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ICES Cooperative Research Report
Rapport des Recherches Collectives

No. 323
February 2015

Alien Species Alert: *Ensis directus*
Current status of invasions
by the marine bivalve *Ensis directus*



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Alien Species Alert: *Ensis directus* Current status of invasions by the marine bivalve *Ensis directus*

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Recommended format for purposes of citation:

Gollasch, S., Kerckhof, F., Craeymeersch, J., Gouletquer, P., Jensen, K., Jelmert, A. and Minchin, D. 2015. Alien Species Alert: *Ensis directus*. Current status of invasions by the marine bivalve *Ensis directus*. ICES Cooperative Research Report No. 323. 32 pp. <https://doi.org/10.17895/ices.pub.5491>

Series Editor: Emory D. Anderson.

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ISBN 978-87-7482-157-1

ISSN 1017-6195

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1 Introduction

The North American bivalve mollusc *Ensis directus* (Conrad, 1843) (Bivalvia, Pharidae) is native to the Northwest Atlantic coasts from southern Labrador to northern Florida (Bousfield, 1960; Theroux and Wigley, 1983; Swennen *et al.*, 1985; Abbott and Morris, 2001; Turgeon *et al.*, 2009; Vierna *et al.*, 2013). This species has been introduced outside its native range, with the first confirmed record from the German Bight in 1979 (Cosel *et al.*, 1982). Thereafter, a subsequent secondary range expansion took place, and the species is presently known to occur from Spain to Norway, including the UK (e.g. Mühlhardt-Siegel *et al.*, 1983; Essink, 1985, 1986; Kerckhof and Dumoulin, 1987; Luczak *et al.*, 1993; Rasmussen, 1996; Brattegard and Holthe, 1997; Eno *et al.*, 1997; Severijns, 2000, 2002, 2004; Wolff, 2005; Dauvin *et al.*, 2007; Houziaux *et al.*, 2011; Arias and Anadon, 2012; Dannheim and Rumohr, 2012; Witbaard *et al.*, 2013) and in the western Baltic (Gürs *et al.*, 1993). The most recent expansion was to the Bay of Biscay (Arias and Anadon, 2012) from where it may be expected to spread further.

E. directus has all the characteristics of a successful “r” strategist invader, including high reproductive capacity, short generation time, and rapid growth. Its expansion is principally due to natural dispersal. It usually occurs in clusters and has wide environmental tolerances (Dannheim and Rumohr, 2012). Moreover, its native predators (e.g. the snail *Polinices heros* and the nemertean *Cerebratulus lacteus*) are absent in Europe (Cosel, 2009). Although *E. directus* is common in its native range, it is more abundant in its introduced range. Further, its exceptional colonization success in Europe is likely related to its use of underutilized tidal habitats that are characterized by exposure to physical disturbance as a consequence of wave action and strong tidal currents. It appears that *E. directus* is one of the few larger benthic invertebrates able to tolerate the unstable sands in the tidal zone (Dekker and Beukema, 2012).

Although there is high annual variability in *E. directus* densities, the species has become a prominent component of the macrobenthos in shallow subtidal sands in Europe. This review describes the current status of the species outside its native range.

2 Identification

Ensis directus (Danish, Amerikansk knivmusling; Dutch, Amerikaanse zwaardschede; English, American razor clam, Atlantic jack knife clam; French, couteau droit, couteau américain; German, Amerikanische Schwertmuschel, Amerikanische Scheidenmuschel; Norwegian, amerikaknivskjell) has also been described with the synonyms *Solen ensis* (Gould, 1841), *Solen directus* (Conrad, 1843), *Solen ensis* var. *americanus* (Gould and Binney, 1870), and *Ensis americanus* (Gould, 1870) (Cosel, 2009).

Known in its native area as *E. directus* (Conrad, 1843), the name was also used when the species was first observed in Europe (Cosel *et al.*, 1982). It should be noted that *E. directus* is also known by some scientists as *E. americanus*, based on a fossil (Miocene) and possibly extinct species (Urk, 1972). However, not all taxonomists agree that the fossil species is different from the current bivalve, so both names are in use (e.g. Urk, 1980; Armonies and Reise, 1999; Jensen, 2010). Cosel *et al.* (1982) and Cosel (2009), in discussing this issue again, provided ample evidence for the use of the name *E. directus*, as at least most of the differences between the Miocene and the recent form, cited by Urk (1972), fall within the variation of the recent form. Also, after a careful comparison of the Miocene fossil material and recent shells, Dall (1900) was “unable to find any constant character with which they can be discriminated”. This view is followed by such authoritative taxonomic databases as the World Register of Marine Species (WoRMS), Cosel and Gofas (2013), and the Check List of European Marine Mollusca (CLEMAM, 2014) (Table 1).

Table 1. The taxonomic status of *Ensis directus* (Source: WoRMS, 2014).

Class	Bivalvia
Subclass	Heterodonta
Order	Euheterodonta
Superfamily	Solenoidea
Family	Pharidae
Genus	<i>Ensis</i>
Species	<i>directus</i>

E. directus is characterized by an elongated (razor-shaped) shell, with both valves connected by a hinge in the anterior end. This hinge has few very small “teeth” and an elastic ligament. The shell shape is best described as slightly curved to almost straight and it grows typically to 16–17 cm in length and 2.5–2.8 cm in width (Figure 1). In Europe, the maximum shell length thus far observed is 18.7 cm in Belgian waters (Vanhaelen, 1993). North American specimens can achieve lengths of up to 25 cm (Cosel, 2009; Abbott and Morris, 2001).

From the inside, the posterior adductor muscle scar is very close to the pallial sinus (only 2–3 mm distance), and the anterior adductor muscle edges can also be seen (Cosel *et al.*, 1982; Voigt, 1999; Jensen, 2010) (Figure 2).

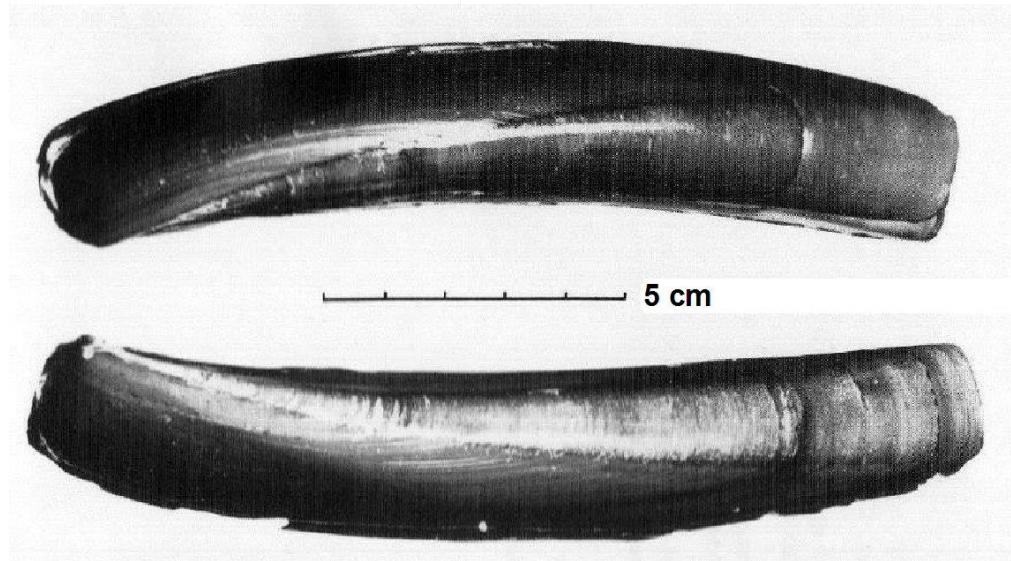


Figure 1. *Ensis directus* shells (source: Mühlenhardt-Siegel *et al.*, 1983).

