Recent findings of wild European flat oysters *Ostrea edulis* (Linnaeus, 1758) in Belgian and Dutch offshore waters: new perspectives for offshore oyster reef restoration in the southern North Sea

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ABSTRACT. The European flat oyster, *Ostrea edulis*, is an emblematic and ecologically important species that was fished to virtual extinction in Belgian and Dutch waters in the 19th century. We report on recent findings of live specimens in Belgian and Dutch waters, an indication for the presence of *O. edulis* in these waters. Though small, these relict populations provide possibilities for natural recovery of *O. edulis* reefs in Belgian and Dutch waters, provided the oyster’s habitat requirements are restored (e.g., exclusion of bottom disturbance). We suggest investigating whether a natural, yet slow, recovery using fisheries closures and gravel bed restoration is a feasible alternative to the currently envisaged human-mediated re-introduction of *O. edulis* in the North Sea. We identify and address the challenge of *O. edulis* detection and identification as an important issue blurring the true presence and distribution of oysters.

KEYWORDS. Coastal, subtidal, endangered species, restoration, recovery, benthos, invertebrates.

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Introduction

The European flat oyster *Ostrea edulis* (Linnaeus, 1758) is an emblematic species that in the past occurred in huge numbers all along most of the European coasts (*Hoeck* 1886; *Korringa* 1952; *Lambert* 1946; *Möbius* 1877; *Olset* 1883) where it formed banks, so-called oyster reefs, a typical biotope known to harbour a high biodiversity (*Möbius* 1877, 1893; *Van Beneden* 1883; *Tesch* 1910) because of their ecosystem engineering features (*Beck et al.* 2011; *Byers et al.* 2006). During the past century and a half, these beds declined massively (*Airoldi & Beck* 2007; *Korringa* 1946; *Van Ginkel* 1996), such that in the Southern Bight of the North Sea natural populations have disappeared. The species
and its habitat are now included on various lists of declining and threatened species (e.g., EC Habitats Directive (92/43/EEC); OSPAR 2009), and national actions towards its protection and restoration are being encouraged.

Prior to the 20th century, *O. edulis* reefs were known to occur in several places in the North Sea (MÖBIUS 1877; OLSEN 1883), including the Hinderbanks (Belgium: HOUZIAUX et al. 2008; LANSZWEERT 1868; VAN BENEDEN 1883) and the Oyster Grounds, a large bank northerly offshore from Terschelling (the Netherlands: MÖBIUS 1877; TESCH 1910). Oysters have always been harvested for food, but it was only from mid-19th century onwards that large scale industrial fisheries targeted these offshore reefs (HOEK 1886; KORRINGA 1946; MÖBIUS 1877; YONGE 1966).

English oystermen, for example, exploited the French part of the North Sea prior to 1862 and gradually moved into Belgian waters. Between 1868 and 1873 English oyster dredgers heavily exploited the Belgian oyster reefs to extinction (“Rapport sur l’administration et la situation des affaires de la ville d’Ostende” series available in the Municipal Archives of Oostende, Belgium). Gustave Gilson, aware of the exceptional biological richness of this site, investigated the Belgian oyster reefs between 1899 and 1910 (collection of the Royal Belgian Institute of Natural Sciences, RBINS). In that collection in the samples containing *O. edulis*, a large array of sizes, from recently settled spat to old specimens, was present (HOUZIAUX et al. 2008). This indicates that at that time settlement and reproduction still occurred but at low levels, in the remnants of the former reefs. The last scientifically documented live *O. edulis* individual was collected by Gilson in 1933 (HOUZIAUX et al. 2008) yet fishermen claim to have caught *O. edulis* in Belgian waters until 1946 (RAPPE 2008). Extensive scientific surveys undertaken since the 1970s (see e.g., CATTRUSSE & VINCX 2001) never reported live *O. edulis* in Belgian waters. The species can thus be considered virtually extinct in Belgian waters since about the mid-20th century.

