

**Invasion ecology of *Marenzelleria cf. wireni* (Polychaeta; Spionidae)
in the Dutch Wadden Sea**

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Abstract

The first record of *Marenzelleria cf. wireni* in estuaries and coastal waters of the European continent was in the Ems Estuary (Eastern Dutch Wadden Sea) in 1983. In the western part of the Dutch Wadden Sea the first specimens was found in 1989.

In the Dollard, a brackish embayment in the inner part of the Ems Estuary with extensive intertidal flats, a significant population developed within a few years time. In 1989-1995 population density at sandy silt sediments amounted to 2 - 3000 *M. cf. wireni*, with a biomass of 8 - 16 grams ash-free dry weight per m². Before the introduction of *M. cf. wireni*, polychaetes made up only 24% of the total biomass, bivalves being dominant with 64%. After the establishment, polychaetes took a 58% share, leaving the bivalves with only 25%. Moreover, the total macrobenthic biomass had increased considerably. Muddy zones high in the intertidal zone act as a nursery area. Here, 130 000 juveniles were per m² found.

In other, generally more saline parts of the Dutch Wadden Sea, development of *M. cf. wireni* was less successful for many years. At the Balgzand intertidal flats in the westernmost part of the Dutch Wadden Sea, *M. cf. wireni* was first recorded in 1989. Here, it took longer, viz. till 1997, before a population of over 2000 *M. cf. wireni* per m² had developed. Locally at Balgzand, the population density showed a sharp increase since then. In the subtidal part of the Dutch Wadden Sea booming of *M. cf. wireni* was delayed till 1999.

The Dollard population of *M. cf. wireni* did strongly decrease after 1995. The remaining population is a few hundreds individuals, or c. 1.5 gram AFDW per m².

In this paper we will discuss the concept of an open niche being available for the invading species. There is no clear-cut case of competitive interaction between the newcomer and the autochthonous benthic community (e.g. *Nereis diversicolor*). Finally, the role of the newcomer in the estuarine food chain (juvenile flatfish, wader birds) will be discussed.

Key-words: Alien species, interspecific competition, empty niche, Ems estuary, brackish, intertidal

Introduction

Polychaetes of the genus *Marenzelleria* were first found in European waters in the Forth Estuary (Scotland) in 1982 (MCLUSKY *et al.*, 1993) and the Ems estuary (The Netherlands) in 1983 (ESSINK & KLEEF, 1988). After having been described initially as *Marenzelleria viridis*, the North Sea populations were identified as *Marenzelleria cf. wireni*. In the Baltic Sea, since 1985, also populations of *Marenzelleria* are present, these having been described as *Marenzelleria cf. viridis*. Parent populations of both species were identified along the Atlantic coasts of North America (BASTROP *et al.*, 1997). As for the North Sea populations an other possible origin, such as boreal and polar waters as well as a cryptic North Sea population (see BASTROP *et al.*, 1997; BICK & ZETTLER, 1997). Presently, *M. cf. viridis* is widely distributed over the Baltic Sea, and since 1996 also in the lower Elbe estuary (North Sea). *M. cf. wireni* occurs along the English east coast (ENO *et al.*, 1997) and along the eastern shores of the North Sea between northern Denmark and Belgium. For tentative dispersal routes see ESSINK (1999).

In the coastal waters of The Netherlands, *M. cf. wireni* has spread in SW direction. By 1991 populations were known from several locations in the Dutch Wadden Sea. In 1995-96, the Rhine-Meuse-Scheldt delta in SW Netherlands was populated, though with low numerical densities (ESSINK, 1999). The rather peculiar record of one specimen found in the 'Binnen IJ' harbour of Amsterdam in 1993 (D. Tempelman, pers. comm.) suggests ship-mediated dispersal from the Wadden Sea either via coastal waters and the IJmuiden-Amsterdam ship canal, or via Lake IJssel.

In the Dollard, a brackish embayment in the Ems estuary (easternmost part of the Dutch Wadden Sea), *M. cf. wireni* has shown a dramatic increase (ESSINK *et al.*, 1998), but in recent years the population strongly declined. In the western part of the Dutch Wadden Sea, the population density is still increasing. The purpose of this paper is to investigate to what extent the development of *M. cf. wireni* in the Dutch Wadden Sea followed and still follows characteristic patterns of invasive species. Furthermore, interactions between the invasive species and the indigenous fauna will be discussed.

