

1 **Environmental factors associated with invasion: modeling occurrence data from a**
2 **coordinated sampling programme for Pacific oysters**

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16

17 **Abstract**

18 Documenting establishment and spread of invasive species requires extensive co-
19 ordinated sampling programmes. Identifying the factors promoting or inhibiting local
20 establishment of an invasive species can improve capacity to predict further spread and
21 underpin strategies to limit spread. Here, a structured sampling programme was used to
22 assess the current distribution of feral populations of Pacific oysters, *Crassostrea gigas*,
23 in Ireland. Sixty-nine sites were sampled using a standardised protocol combining semi-
24 quantitative and quantitative approaches. Sites were chosen to represent variation in
25 proximity to aquaculture and a range of environmental variables. Oyster populations
26 were found at 18 locations, with densities ranging from single individuals to nine
27 individuals per m². The broad size range of oysters found is indicative of more than one
28 recruitment event. Logistic regression indicated that feral oysters were positively
29 associated with the presence of hard substrata or biogenic reef, long residence times of
30 embayments and large intertidal areas. There was also a tendency for oysters to occur
31 disproportionately in bays with aquaculture, but > 500 m from it. Small-scale analysis
32 within sites showed that oysters were almost exclusively attached to hard substrata and
33 mussels. The approach taken here provides a rigorous repeatable methodology for
34 future monitoring and a detailed basis for the prediction of further spread.

35

36 Keywords: logistic regression, environmental variables, *Crassostrea gigas*, aquaculture

37

38 **Introduction**

39 Improving our knowledge of distributions of non-native species assists predictions of
40 spread and allows strategic targeting of management actions for their control (Anderson
41 et al. 2003; Gormley et al. 2011; Simberloff and Rejmánek 2011). Species' distributions
42 are not easy to predict because they are controlled by many factors acting upon different
43 life stages, e.g. hydrodynamics and tides can influence the delivery of spat (Roughgarden
44 et al. 1988; Gaines and Bertness 1992; Dunstan and Bax 2007) whereas habitat
45 availability is important for settlement (Travis and Dytham 1999; Kinlan and Gaines
46 2003) and post-settlement mortality can strongly affect recruitment (Minchinton and
47 Scheibling 1993; Hunt and Scheibling 1997; Jenkins et al. 2009). Furthermore, propagule
48 pressure plays a major role in the early stages of an invasion (Lockwood et al. 2005;
49 Johnston et al. 2009).

50

51 Distributions of invasive species are often documented in a rather fragmented and
52 descriptive way and data are often collated from a number of sources and can be of
53 mixed quality and resolution (Ruiz et al. 2000; Zaniewski et al. 2002; Elith et al. 2006;
54 Hulme and Weser 2011). Interpreting such data requires synthesis and meta-analysis
55 and does not yield unequivocal tests of hypotheses about factors associated with
56 colonisation by the species. It is recommended to use well-designed survey data and
57 analyse functionally relevant predictors (Elith and Leathwick 2009; J Elith unpublished).
58 Thus, extensive coordinated surveys and monitoring and assessment programmes using
59 carefully standardised protocols and well thought-out designs are preferable as they
60 avoid survey bias and result in balanced comprehensive datasets. When a set of sites has
61 been surveyed and presence/absence or abundance has been recorded, generalised
62 linear models encompassing logistic regression are especially useful as additive
63 combinations of predictors and manually selected interaction terms representing

64 interactions between predictors can be included (Elith and Leathwick 2009; Franklin
65 2009).

66

67 Species distribution models (SDM) estimate the relationship between species and spatial
68 and/or environmental characteristics and are widely used to estimate current and
69 potential distributions of species (Elith et al. 2006; Franklin 2009). They have been
70 widely used in terrestrial ecosystems but applications for distribution of species in
71 marine habitats are sparse (Kelly et al. 2001; Garza-Pérez et al. 2004; Beger and
72 Possingham 2008; Robinson et al. 2011). Additionally, including measures of
73 introduction effort is important for assessing on-going biological invasions or for
74 identifying areas that are susceptible to invasion (Herborg et al. 2007; Therriault and
75 Herborg 2008).

76

77 Since the 1980's, world aquaculture production has grown steadily by an average of 9%
78 per year (FAO 2012a). It now produces almost half of the fish and shellfish consumed by
79 humans and will continue to expand in the future (Duarte et al. 2009; FAO 2012a). The
80 expansion of aquaculture also brings with it an increased risk of establishment of wild
81 populations of non-indigenous species.

82

83 The Pacific oyster (*Crassostrea gigas*, Thunberg 1793) has been introduced for
84 aquaculture to many parts of the world and has become one of the world's main
85 aquaculture species (FAO 2012b). In many locations, wild oyster populations became
86 established soon after oyster farming had commenced (Diederich et al. 2005; Brandt et
87 al. 2008; Melo et al. 2010; Troost 2010), often in shallow, enclosed bays, where larval
88 retention might be high. Invasive populations can now be found worldwide in a range of
89 habitats, from coastal sheltered soft-sediment environments to exposed rocky shores

90 (Reise 1998; Diederich 2005; Ruesink et al. 2005; Nehls et al. 2006; Troost 2010). They
91 can have substantial impacts, including saturation of the carrying capacity of estuaries,
92 alterations of habitats and changes in benthic and pelagic communities, food webs and
93 ecosystem processes (Ruesink et al. 2005; Cognie et al. 2006; Troost 2010; Eschweiler
94 and Christensen 2011; Green et al. 2012). Given its rate of spread, there is an urgent
95 need to characterise its pattern of establishment at an early stage and determine which
96 factors are associated with its presence or absence and spread.

97

98 Increasing temperatures have been associated with the spread of Pacific oysters in
99 Europe (Diederich et al. 2005). The northern boundaries of its distribution are
100 expanding, with populations becoming established in England and Wales (Couzens
101 2006), Northern Ireland (Guy and Roberts 2010) and Scandinavia (Wrange et al. 2010).
102 There have also been reports of individuals in the wild in Ireland, where Pacific oysters
103 are extensively farmed around the north, the west and south coasts (Browne et al. 2007),
104 however, the size and distribution of these populations is not yet known.

105

106 In this study, a coordinated national sampling programme was undertaken using a cost-
107 effective, but rigorous and repeatable sampling protocol. It was used at selected sites to
108 firstly, document the current distribution and abundance of Pacific oysters in Ireland
109 and, secondly, build a model using the factors that might be associated with their
110 settlement in the wild. Factors considered here were: embayment residence time,
111 habitat type, wave exposure, distance from aquaculture, latitude and intertidal area. The
112 approach undertaken here might not only improve prediction of the future spread of
113 Pacific oysters but will be broadly applicable to other benthic marine invaders with
114 planktonic larval dispersal.

