

## General patterns in invasion ecology tested in the Dutch Wadden Sea: the case of a brackish-marine polychaetous worm

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### Abstract

The success of invasive aquatic species is determined by a variety of attributes such as wide environmental tolerance, high genetic variability, short generation time, early sexual maturity, high reproductive capacity, and a broad diet. Usually, introduced species, after some time lag since inoculation, show an exponential population increase and expansion. Maintenance of the immigrant species at a high population level will be dependent on interspecific competition with native species and availability of habitat and food. Eventually, the immigrant population may decline, for instance due to increased predation pressure, parasite infestation or loss of genetic vigour. These characteristic patterns in invasive species are reviewed for the case of the North American spionid polychaete *Marenzelleria* cf. *wireni* in the Dutch Wadden Sea. This species was first recorded in estuaries and coastal waters of the European continent in the Ems estuary (eastern Dutch Wadden Sea) in 1983. In the western part of the Dutch Wadden Sea the first specimens were found in 1989. The Ems estuary population showed the typical lag-phase, explosive increase, stabilisation, and eventual decline. In the western part of the Dutch Wadden Sea the latter two phases have not yet developed. The strong development and stabilisation of the population in the Ems estuary may have been caused by the availability of a yet not utilised food source. The species' final decline remains largely unexplained.

### Introduction

There is a vast literature regarding biological invasions and the processes involved. 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., Mooney and Drake 1986; Ashton and Mitchell 1989; Lodge 1993; Ribera and Boudouresque 1995; Carlton 1996; Williamson 1996; Ricciardi and Rasmussen 1998; Parker et al. 1999). Based on information from several publications, Ricciardi and Rasmussen (1998) have drawn up a list of 11 general attributes of invasive aquatic species, allowing hypotheses as to their potential population development pattern in recipient communities. Among these attributes are wide environ-

mental tolerance, high genetic variability, short generation time, early sexual maturity, high reproductive capacity, and a broad diet.

### Phases in population development

In the literature, the following main phases are described for the population development of an introduced species. After the arrival of the first immigrants, the formation of a 'propagule', i.e., the minimum number of individuals able to establish a reproducing population, is essential (MacArthur and Wilson 1967; Ashton and Mitchell 1989). This is also called the settlement phase (Ribera and Boudouresque 1995). During their phase of expansion, a steady increase may lead to a stable equilibrium density. Subsequently, the

population will, as many cases have shown, increase exponentially (Williamson 1996). There is, however, a time lag between arrival and population increase, which may be rather variable between areas as well as between species (Crooks and Soulé, 1999). The increase of the immigrant population during their phase of expansion may lead to a very high and steady population 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; e.g. Parker et al. 1999). Ribera and 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. Other population trajectories are described in the literature, but do not relate much to the case of *Marenzelleria cf. wireni*. 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).

#### *Available habitat or interspecific competition?*

The settlement and subsequent development of an immigrant species will be possible if there is ecological space (often disputably described as vacant or empty niche, see Herbold and Moyle 1986) in the recipient area (Williamson 1996). Sandlund et al. (1999) postulate that ecosystems modified by man generally appear to be more receptive to alien species than undisturbed ecosystems. In a great many cases, invader species seem to have integrated into recipient communities through niche shifts and other mechanisms (Moyle and Light 1996). Alternatively, the newcomer has to compete with, suppress and take over the position of an established native species.

According to the Eltonian invasion model, species-poor communities are more open to introductions than rich ones (Elton 1958). Successful invasion may also be related to the availability of open ecological spaces, such as in the case of the not yet completed post-glacial recolonisation of the Baltic Sea (Leppäkoski 1984). Here, up to 92 non-native species have been reported, about 75% of which have established self-reproducing populations (Leppäkoski and Olenin 2000).

