

ORIGINAL ARTICLE

Long-term patterns in the establishment, expansion and decline of invading macrozoobenthic species in the brackish and marine waters of Southwest Netherlands

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Abstract

The fluctuations in densities or biomass of a number of invading and native polychaete and mollusc species in the Southwest Netherlands were compared over a period of 20 years. For recent invaders a lag phase of 7–10 years occurred after their first appearance, followed by an exponential increase in abundance or biomass for 2–3 years. High numbers and biomass then continued for about 5 years, followed by a strong decline. The total sequence from introduction to decline lasted about 15 years. The densities or biomass of invaders appearing decades or even centuries ago in the Delta area have fluctuated in a similar manner to those of native species, indicating that the densities or biomass of invading species after a 15-year period of strong changes become governed largely by the same environmental factors as native species. The conclusion may be that after some decades, invading species can become part of a balanced co-existence with the native species, and that this may yield a net gain in the overall diversity.

Introduction

An increasing number of invading species has been observed worldwide, and consequent problems have been acknowledged (Streftaris *et al.* 2005; Simberloff 2011). Studies on invading marine species are far less numerous than studies of freshwater and terrestrial species; a Science Direct query for 'Invad*' and 'Exotic' resulted in 52,262 papers, of which only 1016 (2%) discuss the marine realm. However, in the last two decades reports on the appearance and effects of invading and exotic species in the marine realm have also become increasingly numerous (of the 'marine' papers, 82 were published from 1990 to 1994, 134 from 1995 to 1999, 265 from 2000 to 2004, and 457 from 2005 to 2009). The reports mainly acknowledge the rate of range expansions, spatial patterns (globalization of ecosystems), the role of transport vectors, the influence of environmental factors (impact of climate change), the availability of resources

(space and food), the impact on other species in the community and on ecosystem services and the characteristics of successful invaders (see Sakai *et al.* 2001; Stachowicz *et al.* 2002; Troost 2010; and references therein). However, an understudied topic is the long-term population dynamics of an invading species, i.e. the development of a species' population after its introduction or appearance, its (vigorous) increase and eventually its decline and subsequent stabilization or disappearance. A few studies (Stachowicz & Byrnes 2006; Branch *et al.* 2008; Rius *et al.* 2009) mention changes in densities of invading species over a period of a couple of months or years, yet are restricted in their time span and thereby do not show the process to its full extent. The reason might be that it takes long-term sustained observation over many years to assess the full process from appearance to decline. These long-term datasets from sustained observation have been scarce until recently, as it is only during the last two decades, due to national legislation or European

regulations (the Water Framework Directive for example), that a stronger emphasis has been placed on sustained monitoring, which may be able to provide such long-term datasets.

The large-scale monitoring of macrozoobenthic communities of soft sediments during the last 20 years in the waters of the Southwest Netherlands gives an insight into the development of populations, including those of the invading species. The aim of the current study is to evaluate the development over time, from arrival to eventual decrease, of a number of invading species that have recently entered the Dutch Delta area in comparison with both native species and those species that invaded the area many decades or centuries ago.

Material and Methods

The study area is the main outlet of the rivers Rhine, Meuse, and Scheldt in the southwest of the Netherlands known as the Delta area (Fig. 1). After disastrous flooding in 1953, it was decided to turn the estuarine Delta areas into a series of semi-enclosed, more or less stagnant, marine, brackish and freshwater basins (Wijnhoven *et al.* 2008). These basins include the Oosterschelde sea-arm, which was turned into a semi-enclosed marine bay by the building of a storm-surge barrier, and Lake Grevelingen, which was initially turned into a brackish lake and is now a saltwater lake (Nienhuis & Smaal 1994; Engelsma *et al.* 2010).

Since 1959, samples of macrozoobenthos have been taken on a regular basis from the various basins of the Delta by researchers of the NIOZ and their predecessors. All these data are stored in the database of the Monitor Taskforce of the NIOZ (BIS; Benthos Information System, database, version 1.20.0) (Wijnhoven *et al.* 2008).