In the Netherlands, local stocks had already declined as a result of intense fisheries before 1886 in most locations in and around the Wadden Sea (HOEK 1886). At that time, the far offshore Oyster Grounds still covered an area of approximately 27,000 km² in Dutch and German waters (calculated after MÖBIUS 1877 and OLSEN 1883). The spawning stock biomass of oysters must have been in the order of billions of individuals in the open North Sea (BERGHAHN & RUTH 2005; DE VOOYS et al. 2004). However, with the onset of industrial fisheries, these stocks also started to decline (HOEK 1886). Dutch fishermen, for example, landed between 11 and 18 million oysters in the North Sea in 1889 alone (BERGHAHN & RUTH 2005; DE VOOYS 2001). In the southern Dutch delta waters, oyster reefs were observed outside culture areas on the rock dumps at dikes, where trawling was prohibited (HOEK 1886). Today, some estuarine and coastal locations still have a natural oyster stock (SIKKEMA 2016), but offshore oysters are considered extinct (SMAAL et al. 2015).

Given its ecological importance and virtually extinct condition, *O. edulis* is considered a priority species for ecological restoration purposes on the North-East Atlantic Continental Shelf (e.g., ANONYMOUS 1999). In this paper we place recent findings of *O. edulis* specimens in Belgian and Dutch offshore waters into an historical context to speculate on the potential for a natural recovery of *O. edulis* reefs in the area.

**Material and methods**

Dedicated scientific diving campaigns, ship-based surveys and buoy inspections in search of hard substrate epifauna have been undertaken in various research projects in Belgium and the Netherlands since 2001 (Table 1, Fig. 1). The databases of these projects were screened for the presence of *O. edulis*. We verified the identification of the oyster specimens using internal and external morphological characters such as the presence of chomata differentiating the genus *Ostrea* from *Crassostrea* (STENZEL 1971; HARRY 1985; AMARAL & SIMONE 2014). The Belgian confirmed specimens of *O. edulis* were stored in pure ethanol, and lodged in the RBINS Marine Taxonomic Reference Centre’s collection. We
TABLE 1

Overview of recent subtidal hard substrate epifauna research in the Belgian and Dutch part of the North Sea.

| Reference                          | Location                        | Substrate type                          | Method                                | Period        | Frequency of sampling                           |
|-----------------------------------|---------------------------------|----------------------------------------|---------------------------------------|---------------|-----------------------------------------------|
| Mallefet et al. 2008              | Belgian waters                  | Ship wrecks                            | Scraping and visual inspection        | 2003–2005     | once (7 wrecks) or yearly (3 wrecks)           |
| Houziaux et al. 2008              | Hinderbanks, Belgium            | Gravel beds                            | trawling                              | 2005–2007     | Twice                                         |
| De graer et al. 2013              | Belgian offshore renewable energy zone | Wind mills, including erosion protection layer | Scraping and visual inspection | 2008–ctd.     | seasonally (until 2013), then yearly           |
| Norro A., RBINS, unpublished data | Belgian waters                  | Gravel beds and ship wrecks            | Visual inspection and scraping        | 2001–ctd.     | ad hoc                                        |
| Kerckhof F., RBINS, unpublished data | Belgian waters              | Navigational buoys                    | Visual inspection                      | 2001–ctd.     | ad hoc (upon landing, 10-20 buoys per year)   |
| Van Lancker et al. 2016           | Hinderbanks, Belgium            | Gravel beds                            | Grabs and visual inspection           | 2011–ctd.     | yearly                                        |
| Coolen et al. 2015a               | Borkum Reef Grounds, NL         | Gravel beds and rocky reefs            | Scraping, box coring and visual inspection | 2013          | Once                                          |
| Coolen et al. 2015b; Didderen et al. 2013 | Dutch, Belgian and British waters | Ship wrecks and rocky reefs            | Visual inspection                      | 2010 – ctd.   | ad hoc; at least every year on different wrecks |
| Van der Stap et al. 2016          | Dutch waters                    | Oil & gas platforms                    | Video analysis                         | 2005 – 2013   | Once for each location                         |
| Coolen 2017                       | Dutch waters                    | Oil & gas platforms                    | Scraping and visual inspection        | 2014–2015     | Once for each location                         |
| Lengkeek et al. 2013              | Dutch waters                    | Ship wrecks                            | Scraping, photo and visual inspection | 2013          | Once for each location                         |
| Bouma & Lengkeek 2013             | Dutch waters                    | Wind farm                              | Video, photo and scraping              | 2008 and 2011 | Twice                                         |
| Vanagt & Faasse 2014              | Dutch waters                    | Wind farm                              | Video and scraping                     | 2011 and 2013 | Twice                                         |
furthermore estimated the age of the Belgian specimens by counting the growth lines in the ligamental area (STENZEL 1971; RICHARDSON et al. 1993). The Dutch *O. edulis* confirmed specimens that were still available (some specimens had been combusted, and are therefore unconfirmed specimens) were placed in the Wageningen Marine Research Reference collection.

