Helgol Mar Res
DOI 10.1007/s10152-011-0271-2

ORIGINAL ARTICLE

The fate of an immigrant: *Ensis directus* in the eastern German Bight

Jennifer Dannheim · Heye Rumohr

Received: 28 January 2011 / Accepted: 3 August 2011

Abstract We studied *Ensis directus* in the subtidal (7–16 m depth) of the eastern German Bight. The jack-knife clam that invaded in the German Bight in 1978 has all characteristics of a successful immigrant: *Ensis directus* has a high reproductive capacity (juveniles, July 2001: Amrumbank 1,914 m^{-2}, Eiderstedt/Vogelsand: 11,638 m^{-2}), short generation times and growths rapidly: maximum growth rates were higher than in former studies (mean: 3 mm $month^{-1}$, 2nd year: up to 14 mm $month^{-1}$). *Ensis directus* uses natural mechanisms for rapid dispersal, occurs gregariously and exhibits a wide environmental tolerance. However, optimal growth and population-structure annual gaps might be influenced by reduced salinity: at Vogelsand (transition area of Elbe river), maximum growth was lower (164 mm) than at the Eiderstedt site (outer range of Elbe river, $L_\infty = 174$ mm). Mass mortalities of the clams are probably caused by washout (video inspections), low winter temperature and strong storms. *Ensis directus* immigrated into the community finding its own habitat on mobile sands with strong tidal currents. Recent studies on *E. directus* found that the species neither suppresses native species nor takes over the position of an established one which backs up our study findings over rather short time scales. On the contrary, *E. directus* seems to favour the settlement of some deposit feeders. Dense clam mats might stabilise the sediment and function as a sediment-trap for organic matter. *Ensis directus* has neither become a nuisance to other species nor developed according to the 'boom-and-bust' theory. The fate of the immigrant *E. directus* rather is a story of a successful trans-ocean invasion which still holds on 23 years after the first findings in the outer elbe estuary off Vogelsand.

Keywords *Ensis directus* · Introduced species · Competition · Invasion · North Sea · Growth rate

Introduction

Benthic species in the shallow inner German Bight live in a very dynamic environment, characterised by large seasonal and annual temperature variations, storms and tidal currents that lead to sediment erosion and relocations (Dyer et al. 1983; Dörjes et al. 1986; Becker et al. 1992; Kröncke et al. 2001). Moreover, rare events such as extremely cold winters (e.g. Ziegelmeier 1964; Dörjes et al. 1986; Kröncke et al. 1998; Armonies et al. 2001) and anoxia (Niermann et al. 1990; Duineveld et al. 1991; Beukema 1992) affect significantly recruitment and survival of species. Further, benthic communities were changed by several anthropogenic impacts such as fishing disturbance, pollution, eutrophication and invasions by immigrant species, i.e., species that are intentionally or unintentionally introduced by human activity (e.g. Duineveld et al. 1991; Kröncke 1992, 1995; Rumohr and Kujawski 2000). In the last century, many immigrants have settled more or less successfully in the North Sea (e.g. *Crassostrea gigas*, *Marenzelleria* cf. *wireni*, *Eriocheir sinensis*, *Caprella mutica*, *Hemigrapsus sanguineus*).

Communicated by H.-D. Franke.

J. Dannheim (✉)
Alfred Wegener Institute for Polar and Marine Research,
PO Box 12 01 61, 27515 Bremerhaven, Germany
e-mail: Jennifer.Dannheim@awi.de

H. Rumohr
Leibniz Institute of Marine Sciences (IFM-GEOMAR),
Düsternbrooker Weg 20, 24105 Kiel, Germany

Studies on biological invasions, their dynamics, population development and impacts on the communities are numerous (e.g. Carlton 1996; Williamson 1996; Cohen and Carlton 1998; Ricciardi and Rasmussen 1998; Parker et al. 1999; Essink and Dekker 2002). Ricciardi and Rasmussen (1998) listed eleven attributes necessary for an alien species to permit a successful settlement in a new habitat or community: (1) abundant and widely distributed in original range, (2) wide environmental tolerance, (3) high genetic variability, (4) short generation time, (5) rapid growth, (6) early sexual maturity, (7) high reproductive capacity, (8) broad diet opportunistic feeding, (9) gregariousness, (10) possessing natural mechanisms of rapid dispersal and (11) commensal with human activity (e.g. ship ballast-water transport).

The fate of an immigrant depends on several factors. First, the new habitat must be a region where the potential of invasion is given, i.e., species invasion by ballast water, aquaculture product or by release of animals (e.g. Cohen and Carlton 1998). Invasions occur mainly in so-called 'hot spots' (Ricciardi and Rasmussen 1998). These are often regions with intense trans-ocean shipping traffic. The 'Großer Vogelsand', a sandbank in the Elbe estuary situated at the main shipping track to Hamburg harbour, is such a potential invasion region, and invasive species benefit from human-induced dispersal mechanisms by transport in ship ballast water (Gollasch 1996).

Secondly, the new habitat must be similar to the invaders' natural habitat with, e.g., similar climates and habitat structure (Mack 1996). And in the end, space to settle must be given either integrative within the new habitat (e.g. by ecological and spatial adaptation) or suppression and taking over the position of an established native species (Essink and Dekker 2002). The success of an alien species depends on the possibility of expansion of the population and of successful reproduction. Thereby, the invader might become a pest to other species and suppress native species or the population might increase to very high densities and decrease again ('boom and bust' development, e.g. Parker et al. 1999).

The American jack-knife clam, *Ensis directus* (Conrad 1843), originally stems from the Atlantic coast of North America. In 1978, larvae of this species reached the German Bight by water of ballast tanks (von Cosel et al. 1982). The jack-knife clam dispersed rapidly with the northerly directed residual currents along the coast of Germany (North Frisia) and Denmark, but also against the prevailing currents and reached the French and British coast in 1991 and 1989, respectively (Essink 1985, 1986; Van Urk 1987; Howlett 1990; Luczak et al. 1993).

First investigations of this invader in the German Bight were made by von Cosel et al. (1982) dealing with the zoogeography and taxonomy of this species. The abundance and population dynamics of *E. directus* were investigated in the years 1980–1981, 1980–1989 and 1982–1994 by Mühlenhardt-Siegel et al. (1983), Dörjes (1992) as well as Beukema and Dekker (1995). The latest study about *E. directus* in the German Bight (1992–1996) was carried out by Armonies and Reise (1999).