In estuarine areas, with generally low species richness, such habitats may be available for species with a broad environmental tolerance (Olenin and Leppäkoski

1999; Wolff 1999). In artificial water bodies, absence of species with a diet similar to that of the invader may easily provide not utilised resources (Ketelaars et al. 1999). The position an introduced species will take in the food web may be dependent on whether there is a suitable food source available or interspecific competition is unavoidable. An example of a superior competitor is the invader ctenophore *Mnemiopsis leidyi* in the Black Sea. In the more saline Aegean Sea, however, this species seems well controlled by predators (Shiganova et al. 2001).

The major characteristics of invasible habitats, e.g., low diversity of native species, early successional stage of the native community, or habitat disturbance, are thought to be important in determining invasion success. However, there have been few critical tests and also examples that show the opposite (see Kaufman, 1992; Lodge 1993; Cohen and Carlton 1998). Such an example is the San Francisco Bay and Delta ecosystem, where the invasion rate has increased despite a concomitant increase in species richness (Cohen and Carlton 1998), which is consistent with the conviction of Cornell and Lawton (1993) that ecological communities are seldom saturated with species, and the model of 'invasional meltdown' and data supporting this (Simberloff and Von Holle 1999; Ricciardi and MacIsaac 2000). The latter examples and explanatory models, however, do not apply to the Dollard as *M. cf. wireni* is the only invasive species.

#### *Cause of population decline*

For those species that do successfully establish, their population may stabilise or decline. The causes of decline are poorly known. Ribera and Boudouresque (1995) mention some possible causes, e.g., increased predation pressure by native species, increased infestation by parasites, too low genetic variability due to a small sized inoculum leading to loss of genetic vigour by consanguinity and/or elimination of specific alleles. Another possible cause may be overexploitation or depletion of resources.

The purpose of this paper was to investigate the extent of agreement between the population development patterns of *M. cf. wireni* as observed in the different parts of the Dutch Wadden Sea and those described in the literature and to search for explanations for the patterns observed. Among others, interactions between the invasive species and the indigenous fauna will be discussed. Where no specific information on *M. cf. wireni* is available, we will refer to Baltic

*M. cf. viridis* or North American *M. viridis*, as these congeneric species are genetically related (Bastrop et al. 1997), thrive well in similar habitats (e.g., low salinity, rich in organic matter), although they possess different physiological adaptations (Schiedek 1997, 1999).

### The case of *Marenzelleria* cf. *wireni*

#### *Introduction in European waters*

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 and Kleef 1988). After having been described initially as *M. viridis*, the North Sea populations were identified as *M. cf. wireni*. Populations, described as *M. cf. viridis*, have been in the Baltic Sea since 1985. Parent populations of both species were identified along the Atlantic coasts of North America (Bastrop et al. 1997). For the North Sea populations (*M. cf. wireni*), other possible origins can be thought of, such as boreal and polar waters as well as a cryptic North Sea population (see Bastrop et al. 1997; Bick and Zettler 1997). Ballast water transport is considered as a likely vector leading to the initial introductions in the Forth and Ems estuaries (North Sea) and in the Darss-Zingst estuary (Baltic Sea), as there is abundant evidence of spinonid polychaetes found in many ballast water samples (Carlton 1985; Carlton and Geller 1993; Locke et al. 1993; Gollasch 1996; Smith et al. 1999). Secondary introductions are probably mediated by natural water circulation as well as by shipping.

#### *Distribution in Europe*

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).

#### *Populations in the Dutch Wadden Sea*

In the coastal waters of the Netherlands, *M. cf. wireni* has spread from the Ems estuary in southwest direction.

By 1991, populations were known from several locations in the Dutch Wadden Sea. In 1995–1996, the Rhine–Meuse–Scheldt delta in the southwest of the 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, *M. cf. wireni* has shown a dramatic increase (Essink et al. 1998), but in recent years the population has strongly declined. In the western part of the Dutch Wadden Sea, the population density is still increasing.

### Methods

Data on *M. cf. wireni* in the Dutch Wadden Sea and Ems estuary were obtained from two monitoring programmes, taking benthos samples in late winter (ca. March) and early autumn (August–September) at intertidal flats as well as in sublittoral sediments. These programmes are (1) the Rijkswaterstaat Monitoring Programme (MWTL) and (2) 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 of ca. 1 km length (locations: B, PS, HP) or in fixed plots (location: GRON). Within each location plots or transects were a few hundred metres to ca. 2 km apart. At each of the sublittoral locations S1–S3 (2–5 m water depth) samples were taken with a box corer along a fixed 1.5 km long transect. 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 and de Bruin (2000) and Essink (1978).

