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Long-term dynamics and productivity of a successful invader: The first three decades of the bivalve *Ensis directus* in the western Wadden Sea

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ABSTRACT

Results are reported of a long-term and multi-station monitoring study in the western Wadden Sea on numerical densities, biomass, individual weights, and production of populations of the newly (late 1970s) introduced bivalve *Ensis directus*. Data are available on 18 fixed sites, sampled twice-annually ever since 1982 (13 truly intertidal stations and 2 in the transition zone to the subtidal) or 1989 (3 subtidal stations). After a slow start in the 1980s, numbers and biomass rapidly increased during the last 2 decades to reach locally high values in recent years: annual averages of tens of g ash-free dry mass m^{-2} in the subtidal and even of around 100 g AFDM m^{-2} in the transition zone, where it became the dominant species as to biomass and annual production. Temporal and local variability in production (and resulting biomass) could largely be explained by variation in numerical densities of 0-group individuals at the end of the first winter of their life. Highest densities and growth rates were observed in the transition zone. In the true subtidal, recruitment and growth rates were on average lower. In the true intertidal, abundances remained invariably low, as a consequence of relatively low recruitment and in particular poor subsequent survival. Within the “optimal” transition zone along tidal channels, the benthic habitat is highly dynamic, as it is exposed to physical disturbance resulting from both wave action and strong tidal currents. *E. directus* appears to be one of the few large-bodied benthic invertebrate species that can cope with the unstable sands in this zone. Most of its exceptional success may be explained by the occupation of this probably under-utilized habitat in Europe.

1. Introduction

The American Jack-knife or Razor clam *Ensis directus* (Conrad, 1843) (=*E. americanus* (Binney, 1870)) originates from the east coast of North America and was first recorded in Europe in the late 1970s. The find of a few very small (only about 2 or 3 cm shell length) unidentified specimens of an *Ensis* species on a tidal flat in the Dutch Wadden Sea near Terschelling in the summer of 1977 (Beukema and Dekker, 1995) may have been the first record in Europe. The first records in Europe of well-identified specimens were from several locations in the German Bight in the summer and autumn of 1979 (Mühlenhardt-Siegel et al., 1983). Since that time, the species rapidly spread both to the northeast and southwest (Armonies, 2001; Essink, 1985). By now, it is a common and often numerous species along the coasts of a substantial part of Western Europe: from southern Norway up to and including most of Normandy in France (Von Cosel, 2009).

The rapid proliferation of the species resulted in high abundance in shallow waters all along the Dutch coast (Tulp et al., 2010), including the Wadden Sea (Dekker, 2011). The increase continued all over the 1980s, 1990s and 2000s, with highest abundance in the most recent decade (compare Fig. 2 of Tulp et al., 2010 and Figs. 2 and 5 of Dekker, 2011). Locally, the species became a dominant member of the infauna with maximal numerical densities of >1000 ind m^{-2} and biomass values reaching values of several tens of g ash-free dry mass (AFDM) m^{-2}. Maximal abundance was not found at truly intertidal sites, but rather in the shallow subtidal and particularly in the transition zone from intertidal to subtidal parts of the Wadden Sea. In the German Wadden Sea and nearby North Sea, Armonies and Reise (1999) found maximal densities and biomass values of *E. directus* in the shallow subtidal and in the intertidal just below spring low tide level (i.e. in the above defined transition zone). In the Danish Wadden Sea, Freudendahl et al. (2010) found the intertidal distribution to be restricted to a narrow zone around the mean low tide level. The habitats in the transition zones along tidal channels are characterized by strong tidal currents and wave action, resulting in unstable sands with low silt contents. Before the expansion of *E. directus*, such areas were a sparsely occupied habitat in the Wadden Sea with low zoobenthic biomass (Armonies and Reise, 1999; Lackschewitz and Reise, 1998). Nowadays, this invader is the dominant member of the macrozoobenthos in terms of biomass there (Dekker, 2011).