Methods

Data on *Marenzelleria cf. wireni* were obtained from two monitoring programmes, taking benthos samples in late winter (ca. March) and early autumn (Aug.-Sept.) at intertidal flats as well as in the subtidal of the Dutch Wadden Sea including the Ems estuary. These programmes are 1) the Rijkswaterstaat Monitoring Programme (MWTL) and the long-term benthos dynamics programme at Balgzand intertidal flats run by the Netherlands Institute of Sea Research (Texel) (Figure 1)

At intertidal flats samples were taken by hand-operated corers along fixed transects (locations: B, PS, HP) or in fixed plots (location: GRON). At the subtidal location WWS samples were taken with a box corer along fixed transects. The samples were sieved in the field over 1 mm mesh. The remaining residue was either conserved in 6% neutralised formaldehyde before sorting and enumeration, or sorted without conservation within a few days after sampling. For further details on the sampling procedure see BEUKEMA *et al.*, 2000; DEKKER & DE BRUIN, 2000 and ESSINK, 1978.

Results

M. cf. wireni first developed in the Ems estuary at the boarder between Germany and The Netherlands. Within six years a population had developed at Dollard intertidal flats of 2 - 3,000 ind. m⁻² (Fig. 2a). Even higher densities, of over 100,000 of juveniles per m², were found at high muddy flats bordering the saltmarsh. These areas were found to function as "nursery" (ESSINK & KLEEF, 1993). *M. cf. wireni* remained abundant for another six years with a biomass of 10 - 14 g ash-free dry

weight (AFDW) m^{-2} (Fig. 2b) causing an almost doubling of the total macrozoobenthic biomass. During this period the composition of the benthic community also changed drastically. The proportion of bivalves in the total biomass decreased from 64 to 25%, whereas the share of polychaetes increased from 24 to 58% (ESSINK *et al.*, 1998). Since 1995, the population density decreased again, reaching mean densities of c. 500 ind. m^{-2} in 1999 (Fig. 2a) and a mean biomass of 2.1 g AFDW m^{-2} (Fig. 2b).

In the westernmost part of the Dutch Wadden Sea, at Balgzand intertidal flats, *M. cf. wireni* was first observed in 1989. In the years 1995-1999 the population increased (Fig. 3). Locally, along the eastern edge of Balgzand, densities were very high, reaching 13,000 ind. m^{-2} (equalling 63.1 g AFDW m^{-2}) in August 1999.

In the subtidal part of the western Dutch Wadden Sea (transects S1 - S3) densities remained low (a few tens/ m^2) since the first record in 1990 until in August 1999 a sudden increase to 6330 ind. m^{-2} (equalling 3.3 g AFDW m^{-2}) was observed (Fig. 4).

At the other monitoring stations at intertidal flats (PS, GRON - see Fig. 1) no significant populations of *M. cf. wireni* have developed; here, densities remained below 150 ind. m^{-2} (ESSINK, 1999).

Discussion

The general attributes of invasive aquatic species, their patterns of settlement and population development, and their impacts have been extensively described and reviewed (e.g. ASHTON & MITCHELL, 1989; CARLTON, 1996; LODGE, 1993; MOONEY & DRAKE, 1986; PARKER *et al.*, 1999; RIBERA & BOUDOURESQUE, 1995; RICCIARDI & RASMUSSEN, 1998; WILLIAMSON, 1996). In the following we will compare what we know of *M. cf. wireni* with respect to these general invasion characteristics. Where no specific information on *M. cf. wireni* is available we will refer to Baltic *M. cf. viridis* or North American *M. viridis*.

Attributes of a successful invader

Based on information from several publications RICCIARDI & RASMUSSEN (1998) have drawn up a list of 11 general attributes of invasive aquatic species. Among these are wide environmental tolerance, high genetic variability, short generation time, early sexual maturity, high reproductive capacity and a broad diet.

High environmental tolerance of *M. cf. wireni* is apparent from its oligo-mesohaline distribution pattern (ESSINK & KLEEF, 1988 and references therein). Of special significance certainly is its ability to cope with low ambient oxygen and even anoxic conditions by switching to anaerobic metabolic pathways and by formation of sulphide detoxification products (SCHIEDEK, 1999; SCHIEDEK *et al.*, 1997). A similar ability was found in the invader of the Baltic Sea *M. cf. viridis* (BOCHERT *et al.*, 1997b; SCHIEDEK, 1997).

Generation time in *M. cf. wireni* is considered to be 1 - 2 years (ESSINK & KLEEF, 1993). Spawning was observed in the Ems estuary to occur each year in spring (ESSINK & KLEEF, 1993) as was established for populations in Scotland (*M. cf. wireni*; ATKINS *et al.*, 1987) and Nova Scotia (*M. viridis*; GEORGE, 1966), but in contrast to Baltic Sea populations of *M. cf. viridis*, where spawning takes place in autumn. This difference may be genetically determined, but also be a result of different environmental conditions (BOCHERT, 1997).

Females of *Marenzelleria* produce 10,000 - 16,000 (GEORGE, 1966) or even 28,000 - 40,000 eggs (BOCHERT *et al.*, 1997a). Larvae have a long pelagic phase (4 - 12 weeks) enabling them to disperse to places suitable for benthic settlement (cf. BOCHERT, 1997). They also have a well developed physiological adaptation mechanism to cope with various environmental stress (BOCHERT *et al.*, 1997b).

