

1 Optimising recruitment in habitat creation for the native European oyster
2 (*Ostrea edulis*): implications of temporal and spatial variability in larval
3 abundance

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15

16 **Abstract**

17 European oyster (*Ostrea edulis*) restoration often requires the timely deployment of shell habitat for
18 larval settlement. To inform this increasingly popular process, the present study investigated temporal
19 and spatial abundance patterns of *O. edulis* larvae in a rare commercial fishery (Loch Ryan, Scotland,
20 UK). Patterns in larval abundance were analysed against variability in temperature, salinity,
21 chlorophyll, oxygen, tidal/moon phase, light, date, and location.

22

23 ‘Temperature sum’ (sum total of degrees per day above 7°C) was the most significant seasonal
24 predictor of larval abundance; with a peak at 617 degree-days. Oyster larval abundance did not
25 significantly vary between oyster bed and non-bed habitats but was significantly higher in the mid and
26 near-surface part of the water column.

27

28 The findings are discussed in the context of emerging international restoration initiatives and have
29 implications for: where habitat restoration would be successful; the prediction of larval connectivity
30 between sites; and a transferable indicator to optimise shell-habitat deployment timing.

31

32 **Keywords**

33 *Ostrea edulis*, larval behavior, larval dispersal, connectivity, habitat restoration, cultch

34

35 **Introduction**

36 Native European oyster (*Ostrea edulis*) habitats once covered large areas of Europe's coastal seas
37 (Gercken and Schmidt, 2014; Fariñas-Franco et al., 2018; Pogoda et al., 2019, 2020). Unsustainable
38 demand, combined with other stressors, led to the decline of *O. edulis* throughout its range in the 19th
39 and early 20th century (Laing et al., 2005; Airoidi and Beck, 2007; Beck et al., 2011; Thurstan et al.,
40 2013). Today, *O. edulis* is listed as a 'threatened and declining species' by the Oslo and Paris (OSPAR)
41 Convention (Haelters and Kerckhof, 2009). In line with the current United Nations 'Decade on
42 Ecosystem Restoration' (UN, 2020), *O. edulis* restoration is ongoing or planned in several countries
43 across Europe (Pogoda et al., 2019, 2020). These projects aim to recover the important functional role
44 which bivalve shellfish, as ecosystem engineers and filter-feeders, played in coastal environments
45 (Coen et al., 2007; Kent et al., 2016, 2017b, 2017a; McAfee and Bishop, 2019; Lee et al., 2020; zu
46 Ermgassen et al., 2020b).

47

48 One of the most important issues to resolve for the restoration of *O. edulis* populations is the
49 optimisation of shell substrate deployment (zu Ermgassen et al., 2020a) because, after a century of
50 absence, in many cases the shell habitat has long since been lost from these ecosystems (e.g. Fariñas-
51 Franco et al., 2018). The Loch Ryan Oyster Fishery Co. Ltd (LROFC) is the last remaining native oyster
52 fishery in Scotland. Operating since 1701, LROFC is an oyster fishery of scale but is operating at an
53 historically low-level. Therefore, there is scope to enhance the fished population in Loch Ryan but
54 also to learn how to restore oyster beds elsewhere.

55

56 A key aspect of managing sessile marine species that have a planktonic larval phase, such as *O. edulis*,
57 is to better understand their larval dispersal and population connectivity (Levin, 2006; Pineda et al.,
58 2007; Gallego et al., 2013; Gormley et al., 2015; Fitzsimons et al., 2020). There is a general
59 understanding of the biological and environmental processes that may affect larval release (swarming)
60 and dispersal; however, these processes can vary greatly at different temporal and spatial scales
61 (Scheltema, 1986; Kennedy and Roberts, 2006; Pineda et al., 2007; Puckett et al., 2014). Whilst oyster
62 swarming generally occurs during summer months in Europe, it does not appear to be a simple
63 function of any one factor (Korringa, 1940). Korringa (1947) discovered the majority of Dutch larvae
64 swarming maxima occurred about 10 days after full or new moon. Furthermore, higher numbers of
65 larvae have been observed at low slack water (Korringa, 1940) or during flood tides vs. ebb tides

66 (Jessopp and McAllen, 2008). Modelling these historical data from the Oosterschelde in the
67 Netherlands, Maathuis et al. (2020) found temperature sum, day in the lunar cycle, and daily water
68 temperature together, were the best predictors for the larval abundance in a given year.

69

70 Predicting peak larval numbers is crucial for restoration projects because it informs decisions on
71 habitat (cultch) deployment. The availability of suitable substratum for larval attachment during the
72 settlement process is a key factor for determining recruitment success in oyster populations (Korringa
73 1946; Mackenzie 1970; Abbe 1988; Mann and Powell 2007). While *O. edulis* larvae are known to settle
74 on a variety of hard surfaces (natural and man-made), they have been shown to prefer certain
75 materials (Colsoul et al., 2020; van den Brink et al., 2020). Laying of shell cultch, as a form of habitat
76 enhancement, is therefore used commonly by commercial oyster fisheries and restoration
77 programmes for increasing the likelihood of spat settlement (Southworth and Mann, 1998; Colsoul et
78 al., 2020; Fitzsimons et al., 2020).

79

80 The success of cultch deployment, measured as settled larval abundance, varies. If left for too long,
81 shell material appears to be at risk of breaking down further (to a point where larvae would not settle
82 on it), being buried by sediment (Mann and Powell, 2007), or becoming covered by too much algal
83 growth (Galtsoff et al., 1930). The most effective spat collectors in a recent Dutch pilot study were
84 deployed two-three weeks after the first larvae peak (Didderen et al., 2019; van den Brink et al., 2020).
85 Similarly, Cole and Knight-Jones (1939) suggested that collectors should not be laid more than a week
86 or two before spat are due to settle, to ensure they are not covered by mucilaginous algal growth.
87 Some amount of biofilm; however, is probably required, because habitat-associated biofilms have
88 been implicated in inducing more oyster larvae to settle (Rodriguez-Perez et al., 2019). Laying cultch
89 at an optimal time point also increases the chances that it is used by the target species, and the space
90 is not taken by another species causing interspecific competition (Galtsoff et al., 1930; Cole, 1951;
91 Fitzsimons et al., 2019).

