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First records of the dwarf surf clam *Mulinia lateralis* (Say, 1822) in Europe

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Abstract

This paper reports the first records of the dwarf surf clam *Mulinia lateralis* (Say, 1822) outside its native area, which is the western Atlantic Ocean, ranging from the Gulf of St Lawrence to the Gulf of Mexico. In 2017 and 2018 specimens were found in the Dutch coastal waters (North Sea), in the Wadden Sea and in the Westerschelde estuary, in densities of up to almost 6000 individuals per square meter. In view of its ecology and distributional range in the native area *M. lateralis* has the potential to become an invasive species. Its ability to quickly colonize defaunated areas, its high fecundity and short generation time, its tolerance for anoxia and temperature extremes and its efficient exploitation of the high concentrations of phytoplankton and natural seston at the sediment-water interface may bring it into competition with native species for food and space.

Keywords: *Mulinia lateralis*, Bivalvia, Marine, North Sea, Invasive, Competition

Introduction

For at least half a century, the process and the environmental, economic and social impacts of invasions of non-indigenous species are a focus of ecological research (Elton 1958; Rilov and Crooks 2009; Marbuah et al. 2014). As early as 1969 ICES had established a working group to address multiple research and applied issues related to bio-invasions, such as early detection and alerts to potential spread, population dynamics and distribution, ecological impacts, and risk assessments (see WGITMO 2018 for the latest report). Nowadays, many governments set up management goals and regulations to prevent the introduction and spread of alien species (e.g. Canada 2014; EU 2014; Australia 2016).

Meanwhile, many non-indigenous species have been introduced in NW European coastal waters. Gollasch et al. (2008) report 167 species to have been introduced in the North Sea. The authors show that there are relatively many records from the Netherlands and attribute this to the most intensive shipping (Port of Rotterdam) and aquaculture (Oosterschelde estuary) activities in the North Sea region (see also Wolff 2005). The most successful taxa regarding introduction and immigration are polychaetes, bivalves and amphipods (Reise et al. 1999; Zettler et al. 2018).

The number of non-indigenous species is still increasing. In the Netherlands already two new species have been recorded in 2018 (Faasse 2018a, 2018b). Here we report the first records of a new non-indigenous bivalve species in the North Sea: *Mulinia lateralis* (Say, 1822). The vernacular name of *M. lateralis* in English is dwarf surf clam or coot clam. As a Dutch vernacular name for this species, we propose 'Amerikaanse strandschelp', given the Dutch name for other species of the Mactridae in Dutch waters (*Mactra* and *Spisula*), and the American origin.

Detection and distribution

Mulinia lateralis has now been found in coastal waters and estuaries in the Netherlands. The first specimens were found during surveys in the southwestern Dutch coastal zone (the Voordelta) in September 2017, and again in June 2018. In the period of March to June 2018 specimens were also found in the

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Table 1 Records of *Mulinia lateralis* in the Netherlands: year, month, geographical area, geographical positions (WGS84) and density (ind/m^2) (see Fig. 1)

Year	Month	Area	Longitude	Latitude	Tidal zone	Density (n/m2)
2017	October	Voordelta	3.79238	51.75976	sublittoral	1.1
	October	Voordelta	3.81156	51.80296	sublittoral	1260.6
	October	Voordelta	3.80793	51.80274	sublittoral	5872.4
	October	Voordelta	3.79570	51.78147	sublittoral	3.3
	October	Voordelta	3.63029	51.71996	sublittoral	0.1
2018	May	Eems	6.91667	53.35417	intertidal	4.9
	May	Eems	6.91667	53.35833	intertidal	9.8
	May	Eems	6.91667	53.36250	intertidal	9.8
	May	Eems	6.91250	53.39375	intertidal	2.4
	May	Eems	6.91667	53.39583	intertidal	2.4
	June	Voordelta	3.80000	51.80000	sublittoral	1003.1
	June	Voordelta	3.83333	51.77500	sublittoral	7.1
	June	Voordelta	3.83333	51.79167	sublittoral	0.8
	June	Voordelta	3.83333	51.80000	sublittoral	54.8
	May	Waddenzee	5.85000	53.40000	intertidal	2.4
	May	Waddenzee	5.67500	53.34167	intertidal	2.4
	May	Waddenzee	5.66250	53.38125	intertidal	2.4
	May	Waddenzee	5.28333	53.18333	intertidal	2.4
	March	Waddenzee	5.10833	52.98750	sublittoral	0.8
	September	Westerschelde	4.07012	51.36747	intertidal	820.0
	September	Westerschelde	4.06945	51.36606	intertidal	unknown

Wadden Sea and Ems estuary, and in September 2018 in the Westerschelde estuary (Table 1 and Fig. 1).