Successful development of juveniles seems to be guaranteed by the selection of high muddy flats, rich in organic matter, as nursery areas; here up to 130,000 juveniles m^{-2} were found (ESSINK & KLEEF, 1993). In this kind of habitat, avoidance of epibenthic predators (e.g. shrimps, flatfish) may be effective as was indicated by predator exclusion experiments using cages in a USA saltmarsh (R.

Sarda, pers. comm.), and as shown for the tellinid bivalve *Macoma balthica* (BEUKEMA, 1993). The high muddy intertidal fringes of the Dollard, however, were demonstrated to be the preferred place for settlement of post-larvae of the flounder *Platichthys flesus* in May (KLEEF & JAGER, 1999). Besides copepods, these post-larvae consumed also appreciable amounts of polychaetes (VENEMA, 1998). No attempt, however, was undertaken to identify the polychaete fragments found; these may have included juvenile *Marenzelleria*.

According to GEORGE (1966), SANDERS *et al.* (1962) and WHITLATCH (1980) *M. viridis* is a selective deposit-feeder. Suspension-feeding, using its palps, is also possible (DAUER *et al.*, 1981). Also larvae of *Marenzelleria* have a broad food spectrum. Experiments, however, indicate these larvae to be adapted to relatively high food concentrations as usually present in estuarine areas (BURCKHARDT *et al.*, 1997).

Time-lag between arrival and population increase

The first record of *M. cf. wireni* in the Dutch Wadden Sea was in the sublittoral of the Ems estuary in 1983 (ESSINK & KLEEF, 1988). It lasted 2 years before at the Dollard intertidal flats the population started to increase significantly. Within another 3 years the population had dramatically increased, attaining densities of 2 - 3,000 m⁻² (Fig. 2) with a biomass of 8 - 16 g ash-free dry weight (AFDW) m⁻² in 1989-1994 (ESSINK *et al.*, 1998).

In the western Dutch Wadden Sea the first specimens of *M. cf. wireni* were recorded at Balgzand intertidal flats in 1989. By 1997, mean densities had increased till c. 500 m⁻² (Fig. 2). That is a slower development as compared with the one in the Dollard. With *M. cf. wireni* present in the western Dutch Wadden Sea since 1989, it lasted till 1998/1999 before the population really boomed.

A population introduced into a new suitable habitat will, as a rule, increase exponentially (WILLIAMSON, 1996). What then may be the cause of the slower development in the western Dutch Wadden Sea (Balgzand, subtidal) as compared with the Dollard? One explanation might be the difference in species richness of the respective benthic communities. According to the Eltonian invasion model species-poor communities are more open to introductions than rich ones (ELTON, 1958). The species richness of the benthic community of Balgzand intertidal flats is about 3 times as high as that of the Dollard. Also, macrobenthic biomass at Balgzand is higher than in the Dollard. Also, the subtidal of the western Wadden Sea has about twice the species richness as the Dollard intertidal flats. So, these data are in agreement with the Eltonian model. In line with this, WOLFF (1999) considers the paucity of species in brackish water systems as a factor favourable for establishment of introduced species. As a matter of fact, the Dollard as well as the eastern part of Balgzand are under direct influence of discharge of fresh water, from the River Ems and Lake IJssel, respectively.

The invasiveness of the Baltic Sea benthic communities, where colonisation by *M. cf. viridis* of various water bodies (Darss-Zingst estuary, Odra estuary, Vistula lagoon, Curonian lagoon, Gulf of Riga, Gulf of Finland) proceeded within a time frame of 2 - 5 years (OLENIN & LEPPÄKOSKI, 1999; GRUSZKA, 1999; KOTTA & KOTTA, 1998; STIGZELIUS *et al.*, 1997; ZETTLER, 1996, 1997; ZMUDZINSKI, 1996), may be explained by the presence of open spaces due to the not yet completed post-glacial recolonisation of the Baltic Sea (LEPPÄKOSKI, 1984). Up to 92 non-native species have been reported from the Baltic Sea, ca. 75% of which have established self-reproducing populations (LEPPÄKOSKI & OLENIN, 2000). The above mentioned major characteristics of invadible habitats, *viz.* low diversity of native species, and early successional, are among the ones listed by LODGE (1993). The invasion history of the San Francisco Bay and Delta ecosystem sheds a different light to the above concept. If paucity of species, as in the depauperate communities of San Francisco Bay and Delta, offers possibilities for invasions, how then must we understand the observed increase in invasion rate as more species became established in these waters? (COHEN & CARLTON, 1998)