### Results

*Marenzelleria* cf. *wireni* first developed in the Ems estuary, at the border between Germany and the Netherlands. Within 6 years a population had developed at Dollard intertidal flats of 2–3000 ind. m<sup>-2</sup>

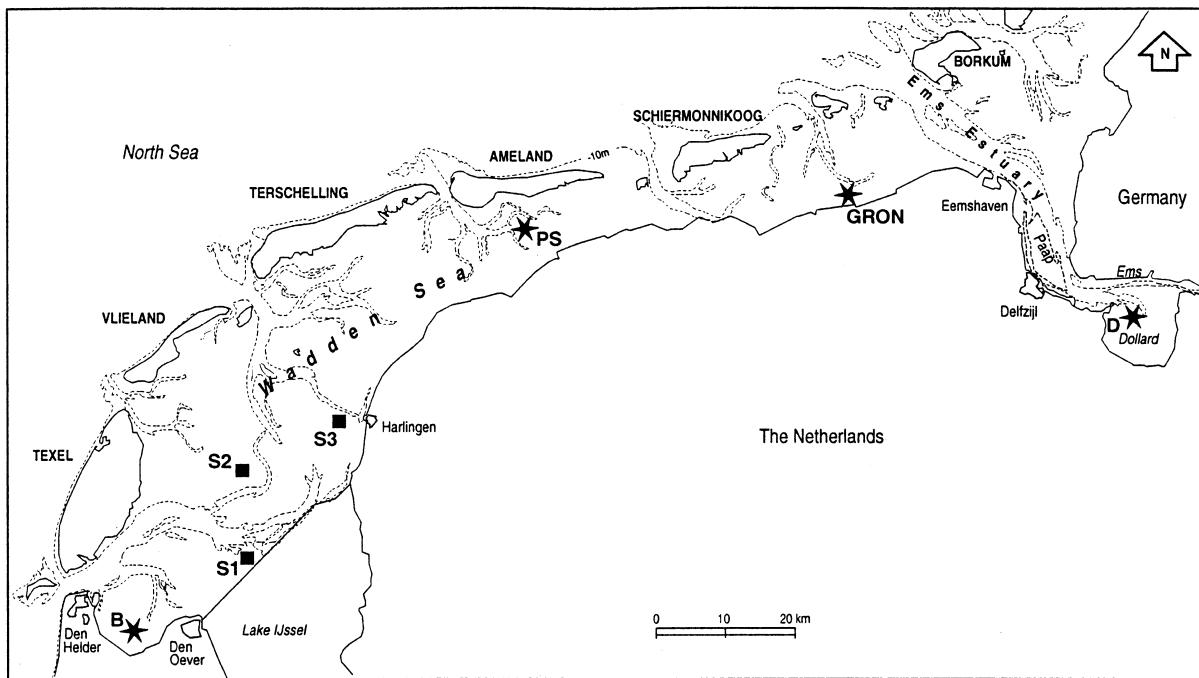


Figure 1. Map of the Dutch Wadden Sea with locations for benthos monitoring at intertidal flats (\*) and in the sublittoral (■). B = Balgzand, S1–S3 = western Wadden Sea, PS = Piet Scheve, GRON = Groningen, D = Dollard. Stippled lines = mean low water.

