. multisetosum is identified as a Group III species. According to Borja et al. (2000) this means that the species is characterized as tolerant to excessive organic matter enrichment. The species may occur under low OM conditions, but populations are stimulated by organic enrichment (slight unbalanced situations). In relation to pollutants, Schütz (1969) considers the species relatively tolerant. Ré et al. (2007) mentioned that the species is sensitive to phenols and metals (but not as sensitive as Daphia magna Straus, 1820 and Paracentrotus lividus (de Lamarck, 1816)), and according to Rodrigues & Quintino (2000) the species should be sensitive to heavy metals and PCB's. Because C. multisetosum is not insensitive for pollutants, but is relatively tolerant, this species is frequently used in toxicity tests and sediment quality evaluations (Quintino et al., 2000; Silva et al., 2004; Castro et al., 2005; Casado-Martínez et al., 2006; Sanz-Lázaro et al., 2008).

## Associated species

Whether species are only associated or also compete for resources and/or space at the same locations is often not clear. Potentially species of the same family might be competitors as they are closely related and might inhabit a similar or partly overlapping niche, with minor differences in preferable conditions. Stock (1952) recorded C. multisetosum together with A. lacustre and at several sites also together with Monocorophium insidiosum (Crawford, 1937) in the Netherlands. The last species might replace C. multisetosum at higher salinity. A. lacustre is frequently observed together with C. multisetosum in England (Ingle, 1963; Taylor, 1994; Hayward & Ryland, 1990), in Germany (Schütz, 1969; Bäthe, 2007) and Poland (Grzelak & Kuklinski, 2010). Jażdżewski (1976) however found that A. lacustre replaces C. multisetosum upstream. Also the earlier mentioned co-occurrences in the Netherlands,

England and Germany show a dominance of A. lacustre especially at lower salinity. Hart (1930) found a special variety of C. volutator, which might have been C. multisetosum. In that case the two species were living at the same sites. C. volutator is in England and Poland more often observed together with C. multisetosum (Ingle, 1963; Jażdżewski, 1976). C. volutator is probably more in favour compared to C. multisetosum at higher salinity (Jażdżewski, 1976). Other Corophiidae found together with C. multisetosum are Apocorophium acutum (Chevreux, 1908) and Monocorophium acherusicum (Costa, 1851), specifically in Portugal (Cunha et al., 1999). Sánches-Moyano & García-Asencio (2010) and Lucena-Moya et al. (2010) did find respectively M. acherusicum, Medicorophium aculeatum Chevreux, 1908, Monocorophium sextonae (Crawford, 1937) (southern Spain) and M. insidiosum, C. orientale Schellenberg, 1928 and M. sextonae (Menorca) in the same region, but never on the same location. Chelicorophium curvispinum (G.O. Sars, 1895) is considered a competing immigrant species in the Netherlands potentially invading C. multisetosum habitat up to a salinity of 6 (Van den Brink & Van der Velde, 1992). A similar pattern is observed in the river Weser where nowadays C. multisetosum and C. curvispinum are largely found along the same river transect (Bäthe, 2007).

C. multisetosum clearly seems to profit from Cordylophora caspia as tubes are often found on these hydroids. Besides Stock (1952), also Crawford (1937) found C. multisetosum (the species described for the River Tamar (England) was later identified by Spooner as C. multisetosum (Ingle, 1963)) on the stolons of the hydroid species. Several other species are identified to be associated or preferring similar environmental conditions as C. multisetosum. Recognized species are the amphipods Bathyporeia pilosa Lindström, 1855, Gammarus duebeni Liljeborg, 1852, G. zaddachi Sexton, 1912 in Poland (Jażdżewski, 1976), the snail Radix peregra (O. F. Müller, 1774), the bivalve Pisidium subtruncatum Malm, 1855 and Tubificidae in Ireland (De Grave & Wilkins, 1994). The snail Potamopyrgus antipodarum (J.

E. Gray, 1843) (syn. P. jenkinsi) was clearly associated with C. multisetosum in both Ireland and England (De Grave & Wilkins, 1994; Taylor, 1994), but is even more an interesting species as it is also frequently found together with C. multisetosum in Portuguese studies (Cunha & Moreira, 1995; Cunha et al., 2000b;) and in France (Cazaux & Labourg, 1973). In these countries also the amphipod Gammarus chevreuxi Sexton, 1913 is often found in the same samples as C. multisetosum (Cazaux & Labourg, 1973; Cunha & Moreira, 1995; Cunha et al., 200b). The amphipod Leptocheirus pilosus Zaddach, 1844 is found in association with C. multisetosum in Germany (Schütz, 1994) and Portugal (Cunha et al., 2000b). Other species found together with C. multisetosum in Portugal are the oligochaete Limnodrilus hoffmeisteri Claparède, 1862, the amphipod Microdeutopus gryllotalpa Costa, 1853, the isopods Cyathura carinata (Krøyer, 1847), Lekanesphaera hookeri (Leach, 1814), the polychaete Streblospio shrubsolii (Buchanan, 1890) and the midge Chironomus spp. (Cunha & Moreira, 1995; Cunha et al., 1999; 2000b; Chainho et al., 2006). In southern Spain particularly C. carinata is found on the same locations as C. multisetosum (Sánches-Moyano & García-Asencio (2010) and in Menorca L. hookeri (Lucena-Moya et al., 2010).

In particular species reworking the sediments might influence the presence and densities of C. multisetosum. The studies of Flach (1992; 1993) and Flach & de Bruin (1993) show negative effects of the presence of the lugworm Arenicola marina (Linnaeus, 1758) and the bivalve Cerastoderma edule (Linnaeus, 1758) on the densities of C. volutator and Corophium arenarium Crawford, 1937, which are subscribed to increased predation risk due to the disturbing activities of A. marina and C. edule.

## New recordings for the Netherlands

C. multisetosum is historically known from three regions in the Netherlands: the area of 'Wieringen' in the northwest, the area surrounding the 'Eem' in the central, and the North Sea Canal in the centralwestern part of the Netherlands (Stock, 1952; Mulder & Stock, 1954). In relation to the status of the species in these regions, it is frequently recorded that C. multisetosum is abundantly present in the Noordzeekanaal (North Sea Canal) (Peeters et al., 2000; Van Dam et al., 2007; Van Wieringen, 2009). Mr. B. Schrieken kindly sent us C. multisetosum collected in 2007 from two small lakes 'Noordelijke Dijkwiel' and 'Zuidelijke Dijkwiel' situated in the 'Wieringen' region. The specimens were collected from soft substrate and the lakes have a salinity of 5.4 to 5.9. The status of the species in the 'Eem' region is less clear. Van Dam et al. (2007) mentions that C. multisetosum is becoming scarce in the hinterland of 'Noord-Holland' to which also the region of 'Wieringen' belongs. They recorded C. multisetosum for the 'Noorder IJ-plas' during inventories in 1991 and 2006, a lake bordering the North Sea Canal, where Lenoir et al. (1996) observed the species in 1996. Van den Brink et al. (1993) mentioned the co-occurrence of C. multisetosum and C. curvispinum in 1990 in the Amsterdam-Rhine Canal, which canal is connected in the north in the Amsterdam region to the North Sea Canal. C. curvispinum was found there on the stones in the littoral zone, while C. multisetosum inhabited the sandy sediment in the deeper parts of the canal. This means clear niche segregation between these two potentially competing species. The onset of the Amsterdam-Rhine Canal near Amsterdam is slightly brackish (Van Wieringen, 2009).

C. multisetosum was not recorded from the southwestern part of the Netherlands before the 1990s although this area harbours a variety of water types which might potentially be suitable for the species. For this study we could check a total of 66,882 species recordings (summation of number of species for all available samples) from the south-western Netherlands for the period 1990-2008. The first record of C. multisetosum in this area was in

1993 in the Hollandsch Diep, a large freshwater body with a minimum of current. In that year the species was found in low densities at two locations on sand containing mud, at depths of 1.1 and 2.8 metres, respectively in the center and in the east of the basin (Klink,1994). Klink (1994) also sampled the Nieuwe Merwede in 1992 and the Dordtsche Biesbosch in 1993, which basins are situated just to the east of the Hollandsch Diep. Other basins in the vicinity which were sampled between 1992 and 1994 are the Dordtse Biesbosch, the Brabantse Biesbosch, the Amer, and more to the east the Getijde Maas and the Zand Maas (fig. 2). In all these water bodies no C. multisetosum was found. The recordings of C. multisetosum in 1993 in the Hollandsch Diep were the only recordings for this basin. In 1993, C. curvispinum was already a common species in the Hollandsch Diep (Van den Brink et al., 1993) and was even found together with C. multisetosum in one of the samples. It is very likely that C. curvispinum has taken over the niche that might have been of C. multisetosum in the Hollandsch Diep before or the species is occasionally present in an environment where it can not maintain very well. With the exception of one observation of C. multisetosum in the Amer in 1997, the species has not been found in the above-mentioned freshwaters east of the Hollandsch Diep where C. curvispinum is abundant. C. multisetosum in the Amer was found in low densities (11 ind. $m^{-2}$) from a muddy substrate with some sand at a depth of 1.2 metres, with C. curvispinum present in the same sample.