Morphological identification

The family Mactridae is characterized by two cardinal teeth in the left valve fused in the shape of a ‘Λ’ (Signorelli and Pastorino 2012a). Our specimens agree with the diagnosis of the subfamily Mactrinae by Signorelli and Carter (2016). In several genera within this subfamily the external ligament has been reduced to a varying degree. According to Gardner (1928) the genus *Mulinia* Gray, 1837 represents the final stage in the reduction of the external ligament to a remnant below the hinge line. We compared the diagnoses of the 25 recent genera within the subfamily Mactrinae (MolluscaBase 2018a) from a number of literature sources with our collected specimens, and conclude they belong to the genus *Mulinia*. An important character of this genus is the absence of an externally visible ligament.

The genus *Mulinia* consists of ten recognized species (MolluscaBase 2018b). The shells of six *Mulinia* species have an oval outline (Signorelli and Pastorino 2011; Coan and Valentich-Scott 2012; Signorelli and Pastorino 2012a; Signorelli and Pastorino 2012b). Four species have shells with a more triangular outline, the anterior and posterior margins being more angular and less rounded, viz. *M. pontchartrainensis* Morrison 1965, *M. cleryana* (d’Orbigny, 1846), *M. pallida* (Broderip & G. B. Sowerby I, 1829) and *M. lateralis* (Say, 1822). The shells of *M. pontchartrainensis*, *M. cleryana* and *M. pallida* have a higher shape than those of *M. lateralis*, with the anterior and posterior end below the middle of the shell height (Morrison 1965; Signorelli and Pastorino 2012b).

Our specimens agree with the following combination of characteristics of *Mulinia lateralis* (Fig. 2), namely (1) triangular shell outline, (2) distinct radial ridge along posterior end of valves, (3) ligament exclusively internal, (4) accessory lamella well developed, (5) anterior lateral teeth in right valve of different sizes, the ventral one longer; two posterior lateral teeth similar in size, (6) shell colour whitish to cream, with thin, yellowish periostracum, may be thickened along the postero-dorsal margin past the

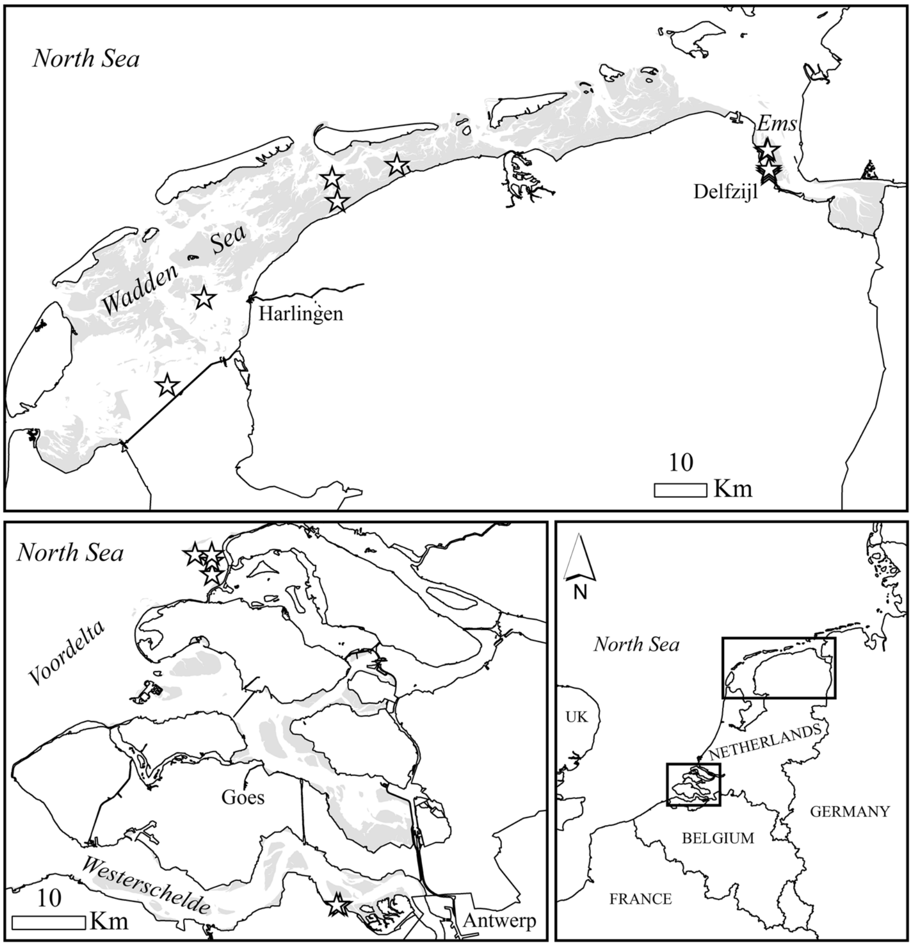

Fig. 1 Map of the Netherlands, with locations where *Mulinia lateralis* has been found

posterior ridge, (7) shell surface smooth with very fine concentric growth lines, (8) shell distinctly convex, (9) cardinal area between beaks broad in large specimens.

Literature sources differ considerably with respect to maximum length given for *M. lateralis*. (Abbott 1974) mentions 12.7 mm (0.5 in.), while the largest length class in a study by (Montagna et al. 1993) was 21 mm. In the Voordelta we found animals between 7.2 and 17.8 mm. Maximum length in the Wadden Sea was 21.2 mm. The specimens in the Westerschelde were smaller, up to 7 mm.

