The non-indigenous window shell *Theora lubrica* Gould, 1861 (Bivalvia: Cardiida: Semelidae) in the delta area of the Netherlands

Marco A. Faasse
Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands;
ecoast Marine Research, Korringaweg 7, 4401 NT Yerseke, The Netherlands; marco.faasse@ecoast.nl
[corresponding author]

Hendrik Gheerardyn
ecoast Marine Research, Korringaweg 7, 4401 NT Yerseke, The Netherlands

Claudia Morys
NIOZ Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems / Utrecht University,
Korringaweg 7, 4401 NT Yerseke, The Netherlands

Ton van Haaren
Eurofins|AquaSense, H.J.E. Wenckebachweg 120, 1114 AD Amsterdam, The Netherlands

Tom Ysebaert
NIOZ Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems / Utrecht University,
Korringaweg 7, 4401 NT Yerseke, The Netherlands;
Wageningen University & Research, Wageningen Marine Research, Wageningen, The Netherlands

Reindert Nijland
Marine Animal Ecology Group, Wageningen University & Research, P.O. Box 338, 6700 AH Wageningen, The Netherlands

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The non-indigenous bivalve *Theora lubrica* has been introduced to the southwestern delta area of the Netherlands. For several years, it has been misidentified as *Abra nitida*, a species with similar appearance. *Theora lubrica* differs from *A. nitida* in the presence of an internal ridge (from umbo to anteroventral margin) and a bifid cardinal tooth in the left valve. In native and newly colonised areas the bivalve is particularly a successful competitor at sites with periodical hypoxic conditions. Ecology and invasiveness are discussed.

Key words: *Theora lubrica*, introduction, Netherlands, northwestern Europe, *Abra nitida*, oxygen, stratification

INTRODUCTION

The southwest of the Netherlands consists of a strongly modified river delta area. Freshwater influx from rivers has been diverted from most former estuaries. After a severe flooding disaster from storm surges in 1953, from 1961 onwards, several former estuaries have either completely or partially been separated from the North Sea by a dam or a storm surge barrier. The result is a region with different types of water bodies with regard to tidal influence, currents and salinity regime (Ysebaert et al., 2016). All water bodies are relatively sheltered and sediments are mainly characterized by fine/medium sand and mud. Two of these water bodies, which are of special interest here, are the tidal Oosterschelde and the non-tidal Lake Grevelingen (Fig. 1). Since 1986, the Oosterschelde is a tidal bay that is still in open connection with the North Sea, but protected against storm surges by a barrier. The Grevelingen was disconnected from the North Sea by the construction of the Brouwersdam in 1971 and is called Lake Grevelingen thereafter. A sluice connects Lake Grevelingen with the North Sea, allowing saline water to enter the lake and creating saline conditions in the lake. The absence of tides in

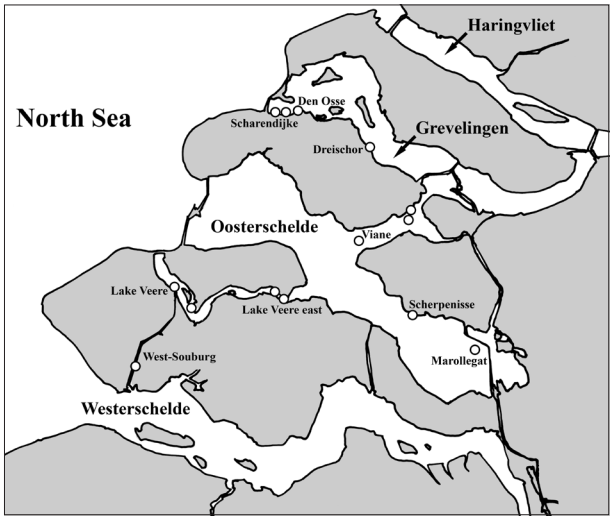

Fig. 1. Map of the southwestern delta area of the Netherlands, with locations where *Theora lubrica* has been collected.

this lake every year leads to stratification during warm and calm summer periods. Stratification results in anoxic conditions close to the sediment surface in depths greater than about 10 meter. This depth depends on and decreases with the duration of the stratification. Both the Oosterschelde and Lake Grevelingen are characterized by relatively high and constant salinities (>25).