Paalvast (2000) found C. multisetosum in the Haringvliet in 1993 and 1994 on locations just east of the Haringvlietdam on mud-poor fine sand substrate, in association with C. volutator. C. multisetosum is not present all over the Haringvliet as shown by the absence of the species in the samples from 1993 and 1994 from the basin checked for this study. However, C. multisetosum was observed on several locations also in the central part of the Haringvliet in 1995 and 1997. Densities varied between 5 and 83 ind. $m^{-2}$, at depths from 0.9 to 6.0 metres on sediments varying from mud to sand. Despite monitoring in 1998, 2001,

2002, 2003 and 2005 C. multisetosum was only observed in 2001 during a study particularly focusing on the western part of the Haringvliet. In 2001 C. multisetosum was found in four samples taken close to the Haringvlietdam from depths of 1.5 to 2.7 metres on fine sands with and without mud at densities of 67 to 133 ind. $m^{-2}$. C. curvispinum is very abundant in the Haringvliet in all years of sampling, with densities of often >1,000 to >10,000 ind. $m^{-2}$, but this species was, with the exception of one of the samples from 1995 where the density of C. curvispinum was low, not present in the samples with C. multisetosum. It seems that C. multisetosum can maintain in the Haringvliet, where C. curvispinum is absent, in particular in the more brackish water close to the Haringvlietdam in the western part of the Haringvliet.

C. multisetosum is also observed in the early 1990s in the most northern river section of the delta, where also a salinity gradient is present. Van den Brink et al. (1993) mentioned C. multisetosum for the oligohaline (salinity 0.5 - 5) parts of the Lower Rhine in co-occurrence with C. cuvispinum. The study probably refers to locations in the Oude Maas, but it is possible that C. multisetosum was also found in the river Lek already in the early 1990s. Paalvast (2000) recorded the species from the Nieuwe Waterweg in 1995 and the Hartelkanaal (which lays just south of the Nieuwe Waterweg, parallel to it) in 1999, on fine sand substrate with not much mud. From the same period we also have several observations in this region. In each of the years at which was monitored (1995, 1999, 2003 and 2009), C. multisetosum was found in all samples of the Nieuwe Waterweg. All observations, which include densities from 6 up to more than 3,500 individuals per $m^2$, are from shallow parts between 0 and 1.2 metres on muddy sediments, on stones and on shore vegetation. Samples were from both the western and the eastern part of the canal. In most samples C. multisetosum was one of the most abundant species, or even the dominant species. On stones, C. multisetosum was always found in association with A. lacustre. In two samples from 1995 from the eastern part of the

canal, on mud and on shore vegetation, C. multisetosum was found together with a few individuals of C. curvispinum, but C. multisetosum outnumbered all other species there.

Although sampled in 2000, 2001 and 2002, C. multisetosum was not found in the extension of the Nieuwe Waterweg eastwards called the Nieuwe Maas. Here the system is rich of organic matter, and Tubificidae are in particular abundant and Corophiidae were not found at all. Further to the east, C. multisetosum was found in the Hollandsche IJssel in the years 1999, 2000 and 2004 (but not during the in between years) and in the river Lek in 2003 (not during monitoring in 1995, 1999 and 2000). In 1999 and 2000 C. multisetosum occurred in the Hollandsche IJssel in singular samples taken from stones; in 2000 together with C. curvispinum. C. curvispinum is found in the Hollandsche IJssel on stones in low densities. In 2004, C. multisetosum was found two times on stones, in one sample also with C. curvispinum. In the Hollandsche IJssel, C. multisetosum was found four times on soft sediment (mud and sand) in 2004 at depths varying between 0.2 and 2.5 metres. No other Corophiidae were found here on soft substrates. In the river Lek, C. curvispinum appeared to be very abundant (>1000 ind. $m^{-2}$) on stones, and some individuals could also be found on soft sediment in 1995. In 1999 the numbers of C. curvispinum were here much lower, but the species was still present in most of the samples, whereas in both years C. multisetosum was not found. In 2000 sampling intensity in the Lek was low, and no C. multisetosum was found. However, in 2003, C. multisetosum was present in all samples from both stones and sandy substrates. The densities varied between 3 and 321 individuals per $m^2$, whereas no C. curvispinum was found. It seems that conditions have changed in the river Lek, which has lead to the decrease of C. curvispinum, making it possible for C. multisetosum to increase. A similar pattern is visible in the Hollandsche IJssel, where C. multisetosum could especially increase their densities on the by C. curvispinum less favoured soft substrates.

The other river transect connected to the Nieuwe Waterweg is the Oude Maas. In contrast to the Nieuwe Maas C. multisetosum was abundantly present there. In 1995 C. curvispinum was here abundantly present especially on stones, but was also found on shore vegetation and on sand, and C. multisetosum was present in three samples. In a vegetation sample it was present in the absence of C. curvispinum. On mud C. multisetosum was in one sample more abundant than C. curvispinum, and the species was also found once on sand in the presence of C. curvispinum. In 1999 C. multisetosum was several times found in the presence of C. curvispinum, but in those cases C. curvispinum was always more abundant. However, in three samples C. multisetosum was the only Corophiid species present at which on mud the densities reached >900 ind. $m^{-2}$. There were also samples with only C. curvispinum present. C. curvispinum was always dominant on stones. From 2001 only samples taken from soft substrates were available. C. multisetosum was present in almost all samples, with the exception of one sample in which C. curvispinum was found, and one sample in which A. lacustre was found. In one of the other samples A. lacustre and C. multisetosum co-occurred with much higher numbers of C. multisetosum. In 2002 only a few samples with a high organic matter content were taken without Corophiidae. In 2003, C. multisetosum appeared to be the dominant Corophiid in all samples, or sometimes even the dominant species, with the exception of one vegetation sample in which only C. curvispinum was found. In two samples respectively taken from the stones and in mud, C. multisetosum co-occurred with A. lacustre, and in one vegetation sample only two specimens of both C. multisetosum and C. curvispinum were present. In 2005 only two samples were taken; Corophiids were lacking in both. However in 2009 it appeared again to be very easy to collect hundreds of specimens of C. multisetosum from bare rather muddy soft substrate at a depth up to 0.5 metres near a reed patch in the Oude Maas. It looks like conditions were fluctuating in the Oude Maas, sometimes favouring C. multisetosum, sometimes favouring C. curvispinum

in transition waters between the freshwater and the brackish water zone. C. curvispinum's competitive power seems to be larger on stones while the species seems to avoid mud more than C. multisetosum. Whereas C. multisetosum was generally found in shallow waters between 0 and 1.2 meters, in 2001 the species was also found in deeper waters up to 13 metres. The deeper observations, with densities varying between 5 and 368 individuals per $m^2$, were all on soft substrates varying from mud to sand with a fraction of mud.

C. multisetosum was also found in low densities in 1999 in the smaller river branch called Wantij situated east of the Oude Maas, a side branch of the Beneden Merwede. 1999 is the only year of monitoring for this water body. The species was always observed on sand with a high amount of mud, and was in one of the four samples accompanied by C. curvispinum. C. curvispinum was also observed in two samples without C. multisetosum. The Beneden Merwede was only monitored in 2002 and no corophiids were found there at all.