Fig. 1. The location of the study areas in the southwest of the Netherlands.

This database currently contains more than 80,000 samples, largely related to the Dutch Delta area. This makes the database highly suitable for analysis of the arrival and development of invading species in the different Delta waters. Since 1990, within the framework of the Monitoring Programme of the National Water Systems (MWTL), the Monitor Taskforce of the NIOZ has monitored the benthic macrofaunal communities of the Dutch Delta in a more standardized way (e.g. Engelsma *et al.* 2010; Wijnhoven *et al.* 2010). Samples are taken twice a year, in spring and autumn, for a minimum of 120 samples from the Oosterschelde and 60 from Lake Grevelingen. Three sediment cores (\varnothing 8 cm) are taken from each station and merged into a pooled sample (total surface area 0.015 m²). Sediment cores are collected directly in the intertidal zone at low water, whereas subtidal cores are taken using a Reineck box corer deployed from a ship. The contents of the cores are gently washed in a 1-mm sieve and the material retained on the sieve is contained, stained with Rose-Bengal and preserved with a 4% buffered formalin solution. The macrofaunal groups are identified to the highest possible taxonomic level.

For the present study all available data on the viewed species were clustered per half year, taking all data for the two different seasons separately but averaging overall strata and/or sub-regions in the basins, and recalculating the data into species densities or biomass (ash-free dry weight) m⁻². To identify the dates of first recordings of species our data have been combined with records available in the literature.

The long-term changes in densities of two groups of species have been compared. First, a group of smaller polychaetes were compared – the recently invading *Syllis gracilis* and *Tharyx marioni* that entered the Delta area in the 1950s, and the native *Exogone naidina*. *Syllis gracilis* was observed in the Netherlands for the first time once in the Oosterschelde in 1940 (Korringa 1951; Wolff 2005). However, the species was not found again until 1990 when it was rediscovered in Lake Grevelingen (own monitoring data available in the BIS database). *Tharyx marioni* was first described for the Netherlands by Korringa in 1951 (at that time called *T. multibranchiis*) and has been common in all Dutch Delta waters including Lake Grevelingen and the Oosterschelde since the 1960s (Wijnhoven & Hummel 2009). *Exogone naidina* is an abundant species native to the Netherlands.

Secondly, from a group of medium-sized suspension feeding bivalves, the recent invader jackknife clam, *Ensis directus*, was compared with the soft-shell clam, *Mya arenaria*, which invaded the Netherlands some centuries ago (Lasota *et al.* 2004; Wolff 2005), and the native cockle *Cerastoderma edule*. *Ensis directus*, originally an American species, was first sighted alive in Dutch waters

in 1981 in the Wadden Sea (Armonies & Reise 1999; Wolff 2005). During the 1980s the species expanded along the North Sea coast to the southern part of the Netherlands. In 1989 the first specimen of *E. directus* in Dutch Delta waters was found in the Oosterschelde. In 1991 the species was also found in Lake Grevelingen (Wijnhoven & Hummel 2009). *Mya arenaria* may already have been introduced from America to Europe in the 13th century, but the first official observation is from 1765 (Streftaris *et al.* 2005; Wolff 2005). This species is now common in all Dutch Delta waters, as is the native *C. edule* (Wijnhoven & Hummel 2009).

Results

Two recently invading species, the polychaete *Syllis gracilis* (Fig. 2a) and the mollusc *Ensis directus* (Fig. 2b), showed a similar pattern of changes in density in Lake Grevelingen as well as the Oosterschelde. After a lag period with very low densities or biomass for 7–10 years after their first recordings, the densities and biomass increased exponentially to high levels over a period of 2–3 years. The high densities and biomass remained for another 3–5 years, after which the populations exhibited marked declines.

The densities and biomass of the invaders that arrived decades or centuries ago in the Delta area have fluctuated in a similar (erratic) way as those of the native species (Fig. 2a and b). These seemingly erratic changes are a normally occurring phenomenon among the benthic species in areas like the Dutch Delta (Coosen *et al.* 1994; Seys *et al.* 1994).