Main diagnostic characters of *Mulinia lateralis* for field identification are its whitish to cream colour, the presence of a radial ridge along the posterior end of the valves, and the distinctly convex shells. In the southern North Sea *Mulinia lateralis* is most likely to be confused with juvenile *Mactra stultorum* or juvenile *Spisula subtruncata*. Therefore, we list main morphological differences with those two species (Table 2) and provide illustrations of all three (Figs. 2, 3 and 4). Furthermore, we provide illustrations of another invasive species of Mactridae, namely *Rangia cuneata* (Fig. 5). Drawings were made with the aid of a drawing mirror on a Wild M5 stereomicroscope, based on following material: 1 specimen of *Mulinia lateralis* (length 21.2 mm) collected in July 2018 from the Wadden Sea, 1 specimen of *Mactra stultorum* (length 21.9 mm) and 1 specimen of *Spisula subtruncata* (length 21.2 mm) collected from the Dutch coastal zone, 1 specimen of *Rangia cuneata* collected on 16 April 2018 from the Galgenweel in Antwerp (length 45.8 mm). Specimens of *M. stultorum* and *S. subtruncata* similar in size to the specimen of *M. lateralis* were chosen for drawing in order to rule out morphological differences related to size. Similar-sized *Rangia cuneata* were not available to us.

Table 2 Main morphological differences between *Mulinia lateralis*, *Mactra stultorum* and *Spisula subtruncata*

	Mulinia lateralis	*Mactra stultorum*	*Spisula subtruncata*
Shell outline	triangular	oval	triangular
Radial ridge along posterior end of valves	distinct	absent	absent
Ligament	exclusively internal	external ligament present	external ligament present
Accessory lamella (between chondrophore and two fused cardinal teeth)	well developed	very weak	very weak
Shell colour	whitish to cream with thin, yellowish periostracum	creamy white with purple hue around umbos and brown radiating rays	dirty white with brown periostracum
Shell surface	smooth with very fine concentric growth lines	smooth	distinct concentric grooves along dorsal line on either side of umbos
Shell convexity	distinctly convex	valves moderately convex	variable, with distinctly convex and less convex forms (van Urk 1959)
Cardinal area between beaks	broad in large specimens	narrow in large specimens	narrow in large specimens

To facilitate identification we provide below a key of all species of the subfamily Mactrinae of the NE Atlantic Ocean and adjacent brackish waters, partly after Tebble (1966).

1.	– external ligament present	2
	– ligament exclusively internal	6
2.	– external ligament separated from internal ligament by a calcareous septum; lateral teeth smooth	3 (*Mactra*)
	– external and internal ligaments not separated by a calcareous septum; upper and lower surfaces of lateral teeth in left valve and inner surfaces of lateral teeth in right valve serrated	4 (*Spisula*)
3.	– anterior cardinal tooth of right valve almost parallel with hinge line; adults normally less than 6.35 cm long	*Mactra stultorum* (Fig. 3)
	– anterior cardinal tooth of right valve not parallel with hinge line; adults normally more than 6.35 cm long	*Mactra glauca*
4.	– pallial sinus shallow, reaching to a point below and behind the middle of the posterior lateral tooth/teeth	*Spisula subtruncata* (Fig. 4)
	– pallial sinus deep, reaching to a point below and in front of the middle of the posterior lateral tooth/teeth	5
5.	– cardinal teeth of left valve reach more than halfway down the hinge plate; dorsal areas about the beaks with fine concentric lines	*Spisula elliptica*
	– cardinal teeth of left valve reach no more than halfway down the hinge plate; dorsal areas about the beaks with fine concentric grooves	*Spisula solida*
6.	– left valve with lamellar lateral teeth, posterior one short (length about one third of postero-dorsal margin); upper and lower surfaces of these teeth smooth or with tiny crenulations, sometimes in indistinct rows; umbo on midline of shell and directed slightly forward at most	*Mulinia lateralis* (Fig. 2)
	– left valve with stout lateral teeth, anterior one L-shaped, posterior one long (almost along entire postero-dorsal margin); upper and lower surfaces of these teeth serrated; umbo in front of midline of shell and directed markedly forward	*Rangia cuneata* (Fig. 5)