The larger water bodies in the south-western part of the delta (Grevelingen, Oosterschelde, Veerse Meer and Westerschelde) were frequently investigated for the macrozoobenthic species composition and were monitored intensively in a standardized way every spring and autumn since 1990. C. multisetosum was however never observed in the four basins, with an exception of a singular observation in 2006 in the northern part of the Oosterschelde near the 'Krammer' sluices. The Oosterschelde is a tidal saltwater body where the salinity varies between 27 and 32, dependent of the location. C. arenarium and M. sextonae are the dominant Corophiidae, C. bonellii (Milne Edwards, 1830), M. insidiosum and C. volutator are locally abundant, and also M. acherusicum is found. Considering the singular observation and the permanent high salinity in the Oosterschelde it is likely that C. multisetosum cannot maintain successfully in this area. The bordering lake Volkerak has a salinity of around 1. It is more likely that the observed specimen originated from there, or was transported with boats from other water bodies. Unfortunately we do not have recent

information on the species composition of the lake Volkerak, but we know that C. curvispinum was present there in 1991 (Frantzen et al., 1994). In the stagnant saltwater lake Grevelingen, salinity since the early 1970s fluctuated between 21 and 34, and since the early 1990s between 26.5 and 34. These continuously high salinities probably make the environment unsuitable for C. multisetosum. In the Grevelingen, M. insidiosum is the dominant corophiid species, Crassicorophium bonellii is abundant, Monocorophium sextonae and M. acherusicum were found in low densities and C. volutator has been observed. In the stagnant lake Veerse Meer, the salinity has always been lower than in the Oosterschelde. However, since the restoration of the connection with the Oosterschelde via a tube in 2004, the salinity has increased (Wijnhoven et al., 2010). The salinity as measured at the surface in the centre of the lake has increased from a yearly range of 10.5 – 21 to a yearly range of 22 – 30. In the Veerse Meer, M. insidiosum appeared to be the dominant corophiid, C. volutator can be abundant, and C. bonellii and C. arenarium were also found. No C. multisetosum was observed here.

The Westerschelde is a tidal inlet with a complete salinity gradient from oligohaline waters upstream in Belgium to euhaline waters in the pre-delta. Comparing the abiotic conditions to those observed at the Portuguese sites where C. multisetosum is very abundant (like Canal de Mira; e.g. Queiroga, 1990; Cunha et al., 2000), the Schelde estuary might be the most promising larger water body in the southwestern Netherlands (due to the full salinity gradient and the variation in dynamics) where the species can be present. The dominant Corophiidae in the system are however C. volutator and C. arenarium, of which particularly the first can be very abundant in densities up to more than 10,000 per $m^2$. Also M. insidiosum and A. lacustre are frequently found, M. acherusicum and C. bonellii are found especially in the western part, and A. lacustre in the eastern part. C. multisetosum might potentially inhabit the upstream oligohaline or fresh water zone in Belgium, but also for this region the species is

never recorded (Ysebaert et al., 1998; 2000). Recently, the species is however recorded for the canal Ghent-Terneuzen. This is a fresh to brackish water salinity gradient with salinities from approximately 1 to 3 extending over a distance of 31 km from Belgium into the Netherlands (Boets et al., 2011). Although the study involved monitoring from 1990 to 2008, the species was only found in 2005. This can however also be a result of the methodology, as species were collected by offering artificial substrates consisting of polypropylene bags filled with bricks of different sizes, which is particularly effective for mobile hard substrate species. It is unclear how abundant C. multisetosum is in this canal. The canal enters the Westerschelde, segregated by sluices, near Terneuzen where the salinity varies between 21 and 27. The prevailing salinity likely forms a barrier for natural extension of the populations into the Westerschelde at this location.

The observations of C. multisetosum from the southwestern part of the Netherlands are on the first sight from a variety of waters (table II). Although the species might be very flexible and can potentially cope with very different abiotic conditions, it is expected that the species will fit in a certain niche, which might be similar in different types of waters. As this also accounts for other species, it is expected that C. multisetosum will fit in certain communities. In this way, the associated species might indicate whether different waters belong to a certain type at which certain characteristics determine the species composition or suitability of the environment to species. Other, seemingly for the communities' relative unimportant, characteristics of the environment, may vary within certain limits without implications for the species composition. In the southwestern part of the Netherlands, C. multisetosum is frequently found in a community dominated in numbers by Tubificidae, the bivalves Pisidium sp. and Corbicula sp., and the oligochaetes Limnodrilus sp. and Potamothrix moldaviensis Vejdovský & Mrázek, 1903, such as in the Hollandsch Diep and the Amer, and several of the locations in the Hollandsche IJssel, the Oude Maas, Wantij, and

in 2001 in the Haringvliet. In the Hollandsche IJssel, the Oude Maas and Wantij, C. multisetosum is also found in association with a community dominated by the midge Thalassosmittia thalassophila (Bequaert & Goetghebuer, 1913), the amphipod Gammarus tigrinus Sexton, 1939, the bivalve Corbicula sp., Tubificidae and C. curvispinum. C. curvispinum is, as indicated before, probably more a species competing with C. multisetosum for the same niche. This community is probably specific for hard substrates and soft substrates dominated by larger grain sizes, while in the same type of water, the earlier described community can be found on sediments containing mud. The two communities are therefore specific for larger riverine environments in the freshwater zone. The described community of hard substrates in also found in the river Lek. In 1995 and 1997, C. multisetosum is found in the Haringvliet in a community dominated by the midge Lipiniella araenicola Shilova, 1961, the snails Valvata piscinalis (O. F. Müller, 1774), and Potamopyrgus antipodarum and the bivalve Pisidium sp.. This might be a variant of the described soft sediment community, but more specific for larger open waters, with low water currents.

A complete different community is found in the Nieuwe Waterweg, and a transition towards the two earlier described communities can be found at some localities in the Oude Maas. This is a community of the riverine mesohaline environment, dominated by the polychaete Nereis sp., the barnacle Amphibalanus improvisus (Darwin, 1854) and the corophiid A. lacustre.

## The Netherlands compared to the rest of Europe

C. multisetosum is recorded from a variety of waters. Where Stock mentions that the species avoids larger open standing waters, this is not supported by the current recordings of the species in the Hollandsch Diep and Haringvliet indicating that the species can do well at a

minimum of current. At low currents the species is however only found in shallow water, as also found by Schütz (1969). The new recordings from the Netherlands (table II) include several observations from hard substrates including stones and vegetation. This is in line with observations of other authors of the species building tubes on hard surfaces (e.g. Stock, 1952; Schütz, 1969; Taylor, 1994). Only at the Iberian Peninsula this behaviour and this substrate choice are not recorded (table III). This might raise the question whether the C. multisetosum from Spain and Portugal is the same species, or at least might be a different population as the one observed in most northwestern European waters.

The new recordings in this study are also from different types of soft substrate, especially mud and fine sands, which is in line with the findings in other countries (e.g. Jażdżewski, 1976; De Grave & Wilkins, 1994; Cunha & Moreira, 1995). However, again on the Iberian Peninsula, the species apparently does not prefer but is found on coarser substrates (Chainho et al., 2006; Sánches-Moyano & García-Asencio, 2010). Also in Ireland C. multisetosum is found on coarse gravel, however in combination with soft mud (Cott et al., 2007). C. multisetosum present on coarse substrates in a part of its geographic region of distribution might be a matter of competition lacking at the Iberian sites, and being more severe at the north-western sites e.g. by C. curvispinum and C. volutator. Again one can also explain the pattern by suggesting different species, at which the Iberian one might even be introduced recently in other regions, like Ireland.

In Germany, Poland and most sites in the UK, C. multisetosum is recorded from freshwater, and oligohaline and lower mesohaline brackish water (fig. 5A). This is similar to C. multisetosum found in the riverine biotopes and the Haringvliet in the southwestern part of the Netherlands. Only Hart (1930) recorded salinities well above 20 and called the species at that time C. volutator (indicated as a light grey bar in fig. 5A). From a salinity point of view one might wonder again whether at least at the high salinity sites the species indeed was C.

volutator. However, in southern Europe (Portugal, Spain and Arcachon basin in France), observations well exceed salinities observed in northwestern Europe. Again such a pattern can be explained by suggesting two separated species, but also differences in competition or better salinity tolerance at higher temperatures are an option. The new observations in the Netherlands (table II) feed the discussion. Particularly the Nieuwe Waterweg case with salinities well above 20 but with flourishing populations of C. multisetosum is remarkable. Is the tolerance of C. multisetosum to salinity also in northwest European regions actually larger, but depending on competition or increased water temperatures as is very likely the case as indicated by studies of Wijnhoven et al. (2008) and Leuven et al. (2009)? Or is it that there are indeed two species or differentiated populations with recent introduction of the Iberian variant in the Netherlands? Another recent observation of C. multisetosum at higher salinity is the singular observation of the species in the northern branch of the Oosterschelde (indicated as a dashed bar in fig. 5A). It is very likely that no population of C. multisetosum is present in the Oosterschelde, as is also the case for the higher salinity waters of the Grevelingen and lake Veerse Meer. That would be in line with the recording of 25 as the upper salinity limit for reproduction (Cunha et al., 2000c), and probably an even lower upper salinity limit for the northwestern populations. The specimen is probably introduced from another region, e.g. via the sluices coming from the Krammer-Volkerak (the freshwater basin situated north of the location of observation separated by sluices; although no recent information about Corophium presence is available), or from other waters using boats as vector. The recording of C. multisetosum presence in the middle of the North Sea, i.e. at the Frisian front (Dewicke et al., 2002), is highly doubtful as even at the Iberian Peninsula the species does not persist at salinities of 34.2. Also the depth at which the species is found is completely out of range (indicated with an X in fig. 5). The recording might be a result of misidentification.

