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Wild gregarious settlements of *Ostrea edulis* in a semi-enclosed Sea Lough; a case study for unassisted restoration

Running Head: *Ostrea edulis* unassisted restoration

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Abstract

Ostrea edulis was once prolific throughout Europe and considered as the continent's native oyster. However, *O. edulis* currently exists in small fragmented assemblages where natural unaided recovery is rarely encountered. This research identified the small semi-enclosed sea lough of Strangford on the north east coast of Northern Ireland as one of the few locations within Europe where the native oyster displayed gregarious natural rejuvenation. On close examination, four influential parameters appeared to assist in concentrated settlement; raised topographical cultch formations, shell coverage, the number of fecund *in-situ* adult's and site protection. If these components were to be combined and managed as part of reintroduction and restoration initiatives, high density settlements and self-sustaining populations may be possible. The research also identified that unregulated harvesting of intertidal *O. edulis* assemblages has the potential to seriously hinder natural recoveries. Indeed, the findings suggest that a review of policy in regards to intertidal hand gathering is necessary. However, naturally occurring high density settlements recorded during this research should be inspirational to all involved in the restoration of the native oyster.

Keywords; high density settlements, multiple attachments, native oyster, spatting pools, unregulated harvesting

Implications for Practice

- Examination of naturally occurring native oyster expansion and the parameters which permit augmentation can provide an insight into which components could be implemented to aid successful assisted restoration.
- A suite of abiotic and biotic conditions can accommodate mass gregarious *Ostrea edulis* settlements; hydrodynamics which allow water retention, adequate coverage of suitable substrate, intertidal topography which provides pool structures, *in-situ* resident adults and policing of settlement sites.
- Unregulated harvesting remains a constant threat to restoration and protection of the species needs to be implemented if a self-sustaining status is to be achieved.

Introduction

Oysters as a species have been important biogenic and economic components within estuarine, coastal and offshore habitats throughout the world (Coen & Grizzle 2007). The immensity of their topographical coverage and economic productivity supported communities for centuries (Trimble et al. 2009). The Roman philosopher Pliny describes the extensive harvesting of oysters in Brittany, France by Sergius Orata at Baiae in 95 BC (Günther 1897; Marzano 2013). In the Persian Gulf circa 250 AD Babylonian fishing fleets were commercially exploiting the pearl oyster *Pinctada radiata* (Carter 2005). The Gulf fishery developed into a considerable financial concern which was valued at £240,000 per annum in 1829, a figure which represents >£25,000,000 today. However, heavy exploitation resulted in the fishery being economically non-viable by the late 1890s (Bowen 1951). Similarly, in the United States of America during the mid-1800s, the *Crassostrea virginica* fishery was under considerable strain (Kirby 2004). In 1869 the Maryland fishery landed >150,000 tonnes of oysters worth \$5,000,000, a current market equivalent of \$80,000,000 (MacKenzie 2007). Likewise, in Europe in the mid-1800s, wild *Ostrea edulis* stocks were undergoing a comparable level of exploitation (Eyton 1958). The scale of harvesting was immense with shell piles at oyster shucking houses regularly containing >1 trillion shells (Goulletquer & Heral 1997). The global demand for oysters led to the classic overfishing scenario whereby demand outweighed resource, culminating in a worldwide collapse of stocks by the early 1900s (Korringa 1946; Thurstan et al. 2013).

The rapid large-scale removal of these primary ecosystem components resulted in several detrimental ecological consequences such as; a deterioration in water quality, an increase in invasive pest species and a prevalence of new disease (Conner & Simon 1979; Jackson et al. 2001). The anthropogenic removal of global oyster reef ecosystems was almost total with an estimated 85% loss over the last 200 years accompanied with a legacy of 85% habitat loss (Beck et al. 2011).

Governments, habitat managers and Non-Governmental Organisations have recognised and accepted that this loss has contributed to the accelerated deterioration of the ecological health of numerous marine ecoregions. As a result, a consensus now exists among concerned stakeholders that active restoration of oyster reefs should be supported and encouraged whenever possible (Alleway & Connell 2015). Indeed, the European Union has identified that biogenic oyster reefs under the Natura 2000 are habitats which require immediate protection, augmentation and restoration (Bostock et al. 2010). As the majority of historic European oyster sites are in a poor state of conservational health, any locations which retain a resident self-sustaining population could offer an important insight into environmental parameters which could be replicated to promote recovery (Carlucci et al. 2010). Presently numerous European countries are attempting to address the dwindling wild stocks through the augmentation of cultured or translocated oysters (Smyth et al. 2018; Pogoda et al. 2019).

