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**A first record of intertidal *Ostrea edulis* 3D structural matrices in Strangford Lough Northern
Ireland - an emergent reef?**

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26 **Abstract**

27 The European flat oyster *Ostrea edulis* once settled in high densities throughout its natural
28 range but now exists only in small fragmented populations. In the Sea Lough of Strangford, Northern
29 Ireland, recent increases in intertidal oyster numbers at historical sites along the north-east shore
30 were recorded in 2018. A substantial number of conjoined oyster settlements were recorded within
31 this density increase. One intertidal site produced numerous three-dimensional (3D) *O. edulis*
32 specific matrices containing > 16 oysters. In contrast, an extensive search of post and pre-1700s
33 literature uncovered relatively few accounts of species-specific 3D *O. edulis* matrices and none
34 relating to intertidal populations. The gregarious 3D settlements discovered during this research
35 represent the first documented evidence of the phenomenon in Ireland. These emergent native
36 oyster reef structures offer an insight into the possible intertidal *O. edulis* formations, which existed
37 pre-1700 and could act as a guide to what may still be obtainable in the future.

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39 **Keywords:** 3D structure; Flat oyster; Oyster; Population; Reef; Restoration.

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51 **1. Introduction**

52 The European flat oyster, *Ostrea edulis*, once supported an immense inshore and offshore
53 commercial fishery throughout its natural range from the 1600s to the late-1800s (Yonge, 1966;
54 Laing et al., 2006). Standing stocks during this period were substantial and by the mid-1800's the
55 Thames Street Fish Market was selling >700 million oysters exclusively to London merchants in 1864
56 (Edwards, 1997). This level of exploitation could not be sustained and by the early-1900s a
57 combination of fishing intensity, disease and anthropogenic stressors resulted in the almost total
58 collapse of European stocks (Yonge, 1966). More than 100 years after this collapse, the native oyster
59 remains functionally extinct at, if not totally absent from, most of its historical sites (Smyth et al.,
60 2009; Beck et al. 2011; Lipcius et al., 2015). Consequently, numerous restoration programmes are
61 underway to address these dwindling wild stocks (Fariñas-Franco et al. 2018; Helmer et al., 2019;
62 Pogoda et al., 2019; <https://nativeoysternetwork.org/>; <https://noraeeurope.eu/>). However, as no
63 reference library exists relating to the biogenic feature forming capabilities of *O. edulis*, much
64 debate persists as to what a rejuvenation might actually look like (Mieszkowska et al., 2013).
65 Therefore, the question arises as to whether *O. edulis*, in a best-case scenario, would be capable of
66 forming interconnected 3D reef structures or solitary unattached beds.

67 It has been presumed that *O. edulis* settles near, but independently of, its neighbours and is
68 not a 3D reef building species (Korringa, 1951). However, this assumption has recently been
69 challenged with the detection of mixed *Crassostrea gigas* and *O. edulis* subtidal reefs along the Dutch
70 sector of the North Sea (Christianen et al., 2018). On the Bulgarian coast of the Black Sea, the
71 discovery of large extinct subtidal *O. edulis* 3D reef structures, known as Ostrak, also contests the
72 solitary settlement theory (Todorova et al., 2009). The Bulgarian reefs were substantial at >7 m high,
73 30-35 m long and 10 m wide with matrices created entirely from *O. edulis* valves (Micu and
74 Todorova, 2007). While local fishermen were harvesting live oysters from the Bulgarian reefs as
75 recently as 2002, there are no living *O. edulis* on these reefs today (Todorova et al., 2009). Prior to

76 these discoveries, it was questioned as to whether *O. edulis* could form 3D structures as no
77 substantial historical evidence of live formations had been recorded (Smyth et al., 2020). However,
78 in 1853 a report by Coste gives vague reference to the condition of fallowed *O. edulis* beds in
79 northern France which, ‘become coarse with barnacles and other parasites and adhere together in
80 thick beds which have to be broken up’ (Eyton, 1858).