A species like C. multisetosum that is this tolerant towards different salinities but that is geographicly bordered in the Baltic region, where salinity cannot be the problem, might be hampered by temperature. The success of Corophiidae in certain environments is probably related to high turnover and productivity. The optimal breeding temperature of C. multisetosum is recorded on 18 °C with more intense breeding between 15 and 20 °C (Cunha et al. 2000a; 2000c). The period with temperatures above 15 °C in areas north of Germany and Poland might be just too short to produce sufficient offspring. However it seems that recent range extensions in the Baltic region, e.g. towards Lithuania, have occurred. This might be the result of increasing water temperatures in the Baltic region, leading to extended periods of suitable breeding conditions (i.e. above 15 °C) as is shown for the Curonian and Vistula Lagoons (Aleksandrov, 2010). Not only at its northern distribution limits but also in other regions an extension of the breeding season can be in favour of the species, as it can increase its competitive abilities relative to other Corophiidae. Wijnhoven et al. (2008) recorded an increase of the water temperature of 0.0348 to 0.0522 °C per year during the period 1959 – 2005 for the Haringvliet - Hollandsch Diep – Biesbosch area. Similar patterns have been observed in the Rhine branches (Leuven et al., 2009) which indicates that the breeding season for C. multisetosum indeed has increased significantly during the last decennia in the entire Dutch southwestern delta. This might explain why C. multisetosum is found to be increasingly successful in the Netherlands and why it did not appear to be so successful before. There is no indication that an extension of the distribution range of C. multisetosum in the south is limited by higher temperatures. Whether the species is present on the African continent is unknown. Natural extensions to the south and into the Mediterranean are probably only hampered by a salinity barrier. This seems to be confirmed by the recent recording of the species for the island of Menorca (Lucena-Moya et al., 2010), where it is likely that the species is coincidently introduced (e.g. by boats or with water plants). Further

range extensions via coincidental introductions towards the eastern Mediterranean are likely to occur and probably just a matter of time.

Other aspects that might explain patterns in presence and absence of C. multisetosum are pollutant levels or levels of eutrophication. C. multisetosum seems to be relatively tolerant towards pollutants and nutrients (e.g. as observed in some of the Dutch and Spanish waters which cannot be considered clean; e.g. Wijnhoven et al., 2008; Tueros et al., 2009), but it might be that recent range extensions in the Netherlands are also made possible by the improvement of the environmental conditions (Wijnhoven et al., 2008). Particularly the competitive abilities under certain environmental conditions might increase at better environmental conditions. As indicated by the situation in the Dutch waters and the absence of C. multisetosum from the Westerschelde, particularly C. volutator seems to be a competing species, particularly favoured at higher salinity. At the lower salinity range C. curvispinum drives C. multisetosum to the soft sediment substrates.

C. multisetosum is recorded in association with A. lacustre in several studies (e.g. Ingle, 1963; Schütz, 1969; Taylor, 1994). Whereas the two species do not seem to be direct competing species, A. lacustre might be in favour at lower salinity as well (Stock, 1952; Jażdżewski, 1976). Among the new recordings for the Netherlands the two species are found together at the Nieuwe Waterweg and the Oude Maas. The species are part of the communities of the riverine mesohaline environment there. A positive regression between the densities of the two species on stones indicates that the two do not seem to be competitors (fig. 3). Moreover, A. lacustre is only found once as the only corophiid species on stones, whereas C. multisetosum is found several times in the absence of A. lacustre. On muddy substrate, C. multisetosum appears to be the dominant species over A. lacustre with A. lacustre only present in 18 % of the samples with Corophiidae in which also always C. multisetosum was present. More upstream, C. multisetosum seems to face a real competitor,

viz. C. curvispinum. C. curvispinum might show a larger productivity and might be less sensitive to enriched and polluted conditions, especially in the riverine environments of the freshwater zone. C. multisetosum disappears from hard substrates when C. curvispinum is present, but is still present on soft sediments, in particularly at oligohaline conditions. C. multisetosum is especially found in the absence or at low densities of C. curvispinum (fig. 4). But the opposite is also true in the same waters. C. curvispinum was especially found in the absence or at low numbers of C. multisetosum. C. curvispinum is dominant on stones and in vegetation (fig. 4), but on sandy or muddy substrates both species are as successful, however generally not found at the same location. Of course, this only accounts for the waters with some salinity influence; going into the oligohaline waters C. multisetosum lacks and C. curvispinum is the only flourishing corophiid species. The success of C. multisetosum in the oligohaline zone in Portugal might be due to the absence of C. curvispinum in those waters.

Further, C. multisetosum is frequently found together with C. volutator, where even a few individuals seem to survive there where C. volutator completely dominates the system (Ingle, 1963; Jażdżewski, 1976). However in the Dutch situation we did not find both species together and it seems that at least so far, C. volutator prevents C. multisetosum entering higher salinity waters. Comparing the communities in which C. multisetosum is found in the Dutch delta to those in other European regions, the species composition at the river Suir in Ireland (De Grave & Wilkins, 1994) shows large similarities with the community as described here as typical for in particular the soft sediments in riverine environments of the freshwater zone. A species found in association with C. multisetosum at several sites over Europe; P. antipodarum (Cazaux & Labourg, 1973; De Grave & Wilkins, 1994; Taylor, 1994; Cunha & Moreira, 1995), was also present in what is described here as the community of the riverine environments of the freshwater zone in the Netherlands, but did not reach densities as high as at the other sites. Further it is found difficult to find the relatives of the associated fauna

observed in Portugal, also in the Netherlands, to indicate potentially suitable habitats for C. multisetosum at higher salinities.

## Hypotheses about the typical pattern of recordings

The European distribution map (fig. 1) shows a remarkable gap in the recordings on C. multisetosum at almost the entire Atlantic coast line of France separating northwestern and southern populations of C. multisetosum. Further some striking differences in the habitats and ecology of the Iberian and the northwestern European populations have been observed. Moreover, particularly the last years C. multisetosum appears to be present in several regions of which it was not known before and these seemingly range extensions might go beyond the Atlantic, North Sea and Baltic coasts. This might make one wonder what is the region of origin of the species and are all recordings of the same species, or at least are we dealing with differentiated populations? It can be argued whether all European regions are monitored for macrobenthic organisms evenly intense and if possibly the attention for the species has increased. It is not sure that the observed pattern is really according to the timeline of distribution and introduction over Europe. It is very well possible that the species has been present along the Portuguese and Spanish coasts long before the early 1980s. Another hypothesis might be that the species has gradually populated the Iberian waters after the early 1970s originating from the basin near Arcachon after its introduction there, in accordance with the direction of the gulfstream along the coast. The species might however also have been overlooked for a while in some northwestern regions. But for several regions and the Dutch delta waters in particular it is clear that the species has been absent for a long time. C. multisetosum lacking from a large part of the central European coast suggests an introduction from the north to the south or vice versa. But as also the ecological niche of the northern and

the southern populations seems to differ, it might be that both populations are separated already for quite some time, if it is the same species we are talking about. The presence of C. multisetosum in Mexico puts the observations in a new perspective. In that case the options are 1) C. multisetosum being an eastern Atlantic species, introduced to the American east coast; 2) C. multisetosum being an amphi-atlantic species with a distribution along both the east and the west Atlantic coast; or 3) C. multisetosum being a western Atlantic species and an exotic species in Europe. All options might involve separations of populations for quite some time, and introductions into Europe of differentiated populations. An extensive genetic study and some species verifications are necessary to clarify the case. An origin from the Gulf of Mexico could elucidate the observation that C. multisetosum populations flourishes in warmer areas more than in temperate areas. The pattern of observations and years of occurrence show a remarkable resemblance with those of the brackish water mussel Mytilopsis leucophaeata (Conrad, 1831), which originated from the Gulf of Mexico and temperate Atlantic coast of North America (Van der Velde et al., 2010; Heiler et al., 2010). Its extension is also from first recordings in Belgium, the Netherlands, northern France and Germany towards the Baltic Sea and later on Great Britain, southern extension till in the Mediterranean, thus in subtropical as well as temperate areas.

