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

Herman Hummel* & Sander Wijnhoven

Monitor Taskforce, Royal Netherlands Institute for Sea Research, Korringaweg 7, 4401 NT Yerseke, Netherlands.

*Corresponding author: herman.hummel@nioz.nl

Publisherҁs version: http://dx.doi.org/10.1111/maec.12085

Keywords: invaders, time-lag, temporal pattern, macrozoobenthos, *Syllis gracilis*, *Ensis directus*

Abstract:

The fluctuations in densities or biomass of a number of invading and native polychaete and mollusc species in southwest Netherlands were compared over a period of 20 years. For recent invaders a lag phase of seven to ten years occurred after their first appearance, followed by an exponential increase in abundance or biomass for two to three years. High numbers and biomass then continued for about five years, followed by a strong decline. The total sequence from introduction to decline lasted about fifteen years. The densities or biomass of invaders appearing decades or even centuries ago in the Delta area have fluctuated in a similar manner to that of native species, indicating that the densities or biomass of invading species after a fifteen year period of strong changes become largely governed 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 of the overall diversity.

Introduction

An increasing number of invading species has been observed worldwide, and the consequent problems 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 2% (1,016) 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 are also becoming 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). Yet an understudied topic is the long-term population dynamics of an invading species, i.e. the development of a speciesôpopulation after its introduction or appearance, its (vigorous) increase and eventually its decline and subsequent stabilization or disappearance. A few studies (Stachowitz & 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 are scarce, however during the last two decades, due to national legislation or European regulations (the Water Framework Directive for example) a stronger emphasis has been given to 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 to both native species and those species that invaded the area many decades or centuries ago.

Materials 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 (Figure 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 the Lake Grevelingen that was initially turned into a brackish lake and which 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). 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, numbering a minimum of 120 samples from the Oosterschelde and 60 from Lake Grevelingen. Three sediment cores (Ø 8cm) are taken from each station and merged into a pooled sample (total surface area 0.015 m^2). Sediment cores are collected directly in the intertidal zone at low water while subtidal cores are taken within 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 at the highest possible taxonomic level. For the present study all available data on the viewed species were clustered per half year, taking together all data for the two different seasons separately yet averaged over all strata and/or sub-regions in the basins, and by 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. Firstly, a group of smaller polychaetes; the recently invading *Syllis gracilis* and *Tharyx marioni* that entered the Delta area in the 1950s, and the native *Exogone naidina* were compared. *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 the species 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 recently invading jackknife clam, *Ensis directus*, was compared to the soft-shell clam, *Mya arenaria,* that invaded the Netherlands some centuries ago (Lasota et al, 2004; Wolff, 2005), and the native cockle, *Cerastoderma edule*. The originally American species *E. directus* 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* for the Dutch Delta waters was found in the Oosterschelde. In 1991 the species was also found in Lake Grevelingen (Wijnhoven & Hummel, 2009). *Mya arenaria* might 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

The recently invading species, the polychaete, *Syllis gracilis* (Fig. 2a) and the mollusc, *Ensis directus* (Fig. 2b), both showed about the same pattern of changes in densities in Lake Grevelingen as well as the Oosterschelde. After a lag period with very low densities or biomass for seven to ten years after their first recordings, the densities and biomass increased exponentially to high levels over a period of two to three years. The high densities and biomass remained for another three to five 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, 2b). These seemingly erratic changes are a normal 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 leveling off and decrease, lasted for about 15 years and was followed by a phase of balanced co-existence amongst 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 as performed in southwest Netherlands with samples taken each half year at many (60 to 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), yet to our knowledge has not been described before for marine macrozoobenthos. Here we have shown a seven to ten year lag phase and two to three 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 might hold true for the presently studied species.

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 become more and more 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 as temperature, currents, food concentration, and parasite or predator occurrence all affecting processes like the 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 affecting the water exchange with the North Sea, do have an impact on the densities of benthic species (Wetsteijn, 2011). Both *C. edule* and *M. 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 elevation of abiotic environmental parameters like temperature, salinity, water currents, turbidity and nutrient levels affecting biotic processes like 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 for the subsequent decline in their densities and leads to them becoming similarly regulated just as 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 help to contribute to models on the rate of species introductions and the success of these biological invasions as described by Wonham & Pachepsky (2006) and Miller et al (2007). It may however be expected that the duration of the lag phase and the period with high invader densities can be environment specific, as indicated by 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 of the diversity, as has also been suggested by Stachowicz and Byrnes (2006).