Even though many European *O. edulis* populations are extremely fragmented and in low densities, the fecundity and life cycle of the oyster suggest that when

abiotic and biotic parameters are optimal the potential for large scale recovery should be possible (Taylor & Bushek 2008). However, rejuvenation within wild *O. edulis* assemblages is rare with only a few remote sites displaying tentative recovery. Nevertheless, those which do exist could offer valuable indicators as to what *in-situ* conditions are required to reinstate or support a restored population (Laing et al. 2006; Christianen et al. 2018). One such location worthy of investigation is the small, semi-enclosed sea Lough of Strangford on the north east coast of Northern Ireland. The native oyster fishery in Strangford Lough was once renowned throughout Ireland for its abundant intertidal and subtidal beds (Day & McWilliams 1991). The Montgomery Records of 1680 (Montgomery 1683) stated that, “the Strangford Lough beds are dredged daily with oyster clumps gathered in deep water as well as on the Lough shore”. Lewis (1837) when discussing the fishery referred to several sites that were renowned for their productivity; Ringhaddy Sound, Cunningburn Milltown and Greyabbey. However, even though Strangford possessed a significant oyster stock it experienced the same overexploitation as the rest of Europe and was considered functionally extinct by the early 1900s (Nunn 1994). Consequently only the occasional solitary individual was recorded up until the late 1990s (Kennedy & Roberts 1999). Though, in 1998 a single spawning event of an *O. edulis* aquaculture assemblage triggered an unintentional rejuvenation of the wild stock (Kennedy & Roberts 1999). The spawning resulted in the Lough’s population growing from an estimated 100 individuals to > 1.5 million in a period of five years (Smyth et al. 2009). Unfortunately, the rapid increase of wild oysters was accompanied by an upsurge in

unregulated commercial harvesting and over the following three years the population declined to <400,000 (Smyth et al. 2009). Nonetheless, the potential for gregarious oyster settlements within the Lough was established and a hydrodynamic larval tracking model confirmed the north east coast as a potential *O. edulis* larval sink (Figure 1) (Smyth et al. 2016).

The Lough has benefited from being studied since the early 1960s and is a designated Marine Conservation Zone (Roberts et al. 2011). Intense trawling activity over *Modiolus modiolus* reefs in the late 1990s was suspected of causing damage to highly diverse biotopes in the north of the Lough (NIOA 2015). As a result the local Government introduced a closed fishing zone in 2008 in an attempt to initiate natural recovery (Roberts et al. 2011). The introduction of this closed zone increased the activities of government enforcement officers and unintentionally the protection of the small remaining resident *O. edulis* assemblages.

Owing to an examination of hydrodynamic regimens in the north of the Lough, and recently reported increases in *O. edulis* densities (Smyth et al. 2009). It was decided to investigate if there had been any evidence of unassisted high density stock recovery. If verified the conditions under which recovery occurred could be examined with the potential to provide test hypotheses for replication in future restoration programmes. The criteria behind choosing the northern region of Strangford is based on the presumption that established assemblages of oysters and increased policing of the marine environment would inadvertently lead to a rejuvenation and augmentation of wild *O. edulis* stocks.

Materials and Methods

Study Area

Strangford Lough is located on the northeast coast of Northern Ireland and lies between 54° 35' N and 54° 20' N and between 5° 41' W and 5° 34' W (Figure 1) enclosing an area of 150 km². The depth ranges from 14-60 m, with substrate varying from bedrock to fine sediments (Kregting & Elsäßer 2014). The Lough can be divided into northern and southern basins. The high retention hydrodynamic regimen in the northern basin is particularly accommodating to larval pooling (Smyth et al. 2016). The entrance to the southern basin is a long, narrow channel, known as The Narrows, where current tidal velocity reaches ~3.5 m/s (Kregting & Elsäßer 2014).

Site Selection

Historical provenance, and recent oyster survey results (Day & McWilliams 1991; Smyth et al. 2009; Roberts et al. 2011; Guy et al. 2018) led to the northern basin of Strangford Lough being selected as an area of possible undetected *O. edulis* bed rejuvenation. Potential sites within the region had to meet habitat suitability requirements as previously outlined in Kennedy and Roberts (1999) these included; sufficient natural shell substrate to accommodate broad-scale settlement, an adequate number of adult oysters for the conveyance of settlement cues and hydrodynamics which would support larval retention. In studies over the preceding

12 years six sites within the northern basin were identified as meeting these requirements to varying degrees.