92

93 Until the 1990s many marine larvae were thought to disperse passively over wide areas, but more
94 recent research has shown larval retention occurs in various species and locations (Roberts, 1997;
95 Jones et al., 1999; Cowen et al., 2006; Levin, 2006; Gerlach et al., 2007). Laboratory based studies on
96 *O. edulis* larvae have found that larval behaviour seems to increase the likelihood of self-recruitment,
97 through increased settlement in the presence of conspecifics (Rodriguez-Perez et al., 2019) and a
98 demersal preference (Rodriguez-Perez et al., 2020), which potentially reduces dispersal distances
99 (North et al., 2008; Sundelöf and Jonsson, 2012; Puckett et al., 2014).

100

101 In the context of habitat restoration and enhancement, the present study aims to investigate the
102 temporal and spatial variation of *O. edulis* larval abundance in Loch Ryan, to inform and optimise the
103 process of shell 'cultch' deployment. It was hypothesised that: i) peak oyster larval abundance can be
104 predicted from environmental parameters, ii) that larvae show a spatial affinity with oyster bed
105 habitats, and iii) that larvae are not homogeneously distributed within the water column. The
106 expectation was that the present findings will inform restoration projects throughout the NE Atlantic.
107

108 **Methods**

109 Loch Ryan (54.933462° -5.027422°) is in the south east Lowlands of Scotland, UK and orientated on an
110 approximate north-south axis (Figure 1). It is a glacial basin with its mouth opening to the north into
111 the Firth of Clyde and the North Atlantic. The loch is approximately 13 km long and 4.8 km wide at its
112 widest point and the southern half is a shallow (< 6 m below chart datum) body of water that has
113 supported a wild fishery for *O. edulis* since at least 1701.
114

115 Weekly samples of surface, mid, and bottom water were taken at eight sites from 7 June to 24
116 September 2019, on 14 separate survey occasions using the oyster fishing vessel, *Vital Spark*. Four
117 sites were on the oyster fishing grounds off Lefnoll Point and four from sites known not to be oyster
118 beds. Sample collection was conducted during daylight hours around low tide of spring and neap tides
119 and adjusted according to weather constraints. Water samples were collected using a pump and trap
120 method (e.g. Miller and Judkins, 1981) whilst the boat was anchored with its dredge. Filter-free
121 diaphragm pumps (Whale Gulper 220) were used to pump water through pipes from the surface, mid,
122 and bottom of the water column at each sample location (Figure 2), at a mean rate of 12.5 L/min.
123 Bottom samples were taken 6 cm off the seabed. In order to sink the hose to the seabed and prevent
124 it becoming clogged with mud or seaweed, a weight, coarse filter head (1 cm slots), and skid plate,
125 was used. Surface samples were taken from a depth of 30 cm and mid-water samples from half the
126 water depth under the keel. Pumps were run for a minimum of two minutes before filtration, to ensure
127 the sample contained water from the target depth only. Water was then filtered through 90 µm
128 plankton nets (Duncan & Associates, UK, code 438 001) to ensure *O. edulis* larvae were collected with
129 minimal smaller additional plankton species: the diagonal mesh opening was approximately 127 µm
130 whilst the smallest *O. edulis* larvae measured by Loosanoff et al. (1966) was 168 x 154 µm (L x W).
131 Plankton nets were suspended over 210 L water butts, enabling 200 L of filtrate to be measured from
132 each sample as it was pumped through the net. Concentrated plankton samples were transferred from

133 the net to 50 ml containers, immediately refrigerated in a cool-box and subsequently transferred to a
134 4°C laboratory refrigerator at the St Abbs Marine Station.

135

136 Throughout the sampling period, loggers were placed in weighted gabion cages on the seabed at the
137 oyster bed and non-oyster bed sites. Loggers measured water temperature, conductivity (ONSET
138 HOBO - U24-002-C), light (ONSET HOBO - UA-002-08), and dissolved oxygen (ONSET HOBO - U26-001).
139 Conductivity loggers were standardised from water samples taken in the field and validated in the
140 laboratory with a handheld multiparameter probe (YSI ProDSS Digital Sampling System - SKU 626909-
141 1). Daily Sea Surface Temperatures (SST) were also obtained from the National Oceanic and
142 Atmospheric Administration (NOAA) ([dataset] Huang et al., 2020) and used to calculate 'temperature
143 sum' for each sampling event following Maathuis et al. (2020), i.e. the sum total number of degrees
144 per day over 7°C starting from 1st January. During sampling, sea temperature and salinity were also
145 measured on the sample pipe in-take (ONSET HOBO - U24-002-C) or from freshly pumped water (YSI
146 ProDSS SKU 626909-1, or YSI Model 85), depending on sensor availability. Chlorophyll (Turner Designs
147 HHLF FluoroSense-Chlorophyll) was measured at each location and depth sampled.

148

149 The day in the lunar cycle and tidal range were recorded for each sampling day. The day in lunar cycle
150 was categorised into three factors: spring (day 3 and 4 in lunar cycle), neap (day 9 and 10), and mid
151 (day 13 and 14) tide. Time since (before or after) low tide, latitude and longitude for each sample was
152 also recorded.