115

116 **Methods**

117 *Sampling programme*

118 A sampling programme was undertaken from May until September 2009 at 69 sites
119 around the coast of Ireland (coordinates provided in Online Resource 1). The sites were
120 selected to represent variation in distance from aquaculture, latitude, wave exposure,
121 embayment residence time, intertidal area (shore width) and habitat type (Table 1 and
122 Online Resource 1). Sites ranged in area between approximately 3500 m² (narrow rocky
123 shores) and 40000 m² (mussel beds) and salinities ranged between 22.5 and 35 psu.

124

125 Sites were visited and sampled during spring low tides. The sampling methodology was
126 designed to be flexible, repeatable and efficient. *Phase 1* of the methodology involved a
127 timed semi-quantitative sample of oysters at each site and a simple characterisation of
128 the habitats available at that site. It could be completed within 40-45 min maximising
129 the number of sites it was possible to visit in the available time. *Phase 2* was only used at
130 sites where oysters were found. It involved a more detailed quantitative survey of the
131 area of greatest density of oysters to enable comparisons among sites and between
132 present and future surveys. In addition, it also provided the basis for analyses of small-
133 scale associations between oysters and features of the biotic and abiotic environment.
134 Further details of these phases are provided below.

135

136 *Phase 1:* At each site the first 40-45 min were spent identifying the habitat types in the
137 lower intertidal, searching for Pacific oysters within those areas and assessing their
138 abundance using the SACFOR scale (Connor et al. 2004). The abundance categories used
139 were: Superabundant (100-999/m²), Abundant (10-99/m²), Common (1-9/m²),
140 Frequent (0.1-0.9/m²), Occasional (0.01-0.09/m²), Rare (< 0.009/m²) and Absent. After
141 the timed search, each location was classified using a modified EUNIS framework of

142 habitat types (Connor et al. 2004) to better describe the types of substratum
143 encountered in the habitats studied here. The modified categories were: bedrock;
144 boulders (25.6 cm – 102.4 cm); cobbles and pebbles (25.6 cm – 1.6 cm); gravel (1.6 cm –
145 0.4 cm); sand (0.063 mm – 4 mm); mud (< 0.063 mm); mixed sediment; biogenic reef
146 (mussel beds, *Sabellaria* reefs); and macroalgae-dominated sediment (from here
147 onwards referred to as ‘macroalgae’). More than one habitat was noted for a site if the
148 type of substratum changed significantly (visual estimation) (see Online Resource 1).
149 Coverage by different types of substratum was expressed in % of the area by visual
150 estimate, generally in increments of 10%, except in a few cases where increments of 5%
151 were used.

152

153 Aquaculture was categorised as absent, close (trestles with Pacific oysters were
154 encountered during the timed search) and far (known to be present in the embayment,
155 but generally > 500 m from the study site) based on licensing information from Bord
156 Iascaigh Mhara, the Irish Sea Fisheries Board. Wave fetch was used as an index of wave
157 exposure; it was defined as the closest distance to the land in 16 angular sectors
158 (average in km), and calculated after the method developed by Burrows et al. (2008).

159 Residence time was determined using the formula developed by Hartnett et al. (2011):

160
$$R = \frac{V}{B_0 L} \left(\frac{1}{TPR} - 1 \right)$$

161 . TPR is the tidal prism ratio, which
162 was derived from the volume of water between low water and high water [m³] divided
163 by the volume of the embayment at high water [m³]; B₀ is the width of the mouth of the
164 embayment [km]; and L is the length of the embayment along the longitudinal axis [km].

164 Each site’s intertidal width was categorized into 1 = 0-50 m, 2 = 51-100 m, 3 = 101-
165 150 m, 4 = > 151 m, based upon measurements from high water line to the lowest water
166 line. Each site was classified according to each of the variables described above with up
167 to three habitats per site (see Table 1 and Online Resource 1 for details).

168

169 *Phase 2:* When oysters were present at overall densities greater than 0.1 individuals/m²
170 (i.e. abundance category Frequent or above), two transects of 30 m x 1 m were randomly
171 placed in the habitat of greatest oyster density. In each transect, the numbers of oysters,
172 the sizes of oysters to the nearest mm (Vernier callipers) and substrata to which they
173 were attached were recorded. If more than 100 oysters were found in the first transect,
174 only counts and attachments to substrata but no further size measurements were
175 recorded in the second transect. On mussel beds, 17 random quadrats of 1 m x 1 m were
176 taken in each transect as densities were too high to account for every single oyster
177 within a transect line. Conversely, in the Shannon Estuary, extended transects were run
178 on two rocky shores to ensure that sufficient length measurements were collected for
179 size frequency analysis.

180

181 To estimate substratum availability, substrata were recorded quantitatively along two
182 10 m tapes placed haphazardly in the habitat where oysters occurred. The distances
183 along the tape at which the substratum changed from one type to another were
184 recorded, and these distances were converted into estimates of the percentage area
185 covered by different substrata. These data were used in conjunction with the data
186 collected on oysters and the substratum they were attached to. This enabled tests of
187 small-scale associations between oysters and biotic and abiotic features of habitat.

188

189 Teams of researchers from the different institutions were trained in the use of the
190 protocols by the coordinator of the project, who also accompanied each team on its first
191 sampling trip to ensure consistency of methodology. Each team was assigned a number
192 of specific sites to survey in a sequence that ensured minimal temporal and observer
193 bias with respect to the site variables described above. Each team surveyed a maximum

194 of two sites on each day, with pairs of sites selected to be in close proximity to each
195 other. Each site visit was timed such that the low shore could be visited within 20
196 minutes of a spring low tide. In any given day, a *Phase 1* survey was initiated one hour
197 before predicted low water, with the timed search gradually progressing down the shore
198 in step with the receding tide. If oysters were found at that site, the *Phase 2* survey was
199 completed during the incoming tide. If no oysters were found, the team moved on to the
200 second site for the day and completed a *Phase 1* survey during the incoming tide.