As mentioned, Lake Grevelingen experiences regular seasonal stratification leading to oxygen depletion in bottom waters (Hoeksema, 2002; Wetsteijn, 2011). During observations of such an event on 13 August 2016, many little transparent bivalves superficially similar to *Abra nitida* (O.F. Müller, 1776) were observed on the muddy sediment surface. One specimen was collected for future reference and this bivalve was identified as *Theora lubrica* Gould, 1861, at that moment the first record of *T. lubrica* from NW Europe.

Theora lubrica is a West Pacific bivalve which has been introduced to other parts of the world. It has been reported as an introduced species from Australia (Port Phillip Bay, Victoria) in 1958 (Hewitt et al., 2004), from California (Sunset Bay) in 1968 (Seapy, 1974), from New Zealand in 1971 (Climo, 1976), from Italy (Livorno) in 2001 (Campani et al., 2004), from Israel (Haifa) in 2006 (Bogi & Galil, 2007), from the Atlantic coast of Spain (Basque Country) in 2010 (Adarraga & Martínez, 2011) and from southeastern England in 2018 (APEM, 2018). Being categorised as an invasive species, its ecological consequences are here discussed.

Because of the similarity with *A. nitida*, we considered it possible that *Theora lubrica* has been mistakenly identified as *A. nitida* in the past. Therefore, specimens in collections and photos from 2003 to 2017 labelled as *A. nitida* from the southwestern delta area of the Netherlands were studied to investigate possible earlier recordings of *T. lubrica*. Additional benthic samples taken in September 2018 with the R/V Navicula in Lake Grevelingen and Oosterschelde were screened for the presence of *T. lubrica*. In November and December 2018 additional benthic samples were taken during SCUBA dives.

MATERIAL AND METHODS

Collections and photos

The collections of Wageningen Marine Research (WMR), Royal Netherlands Institute for Sea Research (NIOZ), Eurofins|AquaSense, Rijkswaterstaat CIV, Hydrobiologisch Laboratorium and the private collection of the first author were searched for specimens labelled as *Abra nitida* from the delta area of the Netherlands. The photo collection of Eurofins|AquaSense was searched for *Abra nitida* photos from the delta area. An internet search for underwater photos of presumed *Abra nitida* by SCUBA-divers was performed.

Sampling

In 2018 samples were collected with a box core sampler or by SCUBA diving. In September 2018 benthic samples were taken with the R/V Navicula in Lake Grevelingen and the Oosterschelde using a Reinecke box core sampler with a surface area of 0.077 m². Subsequently the sediment was sieved through a 1 mm mesh sieve. The residue including the benthos was temporarily preserved in 4% buffered formol. After removing the benthos from the sediment and identification, biomass (ash-free dry weight) of the bivalves was determined by weight loss on ignition.

The SCUBA diving samples were collected in November and December 2018 in Lake Grevelingen and the Oosterschelde by scraping the uppermost surface layer (approximately 1 cm) of the sediment with two sample pots, containing a total volume of 300 ml. Hence, the surface area sampled during each sampling event covers about 0.03 m². Multiplying the number of bivalves in each sample by 33, gives a very rough estimate of density per m². Treatment of the samples was different from the boxcorer samples: bivalves were removed from the sediment on the day of sampling. Bivalves were preserved in 96% ethanol for sequencing (2 specimens on 30 November 2018 and 1 specimen on 14 December 2018) or in 70% ethanol for morphological study. Sampling details are given in Table 2.

Drawings were made with the aid of a drawing mirror on a Wild M5 stereomicroscope. Photographs were taken with a Canon 5DII camera and MP-E 65 mm macrolens.

DNA based identification

DNA was analysed from 2 specimens collected on November 30th and 1 specimen on December 14th, 2018 in Lake Grevelingen (Table 2: "seq"). For 1 specimen, soft tissue