The dorsal and ventral margins are almost parallel. The anterior end is rounded while the posterior end is truncate. The pallial sinus is not symmetrical, and the dorsal half is indented. At its upper part, *E. directus* has its innermost point below the dorsal pallial sinus (Cosel *et al.*, 1982; Cosel, 2009). In the European populations, that point is situated more ventrally, almost in mid-shell height (Cosel, 2009). Besides the characteristic shape and size (Figure 1), this makes adult *E. directus* easily distinguishable from most native bivalves. Although apparently easily distinguishable, *E. directus*, especially the straight-shaped specimens, can be and have been confused with native *E. magnus* (formerly known as *E. arcuatus*); however, an internal inspection of the shells reveals clear differences. Compared with *E. magnus*, the pallial sinus in *E. directus* has a wide and shallow shape that forms a distinct wave (see no. 5 in Figure 2). The anterior adductor depression muscle scar is much shorter, and the posterior adductor muscle scar is situated much closer to the pallial sinus.

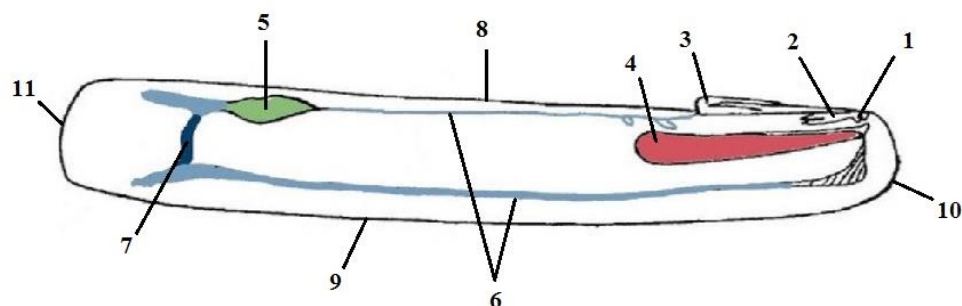


Figure 2. *Ensis directus*, pallial sinus – a feature to distinguish it from *Ensis magnus* (Severijns, 2002). Legend: 1, vertical teeth of hinge; 2, horizontal teeth; 3, hinge ligament; 4, anterior of muscle scar; 5, posterior muscle scar; 6, pallial line; 7, pallial sinus; 8, dorsal surface; 9, ventral surface; 10, anterior; 11, posterior.

The shell of *E. directus* is wider and usually curved, or partly so, not as curved as in *E. ensis*. It seems that one of the important features for identification in the field is the pallial sinus, which is more easily seen when the shell is dry (Figure 2). In young individuals, marks are indistinct and difficult to see (Jensen, 2010).

While adult *E. directus* can easily be distinguished from native species, specialist knowledge is required to identify juveniles. As for many bivalves, larval stages (pelagic

veliger) are difficult to identify to species level (Voigt, 1999). To solve taxonomical uncertainties, a multiplex *polymerase chain reaction* (PCR) technique using specific primers may be used for the identification of *Ensis* spp. by different sizes of the species-specific amplicons separated in an electrophoresis. This method provides a simple, reliable, and rapid identification of *Ensis* spp. (Fernández-Tajes *et al.*, 2010).

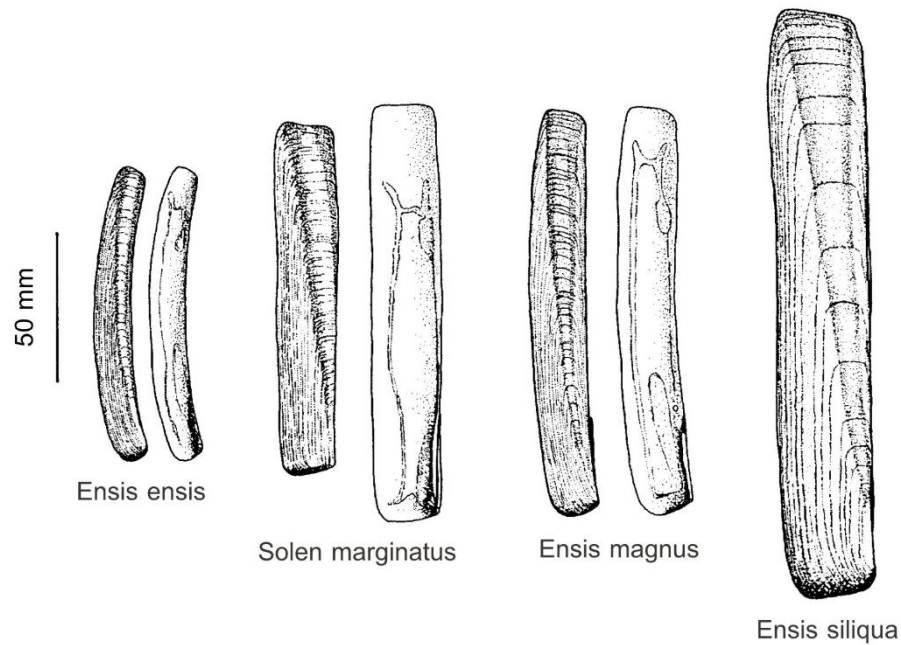


Figure 3. Native European bivalves with shells similar in shape to the *Ensis directus*. (Sources: Hayward and Ryland, 1996; Voigt, 1999.)

3 Biology in the native range

The distribution in the native range of *E. directus* along the eastern coast of North America extends from Labrador (60°N) in the north to South Carolina (34°N) in the south (Bousfield, 1960; Cosel *et al.*, 1982; Swennen *et al.*, 1985; Coan *et al.*, 2000). There are reports of its presence even farther south off northern Florida (Theroux and Wigley, 1983; Abbott and Morris, 2001; Turgeon *et al.*, 2009; Vierna *et al.*, 2013). However, the northern limit of the species' native range is currently unclear because it is unknown whether *E. directus* and *E. terranovensis* co-occur off Canadian and north-eastern US waters (Vierna *et al.*, 2013). Baqueiro *et al.* (2004) recorded *E. directus* off Yucatan.

The free-swimming larvae are produced in spring. Juveniles settle on clean fine sands with small amounts of silt in the lower zone of the intertidal areas where they filter-feed on plankton and detritus.

The larval phase lasts 10–27 days (Cosel, 2009). Spat survival is limited to areas below mean low tide (Beukema and Dekker, 1995), but older clams may be found in the low intertidal areas.

E. directus are known to burrow rapidly deep into the sediment when disturbed. This behaviour makes it difficult to capture them alive and undamaged (Drew, 1907; Truman, 1967). Valve movements during burrowing cause change in viscosity of the sediment surrounding the clam, which reduces drag and facilitates rapid penetration to depths greater than expected, considering the muscular strength of the clam (Winter *et al.*, 2012). The species has a unique burrowing strategy to move in sediment whereby the “foot” is used to manipulate its position in the sediment (Figure 4). Jung *et al.* (2011) describes a burrowing model that uses deformations of the *E. directus* body to cyclically loosen and repack the surrounding sediment to manipulate burrowing drag locally (Figure 4).

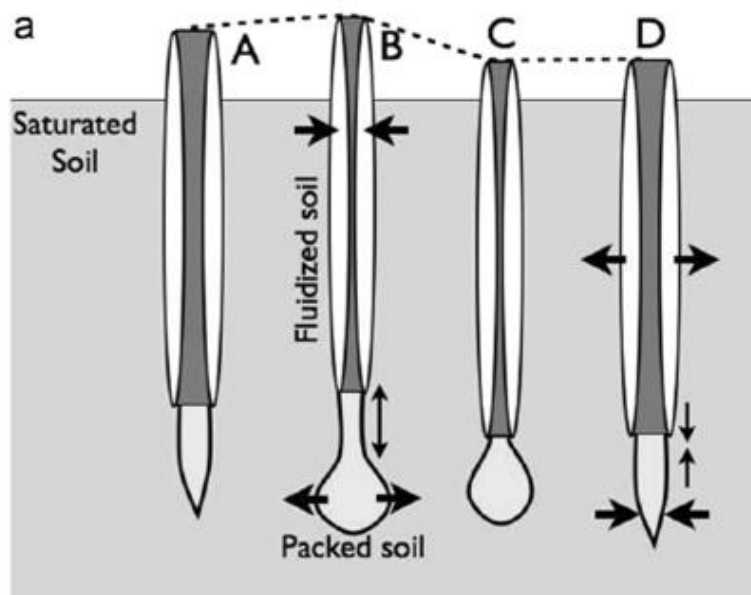


Figure 4. Burrowing strategy of *Ensis directus* in sediment (Modified from Jung *et al.*, 2011).