201

202 *Data Analysis*

203 Logistic regression allows multiple explanatory variables, and their interactions to be
204 included in a single model (Vittinghoff et al. 2005). Here, logistic regression was used to
205 find a set of environmental variables that could be used to predict oyster
206 presence/absence. In the 69 sites visited during the sampling programme, 127 habitats
207 were identified (*Phase 1*) and classified for presence/absence of oysters and the
208 environmental conditions encountered, including proximity of aquaculture (see Online
209 Resource 1). Our model was based on this set of 127 observations.

210

211 Prior to running the model, Spearman rank correlations (ρ) were calculated among all
212 pairs of environmental variables. When a Spearman rank correlation exceeded an
213 absolute value of 0.35, one of the pair of variables was omitted from the model to avoid
214 co-linearity (Dormann et al. 2012). The following pairs of variables had $|\rho| > 0.35$:
215 Macroalgae with Rest ($\rho = -0.63$), Latitude with Residence ($\rho = 0.46$), Rest with Width
216 ($\rho = 0.46$) and Macroalgae with Hardreef ($\rho = -0.35$), where 'Rest' refers to the EUNIS
217 categories sand, gravel, mixed sediment and mud, 'Hardreef' refers to bedrock, cobble,
218 pebble and biogenic reef, 'Residence' refers to residence time and 'Width' refers to shore
219 width. Latitude, Rest and Macroalgae were therefore omitted from the model. The

220 variables used in the full model were % cover of bedrock, cobble, pebble and biogenic
221 reef (called Hardreef), proximity to aquaculture (called Aquaculture with levels: absent,
222 far and close), residence time (called Residence), wave fetch (called Fetch) and shore
223 width (called Width with levels < 50 m and \geq 50 m)(see also Table 1).

224

225 The full logistic model used a logit link function and a model equation

226 $Oysters \sim 1 + Width + Fetch + Aquaculture + Residence + Hardreef + Hardreef:(Fetch + Width +$
227 $Residence + Aquaculture) + Fetch:Width$

228

229 The variable Oysters is 1 if oysters are present and zero otherwise, the other variables
230 are explained in Table 1 and ‘:’ indicates an interaction between two variables. All
231 interactions between Hardreef and the other variables are included in this full model
232 because oysters attach almost exclusively on hard substrata. Additionally, an interaction
233 between Fetch and Width was included because the extent of the shore is not considered
234 in the calculation of wave fetch and can be important when shores are wider than 100 m
235 (see Burrows 2008). Starting from this full model, backward stepwise selection was used
236 with Akaike’s Information Criterion (Akaike 1974) to arrive at a ‘best fit’ model. The
237 performance of the ‘best fit’ model to correctly classify oyster presence/absence at a
238 habitat unit was quantified using ROC curves and their AUC values (Fielding and Bell
239 1997). Additionally, we selected a probability threshold that gave a classifier that
240 weighed omission errors (false negatives, where oysters are incorrectly predicted to be
241 absent) more than commission errors (false positives, where oysters are incorrectly
242 predicted to be present) as this type of classifier is mostly desirable for invasive species
243 (Gormley et al. 2011).

244

245 χ^2 analysis (goodness-of-fit test) was used to test hypotheses about small-scale

246 associations between oysters and different types of substratum (using data obtained
247 during *Phase 2*).

248

249 Logistic model calculations were performed with R, using the MASS and pROC packages
250 (R Development Core Team 2011). For calculations of residence time and wave fetch,
251 detailed descriptions can be found in the original papers (Burrows et al. 2008; Hartnett
252 et al. 2011).

253

254 **Results**

255 *Distribution, densities and sizes of feral Pacific oysters*

256 Pacific oysters occurred at 18 of the 69 sites (Figure 1). No oysters were found at sites in
257 the south. Most oysters were found in the large estuaries of Lough Swilly, Lough Foyle
258 and the Shannon, with many sites scored Common or Frequent for the abundance of
259 oysters. Oysters were Occasional or Rare at five sites in Galway Bay and single
260 individuals of oysters were found at one site in Tralee Bay and another site in Ballynakill
261 Harbour, which therefore scored Rare on the SACFOR scale.

262

263 Oyster densities in the different habitats varied from single individuals to 8.5 ind./m²
264 (Table 2). Sites in Lough Swilly and Lough Foyle had the highest densities whereas sites
265 in the Shannon Estuary, Galway Bay, Tralee Bay and Ballynakill Harbour oysters were
266 found in lower densities (Table 2). Pacific oysters were mostly found in the lower
267 intertidal. During an exceptionally low spring tide, a subtidal mussel bed could be
268 accessed at Rathmelton in Lough Swilly, where densities were estimated at 12.5 ind./m².

269

270 At all of the sites with oysters > 0.1 ind./m², the range of sizes of oysters found exceeded
271 120 mm (Figure 2). In Lough Swilly, oyster sizes ranged from 13.8 mm – 125.7 mm on a

272 mussel bed (n = 147) and from 25.3 mm – 135.0 mm on a rocky shore (n = 182). Similar
273 sizes of oysters from 23.0 mm – 135.5 mm (n = 182) were also measured on a mussel
274 bed in Lough Foyle. In the Shannon Estuary slightly larger oysters were found, with the
275 smallest and largest oyster measuring 43.4 mm and 146.2 mm (n = 125) respectively at
276 Loghill. At Glin, oyster sizes ranged from 40.4 mm – 123.0 mm (n = 101).

277

278 *Associations between oysters and environmental variables at the scale of sites (Phase 1)*

279 127 different habitats were identified at the 69 sites of which there were 27 with oysters
280 present and 100 where no oysters were found (Figure 3). Four variables (Aquaculture,
281 Width, Hardreef and Residence) and no interactions were retained in the best-fit logistic
282 regression model (Table 3). Comparing the best-fit model's predictions against the
283 oyster presence/absence data gave an AUC of 0.9. Applying a classification probability
284 threshold of 0.1 to this model (corresponding to the threshold that maximised the sum
285 of specificity and sensitivity) gave 25 true positives, 71 true negatives, 29 false positives
286 and two false negatives for our oyster presence/absence data. Another approach to
287 estimate model performance is Cohen's kappa (Cohen 1960). Cohen's kappa is
288 maximised for our model at a threshold of 0.48. However, classification performance
289 with this threshold had less true positives and more false negatives and was therefore
290 not considered as the best classifier. Oyster presence was positively associated with
291 Hardreef (bedrock, boulders, cobbles, pebbles or biogenic reef), Residence and Width
292 ≥ 50 m. 'Aquaculture far' was also positively associated with oyster presence ($p = 0.035$,
293 Table 3). Removing 'Aquaculture absent' from the model did not affect the other
294 coefficients, indicated by a high standard error on the regression coefficient (Table 3). It
295 is important to note that Latitude, Rest and Macroalgae, which were omitted from the
296 full model due to co-linearity, could equally well underlie the same associations as the

297 terms that were left in the model in their place (i.e. Residence, Width and Hardreef
298 respectively). Thus, Latitude might equally be positively associated with oyster presence
299 whereas Macroalgae or a low % cover of Rest might be negatively associated with oyster
300 presence. Fetch was in the full model but was not kept in the best-fit model owing to its
301 low explanatory power.