The sites of Ballyreagh, Cuningburn and Greyabbey consistently produced high density oyster settlements on a *Mytilus edulis* shell dominant substrate (Figures 2 to 5). Kircubbin, Pig Island and Ringhaddy were considered low density *O. edulis* sites in comparison with a predominantly mud and shell fragment substrate (Kennedy & Roberts 1999; Smyth et al. 2018). All sites were intertidal as extensive dive surveys in the region between 2008 and 2011 had shown the subtidal substrate to consist of heavy mud absent of a shell mix and therefore unsuitable for *O. edulis* larval settlement (Roberts et al. 2011). The one exception was Ringhaddy a subtidal site mentioned in the historical accounts of Lewis (1837). However, when examined in 2010 (Roberts et al. 2011) any available hard substrate had succumbed to heavy siltation leaving potential settlement surfaces in a poor state to accommodate high density larval attachments, thus the site was sampled along the intertidal only.

All sites were located in the northern basin of the lough in close proximity to a governmental Department of Agriculture sub-surface coastal monitoring buoy. The recorded physical parameters which encompassed all waters within the survey sites hydrodynamic regime included; water temperature of 2–17.6 °C, a mean salinity of 33, mean nutrient concentrations ($\mu\text{mol l}^{-1}$) of 2.8 ammonium, nitrate 13.5, phosphorus 2, and silicate 4.3 and a mean nutrient load (ton year^{-1}) of 1,202 nitrogen and 126 phosphorus (www.afbini.gov.uk/costal-monitoring).

Survey Techniques

Data collection from 2002-2014 were conducted as per those outlined in Kennedy & Roberts (1999) the protocol was replicated again in 2018. Surveys were undertaken in November during low spring tides of <0.5 m below chart datum. A random belt transect and timed search methodology was employed with sampling taking place parallel to the low water mark within three 30 × 10m plots. Digital still images were taken *in-situ* of gregarious settlement to record any *O. edulis* clusters (>2 oysters adhered together) known locally as 'clocks' (Figure 4). Oyster size was recorded *in-situ* using a Vernier® caliper with measurements taken from the umbo to the ventral front edge of the shell.

The influence of topographical variations on micro-hydrodynamics and *O. edulis* larval settlement success has seldom been researched. During the 16-year survey period, accumulations of conjoined oysters were recorded in high densities at sites where high elevations of shell cultch dipped to form depressions within the shell substrate. Therefore, a simple snap-shot topographical survey of site plots was undertaken using a Nedo® F-series builders level and two York® ranging poles. This allowed for the quantification of noticeable elevations and depressions of substrate coverage from the horizontal plane (Figure 5 a-d). An area of >3m² of elevation / depression was required at sites to be considered for analysis.

Data Analysis

Multi-variate PERMANOVA of Bray-Curtis similarity matrices was used throughout with 9999 permutations to determine the similarities of square root transformed data of single and conjoined oyster settlements per; site, year, percent shell cover /m², harvesting protection and snapshot topographical features. The total area coverage m² of conjoined oysters per site and year was also examined using the same analytical techniques. All statistical test were undertaken using PAST 3.25[©] (Hammer et al. 2001).

Results

Single Settlement

The number of single settlements over the survey period was shown to be significantly different between sites ($F = 14.58$, $P = 0.0001$). Pairwise post-hoc analysis (Table S1) identified Ballyreagh, Kircubbin, Ringhaddy and Pig Island as significantly different ($P < 0.0005$) from all sites. Differences in the number of single settlements at Cunningburn and Greyabbey proved to be non-significant ($P > 0.1$). Differences in the number of single *O. edulis* settlements per year over the survey period was shown not to be significant ($F = 1.72$, $P > 0.1$).

The most northerly site of Ballyreagh produced the highest settlement densities between 2002 and 2010 for single attachments over all five size cohorts (0-29, 30-59, 60-89, 90-119, 120-149 mm). However, settlements at Ballyreagh regressed

rapidly between 2014 and 2018. Cunningburn and Greyabbey proved to be the most prolific single settlement sites post-2010 (Figure 2). Kircubbin, Pig Island and Ringhaddy remained low density settlement sites throughout the survey period (Figure 2).