(Figure 2a). Even higher densities, of over 100,000 of juveniles per  $\text{m}^2$ , were found at high muddy flats bordering the saltmarsh. These areas were found to function as 'nursery' (Essink and Kleef 1993). *M. cf. wireni* remained abundant for another 6 years with a mean biomass of 10–14 g ash-free dry weight (AFDW)  $\text{m}^{-2}$  (Figure 2b), causing an almost doubling of the total macrozoobenthic biomass. At the same time, the composition of the benthic community changed drastically. Due to the increased share of polychaetes from 24% to 58%, the proportion of bivalves in the total mean biomass decreased from 64% to 25% (Essink et al. 1998). Since 1995, the population density of *M. cf. wireni* has decreased again, reaching mean densities of ca. 500 ind.  $\text{m}^{-2}$  in 1999 (Figure 2a) and a mean biomass of 2.1 g AFDW  $\text{m}^{-2}$  (Figure 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 (Figure 2). Locally, along the eastern edge of Balgzand, densities were very high, reaching 13,000 ind.  $\text{m}^{-2}$  (equalling 63.1 g AFDW  $\text{m}^{-2}$ ) in August 1999.

In the subtidal part of the western Dutch Wadden Sea (transects S1–S3) densities remained low

(a few tens  $\text{m}^{-2}$ ) since the first record in 1990 until in August 1999 a sudden increase to 6330 ind.  $\text{m}^{-2}$  (equalling 3.3 g AFDW  $\text{m}^{-2}$ ) was observed (Figure 2).

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

## Discussion

### *Attributes of a successful invader*

The introduced polychaete *M. cf. wireni* has a number of attributes that are thought to be characteristic of successful invaders. The rather quick population increase in the Dollard seems related to the high environmental tolerance of *M. cf. wireni* to oligomesohaline conditions (cf. Essink and Kleef 1988 and references therein). Of special significance is the species' 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 et al. 1997; Schiedek 1999). A similar ability was found in the invader of the

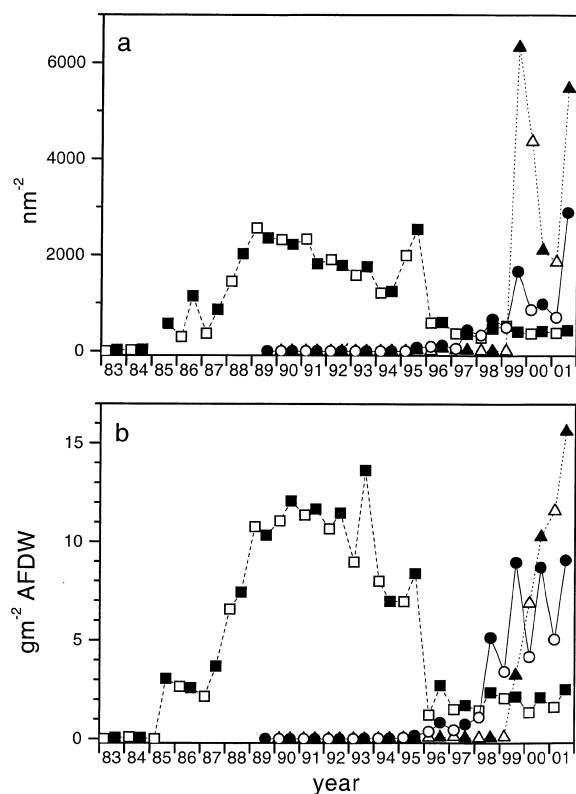


Figure 2. Mean abundance ( $\text{N m}^{-2}$ ); (a) and mean biomass ( $\text{g AFDW m}^{-2}$ ); (b) of *M. cf. wireni* at the intertidal flats of Dollard (squares), Balgzand (circles) and the subtidal of the western Dutch Wadden Sea (triangles). Closed symbols: early autumn; open symbols: late winter. No late-winter abundances are available for the Dollard in 1985.

Baltic Sea *M. cf. viridis* (Bochert et al. 1997b; Schiedek 1997).

Once started, population increase was fast at all sites studied. This has to be based on a short generation time, high reproductive capacity and successful development of juveniles. Indeed, Essink and Kleef (1993) found a generation time of 1–2 years in *M. cf. wireni* in the Dollard. Spawning was observed in the Ems estuary to occur each year in spring (Essink and Kleef 1993) as was established for populations in Scotland (*M. cf. wireni*; Atkins et al. 1987) and Nova Scotia (*M. viridis*; George 1966). This contrasted, however, to Baltic Sea populations of *M. cf. viridis* with spawning taking place in autumn. This difference may be genetically determined, but also be a result of different environmental conditions (Bochert 1997).