81 If such 3D *O. edulis* reefs currently exist, they would most likely be in remote regions that
82 once accommodated abundant wild stocks and still receive a sufficient larval supply. A location
83 worthy of consideration as a possible site for 3D intertidal *O. edulis* structural settlements is the
84 small, semi-enclosed sea lough of Strangford in Northern Ireland, UK. The Lough once held a
85 historically renowned Irish stock of *O. edulis* in both the intertidal and subtidal (Day and McWilliams,
86 1991). In addition, Kennedy and Roberts (2006) and Smyth et al. (2020) recorded multiple *O. edulis*
87 attachments of up to five oysters (known locally as ‘Cloks’ where traditionally fishermen said more
88 than three joined oysters made a Clok) in remote unfished areas of the Lough.

89 Gregarious settlements of *O. edulis* generally require five key parameters; historical
90 provenance of prolific oyster assemblages, a low-flush high retention hydrodynamic regimen, larval
91 supply, suitable settlement substrate with adequate coverage and a resident fecund assemblage of
92 adult oysters (Kennedy and Roberts, 2006). Strangford Lough meets these important criteria that
93 would assist high density oyster settlements. Firstly, the Lough is a designated Marine Conservation
94 Zone recognised under European legislation and considered to be in a good state of environmental
95 health (Roberts et al., 2011). It also benefits from a zone of approximately 90 km² which is closed to
96 static and mobile fishing which is patrolled regularly by the authorities (Johnson et al., 2008).
97 Furthermore, the north of Strangford Lough possesses a mean flow < 0.15 m/s, hydrodynamic
98 conditions low enough to initiate larval pooling while also providing suitable intertidal settlement
99 substrate (Kregting and Elsäßer, 2014; Smyth et al., 2016, 2020). Moreover, the small resident
100 population of *O. edulis* estimated at < 800,000 within the 75 km² northern basin of the Lough (Smyth

et al. 2016), could produce a substantial spawning response to high sea temperatures, such as those experienced in 2014 (MCCIP, 2017), thereby creating a situation which could be conducive to mass concentrated settlements. Therefore, it was decided to quantify the abundance of 3D structural aggregations of *O. edulis* in the intertidal zone of the Lough (Fig. 1), which may have formed 3D matrices with the potential to develop into reef formations akin to pre-1700s. This information will be invaluable for restoration and conservation management decisions.

Figure 1. Historically renowned intertidal *Ostrea edulis* sites (Smyth et al. 2009) and associated substrate composition as per Smyth et al. (2018) in Strangford Lough, Northern Ireland, UK.

112 **2. Materials and Methods**

113 **2.1. Site selection**

114 Historical verification of oyster sites renowned for prolific harvests in Strangford Lough were
115 taken from the Ordnance Survey Memoirs for the Parish of Killinchy (Lewis, 1837) which identified
116 Ringhaddy Sound, Cunningburn and Greyabbey as notable locations for “the harvesting of oysters
117 from the high and low shore in both summer and winter” (Day and M^c Williams, 1991). Smyth et al.
118 (2016) confirmed that the hydrodynamics and substrate type associated with the three sites would
119 be conducive to larval retention and potential gregarious settlements. Oyster population density
120 data was also available for all three sites from 2010-2014. It was therefore decided that the lower
121 intertidal areas at Ringhaddy, Cunningburn and Greyabbey (Fig. 1) would be selected for
122 investigation.

123 **2.2 Survey Techniques**

124 Surveys were undertaken during October 2010 and November 2014 and 2018 on low spring
125 tides of <0.5 m chart datum as per the 2010 protocol established by Smyth et al., (2009). A random
126 belt transect and timed search methodology was employed at each site with sampling taking place
127 parallel to the low water mark within three 30 x 10 m plots. Multiple attachments of two or more
128 oysters were recorded both as size of individuals measured from the umbo to the ventral front edge
129 of the shell using a Vernier caliper to the nearest mm and as total number attached.

130 **2.3. Data Analysis**

131 A PERMANOVA which employed a Bray-Curtis similarity matrix, with 9999 permutations was
132 used to determine the similarities of square root transformed densities of multiple
133 attachments/Cloks of oysters in relation to the factors site and year. Statistical analyses were carried
134 out using PAST 3.25[®] (Hammer et al., 2001). The age of each oyster was estimated from the size
135 data to determine the average age for Clok assemblage. All age estimates were assigned as per
136 Richardson et al. (1993).