The relatively short siphons indicate that their usual position in the sediment is near the surface. At low tide, *E. directus* are frequently found with the posterior end protruding from the sediment a few centimetres (Swennen *et al.*, 1985).

3.1 Natural history

The preferred habitat of *E. directus* within its native range includes the gently sloping subtidal region on low gradient shifting sands (Gosner, 1979), but it can also be found in mud and gravel. In eastern Canada, the identified subtidal clam beds are primarily located at depths of 5–8 m where currents are typically low–moderate (Kenchington *et al.*, 1998), but it has also been found down to 100 m depth (Theroux and Wigley, 1983). In North America, *E. directus* is known to be pollution-sensitive (Callier *et al.*, 2008).

The species shows large annual temperature tolerances, but low winter temperatures seem to limit its development (Essink, 1994). Its salinity tolerance is 7–32 psu (Maurer *et al.*, 1974); therefore, it occurs in both marine and estuarine areas (Beukema and Dekker, 1995). *E. directus* shows a limited tolerance to reduced oxygen conditions (Schiedek and Zebe, 1987).

In its native range, *E. directus* is a preferred prey of the sea star *Leptasterias polaris* (Thompson *et al.*, 2005). Large carnivorous snails also prey on *E. directus*, including moon snails (*Polinices* spp.) (Clements *et al.*, 2013) and whelks (*Busycon* spp.). *E. directus* may also be affected by the predatory nemertean *Cerebratulus lacteus* (McDermott, 1976; Thompson *et al.*, 2005; Cosel, 2009) as well as by several bird species, including sea gulls (Cadée, 2000a).

3.2 Growth rate

There is little information available on the shell growth of *E. directus* within its natural range. Kenchington *et al.* (1998) evaluated *E. directus* as a potential aquaculture species and characterized the species as being relatively fast-growing. In an experimental setup, juvenile *E. directus* were observed to be in the size range of 7–9 mm at three months post fertilization.

3.3 Reproduction

E. directus is dioecious (Loosanoff and Davis, 1963), but males and females cannot be distinguished externally. Males release sperm into the water, and the sperm enters the females through the inhalant siphon. Eggs are fertilized in the interior of the gill, and newly-fertilized zygotes develop into larvae, which are then released in the water. The zygotes develop into trochophores as naked pear-shaped, translucent free-swimming larvae, which develop further into lightly-shelled “D” veliger larvae that become more rotund with age to form the umbonate stage. The final larval stage is a pediveliger, which is capable of swimming and crawling with a “foot”. The planktonic stage of *E. directus* lasts 10–27 days, resulting in its dispersal by currents over long distances. After the larval stage, young individuals settle onto sandy or muddy habitats and begin their development into adults. Most *E. directus* achieve sexual maturity in their first year. Reproduction occurs between May and September, based on rising water temperatures (Sullivan, 1948; Kenchington *et al.*, 1998; Cosel, 2009). Unprovoked spawning occurs at temperatures of ca. 15–22°C; at 30°C, spawning seldom takes place unless triggered by the presence of sperm (Loosanoff and Davis, 1963).

The settlement of *E. directus* takes place once larvae attain ~210 µm. At 24°C, this often occurs only about 10 days after fertilization. However, some larvae remain swimming until they reach a much larger size before undergoing metamorphosis, which may extend up to 27 days after fertilization; at this time, they have a powerful velum and a well-developed foot (Loosanoff and Davis, 1963).

The species is relatively long-lived for a bivalve, with an estimated maximum age (based on shell morphology) of up to 20 years (Cosel, 2009).

4 Non-native distribution

In Europe, *E. directus* occurs in clean, muddy, and coarse sand with shell debris, being found in exposed as well as more sheltered environments. It can bury in sediments to a depth of up to 50 cm (Richards, 1938; Armonies and Reise, 1999; Tulp *et al.*, 2010). However, it prefers wave- and current-swept cleaner sands (Beukema and Dekker, 1995) with small amounts of silt (Kennish *et al.*, 2004; Dauvin *et al.*, 2007).

The first strong year class in Europe (German Bight, Elbe Estuary) was documented in 1979 (Figure 5) and was presumed to have arrived as larvae transferred in the ballast water of ships from the east coast of the US, most likely during 1978 (Cosel *et al.*, 1982; Mühlenhardt-Siegel *et al.*, 1983; Urk, 1987). However, in 1977, a few small *Ensis* spp. were found on tidal flats in the Dutch Wadden Sea near Terschelling, but the species identification of these specimens is unclear (Beukema and Dekker, 1995). The 1977 findings may have been the first European record, but the first taxonomically confirmed European record is from the German Bight in summer and autumn 1979 (Mühlenhardt-Siegel *et al.*, 1983; Dekker and Beukema, 2012). Swennen *et al.* (1985) also assumed that the introduction of *E. directus* into Europe took place before 1978, but that the first strong year class in Europe originated in 1979.

Since its early records, the species had spread rapidly in the North Sea region, with a range expansion along the coast of Germany and the western coast of Denmark. It reached the Ems Estuary (Dutch and German border) in 1981, Texel and Schiermonnikoog (The Netherlands) and the complete Dutch coast in 1982. In the Dutch southern Delta area (Eastern Scheldt), first records were reported in the early 1990s (P. van Avesaath, pers. comm.). The first Danish records were in 1982 from the Kattegat and east coast (Knudsen, 1989; Jensen, 2010). The entrances to the Great Belt and the Sound were reached in 1988, and the entrance to the Little Belt in 1994 (Knudsen, 1997; K. Jensen, pers. comm.), and it was also found in the Limfjord near Nykøbing and Fur Island, along the northern coasts of Fyn and Zealand, and in the Flensborg Fjord near Sønderborg (K. Jensen, pers. comm.). The first record on the Belgian coast was in 1986 (Kerckhof and Dumoulin, 1987; Kerckhof *et al.*, 2007). It was also observed in Sweden in 1982 and in Norway in 1989 (Brattegard and Holthe, 1997; Ovcharenko *et al.*, 2009; Jensen, 2010). In the United Kingdom, it was first recorded in 1989 (Howlett, 1990; Eno *et al.*, 1997; Palmer, 2003; Minchin *et al.*, 2013); at Southend-on-Sea (Essex), it was reported to be one of the most common living bivalves on the shore in 1995 (Ovcharenko *et al.*, 2009). At present, *E. directus* is known at the eastern coast of the United Kingdom, stretching from the Humber and the Wash (Palmer, 2003, 2004; Ashelby, 2005) to the eastern coast of Kent (Killeen, 2003). Additional records from the United Kingdom indicate the spread of *E. directus* to the Firth of Forth near Edinburgh in 2000 (Smith, 2000), in Angle Bay, the western part of Milford Haven (South Wales) in 2002 (Killeen, 2003), and in several locations of Liverpool Bay in 2011 (Dansey, 2011).

Adults were also reported in France in 1991, with the first record close to Dunkerque (Gravelines) in the southern region of the North Sea (Luczak *et al.*, 1993), in Boulogne and Hardelot in 1992 and 1993, respectively, and then in the Bay of Somme and Bay of Seine in 1996 and 1998, respectively (Dewarumez *et al.*, 2011). By the 1990s, *E. directus* had spread along the coasts of the English Channel (Davoult *et al.*, 1999), with a progressive and continuous expansion along the northern French coastline to Normandy (Severijns, 2000). The species is now commonly found along the northern French coastline and in several parts of the English Channel (e.g. Rye Bay), but it has not yet been observed along the Brittany coastline (e.g. Bay of Saint Malo) (OBPNB, 2010).

Arias and Anadon (2012) reported *E. directus* from the southwest part of the Bay of Biscay, with findings in three localities in 2011. Moreover, with an overlapping distribution with shellfish rearing areas, further spread might be facilitated by commercial shellfish transfers.

Estimates of the spread of the clam from the German Bight, where it was first recognized, vary from 125 km year⁻¹ northwards and westwards, against the direction of residual current flow, at 75 km year⁻¹ (Armonies, 2001).