153

154 All subsequent enumeration of *O. edulis* larvae was undertaken with live larvae to aid identification
155 (see Korringa, 1940). The volume of each refrigerated sample was measured then transferred multiple
156 times between containers to mix the sample thoroughly. A minimum of three separate 1 ml
157 subsamples were pipetted into a Sedgewick rafter counting cell (Camlab, UK, Part No: 1169034). All
158 bivalve larvae, including cockle, mussel, native oyster, and saddle oyster in each subsample were
159 counted and photographed (see: Kennedy and Roberts, 2006; McGonigle et al., 2016) (Figure 3).
160 Empty shells of bivalve larvae were not included. A compound (Leica DM750) or large field microscope
161 (Leitz Wetzlar Orthoplan 894799) with microscope camera (Leica MC170 HD or Bunnell Microscopes
162 Ltd p/n 502000A-P SPCMOS) was used throughout. The grids on the counting cell were used to
163 systematically search each subsample. The average number of bivalve larvae was calculated per
164 condensed sample and scaled to mean bivalve larvae per 200 L of seawater. Morphometric
165 measurements of larvae were taken from still images using the image processing programme ImageJ
166 (National Institutes of Health and the Laboratory for Optical and Computational Instrumentation,

167 v1.51k). Measurements were taken of the greatest length of the shell parallel to the hinge (Hendriks
168 et al., 2005). Larvae in the *O. edulis* size range of 160-329 μm were assigned to 'yes'/ 'maybe'/ 'not'
169 *O. edulis* categories based on matching morphological characteristics. Each identification and
170 photographic record was independently screened by an expert with 8 years' experience in the
171 identification of oyster larvae in plankton samples (author Cass Bromley).

172

173 *Data handling and analysis*

174 R studio (version 1.0.153) and R (version 3.6.3) were used for data exploration and all analysis. The
175 presence of outliers, zero inflation, collinearity, relationships, and independence between variables,
176 was assessed with boxplots, Cleveland dotplots, frequency plots, pairplots, Pearson correlation
177 coefficients, multi-panel scatter plots, conditional boxplots, and plotting *O. edulis* counts versus time
178 and space (Zuur et al., 2010).

179

180 To inform predictions of larval abundance, Generalized Additive Mixed Models (GAMMs) were created
181 and compared in R with the *mgcv* package (Wood, 2017). A negative binomial distribution with log
182 link was used, alongside Restricted Maximum Likelihood (REML) as the smoothness selection method.
183 Sampling site and depth collection were included as random effects to allow predictions of generalised
184 larval densities, irrespective of where water samples were collected within Loch Ryan. All other
185 variables (day in year, chlorophyll, water temperature, temperature sum, salinity, light, dissolved
186 oxygen, time since low tide, tidal range) were included as smoothers, except day in lunar cycle, which
187 was converted to a factor variable with three levels, due to the limited number of moon ages on which
188 sampling occurred and was included as a non-smoothed linear effect. Variable and model selection
189 were carried out using the significance of smooth terms (approximate *p*-values and visual inspection
190 of partial effect plots), adjusted R^2 values, Akaike Information Criterion (AIC), concurvity tests (a
191 generalisation of collinearity in GAMs), prediction practicalities, and biological relevance (i.e. results
192 from Maathuis et al. (2020)).

193

194 Kruskal-Wallis rank sum tests followed by pairwise comparisons using Wilcoxon rank sum tests (due
195 to failure to meet parametric test assumptions) were used to compare larval counts, lengths, and
196 environmental variables at each sampling site and depth. An ordinal logistic regression and stepwise
197 AIC function from the *MASS* package (Venables and Ripley, 2002) in R were used to examine the
198 influence of environmental variables (oyster bed vs non-oyster bed, chlorophyll, temperature, time
199 since low tide, and day in year) and larval size on the vertical distribution of oyster larvae.

200

201 **Results**

202 The mean number of *O. edulis* larvae per 200 L water sample varied between 0 and 1,015. Salinity
203 measurements taken from each sample location varied between instruments; therefore, daily
204 averages of the salinity measurements from the seabed logging stations were used instead to
205 investigate predictors of larval abundance (see Table 1 for all variables used and their correlation
206 coefficients). Temperature sum and the day in year variables were fully correlated ($r_s = 1$, $p < 0.001$);
207 therefore, only temperature sum was used in analysis, as it is a more ecologically meaningful
208 predictor. Dissolved oxygen was also not used in the analysis, as it had a high collinearity with
209 temperature sum ($r_s = -0.82$, $p < 0.001$). Tidal range and day in the lunar cycle were slightly correlated
210 ($r_s = -0.71$, $p < 0.001$), as was tidal range and temperature sum ($r_s = -0.59$, $p < 0.001$); therefore, day in
211 lunar cycle was used over tidal range. Mean daily sea temperature taken from the logging stations was
212 not used in the models, as it had a high collinearity with the onsite water temperatures taken during
213 sampling at each depth ($r_s = 0.85$, $p < 0.001$), indicating reasonably well mixed water during the study
214 period.

215

216 The GAMM with the lowest AIC (2244.275) included temperature sum as its only explanatory variable,
217 had an adjusted R^2 of 0.182 and explained 32.8% of the deviance. Day in lunar cycle and water
218 temperature were found to not be significant ($p > 0.05$ and higher AICs). Water temperature also
219 showed some problems of concurvity with temperature sum. The raw data indicated more *O. edulis*
220 larvae at 16-18°C (Figure 4).

221

222 The first plateau of larval abundance is predicted at 481 to 511 degree days, and the peak at 617
223 degree days (Figure 5).

224

225 There was no significant difference in larval numbers (chi-squared = 3.426, $p > 0.1$, $df = 7$) or
226 environmental variables (chi-squared, $p > 0.1$, $df = 7$) between any of the sample locations, on or off
227 the oyster bed.

228

229 Larval numbers differed significantly between depths (chi-squared = 39.773, $p < 0.001$, $df = 2$), with
230 significantly lower numbers at the bottom compared to both mid ($p < 0.001$) and surface ($p < 0.001$)
231 sampling depths. There was no significant difference between the surface and mid depth ($p > 0.1$)
232 (Figure 6). There was no significant difference in environmental variable between depths (chi-squared,
233 $p > 0.05$, $df = 2$).

234

235 *O. edulis* larval length ranged from 148.053 to 283.4557 μm , indicating all larval stages may have been
236 present. There was no significant difference in larval length between depths (chi-squared = 1.947, $p >$
237 0.1, $df = 2$).