Phases in population development

The Dollard population of *M. cf. wireni* clearly shows three developmental phases: 1) an initial increase, 2) a stabilisation period, and 3) a period of decline. In the literature the following main phases are described for an introduced species. After the arrival of the first immigrants the formation of a 'propagule', *i.e.* the minimum number of individuals able to found a reproducing population, is

essential (MACARTHUR & WILSON, 1967; ASHTON & MITCHELL, 1989). This is also called the settlement phase (RIBEIRA & BOUDOURESQUE, 1995). A subsequent steady increase of the immigrant population during their phase of expansion may lead to a stable equilibrium density. In some cases, these high densities become a pest to other species in the invaded community, e.g. the Zebra mussel *Dreissena polymorpha* (RICCIARDI *et al.*, 1998). Alternatively, the population may increase to very high densities, and then decline to lower levels ('boom and bust' development; PARKER *et al.*, 1999). RIBEIRA & BOUDOURESQUE (1995) describe a stabilisation either at a lower level than the maximum attained during expansion or at a plateau closed to that attained maximum. After establishment of a 'propagule' or further developed population in a water body, this population may act as a new 'donor' region for further invasions (CARLTON, 1996).

The development pattern of the Dollard population of *M. cf. wireni* is kind of intermediate between the 'increase to a stable equilibrium density' and the 'boom and bust' pattern. Although the macrobenthic community structure was significantly changed (see above), the species never became detrimental to other species, although there were some indications of competitive interactions with native species.

Competitive interaction with native populations

Concurrent with the development of an increasing population of *M. cf. wireni* at the intertidal flats of the Dollard not only the structure of the macrozoobenthic community changed (see above). Also, changes in abundance occurred in some species, especially the bivalves *Mya arenaria* and *Macoma balthica*, the amphipod *Corophium volutator* and the polychaete *Nereis diversicolor* (ESSINK *et al.*, 1998). The observed decrease of neither *M. arenaria* nor *M. balthica* could be related to the increase of *M. cf. wireni*. Concurrent with the increase of *M. cf. wireni* an increase of *C. volutator* was observed. A positive effect, however, of the newcomer *M. cf. wireni* on this native amphipod could not be made plausible. Only in the case of *Nereis*, during the period of high abundance of *M. cf. wireni* (1989-1994), a significantly negative relationship was found between the annual mean biomass of *M. cf. wireni* and that of *N. diversicolor* (+ *N. succinea*) (ESSINK *et al.*, 1998). This may be related to competition for food as both species are known as surface deposit-feeders and filter-feeders (GOERKE, 1966, 1971; DAUER *et al.*, 1981).

For the Tay estuary (Scotland), ATKINS *et al.* (1987) report negative correlations between *Marenzelleria* and all common zoobenthic species, and suggest *Marenzelleria* to be an isolated functional entity in the estuarine community

In Balgzand intertidal flats no negative correlations between the newcomer *M. cf. viridis* and native benthos species were found. A similar absence of apparent interaction was reported from several coastal waters of the Baltic Sea (KOTTA & KOTTA, 1998; KUBE & POWILLEIT, 1997; ZETTLER, 1996). One exception is the Vistula lagoon, where the soft bottom community structure was totally changed. Here, native chironomids and oligochaetes dramatically decreased in favour of *M. viridis* constituting 95% of the total community biomass (ZMUDZINSKI, 1996).

Since the decline of the *M. cf. wireni* population in the Dollard started in 1995, no obvious response of *N. diversicolor* was observed. It lasted till autumn of 1999 before a relatively good recruitment of *N. diversicolor* occurred causing the population density to increase from 260 to 673 ind. m⁻². So, in the benthic community of the Dollard a functional link between both species, if any, seems to be rather weak.

Availability of an empty niche

The settlement and subsequent development of an immigrant species will only be possible if there is ecological space (a vacant or empty niche) in the recipient area (WILLIAMSON, 1996). Otherwise, the newcomer has to suppress and take over the position of an established species.

The data from the Dollard do indicate to some extent the existence of a competitive interaction between *M. cf. wireni* and *N. diversicolor*. The latter species, however, was never replaced. Yet, *M. cf. wireni* succeeded in developing a significant population, causing a doubling of the total macrozoobenthic biomass. The observations in the Tay estuary by ATKINS *et al.* (1987) do not suggest a real functional interaction with the native fauna either. Therefore, we are apt to conclude that the *Marenzelleria* sp. has found vacant niches in European waters, with ample food available not exploited by other benthic species. At the subtidal transects S1 - S3 in the Dutch Wadden Sea, the late booming of *M. cf. wireni* in the second half of 1999 seems to be mediated by the strong decline earlier that year of the dense *Hydrobia ulvae* population (DEKKER & DE BRUIN, 2000), thus providing physical and ecological space. The availability of empty niches in the Baltic Sea is a likely result of the not yet completed post-glacial colonisation (LEPPÄKOSKI, 1984). In estuarine areas, with generally low species richness, empty niches may be available for species with a broad environmental tolerance (OLENIN & LEPPÄKOSKI, 1999; WOLFF, 1999). In artificial water bodies, absence of species with a similar diet may easily provide an empty niche (KETELAARS *et al.*, 1999).