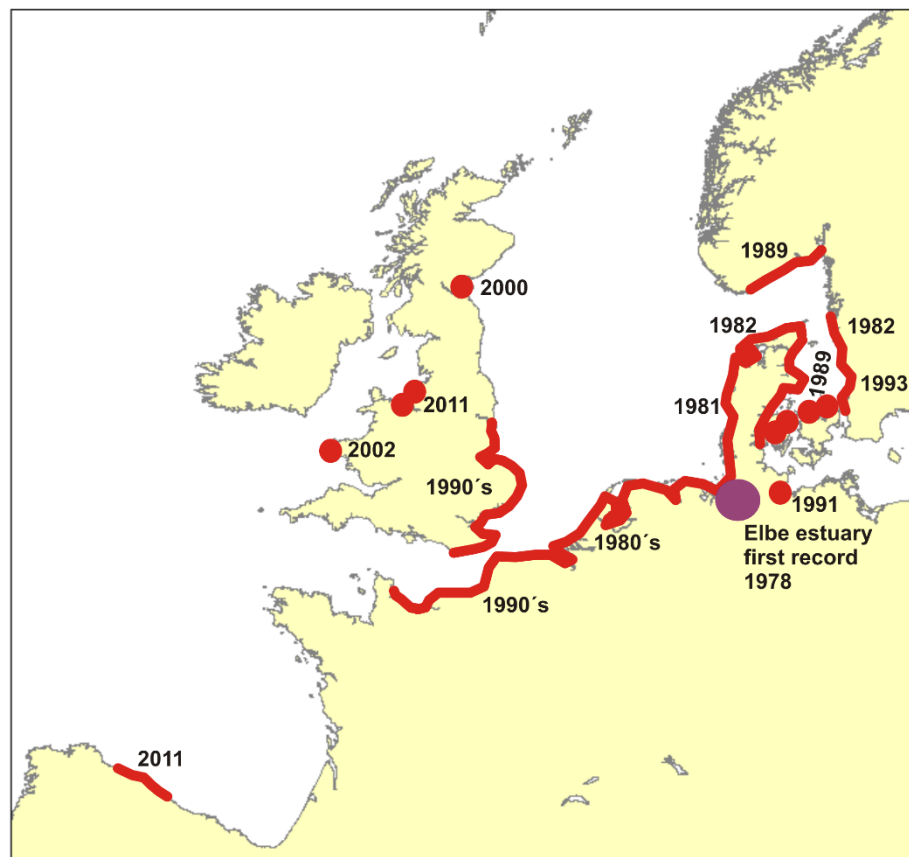


Figure 5. *Ensis directus* distribution in Europe, also indicating the confirmed first record in the Elbe estuary (Germany) (see text for references).

4.1 Natural history in the recipient region

In the Netherlands, *E. directus* was observed to have a long lag phase. These high densities may be found over a period of >2 years – the exponential phase (Hummel and Wijnhoven, 2014). The species is very abundant, with juvenile densities amounting to several tens or hundreds m⁻² (Beukema and Dekker, 1995; Witbaard *et al.*, 2013). Dense populations (thousands of individuals m⁻²) were reported by Essink (1994) (Figure 6). Mass developments in the Wadden Sea have occurred in various years, during which biomass and production values exceeded 10 g AFDW (ash-free dry weight) m⁻² (Beukema and Dekker, 1995; Armonies and Reise, 1999), and *E. directus* is among the dominant biomass species in the Dutch Wadden Sea (Compton *et al.*, 2013). The species reached a maximum recorded biomass of >100 g AFDW m⁻² in 2006 (Figure 7) (Dekker and Beukema, 2012).

The population development of *E. directus* has been remarkable in the Wadden Sea, especially around the low watermark at spring tide (i.e. the transition zone of intertidal

and subtidal parts), where the clam increased in biomass from zero to locally $\approx 90\%$ of the total macrozoobenthic biomass (Dekker and Beukema, 2012). Since 2002, *E. directus* has been the most common mollusc species in the Dutch coastal zone (Tulp *et al.*, 2010).



Figure 6. Massive amounts of *Ensis directus* shells washed ashore near Skallingen, western coast of Denmark in 1983 (left and bottom right; source: Mühlenhardt-Siegel *et al.*, 1983) and in 2005 along the west coast of the German Sylt Island (top right; source: Stephan Gollasch).

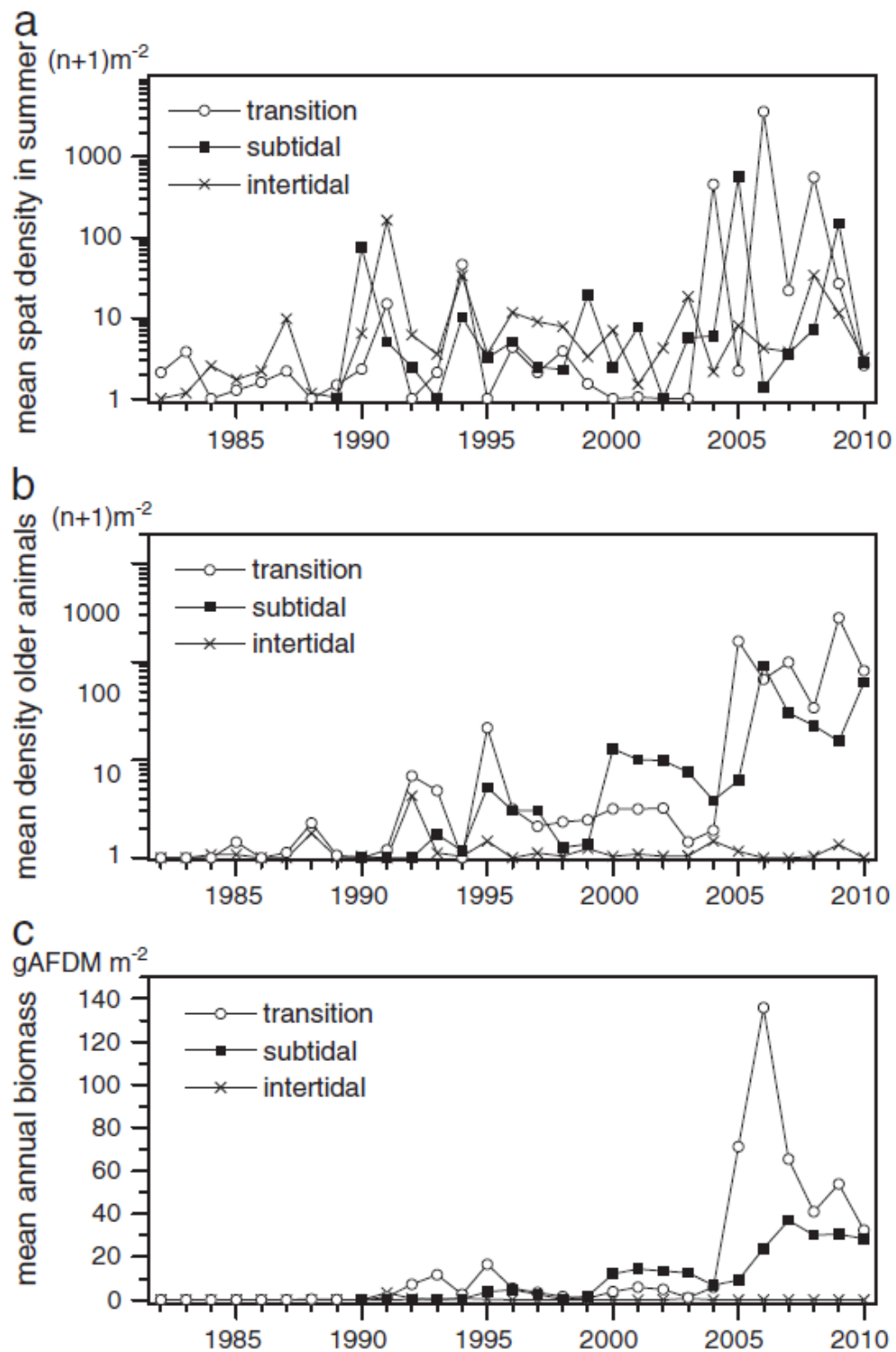


Figure 7. *Ensis directus* 1982–2010 annual estimates of numbers and biomass of populations in three areas of the Dutch Wadden Sea, i.e. crosses = 13 intertidal sites, open circles = two transition sites, and solid squares = three subtidal sites. Panel a = mean densities of spat-sized individuals (late summer); Panel b = densities of older individuals (after the first winter); and Panel c = soft part biomass of the entire populations. (Source: Dekker and Beukema, 2012.)