Here, we investigate attributes necessary for *E. directus* as an alien species to settle successfully, i.e., population size and mortality, species growth and size as well as potential suppression of native species. These attributes enable to assess whether *E. directus* population dynamics followed the 'boom-and-bust' development or whether the species remained stable in population size by either suppressing native species or rather by integrating successfully in the native benthic community after 23 years.

Materials and methods

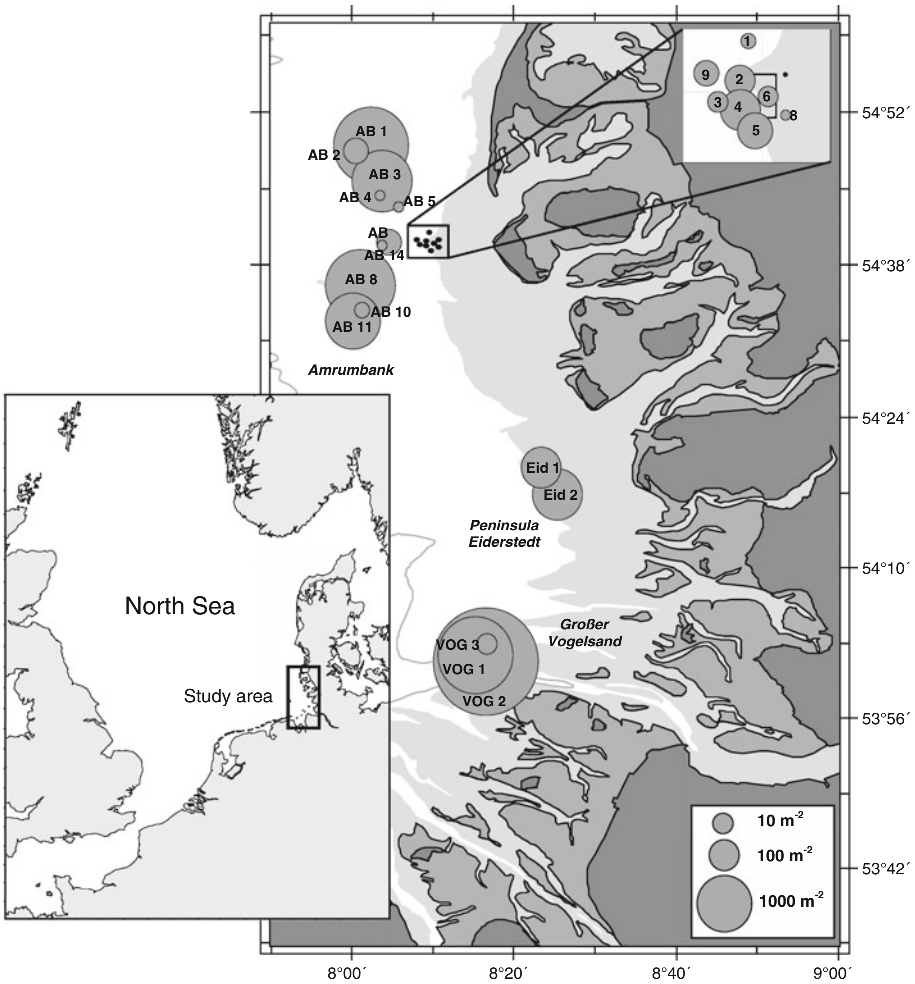
The study area is situated in the inner German Bight in the subtidal between 7 and 16 m water depth along the coast of North Frisia. Sediments vary from coarse sand to fine and silty fine sand. In total, 28 stations (3 replicates per station) were sampled which can be divided into three regional areas: the 'Amrumbank' (and north of it, 23 stations), 'Eiderstedt' close to the homonymous peninsula (2 stations) and the 'Großer Vogelsand' (3 stations) at the Elbe estuary where *E. directus* was found at first (Fig. 1).

Sampling was carried out three times per year in 2000 and 2001 (2000: March, August and November; 2001: March, May and July) with a 70 kg Van-Veen-grab (0.1 m^2). Sampling and further processing followed the ICES method recommendations (Rumohr 1999). All samples were sieved on board through a 1-mm sieve and fixed in a 4% formalin-seawater solution. Upon return to the laboratory, sampled specimens were determined to the lowest possible taxonomic level, and species abundances were standardised to 1 m^2.

Length and width of *E. directus* specimens were measured to the nearest 0.1 mm, maximal 100 specimens from a subsample. *Ensis directus* lives with the posterior end just below the sediment surface (Drew 1907; Stanley 1970), but retracts quickly deeper in its burrow if disturbed. More often than not, larger specimens of *E. directus* are cut by grabs. Hence, length of these larger individuals was calculated by a length/width relationship (see Fig. 2), a constant and established identification characteristic (von Cosel et al. 1982).

In order to study potential suppression of *E. directus* on native species, we correlated its abundance with the abundance of 59 species that occurred with a presence of >20% in the study area and looked for significant ($P < 0.05$) negative correlations.

Fig. 1 Map of investigation area and mean abundance (m^{-2}) of *E. directus*. The *upper right* corner shows the stations Spi *1–9*



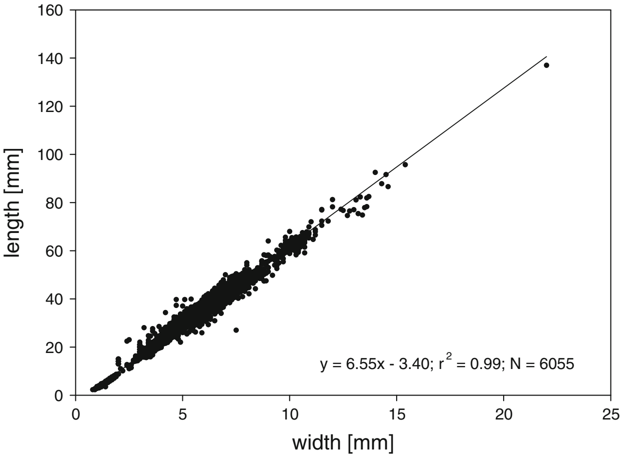


Fig. 2 Length/width relation of *E. directus* in the study area

Growth rates were calculated by increase in size between mean length within cohorts at each sampling. The month March/April when spawning of *E. directus* occurs (Mühlenhardt-Siegel et al. 1983) was set to zero. Weighted mean values for each year were calculated, and the von Bertalanffy model was used to describe growth of the clams over its lifespan:

$$L_t = L_\infty * \left(1 - e^{-k^*(t-t_0)}\right) \qquad (1)$$

where L_t is the length of *E. directus* at age t, L_∞ is the maximum length achievable, k is the species growth rate. For the Amrumbank only, we were able to calculate seasonal growth over the two sampling years by following four distinct cohorts. A Gaussian distribution (with 3 parameters) was fitted to the data to describe growth rates (mm month^{-1}) over age.