302

303 *Small-scale associations between oysters and habitat within sites (Phase 2)*

304 Oysters were disproportionately associated with hard substrata (boulders, cobbles,
305 pebbles and mussels) given their availability relative to that of macroalgae, sand,
306 *Sabellaria* tubes and mud (Table 4). Oysters were never found attached to macroalgae
307 (with one single exception (J Kochmann, pers. obs.).

308

309 **Discussion**

310 The structured framework and sampling protocol here was used in cooperation with
311 relevant state agencies in Ireland and allowed rigorous analysis of the extent of spread
312 and factors influencing the distribution of Pacific oysters. Its cost-effectiveness and
313 repeatability make it valuable and widely applicable for future assessments and also
314 relevant for other marine benthic species with similar life-history traits.

315

316 Unlike the situation in many other European countries, no dense intertidal reefs of Pacific
317 oysters are established yet in Ireland, despite extensive aquaculture. Pacific oysters were
318 found at 18 of 69 sites. Densities at those sites ranged from single individuals to 8.5 ind./m² in
319 the intertidal; they were also observed at higher densities in the shallow subtidal in Lough
320 Swilly (J Kochmann, pers. obs.) and are known to occur in subtidal areas in Loughs Foyle and
321 Swilly (McGonigle et al. 2011; Marine Institute and BIM 2012). Comparably low densities
322 of 0.01-42.44 ind./m² were found, e.g. in Sweden and Denmark (Wrange et al. 2010), the

323 Wadden Sea (Reise 1998; Wehrmann et al. 2000; Diederich et al. 2005) or Argentina
324 (Orensanz et al. 2002) in the early stages of invasion. Guy and Roberts (2010) found
325 densities of one individual per m² in Northern Ireland with the largest oysters reaching lengths
326 of 155 mm. Based on their analysis of age-size relationships in Strangford Lough (Northern
327 Ireland), we would estimate that the largest oysters found in our study were approximately 6
328 years old. However, age-size relationships of *C. gigas* can vary among sites (references in
329 Diederich 2006), so this inference is tentative. In the Wadden Sea, Pacific oysters usually
330 reach 20-50 mm in the first year and 30-80 mm in the second year on mussel beds (Reise
331 1998; Schmidt et al. 2008; Fey et al. 2010) which are the lower size ranges also found in this
332 study. Little evidence of recruitment was found in 2008 at the sites where transects were
333 sampled, with few individuals found < 50 mm. New recruitment (oysters < 15 mm
334 length) has since been observed in the intertidal in 2011 (J Kochmann, pers. obs). The
335 range in sizes observed at individual sites (> 100 mm in four of the sites sampled, e.g.
336 from 25.3 mm to 135.0 mm mm at Lough Swilly) is greater than would have arisen in a
337 single cohort and is indicative of successful recruitment of Pacific oysters in more than
338 one year in several bays in Ireland.

339

340 Colonization of sessile benthic invertebrates often starts with a few individuals settling
341 onto pieces of hard substratum and is widely known for oysters (Reise 1998; Escapa et
342 al. 2004; Diederich 2005; Nehls et al. 2006). Similarly, in the current study oysters were
343 always found attached to bare boulders, cobbles, pebbles or biogenic reef (live or dead
344 material) and were very rarely found under macroalgae. Due to the co-linearity of
345 Macroalgae and Hardreef, the positive association of Hardreef with oyster presence
346 could also be a negative association with the % cover of macroalgae. However, when
347 both factors were kept in the full model, Hardreef was kept in the 'best-fit' model
348 indicating it as a better predictor than Macroalgae. Field studies with barnacle larvae

349 have shown that algal fronds can inhibit settlement on their surfaces by exuding
350 metabolites (Brock et al. 2007) and that macrophyte canopies could prevent larvae from
351 settling on rocks underneath them because they sweep the surface and limit access to
352 the substratum (Jenkins et al. 1999). These effects might also play a role in the
353 settlement patterns of oysters affecting recruitment and mortality (Thomsen and
354 McGlathery 2006) and interfering with filter-feeding apparatus (Cadée 2004). The
355 positive correlation of Width with Rest might be an indication of the characteristics of
356 the larger intertidal areas surveyed; they were often extensive intertidal mud- or
357 sandflats. Consequently, as intertidal shore width (> 50 m) was positively associated
358 with oyster presence, the model also captured the likelihood of oysters being found on
359 extensive, intertidal sedimentary shores.

360

361 For marine species with planktonic life-stages, the duration of the larval stage
362 determines the length of time that the larvae are subject to movement by currents and
363 exposed to sources of mortality (Pechenik 1999; Pineda et al. 2007). High reproductive
364 rates, spawning in multiple seasons or years and short development times can facilitate
365 retention (Byers and Pringle 2006). Even if larvae do not necessarily behave as passive
366 particles (e.g. Knights et al. 2006), flushing characteristics of coastal waterbodies such as
367 residence times can help in the identification of areas likely to retain larvae (see Dyer
368 and Orth 1994). Indeed, limitations in larval supply resulting from the interactions
369 between spawning location and local hydrodynamics may impede the proliferation of
370 introduced species (Dunstan and Bax 2007; Brandt et al. 2008; Rigal et al. 2010). The
371 dynamics of retention will not only differ between bays but also between species and
372 will influence their range expansion. For example, the larval duration of the invasive
373 seastar *Asterias amurensis* (Lütken, 1871) can take 120 days (Dunstan and Bax 2007),
374 whereas spores of the Asian kelp *Undaria pinnatifida* (Harvey) Suringar might last only

375 several hours in the watercolumn (Hay and Luckens 1987). The planktonic larvae of
376 Pacific oyster can spend three to four weeks in the water column before they reach
377 competence to settle (Quayle 1988). Thus, enhanced oyster settlement could be
378 expected to occur in bays exceeding the residence time of 21 days as larvae may be
379 entrained for the duration of their planktonic phase. Except for two bays, Ballynakill and
380 Tralee Bay, where single individuals of oysters were found, oysters were present in bays
381 with residence times of more than 21 days.