The total sequence of events from the first appearance of an invading species, through the time-lag, the exponential increase phase and then levelling off and decrease, lasted for about 15 years and was followed by a phase of balanced co-existence among the native species. This sequence can be visualized in a generalized pattern of population development for invasive species after arrival in a new environment (Fig. 3).

Discussion

The kind of long-term sustained monitoring programmes followed in the Southwest Netherlands, with samples taken each half year at many (60–120) stations per basin, has been instrumental in obtaining a sufficiently long record to be able to compare the long-term population dynamics of newly invading species from arrival to expansion and subsequent decline, coupled with the fluctuations of other macrobenthic species.

A lag phase between initial colonization and the onset of rapid population growth, followed by an exponential

increase, is a common phenomenon in plants (Sakai *et al.* 2001 and references therein), but to our knowledge it has not been described before for marine macrozoobenthos. Here we have shown a 7- to 10-year lag phase and a 2- to 3-year exponential increase phase. The lag phase for plants has been attributed to the sorting and evolution of the best adaptive ecotypes of a species following a (multiple) colonization effect (Sakai *et al.* 2001), and the same may hold true for the studied species here.

The sequence of events in the densities and biomass of recent invaders, together with the observed fluctuations of earlier invaders resembling the pattern of native species, indicates that after a lag phase and exponential growth, invading species gradually become governed by the same (environmental) factors determining their population densities. Annual changes in densities and biomass are a regular phenomenon among the benthic species in areas like the Dutch Delta, primarily caused by the interplay of environmental variables and biotic interactions such as temperature, currents, food concentration, and parasite or predator occurrence, all affecting processes like reproduction, growth, dispersal or competitive capacities of species (Coosen *et al.* 1994; Seys *et al.* 1994). Moreover, in the Dutch Delta, anthropogenic impacts such as the control of the sluice regime for Lake Grevelingen, which affects the water exchange with the North Sea, have an impact on the densities of benthic species (Wetsteijn 2011). Both *Cerastoderma edule* and *Mya arenaria* showed increased densities after a period of higher water exchange. Minor fluctuations in densities or biomass are generally the result of differences in timing or are the effect of increased abiotic environmental parameters such as temperature, salinity, water currents, turbidity and nutrient levels on biotic processes such as reproduction, growth, dispersal and competitive capacities.

A lack of competitors and natural enemies (including diseases) is frequently mentioned as a reason for the exponential growth of invaders (e.g. Bax *et al.* 2001; Troost 2010). The adaptation of predators to consume the new invaders and the evolution of parasites may then be important factors in the subsequent decline in the density of invaders and result in them becoming regulated similarly to native species.

The information on the duration of the lag phase, expansion, and period with high numbers and biomass, as observed in our study for two species, may contribute to models on the rate of species introductions and the success of these biological invasions, as described by Wonham & Pachevsky (2006) and Miller *et al.* (2007). However, it might be expected that the duration of the lag phase and the period with high invader densities is environment-specific, as indicated by