Multiple Attachment

The number of multiple attachments/clocks in relation to site during the survey period was shown to be significant ($F = 3.28$, $P < 0.005$) (Figure 3). Pairwise post-hoc analysis identified Cunningburn, Kircubbin, Ringhaddy and Pig Island as significantly different ($P < 0.05$) (Table S2).

A significant difference ($F = 2.08$, $P < 0.05$) was detected in the number of multiple attachments/clocks in relation to year, post-hoc analysis identified 2018 as the survey year which was significantly different ($P < 0.05$) (Table S3).

The total area of coverage in m^2 attributed to conjoined oyster attachment was shown to be significantly different ($F = 1.58$, $P < 0.005$) between sites. Post-hoc analysis revealed Cunningburn, Kircubbin, Ringhaddy and Pig Island to be significantly different ($P < 0.05$) in area m^2 of conjoined settlement (Table S4). Analysis of area m^2 of conjoined oyster settlement and year proved not to be significant ($F = 1.08$, $P = 0.3631$).

Percentage of Shell Coverage

The percentage of available shell substrate within a site has been recognised by numerous researchers as an influencing factor in the settlement success of *O. edulis* (Bayne 1969; Kennedy & Roberts 1999; Christianen et al. 2018). Analysis revealed a highly significant difference ($F = 5.296$, $P = 0.0001$) between the total percentage of shell cover (no differentiation was made between shell types) per site and the total density of annual oyster settlement. A pairwise post-hoc identified Kircubbin, Ringhaddy and Pig Island as being significantly different ($P < 0.05$) (Table S5).

Site Protection from Harvesting

Active site protection of commercial molluscan assemblages is a proven management measure which can deter unregulated harvesting (Crawford et al. 2010). During the surveys Cunningburn had an assemblage of *O. edulis* within a protected site. Site protection and settlement densities per site revealed a significant difference ($F = 4.041$, $P = 0.012$).

Density of Fecund Oysters (>60-150mm) in Relation to Total Density

The average total density per site of oysters considered fecund (>60mm/year 2, based on Walne 1964) was compared in relation to total overall density per site and year no significant difference was detected ($F = 8.066$, $P = 0.061$).

Substrate Topography

The survey identified four sites with topographical height variations from the horizontal plane of $> 3\text{m}^2$ in area: Cunningburn 68-72mm, Ballyreagh 27-32mm, Pig Island 10mm, Kircubbin 10-14mm. No variations in shell height from the horizontal plane were detected at Greyabbey and Ringhaddy. A significant difference ($F=3.029$, $P=0.0003$) was detected in oyster clump/clock density in relation to topographical height. Post-hoc analysis showed Cunningburn to be significantly different ($P<0.05$) from the remaining five sites and Pig Island significantly different ($P<0.05$) from Greyabbey and Ringhaddy (Table S6).

Discussion

At Strangford Lough the site of Cunningburn was identified as accommodating the most gregarious settlements over the 16 year survey period. The most prolific solitary and clumped *O. edulis* settlement areas were all located on substrate complexes dominated by shell. The lowest oyster densities were at sites where the predominant substrate coverage was mixed mud. The most northerly site of Ballyreagh showed high density settlements pre-2010 but experienced a dramatic decline post-2006 particularly within the 30-59 mm size cohort. *O. edulis* densities continued to decline at Ballyreagh throughout the survey period. With the site eventually becoming the least populated of the six by 2018. The three low density

sites, Ringhaddy, Kircubbin and Pig Island remained relatively static in regards to *O. edulis* settlements throughout the 16 year period.

One of the most striking changes in the Strangford Lough oyster population was the rapid density decline observed at Ballyreagh post-2006. Prior to 2002 (Nunn 1994; Kennedy & Roberts 1999) no historical accounts of *O. edulis* settlements existed for Ballyreagh. However, by 2004 an estimated population of >300,000 *O. edulis* had settled in densities of >30 m² (Smyth 2009) although by 2018 <20 individuals remained. Pathogen or pollution induced mortalities can be disregarded as an explanation for population decline as no empty oyster valves were recorded and shell debris would have lingered within the low-velocity, low-flush regimen. Numerous witnessed reports from members of the general public of shellfish gatherers in the vicinity of Ballyreagh between 2004 and 2006 suggest that sporadic subsistence and commercial harvesting was the overriding influencer in population declines (Smyth et al. 2009).