Collection / photographer	Sampling date	Locality	Coordinates	*T. lubrica*
Coll. Eurofins|AquaSense	20.v.2003	Kanaal door Walcheren, West-Souburg	51°27'31.6"N, 3°35'27.6"E	2
Photo M.A. Faasse	06.x.2007	Oosterschelde, Scherpenisse	51°31'27.8"N, 4°5'40.9"E	1
Coll. Eurofins|AquaSense	21.ii.2008	Oosterschelde, Marollegat	51°29'3.8"N, 4°11'23.5"E	1
Coll. NIOZ	01.x.2012	Lake Grevelingen	51°44'50.2"N, 3°53'52.9"E	3
Photo Eurofins|AquaSense	03.iv.2013	Lake Veere east	51°32'33.3"N, 3°51'22.0"E	20
Coll. Rijkswaterstaat CIV and photo Eurofins|AquaSense	03.iv.2013	Lake Veere east	51°33'9.7"N, 3°50'19.1"E	13
Photo Eurofins|AquaSense	04.iv.2013	Lake Veere	51°32'4.1"N, 3°41'47.9"E	7
Photo Eurofins|AquaSense	16.ix.2014	Oosterschelde	51°37'26.6"N, 4°3'49.2"E	9
Photo M. Haarsma	25.vii.2016	Lake Grevelingen, Dreischor	51°42'30.7"N, 4°0'1.6"E	1
Private coll. M.A. Faasse	13.viii.2016	Lake Grevelingen, Dreischor	51°42'30.7"N, 4°0'1.6"E	1
Photo M. Otten	15.viii.2016	Lake Grevelingen, Dreischor	51°42'30.7"N, 4°0'1.6"E	1
Coll. Rijkswaterstaat CIV	26.ix.2016	Lake Veere	51°33'9.1"N, 3°39'58.6"E	≥1
Coll. Rijkswaterstaat CIV	13.ix.2017	Oosterschelde	51°37'19.7"N, 4°4'4.3"E	3

Table 1. Sampling dates, localities and number of *Theora lubrica* specimens found in older collections and underwater photos.

Sampling date	Locality	Coordinates	Depth (m)	*T. lubrica*	*M. lateralis*	*R. philippinarum*
18.ix.2018	Oosterschelde, Viane	51°36'24.9"N, 3°59'2.7"E 51°36'24.1"N, 3°59'1.8"E 51°36'23.6"N, 3°59'3.9"E	10	14 (2-9 mm)		
20.ix.2018	Lake Grevelingen	51°44'24.5"N, 3°51'46.6"E 51°44'24.4"N, 3°51'47.7"E	2		7 (1-2 mm)	1 (1 mm)
20.ix.2018	Lake Grevelingen	51°44'58.1"N, 3°52'22.3"E 51°44'58.4"N, 3°52'22.6"E	1-2			4 (1-2 mm)
30.xi.2018	Lake Grevelingen, Den Osse	51°44'36.2"N, 3°52'44.5"E	14	4 (2-3 mm) 2 seq		
14.xii.2018	Lake Grevelingen, Den Osse	51°44'36.2"N, 3°52'44.5"E	12-14	1 (5 mm) seq	34 (1-3 mm)	
22.xii.2018	Lake Grevelingen, Dreischor	51°42'30.7"N, 4° 0'1.6"E	10-12		2 (1-2 mm)	
27.xii.2018	Lake Grevelingen, Scharendijke	51°44'25.0"N, 3°50'2.2"E	10-12	1	5 (1-3 mm)	12 (1-3 mm)
29.xii.2018	Oosterschelde, Zierikzee	51°37'45.2"N, 3°54'27.9"E	8-10		3 (1-2 mm)	9 (1-3 mm)

Table 2. Sampling dates, localities, depth, number (and shell length) of *Theora lubrica* (seq = sequenced) and co-occurring non-indigenous bivalve species, *Mulinia lateralis* and *Ruditapes philippinarum*, from box corer samples taken during a Navicula cruise in September 2018 (three replicates per station) and samples collected during SCUBA-dives in November and December 2018.