The mortality was estimated by the decrease of individual numbers within cohorts (only cohorts from 2000 and 1999):

$$M = \left(1 - \frac{N_0}{N_t}\right) * 100 \qquad (2)$$

where M is the mortality of the cohort, N_0 the individuals density at first recording and N_t the density at last recording. Monthly mortality rates were calculated by using the densities between the consecutive sampling dates.

Results

Accompanying fauna

Ensis directus was the most dominant (Amrumbank: 67%, Eiderstedt: 48%, Vogelsand: 83%) and most frequent species (Amrumbank: 64%, Eiderstedt: 100%, Vogelsand: 100%) in the study area (Table 1). The accompanying fauna consisted of typical fine-sand species of the *Tellina-fabula*-association (*sensu* Salzwedel et al. 1985; Rachor et al. 2007). Besides *E. directus*, mainly tube-building worms such as *Spiophanes bombyx* (7%), *Magelona johnstoni* (6%) and *Lanice conchilega* (3%) occurred in high densities at Amrumbank. At the Eiderstedt site, *Macoma balthica* (14%) and small polychaetes such as *Spio goniocephala* (8%) and *Scoloplos armiger* (5%) were predominant. According to Salzwedel et al. (1985) and Rachor et al. (2007), the Vogelsand fauna belongs to the *Nucula-nitidosa*-association. However, the dominant species accompanying *E. directus* were similar to those of the *Tellina-fabula*-association: *L. conchilega* (8%), *T. fabula* (6%) and *Nephtys hombergii* (1%).

Table 1 Dominance (%), mean abundance ± SD (m^{-2}) and presence (%) of the five most dominant species in the study area

Species	Dominance (%)	Mean abundance ± SD	Presence (%)
Amrumbank			
Ensis directus	66.5	699 ± 1,956	63.8
Spiophanes bombyx	7.0	73 ± 253	46.6
Magelona johnstoni	6.2	65 ± 133	53.4
Lanice conchilega	3.0	31 ± 143	20.7
Asterias rubens	2.1	22 ± 168	6.9
Eiderstedt			
Ensis directus	48.4	475 ± 855	100.0
Macoma balthica	13.7	109 ± 14	100.0
Spio goniocephala	8.0	79 ± 205	50.0
Scoloplos armiger	5.1	50 ± 52	100.0
Spiophanes bombyx	3.6	26 ± 4	100.0
Vogelsand			
Ensis directus	82.5	6,575 ± 10,980	100.0
Lanice conchilega	7.9	626 ± 1,206	60.0
Tellina fabula	6.0	478 ± 425	100.0
Nephtys hombergii	1.3	105 ± 45	100.0
Abra alba	0.7	58 ± 95	80.0

Abundance of *E. directus*

The mean abundance of *E. directus* in the study area was 1,087 ± 3,521 m^{-2}. The highest density occurred on the Vogelsand (6,575 ± 10,980 m^{-2}). At the Amrumbank, the abundance of the American jack-knife clam was 699 ± 1,956 m^{-2}; the Eiderstedt site had a density of 475 ± 855 m^{-2} (Table 1). The species occurred at almost all stations in the investigation area except at those with coarse sand (Figs. 1, 3). Density of *E. directus* depended on sediment and depth (Fig. 3). Highest abundances were recorded on silty fine (2,821 ± 7,082 m^{-2}) or fine (1,599 ± 2,757 m^{-2}) sands, as well as at 10 m (2,039 ± 6,090 m^{-2}) and 12 m (1,474 ± 2,969 m^{-2}) depth.

Clams' densities were strongly variable by the pronounced seasonal development (Fig. 4). Population-structure development differed between Eiderstedt/Vogelsand and Amrumbank sites. At Eiderstedt/Vogelsand, density was highest in March 2000 (696 m^{-2}) owing to individuals that derived mainly from 1999. Consecutively, the abundance of this cohort decreased until May 2001 (9 ± 1 m^{-2}). At Amrumbank, density increased from August 2000 (613 ± 1,861 m^{-2}) to November 2000 (1,285 ± 2,350 m^{-2}) by the recruitment of this year's cohort. During 2001, the density of this cohort decreased again (March 2001: 798 ± 1,424 m^{-2}; May 2001: 98 ± 314 m^{-2}).

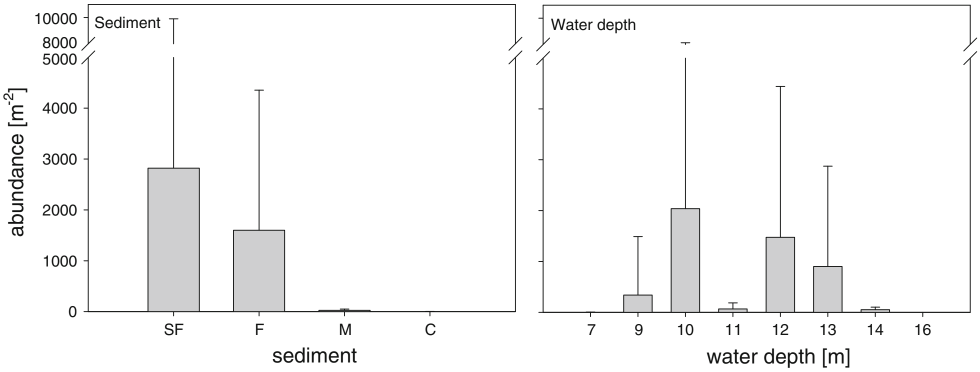


Fig. 3 Distribution of *E. directus* (m^{-2}) subject to sediment (*SF* silty fine sand, *F* fine sand, *M* medium sands, *C* coarse sand) and water depth (m)

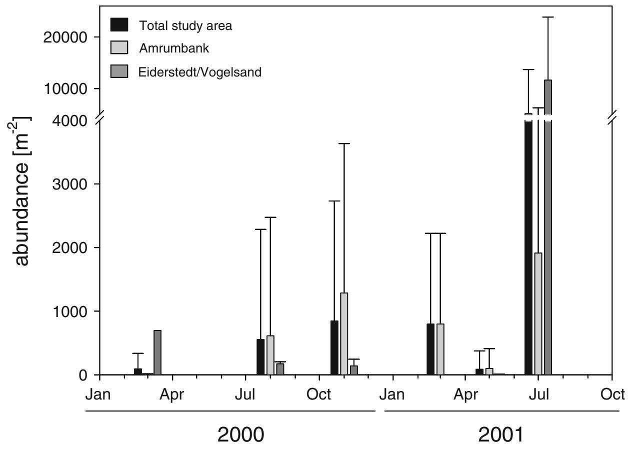


Fig. 4 Mean abundance ± SD (m^{-2}) of *E. directus* in the study area over time of investigation (March 2000 until July 2001)

At both sites, densities strongly increased in July 2001 with highest abundances during study time (Amrumbank: 1,914 ± 4,360 m^{-2}; Eiderstedt/Vogelsand: 11,638 ± 12,213 m^{-2}) caused by freshly settled larvae.