The reproductive capacity of *Marenzelleria* is high. Females 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). For the maintenance of populations in extreme estuarine habitats, however, dispersal of young benthic stages rather than pelagic larvae seem to be important, as is suggested for the Curonian lagoon (Daunys et al. 2000).

In the Dollard, 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  $\text{m}^{-2}$  were found (Essink and 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 predation on the tellinid bivalve *Macoma balthica* by the brown shrimp *Crangon crangon* (Beukema 1993). The high muddy intertidal fringes of the Dollard, however, were observed to be the preferred place for settlement of post-larvae of the flounder *Platichthys flesus* in May (Kleef and 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*.

As to the broadness of its diet, George (1966), Sanders et al. (1962) and Whitlatch (1980) report that *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 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

*Marenzelleria cf. wireni* was first accidentally recorded in the sublittoral of the Ems estuary in 1983 (Essink and Kleef 1988), where no population development was documented. However, at the Dollard intertidal flats the population increased strongly two years later. Within another three years the population had dramatically increased, attaining densities of 2000–3000 ind.  $\text{m}^{-2}$  (Figure 2) with a biomass of 8–16 g AFDW  $\text{m}^{-2}$  in

1989–1994 (Essink et al. 1998). In contrast, the population of *M. cf. wireni* in the western Dutch Wadden Sea (Balgzand intertidal flats) did not increase substantially until approximately 10 years after the first specimens were recorded in 1989, attaining densities of  $>500$  ind.  $m^{-2}$  in 1998/1999 (Figure 3).

Differences in time lag may be related to differences (natural or anthropogenic) in environmental factors or ecological conditions that favour the development of an introduced species, and to differences in genetic factors, such as the fitness of the newcomer in the novel environment (Crooks and Soulé 1999). The species richness of the recipient community may be one of those ecological conditions (cf. the Eltonian invasion model). The species richness of the benthic community of Balgzand intertidal flats is about three times as high as that of the Dollard (ca. 23 and 15 species, respectively). Also, macrobenthic biomass at Balgzand (well over 100 g AFDW  $m^{-2}$  in August) is higher than in the Dollard (ca. 10 g AFDW  $m^{-2}$  in August). Similarly, the sublittoral of the western Wadden Sea has about twice the species richness (ca. 25 species) as the Dollard intertidal flats. These observations are also in line with Wolff's (1999) conclusion on the paucity of species in brackish water systems as a favourable factor for the 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. Indeed, the Dollard is characterised by low macrobenthic diversity (ca. 15 species); the eastern part of Balgzand lacks species like *Lanice conchilega* and *Urothoe poseidonis*, which have a preference for a higher salinity environment.

In the Baltic Sea, 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 (Zettler 1996, 1997; Zmudzinski 1996; Stigzelius et al. 1997; Kotta and Kotta 1998; Olenin and Leppäkoski 1999; Gruszka 1999), the invasiveness of indigenous benthic communities may be explained by the presence of open ecological spaces due to a not yet completed post-glacial recolonisation (Leppäkoski 1984).

#### *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.

This pattern of development is intermediate between the 'increase to a stable equilibrium density' (Ribera and Boudouresque 1995) and the 'boom and bust' pattern (Parker et al. 1999). Although the macrobenthic community structure was significantly changed by an almost doubling of the total biomass and a drastic change in bivalve : polychaete biomass ratio, *M. cf. wireni* never became detrimental to other species, although there were some indications of competitive interactions with native species (Essink et al. 1998 – see below).