238

239 Following stepwise selection, day in year was the only explanatory variable inputted into the ordinal
240 logistic regression model that was found to have an influence on vertical distribution of oyster larvae
241 (AIC = 1027.766), but it was not statistically significant (chi-squared = 2.0289, $p > 0.1$, $df = 1$).

242 **Discussion**

243 The present study aimed to investigate the temporal and spatial variation in the abundance of *O.*
244 *edulis* larvae to inform the restoration and enhancement of oyster populations and, specifically, to
245 optimise the process of shell 'cultch' deployment. Temperature sum was the most appropriate
246 predictor for peak oyster larval abundance: occurring at 617 degree-days. Other variables had no
247 predictive potential. Therefore, the hypothesis that peak oyster larval abundance can be predicted
248 from environmental parameters was accepted. *O. edulis* larvae were distributed similarly between the
249 oyster bed and non-oyster bed sites across the loch at distances of 2-5 km. The hypothesis that *O.*
250 *edulis* larvae show a spatial affinity with oyster bed habitats in Loch Ryan was therefore rejected.
251 However, as hypothesised, larvae were not homogeneously distributed within the water column,
252 which, in agreement with other studies (e.g. Wood and Hargis, 1971; Peteiro and Shanks, 2015),
253 suggests that they are not behaving as passive, neutral particles.

254

255 Maathuis et al. (2020) modelled historical data collected daily between 1935 and 1946 by Korringa
256 (1947) from the Oosterschelde in the Netherlands. Temperature sum, day in the lunar cycle, and daily
257 water temperature were the best predictors for maximum oyster larval abundance in a given season
258 (Maathuis et al., 2020). In the present study, over one season, day in lunar cycle and water
259 temperature were not found to be significant predictors that improved the model, although, if data
260 were collected for multiple years, other factors might become significant. Nonetheless, temperature-
261 sum was clearly the strongest predictor and, since it was previously identified in the Dutch study
262 (Maathuis et al., 2020), it is very likely to be a widely transferable indicator of seasonal peaks in larval
263 abundance.

264

265 Using the Korringa (1947) data, larval peaks in the Oosterschelde occurred between 493 and 661
266 degree-days (Maathuis et al., 2020). An oyster restoration pilot in Voordelta, Netherlands used the
267 593 and 660 degree-day predictors (see Maathuis, 2018) from Oosterchelde and Grevelingenmeer
268 data, respectively, and larvae were first detected around 593 degree-days and peaks occurred within

269 11, one, and five days of the 660 degree-days prediction in three consecutive years (Didderen et al.,
270 2019). Temperature sum predictions are, however, based on a 6.75-7°C gonad development threshold
271 (Mann, 1979; Wilson and Simons, 1985) that may vary between sites. In the present study a 41 degree-
272 days difference was found with Maathuis et al.'s (2020) best model predicting a 576 degree day peak;
273 highlighting the potential need for adjusting the temperature sum predictor for site-specific responses
274 of local populations in different latitudinal and therefore climatic settings. Indeed, historically *O.*
275 *edulis* populations occurred over 30 degrees of latitude in the Atlantic with implications for local
276 adaptation to thermal range. The difference of 3 degrees of latitude between the present and the
277 previous Dutch study sites may account for some site-specific variation. By implication, changing
278 climate may also be expected to affect the temperature sum predictor in future, as well as the sex
279 ratio of *O. edulis* populations seen previously (see Eagling et al., 2018), adding to the future
280 management implications of marine protected areas (Frost et al., 2016).

281

282 There was no significant difference in abundance of oyster larvae on and off the fished oyster bed in
283 Loch Ryan. Larval dispersal depends on a range of factors, including larval behavioural adaptations,
284 current transport, and water mixing (Korringa, 1940; Wilson, 1987; North et al., 2008; Sundelöf and
285 Jonsson, 2012; Smyth et al., 2016; Rodriguez-Perez et al., 2020). However, the homogeneous
286 distribution of larvae contrasted with the eastern distribution of adult oysters in Loch Ryan (which is
287 well known to the active fishers (LROFC pers. comm.)). Tidal flow floods SE and ebbs NW in the loch,
288 with peak tidal flows between 0.4 and 0.7 ms⁻¹ (neap vs spring tides), and a residual SE displacement
289 of 1.5 to 2.4 km respectively (Cefas and Food Standards Agency Scotland, 2013). Sediment suspension
290 models also show a residual southern flow adjacent to the eastern shore then clock-wise round the
291 loch (Royal Haskoning, 2012). The apparent homogeneous *O. edulis* larvae distribution on and off the
292 oyster beds is consistent with their negligible horizontal swimming ability (Rodriguez-Perez et al.,
293 2020) and the moderately high tidal flows that appear to have dispersed them in this case.
294 Furthermore, the distribution of oyster larval in the water column may have added to their wider
295 dispersal off the bed.

296

297 The vertical distribution of oyster larvae was not homogenous, with a greater number of larvae found
298 at the surface and mid-water depths compared to bottom waters. No variables measured (day in year,
299 oyster bed vs non-oyster bed, chlorophyll, temperature, time since low tide, or larval length)
300 significantly explained the difference in vertical distribution. The importance of chlorophyll and
301 temperature in the vertical distribution of bivalve larvae has been seen elsewhere (Raby et al., 1994;
302 Thomas et al., 2012), but in the present study, no stratification was indicated by differences in