DNA based identification

DNA was analyzed from 3 specimens collected in September 2018 in the Westerschelde. Soft tissue was removed from the shell, and conserved in 96% Ethanol as soon as possible after collection. DNA was isolated from this tissue using the DNeasy Blood and Tissue kit (Qiagen) as per manufacturers protocol. 0,5 µl of the isolated DNA was used as a template in a 25ul PCR reaction to amplify the 16S gene of the mitochondrial DNA (primers 16S-F-ONT and 16S-R-ONT, containing an extension to allow for the addition of Oxford Nanopore Barcodes in a subsequent PCR step (Pomerantz et al. 2018); Phire Tissue Direct PCR master mix (Thermo Fisher). The amplification program was as follows: Initial denaturation, 3 min at 98 °C, 30 amplification cycles of 98 °C, 8 s; 61 °C, 8 s; 72 °C, 20 s; and 2 min final extension at 72 °C. 4 µl of this PCR mixture was directly used in a second 20ul barcoding PCR using the PCR barcoding expansion kit EXP-PBC096 (Oxford Nanopore) according to the manufacturers protocol, and again using Phire tissue direct PCR master mix. Barcoded PCR products were purified using the QIAquick PCR Purification Kit (Qiagen), and DNA was eluted in 15 µl EB. DNA concentrations and purity were checked using Nanodrop (Thermo Fisher) and Qubit dsDNA HS DNA Assay kit (Thermo Fisher). Samples were pooled in equimolar ratios with several other samples and a sequencing library was prepared using the SQK-LSK108 sequencing kit (Oxford Nanopore) according to the manufacturers protocol. The DNA library was sequenced on a R9.4.1 flowcell in the MinION MK1b sequencer using MinKNOW 2.2.1 for 1 h, with live base calling enabled. Obtained sequences were filtered on read length and quality using NanoFilt (De Coster et al. 2018) with settings to retain only reads between 500 and 800 nucleotides and a minimum q score of 9. Filtered reads were

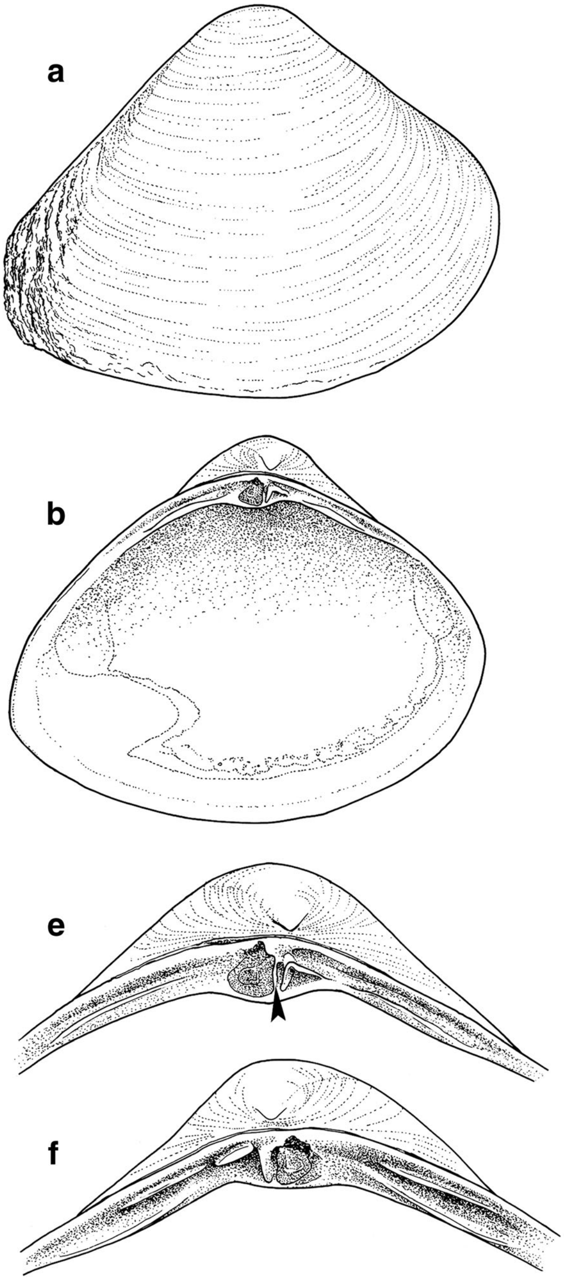

Fig. 2 *Mulinia lateralis*. **a** outside view of right valve; **b** inside view of left valve; **c** view of anterior regions of the two valves; **d** view of dorsal regions of the two valves (radial ridge arrowed); **e** hinge and umbonal region of left valve (accessory lamella arrowed); **f** hinge and umbonal region of right valve

trimmed of their sequencing adapters and barcodes and demultiplexed using Porechop (Wick et al. 2017). Approximately 50.000 reads were obtained for each of the three specimens. The first 100 reads were used to build a de novo consensus sequence using Canu V1.7 (Koren et al. 2017) with settings only correct reads, and optimized for short amplicons (canu -correct; genomeSize = 1000, minReadLength = 400 minOverlapLength = 300). From the corrected reads the top one was used as a reference to further polish the sequence. First, 500 reads from the obtained amplicons were aligned to the reference using minimap2 (Li 2018) and this alignment was used as input for further polishing with Racon (Vaser et al. 2017).