Suppression of other species

Potential suppression of other species by *E. directus* was tested with density correlations between the 59 most frequent species and the jack-knife clam at all stations investigated ($N = 28$). The results of the five most dominant bivalves and the species *L. conchilega*, *N. hombergii*, *Spio martinensis* are listed in Table 2. *Ensis directus* did not show any suppression of any species including the dominant bivalves. Densities of *M. balthica*, *Spisula solida* and *Kurtiella bidentata* neither were high at low density of *E. directus* nor low at high densities of the jack-knife clam. On the contrary, *E. directus* seemed to favour the appearance of some species. *T. fabula* and *Abra alba* showed higher abundances at stations with higher densities of *E. directus* ($P < 0.05$; *T. fabula* $r^2 = 0.85$; *A. alba* $r^2 = 0.17$). The same relation was observed with the tube building polychaetes *L. conchilega* and *S. martinensis* ($P < 0.05$; *L. conchilega* $r^2 = 0.85$; *S. martinensis* $r^2 = 0.52$), as well as the predatory polychaete *N. hombergii* ($P < 0.05$; $r^2 = 0.61$).

Size spectra and growth rates

Growth of *E. directus* was described by a von Bertalanffy model calculated with weighted mean length over age-years separately for the three investigated study sites (Fig. 5). At the Amrumbank, we identified four well distinguishable age groups of clams (cohorts: 1998, 1999, 2000, 2001), whereas in the Eiderstedt/Vogelsand region, only two cohorts were observed (1999, 2001). The cohort from 2000 was predominant at the Amrumbank, whereas at the Eiderstedt/Vogelsand sites, this 2000 cohort was totally missing and the cohort from 1999 was more abundant.

Individuals of the American jack-knife clam grew larger at the Amrumbank (recorded maximum length of 172 mm, 4 years). Estimated maximum length by the von Bertalanffy model was 254 mm. In the Eiderstedt region, the recorded maximum length was 144 mm (calculated length by model: 174 mm), but most animals did not become larger than 70 mm (2 years). At the Vogelsand, most individuals did not achieve a length larger than 100 mm (3 years). The model calculated a maximum length of 164 mm, but largest individual found at the site was only 120 mm.

A mean growth rate of 3.5 mm $month^{-1}$ at in the whole study area and over the whole year was determined. The von Bertalanffy model showed differences in growth rates between the study areas (Fig. 5). Relative growth was lowest at the Amrumbank with 2.4 mm $month^{-1}$, the Vogelsand population showed a growth rate of 2.8 mm $month^{-1}$, and highest relative growth was recorded at the Eiderstedt site (4.1 mm $month^{-1}$).

Ensis directus showed a strong seasonal variability in growth with highest growth rates (up to 14 mm $month^{-1}$)

Table 2 Slopes, intercepts, correlation coefficient (r^2 values) and significance (*F* and *P* values of correlations between the abundance of the five most dominant bivalves and species that showed significant correlations ($P < 0.05$, bold) with the density of *E. directus* (m^{-2}) ($N = 28$ stations)

Species	Slope	Intercept	r^2	*F*	*P*
Dominant bivalves					
Abra alba	0.004	4.65	0.17	$5.38_{1,27}$	**0.03**
Macoma balthica	-8.73^{E-05}	11.36	4.68^{E-05}	$0.001_{1,27}$	0.97
Kurtiella bidentata	0.001	3.39	0.04	$1.20_{1,27}$	0.28
Spisula solida	-1.89^{E-04}	5.51	0.006	$0.17_{1,27}$	0.68
Tellina fabula	0.06	−12.12	0.85	$152.54_{1,27}$	**<0.01**
Other species (sign. correlations)					
Lanice conchilega	0.18	−72.16	0.85	$156.84_{1,27}$	**<0.01**
Nephtys hombergii	0.01	3.91	0.61	$43.02_{1,27}$	**<0.01**
Spio martinensis	0.01	4.03	0.52	$29.54_{1,27}$	**<0.01**

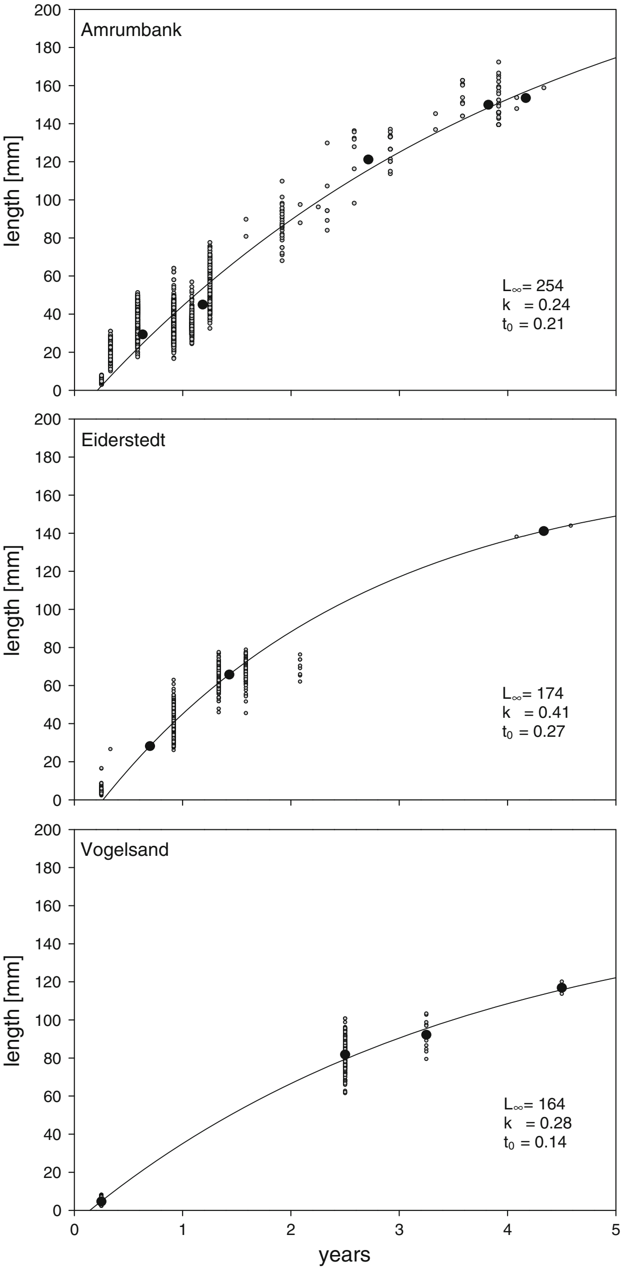


Fig. 5 Length distribution of cohorts of *E. directus* on the Amrumbank, at the Eiderstedt site and on the Vogelsand. Growth is described as von Bertalanffy model with weighted mean values for every single year of lifespan (spawning time in March/April is set to zero). *Grey dots* mark raw data, *black filled circles* mark weighted annual mean value