After these rapid developments, the populations exhibited substantial declines (Figure 7). Mass mortalities also took place, possibly as a result of the washout of older *E. directus* from the turbulence caused by strong storms (Armonies and Reise, 1999; Dann-

heim and Rumohr, 2012). Once the species has been completely washed out of the sediment, reburrowing is difficult (Cadée, 2000b). Furthermore, low winter temperatures can cause mortality (Armonies and Reise, 1999; Dannheim and Rumohr, 2012). Long-term monitoring in the Dutch Wadden Sea has indicated that survival of the first winter is crucial to successful recruitment, which highlights the importance of low winter temperatures on its survival (Dekker and Beukema, 2012). These mass mortalities are also known from its native region (Cadée, 2000b).

In Dutch coastal waters, *E. directus* was found over a wide coastal area and was recognized since the time that shellfish stock assessments began. Over the past 15 years, the total standing stock of *E. directus* has greatly increased. Biomass fluctuates considerably between years and shows sudden increases, as in the case of 2002 (Figure 8). However, in the Dutch Eastern Scheldt, a peak in density already occurred in the mid-1990s (P. van Avesaath, pers. comm.).

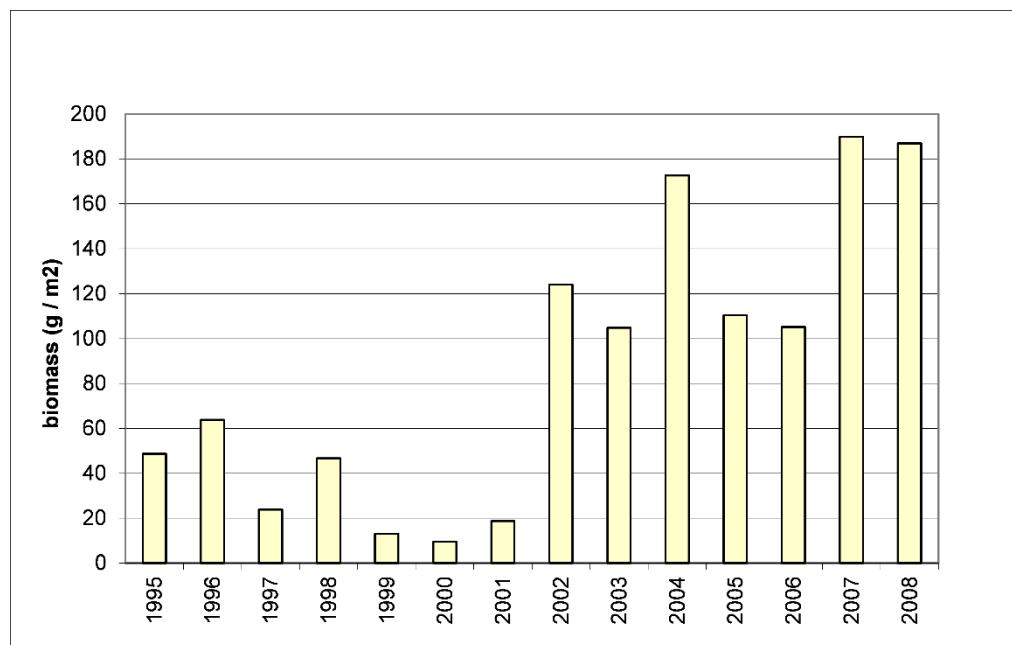


Figure 8. Standing stock of *Ensis directus* in Dutch coastal waters in the period 1995–2008 (unpublished data, IMARES) based on yearly stock assessments with modified hydraulic dredge or trawled dredge; sampling efficiency for *E. directus* is estimated at 50% (Craeymeersch, Perdon, Goudswaard, unpublished; Tulp *et al.*, 2010; Witbaard *et al.*, 2013).

The *E. directus* distribution in the Wadden Sea is patchy and variable (Figure 9). Mass mortalities and large spatfalls are known (Dannheim and Rumohr, 2012), with the main distribution and abundance close to the coast.

In Belgian waters, after its first observation in 1987, *E. directus* rapidly colonized all coastal sandy sediments. Millions of shells and dying specimens are now frequently observed washed onto Belgian beaches (Houziaux *et al.*, 2011).

The population genetics of *E. directus* have shown high variability within their introduced range (Vierna *et al.*, 2012; ICES, 2013), including several haplotypes unique for European populations. Hence, a source population could not be identified, and multiple introductions may have taken place. This assumption is also supported by the recent disjunct European distribution of *E. directus*. Furthermore, the cytogenetics of this species have been studied, showing lower numbers of telocentric and higher numbers

of subtelocentric chromosomes in *E. directus* than in three native European *Ensis* species (González-Tizón *et al.*, 2013).