The obtained consensus sequences had a length of 519, 516 and 511 bp. Blast was used to search for homology in NCBI nt database. The obtained consensus sequences were all 99% homologous to the *M. lateralis* references, despite some remaining homopolymer errors

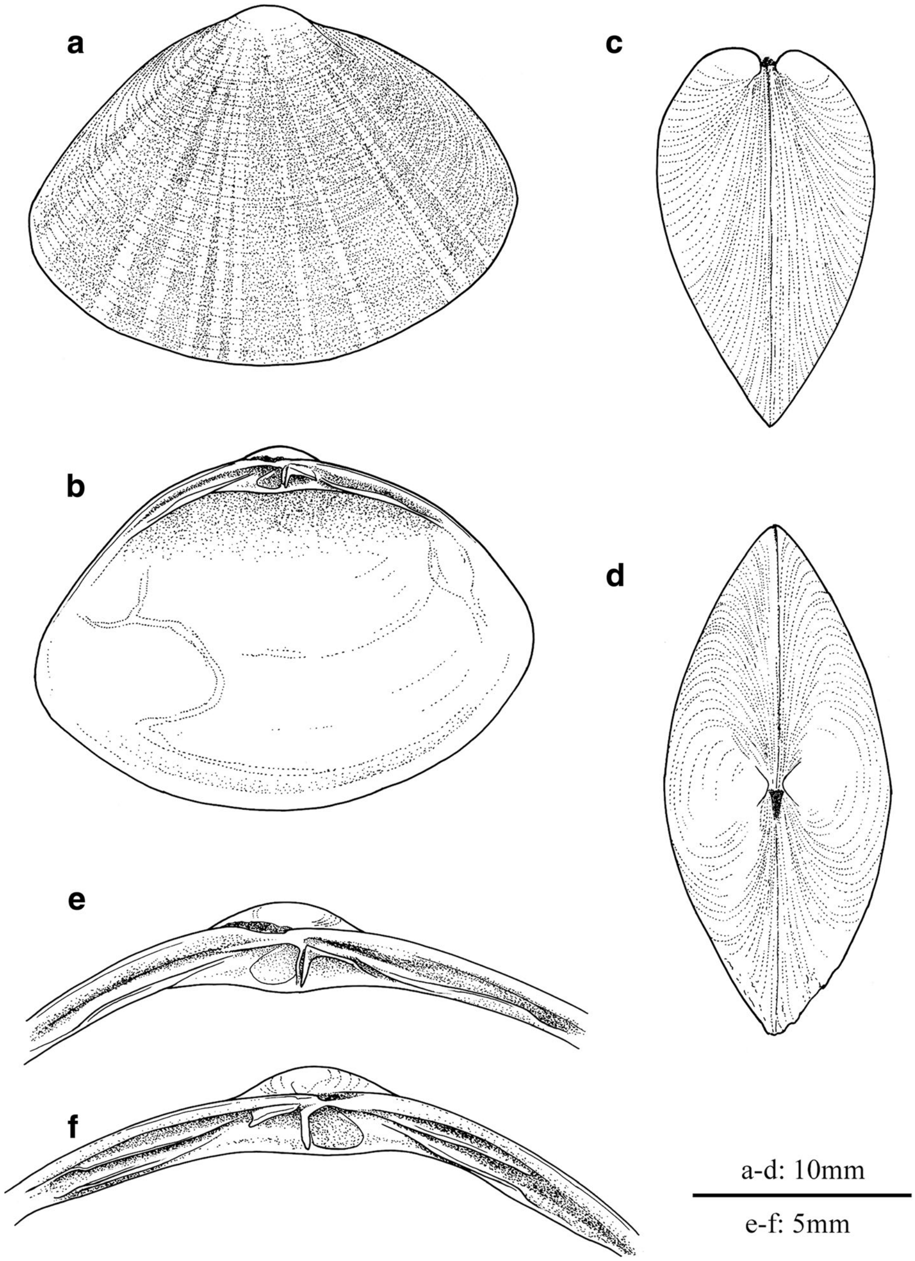

Fig. 3 *Mactra stultorum*. **a** outside view of right valve; **b** inside view of left valve; **c** view of anterior regions of the two valves; **d** view of dorsal regions of the two valves; **e** hinge and umbonal region of left valve; **f** hinge and umbonal region of right valve

in the nanopore consensus. The best hits in NCBI nt not being *M. lateralis* were *Rangia cuneata* (sequence homology of 88%) and *Spisula solida* (homology of 84%). Sequences obtained from the three specimens were manually corrected for the homopolymer errors based on an alignment with *M. lateralis* reference sequences KT959479 and KX713236, and the resulting sequences are deposited at Genbank, accession numbers: MK026966-MK026968.