382

383 Although not explicitly considered here, temperature also plays an important role for
384 the timing and magnitude of population growth through its influence on reproduction,
385 survival of planktonic stages and on dispersal distances (Gillooly et al. 2002; O'Connor et
386 al. 2007). It is widely assumed that large recruitment events of introduced species have
387 been favoured by increasing summer temperatures and led to an increase in population
388 growth, e.g. in the Australian barnacle *Austrominius modestus* (Darwin, 1854) (Witte et
389 al. 2010) and the slipper limpet *Crepidula fornicata* (Linnaeus, 1785) (Thieltges et al.
390 2003). Similarly, there is considerable evidence in support of this contention for Pacific
391 oysters (Diederich et al. 2005) and temperature has been used to predict its potential
392 geographic range (Carrasco and Barón 2010). If latitude were considered a broad proxy
393 for temperature, our finding of greater densities of feral Pacific oysters in northern sites
394 than southern sites might be considered surprising. In fact, local temperatures and
395 biogeographic patterns cannot simply be predicted by latitude (Helmuth et al. 2002;
396 Dutertre et al. 2010) and temperature data from the Irish Environmental Protection
397 Agency (EPA), which was available for some bays, suggests that averages of maximum
398 summer temperatures cannot be simply characterized by latitude but vary between
399 bays. Thus, the high correlation of residence time and latitude suggests that any
400 influence of latitude in the current study might be more related to bay features than to

401 temperature. Certainly, bay features can also be related to temperature and part of the
402 reason for a positive association between residence time and oyster occurrence in the
403 current study may be that extensive shallow bays tend to be warmer at certain times
404 than smaller deeper ones. Generally, even if temperature regimes might be favourable
405 and spawning could be initiated, planktonic larvae might be carried away before they
406 attain competence to settle. Thus, residence time, which takes different bay features into
407 account, should be considered more relevant as a predictor for the presence of benthic
408 species with planktonic larval stages than average depth of a bay or a physiological
409 temperature threshold only.

410

411 Another hydrodynamic factor that can influence intertidal communities and abundance
412 patterns of introduced species is exposure to wave action (e.g. Andrew and Viejo 1998;
413 Branch et al. 2008). Although abundance patterns of Pacific oysters on rocky shorelines
414 can differ between sites of different exposure (Ruesink 2007), in this study, wave
415 exposure (quantified by wave fetch) played no role in our selected model of oyster
416 presence. It could be argued that wave exposure indices based on wave fetch alone might
417 not prove to be as powerful as including other aspects of wave climate, e.g. variations
418 due to wind climate (Davies and Johnson 2006). However, this would involve more
419 complex physical models and until those can be widely applied, wave fetch indices
420 remain useful for ecologists (Burrows et al. 2008). As shown by Burrows et al. (2008),
421 the extent of the shore is not considered in the calculation of wave fetch and can be
422 important when shores extend > 100 m. This might be especially important when
423 extensive intertidal areas offer some kind of hard substratum for attachment. Thus,
424 intertidal width was additionally used as a proxy for settlement area and the model
425 selection showed that intertidal width was a better predictor of oyster presence than
426 wave fetch with a shore width smaller than 50 m being negatively associated with oyster

427 presence.

428

429 Although aquaculture provides considerable economic and social benefit, the use of non-
430 native species in aquaculture increases the risk of unintentional escapes into ecosystems
431 (Carlton 1996; Naylor et al. 2001). A wide range of non-indigenous species are already
432 cultivated (FAO 2012a) and many additional species are being trialled for aquaculture in
433 countries outside their native range (see review Cook et al. 2008). Improved
434 understanding of the risks of escapes from aquaculture is clearly needed. Although more
435 oysters were expected in close proximity to oyster racks and aquaculture sites, a
436 tendency of oysters to be present more frequently far from aquaculture was found
437 ($p = 0.035$, Table 3). Cognie et al. (2006) suggested that farmers' upkeep activities might
438 explain the low biomass of oysters on used racks and might have also played a role in
439 our observations with a negative association of close proximity to aquaculture and
440 oyster presence. In this study, most of the sites visited (62 of 69) were located in bays
441 where aquaculture of Pacific oysters was present and only one single individual of Pacific
442 oyster was found in a bay without aquaculture. It will be important to sample more bays
443 where aquaculture is absent to draw more detailed and robust conclusions about
444 associations of aquaculture and Pacific oysters in the wild. However, the fate of
445 established non-native populations may not depend on reproduction success of farmed
446 counterparts (e.g. Kochmann et al. 2012); the overall significance of aquaculture might
447 be high in the initial establishment phase but less in subsequent spread. Therefore,
448 monitoring environmental factors that are related to recruitment success and
449 incorporating distances to sites where establishment has occurred might be more
450 important to follow spread than focusing only on potential initial introduction sources.

451

452 Recently, surface seawater and atmospheric temperature records were used to predict

453 the potential geographic range of the Pacific oyster in South America (Carrasco and
454 Barón 2010). However, the authors averaged monthly near-coast temperatures over
455 several years and acknowledged that in some locations, especially in estuaries and tidal
456 flats, their predictions of oyster occurrence did not match the real situation, most likely
457 because of a mismatch between local and near-coastal temperature regimes. Predictor
458 variables such as embayment characteristics and habitat availability might increase the
459 effectiveness for spatial predictions, particularly to discriminate among sites with
460 similar temperature regimes. On the basis of the current study, we would anticipate that
461 the sites most likely to develop populations of oysters would (a) be in embayments with
462 aquaculture and with temperature regimes allowing for oyster spawning and larval
463 development and with long residence times, (b) have hard substrata, e.g. mussel beds
464 and rocky shores, (c) not have extensive cover of macroalgae and d) be intertidal areas
465 > 50 m wide. The predictive performance of the model could be tested easily elsewhere
466 as oyster populations have been found in places worldwide outside their native range for
467 at least 40 years (Ruesink et al. 2005; Carrasco and Barón 2010).