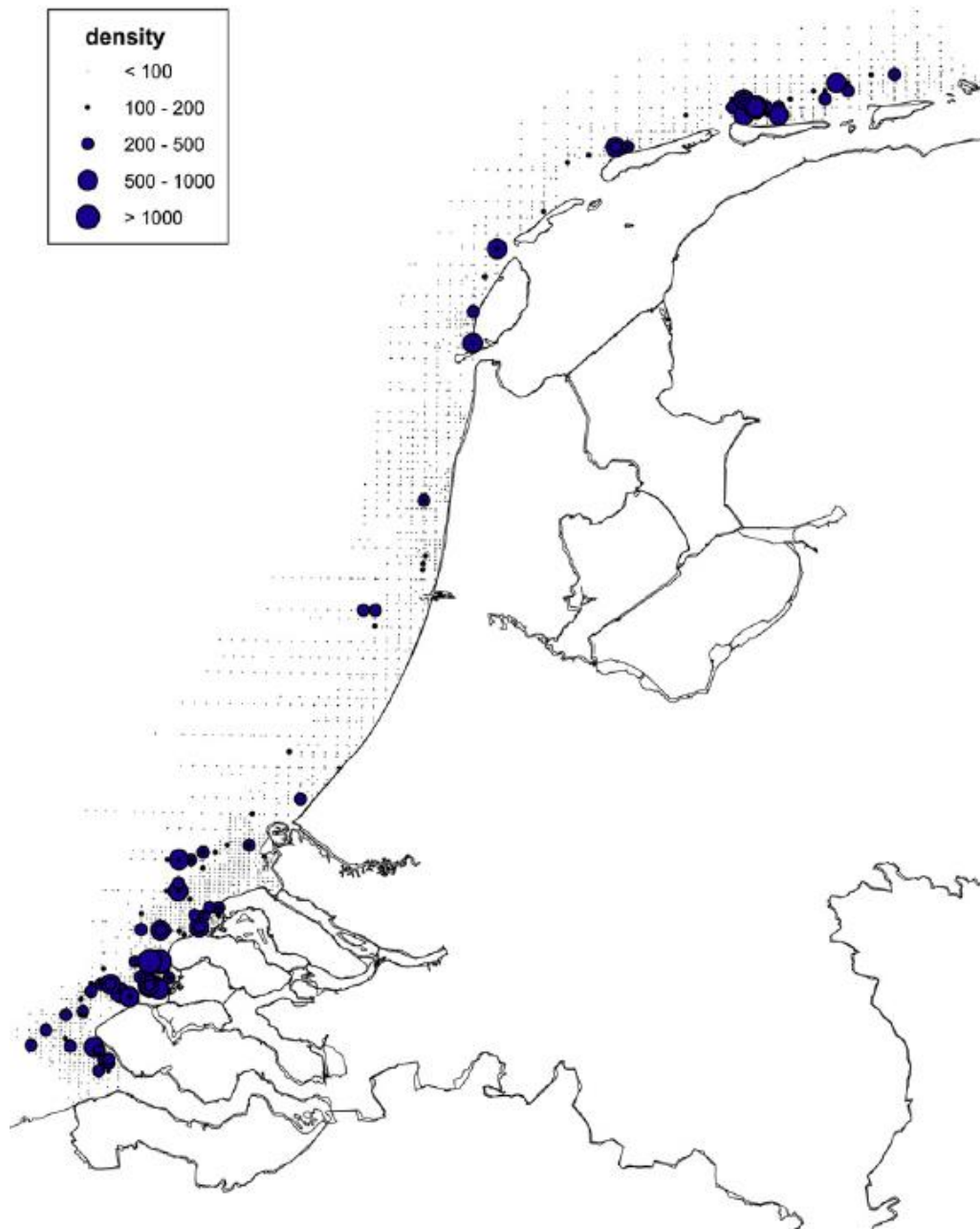


Figure 9. *Ensis* spp. spatial distribution and maximum densities (no. m⁻²) in the Dutch coastal zone (1995–2008), excluding inner Scheldt records. Each small dot on the map represents a sampling station (Source: Tulp *et al.*, 2010).

4.2 Habitat and behaviour

The preferred habitat of *E. directus* in its native range includes gently sloping beaches with wave- and current-swept clean sands, at depths of 5–8 m (Beukema and Dekker, 1995; Cosel, 2009) and with small amounts of silt (Kennish *et al.*, 2004). *E. directus* are also found in lower intertidal areas as well as in deeper waters, including muddy or coarse sediments (Armonies and Reise, 1999; Cosel, 2009), and can thus be independent of sediment characteristics (Dauvin *et al.*, 2007).

Young *E. directus* move out of the sediment and propel themselves along the seabed in response to their environment, becoming stressful either biochemically or through the threat of physical displacement (Muir, 2003). The clams are able to propel themselves over the sand by a series of vigorous lashes with the foot (Figure 4), combined with rapid ejections of water along the vertical side of the foot (Schneider, 1982). Post-larval stages may re-enter the water column for secondary dispersal in summer for up to 6–8 weeks. Furthermore, postlarval juveniles of *E. directus* are able to swim and use byssus threads as draglines, enabling drifting (Swennen *et al.*, 1985; Armonies, 1992; Ovcharenko *et al.*, 2009). Byssus-thread drifting *E. directus* were almost sevenfold more abundant at night than in daylight (Armonies, 1992), demonstrating vertical migration between the sediment and the water column. Nocturnal swimming of adult clams may also facilitate dispersal (Ovcharenko *et al.*, 2009).

In the North Sea, *E. directus* have been found down to depths of 26 m (Mühlenhardt-Siegel *et al.*, 1983; Swennen *et al.*, 1985; Dörjes, 1992). This is much less than its greatest known depth within its native range (Theroux and Wigley, 1983). Because of its rapid burrowing ability, it can live in the unstable sands (Swennen *et al.*, 1985) that are seen frequently in shallow water.

According to habitat suitability mapping of *E. directus* in Dutch coastal waters, there is a preference for depths of 5–25 m, fine sediments, and for areas where current velocities are not high. The resulting map (Figure 10) shows that *E. directus* might occur extensively along the Dutch coastal zone (De Mesel *et al.*, 2011).

Long-term monitoring in the Dutch Wadden Sea indicates that the success of *E. directus* is due to its colonization of previously underutilized habitat formed by highly dynamic, unstable sands (Dekker and Beukema, 2012).

In the Belgian coastal area, habitat suitability models show a positive relationship between clam occurrence and bottom shear stress, water depth, and sand fraction (

Figure 11). These are considered to be the most important factors that enable its colonization (Mangelsdorf *et al.*, 1990; Kenchington *et al.*, 1998). The likely areas for further colonization are subtidal and lower intertidal areas (Ovcharenko *et al.*, 2009).

In Danish waters (Horns Rev), *E. directus* were (positively) linked to water depth, areas with relatively flat terrain, and carrying capacity index (Skov *et al.*, 2008).

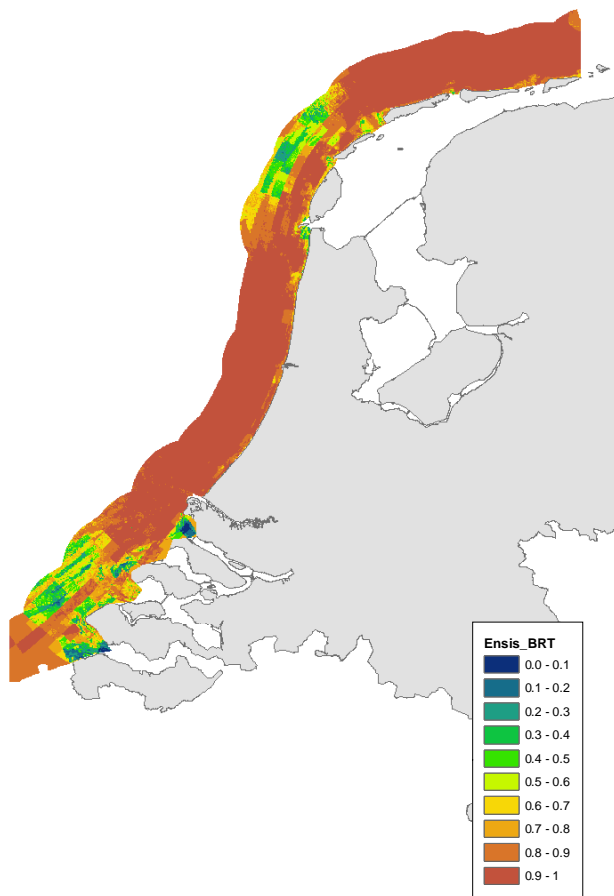


Figure 10. *Ensis directus* habitat suitability mapping (Boosted Regression Tree model; De Mesel *et al.*, 2011).

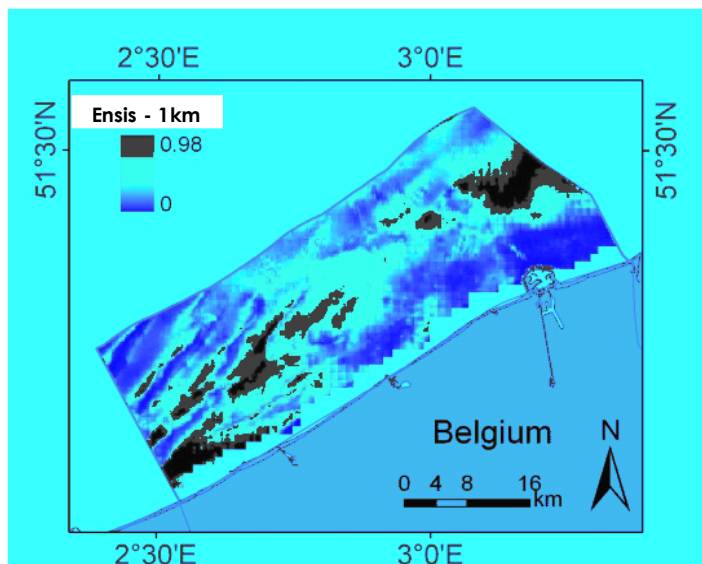


Figure 11. *Ensis directus* 1 km habitat suitability model for the Belgian coastal area (Houziaux *et al.*, 2011).

4.3 Reproduction

E. directus reach early sexual maturity after one year (Mühlenhardt-Siegel *et al.*, 1983).

In the Wadden Sea, spawning takes place between March and April (Beukema and Dekker, 1995). The main spawning period in both 2011 and 2012 took place shortly after the spring plankton bloom (Witbaard *et al.*, 2013). Planktonic larvae were identified in the Isefjord, Denmark in June (Larsen *et al.*, 2007). Observations in the Wadden Sea showed that a second spawning may occur in July/August (Armonies, 1996; Wijsman *et al.*, 2006). The free-swimming larvae are distributed by currents in spring. The larval phase is 10–27 days, depending on water temperatures (Cosel, 2009).