## Conclusions

Corophium multisetosum is distributed over a large geographic range and is found in a variety of waters and environmental conditions. The current study shows that the first observation of the species from the southwestern part of the Netherlands was made in 1993, followed by an increasing number of observations from known and new areas in the region. This raises the question whether the species has extended its range in this part of the

Netherlands, or that the species was overlooked before. Taking monitoring intensity into account it can be concluded that C. multisetosum must have extended its range into the southwestern part of the Netherlands before, but not long before 1993. Range extension must have been possible by introduction via shipping activities or with water plants, but successful establishment is probably made possible by a gradual increase of the water temperature and an improved water quality during the last decennia leading to an extension of the breeding season and an improved competitive position. The riverine fresh- to mesohaline waters are potentially all suitable habitats, which are gradually colonized during the 1990s. However the conditions are not such that C. multisetosum becomes a dominant species here, as is the case in several estuaries in Portugal and Spain. The range of distribution and locations of occurrence are especially determined by competition with C. curvispinum, which when present excludes C. multisetosum from the shallow hard substrates and restricts the latter species to the soft substrates. In the oligohaline to mesohaline riverine waters C. multisetosum succeeds to withstand C. curvispinum and reaches the highest densities. For the larger basins to the south, the combination of high salinities (Oosterschelde, Grevelingen and Veerse Meer) and the abundant presence of C. volutator (Westerschelde), probably prevents the successful settlement of C. multisetosum in the region. Increased water temperature over the last decades has probably also led to range extensions at the northern limits of its geographic range of distribution (i.e. in the Baltic). Recently the species seems to have been introduced into the Mediterranean (i.e. Menorca) where further range extensions can be expected. The clear spatial separation between a northern (northwest European) and a southern (Iberian) population co-occurring with striking differences in displayed ecological ranges and behaviour at least suggests the presence of two differentiated populations separated for a long time. Most striking are differences in salinity tolerance and tube-building behaviour between populations. Recent recordings of the species from Mexico put the findings in a new

perspective and might indicate a pattern of (re-)introductions from one to the other continent and vice versa with specimens of different origin. A few range extensions in northwestern Europe might even be the result of the introduction from a southern subtropical population.

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FIGURE CAPTIONS

Fig. 1. Map of Europe with locations indicated where Corophium multisetosum Stock, 1952 is recorded with the first year of observation.

Fig. 2. Observations of Corophium multisetosum Stock, 1952 in the Netherlands. a, the regions where the historic observations of C. multisetosum are done by Stock (1952) and Mulder & Stock (1954), and the region with new recordings in the South-Western part of The Netherlands are indicated; b, locations where C. multisetosum is recently observed in the South-Western part of the Netherlands with the first year of observation indicated. Other monitored water bodies where no C. multisetosum is found are indicated in a small font.

Fig. 3. Relationships between Corophium multisetosum Stock, 1952 and Apocorophium lacustre (Vanhöffen, 1911) for the waters (Oude Maas and Nieuwe Waterweg) on the locations where they co-exist. a, relationship between the densities of both species in samples from mud and stones; whereas A. lacustre is almost always absent in the samples with C. multisetosum on mud, on stones a significant positive regression is found between the two ($p = 0.004$, $R^2 = 0.582$); b, proportional distribution of the presence of each of the species in the samples with Corophiidae.

Fig. 4. Relationships between Corophium multisetosum Stock, 1952 and Chelicorophium curvispinum (G.O. Sars, 1895) for the waters (Oude Maas, Nieuwe Waterweg, Hollandsch Diep, Haringvliet, Wantij, Amer and Hollandsche IJssel) for the locations where they co-exist. a, relationship between the densities of both species in samples from sand, mud, stones and vegetation with in the smaller graph a detail the low densities part of the larger graph.

When one species is present generally the other is absent or only present in small numbers. b, proportional distribution of the presence of each of the species in the samples with Corophiidae.

Fig. 5. Salinity (a) and depth (b) range as observed for Corophium multisetosum Stock, 1952 in different regions of its geographic range. A distinction has been made between the historic recordings for the Netherlands and the recordings for the Netherlands since the early 90s. Intertidal locations have been designated a depth of 0 m.

TABLES

Table I

Years in which sampling of macrobenthic fauna has taken place in each of the basins. The geographic positioning of the basins is indicated in Fig. 2b. X = Corophium multisetosum Stock, 1952 observed in at least one of the samples; 0 = no C. multisetosum found.

| | 1990 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 2000 | 01 | 02 | 03 | 04 | 05 | 06 | 07 | 08 | 09 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hollandsche IJssel | | | | | | | | | | X | X | 0 | 0 | 0 | X | | | | | |
| Nieuwe Waterweg | | | | | | X | | | | X | | | | X | | | | | | X |
| Nieuwe Maas | | | | | | | | | | | 0 | 0 | 0 | | | | | | | |
| Lek | | | | | | 0 | | | | 0 | 0 | | | X | | | | | | |
| Oude Maas | | | | | | X | | | | X | | X | 0 | X | | 0 | | | | X |
| Wantij | | | | | | | | | | X | | | | | | | | | | |
| Beneden Merwede | | | | | | | | | | | | | 0 | | | | | | | |
| Boven Merwede | | | | | | | | | 0 | | | | | | | | | | | |
| Zand Maas* | | | 0 | | | | 0 | 0 | | | 0 | | | | 0 | | | | | |
| Haringvliet | | | | 0 | 0 | X | | X | 0 | | | X | 0 | 0 | | 0 | | | | |
| Hollandsch Diep | | | | X | 0 | | | | 0 | | | | 0 | | | | | | | |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dordtse Biesbosch | | | | 0 | | | | | | | | 0 | | | | | | | | |
| Sliedrechtse Biesbosch | | | | | | | | | | 0 | | 0 | | | | | | | | 0 |
| Brabantse Biesbosch | | | | 0 | 0 | | | | 0 | | | 0 | 0 | | | | | | | |
| Nieuwe Merwede | | | 0 | 0 | | 0 | | | | 0 | | | | 0 | | | | | | |
| Amer | | | | 0 | | | | X | | | | | | | | | | | | |
| Getijde Maas | | | 0 | | | | 0 | 0 | 0 | | 0 | 0 | | | 0 | | | | | |
| Grevelingen | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Oosterschelde | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 |
| Veerse Meer | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Westerschelde | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

* Situated east of the Boven Merwede, out of the map range of fig. 2B.

Table II

New recordings of Corophium multisetosum Stock, 1952 in the Netherlands, indicating the year of observation, waterbody characteristics (type, salinity, other corophiid spececies observed during the same campaign), sample site characteristics (substrate and depth) observed densities of C. multisetosum, number of samples with C. multisetosum and possible co-occurring Corophiidae in the same samples.

| Water body | Year | Water type | Salinity | Substrate* | Depth (m) | Densities ($n/m^2$) | N samples | Other Corophiidae | Corophiidae in same sample |
|---|---|---|---|---|---|---|---|---|---|
| Hollandsch Diep | 1993 | large freshwater lake | 0.2 | muddy sand | 1.1 - 2.8 | 5 - 11 | 2 | C. curvispinum | C. curvispinum |
| Amer | 1997 | river | 0.4 | mud with sand | 1 .2 | 11 | 1 | C. curvispinum | C. curvispinum |
| Haringvliet | 1995 | large freshwater lake | 0.1 - 0.3 | mud - sand | 0.9 - 6 | 5.7 - 16.7 | 5 | C. curvispinum & C. volutator | C. curvispinum |
| | 1997 | | | mud - sand | 0.5 | 12 - 83 | 2 | C. curvispinum | |
| | 2001 | | | mud - fine sand | 1.5 - 2.7 | 66.7 - 133.3 | 4 | C. curvispinum | |
| Nieuwe Waterweg | 1995 | canal with salinity gradient | 14.4 – 23.4 | mud, stones & vegetation | 0.03 - 1 | 7 - 744 | 5 | C. curvispinum & A. lacustre | C. curvispinum & A. lacustre |
| | 1999 | | | mud, stones & vegetation | 0.4 - 1.2 | 8 - 3552 | 6 | C. curvispinum | A. lacustre |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | & A. lacustre | |
| | 2003 | | | mud & stones | 0 | 9 - 32 | 5 | C. curvispinum | A. lacustre |
| | | | | | | | | & A. lacustre | |
| | 2009 | | | fine sand with little mud & stones | 0 - 0.5 | 90 | 1 | | |
| Hollandsche | 1999 | river | 0.2 | stones | 0.5 | 8 | 1 | C. curvispinum | |
| IJssel | 2000 | | | stones | 0.5 | 1 | 1 | C. curvispinum | C. curvispinum |
| | 2004 | | | clay - sand & stones | 0.2 - 2.5 | 1 - 527.8 | 6 | C. curvispinum | C. curvispinum |
| Lek | 2003 | river | 0.1 - 0.3 | sand & stones | 0 | 3 - 321 | 6 | | |
| Oude Maas | 1995 | river | 0.2 – 5.4 | mud, sand & vegetation | 0.8 - 1 | 1 - 44 | 3 | C. curvispinum | C. curvispinum |
| | 1999 | | | mud, sand, vegetation & stones | 0.5 - 1.2 | 1 - 939 | 7 | C. curvispinum | C. curvispinum |
| | 2001 | | | mud - sand with little mud | 0.29 - 13.15 | 5.8 - 368.0 | 9 | C. curvispinum & A. lacustre | A. lacustre |
| | 2003 | | | mud, sand, vegetation & stones | 0 | 1 - 3720 | 12 | C. curvispinum & A. lacustre | C. curvispinum & A. lacustre |
| | 2009 | | | sandy mud with clay | 0 - 0.5 | >100 | 1 | | |
| Wantij | 1999 | small river | 0.7 | muddy sand | 2 - 4.2 | 5.7 - 22 | 4 | C. curvispinum | C. curvispinum |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Oosterschelde | 2006 | tidal saltwater bay | 27 - 32 | muddy fine sand with shells | 6.6 | 66.7 | 1 | C. arenarium, M. sextonae, C. bonellii, M. insidiosum, C. volutator, M. acherusicum |