Food-web relationships

Stomachs of post-larval flounder *Platichthys flesus* caught at the high muddy fringes of the Dollard did contain many polychaete fragments (VENEMA, 1998). The species involved, however, were not identified. In stomachs of larger, juvenile plaice *Pleuronectes platessa* and flounder *P. flesus* foraging at mixed intertidal flats where adult *M. cf. wireni* dominate it was shown that the newcomer was consumed by these flatfish (ESSINK & KLEEF, 1993), and was consequently incorporated in the estuarine foodweb. Yet, these flatfish kept the amphipod *Corophium volutator* as their staple diet. Direct predation by birds on the highly productive polychaete, *Marenzelleria viridis* having the highest P/B ratio known among marine polychaetes (SARDA *et al.*, 1995a), is not described. Potential consumers of *M. cf. viridis* in the Dollard are dunlin (*Calidris alpina*), teal (*Anas crecca*) and shelduck (*Tadorna tadorna*) (PROP, 1998).

Cause of population decline

The cause of the decline of the population of an introduced species is poorly known. RIBERA & BOUDOURESQUE (1995) mention some possible causes. In the Dollard we have no indication of increased predatory pressure on *M. cf. wireni*. And no trematode metacercariae were found in *M. cf. wireni* (G. Lauckner, pers. comm.) ruling out increased infestation by parasites as a likely cause. Remaining possibilities relate to low genetic variability, due to the small size of the inoculum in 1983, and decline in genetic vigour (due to consanguinity) and/or elimination of specific alleles, as to none of which we have relevant data available.

One possible cause may relate to changes in organic waste loading of the Dollard (cf. ESSELINK *et al.*, 1989; ESSINK & KEIDEL, 1998; ESSINK *et al.*, 1998). In the mid-1980s, the discharge of organic waste originating from the Dutch potatoflour industry had considerably decreased. Such a change in a recipient area may have created chances for invasive species, such as *M. cf. wireni* (CARLTON, 1996). From 1991 onwards, the pollution load had further decreased to very low levels, possibly impacting the food resource of *M. cf. wireni*. For the other polychaetes in the Dollard, a decreasing trend in their total biomass, concurrent with the decrease in organic loading, was demonstrated (PROP, 1998).

Perspectives

The population development as observed at the Dollard intertidal flats may be typical. A similar 'increase-peak-decline' pattern, with peak abundance and distribution reach 3-4 years after the first findings, was observed in *M. cf. viridis* in the Curonian Lagoon, Lithuania (S. Olenin, pers. comm.). Therefore, we may expect a similar population development elsewhere, *viz.* some years of further increasing or high densities at the Balgzand intertidal flats and the sublittoral of the western Dutch

Wadden Sea. Brackish locations in coastal waters, especially near shipping harbours, will reveal new populations of *Marenzelleria*.

Conclusions

In the Dutch Wadden Sea, the newcomer *Marenzelleria* cf. *wireni* has shown one of the typical patterns of population development known in invasive species: 1) a lag-phase following the first observation, 2) an almost explosive increase of the population, 3) a stabilisation phase, and 4) a phase of decline. These phases were most clear in the Ems estuary (Dollard). In the western part of the Dutch Wadden Sea phases (3) and (4) have not yet developed. In more saline parts of the Wadden Sea no significant populations have developed.

The strong development and stabilisation of the population at a high level is not a likely result of a strong competitive power of the newcomer. Having observed the dramatic increase in biomass of this highly productive polychaete we rather conclude to the availability of a vacant niche, including a not exploited food source. The species' final decline remains unexplained. There are no indications of increased predation or infestation by parasites. Changes in environmental conditions due to a decrease in organic waste discharge, may have played a role.