468
469 Our sampling methodology differs from other approaches in marine bioinvasions, such
470 as passive sampling methods that use settlement plates, or rapid assessments that
471 record only presence or absence and do not quantify densities (see Campbell et al.
472 2007). Furthermore, when species-environment relationships are studied the scale of
473 analysis should match the scale of a species' response to its environment (De Knecht et al.
474 2009). Our methodology incorporated factors that correspond to the spatial scale
475 relevant for the different life-stages of invertebrates, such as larval supply, settlement
476 and recruitment. Rather than using only fixed levels of environmental factors, our
477 approach also allowed inclusion of continuous covariates (substratum, wave fetch and
478 residence time). This resulted in more degrees of freedom in the model as only the slope

479 for a continuous variable and not a coefficient for each level had to be calculated. The
480 AUC of 0.9 and also the individual classification threshold indicate a high discriminatory
481 ability of our model (Fielding and Bell 1997). However, the same data were used to fit
482 the model and to calculate model performance, which is not an independent validation
483 of the model. Several sites were sampled within individual embayments, and several
484 habitats were sometimes sampled within sites, thus, sampling locations were spatially
485 clustered and could lack independence. This might have led to spatial autocorrelation,
486 which can cause Type I error. However, initial results from mixed-model logistic
487 regression that correct for spatial autocorrelation with a random effect of site on the
488 intercept did not change results, i.e. estimated coefficients remained qualitatively the
489 same as in the logistic model, which justified the use of a non-spatial model. Seeing the
490 same qualitative outcome in the mixed-model suggests that oyster presence is affected
491 by local differences in habitat (within site), and makes sampling of more than one
492 habitat per site important.

493

494 The presence of non-native species and also their abundances at sites cannot be
495 explained exclusively by single factors. Beside sources of introduction, a comprehension
496 of the early stages of spread requires a broad understanding of abiotic and biotic factors.
497 Large-scale dynamics affect pelagic larvae and benthic juveniles, and biological, small
498 scale interactions affect their survival and recruitment to the benthos. Statistical and
499 process-based models are valuable tools for estimating the relative importance of
500 multiple factors and combining them into 505 future invasion scenario predictions.
501 Foremost, investigations of population dynamics at an early stage of marine bioinvasion
502 are extremely valuable to allow early action to reduce the risk of invasion (Simberloff et

503 al. 2013). Carefully designed sampling programmes using cost-effective methodologies
504 and coordinated over large areas to encompass variation in a range of predictor
505 variables, could make valuable contributions to such investigations. Furthermore, these
506 programmes should provide for robust outputs that can be easily communicated to
507 stakeholders and managers so that any subsequent management measures that target
508 relevant risk factors are suitably informed and justified.

509

510 **Acknowledgements:**

511 We are grateful to everyone who helped in the field, and to Grainne O'Brien and the
512 regional officers of BIM (Irish Sea Fisheries Board) for access to their aquaculture
513 databases and for putting us into contact with aquaculture operators. We would also like
514 to thank Ciaran McGonigle from the Loughs Agency and members of staff for their
515 extensive help in Northern Ireland and Donegal. Many thanks are due to Mike Burrows
516 who calculated wave fetch and Tomasz Dabrowski, Marine Institute, who calculated
517 residence times. Claire Guy and Dai Roberts from Queen's University Belfast and Heike
518 Büttger from BioConsult in Husum, Germany, helped during the initial planning of the
519 survey. This work was supported by the Graduate Research Education Programme in
520 Sustainable Development at University College Dublin, which was funded by the Irish
521 Research Council for the Humanities and Social Sciences (IRCHSS) and the Irish Research
522 Council for Science, Engineering and Technology (IRCSET). The work was also done in
523 association with the SIMBIOSYS (2007-B-CD-1-S1) project as part of the Science,
524 Technology, Research and Innovation for the Environment (STRIVE) Programme,
525 financed by the Irish Government under the National Development Plan 2007–2013,
526 administered on behalf of the Department of the Environment, Heritage and Local
527 Government by the Irish Environmental Protection Agency (EPA). We also thank two
528 reviewers and the editor, Jennifer Ruesink, whose suggestions improved this paper

529 substantially.

530

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- 776

777 **Table1** Categories of environmental variables and aquaculture. The number of habitats with oysters
 778 present and absent is only shown for categorical variables. Note that categories for Width with the same
 779 superscript letters were combined for the logistic regression. Latitude was not included in the model and
 780 Hardreef was the only Substratum cover used in the full model. More details of the variables are provided
 781 in the text
 782

Variable	Category	Oysters present	Oysters absent
Latitude	low: N51°- N52.3°	1	41
	medium: N52.3°- N54°	12	38
	high: N55°	14	21
Aquaculture	absent	1	12
	close	5	52
	far	21	36
Width	0-50 m ^a	5	28
	51-100 m ^b	10	31
	101-150 m ^b	5	12
	>151 m ^b	7	29
Fetch	log ₁₀ (km) transformation, continuous		
Substratum cover (Hardreef)	%, arcsine transformation, continuous		
Residence	days, continuous		

783

784 **Table2** Density of Pacific oysters estimated by transects (2 x 30 m²) or random quadrats (2 x 17 x 1 m² on
 785 mussel beds) in intertidal areas with the highest density of oysters at each site at which oysters were
 786 found. The locations of sites can be seen in Figure 1. At sites scored rare or occasional on the SACFOR scale
 787 (see methods), no transects were used as densities were too low. In those cases, the SACFOR values are
 788 given in the table as Occasional = 0.01-0.09/m² or Rare = < 0.009/m²
 789
 790

Location	No. of oysters m ⁻² (± SD)
<u>Lough Foyle</u>	
Muff, mussel bed	5.35 (0.42)
Longfield	0.38 (0.04)
Ball's Point	0.38 (0.37)
Moville	rare
<u>Lough Swilly</u>	
Rathmelton, rocky shore	6.32 (0.31)
Rathmelton, mussel bed	8.53 (0.17)
Inch Island	0.76 (0.17)
Ballybagley	0.85 (0.07)
<u>Galway Bay</u>	
Ballynacorty	rare
Dunbulcaun	rare
Parkmore	rare
Finvarra	occasional
Ballyvelaghan	rare
<u>Shannon Estuary</u>	
Glin	0.72 (0.49)
Loghill	0.68 (0.31)
Tarbert	rare
<u>Tralee Bay</u>	
Black Rock, Spa	rare
<u>Ballynakill Harbour</u>	
Letterfrack	rare

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809 **Table3** Coefficients, Standard Errors and p-values from the 'best fit' logistic regression model. The
810 intercept corresponds to Width \geq 50 m, Aquaculture close, Residence = 0, Hardreef = 0
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	Estimate	Standard Error	p-value
Intercept	-4.63	0.86	<0.001
Width < 50 m	-2.28	0.93	0.010
Aquaculture far	1.41	0.67	0.035
Aquaculture absent	-0.37	1.31	0.780
Residence	0.06	0.02	0.001
Hardreef	2.69	0.85	0.002