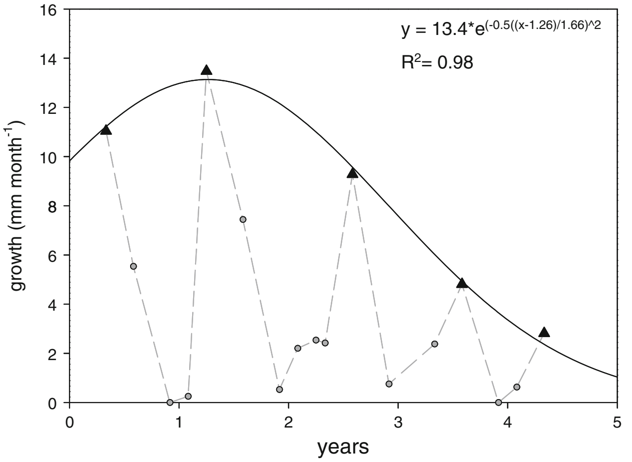


Fig. 6 Growth of *E. directus* at the Amrumbank over age. *Grey circles* show seasonal development of growth. *Black triangles* mark maximum growth in summer/autumn for every year. Growth over years is described by a Gaussian distribution with three parameters. Date of spawning (March/April) is set to zero

in summer/early autumn and lowest (0–2 mm month^{-1}) in winter/spring (Fig. 6). In order to describe growth over lifespan of the American jack-knife clam, maximum growth rates (summer/autumn) were fitted to a Gaussian distribution (Fig. 6). In the year 0 (year of settlement), a maximum growth of 11 mm month^{-1} was recorded. Highest growth rate over lifespan was observed in the first year (14 mm month^{-1}) and consecutively growth decreased over the years: 2nd year: 9 mm month^{-1}; 3rd year: 5 mm month^{-1}; 4th year: 3 mm month^{-1}. The Gaussian model showed a peak of 13.4 mm month^{-1} (August 1st year; see Fig. 6: $x = 1.26$) followed by a decrease to 1 mm month^{-1} at an age of 5 years.

Mortality

It was difficult to estimate the mortality of *E. directus* because the investigation time was very short and only a few cohorts could be followed, the distribution of *E. directus* is patchy and, finally, it is questionable whether the grab sampled all jack-knife clams as the clam is able to move quickly into the sediment. However, at the Amrumbank, we estimated a mortality of 74% year^{-1} (6% per month^{-1}) for the cohort of 2000, the 1-year-old clams. In the Eiderstedt/Vogelsand region, the mortality amounted to 85% year^{-1} (7% month^{-1}) for the 2-year-old clams (cohort of 1999). The highest loss of clams occurred from March until May (30–35% month^{-1}).

Discussion

Twenty-three years after its first appearance, *E. directus* is still an important and dominant member of the benthic fauna in the German Bight.

The mean abundance on Vogelsand, the region of the first observation of *E. directus*, today is higher than in the past (this study: 6,575 m^{-2}, Mühlenhardt-Siegel et al. 1983: <500 m^{-2} (1979–1982)). Highest density found due to a spatfall was also higher (this study: 25,513 m^{-2}; Mühlenhardt-Siegel et al. 1983: 15,440 m^{-2}). Mean density found by Armonies and Reise (1999) (440 m^{-2}) in the intertidal near the island Sylt is comparable to densities found in this study on the Amrumbank (699 m^{-2}). In parts, these differences between abundances were caused by seasonal differences (e.g. massive spat fall in July 2001) or by a patchy distribution. Schröder (2003) recorded a permanent population of the American jack-knife clam from 1995 onwards at a station in the outer range of the Elbe river.

Ensis directus managed this establishment by finding its own habitat in mobile fine and silty fine sands of highly energetic habitats along the Frisian coast, as the jack-knife clam is very mobile and can burrow quickly and deep (Drew 1907). In contrast to the study of Armonies and Reise (1999) in the intertidal, *E. directus* did not suppress other bivalves in the subtidal but favoured a few species, mainly deposit feeders. The reasons for benthic fauna changes are complex: altered flow rates within the habitat might increase sedimentation rates within the mussel habitat or organic enrichments by biodeposits might change sediment chemistry (Markert et al. 2010). Dense mats of the American jack-knife clam might have stabilised the sediment and function as a sediment-trap, i.e., collecting particular organic matter. Other deposit feeding species, however, did not correlate with *E. directus* densities (e.g. *Spiophanes bombyx*, *Magelona johnstoni* or small amphipods).

Only a few suppression examples by invasive species are known in the North Sea (see Essink and Dekker (2002) for *Marenzelleria viridis* example), but hitherto no species extinction by alien species is recorded (Beukema and Dekker 2011 and citations therein). In contrast, recent studies of Markert et al. (2010) and Troost (2010) on mussel beds of *Crassotrea gigas*, as well as Beukema and Dekker (2011) and this study on sandy habitats with *E. directus*, found increased species numbers, abundances, biomass and diversity in mussel habitats changed by the invasive species in the North Sea. Nevertheless, *E. directus* is patchy distributed and variable in occurrence, e.g., mass mortalities and large spat falls (this study, Beukema and Dekker 2011). Our correlations are based on a limited station number ($N = 28$) over a rather short study period and thus display only a snapshot at a certain time. Monitoring of *E. directus* densities and the associated fauna over longer time scales might be a better and sound base for species occurrences dependent on the occurrence of American jack-knife clams.

As densities nowadays are throughout higher than in former studies with similar study sites, we can assert that *E. directus* has established a robust population in the German Bight after 23 years. The clam integrated into the community without specific adaptations to the new habitat as the original habitat at the US coast is also fine sand with medium to strong currents (Bousfield 1960; Stanley 1970). Settling of invaders needs ecological space and the American jack-knife clam integrated into the community without suppressing or taking over the position of an established native species in the subtidal of the Frisian coast.