was removed from the shell, and conserved in 96% ethanol as soon as possible after collection, the other samples were conserved in 96% ethanol inside their shells. DNA was isolated from this tissue about 6 weeks after collection 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 20 µl PCR reaction to amplify a part of the 28S gene of the genomic DNA, using Phire Tissue Direct PCR master mix (Thermo Fisher), and primers designed based on the only *T. lubrica* 28S sequence available at NCBI (sequence ID: AB746872.1), Tlubrica_28S-fw: GAACTTTGAAGGGAGAGTTCAACAG and Tlubrica_28S-rv: CACCTTTTATGGTATCTCATGAGCG. These primers will amplify a fragment of the 28S gene of 1087 bp. The amplification program was as follows: Initial denaturation, 3 min at 98°C, 33 amplification cycles of 98°C, 8 sec; 59°C, 8 sec; 72°C, 20 sec; and 2 min final extension at 72°C. The resulting PCR products were purified using the QIAquick PCR Purification Kit (Qiagen). DNA for two specimens was send for Sanger sequencing at Eurofins Genomics using their Mix2seq service. Each sample was sequenced twice, with either primers Tlubrica_28S-fw or Tlubrica_28S-rv included as sequencing primers. Resulting fw- and rv-sequences of a specimen were aligned in Geneious Prime 2019.0.4 and manually trimmed and corrected where needed.

RESULTS

Records from the Netherlands

In most of the available collections and in a number of underwater photographs from the delta area taken by different photographers, several specimens of *T. lubrica* labelled as *Abra nitida,* could be traced (Table 1). In the collection of Wageningen Marine Research, no specimens labelled as *A. nitida* from the delta area could be found. In the collection of Eurofins|AquaSense two samples containing *T. lubrica* were found. One sample from a brackish canal (Kanaal door Walcheren) near West-Souburg, collected on 20 May 2003, contained two specimens. Another sample from the eastern Oosterschelde (Marollegat) contained one specimen. In the NIOZ reference collection, a sample of 1 October 2012 from Lake Grevelingen was re-examined and found to contain 3 specimens of *T. lubrica*, labelled as *Abra nitida*. In the collection of the first author, a single specimen of *Theora lubrica* collected during a SCUBA-dive on 13 August 2016 at Dreischor (Lake Grevelingen) is present. The photo collection of Eurofins|AquaSense contains several bivalve photos from the delta area which could be identified as *T. lubrica*. These photos were taken from three samples in Lake Veere on 3 and 4 April 2013 and one from the Oosterschelde on 16 September 2014. A larger number of photos in the photo collection of Eurofins|AquaSense from Lake Grevelingen, Oosterschelde and Lake Veere showed specimens which could not be identified with certainty, but probably belong to *T. lubrica* as well. Often a trace of the internal ridge is visible. The corresponding specimens are not available because biomass has been determined by weight loss on ignition.

On a bivalve photo taken by the first author in the eastern Oosterschelde (Scherpenisse, Tholen) on 6 October 2007, the internal ridge of *T. lubrica* is visible. On a bivalve photo taken by M.J. Otten in Lake Grevelingen (Dreischor) on 15 August 2016, the internal ridge of *T. lubrica* is visible as well (Otten, 2017). On a photo taken by M. Haarsma on 25 September 2016 near Dreischor a specimen of *T. lubrica* is visible. On another photo by her, eight similar shells are visible on a bottom surface area of about 5 × 5 cm.

Analysis of box corer samples taken in Lake Grevelingen and Oosterschelde in September 2018 yielded fourteen specimens of *T. lubrica* in three box corer samples from Viane (Oosterschelde). Juveniles of 1-2 mm length of two other introduced bivalve species were found as well: seven specimens of *Mulinia lateralis* (Say, 1822) in one box corer sample from Lake Grevelingen and five specimens of *Ruditapes philippinarum* (A. Adams & Reeve, 1850) in two box corer samples from Lake Grevelingen (Table 2).

During SCUBA-dives in November and December 2018, six specimens of *Theora lubrica* were collected from two localities in Lake Grevelingen (Den Osse, Scharendijke) (Table 2). Juveniles of 1-3 mm length of two other introduced bivalve species were collected together with *T. lubrica*, namely *Mulinia lateralis* in densities up to about 1000/m² and *Ruditapes philippinarum* in densities up to about 400/m². The only native bivalve species in these samples were *Corbula gibba* (Olivi, 1792) and *Kurtiella bidentata* (Montagu, 1803), present as specimens of 3 mm at most.

Morphology

Adams' (1864) diagnosis of the genus *Theora* H. Adams & A. Adams, 1856 is very short: "Shell thin, smooth, pellucid, gaping at both sides. Hinge with an oblique cartilage-pit in each valve; primary teeth none. Valves simple within.". After the diagnosis, he further mentions the deep sinus of the pallial line. Adams (1864) established the subgenus *Theora* (*Endopleura*) A. Adams, 1864 to accommodate the single species *T. lubrica* and provided the following diagnosis: "Shell pellucid, gaping at both sides. Hinge with a bifid primary tooth in front of the oblique cartilage–pit. Valves with an internal rib extending from the beaks obliquely towards the anterior side.". He does not mention the two short cardinal teeth in the right valve.