The strong proliferation of *E. directus* may be another example of a successful alien that exerts substantial impacts on the recipient ecosystem (Ruesink et al., 2006; Simberloff, 2011), as did another recent invader, *Crassostrea gigas*, in the Wadden Sea (Troost, 2010). The

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expected significance of effects of highly successful introduced species on ecosystem structure and functioning (Reise et al., 2006) makes it worthwhile to quantify as good as possible the role of *E. directus* in the invaded ecosystem. Because the ecological role of a species can be judged best from its share in the productivity of the ecosystem, we assessed not only biomass but also estimated annual production values of *E. directus* populations from twice-annually gathered data on numerical densities and mean weights of aged individuals of successive cohorts. Continuous data series on this species from our long-term monitoring program are available for 29 years (1982–2010 period) at 15 sampling sites in the intertidal and transition zone and for 22 years (1989–2010) at 3 subtidal sites, allowing a genuinely long-term record of dynamics, growth and productivity of the species. As far as we are aware, published long-term studies on the species are limited to about 10 years (Dörjes, 1992) and indicate a highly variable abundance as a consequence of erratic recruitment and occasional mass mortalities (Armonies and Reise, 1999).

2. Methods

Since the 1970s, the macrozoobenthos community has been monitored at 15 fixed sampling sites at a 50-km^2 tidal-flat area called "Balgzand", in the westernmost part of the Dutch Wadden Sea (at about 53° N and 5° E). Among these 15 sites, 13 (crosses in Fig. 1) were situated within the true intertidal (i.e. between mean high-tide level MHTL and mean low-tide level MLTL) and 2 (open circles in Fig. 1) in the transition zone to the subtidal (i.e. between MLTL and lowest astronomical tide). Starting from 1989, 3 subtidal transects in the western Wadden Sea (20–40 km NE of Balgzand) were added to the monitoring program: solid squares in Fig. 1. The monitoring program comprises twice-annual (late winter: mostly March and late summer: mostly August) estimates of numbers and biomass of all macrobenthic (those retained on 1-mm sieves) invertebrate species.

At Balgzand, samples were taken with hand-operated corers of ~0.02 and 0.01 m^2. Larger samples were taken in winter (~1 m^2 per site) than in summer (~0.5 m^2 per site), because numerical densities were generally lower in winter than in summer. Details on sampling sites and methods can be found in earlier publications (e.g. Beukema and Cadée, 1997). At the subtidal sites samples were taken from a ship with a 0.06 m^2 Reineck boxcorer. Each subtidal site is a transect of 15 cores in line with a distance of ~100 m between the cores. Therefore, each site covered 0.9 m^2. Depending on the penetrability of the sediments, the core depth of the boxcore samples varied between 15 and 45 cm. All core samples were sieved on board over 1-mm sieves. For details of sampling procedures see Dekker (2011).

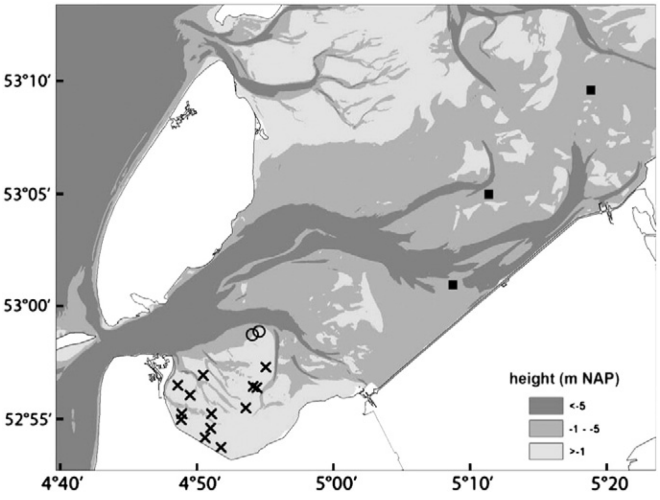

Fig. 1. Location of sampling sites in the westernmost part of the Wadden Sea: (crosses) 13 intertidal stations on Balgzand, (open circles) 2 stations at the transition of intertidal to subtidal parts of Balgzand, and (solid squares) 3 truly subtidal stations. NAP in the legend is Mean Tidal Level (MTL).