Juveniles settle on clean fine sands with small amounts of silt in the lower zone of the intertidal areas, where they filter-feed on plankton and detritus (Beukema and Dekker, 1995; Swennen *et al.*, 1985).

The settlement of larvae is usually reported for May/June, and the settling density in this area was observed to be ca. 150 individuals m^{-2} by Beukema and Dekker (1995), although other authors report higher values: 440 individuals m^{-2} (Mühlenhardt-Siegel *et al.*, 1983), >3000 individuals m^{-2} (Dauwe *et al.*, 1998), or even 6500 individuals m^{-2} . The highest numbers due to a spatfall (>25 000 individuals m^{-2}) were reported by Dannheim and Rumohr (2012). In France, *E. directus* was reported to have a density of 5–15 individuals m^{-2} in 1998, an increase to 100 individuals m^{-2} , and found at 81 stations out of 706 sampled in the Bay of Seine in 2006 (Dauvin *et al.*, 2007). Density has reached as high as >1000 individuals m^{-2} in several areas. Densities up to 30 000 individuals m^{-2} were reported after settlement, with adult populations reaching >1000 individuals m^{-2} in several areas (e.g. Gravelines close to Dunkerque), and mass strandings of juveniles occur all along the Belgian coast (F. Kerckhof and P. Gouletquer, pers. comm.).

Spat survival is limited to areas below the level of mean low tide (Beukema and Dekker, 1995). Recruitment may be very low or even absent following cold winters (Armonies *et al.*, 2001).

4.4 Growth rate

Migrating juveniles are mostly 1–3 mm long, occasionally up to 5 mm (Armonies, 1992). They reach about 6 cm in length after the first winter. *E. directus* exhibits retarded growth in the first year (size: 30–50 mm) and faster growth in the second year. Lifespan is up to five years in the North Sea, although this is rarely observed (Swennen *et al.*, 1985).

A relatively fast (initial) growth rate in *E. directus* is known for some European populations, where anterior to posterior shell-growth measurements vary from 5.27 $cm\ year^{-1}$ in the first year to 1.08 $cm\ year^{-1}$ in the fifth year (Cardoso *et al.*, 2013). Normally for bivalves, relative growth is age (size)-dependent (e.g. Ramón and Richardson, 1992).

In the Wadden Sea, significant shell growth begins late in the year at minimum water temperatures of 12–14°C (Witbaard *et al.*, 2013). During the first two years of life, growth is rapid, with maximum mean growth rates of 3 $mm\ month^{-1}$ in the first year and up to 14 $mm\ month^{-1}$ in the second year. Growth is variable per season, being highest in summer/early autumn (Dannheim and Rumohr, 2012). Stable isotope studies indicate that growth ceases at about 6°C. Growth is greatest at temperatures above 14°C (Cardoso *et al.*, 2013).

In laboratory experiments (Kamermans *et al.*, 2013), the maximum daily growth rate of *E. directus* was found to be 0.24 mm for shell length and a 2% increase in wet weight

day⁻¹. A ten-week experimental exposure to silt concentrations of 300 mg l⁻¹ documented a significantly higher growth rate compared to a 150 mg l⁻¹ treatment. Therefore, it appears that high silt concentration stimulates growth. In a further experiment, *E. directus* was exposed to different concentrations of chlorophyll in water for ten weeks at a level of 6.5 µg chlorophyll l⁻¹; shell growth was reduced by ca. 40% when compared with growth at 16.5 µg chlorophyll l⁻¹. Kamermans *et al.* (2013) concluded that *E. directus* is more sensitive to a reduction in algal concentration than to an increase in silt concentration in water.

4.5 Impacts

Although dense *E. directus* populations may change the community structure of the benthic fauna or compete for space and food, there have been no reports of significant interactions with native species (Dekker and Beukema, 2012), perhaps because this aspect has not been specifically studied. However, there is some circumstantial evidence to suggest impacts. For example, in the so-called *Abra alba* community (Van Hoey *et al.*, 2004) along the Belgian coast, *E. directus* is now the most common species. There have been declines in abundance of other bivalves such as *Macra stultorum* and *Cerastoderma edule*, and tellinids have been observed since the introduction of *E. directus*. Furthermore, the presence of *E. directus* seems to support the settlement of deposit feeders in general, and dense clam clusters may stabilize the sediment and act as sediment traps (Dannheim and Rumohr, 2012). Similarly, in the mid-2000s in both Belgium and The Netherlands, a decline in abundance of the bivalve *Spisula subtruncata* has coincided with a strong increase in the biomass of *E. directus*. A link between these events has been suggested, with the invader reducing the abundance and local distributions of native species through competition for space and food (Houziaux *et al.*, 2011). In dense beds of *E. directus*, fine sediment particles accumulate, which may alter polychaete abundance (Armonies and Reise, 1999). For example, there was found to be a shift from *Lanice conchilega* to *Owenia fusiformis* (Houziaux *et al.*, 2011), but the full impact on native biota requires further study. Although no extinctions have officially been reported, the indigenous species *E. minor* seems to have disappeared along the Belgian coast (F. Kerckhof, pers. comm.).

In France and Belgium, the native *E. magnus* has been largely replaced by *E. directus*, and the distribution of the former is now mainly confined to areas offshore (Houziaux *et al.*, 2011). Trophic competition occurs between both species, and the distribution of both overlaps (Dewarumez *et al.*, 2011). In contrast, *E. directus* has demonstrated its ability to colonize higher intertidal habitats such as sparsely faunated sand and channels exposed to strong currents where native *Ensis* species are absent (Armonies and Reise, 1999; Arias and Anadon, 2012).

Apparently, *E. directus* has created an ecological niche in areas almost unoccupied by native *E. minor*, i.e. the lower intertidal and shallow subtidal parts of the vast flats of fine sand or muddy sand in the Danish, German, and Dutch Wadden Sea (Cosel, 2009) and even in semi-enclosed water bodies such as the Spuikom in Oostende (F. Kerckhof and K. Jensen, pers. comm.). The species also entered semi-enclosed systems, like the Eastern Scheldt, Lake Grevelingen, and Lake Veere (Hummel and Wijnhoven, 2014).

As summarized by Voigt (1999), Ovcharenko *et al.* (2009), and Jensen (2010), additional various potential impacts include:

- Dense populations may change the benthic community structure due to their burying activities (bioturbation).
- Competition for space and food.

- Dense populations may have an impact on the sediment structure.
- Damage to fishing gear netting from sharp shells.
- Cuts to bathers stepping on *E. directus* in shallow water. Cuts and deep laceration may lead to infections. Other species of razor clam can also cause such conditions.
- Provision of a hard substratum for sessile biota such as barnacles (Donovan, 2011). Fouling of the anterior exposed end of shells can take place (Figure 12). Fouling also takes place on shell material washed out of sediment (F. Kerckhof and K. Jensen, pers. comm.).



Figure 12. *Ensis directus* with epifauning in Fur Island, central Limfjord, Denmark, collected 22 May 2005 by Ole S. Tendal and Kathe Jensen. The polychaete tubes in the left photo are *Pomatoceros triqueter*; the barnacles in the right photo are *Balanus crenatus* (courtesy of Kathe Jensen).

The species can provide an abundant food source for birds, particularly eider ducks (*Somateria mollissima*) (Caldow *et al.*, 2007), gulls (Cadée, 2000a), scoters [common scoter (*Melanitta nigra*) and velvet scoter (*M. fusca*)] (Dekker and Beukema, 2012), waders and corvids (Tulp *et al.*, 2010), but also sea stars (Thompson *et al.*, 2005), thereby interacting with the trophic chain. Following the disappearance of the preferred scoter prey (*Spisula*), scoters adapted to consume the less preferred *E. directus*. The first evidence of common scoters effectively feeding on *E. directus* was observed in 2003 when scoters were seen diving and bringing up *E. directus* at the Brouwersdam in the southern part of the Netherlands (Leopold and Wolf, 2003; Wolf and Meininger, 2004). This was also observed in Belgium, after 2006, when scoters were seen taking *E. directus* in near-coastal waters. For common scoter predation, the optimum length of *E. directus* for foraging was 3–9 cm. While it took some time for scoters to adapt to the new food source (e.g. Houziaux *et al.*, 2011), despite the low density of *E. directus*, oystercatchers (*Haematopus ostralegus*) also adapted to this food source and became specialist predators in selecting *E. directus*, thereby reducing the pressure on the declining stocks of cockles (*Cardium edule*) (Swennen *et al.*, 1985; Freudendahl *et al.*, 2010).