Oyster densities at the remaining five sites fluctuated over the 16 years though not to the extent experienced at Ballyreagh this may have been because of an increase in policing. However, it would be assumptive to attribute the maintenance of oyster densities to policing alone. It may be simply that stocks had become non-viable for harvesting due to the low Catch Per Unit Effort (CPUE). Similar harvesting scenarios have been described for other intertidally accessible species; *Amiantis purpurata*, *Cymbula granatina*, *Lucina pectinata*, *Panopea abrupta*, *Perna perno* (Kyle et al. 1997; Tomalin et al. 1998; Rondinelli & Barros,

2010). Continuous low-level subsistence gathering of at sites may be impeding recovery and keeping standing stocks stagnant. Monthly observations of accessible assemblages of market sized oysters would assist in the monitoring of shellfish gathering and give a better understanding to the population dynamics of native oysters within Strangford.

A further detrimental effect of harvesting pressure on mature oysters is the fragmentation of fecund standing stock (Rondinelli & Barros 2010). This can result in a compromised Allee effect and a decrease in successful spawns. Eventually leaving population dynamics inert and as natural mortality ensues the species eventually becomes reproductively non-functional (Marshall et al. 2003; Turra et al. 2016). Guy et al. (2018) showed that *O. edulis* is particularly susceptible to this chain of events, as a nearest neighbour of < 1.5 m brooded significantly more larvae than those with a nearest neighbour of > 1.5 m. The findings at the low-density sites and the heavily harvested site of Ballyreagh concur with Guy et al. (2018). As adult oysters were removed from the population post-2006 recruitment slowed significantly with the Ballyreagh stock virtually non-existent by 2018.

During the research a significant increase in the gregarious nature of larval settlement at Cuningburn was noticed. The site produced settlement complexes of > 16 conjoined oysters and a total area coverage of clumps within the survey plots of 6.8 m². This was unique among survey sites and represents the first documented occurrence of conjoined *O. edulis* settlements in this density in Ireland. Cuningburn had site properties similar to both Ballyreagh and Greyabbey however the volume of

post-2014 oyster clump settlements suggested site specific properties had influenced the attachments. A comparison between sites identified Cunningburn as possessing some distinctive characteristics which may have influenced the gregarious behaviour most notably; topographical shell formations, % shell substrate coverage, number of *in-situ* fecund adults and protection from harvesting.

The topographical nature of the shell substrate accumulations at Cunningburn were markedly different from the other sites. Although shell coverage /m² was similar at Greyabbey and Ballyreagh the *M. edulis* concentrations at Cunningburn formed undulating banks which created a network of large intertidal pools. These pools held the majority of oysters found at the site and appeared to have acted as natural spatting ponds. It is possible that the formations provided a containment area for larvae to concentrate in high densities thereby increasing the potential for focused gregarious settlement within these Cunningburn pools, which would have several advantages to reduce mortality. The ponds would provide protection against; air exposure over tidal cycles, low winter temperatures and visual detection from harvesters.

The use of natural spatting ponds or “polls” in oyster culture has been considerable, with records dating as far back as A.D. 43. when Romans stocked naturally occurring pools in Northern France to act as primitive mariculture systems (Horváth et al. 2012). Historically, the spatting pond was the stock enhancement technique of choice in many regions of Europe (Hedgecock & Davis 2007). However, concerns regarding the genetic fitness of the progeny, high density disease transfer

and the development of improved hatchery culture led to their demise (Lallias et al. 2010). The intertidal pool structure and high-density settlements discovered during this study present a hypothesis worthy of testing for future native oyster rejuvenation/reintroduction programmes. If a section within a restoration cultch lay was formed into an undulating bank of shell it could provide the micro hydro-dynamics suitable to replicate the larval settlement at Cunningburn.

The availability of shell, as opposed to shell type, has been shown to be influential in settlement success (Smyth et al. 2018). A significant higher density of *O. edulis* attachments were discovered at Cunningburn post-2014 when compared to other sites. In contrast to the findings of Smyth et al. (2018) the survey showed that when available, at Strangford Lough *O. edulis* pediveligers attachment material of choice was the living edge of a live oyster. Researchers have emphasised this fact previously in relation to larval settlements within Ostrediae spat (Breitburg et al. 2000; Tamburri et al. 2008).