303 temperature or chlorophyll, and it would not be expected with the tidal flows and shallow waters of
304 the site. Whilst models of *Crassostrea virginica* larvae in well mixed water, predicted greater numbers
305 of small larvae to be found closer to the surface and larger larvae in the lower regions of the water
306 column (Dekshenieks et al., 1996), this was not observed here. Independent of larval stage, in previous
307 laboratory studies *O. edulis* larvae, were most often located very close to the bottom (Rodriguez-Perez
308 et al., 2020), but they can only control their behaviour in the water column if current speeds are below
309 0.5 ms^{-1} (Finelli and Wethey, 2003; Peteiro and Shanks, 2015), and, clearly this is not always the case
310 in Loch Ryan. At this site, actions that contribute to demersal larval behaviours may be overwhelmed
311 by the prevalent tidal conditions. As observed with *C. virginica*, larvae may have propelled themselves
312 upwards in response to strong turbulence and waves, which is representative of sheltered tidal inlets
313 and estuaries (Fuchs et al., 2015) and therefore likely to be a characteristic feature of Loch Ryan. It is
314 also possible that the rugosity of the Loch Ryan oyster bed was insufficient to increase the benthic
315 boundary layer and facilitate demersal larval retention (*cf* Whitman and Reidenbach, 2012), because
316 the area had been fished within the last year; and dredging is known to reduce the complexity of
317 shellfish habitats (Cook et al., 2013). Styles (2015) showed that for *C. virginica* beds, the physical
318 bottom roughness is equal to five times the average height of the oysters. Elsewhere, Folkard and
319 Bouma (2016) found higher mussel (*Mytilus edulis*) density increased turbulence and downward-
320 mixing of planktonic food, whilst Kitsikoudis et al. (2020) showed the drag coefficient associated with
321 bed shear stress in *C. virginica* oyster reefs was almost twice that of degraded reefs and almost an
322 order of magnitude greater than those observed at sand and mud beds. Overall, the fished moderate
323 tidal habitat in the present study may not provide the conditions required to observe retentive,
324 demersal larval behaviours reported in the laboratory. Indeed, there are very few examples of
325 undisturbed *O. edulis* habitats; most are small in scale compared to historical records and at relatively
326 low densities (Pogoda et al., 2020).

327

328 **Conclusion**

329 Overall, the present study shows that temperature sum is a transferable indicator of peak oyster larval
330 abundance. This is important in the context of oyster restoration management because the timely
331 deployment of appropriate habitat to encourage settlement is a balance between early deployment,
332 with colonisation by competitors, and late deployment that does not allow for the sufficient
333 development of attractive biofilms or the larvae of the target species no longer being present (e.g.
334 Rodriguez-Perez et al., 2019; Colsoul et al., 2020 and references therein). There is emerging evidence
335 that optimisation of habitat deployment timing can make as much as a threefold difference to
336 subsequent recruitment of planktonic larvae in some temperate biogenic habitats (Cook et al., 2021).

337 Furthermore, from the present study, the restoration of habitats within 5 km of a natal bed in a
338 moderate tidal flow setting ($> 0.5 \text{ ms}^{-1}$) might be expected to receive a reasonably homogeneous larval
339 supply. Whether habitat restoration would be successful at such sites would also depend on survival
340 (e.g. seabed dynamics, predation, protection from harvesting), growth (phytoplankton and suspended
341 particles), reproduction (e.g. density of fecund oysters), and subsequent continued recruitment (e.g.
342 linked to percent shell cover, presence of conspecifics) (e.g. Kennedy and Roberts, 1999; Kamermans
343 et al., 2018; Fitzsimons et al., 2019; Smyth et al., 2020). Indeed, a spatfall survey conducted in 1999
344 showed good recruitment both on and off the main oyster bed in Loch Ryan (Hugh-Jones, 2003).

345

346 Finally, the potentially retentive demersal behaviour of oyster larvae seen in previous laboratory
347 experiments is not apparent in the present tide-swept study site and deserves closer investigation,
348 since the variation in vertical distribution seen here nevertheless implies that larvae are not behaving
349 as passive neutrally dense particles and this has implications in predicting the connectivity and longer-
350 term resilience of restored populations (e.g. Gormley et al., 2013; Rodriguez-Perez et al., 2019, 2020).

351

352 If the ambitions of a decade on Ecosystem Restoration (UN, 2020) are to be realised in the marine
353 environment, optimisation studies of habitat restoration, such as those presented here, are important
354 pre-cursors to habitat restoration work 'at-scale' and has the potential to significantly increase the
355 likelihood of successful outcomes.

356

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373

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614

615 **Figure captions**

616 **Figure 1.** Water sample (o = on the oyster bed, x = off the oyster bed) and logger (s) locations in Loch
617 Ryan, Scotland, UK.

618

619 **Figure 2.** Water sample collection schematic.

620

621 **Figure 3.** A) Water sample collection aboard *Vital Spark*. B) Different species of bivalve larvae collected
622 on 2019/07/11 from surface water of a non-oyster bed site; three identified *O. edulis* marked with *.
623 C) Confirmed *O. edulis* larva collected on 2019/07/26 from the middle of the water column at an oyster
624 bed site. D) Adult oyster (*Ostrea edulis*), circled, at Leffnol Point sampling site with associated epifauna
625 (Photo Richard Shucksmith).

626

627 **Figure 4.** Number of *Ostrea edulis* larvae at each sea temperature during the summer of 2019 in Loch
628 Ryan, Scotland. Data from three depths at eight sites.

629

630 **Figure 5.** *Ostrea edulis* larvae abundance predictions for temperature sum (solid line), shown with
631 standard error estimates (dashed lines), and raw data collected from Loch Ryan in 2019 (dots).