Discussion

The native distribution of *Mulinia lateralis* is the western Atlantic Ocean, ranging from the Gulf of St Lawrence to the Gulf of Mexico (Brunel et al. 1998; Turgeon et al. 2009). It is widely reported from bays along the Atlantic and Gulf coasts of the U.S., in a large range of salinities, from 5 to 80 ppt (Parker, 1975 in Montagna et al. 1993). It appears, however, to be a mainly estuarine species (Walker and Tenore 1984; Montagna and Kalke 1995). In

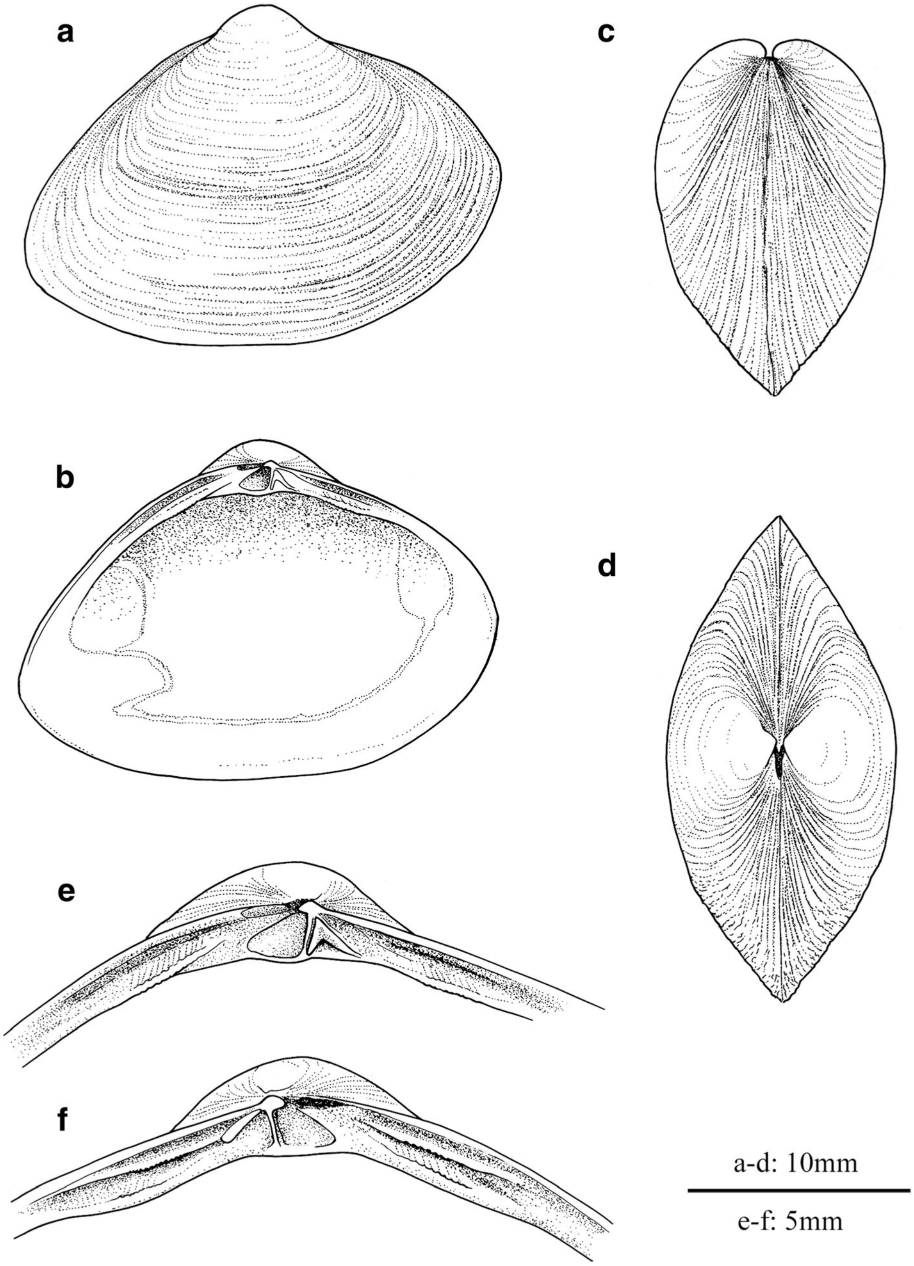

Fig. 4 *Spisula subtruncata*. **a** outside view of right valve; **b** inside view of left valve; **c** view of anterior regions of the two valves; **d** view of dorsal regions of the two valves; **e** hinge and umbonal region of left valve; **f** hinge and umbonal region of right valve

samples collected by Montagna and Kalke (1995) *M. lateralis* was dominant at four stations where there was freshwater influence, while at two other stations other bivalves were dominant. McKeon et al. (2015) report that *M. lateralis* composes a large portion of the total bivalve abundance at mixohaline sites (5–30 ppt) but quickly decreases in euhaline sites. They found *M. lateralis* has the most variable occurrence of all bivalve species they studied. They suggest that the tremendous variability seen in this species' occurrence could be a result of salinity 'windows of opportunity' for the larvae to colonize polyhaline sites. The Voordelta is mostly saline, but in periods of high freshwater discharges, salinity in some parts becomes less than 25 ppt for several days, among others in the area where dwarf surf clams were found. Both the Westerschelde and the Wadden Sea can be characterized as estuarine environments. The eastern part of the Westerschelde, where *M. lateralis* was found, is brackish.