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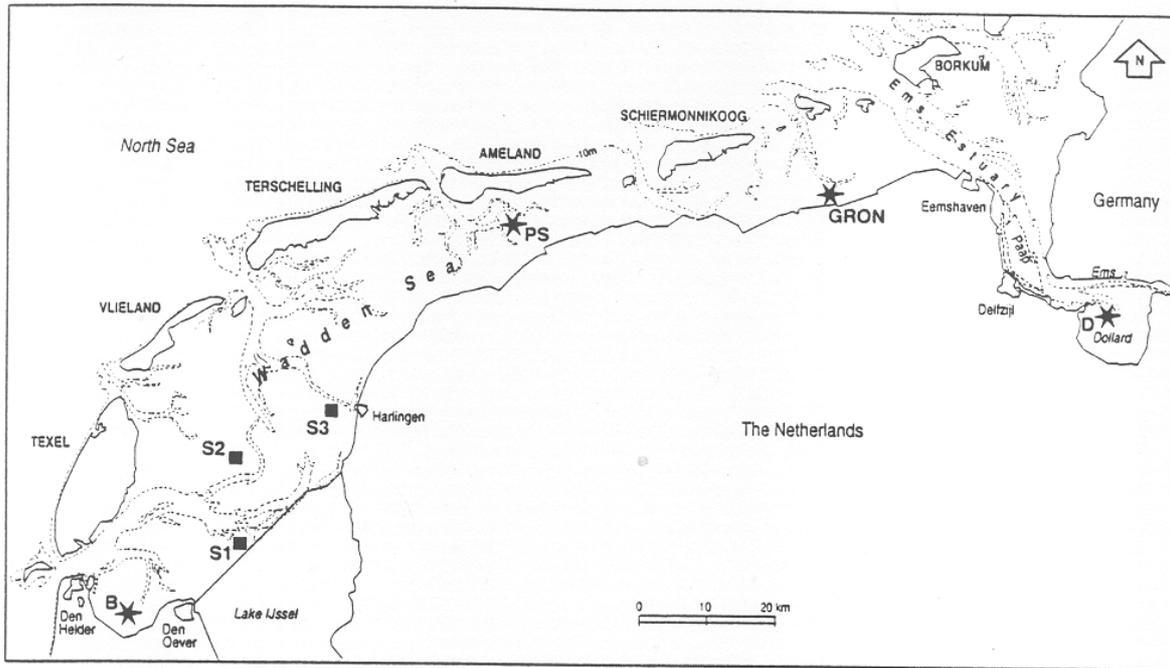


Figure 1. Map of the Dutch Wadden Sea with locations for benthos monitoring at intertidal flats (*) and in the subtidal (■). B = Balgzand, S1 - S3 = Western Wadden Sea, PS = Piet Scheve, GRON = Groningen, D = Dollard. Stippled lines = Mean Low Water .