Acknowledgements:

We are grateful to the Directorate General ôRijkswaterstaat (RWS)ö of the current Dutch Ministry of Infrastructure and the Environment who funded the MWTL sampling program used for this study. Special thanks to the Invasive Species Team of the current Dutch Ministry of Economic Affairs, Agriculture and Innovation who made the desktop study on the invading species in the Dutch Delta waters possible. We thank Thomas Scott for his contributions to the text. This is publication 5157 of the Netherlands Institute of Ecology (NIOO-KNAW) and Monitor Taskforce Publication Series 2011-13.

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Figure 1. The location of the study areas in the south-west of the Netherlands

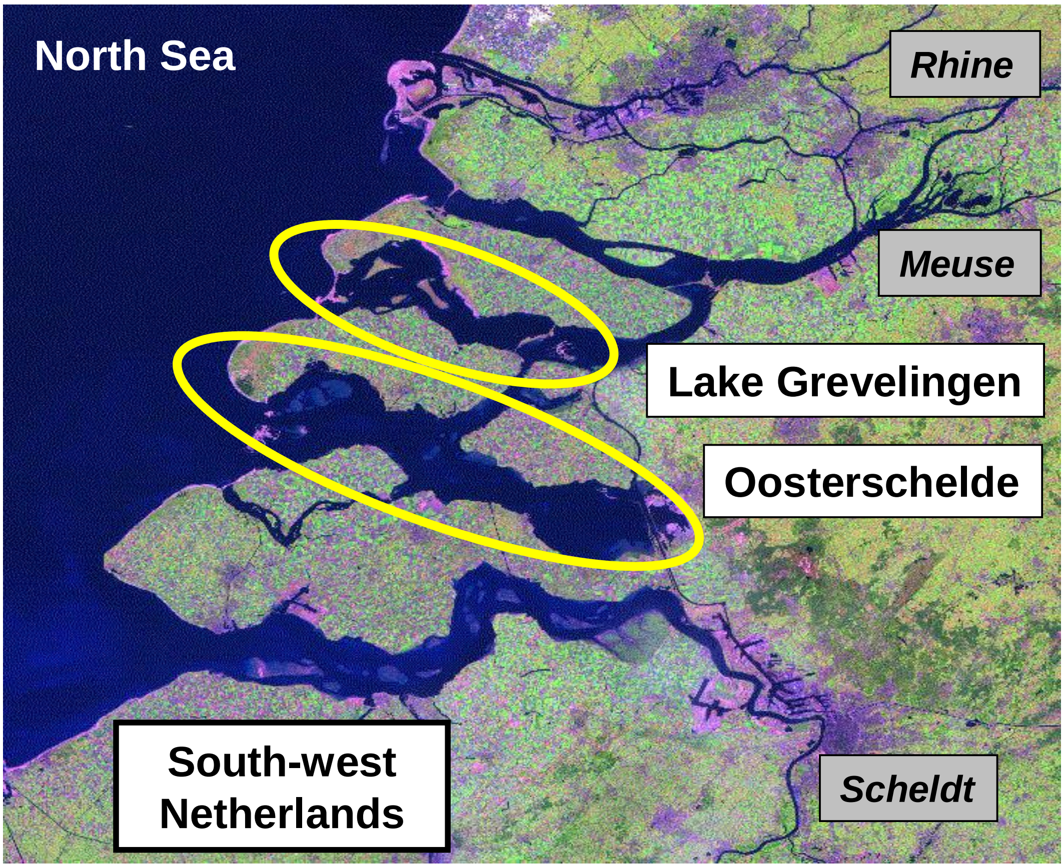
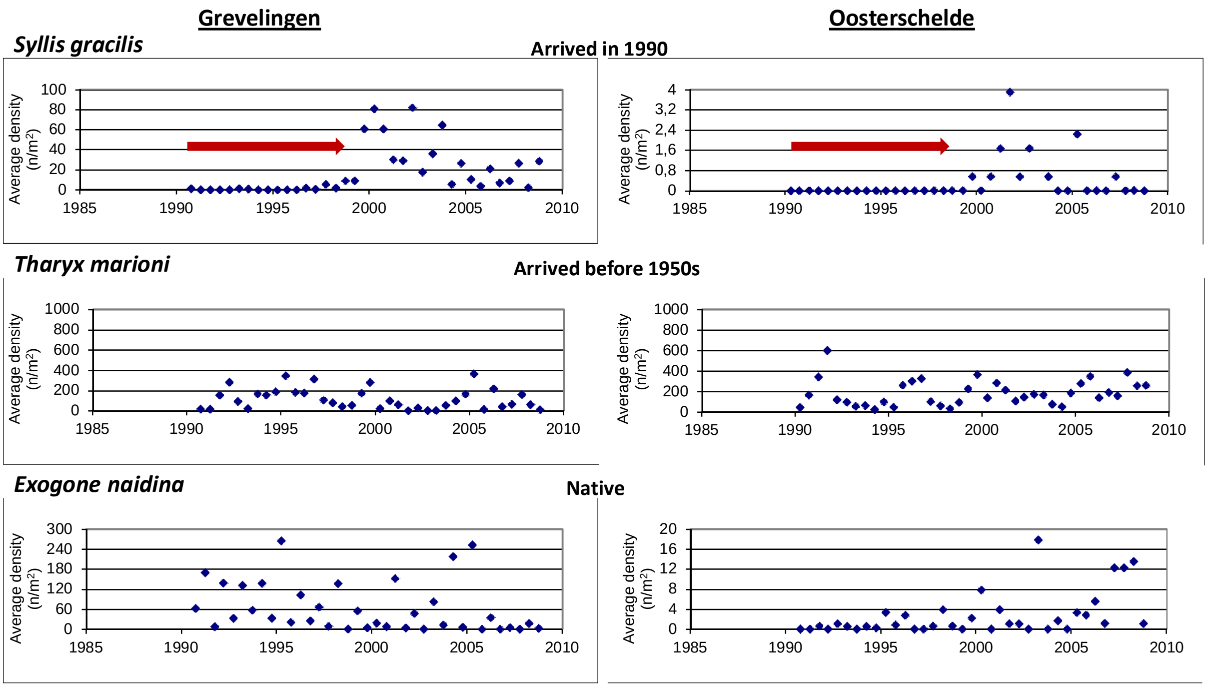