The high density of oysters >60mm at Cunningburn and their associated conspecific chemical cues may have also had an influence on settlement behaviour (Rodriguez et al. 2019). An overview of the three hypotheses related to *O. edulis* and adult density related chemical cues can help explain. The first indicates conspecifics as the source therefore a high-density mature population is required (Keck et al. 1971). The second suggests the importance of biofilms on oyster shells, therefore high density of shell material is required (Bonar et al. 1990). The third identifies high densities of both live oysters and biofilms on shell, as producing settlement inducing

cues which act synergistically (Tamburri et al. 2008). The *O. edulis* aquaculture and mariculture sector concurs with the hypothesis of high densities of conspecifics as an explanation for increased oyster settlements (Hugh-Jones 2003; Galley et al. 2017). Oyster growers have long considered live and dead oyster valves as the most effective settlement surfaces (Yamaguchi 1994). At the Loch Ryan *O. edulis* fishery in Scotland, >100 spat have been recorded on a single live oyster (Hugh-Jones 2003). In Ireland, at the Bertraghboy fishery, >80 spat have been recorded regularly on wild *O. edulis* (Barry 1981). There are similar reports from aquaculturists throughout Europe of high density spat attachments on living *O. edulis* within hatcheries (Drinkward 1998; Culloty & Mulcahy, 2007). The findings of this present research are certainly worthy of further investigation as the densities of live adult *O. edulis* may be an important factor when attempting to establish gregarious settlement events.

The active protection from illicit harvesting at Cunningburn was considered as a dominant influence. The location of the *O. edulis* population is in close proximity to a private yacht club where trespassers onto the adjacent foreshore are actively challenged by club members. This acts as a powerful deterrent. Nevertheless, as wild stocks at other unrestricted sites decline and CPUE decrease, the concentrated assemblages at Cunningburn will become an attractive proposition worthy of trespass for unscrupulous harvesters. Unregulated harvesting events such as those described at Ballyreagh where, 300,000 individuals were removed, can have a devastating impact on a conservation project (Bostock et al. 2010; Guy et al. 2018).

Presently throughout Europe a significant amount of time, effort and finance have been committed to restoring *O. edulis* to a self-sustaining status (Helmer et al. 2019; Pogoda et al. 2019). It is vital that NGO's, Habitat Managers and Governments recognise the detrimental consequences of mass removal events and produce preventative measures to counter such actions.

Historical European native oyster regions, experience a suite of hindrances in regards to recruitment and reintroduction; a lack of effective larval density, water quality, disease, anthropogenic disturbance and substrate availability (Laing et al. 2006). The observations described during this survey have highlighted a number of aspects of *O. edulis* settlement dynamics which are not fully understood and a considerable knowledge gap exists which therefore warrant trial when investigating restorative gregarious, *O. edulis* settlements.

It may be, that historical accounts such as those described by Orton (1937) which refer to the North Sea grounds as; "being built of oysters, knitted and interlaced with countless other invertebrates with the bottom hardened as a living crust" (Houziaux et al. 2008) are beyond the capabilities of present restoration initiatives. However, the tentative high-density bed settlements and the number of clumped oysters recorded during this research should be considered inspirational to all those involved in the re-establishment of *Ostrea edulis*. As the task which was once considered almost unachievable has now been revealed as possibly attainable.

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FIGURES

Figure 1. Strangford Lough and the six survey sites with substrate constitution at sample plots.

Figure 2. Individual *Ostrea edulis* density per size cohort at sites between 2002 and 2018. (Site codes are: C- Cunningburn, B- Ballyreagh, G- Greyabbey, K- Kircubbin, R- Ringhaddy, P- Pig Island).

Figure 3. Total area m² of multiple attachment *Ostrea edulis* settlement per site and year.

Figure 4. *Ostrea edulis* clumps/clocks at intertidal pools Cuningburn

Figure 5. Lateral cross-section schematics and *in-situ* image of undulating mussel bank (*Mytilus edulis*) formations at Cuningburn site.

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a. Movement of *O. edulis* veliger and pediveliger larvae during incoming high spring tide

b. *O. edulis* veliger and pediveliger containment during the ebbing tide

c. *O. edulis* veliger and pediveliger become more densely concentrated within the intertidal mussel pools during the lowest ebb. The undulating mussel banks maintain this level of tidal retention throughout the tidal cycle.

d. Figure 5. Lateral cross-section schematics and *in-situ* image of an undulating mussel bank (*Mytilus edulis*) formation at Cuningburn.