E. directus forms an important food source for gulls (*Larus* spp.). Within the native range of *E. directus*, gulls are frequently seen feeding on displaced specimens (Schneider, 1982). This is also the case within the introduced range (Cadée, 2000a,b), where

decaying and moribund *E. directus* form an important food source (François, 1993; Knudsen, 2001; Kerckhof pers. comm.). During mass mortalities, *E. directus* partly leaves its burrow, and the protruding clams are unable to reburrow, thus becoming an easy prey for herring gulls (*Larus argentatus*) at low tide (Cadée, 2000a,b).

Along the American east coast, *E. directus* is preyed upon by birds and further affected by the snail *Polinices heros*, which drills into shells of living individuals. Similar snails are capable of drilling into *E. directus* shells on the European coasts, such as *Polinices catena*, which ranges from the north to the Mediterranean Sea. This species is smaller than *P. heros*, but it is known to avidly feed on bivalves (Clements *et al.*, 2013).

Fish are also known to feed on *E. directus* (Ashelby, 2004; Tulp *et al.*, 2010), with *E. directus* forming up to 90% of the volume in the gut contents of some flatfish (Tulp *et al.*, 2010) and cod (*Gadus morhua*). Cod readily feed on the great numbers that drift near the seabed following storms, when *E. directus* have been washed out of the sediment and their soft tissues became separated from the shells (F. Kerckhof, pers. comm.).

Tulp *et al.* (2010) concluded that the introduction of *E. directus* caused a major change in food interrelationships in the invaded region.

5 Prospects for further invasions

E. directus was included in the list of the 100 most invasive species in Europe (Ovcharenko *et al.*, 2009). Owing to its life history with free-swimming larvae, it is a good candidate for continued range expansion, with water currents or ballast water being the most likely vectors. Because of its potential to be transported with ballast water, it became recorded in the updated “next pest” list of Australia. This list covers those species that have not yet been introduced to Australia (Hayes *et al.*, 2005).

Hummel and Wijnhoven (2014) took *E. directus* and other non-indigenous species in the Dutch Wadden Sea as examples to conclude that invasions may, over time, reach balanced coexistence with native species, possibly resulting in a localized net diversity gain. However, the impacts of non-indigenous species should not be neglected, especially during their mass developments.

Additional likely areas for *E. directus* colonization include temperate subtidal and lower intertidal areas. Areas that *E. directus* colonizes are relatively exposed, with usually a lower level of macrozoobenthos. Their distribution is presently discontinuous along the Atlantic coastline. However, continuous distribution is likely to occur in the near future because of the available and suitable habitat for this species and because of its pelagic life history phase (Lazure and Jegou, 1998; Puillat *et al.*, 2004). Considering its depth distribution in its native range, *E. directus* has the potential to colonize the entire German Bight (Armonies, 2001) and large areas of the Iberian Peninsula and Bay of Biscay (P. Gouletquer, pers. comm.). The authors believe immigration to the Mediterranean Sea is also possible.

The spread of *E. directus* may also arise from the discarding of live specimens intended for human consumption. Large numbers of *E. directus* captured in Dutch waters are marketed in southern Europe, and the possibility of a new range extension from this source may take place. Vacant shells of *E. directus* were found on a beach near Lisbon in 2012 together with the remains of other non-native Mollusca (F. Kerckhof, pers. comm.).

It is interesting to note that *E. directus* has not (yet) colonized suitable habitats on other continents, which highlights its potential to become introduced to habitats outside Europe. Considering the habitat preferences as well as temperature and salinity tolerances of *E. directus*, new potential areas of colonization may be found in South America, along the North American west coast, southern Africa, Asia, Australia, and New Zealand.

6 Prospects for control or management where introductions occur

As with most introduced species, after establishment in a new region, control or mitigation options are minimal. This is especially true for species that have developed massive population densities or have become widely distributed. Both of these scenarios occurred with *E. directus* in the Wadden Sea and elsewhere along the European coastline. Indeed, the abundance and ease of inducing spawning of *E. directus* has made it a potential candidate for aquaculture in the maritime region of North America (Kenchington *et al.*, 1998), where there is a small commercial fishery (Leavitt *et al.*, 2005).

A control option to avoid reintroductions from its native range might be achieved by mid-ocean exchange of ballast water or other effective ballast water management measures. Furthermore, the potential of local predators (e.g., *Polinices* spp.) to partially control populations could be considered unless this interferes with production from fishing.

In Europe, a commercial fishery on *E. directus* exists in the Netherlands (Houziaux *et al.*, 2011), and this species is frequently found on restaurant menus in Wadden Sea countries. The results of Houziaux *et al.* (2011) suggest that a yield of ≈ 2 kg m⁻² of marketable *E. directus* specimens can be expected annually, and Hervás *et al.* (2012) determined that the *E. directus* fishery by the Dutch Fishermen's Association was certified according to the Marine Stewardship Council Principles and Criteria for Sustainable Fisheries. However, the fishing activities will unlikely depress the *E. directus* population because no intensive fishing efforts have yet been authorized. In Belgium, targeted fishing of this shellfish is prohibited (F. Kerckhof, pers. comm.).

Attempts to develop aquaculture using *E. directus* were abandoned because of low market value and insufficient demand in France (P. Gouletquer, pers. comm.). Targeted *Ensis* spp. fishing (on native species) is reported for, e.g. the Bay of Biscay populations, with larger specimens collected for direct human consumption and small individuals used as bait (Arias and Anadon, 2012). On the Dutch coast, densities of up to 91 individuals m⁻² have been obtained, demonstrating that this species may continue to support a viable and sustained fishery (Witbaard *et al.*, 2013). However, it should be evaluated whether the disturbance caused by fishing effort makes the harvest viable. Trials of different fishing methods, e.g. hydraulic dredging and electrical fishing, have been carried out in Scotland (Addison *et al.*, 2006; Breen *et al.*, 2011). The potential for *Ensis* aquaculture has also been investigated in the Limfjord, Denmark (Freudentahl and Nielsen, 2005); so far this has been unsuccessful, likely because of the difficulties in capturing this species that is only accessible at very low tides.

Establishing a commercial fishery on this species is also seen as controversial as this may support the spread of *E. directus* when live clams are actively moved to places where they were previously absent to create new fisheries. In this sense, the *E. directus* case study is similar to other invasive species relative to a marketable approach to manage such populations, as in the case of the fishery developed for the predatory snail *Rapana venosa* in the Black Sea (ICES, 2004), a debatable question emphasized by Nunez *et al.* (2012).

In laboratory experiments, Thompson *et al.* (2005) demonstrated that the sea star *Lepasterias polaris*, native to the Northwest Atlantic (Gaymer *et al.*, 2001), prefers *E. directus* as prey over *Mya truncata* and *Spisula polynyma*. However, attempts to control the *E. directus* population with imports of a non-indigenous sea star should be strongly discouraged as this intentional introduction may result in unexpected negative impacts, and its diet may not be selective and might include native European species. On the

contrary, better understanding of potential native European predators should be obtained to evaluate whether biocontrol efforts should be considered for *E. directus*.

7 Acknowledgements

This document was prepared at the meeting of the ICES Working Group on Introductions and Transfers of Marine Organisms (WGITMO) held in Klaipeda, Lithuania 19–21 March 2014. Members of the Working Group, in addition to the authors, provided editorial review.

We thank P. van Avesaath (NIOZ, the Netherlands) for providing additional Dutch distribution records of *Ensis directus* and G. H. Copp (Cefas, UK) for his comments on the text as well as for improving the English. Furthermore, the authors thank Ute Mühlenhardt-Siegel (University of Hamburg, Zoological Museum, Hamburg, Germany) for her critical review of the text.

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