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823 **Table4** Observed and expected numbers of oysters depending on availability of substrata at sites where
 824 transects or quadrats were sampled (*Phase 2* of the protocol). Chi² goodness-of-fit test was used and p-
 825 values were simulated when expected values were smaller than 5
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Location	Available substratum (%)	No. of oysters		Chi ²	p
		observed	expected		
<u>Shannon Estuary</u>					
Glin	mud, sand (60%)	0	60.60	171.97	< 0.001
	boulders or cobbles (37%)	101	37.37		
	macroalgae (3%)	0	3.03		
Loghill	boulder, cobble (80%)	125	100.00	31.25	< 0.001
	mud (10%)	0	12.50		
	macroalgae (10%)	0	12.50		
<u>Lough Swilly</u>					
Rathmelton, mussel bed	mussels (47%)	267	126.90	292.11	<0.001
	boulder or cobbles (10%)	3	27.00		
	mud (28%)	0	75.60		
	macroalgae (15%)	0	40.50		
Rathmelton, rocky shore	boulder, cobbles, pebbles (52%)	373	196.56	330.07	< 0.001
	Sabellaria (26%)	5	98.28		
	mud (22%)	0	83.16		
Inch Island	mussels (78%)	22	17.16	6.21	< 0.050
	mud (22%)	0	4.84		
Ballybagley	mussels (35%)	26	17.85	98.28	< 0.001
	boulder or cobbles (11%)	25	5.61		
	mud (13%)	0	6.63		
	macroalgae (41%)	0	20.91		
<u>Lough Foyle</u>					
Muff, mussel bed	mussels (90%)	156	140.40	17.33	< 0.001
	mud (10%)	0	15.60		
Ball's Point	mussels (50%)	8	4.00	8.00	< 0.010
	mud(50%)	0	4.00		
Longfield	mussels (92%)	13	11.96	1.13	> 0.050
	sand (8%)	0	1.04		

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828 **Figures**

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830 **Fig.1** Sampling sites and abundance of feral Pacific oysters in Ireland in 2009. Sites are categorised on the
831 SACFOR scale on the basis of timed searches (see methods) by symbols. Open circle: Absent; grey triangle:
832 Rare; black triangle: Occasional; black circle: Frequent; grey circle: Common. Names of embayment where
833 oysters were found are given

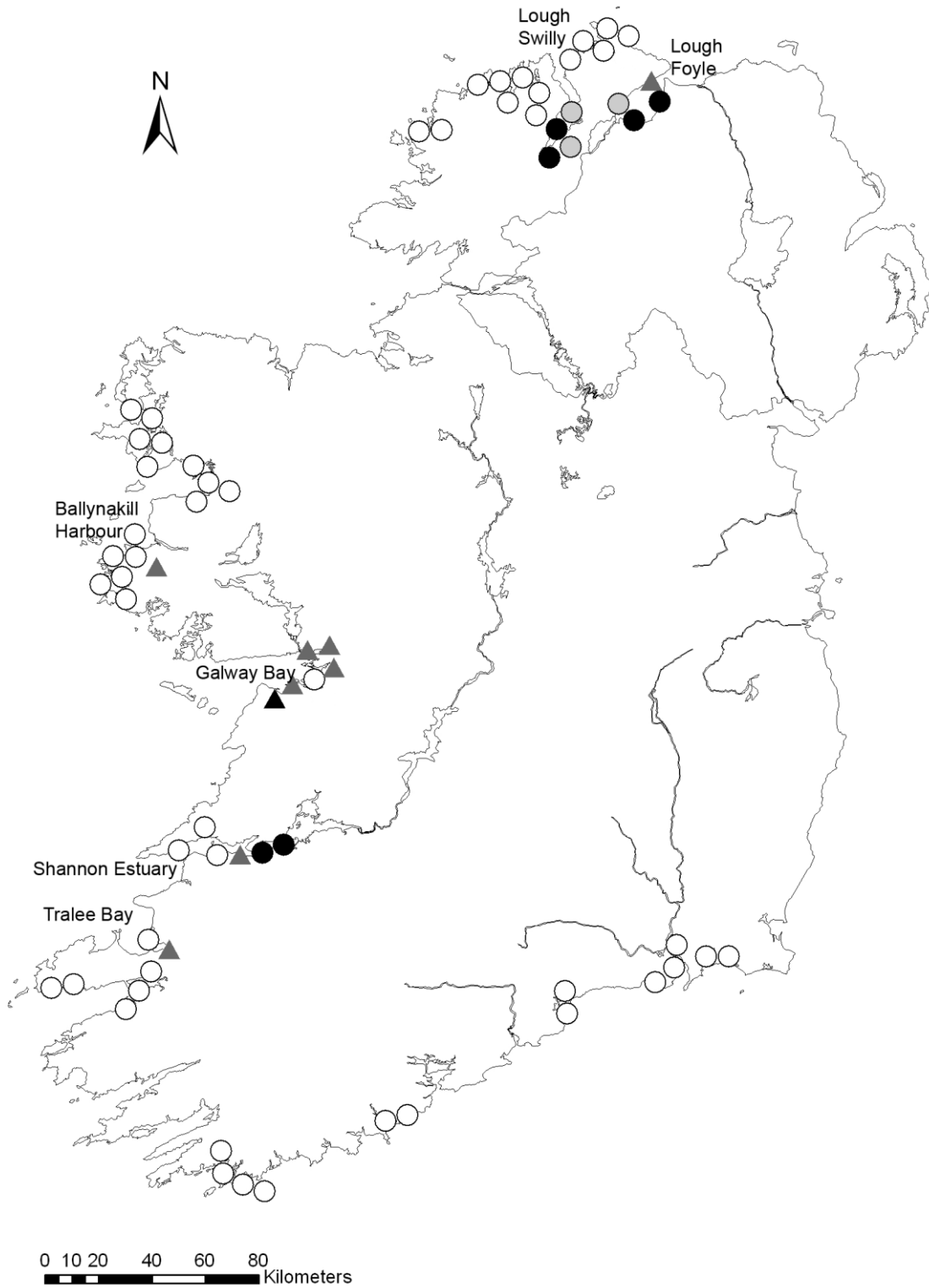
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835 **Fig.2** Size-frequencies of Pacific oysters in 5 mm size intervals at different locations, a Lough Swilly,
836 Rathmelton, rocky shore, b Lough Swilly, Rathmelton, mussel bed, c Shannon Estuary, Loghill, d Shannon
837 Estuary, Glin, e Lough Foyle, Muff, mussel bed. Measurements were taken from transects (see methods),
838 n = number of oysters