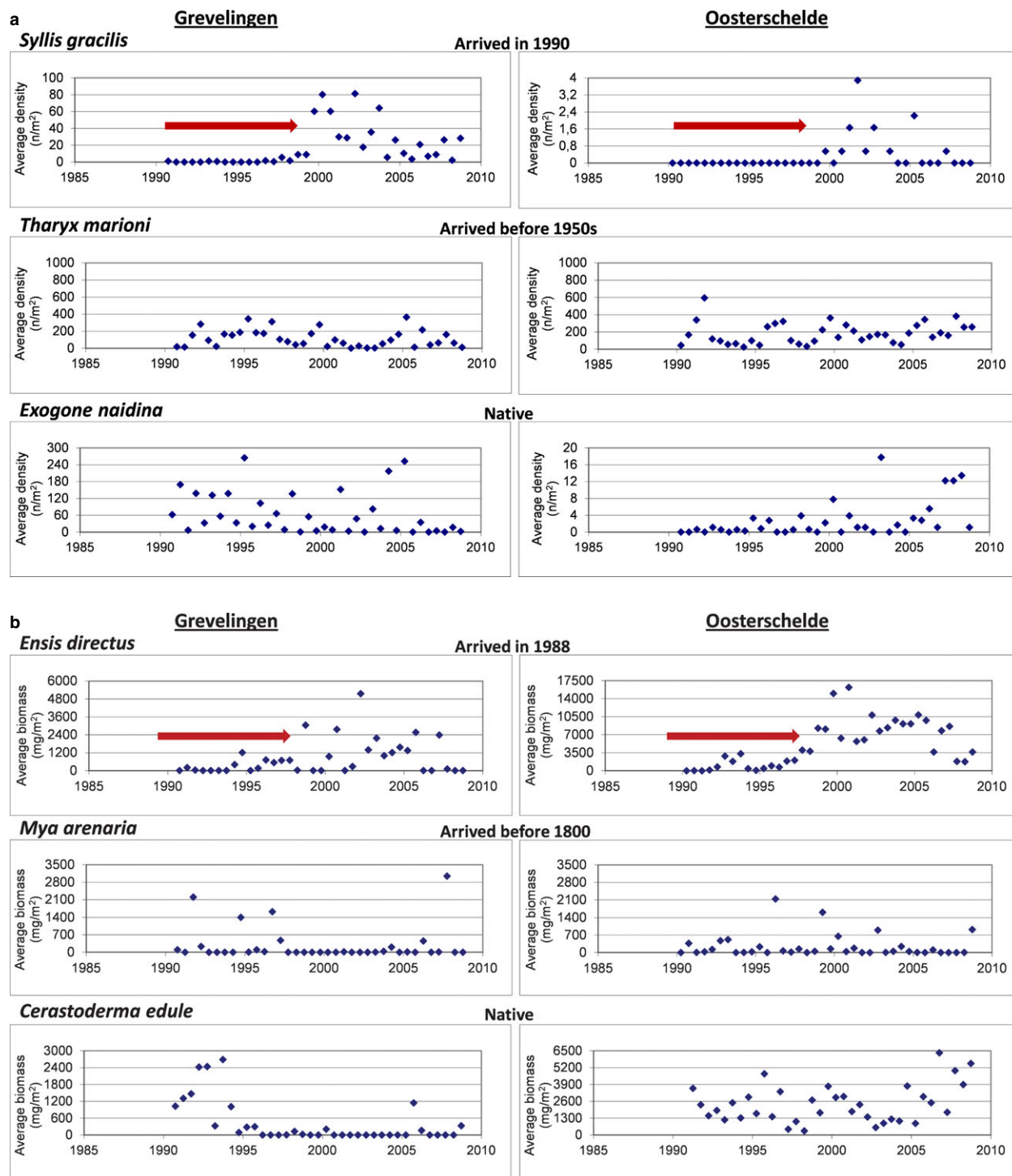


Fig. 2. The fluctuations in densities of a recent invading polychaete (a) and in biomass of a recent invading mollusc (b) compared with the fluctuations in earlier invading and native species.

observed differences in susceptibility between systems (Vermonden *et al.* 2010) and observations of recurrent and consecutive invasions in certain systems (e.g. Leuven *et al.* 2009).

We conclude that invasions can eventually result in a balanced co-existence with the native species, and that this may yield a localized net gain in diversity, as has also been suggested by Stachowicz & Byrnes (2006).

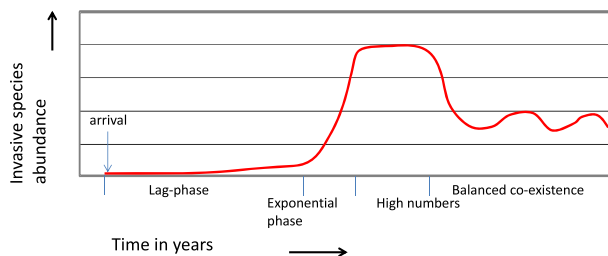


Fig. 3. Conceptual pattern of population development for invasive species after arrival in a new environment.

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