#### *Competitive interaction with native populations*

At the same time the population of *M. cf. wireni* at the intertidal flats of the Dollard increased, the abundance of a number of species changed, 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 *M. arenaria* and *M. balthica* could not be related to the increase of *M. cf. wireni*. The decline of these bivalve species is rather related to successive years of poor recruitment and mortality in severe winters (Essink et al. 1998). As to the observed increase of *C. volutator*, there is no clue to a causal relationship. For *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 relate to competition for food as both species are known as surface deposit-feeders and filter-feeders (Goerke 1966, 1971; Dauer et al. 1981). Organic matter, however, either in suspended form or incorporated in the sediment, is not very likely to be a limiting resource in the Dollard where suspended organic matter does accumulate (e.g., van Leussen 1994). A proper experimental approach to resolve this problem (cf. Talman and Keough 2001) was not carried out.

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* caused 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.

For the Tay estuary (Scotland), Atkins et al. (1987) reported negative correlations between *Marenzelleria*

and all common zoobenthic species, and suggested *Marenzelleria* to be an isolated functional entity in the estuarine community, in other words a species without significant interaction with other species. At Balgzand intertidal flats no negative correlations between the newcomer *M. cf. viridis* and native benthos species were found, nor in several coastal waters of the Baltic Sea (Zettler 1996; Kube and Powilleit 1997; Kotta and Kotta 1998). 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).

#### *Availability of habitat or resources*

The data from the Dollard suggest 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 interaction with the native fauna either. Therefore, we are apt to conclude that *Marenzelleria* sp. has found available space in European waters, with ample food available not exploited by other benthic species. For the Dollard, suitable habitat may have developed due to the first reduction of organic waste loading, improving ambient oxygen conditions (Essink et al. 1998; Essink 2003). Such a change in a recipient area may have created chances for invasive species, such as *M. cf. wireni* (cf. Carlton 1996). There is no data supporting the theory of fluctuating resources as facilitator of invasions in plant communities (Davis et al. 2000) or the theory of increase of a limiting resource enabling the invasive species to rapidly develop (Crooks and Soulé 1999).

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: from ca. 125.000 to 35.000 ind. m<sup>-2</sup> (Dekker and de Bruin 2000), thus providing at least physical space.

#### *Food-web relationships*

Introduced species may cause changes in the food-web of the recipient system. In the Dolard, stomachs

of post-larval flounder *P. flesus* caught at the high muddy fringes did contain many polychaete fragments (Venema 1998). The species involved, however, were not identified. At mixed intertidal flats where adult *M. cf. wireni* dominate the newcomer was found in stomachs of larger, juvenile plaice *Pleuronectes platessa* and flounder *P. flesus* (Essink and Kleef 1993). Yet, these flatfish kept the amphipod *C. volutator* as their staple diet. Direct predation by birds on the highly productive polychaete, *M. viridis* having the highest P/B ratio known among marine polychaetes (Sarda et al. 1995a), is not described. Potential consumers of *M. cf. viridis* among the birds in the Dollard are dunlin (*Calidris alpina*), teal (*Anas crecca*) and shelduck (*Tadorna tadorna*) because of their known diet and feeding behaviour (Prop 1998). So, *M. cf. viridis* is likely to have become merely an additional food resource for various predators.

#### *Cause of population decline*

The causes of decline of a species after a period of successful development and expansion is not well known. Possible causes are (1) predators in the recipient community get accustomed to the new prey, (2) an increased abundance of indigenous predators or parasites, (3) low genetic variability leading to poor adaptive strength and (4) decline in genetic vigour (due to consanguinity) or loss of specific alleles (Boudouresque 1994). In the Dollard, we have no indication of an increased predation pressure as the cause of the decline of *M. cf. wireni* since 1995. No trematode metacercariae were found in *M. cf. wireni* (G. Lauckner, pers. comm.) ruling out increased infestation by parasites as a likely cause. As to the other possible causes mentioned relevant data are lacking.

One other possible cause of population decline may relate to changes in organic waste loading of the Dollard (cf. Esselink et al. 1989; Essink and Keidel 1998; Essink et al. 1998; Essink 2003). In the mid-1980s, the discharge of organic waste originating from the Dutch potato flour industry had considerably decreased, largely eliminating the regular occurrence in the Dollard of unfavourable oxygen conditions. 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).

## 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 not yet utilised resources, however without a clue as to its specific nature. 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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