At Balgzand, the sampling sites were scattered (almost) randomly over the tidal flats of the Balgzand area and covered the entire intertidal depth range (compare Fig. 1b of Beukema and Cadée, 1997), which runs on average from about $+6$ to -8 dm, compared with mean-tide level (MTL). The levels of the 13 sites in the true intertidal were between $+5$ and -8 dm, those of the 2 in the transition area between -8 and -12 dm. The sites in the subtidal area were at depths between 16 and 47 dm below MTL. The sampling sites covered a wide range of sediment composition. Silt (material <16 µm) content of the top 5 cm of the sediment ranged from $>10\%$ to ~2% in the intertidal, was ~1% in the transition zone and ranged from ~10 to ~2% at the subtidal sites.

In the present paper, we use data on *E. directus* of the homogeneous 29-y series 1982–2011 in the intertidal and transition area and the 22-y series 1989–2011 in the subtidal area. All data on abundance are expressed in $n\ m^{-2}$, on biomass in g AFDM m^{-2} and on production in g AFDM $m^{-2}y^{-1}$. All *E. directus* were sorted from the sieved samples, measured and opened by short immersion in boiling water to remove the soft parts. These were dried (two or three days at 60 º C in a ventilated stove), weighed (individually or per 1-mm shell-length class), and incinerated. Ash-free dry mass (AFDM) is soft-parts dry weight minus ash weight (after incineration at 560 °C). Data on individual weights and length were used to calculate "condition" of individuals as body-mass index (BMI): individual AFDM divided by third power of shell length, in mg cm^{-3}. The shells were assigned to age classes by external examination of the number of year marks on the shells. We are confident that the marks read were truly annual, because strong cohorts could be easily traced as peaks in the length-frequency distributions for several years after their appearance. Numerical densities ($n\ m^{-2}$) of all cohorts thus could be assessed with half-year intervals. Young-of-the-year are called recruits and the time of sampling is indicated (summer recruits of ~4 months old and hardly larger winter recruits of an age of ~6 more months that had survived their first winter).

Values of (somatic) production were estimated following the weight-increment summation method as described by Van der Meer et al. (2005). We made separate calculations for half-year periods and for individual sampling sites. As annual estimates (March–March) we used the sum of two successive seasonal estimates, i.e. March–August (growing season with mostly positive values) and August–March (weight-loss season with mostly negative values). For each of the sites and half-year periods (t to $t+1$), we defined production P as the product of mean numerical density ($0.5\ N_t + 0.5\ N_{t+1}$) and weight change ($w_{t+1} - w_t$), where N_t and N_{t+1} are the numerical densities ($n\ m^{-2}$) at the start and end of the production period, respectively, and w_{t+1} and w_t are the mean soft-parts AFDM per individual at these times. Estimates of N and w were obtained separately per year class (or cohort: all individuals born in the same year, almost exclusively in spring). We did not succeed in estimating production during the first growing season. The first estimates on N and w available were of spat-sized animals in August, ~3 months after their settlement. At that time a substantial part of the growth in the first growing season was already completed. A minimal estimate of spat production before August would equal the spat biomass found in August, but the true production (including their biomass at settlement and production by spat that had died between settlement in May/June and sampling in August) must have been higher, maybe twice the biomass observed in August. We arbitrarily adopted a value of 2 times spat biomass in August (i.e. the product of their numerical density times their mean individual weight in August) as a rough estimate of production of spat-sized animals in their first growing season (between settlement in May and first sampling in August).