137 3. Results

138 Two-way PERMANOVA revealed significant differences in Clok density with regards to the
 139 factors 'Site' ($F_{(2,18)} = 8.77, P < 0.001$) and 'Year' ($F_{(2,18)} = 2.51, P < 0.05$) as well as a significant
 140 interaction between the factors ($F_{(4,18)} = 4.49, P < 0.001$) (Table 1).

141

142 Table 1. Two-way PERMANOVA summary table of Clok density per site and year.

Source	Sum Sq	df	Mean Sq	<i>F</i>	<i>P</i>
Site	1.39	2	0.696	8.77	0.0001
Year	0.39	2	0.199	2.51	0.028
Interaction	1.42	4	0.356	4.49	0.0001
Residual	1.42	18	0.079		

143

144 An increase in the number of Cloks was recorded at all sites in 2018 compared to previous
 145 years (Fig. 2). The greatest abundance of Cloks across all years was observed at the Cunningburn
 146 site with the greatest number recorded in 2018 (Fig. 2) where the dominant substrate was *Mytilus*
 147 *edulis* (Fig. 1). This location also contained the highest variation in the number of oysters per Clok
 148 (Fig. 2 & 3). Cunningburn site was also the only site which produced Cloks with >4 individuals and
 149 was unique with >10 individuals per Clok recorded for the first time in 2018. Indeed, one conjoined
 150 oyster attachment at Cunningburn had >16 oysters ranging from 80-120 mm (Fig. 3d). The remaining
 151 sites of Ringhaddy and Greyabbey did not produce multiple attached settlements in quantities
 152 which could be considered as ecosystem engineers producing 3D biogenic structures.

153

154 Figure 2. Frequency of each Clok (classified by the number of live oysters attached together in a
 155 single matrix) for the categories 2 – 4, 5 – 7, 8 – 10 and >10 oysters per Clok for Cunningburn (C),
 156 Greyabbey (G) and Ringhaddy (R) sites in 2010, 2014 and 2018. Means $\pm$ SD (n = 3).

157

158 Figure 3. Digital images (a-d) from Cunningburn site (2018) showing multiple *Ostrea edulis* Cloks on
 159 a *Mytilus edulis* dominant mixed shell substrate.

160 The size of individual oysters within Clok assemblages of 4, 6 or >6 at the Cunningburn site
 161 ranged from 1 – 13 cm (Fig. 4). The average estimated age of the Clok assemblages ranged from 3.3
 162 - 9.7 years.

163
 164 Figure 4. Size of *Ostrea edulis* individuals within conjoined / Clok assemblages of > 4 oysters at
 165 Cunningburn 2018. Numbers denote the average age of Clok/multiple attachment assemblage
 166 based on Richardson et al. (1993) and letters denote every individual Clok.

169 4. Discussion

170 The European native oyster has been regarded as a bed forming bivalve with individuals
171 creating assemblages rather than as interconnected bio-structural features (Korringa, 1946; Walne,
172 1964). Recent discoveries have identified extant mixed oyster reefs in the Netherlands and extinct
173 subtidal *O. edulis* specific structures in Bulgaria (Micu and Todorova, 2007; Christianen et al., 2018).
174 However, there has been no indications of intertidal *O. edulis* specific reef formations in the UK and
175 Ireland, until now. The discovery of intertidal oyster settlements at Cunningburn clearly
176 demonstrated that there is potential for *O. edulis* to form reef formations (Figs. 2-4).

177 Literature related to *O. edulis* when densities would have existed in numbers capable of
178 forming 3D reef matrices pre-1700s, is almost absent from the archives. The few existing accounts
179 use ambiguous terminologies and do not confirm if structural matrices were formed. The lack of
180 clarity within the archives regarding *O. edulis* specific structures highlights the importance of this
181 current discovery and those of Micu and Todorova (2007) and Christianen et al. (2018). The small
182 intertidal multiple attachments discovered at Cunningburn are diminutive in comparison to the
183 extinct Black Sea reefs (Micu and Todorova, 2007). However, the discovery within the current study
184 confirms that *O. edulis* has the capability to form multiple attachments both in the intertidal as well
185 as the subtidal. Further, the variation of size within the settled assemblages show that Clok
186 formation was over numerous spawning events and not from a single spat-fall.