Figure 2

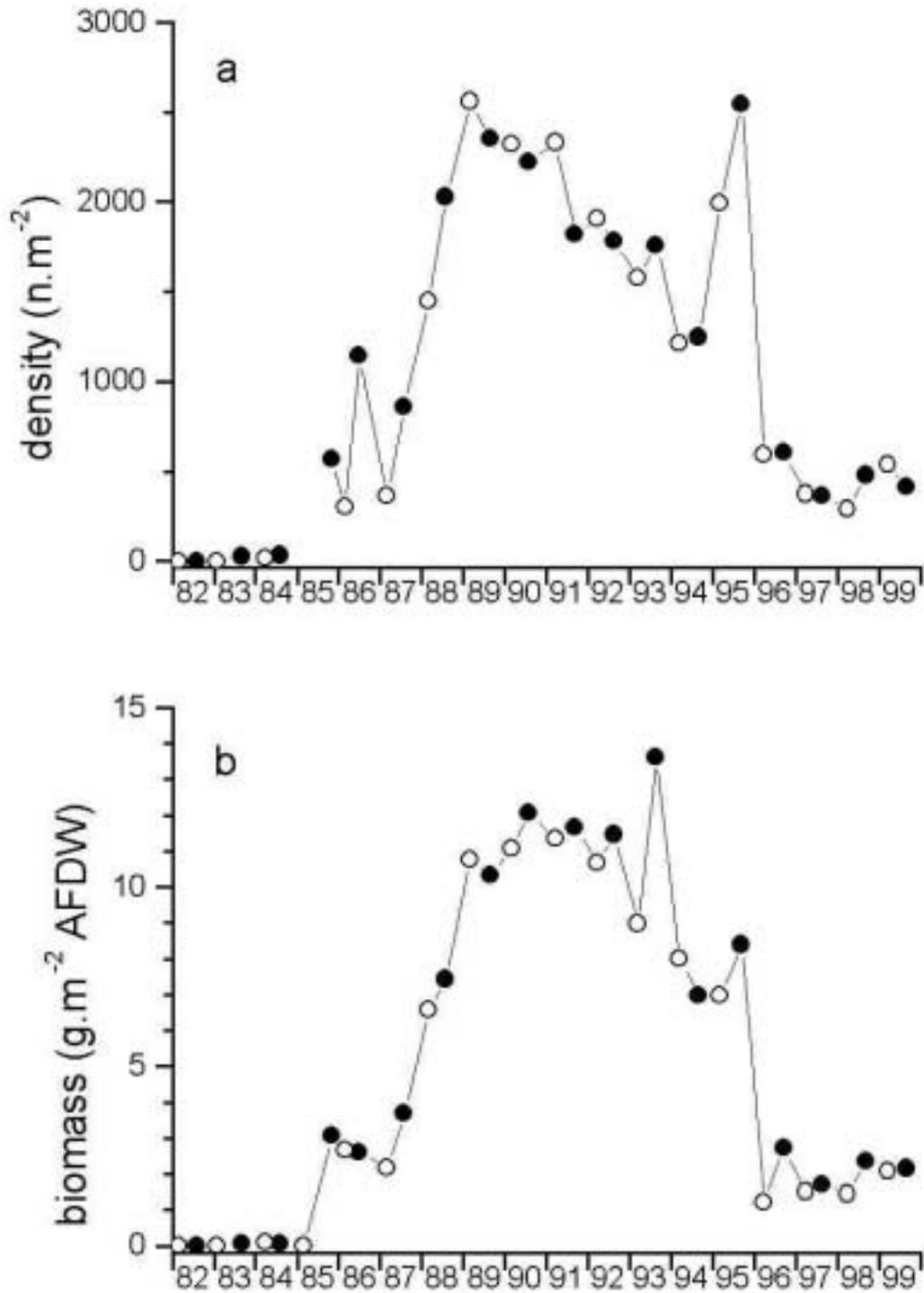


Figure 2. Population development of *M. cf. wireni* at three intertidal transects in the Dollard (Ems estuary). a) mean abundance (N m^{-2}), b) mean biomass (g AFDW m^{-2}). Closed symbols: late winter; open symbols: early autumn. Mean values for three transects. No late-winter abundances are available in 1985

Figure 3

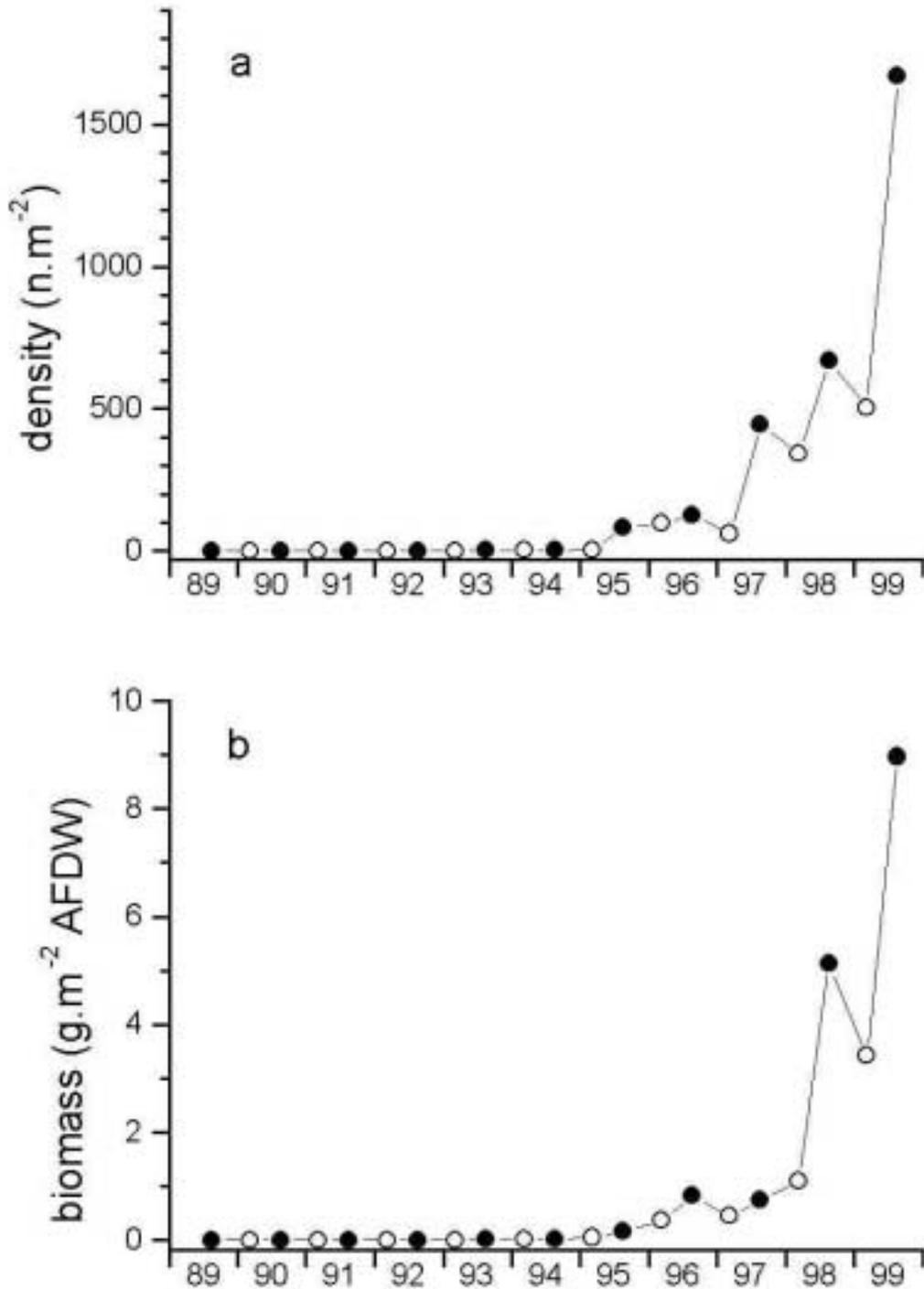


Figure 3. Population development of *M. cf. wireni* at Balgzand intertidal flats (Western Dutch Wadden Sea). a) mean abundance ($N \cdot m^{-2}$), b) mean biomass ($g \cdot AFDW \cdot m^{-2}$). Closed symbols: late winter; open symbols: early autumn. Mean values for 12 transects and 3 permanent squares.