* Mud – sand indicates that C. multisetosum is observed on substrates covering the whole gradient from mud to sand and the various types in between.

Table III

Range of substrates and water types and the mode of living observed for Corophium multisetosum Stock, 1952 in different regions of its geographic range. A distinction has been made between the historic recordings for the Netherlands and the recordings for the Netherlands since the early 90s.

| | **Poland & Germany** | **Netherlands (historic)** | **United Kingdom & Ireland** | **Portugal & Spain** | **Netherlands (recent)** |
|---|---|---|---|---|---|
| **Substrate:** | | | | | |
| mud | x | x | x | | x |
| muddy sand | x | x | x | x | x |
| medium sand | x | x | x | x | x |
| coarse sand | | | x | x | |
| vegetation | x | x | x | | x |
| hard substrate | x | x | x | | x |
| **Mode of living:** | | | | | |
| In sediment | x | x | x | x | x |
| Tube building | x | x | x | | x |
| **Water type:** | | | | | |
| canal | x | x | | x | x |
| river | x | x | x | x | x |
| estuary | | | x | x | (x) |
| lagoon/lake | x | | | x | (x) |
| sea | | | | | (x) |

Table IV

Recordings of Corophium multisetosum Stock, 1952 in literature including year, place and country of observation. Year of first observation for the location is shown when noticed in the article. For some regions it is unclear when C. multisetosum is first observed than an indication is given of when the species was present for sure. Several articles refer to earlier work, observations or unpublished observations. These are indicated when relevant towards the first year of observation. Locations indicated in map of Europe (fig. 1).

| Reference | Reported by | Country | Region | Area | First observation | Other observations |
|---|---|---|---|---|---|---|
| De Grave & Wilkins, 1994 | Ingle | UK | | | 1904 | |
| Stock, 1952 | Stock (vessel Meerval) | Netherlands | Zuiderzee | near Eem | 1921 | |
| Stock, 1952 | Stock (vessel Meerval) | Netherlands | Zuiderzee | near Eem | 1926 | |
| Hart, 1930 | Hart | England | North Sea | Whitby harbour | 1929 | |
| Ingle, 1963 | Spooner re-examined Crawford (1937) | England | English Channel | River Tamar | 1937 | |
| Ingle, 1963 | Spooner | England | English Channel | River Plym | 1938 | |
| Stock, 1952 | Stock | Netherlands | North Sea | North Sea Canal | 1950 | |
| Stock, 1952 | Stock | Netherlands | North Sea | North Sea Canal | 1951 | |
| Stock, 1952 | Stock | Netherlands | North Sea | North Sea Canal | 1952 | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Schütz, 1969 | Schütz | Germany | Baltic Sea | Nordostseekanal (Canal of Kiel) | 1952 | |
| Mulder & Stock, 1954 | Mulder & Stock | Netherlands | North Sea | Normert (Wieringen) | 1954 | |
| Jażdżewski, 1976 | Spooner | UK | | | 1957 | |
| Ingle, 1963 | Crawford | England | English Channel | River Adur | <1959 | |
| Ingle, 1963 | Gurney | England | North Sea | River Bure | <1959 | |
| Taylor, 1994 | Taylor | England | North Sea | River Bure | | 1990-1992 |
| Ingle, 1963 | Gurney | England | North Sea | River Yare | <1959 | |
| Ingle, 1963 | Anderton | England | Straits of Dover | River Stour | 1959 | |
| Ingle, 1963 | Ingle | England | Straits of Dover | River Stour | 1959 | |
| Jażdżewski, 1976 | Jażdżewski | Poland | Baltic Sea | Martwa Wisla (Dead Vistula) | 1962 | |
| Jażdżewski, 1976 | Ingle | UK | | | 1963 | |
| Ingle, 1963 | Crawford | England | English Channel | Whitsam and Haye | | |
| Ingle, 1963 | Crawford | England | English Channel | Cotehele Quay | | |
| Ingle, 1963 | Crawford | England | English Channel | Calstock | | |
| Jażdżewski, 1976 | Hamond | UK | | | 1967 | |
| Jażdżewski, 1976 | Jażdżewski | Poland | Baltic Sea | Canal mouth Resko lake | 1968 | |
| Cazaux & Labourg, 1973 | Cazaux & Labourg | France | NE Atlantic | Teich - fishpond near Arcachon | 1973 | |
| Altuna et al., 1983 | Altuna et al. | Spain | NE Atlantic | Ria de Bidasoa (Guipuzcoa) | | 1982 |
| Junoy & Viéitez, 1990 | | Spain | NE Atlantic | Ria de Foz | | 1984 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Queiroga, 1990 | Queiroga | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | 1985-1986 |
| Queiroga, 1990 | Marques & Bellan-Santini | Portugal | NE Atlantic | Sado estuary | | 1985 |
| Queiroga, 1990 | Marques & Bellan-Santini | Portugal | NE Atlantic | Mondego estuary | | 1985 |
| Cunha & Moreira, 1995 | Cunha & Moreira | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | 1988-1989 |
| Cunha et al., 2000a | Cunha et al. | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | 1988-1989 |
| Bäthe, 2007 | Herbst & Bäthe, 1993 | Germany | North Sea | River Weser | 1987 | |
| Taylor, 1994 | | England | North Sea | River Bure | | 1990-1992 |
| Hayward & Ryland, 1990 | | England | English Channel | | | |
| Van Dam et al., 2007 | | Netherlands | North Sea | North Sea Canal (Noorder IJ-plas) | | 1991 |
| Anonymus, 1993 | | Spain | NE Atlantic | Ria Fazouro (Lugo) | | |
| Cunha et al., 2000b | Chatwin, 1991 | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | |
| Cunha et al., 2000b | Flach 1992, 1993, & Flach and de Bruin, 1993 | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | |
| Cunha et al., 2000b | Cunha unpublished | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | |
| De Grave & Wilkins, 1994 | De Grave & Wilkins | Ireland | NE Atlantic | River Suir | | 1994 |
| Dewicke et al., 2002 | | Netherlands | North Sea | Frisian front (North Sea) | 1994 | |
| Janta, 1995 | several authors | overview | in general | | | |
| Cunha et al., 1999 | Cunha et al. | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | 1995-1996 |
| Ré et al., 2007 | Ré, 1996 | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Lenoir et al., 1996 | | Netherlands | North Sea | North Sea Canal (Noorder IJ-plas) | | 1996 |
| Peeters et al., 2000 | | Netherlands | North Sea | North Sea Canal | | 1998 |
| Zettler, 2002 | Zettler & Gosselck et al. | Germany | Baltic Sea | Greifswalder Bodden (Mecklenburg-Vorpommern) | | 1997 |
| Zettler, 2002 | Zettler & Gosselck et al. | Germany | Baltic Sea | Peenestrom (Mecklenburg-Vorpommern) | | 1998 |
| Buckley et al., 2004 | Buckley et al. | England | Straits of Dover | Kentish Stour Estuary | 1999 | |
| Cunha et al., 2000c | | Portugal | NE Atlantic | Canal de Mira (Ria de Aveiro) | | |
| Quintino et al., 2000 | | Portugal | NE Atlantic | | | |
| Rodrigues & Quintino, 2000 | | Portugal | NE Atlantic | | | |
| Sánchez-Moyano & García-Asencio, 2010 | | Spain | NE Atlantic | Guadiana estuary (Spanish south-coast) | 2000 | |
| Chainho et al., 2006 | | Portugal | NE Atlantic | Mondego estuary | | 2001 |
| Gomes de Sousa, 2003 | | Portugal | NE Atlantic | Rio Lima | | 2002 |
| Arcas, 2004 | | Spain | NE Atlantic | River Miño estuary | | |
| Castro et al., 2006 | | Portugal | NE Atlantic | Ria de Aveiro | | |
| Casado-Martínez et al., 2006 | | Spain | NE Atlantic | | | |
| Belzunce-Segarra et al., 2008 | | Spain | NE Atlantic | Basque estuaries | | |
| Grzelak & Kuklinski, 2010 | | Poland | Baltic Sea | Gulf of Gdansk | | 2007 |