**Results**

Since the 1970s, no live *O. edulis* individuals were reported in Belgian and Dutch waters until 2010, when several specimens were found on a navigational buoy located approximately 48 km off the Belgian coast. After this first finding, *O. edulis* was detected on four confirmed and another two unconfirmed occasions (Table 2).

While *O. edulis* was detected on the Twin buoy in 2010 (853 days in the water) and 2014 (729 days), we did not find the species in 2004 (740 days), 2006 (796 days) and 2012 (575 days).

*Ostrea edulis* was detected on a piece of scrap metal recovered from the wreck of the Kilmore during a scientific diving course on July 19th 2010. The non-identified Ostreidae reported from the Kilmore in 2004 (ZINTZEN & MASSIN 2010), were reinvestigated and the small individuals (6 and 11 mm) showed no traces of chomata and thus are not *O. edulis*.

Fig. 1 – *Ostrea edulis* (Twin Buoy, 5 October 2010) and *Crassostrea gigas* (groyne Harbour Oostende, 20 March 2017). A–B. Internal view. C–D. Habitus. External view of the upper (right) valve of *O. edulis* (C) and *C. gigas* (D). Internal view of the hinge part of the upper (right) valve of *O. edulis* (A) with chomata indicated by a white arrow and *C. gigas* (B) where the white arrow points to the lack of chomata.
In Dutch waters a specimen of *O. edulis* was detected in 2012 on the Christian Huygens wreck, attached to an unidentified part of the wreck. The specimen was left *in situ* and only identified using external morphological characters. Another specimen collected in summer 2013 on the wreck of HMS Aboukir was an empty doublet that had died only recently. The valves were open, exposing the glossy white inside of the shell without any encrustations, making it obviously visible in an otherwise rather drab environment.

**Discussion**

**Problematic *Ostrea edulis* detection and identification**

False negative detections may compromise an accurate view on *O. edulis* presence. Oysters can indeed easily be overlooked by divers as their shells are usually fully overgrown by other epifouling organisms (KORRINGA 1951; SMYTH & ROBERTS 2010), thus masking their presence. This holds true for *O. edulis* individuals found on the Twin buoy and Christian Huygens wreck, where the specimens were hidden under a thick layer of Jassa turf. Furthermore, being flat and tightly glued to the surface, oysters are often noticed only after the valves are opened. Also the individual on the piece of scrap was not actually detected by the divers and its presence among the epifaunal growth was noted only later when samples were inspected in detail in the lab. The observation that divers do not necessarily detect oysters during routine sampling surveys clearly indicates that visual inspection of epifauna has to be carefully evaluated before conclusions on their absence can be drawn. While oysters were first rediscovered in Belgian and Dutch waters in 2010, they may have been present in the area before then. This assumption is further strengthened by the poor attention that was paid to hard substrate epifauna in the second half of the 20th
Historically certain recruitment described in this paper. While artificial hard substrates in offshore waters provide a suitable environment for successful larval settlement or smother the larvae shortly after settlement (Kerckhof F., unpublished data). Oysters from the Prinses Amalia wind farm (the Netherlands) originally identified as *Ostrea edulis* (Vanagt et al. 2013) proved to be *C. gigas* after closer inspection (Vanagt & Faasse 2014). Internal inspection for the presence of chomata, indicative for *Ostrea*, hence is crucial (Fig. 1), and, at least for doubtful specimens, internal inspection of the hinge region is needed for correct identification, as performed in this study.