In the NE Atlantic, *Theora lubrica* is most likely to be confused with another semelid bivalve species, *Abra nitida*. Both species have a similar elongate oval shell outline and the beaks are almost on the midline of the shell.

< **Fig. 2.** *Theora lubrica*, 13.vii.2016, Dreischor, Grevelingen, The Netherlands. Shell length 8 mm. Collection M.A. Faasse.

Fig. 3. *Theora lubrica*, 14.xii.2018, Den Osse, Grevelingen, The Netherlands. Lateral view on right side. Shell length 5 mm. Collection M.A. Faasse.

The most prominent character in which *T. lubrica* differs from *A. nitida* is the presence of a ridge on the internal surface of the valves, from the umbo in the direction of the lower frontal margin (Fig. 2). The ridge is even visible externally in living and fresh specimens (Fig. 3). A second difference is the bifid single cardinal tooth in the left valve of *T. lubrica* (Fig. 4) and the blunt cardinal tooth in the left valve of *A. nitida* (Fig. 5). The original description of *A. nitida* by Müller (1776: 245) says: "testa ovali alba, laevi, dente obtuso in utroque cardine" (translation: shell oval, white and smooth, blunt tooth on both sides of the hinge). A further difference is the more transparent shell of living *T. lubrica*. However, it should be noted that preservation in formol and/or drying decreases transparency. According to Adarraga & Martínez (2011), the umbo is close to the midline in *T. lubrica* and a little posterior of the midline in *A. nitida*. However, we find this difference less useful for routine identifications without actual measurements of the distance of the umbo to the midline.

DNA-based identification

PCR on DNA isolated from all three tested specimens yielded a fragment of a little over 1000bp, indicating good specificity of the used primers. Amplicons of two specimens were sequenced at Eurofins Genomics. The obtained consensus sequences for the 28S gene fragments after alignment, trimming and manual correction had a length of 1016 and 1015 bp respectively. Blast was used to search for homology in the NCBI nt database. The sequences were respectively 99.5% and 99.7% identical to the single *T. lubrica* 28S sequence present in the database. The next hits in NCBI nt were several *Abra* species, with a sequence homology of 94%. These results confirm the identification of the analysed specimens based on their morphological characteristics. Our newly obtained *T. lubrica* 28S sequences are deposited at Genbank, accession numbers MK510951 and MK510952.

DISCUSSION

Ecology

Theora lubrica shows several characteristic traits of an invasive species, e.g. low sensitivity to adverse conditions (pollution and low oxygen concentrations), high fecundity and short generation time (Johnston, 2005). In the native environment in Japan, *T. lubrica* is the macrobenthic species with the highest tolerance with regard to low oxygen levels during stratification in late summer (Imabayashi, 1990). Saito (2006) states that the species is an indicator for polluted or eutrophic waters. Although it has been repeatedly suggested that reproduction occurs year-round (Campani et al., 2004; Bogi & Galil, 2007), Imabayashi (1990) and Johnston (2005) found that the main period of settlement is from late spring to mid-summer. In Lake Grevelingen, *T. lubrica* occurs together with other introduced species that are particularly tolerant to low oxygen levels, such as the American bivalve *Mulinia lateralis*, the Californian sabellid worm *Euchone limnicola* Reish, 1959 and the Pacific polydorin worm *Pseudopolydora paucibranchiata* Okuda, 1937. Juveniles