The population structure was different between the studied sites. At the Amrumbank, age classes from 1997 to 2001 were found. At the Vogelsand and Eiderstedt site, only two generations (2001, 1999) were observed. Dörjes (1992) stated that mainly two generations (maximum three) could be found at one station and that annual gaps are usual. He found annual gaps in the year 1981 and 1988, in this study, the gap was in 2000. All these years had a high runoff of the river Elbe in March and April (around 3,000 m^3/s; Kappenberg 2006). The Vogelsand and Eiderstedt site are situated in the river Elbe area and Eiderstedt supplementary in the zone of the river Eider. Hence, it might be that reduced salinity or higher sediment resuspension influenced the succession of recruitment. However, transitions in benthic communities by changing recruitment success were recorded in various parts of the North Sea (Austen et al. 1991; Kröncke et al. 2001), and thus, other environmental factors might be responsible for different recruitment success as well.

The von Bertalanffy model showed that *E. directus* has the potential to grow up to a length of 164–254 mm, comparable to length in its original habitat (Stanley 1970; Morris 1973; Abbott 1974). Maximum modelled length might be an overestimation (Amrumbank) for the lack of older individuals and the problem of age classification of larger animals (no definite ageing by shell growth marks possible). However, largest specimens occurred at Amrumbank up to an age of 4 years, which is common for the North Sea and goes along with other investigations (Table 3). Sizes of *E. directus* at the end of each age-year were also comparable to other investigations (Table 3).

Modelled maximum length at the Eiderstedt and Vogelsand site lays also well within the reported size range for the European *E. directus* (Mühlenhardt-Siegel et al. 1983; Dörjes 1992; Armonies and Reise 1999). Dörjes (1992) assumed a maximum length up to 100 mm (2 years) for the Vogelsand. Mühlenhardt-Siegel et al. (1983), Swennen et al. (1985) and Palmer (2004) found also different maximum lengths at different study sites (Table 3). However, at both study sites, most individuals did not reach the maximum size. Optimal growth for the European *E. directus* is assumed generally in the deeper eulittoral respectively shallow sublittoral between 0 and 20 m depth (Swennen et al. 1985; Beukema and Dekker 1995; Armonies and Reise 1999).

The Amrumbank stations are situated at 12 m depth, whereas the Eiderstedt (10 m) and Vogelsand stations (9 m) are slightly shallower which might influence optimal growth. Differences in sediment structure, i.e., Eiderstedt and Vogelsand stations consists of more silty fine sand, might also effect optimal growth. Dörjes (1992) suggested that pollution might be a factor reducing growth capacity. We think that reduced salinity in this transition area of the Elbe estuary might also influence growth of the jack-knife clam. Lowest maximum size was recorded directly in the Elbe estuary on the Vogelsand with highest influence of freshwater; the Eiderstedt site is situated in the outer range of the Elbe zone but influenced by the river Eider. Largest individuals of the American jack-knife were found at the Amrumbank with no direct freshwater influence. We checked other potential environmental factors (see Schröder 2003) but were not able to find an event that might have influenced growth. However, testing freshwater influence on *E. directus* was beyond the scope of this study, but might be worth to be proven by others.

The reproduction of the American jack-knife occurs in March/April and is followed by a planktonic stage of 2–4 weeks (Mühlenhardt-Siegel et al. 1983; Dörjes 1992). High recruitment variability is common for *E. directus* (in this study reflected by missing cohorts). Strasser and Günther (2001) provided evidence that recruitment variability depends on winter temperatures and the temporal mismatch with epibenthic predators. Settlement of the larvae occurs usually in May/June at a length of 1–3 mm (Beukema and Dekker 1995). Smallest clams found in this study, mean length of 4.8 ± 1.1 mm, thus must have recently settled. During the first 2 years of lifespan, growth rates were high but seasonally variable. Maximum growth (up to 14 mm month^{-1}) in summer/early autumn was much higher than in former studies in the German Bight (Mühlenhardt-Siegel et al. 1983: 5 mm month^{-1}). Other species of the Pharidae show a very rapid length growth after metamorphosis and settlement, too (Rumohr 1980). The American jack-knife clams showed higher growth rates in the first but particularly within the 2nd year (catching up phenomenon) and reported also for other clams (Kristensen 1957; Lammens 1967). This development was demonstrated by the Gaussian model, and the growth-capacity decrease with age which was reflected by the decreasing amplitude of seasonal variability over the lifespan of the American jack-knife clam.

Mass mortalities of *E. directus*, mainly in late winter or late spring, are common (Mühlenhardt-Siegel et al. 1983; Beukema and Dekker 1995; Essink 1998; Armonies and Reise 1999). In particular, young clams show low survival rates in the first winters/springs of their lifespan (this study; Beukema and Dekker 1995; Essink 1998; Armonies and Reise 1999). Although mass mortalities are well known from *E. directus*, hitherto there is no established reason for this. According to Mühlenhardt-Siegel et al. (1983), high mortalities might be caused by exhaustion after spawning. Many bivalves invest 90% of their net production in reproduction (Ansell 1982). Armonies and Reise (1999) suggest two possible reasons for mass mortalities: 1. the European *E. directus* has reached its most northern limit of distribution in the North Sea and 2. *E. directus* could be washed out by offshore waves caused by strong westerly or north-west winds that do not appear at the American Atlantic coast. In principle, *E. directus* is able to survive

Table 3 Mean lengths (mm) of *E. directus* in the North Sea

Literature	Study side	Years			
		1	2	3	4
Mühlenhardt-Siegel et al. (1983)	DK, Blåvandshuk-beach	48	109	137	152
	D, Sylt	43	94	124	–
Swennen et al. (1985)	D, Langeness (intertidal)*	27–30	78–84	–	–
Dörjes (1992)	D, Großer Vogelsand**	10–50	60–105	–	–
Luczak et al. (1993)	F, Dunkerque***	35	–	–	–
Cadée et al. (1994)	NL, Sublittoral	59	120	134	–
Beukema and Dekker (1995)	NL, lower intertidal	64	126	144	–
Armonies and Reise (1999)	D, Sylt (intertidal)	43	97	127	133
This study	Amrumbank	35	88	129	149
	Eiderstedt	40	70	–	138
	Vogelsand	–	82^{+}	92^{++}	117^{+}

Table modified after Armonies and Reise (1999)

* Range of average from three sites

** Range of average from three sites studied over 10 years, estimated from graph

*** Age: ½ year

$^{+}$ Age: 2 ½ and 4 ½ years respectively

$^{++}$ Age: 3 ¼ years

sedimentation (Rauck 1982; Swennen et al. 1985; Schiedek and Zebe 1987), because it is very agile (Drew 1907). However, low temperatures in winter could slow down motility. Video inspections from this study (unpublished data) showed older individuals of *E. directus* also burrowed only halfway in. Thus, it is more than likely that the washout accompanied by low temperature and strong storms are responsible of these low survival rates.