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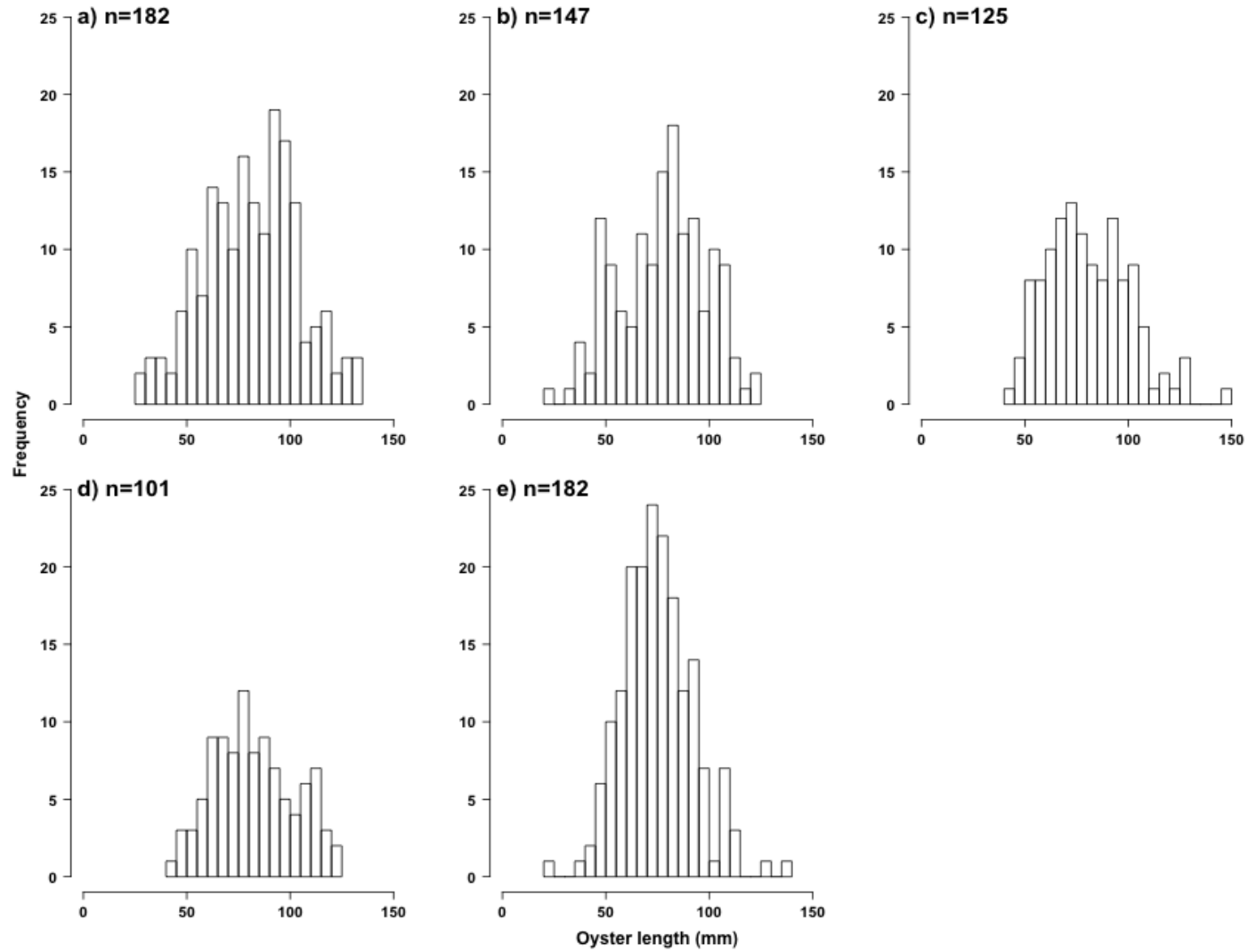
840 **Fig.3** Visualized results of estimated types of substratum from all collected habitats with and without
841 oysters. The number of habitats with and without oysters is given in brackets

842 Figure 1.
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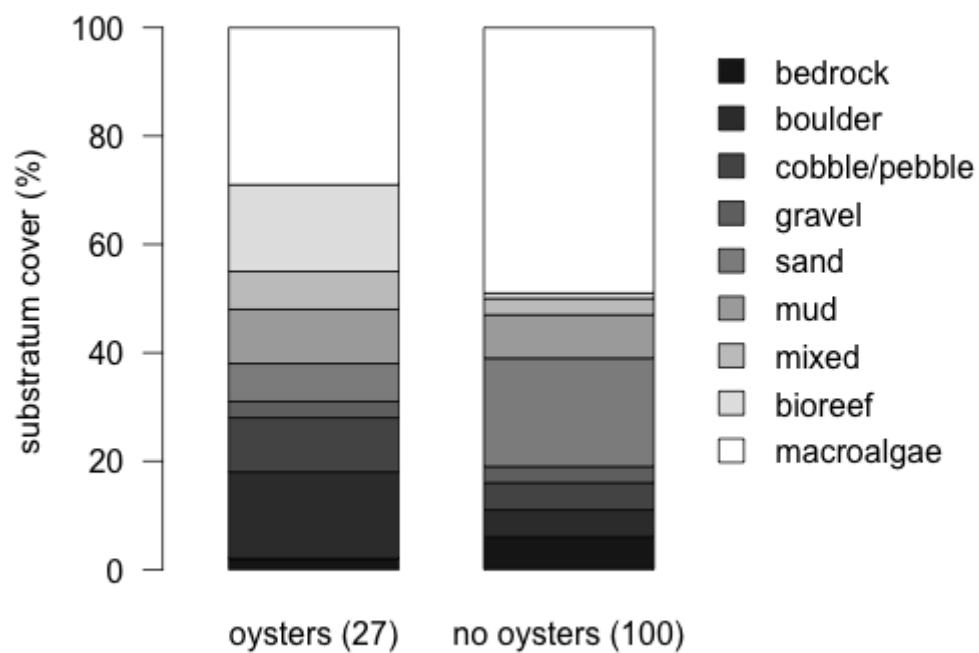
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846 Figure 2.



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848 Figure 3.
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