**Possible *Ostrea edulis* source populations for Belgian and Dutch waters**

While *O. edulis* is considered virtually extinct in Belgian and Dutch offshore waters, a relict brood stock must still be present in the vicinity. *Ostrea edulis* larvae stay in the water column for only a short period of about 12–10 days at temperatures between 18° C and 20° C, even shorter at higher water temperatures (Bergahn & Ruth 2005; KorrinG & Ruth 1952), corresponding to a dispersal range of more than ten kilometres (Bergahn & Ruth 2005). Adult *O. edulis* oysters should hence be present either in the Belgian and Dutch waters, or in the neighbouring marine waters as can be deduced from the successful recruitment described in this paper. While *O. edulis* is no longer cultivated in the area, large wild individuals, caught in the eastern English Channel, are being sold in the harbours of Le Tréport (France) and occasionally Oostende (Belgium) (Kerckhof F., unpublished data) and the species still occurs in the Solent region (Harding et al. 2016). Feral populations have survived for centuries in Lake Grevelingen and the Oosterschelde (the Netherlands; Hoek 1886; Van Banning 1991; Daan et al. 2013). These three sites could be the sources of the European oysters found in Belgian and Dutch waters. However, the exact origin of the recently found *O. edulis* individuals remains unknown. Given that (1) the offshore part of the Belgian and Dutch water is under the direct influence of clear Atlantic Channel water (M’harzi et al. 1998; Lacroix et al. 2004) and (2) the residual current in the area is north-eastly (i.e., from the English Channel into the North Sea), it may be expected that the source population of the individuals in Belgian and Dutch offshore waters is to be found in the (eastern) English Channel. The recently discovered mixed *Crassostrea* - *Ostrea* oyster bed close to the Brouwersdam in the Netherlands most probably originated from nearby populations in the Grevelingen (Sikkema 2016). Further population genetic analyses may provide clarification of the origin of these populations.

**Ostrea edulis** habitat requirements in Belgian and Dutch waters

Our findings illustrate that at least artificial hard substrates in offshore waters provide a suitable environment for *O. edulis* recruitment and subsequent growth. Both Belgian sites where *O. edulis* was recently encountered are situated in Atlantic water. This water mass is much clearer than the silt-loaded coastal waters (Dauvin 2012; Brockmann et al. 1990). The historical *O. edulis* reefs in Belgian and Dutch waters, e.g., on the Hinderbanks (Lanszweert 1868) and Central Oyster Grounds (Hoek 1886; Möbius 1877), were also in offshore clear Atlantic waters. Clear water seems to be a prerequisite for successful *O. edulis* colonization as high silt concentrations in the water column and on the bottom prevent *O. edulis* larval settlement or smother the larvae shortly after settlement (KorrinG 1946). Historically certain *O. edulis* reefs were situated closer to the Belgian and Dutch coastline (Houziaux 1946).
et al. 2008; Olsen 1883), however, the siltation of these waters due to human activities (e.g., dredging and harbour wall constructions) during the last century, as suggested by Houziaux et al. (2011), may have rendered these less suitable for O. edulis.

Oysters need a hard substrate to settle and grow. In natural circumstances in Belgian and Dutch waters, this habitat was gravel beds with a certain small amount of silt that also held a large fraction of shell hash, old shells that are suitable for the settling of Ostrea-larvae. The presence of O. edulis on Belgian gravel beds was documented by Gilson (Houziaux et al. 2008). The present findings of O. edulis on artificial hard substrates (i.e., scrap metal of wrecks and buoys) may hence be considered unusual. However, Gilson also collected two hull-fouling O. edulis specimens on the Wandelaar lightship in offshore Belgian waters in 1908. They are lodged in the RBINS collection (Houziaux et al. 2008). The current reports (albeit anecdotal) of the presence of Ostrea on buoys may be explained by the need of Ostrea larvae for free space and a smooth surface to settle, which would make heavily fouled objects such as wrecks less suitable for settlement than buoys that are cleaned about once every two years. In both cases where O. edulis was detected on buoys (2010 and 2014), the specimens’ growth rings hinted towards individuals in their second growing season. This corresponds with settlement shortly after the buoys were newly deployed (June 2008 and May 2012) and hence relatively devoid of epifaunal growth.