Summing-up, we may assert that *E. directus* shows all characteristics of a successful invader. It is gregariously abundant and exhibits a high environmental tolerance and has settled by immigrating into the community finding its own habitat on mobile sands with strong tidal currents. Rapid burrowing capability is the key of the adaptation to life at such high energetic habitats. The jack-knife clam has a high reproductive capacity, short generation time, rapid growth and early sexual maturity (after 1 year according to Mühlenhardt-Siegel et al. 1983). Another characteristic for a successful immigrant is a broad diet or opportunistic feeding strategy. We did not investigate feeding of *E. directus*, but in principle, the North Sea system is only moderately limited in nutrients (Kröncke et al. 2004). Hence, plankton and detritus for *E. directus* as a detritus feeder are not limited as well. Therefore, physiological stress such as a lack of food is relatively low. Thus, the need for *E. directus* for an opportunistic feeding strategy is of lower importance for a successful immigration. Moreover, an alien species must have the capacity of using natural mechanisms for rapid dispersal. Many studies in the last decade have shown how fast *E. directus* used the predominant remaining currents, and even against those, to spread all along the coast of the North Sea (Essink 1986).

Although the American jack-knife clam would have the potential to cover the whole North Sea (Armonies and Reise 1999), it did not (Rachor and Nehmer 2003) and can only be found no deeper than the shallow subtidal. The density of *E. directus* is highly variable, as well as the recruitment and, especially at the Vogelsand, individuals are smaller or rather do not reach maximum length such as in the original habitat. But 23 years after the invasion, *E. directus* is still successful.

Although mass mortalities of the jack-knife clam are common in the North Sea, there is no hint of a 'boom and bust' development (according to Parker et al. 1999). Quite the contrary, there are no factors mentioned by Essink and Dekker (2002) which might cause a decline in population density (e.g. increasing predation pressure, parasites, overexploitation or depletion of resources). On the other hand, alien species have the potential to become a nuisance to other native species in the community such as the zebra mussel *Dreissena polymorpha* (Ricciardi et al. 1998). However, as far as we can say, the American jack-knife clam did integrate well into the existing community without suppressing native species.

The fate of this immigrant, *E. directus*, is a story of a successful trans-ocean invader which still stays successfully within the benthic community of the eastern German Bight, 23 years after its first findings.

Acknowledgments The samples were taken along with a PESCA project funded by the Fischereiamt, Kiel. We would like to thank Marco Bruhn, Monika Kock and Renate Schütt for their help while expeditions and sorting in the laboratory, as well as their support identifying the fauna. We are grateful to Dieter Piepenburg for his support during my (JD) diploma thesis. We thank the crew of *RV Littorina* for their help during sampling cruises. Further thanks go to Lars Gutow and Alexander Schröder for helpful comments on this manuscript.

References

Abbott RT (1974) American seashells. Van Nostrand Reinhold, New York

Ansell AD (1982) Experimental studies of a benthic predatory prey relationship. II. Energetics of growth and reproduction, and food-conversion efficiencies, in longterm cultures of the gastropod drill Polinices alderi (Forbes) feeding on the bivalve Tellina tenuis (da Costa). J Exp Mar Biol Ecol 61:1–29

Armonies W, Reise K (1999) On the population development of the introduced razor clam *Ensis americanus* near the island of Sylt (North Sea). Helgol Meeresunters 52:291–300

Armonies W, Herre E, Sturm M (2001) Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the Island of Sylt. Helgol Mar Res 55:170–175

Austen MC, Buchanan JB, Hunt HG, Josefson AB, Kendall MA (1991) Comparison of long-term trends in benthic and pelagic communities of the North Sea. J Mar Biol Ass UK 71:179–190

Becker GA, Dick S, Dippner JW (1992) Hydrography of the German Bight. Mar Ecol Prog Ser 91:9–18

Beukema JJ (1992) Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. Neth J Sea Res 30:73–79

Beukema JJ, Dekker R (1995) Dynamics and growth of a recent invader into European coastal waters: the American razor clam, *Ensis directus*. J Mar Biol Assoc UK 75:351–362

Beukema JJ, Dekker R (2011) Increasing species richness of the macrozoobenthic fauna on tidal flats of the Wadden Sea by local range expansion and invasion of exotic species. Helgol Mar Res 65:155–164

Bousfield EL (1960) Canadian Atlantic seashells. National Museum of Canada, Ottawa

Cadée GC, Cadée-Coenen J, Witte JIJ (1994) Massale sterfte van *Ensis directus* op Schanserwaard en elders blijft raadselachtig. Corresp Nederlandse Malacol Vereiniging 279:86–93

Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biol Conserv 78:97–106

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Dörjes J (1992) Die amerikanische Schwertmuschel *Ensis directus* (Conrad) in der Deutschen Bucht. III. Langzeitentwicklung nach 10 Jahren. Senckenb Marit 22:29–35

Dörjes J, Michaelis H, Rhode B (1986) Long-term studies of macrozoobenthos in the intertidal and shallow subtidal habitats near the island of Norderney (East Frisian coast, Germany). Hydrobiologia 142:217–232

Drew GA (1907) The habits and movement of the razor shell clam, *Ensis directus*, Conrad. Biol Bull 12:127–138

Duineveld GCA, Kuenitzer A, Niermann U, De Wilde PAJ, Gray JS (1991) The macrobenthos of the North Sea. Neth J Sea Res 28:53–56

Dyer MF, Fry WG, Fry PD, Cranmer GJ (1983) Benthic regions within the North Sea. J Mar Biol Assoc UK 63:683–693

Essink K (1985) On the occurrence of the American jack-knife clam *Ensis directus* (Conrad 1843) (Bivalvia, Cultellidae) in the Dutch Wadden Sea. Basteria 49:73–80

Essink K (1986) Note on the distribution of the American jack-knife clam *Ensis directus* (Conrad, 1843) in N.W. Europe (Bivalvia, Cultellidae). Basteria 50:33–34