Figure 2: The fluctuations in densities of a recent invading polychaete (a) and in biomass of a recent invading mollusc (b) compared to the fluctuations in earlier invading and native species

2.a. Polychaetes



2.b. Molluscs

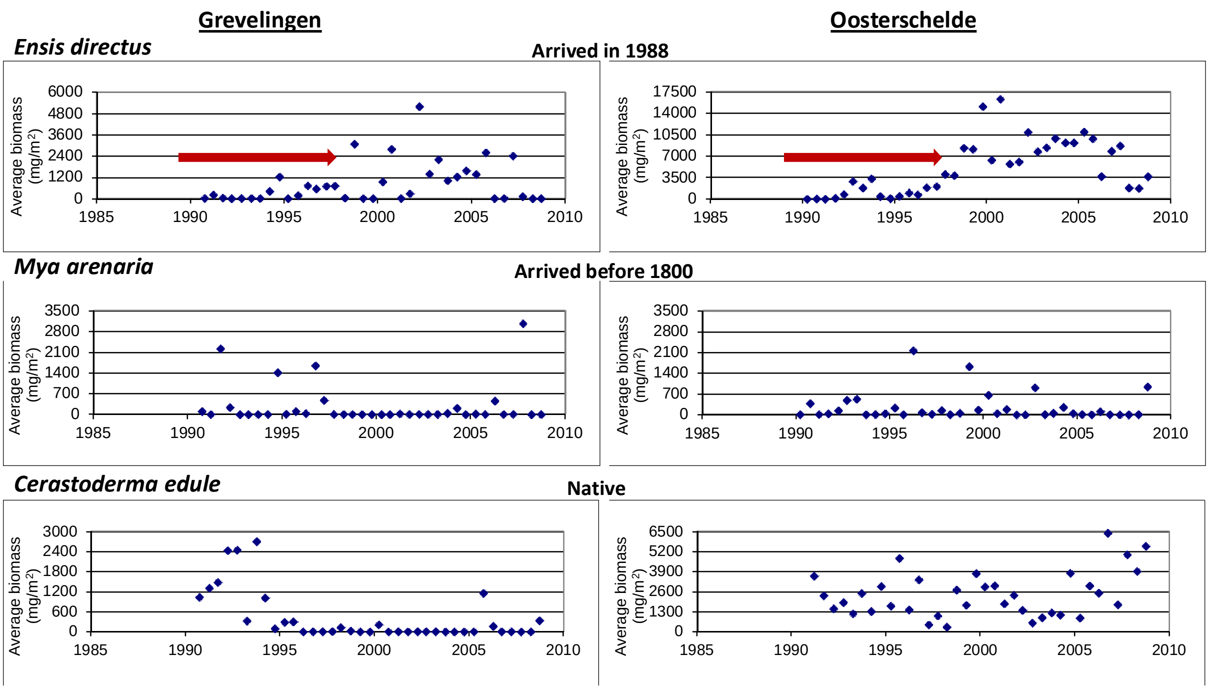


Figure 3: Conceptual pattern of population development for invasive species after arrival in a new environment