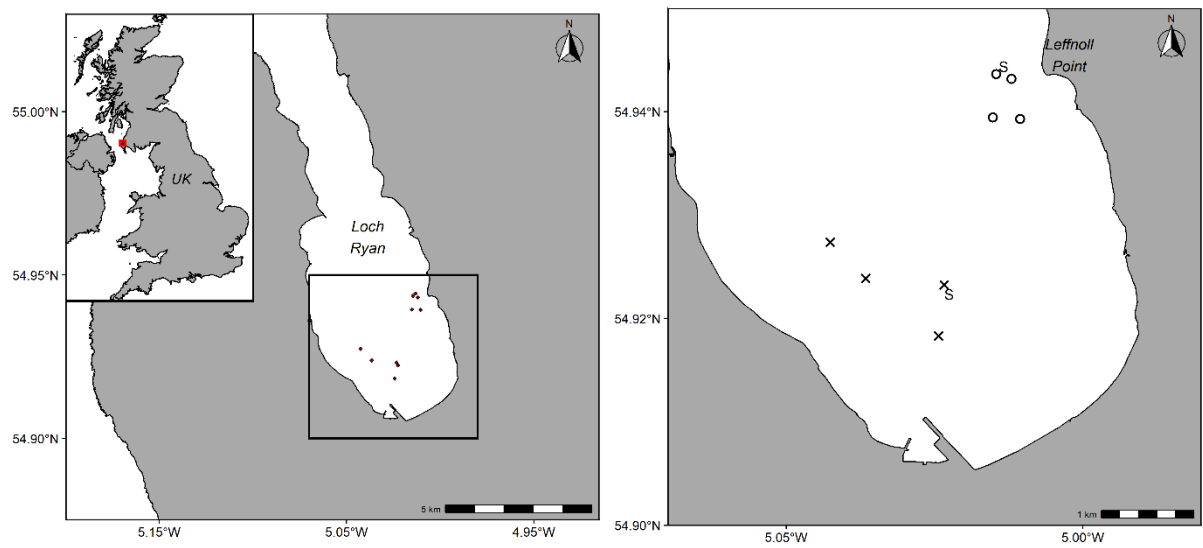
632

633 **Figure 6.** Vertical distribution of *Ostrea edulis* larvae at three different depths in Loch Ryan, Scotland.
634 Depths that differ in A/B notation were significantly different ($p < 0.001$).