Essink K (1998) On the dispersal of *Marenzelleria* spp. (Polychaeta: Spionidae) and *Ensis americanus* (Bivalvia: Cultellidae) in NW Europe. ICES Working Group on Introduction of Marine Organisms (WGITMO) 11

Essink K, Dekker R (2002) General patterns in invasion ecology tested in the Dutch Wadden Sea: the case of a brackish-marine polychaetous worm. Biol Invasions 4:359–368

Gollasch S (1996) Untersuchungen des Arteintrages durch den internationalen Schiffsverkehr unter besonderer Berücksichtigung nichtheimischer Arten. Ph.D. Thesis, University of Hamburg, Germany

Howlett DJ (1990) The arrival in Britain of *Ensis americanus*. Conchol Newsl 114:301–302

Kappenberg J (2006) Elbe discharge and runoff (Neu-Darchau), services (Elbe runoff dataset, online). http://w3g.gkss.de/staff/kappenberg/elbe/abfluss/elbe.abfluss

Kristensen I (1957) Differences in density and growth in a cockle population in the Dutch Wadden Sea. Archs Néerl Zool 12:351–453

Kröncke I (1992) Macrofauna standing stock of the Dogger Bank. A comparison: III. 1950–54 versus 1985–1987. A final summary. Helgol Meeresunters 46:137–169

Kröncke I (1995) Long-term changes in North Sea benthos. Senckenb Marit 26:73–80

Kröncke I, Dippner JW, Heyen H, Zeiss B (1998) Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar Ecol Prog Ser 167:25–36

Kröncke I, Zeiss B, Rensing C (2001) Long-term variability in macrofauna species composition off the island of Norderney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. Senckenb Marit 31:65–82

Kröncke I, Stoeck T, Wieking G, Palojärvi A (2004) Relationship between structural and functional aspects of microbial and macrofaunal communities in different areas of the North Sea. Mar Ecol Prog Ser 282:13–31

Lammens JJ (1967) Growth and reproduction in a tidal flat population of Macoma balthica (L.). Neth J Sea Res 3:315–382

Luczak C, Dewarumez J-M, Essink K (1993) First record of the American jack knife clam *Ensis directus* on the French coast of the North Sea. J Mar Biol Assoc UK 73:233–235

Mack RN (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches: invasion biology. Biol Conserv 78:107–121

Markert A, Wehrmann A, Kröncke I (2010) Recently established *Crassotrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). Biol Invasions 12:15–32

Morris PA (1973) A field guide to the shells of the Atlantic and Gulf coasts and the West Indies. Houghton Mifflin, Boston

Mühlenhardt-Siegel U, Dörjes J, von Cosel R (1983) Die amerikanische Schwertmuschel Ensis directus (Conrad) in der Deutschen Bucht. II. Populationsdynamik. Senckenb Marit 15:93–110

Niermann U, Bauerfeind E, Hickel W, von Westernhagen H (1990) The recovery of benthos following the impact of low oxygen content in the German Bight. Neth J Sea Res 25:215–226

Palmer DW (2004) Growth of the razor clam *Ensis directus*, an alien species in the wash on the east coast of England. J Mar Biol Assoc UK 84:1075–1076

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Rachor E, Nehmer P (2003) Erfassung und Bewertung ökologisch wertvoller Lebensräume in der Nordsee. BfN-Projekt-Bericht, Alfred Wegener Institute Bremerhaven, Germany

Rachor E, Reiss H, Degraer S, Duineveld GCA, van Hoey G, Lavaleye M, Willems W, Rees HL (2007) Structure, distribution, and characterising species of the North Sea macrozoobenthos communities in 2000. In: Rees HL, Eggleton JD, Rachor E, Vanden Berghe E (eds) Structure and dynamics of the North Sea benthos, ICES Coop Res Rep 288, pp 46–59

Rauck G (1982) Massensterben der Messerscheiden-Muscheln (*Ensis* spp.) an der niedersächsischen und schleswig-holsteinischen Küste. Inf Fischwirtsch 29:65–66

Ricciardi A, Rasmussen JB (1998) Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can J Fish Aquat Sci 55:1759–1765

Ricciardi A, Neves RJ, Rasmussen JB (1998) Impending extinctions of North American freshwater mussels (Unionidae) following the zebra mussel (Dreissena polymorpha) invasion. J Anim Ecol 67:613–619

Rumohr H (1980) Der Benthosgarten in der Kieler Bucht - Experimente zur Bodentierökologie. Reports Sonderforschungsbereich 95. Wechselwirkungen Meer - Meeresboden 55:179

Rumohr H (1999) Soft bottom macrofauna: collection, treatment, and quality assurance of samples. ICES Tech Mar Ecol Stud 27:1–19

Rumohr H, Kujawski T (2000) The impact of trawl fishery on the epifauna of the southern North Sea. ICES J Mar Sci 57:1389–1394

Salzwedel H, Rachor E, Gerdes D (1985) Benthic macrofauna communities in the German Bight. Veröff Inst Meeresforsch Bremerh 20:199–267

Schiedek D, Zebe E (1987) Functional and environmental anaerobiosis in the razor-clam *Ensis directus* (Mollusca: Bivalvia). Mar Biol 94:31–37

Schröder A (2003) Community dynamics and development of soft bottom macrozoobenthos in the German Bight (North Sea) 1969—2000. Ph.D. Thesis, University of Bremen, Germany

Stanley SM (1970) Relation of shell form to life habits of the Bivalvia (Mollusca). Geol Soc Am Mem 125:296

Strasser M, Günther CP (2001) Larval supply of predator and prey: temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. J Sea Res 46:57–67

Swennen C, Leopold MF, Stock M (1985) Notes on growth and behavior of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. Helgol Meeresunters 39:255–261

Troost K (2010) Causes and effects of a highly successful marine invasion: case-study of the introduces Pacific oyster *Crassotrea gigas* in continental NW European estuaries. J Sea Res 64:145–165

Van Urk RM (1987) *Ensis americanus* (Binney) (Syn. *E. directus* auct. non Conrad) a recent introduction from Atlantic North-America. J Conch 32:329–333 von Cosel R, Dörjes J, Mühlenhardt-Siegel U (1982) Die amerikanische Schwertmuschel *Ensis directus* (Conrad) in der Deutschen Bucht. I. Zoogeographie und Taxonomie im Vergleich mit den einheimischen Schwertmuschel-Arten. Senckenb Marit 14:147–173

Williamson M (1996) Biological invasions. Chapman and Hall, London

Ziegelmeier E (1964) Einwirkungen des kalten winters 1962/63 auf das Makrobenthos im Ostteil der Deutschen Bucht. Helgol Mar Res 10:276–282