| | | | | | |
|---|---|---|---|---|---|
| Cott et al., 2007 | Ireland | NE Atlantic | River Lee (Cork) | | 2007 |
| Van Wieringen, 2009 | Netherlands | North Sea | North Sea Canal | | 2009 |
| Sanz-Lazáro et al., 2008 | Spain | NE Atlantic | | | |
| Det Digitale Randers, 2006 | Denmark | Kattegat | Randers Fjord | 2002 | |
| Århus Amt, 2007 | Denmark | Kattegat | Randers & Mariager Fjord | | |
| Boets et al., 2011 | Belgium/Netherlands | North Sea | Canal Ghent-Terneuzen | 2005 | |
| Raudonikis et al., 2009 | Lithuania | Baltic Sea | South coast | 2009 | |
| Ardisson & Castillo-Fernández, 2004 | Mexico | Gulf of Mexico | Progreso, Yucatán | 2004 | |
| Lucena-Moya et al., 2010 | Spain | Medditeranean | Menorca | 2008 | |

FIGURES

Fig. 1.

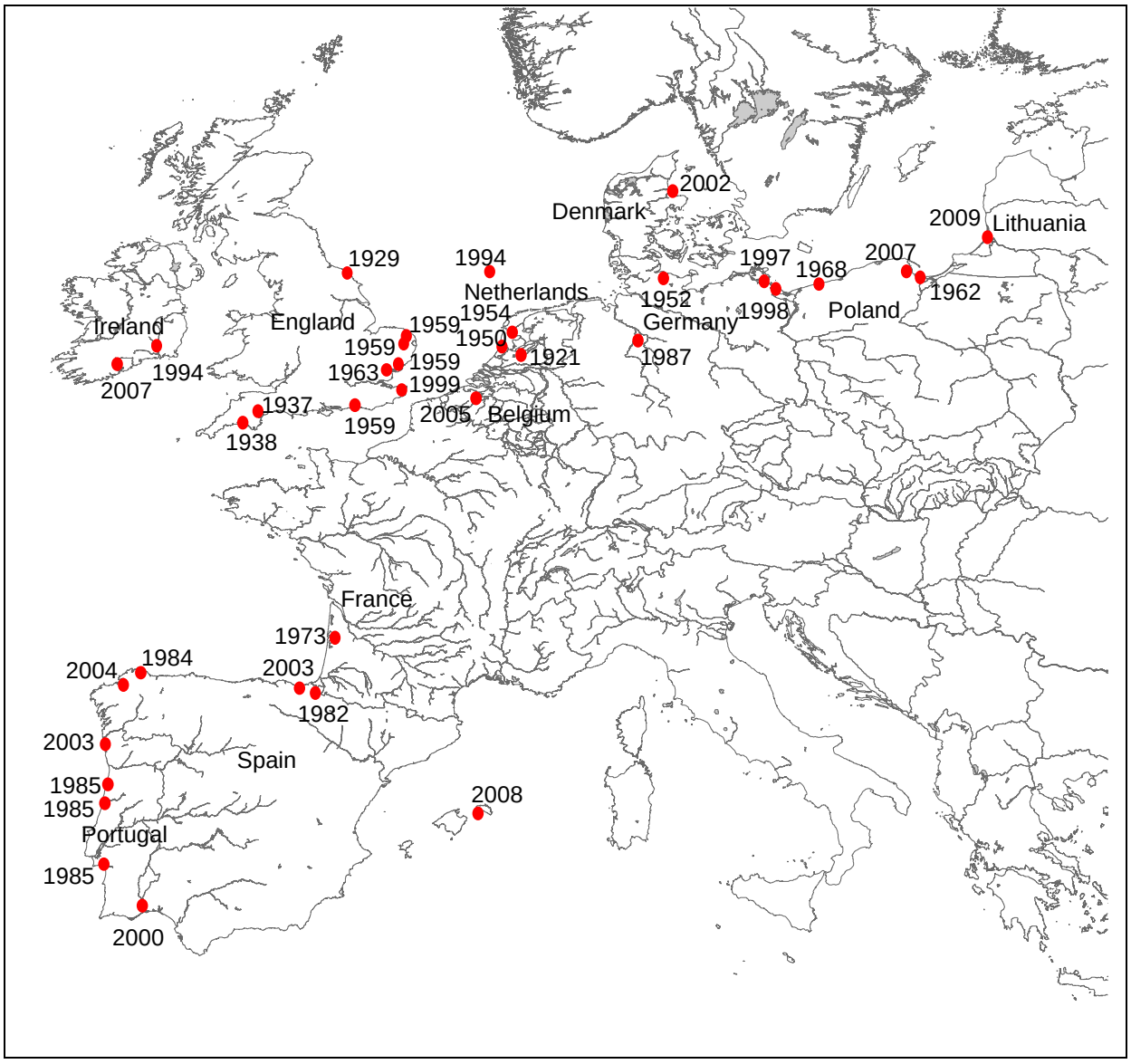


Fig. 2.

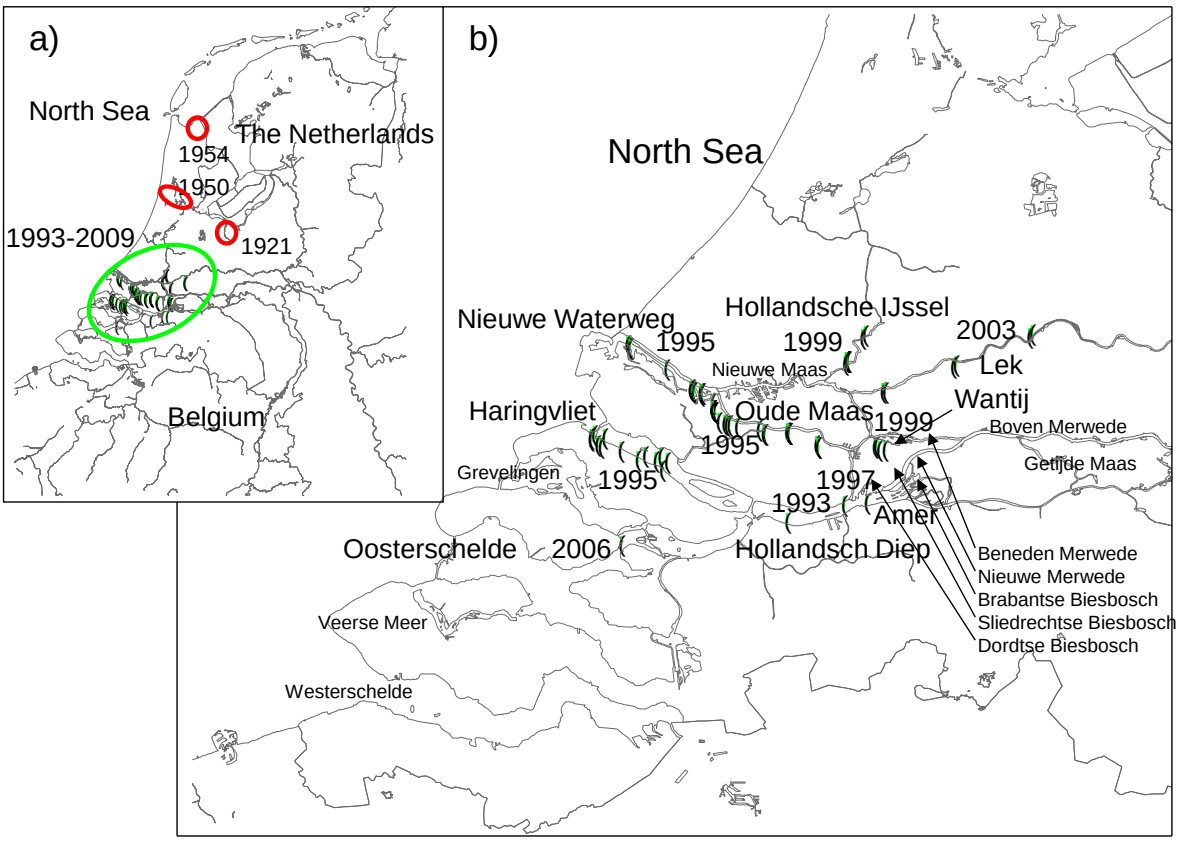

a)
North Sea
The Netherlands
1954
1950
1921
1993-2009
Belgium
b)
North Sea
Nieuwe Waterweg
1995
Hollandsche IJssel
1999
2003
Lek
Nieuwe Maas
Wantij
Haringvliet
Oude Maas
1999
Boven Merwede
1995
Grevelingen
1995
1997
Getijde Maas
1993
Amer
Oosterschelde
2006
Hollandsch Diep
Beneden Merwede
Nieuwe Merwede
Brabantse Biesbosch
Sliedrechtse Biesbosch
Dordtse Biesbosch
Veerse Meer
Westerschelde

Fig. 3.