With respect to introduced species, most attention is being paid to species that become invasive, i.e. having

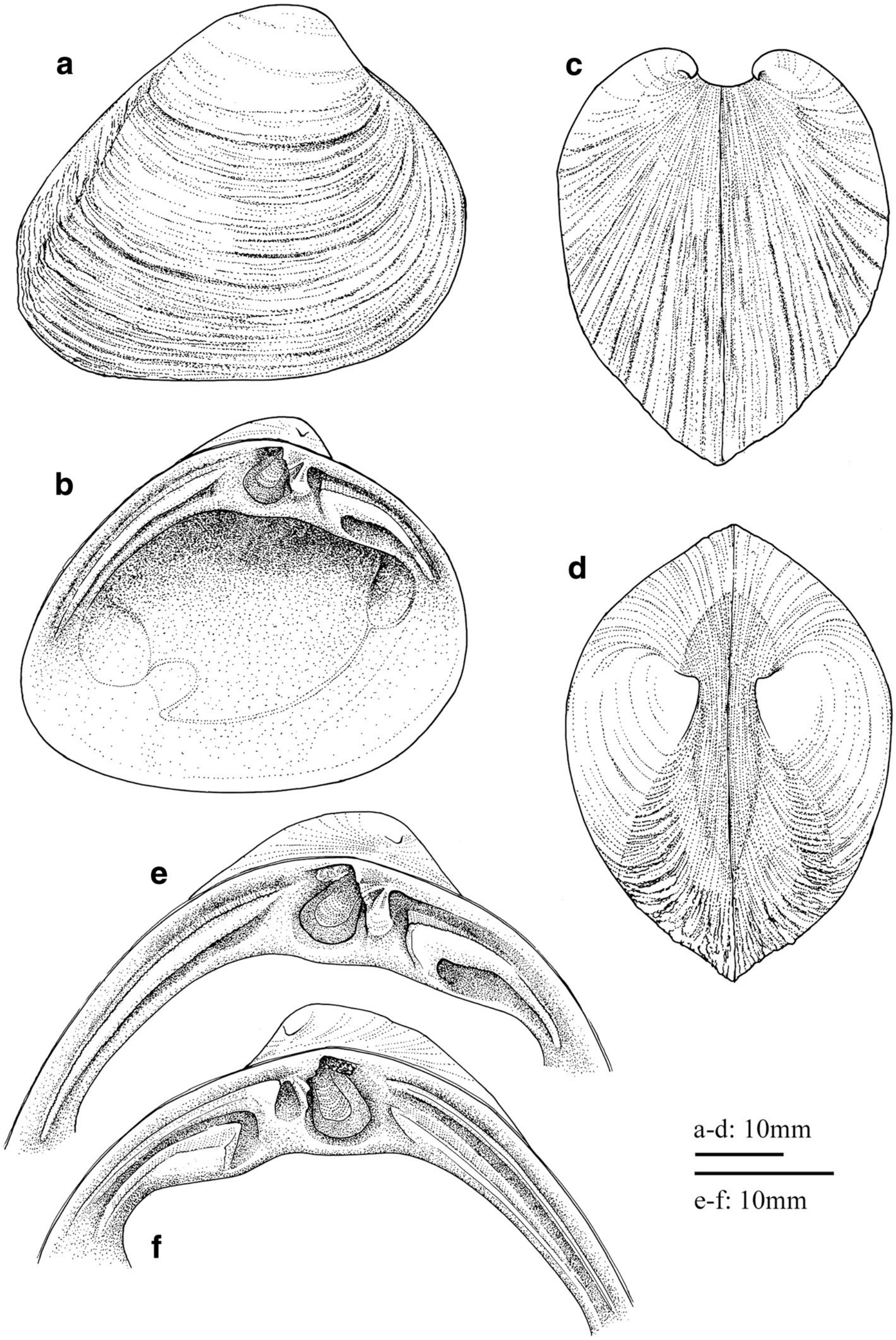

Fig. 5 *Rangia cuneata*. **a** outside view of right valve; **b** inside view of left valve; **c** view of anterior regions of the two valves; **d** view of dorsal regions of the two valves; **e** hinge and umbonal region of left valve; **f** hinge and umbonal region of right valve

negative ecological and/or economic impact. Examples of invasive species in the North Sea coastal waters are the razor shell *Ensis leei* (Beukema and Dekker 1995; Tulp et al. 2010; Gollasch et al. 2015; Witbaard et al. 2015). the Pacific oyster *Crassostrea gigas* (Smaal et al. 2005; Nehls and Büttger 2007; Troost 2010) and the Asian shore crabs *Hemigrapsus sanguineus* and *H. penicillatus* (Noël et al. 1997; Gollasch 1999; Jungblut et al. 2017). Will *Mulinia lateralis* become the next invasive species? Although no generalizations should be made about links between species' attributes and its invasive ability (Manchester and Bullock 2000), its native range and ecology in that area might give some first indications.