187 When casting doubt on the reef forming potential of *O. edulis*, the cementation and settlement
188 biology of its larvae should not be ignored as it has been shown, on numerous occasions, that
189 pediveligers favour the living shell edge of conspecifics (Korringa, 1941; Cranfield, 1973; Rodriguez-
190 Perez et al., 2019). This behavior supports previous work conducted in Northern Ireland (Smyth et
191 al. 2020). It is therefore quite plausible that in a situation when all the key settlement components
192 are in place that multiple oyster attachments could result in 3D reef-like matrices. However, in
193 Europe the current biological status of many *O. edulis* stocks would not permit the spawning

194 intensity required for high density multiple attachments. Nonetheless, it would be flippant not to
195 postulate that native oysters, during the epochs of their maximum densities, would not have created
196 expansive structures like those discovered in the Black Sea. This is also supported by the numbers
197 of oysters removed from heavily fished areas such as the Solent where ~15 million oysters were
198 fished in 1978. The oysters must have been forming reefs as the square meterage of the suitable
199 habitat would not allow for this number of oysters to be caught if there was not this kind of
200 settlement (Jensen, 2000).

201 Furthermore, misinterpretations of the historical vocabulary used to describe *O. edulis*
202 accumulations during periods of peak densities have probably added to the confusion surrounding
203 the bioengineering capabilities of the native oyster. The Irish and English Fishery Commission
204 reports of the 1800s referred to both “oyster beds and banks” (Went, 1962; Edwards, 1997). In the
205 early 1800s, oysters were said to lay as banks throughout the English Channel (Olsen, 1883). The
206 North Sea fishermen of the era stated that “oysters lay in beds” (Metzger, 1873; Houziaux et al.,
207 2008). Murie (1911) reports that in the 1870s fishermen from Essex, England were concerned about
208 the dwindling oyster banks and reefs of the Blackwater and Korringa (1951) refers to the oyster
209 banks of the Crouch.

210 An examination of the etymology of the words used to describe *O. edulis* accumulations gives
211 some insight into the subtle differences in meanings. Usage of the word bank can be traced back to
212 c. 1200 and finds its origin in both the Old Norse ‘*bank*’ and Old Danish ‘*banke*’ which refer to “a
213 rising of ground in a sea” (Fowler, 1994). The word bed originated from a Middle High German
214 interpretation of the Danish word ‘*bed*’ which meant “laying place or bottom of lake or sea” (Klein,
215 1971). Therefore, bank would suggest a raised topography formed by oysters whereas bed would
216 be the place where the oysters were found. The word reef originating from the Old Norse ‘*rif*’
217 meaning “ridge in the sea” was not commonly used to describe the European oyster but was
218 directed more towards below water rock formations which became visible at low water. However,

219 a description of the benthos relating to the North Sea oyster grounds in the 1830s describes them
220 as; “being built of oysters, knitted and interlaced with countless other invertebrates with the bottom
221 hardened as a living crust” (Orton, 1937; Houziaux et al., 2008), a narrative that could be interpreted
222 as a structured reef matrix. The lack of evidence confirming the native oyster as an active reef
223 builder is not surprising when the intensity of the dredge fishery between the 1700s and late-1800s
224 is taken into consideration.

225 The current status of *O. edulis* populations and the conditioning of the associated scientific
226 community to the prevalence of fragmented low stock assemblages has left many in the field, with
227 good reason, to doubt if *O. edulis* was ever a species capable of structural conjoined settlements.
228 However, the unique Cunningburn discovery at Strangford shows that if conditions are suitable,
229 *Ostrea edulis* has the potential to bioengineer a 3D reef matrix within the intertidal. However, the
230 debate as to whether attachments such as Cunningburn should be considered reefs or beds is
231 premature as currently, most oyster assemblages do not exist in sufficient densities to allow for
232 gregarious settlements of this nature. Nonetheless, the discoveries of this survey suggest the debate
233 of reef or bed may not be too far-off and that potentially, *O. edulis* can form reefs.

234

235

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