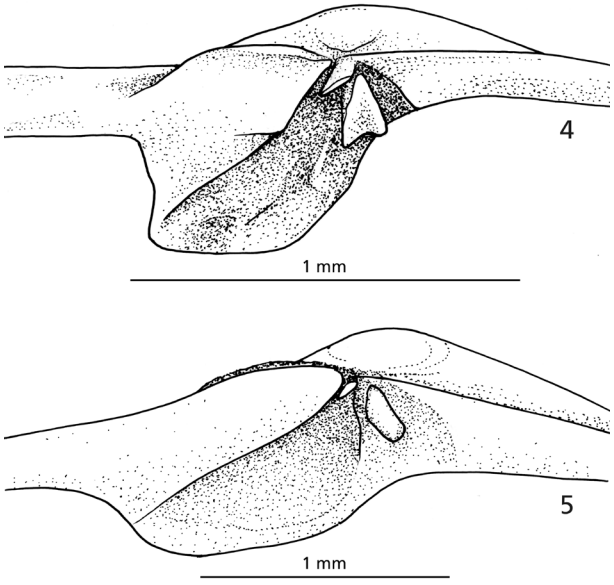

Fig. 4. *Theora lubrica*, collected 1 October 2012, Grevelingen, The Netherlands; collection NIOZ. Left valve hinge. Shell length 9 mm.

Fig. 5. *Abra nitida*, collected 12 February 2019, Friese Front (station 109), North Sea, The Netherlands; collection Rijkswaterstaat CIV, Hydrobiologisch Laboratorium. Left valve hinge. Shell length 11 mm.

of *Mulinia lateralis* were collected in December 2018 at all three localities in Lake Grevelingen where *T. lubrica* was found. *Mulinia lateralis* has recently been recorded from the Netherlands and Europe for the first time (Craeymeersch et al., 2019), and the present records further extend its known distributional range. *Euchone limnicola* was abundant at Dreischor and Den Osse in March 2016 (van Haaren et al., 2017) and at low oxygen concentrations which caused die-off of most marine life in summer and autumn 2016 and 2017 (Faasse, unpublished observations). *Pseudopolydora paucibranchiata* has been found to be highly abundant at both localities in 2017 (Faasse, unpublished observations). Reish (1955) emphasizes the hardiness of the latter species with respect to organic enrichment and pollution.

Apparently, *T. lubrica* is not restricted to areas with periodical hypoxic conditions like Lake Grevelingen. It occurs as well in the sheltered eastern part of the Oosterschelde where stratification does not exist and hypoxic conditions almost never occur. However, it does not belong to the dominant bivalves in this area.

Invasiveness

Release of larvae with ballast water is usually proposed as an explanation for the introduction of *T. lubrica* to new areas (Bogi & Galil, 2007; Adarraga & Martínez, 2011). In the Netherlands, *T. lubrica* occurs in the delta area, which is situated between two large international ports, Rotterdam and Antwerp. Not only, in its native environment (Imabayashi & Wakabayashi 1992), but in invaded areas as well, the bivalve reaches very high densities. Imabayashi & Wakabayashi (1992) found that in their study area, *T. lubrica* accounted for 61-67% of macrobenthos density, and its maximum density reached 2038 individuals per m^2 in June. In California embayments, Ranasinghe et al. (2005) found that non-native species (4.3% of a total of 633 taxa) contributed 27.5% of macrobenthic density. There, *Theora lubrica* contributed 18.2% to the density of non-native species, only third in rank after *Pseudopolydora paucibranchiata* (51.9%) and *Arcuatula senhousia* (Benson, 1842) (21.7%). Adarraga & Martínez (2011) state that *T. lubrica* belongs to the worst invasive species in Europe and in the 'Scottish List of Invasive Non-Native Species Priorities' it is mentioned as one of ten marine high-risk species (Scottish Natural Heritage, n.d.). The recent record of 27 specimens of *T. lubrica* from Lowestoft in SE England (APEM, 2018) suggests the bivalve may be more widespread in Europe than is currently known.

Status in the Netherlands

According to de Bruyne et al. (2013), *Abra nitida* has long been known from the northern section of the Netherlands' part of the North Sea and has colonised the southwestern delta area from 1985 onwards. We were unable to trace any *A. nitida* from the delta area in collections of institutions that have done research in the delta area. The few samples from the delta area in collections labelled as *A. nitida* all belong to *T. lubrica*. Therefore, the presence of *A. nitida* in the delta area should be reconfirmed. Possibly as early as 1985 (cf. de Bruyne et al., 2013), and with certainty from 2003 onwards, the species *T. lubrica* has been present in the delta area. The record from 2003 constitutes the first record from the Atlantic coast of Europe, two years after the very first record from Europe. As a vernacular name in Dutch for *T. lubrica* we propose 'vensterglasschelp'.

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