Mulinia lateralis is a typical r-selected species (Williams et al. 1986). It has a very short generation time, individuals being able to spawn at a length of 3 mm and at an age of 60 days, and probably more than once a year (Calabrese 1970). It has a short life span, up to 2 years, and a high fecundity (Lu et al. 1996). The species has a pelagic planktotrophic larval stage that lives in the plankton from 7 to 22 days (Mann et al. 1991) and, thus, a generation time of about 3 months (Guo and Allen 1994). In some areas, however, a continuous period of settling from a single spawning cycle has been reported, as well as year-round spawning (Montagna et al. 1993). It is a rapid colonizer after different types of disturbance. It has been found to be one of the numerically dominant species in Tampa Bay after summer defaunations (Santos and Simon 1980), likely because it is well-adapted to short-term anoxia (Shumway et al. 1983). McKeon et al. (2015) observed that *M. lateralis* was most abundant at sites with 'poor water quality', and has a tolerance for "muck" at poor water quality sites.

In conclusion, *M. lateralis* seems to have many characteristics to become a successful invader, as was the case for *E. leei* in the NE Atlantic (Dannheim and Rumohr 2012; Gollasch et al. 2015): planktonic larvae, short generation time, rapid growth. However, success will also depend on, among others, predation, available habitats and competition with native shellfish. At the moment *M. lateralis* is only known from a restricted area in the Northeast Atlantic. However, some species may be present for many years before they exhibit invasive characteristics (Aikio et al. 2010; Piria et al. 2017).

In its native range, *M. lateralis* is a desirable prey for crabs and fish (Calabrese 1970; Montagna et al. 1993). Even large *Mulinia* live very close to the sediment surface and are thus easily available to predators. Predation by crabs and fish is probably the major factor controlling adult population size, at least during warmer months (Virnstein 1977, 1979). We expect this to be the same in European waters, as has been documented for native species (Sanchez-Salazar et al. 1987; Hiddink et al. 2002; Andresen and van der Meer 2010). It is also an important food item for starfish (Mcclintock and Lawrence 1985), ducks (Cronan 1957; Montagna and Kalke 1995; Berlin 2018) and shorebirds (Britton and Morton 1989; Smith et al. 2016). Thus, in North Sea coastal waters, the species might be a new and/or alternative prey for shorebirds (such as oystercatcher, sanderling and red knot) and sea-ducks (such as common scoter, common eider, greater scaup).

Introductions can also have marked effects on populations of native species and biodiversity, and modify native habitats (Manchester and Bullock 2000; Bax et al. 2003). The most obvious is by modifying the habitat, or through increasing predation on native organisms. Intra-guild predation of *Hemigrapsus sanguineus* upon *Carcinus maenas* may be one of the reasons *H. sanguineus* outnumbered *C. maenas* at some places, besides enhanced larval settling rates and competition for space (i.e. sheltered areas) (Jungblut et al. 2017). Filter feeding non-native bivalves may compete for space and food with native bivalves, especially if the non-native species can easily spread into all available habitats at high population densities. In the Venice lagoon, for instance, the non-native Manila clam, *Ruditapes philippinarum*, is now the dominant bivalve species, and native species such as *Ruditapes decussatus* are now rare (Pranovi et al. 2006). This also seems to be a realistic scene for the opportunistic *Mulinia lateralis*. Most bivalve species largely utilize the same food source and are therefore competitors for food. Whether food competition leads to an introduced species out-competing indigenous species is dependent on many factors such as filtration capacity, selection and absorption efficiency, and energy demand (Shumway and Newell 1984; Troost 2010). *M. lateralis* is adapted to quickly exploit the high concentrations of phytoplankton and natural seston which occur at the sediment-water interface but has a relatively high energy demand and an apparent inability to catabolize protein during prolonged periods of starvation which may be the cause of observed mass mortalities (Shumway and Newell 1984). *M. lateralis* may therefore be a weak competitor for food. In the Voordelta *M. lateralis* was found together with *Spisula subtrucata*. At the same station the highest density of both *M. lateralis* (5872 ind/m^2) and of *S. subtruncata* (955 ind/m^2) was found. In the Westerschelde *M. lateralis* (820 ind/m^2) was found together with high densities of small *Cerastoderma edule* (1756 ind/m^2). Apparently, as *M. lateralis* seems to settle in high densities together with other bivalves, it will compete both for space and food with native bivalves.

Conclusion

Mulinia lateralis has established populations in estuarine areas and coastal waters of the Netherlands. In view of its ecology and distributional range in the native area it has the potential to become an invasive species. For the same reasons dispersal to other areas in Europe is likely.

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Availability of data and materials

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request. At a later stage the data will become publicly available, through the Dutch Marine Information and Data Centre (IHM) (https://www.informatiehuismarien.nl/uk/).

Authors' contributions

JC and KT are project leaders of the main monitoring programs. MF and HG made the identification key. KT made Fig. 1, HG made the Figs. 2, 3, 4 and 5. MF, HG, AE, KP, DvdE and JvZ were involved in the field work, found the new species and contributed to the final identification. RN did the DNA based identifications, and wrote the parts of the ms about these analyses. All authors were involved in the setup of the manuscript, lead by JC. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Publisher's Note

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