635

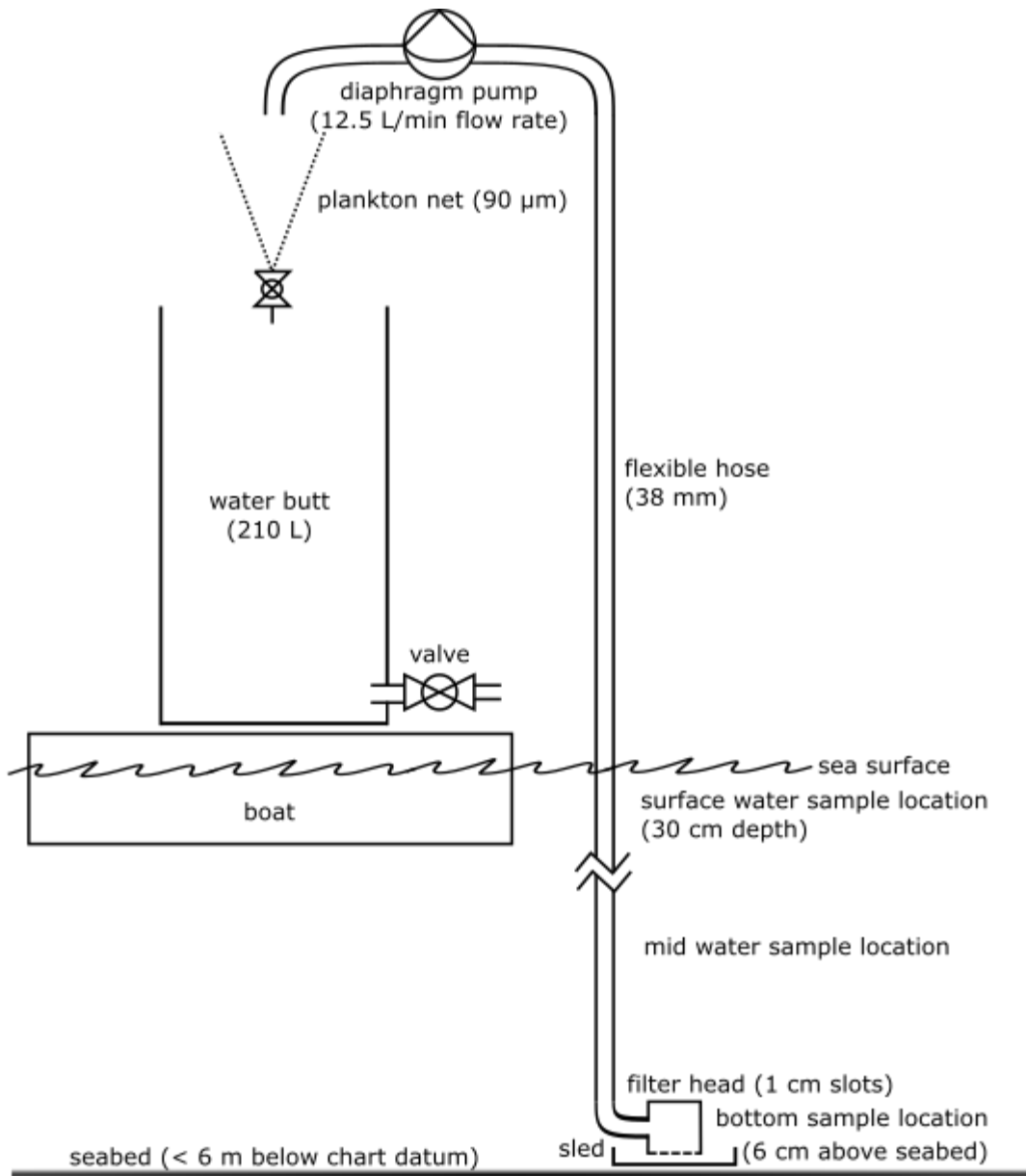
636 **Figures**

637



638

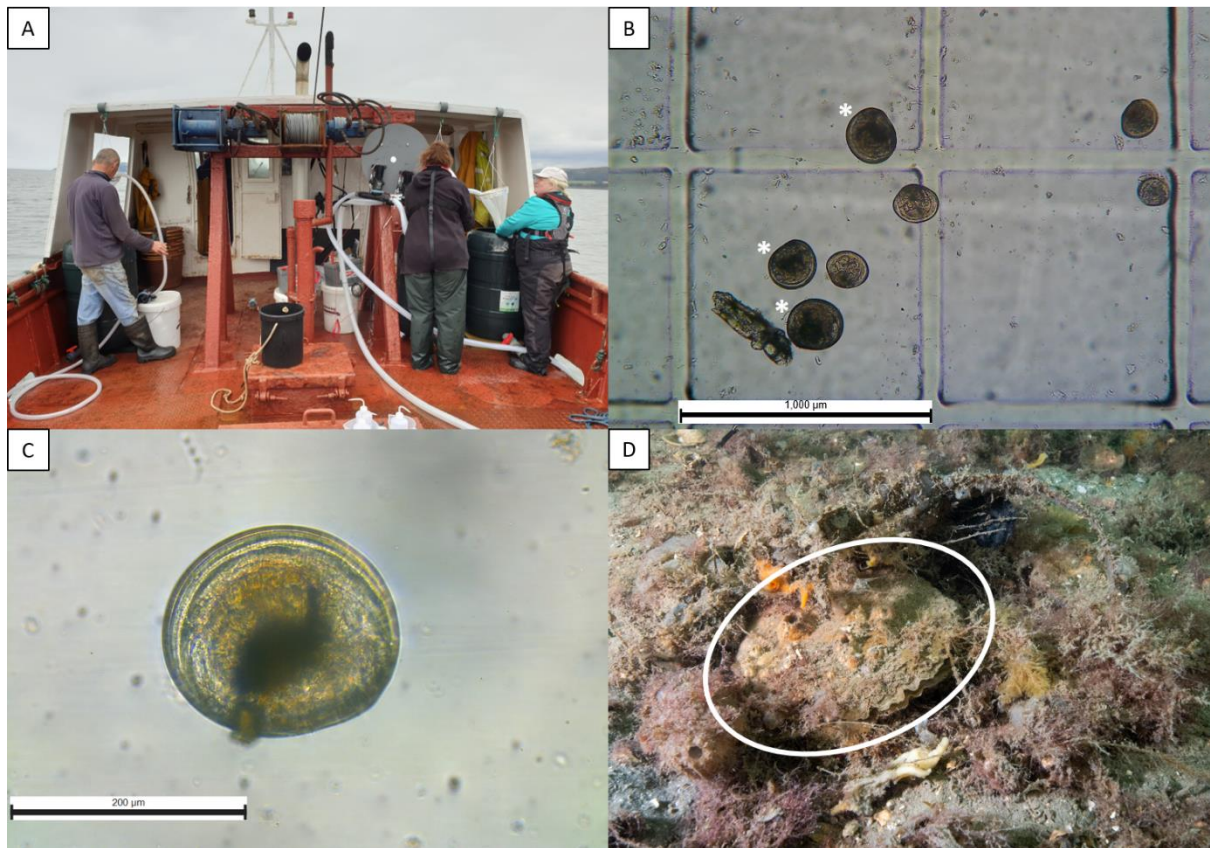
639 **Figure 1 (2 columns)**



640

641 Figure 2 (1 column)

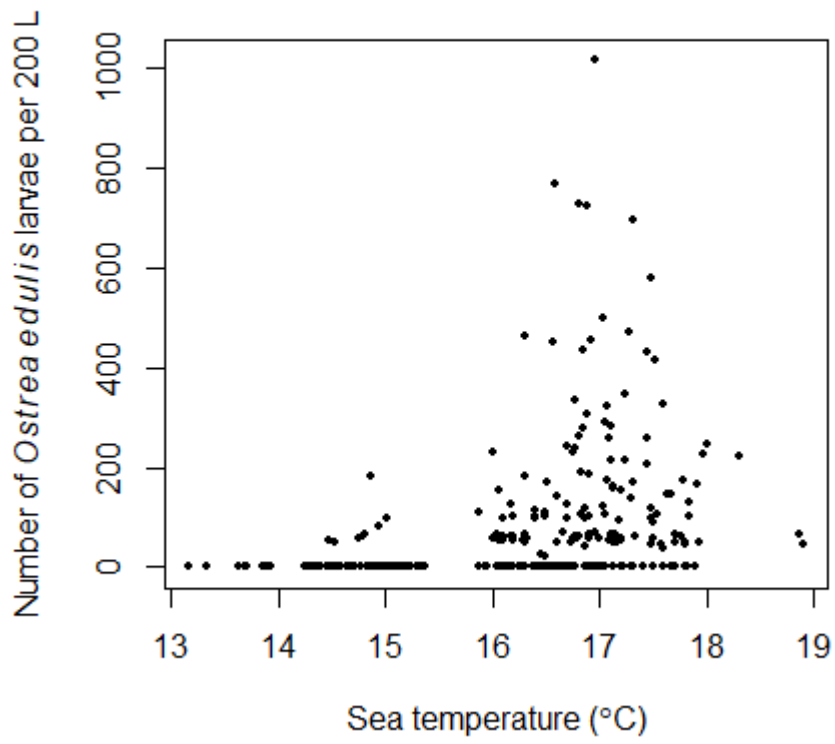
642



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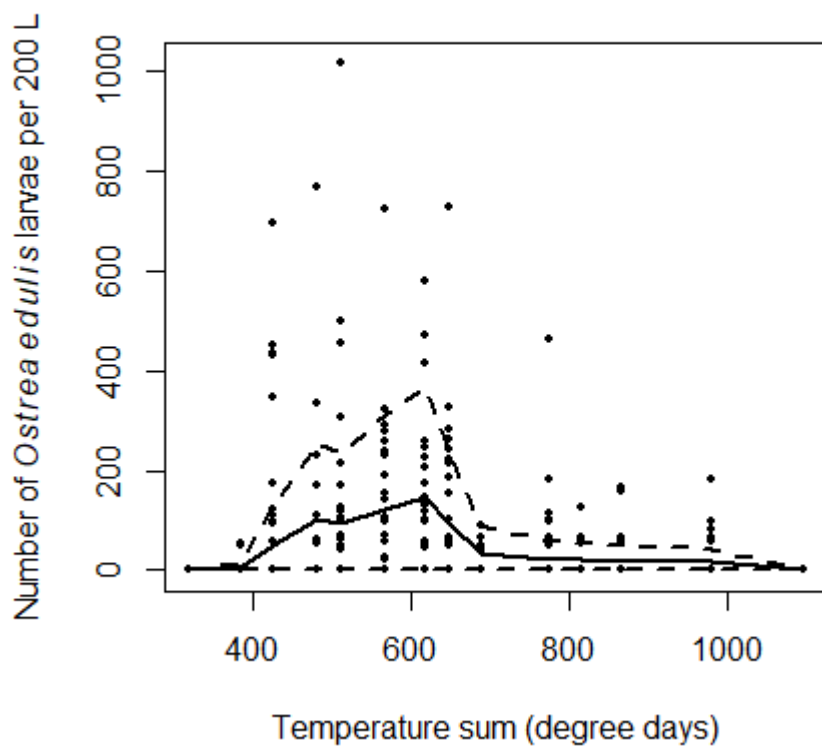
644 Figure 3 (2 columns)

645



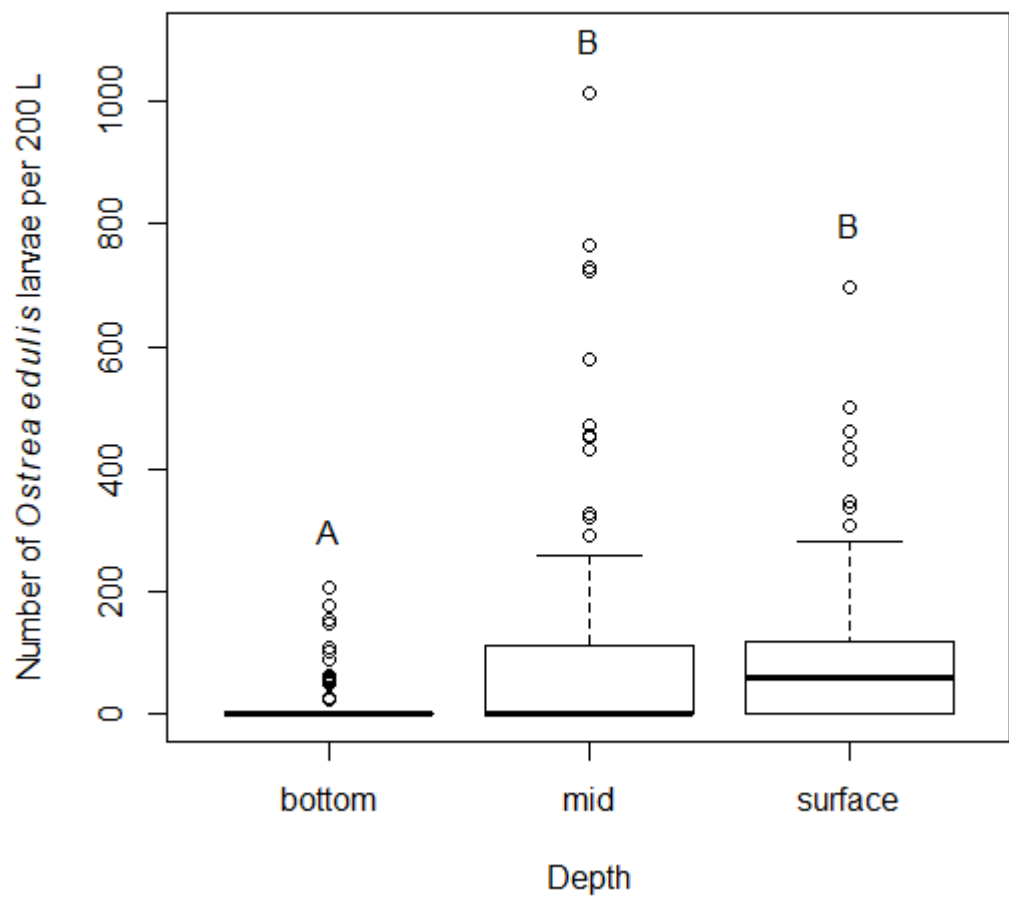
646

647 Figure 4 (1 column)



648

649 Figure 5 (1 column)



650

651 Figure 6 (1 column)

652 **Table captions**

653

654 **Table 1.** Spearman's rank correlation coefficients. p-values shown as *** 0-0.001, ** 0.001-0.01, *
655 0.01-0.05, + 0.05-0.1, no symbol 0.1-1.0. Shaded cells indicate variables used in the Generalised
656 Additive Mixed Model (GAMM) and bold text indicates higher correlation values used for variable
657 selection.

Variables	Day in year	Chlorophyll	Water temperature	Temperature sum	Logger salinity	Logger temperature	Light	Dissolved oxygen	Day in lunar cycle	Time since low tide	Tidal range
Day in year		0.09 +	0.02	1 ***	0.06	0.26 ***	-0.55 ***	-0.82 ***	0.41 ***	-0.14 *	-0.59 ***
Chlorophyll			-0.05	0.09 +	0.02	0.07	-0.33 ***	-0.23 ***	0.31 ***	-0.03	0.07
Water temperature				0.02	0.23 ***	0.85 ***	-0.09	-0.20 ***	0.14 *	0.01	0.03
Temperature sum					0.06	0.26 ***	-0.55 ***	-0.82 ***	0.41 ***	-0.14 *	-0.59 ***
Logger salinity						-0.04	0.20 ***	-0.01	-0.11 +	-0.03	-0.01
Logger temperature							-0.31 ***	-0.43 ***	0.21 ***	-0.01	0.06
Light								0.72 ***	-0.36 ***	0.20 ***	0.19 ***
Dissolved oxygen									-0.40 ***	0.16 **	0.31 ***
Day in lunar cycle										-0.15 ***	-0.71 ***
Time since low tide											0.16 **
Tidal range											