While gravel beds are still present in the Belgian and Dutch waters (Houziaux et al. 2008; Coole et al. 2015a), O. edulis reefs have long been gone from this originally natural habitat and even individual O. edulis specimens seem no longer to occur on gravel beds in the area. The most obvious explanation for the lack of recovery in its natural habitat may be the heavy bottom-trawling fisheries that operate in these waters, physically disturbing the sediment surface preventing long-lived organisms such as O. edulis from developing to maturity.

**Possibilities for natural recovery of Ostrea edulis reefs in Belgian and Dutch waters**

Historical and recent finds of O. edulis in Belgian and Dutch waters show that, while O. edulis reefs were destroyed about a century ago, hampering subsequent successful recruitments (e.g., Gross & Smyth 1946), some O. edulis larvae still reach Belgian and Dutch waters and are able to settle and grow under the current environmental conditions. The most critical environmental condition, however, seems to be the presence of physically undisturbed, natural hard substrate such as gravel and shell hash beds. This raises the question whether exclusion of bottom-disturbing human activities would enable natural recovery of O. edulis reefs in Belgian and Dutch waters or whether active re-introduction by transplantation would be necessary. Choosing between the two options is timely given that many North Sea countries are currently making plans for O. edulis reef restoration. For example, the feasibility of recovery of native oyster stocks in Dutch waters is being explored at the request of the Dutch government (Smaal et al. 2015). Also in most other countries surrounding the North Sea similar plans are under investigation such as in UK waters (Harding et al. 2016; Laing et al. 2005, 2006) and the German part of the North Sea (Gercken & Schmidt 2014).

Even if bottom-disturbing human activities were halted near the remaining gravel beds, their condition and extent may prove to be too degraded for O. edulis recolonization. Belgian gravel beds for example suffered heavily from the removal of stones by bottom trawlers to clean up so-called “dirty” fishing grounds (Haelters et al. 2007). When considering O. edulis reef restoration, stone replacement may be a valid managerial action to upgrade the current physical condition of gravel beds, making them again suitable for O. edulis settlement and growth. Such plans are being developed or already exist in several countries, e.g., Belgium (Vande Lanotte et al. 2012: Actieplan Zeehond), Denmark (Naturstyrelsen 2013: Blue Reef) and the Netherlands (Lengknek et al. 2017).

In addition to exclusion of physical disturbance of gravel beds and potential restoration of suitable habitat for O. edulis, we suggest an in-depth investigation of the natural recovery potential of O. edulis reefs in Belgian and Dutch waters as a potentially valuable alternative to human-mediated re-introduction.
of the species. Reintroducing any species in an area always poses a risk of co-introducing parasites and diseases (e.g., Bonamia ostreae; Van Banning 1991) and genetic contamination of the local and hence possibly locally-adapted O. edulis population (Launey et al. 2002; Sanford & Kelly 2011). We, however, acknowledge that any natural recovery of the oyster reefs is likely to be slow given O. edulis larvae are short-lived and do not disperse over large distances (KorrinGa 1952). Policy initiatives such as the currently negotiated restriction of bottom-disturbing human activities in Belgian and Dutch waters (e.g., Flemish Banks and Cleaver Bank fisheries closures, respectively), could be regarded as hands-on experiments and closely monitored for O. edulis reef recovery.

In conclusion, our detection of young European flat oysters proves reproduction still takes place in the southern North Sea and/or the eastern English Channel. This suggests potential for a natural recovery of oyster beds in the area. Successful restoration of the European flat oyster beds, however, strongly depends on the availability of a sufficient number of suitable and undisturbed marine areas, where oysters can settle, grow and reproduce. That would at least imply the exclusion of seabed-disturbing activities such as bottom trawling or sand and gravel extraction. Suitable marine protected areas have to be designated and managed with the specific aim of serving European flat oyster restoration. Furthermore, these populations cannot persist in isolation and therefore the possible connectivity between the restored bed(s) and relict populations that still are present in the southern North Sea and English Channel, has to be assessed. The recently established European-wide Native Oyster Restoration Alliance (NORA) aimed at the restoration of the native European flat oyster beds, with international voluntary representation from nature conservation agencies, science institutes, non-governmental organisations as well as oyster farmers, may significantly contribute to the indispensable cross-boundary approach towards this goal.

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