Figure 4

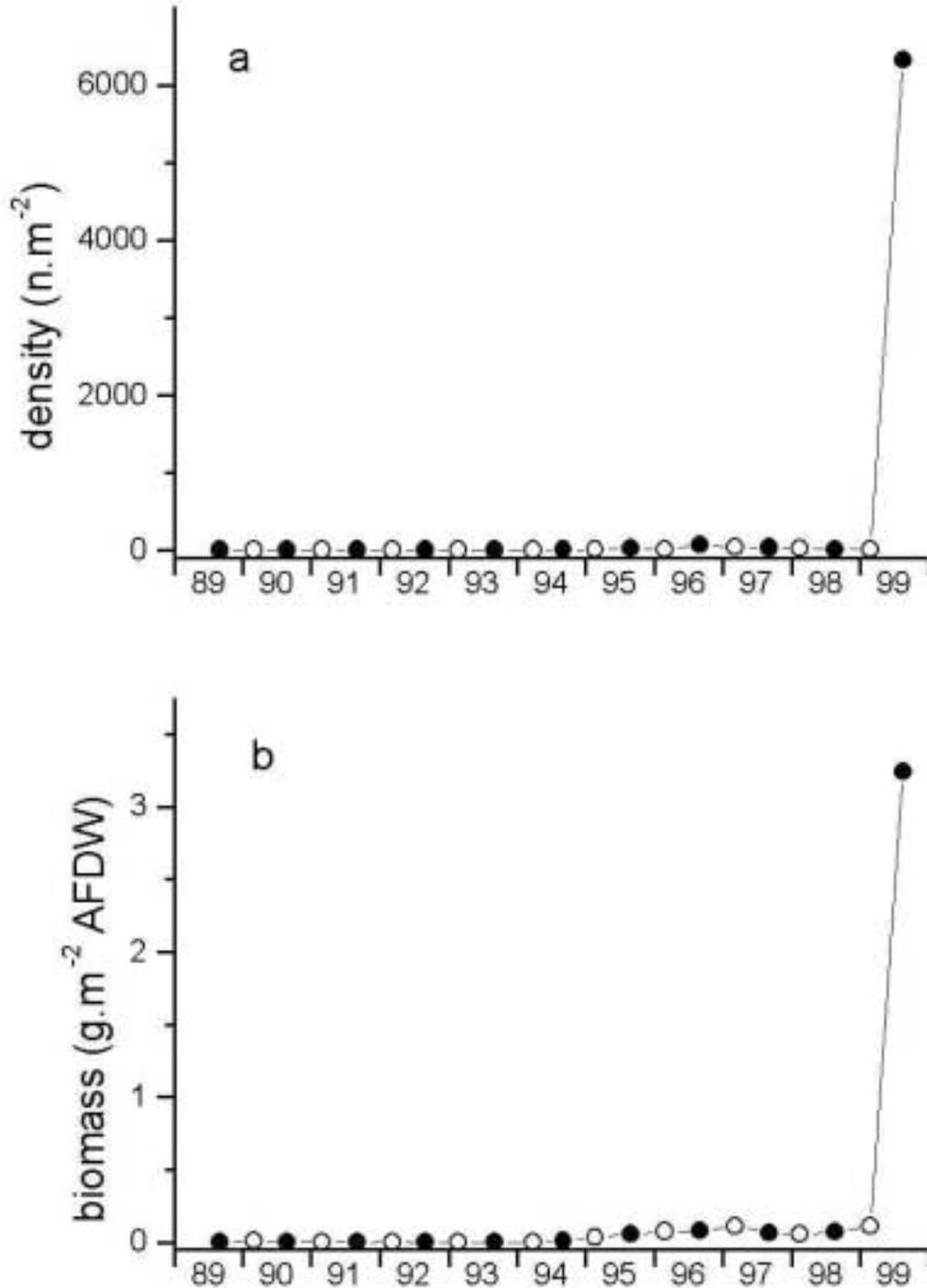


Figure 4. Population development of *M. cf. wireni* at three transects (S1 - S3) in the sublittoral western Dutch Wadden Sea. a) mean abundance ($N \cdot m^{-2}$), b) mean biomass ($g \text{ AFDW } m^{-2}$). Closed symbols: late winter; open symbols: early autumn. Mean values for three transects.