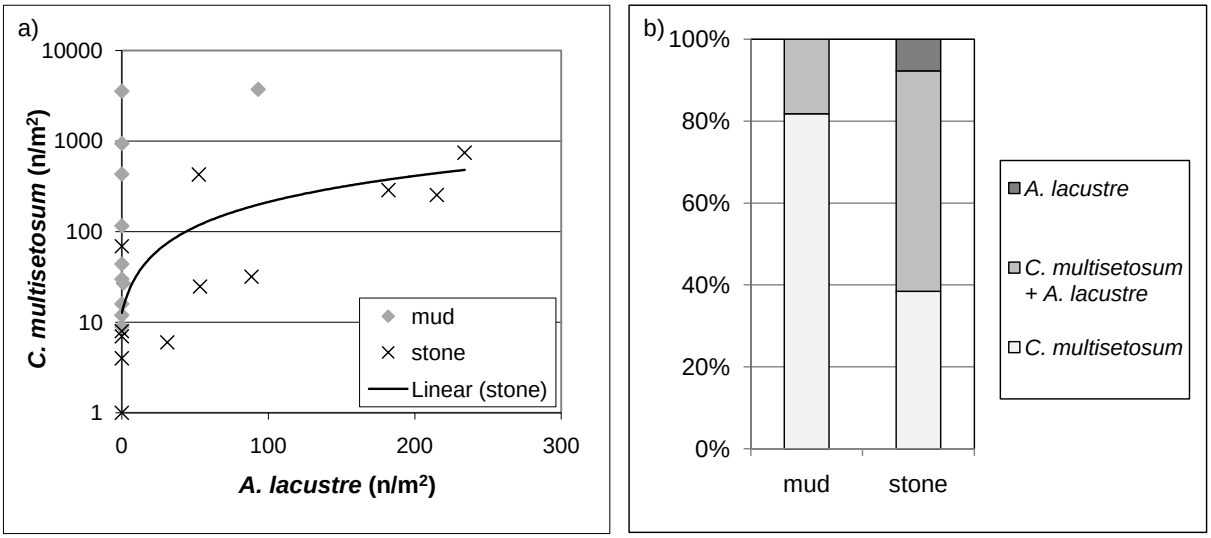

a)
10000
1000
100
10
1
C. multisetosum (n/m²)
0
100
200
300
A. lacustre (n/m²)
mud
stone
Linear (stone)
b)
100%
80%
60%
40%
20%
0%
mud
stone
A. lacustre
C. multisetosum + A. lacustre
C. multisetosum

Fig. 4.

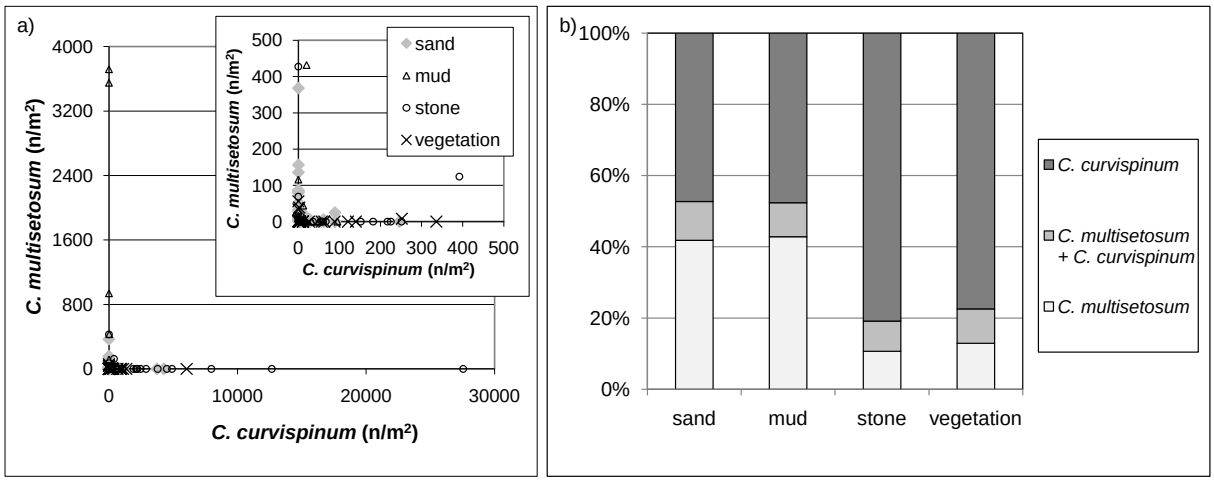
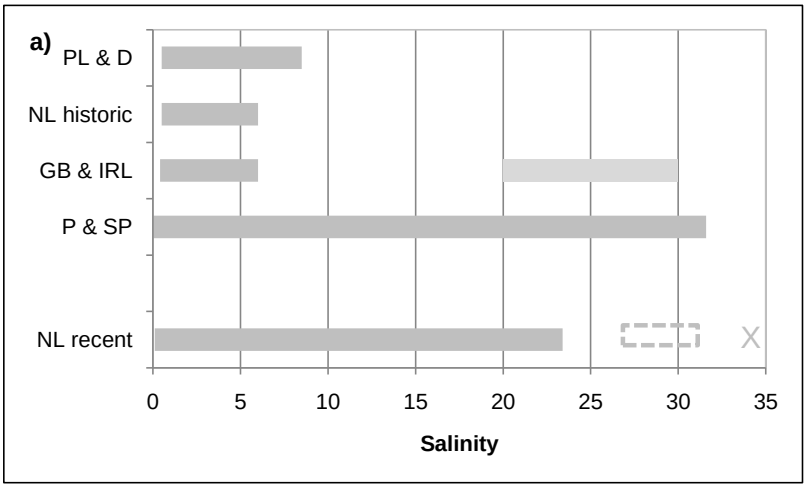
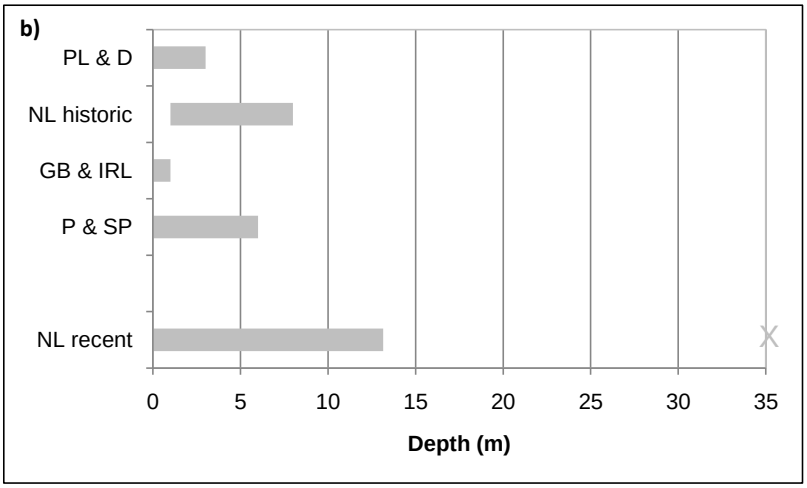

a)
4000
3200
2400
1600
800
0
C. multisetosum (n/m²)
0
10000
20000
30000
C. curvispinum (n/m²)
500
400
300
200
100
0
0
100
200
300
400
500
C. multisetosum (n/m²)
C. curvispinum (n/m²)
sand
mud
stone
vegetation
b)
100%
80%
60%
40%
20%
0%
sand
mud
stone
vegetation
C. curvispinum
C. multisetosum + C. curvispinum
C. multisetosum

Fig. 5.


a)
PL & D
NL historic
GB & IRL
P & SP
NL recent
0
5
10
15
20
25
30
35
Salinity


b)
PL & D
NL historic
GB & IRL
P & SP
NL recent
0
5
10
15
20
25
30
35
Depth (m)