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 asscociated 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 . TPR is the tidal prism ratio, which

161 was derived from the volume of water between low water and high water [m^3] divided

162 by the volume of the embayment at high water [m^3]; B_0 is the width of the mouth of the

163 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/m^2

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 ≥ 50 m)(see also Table 1).

224

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

226   Oysters~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./m^2

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./m^2.

269

270 At all of the sites with oysters > 0.1 ind./m^2, 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./m^2 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 m^2 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

14

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 and 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 Knegt 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

529   substantially.

530

531   **References**

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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

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

Location	No. of oysters m⁻² (± SD)
Lough Foyle	
Muff, mussel bed	5.35 (0.42)
Longfield	0.38 (0.04)
Ball's Point	0.38 (0.37)
Moville	rare
Lough Swilly	
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)
Galway Bay	
Ballynacorty	rare
Dunbulcaun	rare
Parkmore	rare
Finvarra	occasional
Ballyvelaghan	rare
Shannon Estuary	
Glin	0.72 (0.49)
Loghill	0.68 (0.31)
Tarbert	rare
Tralee Bay	
Black Rock, Spa	rare
Ballynakill Harbour	
Letterfrack	rare

809 **Table3** Coefficients, Standard Errors and p-values from the 'best fit' logistic regression model. The
810 intercept corresponds to Width ≥ 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). Chi^2 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),
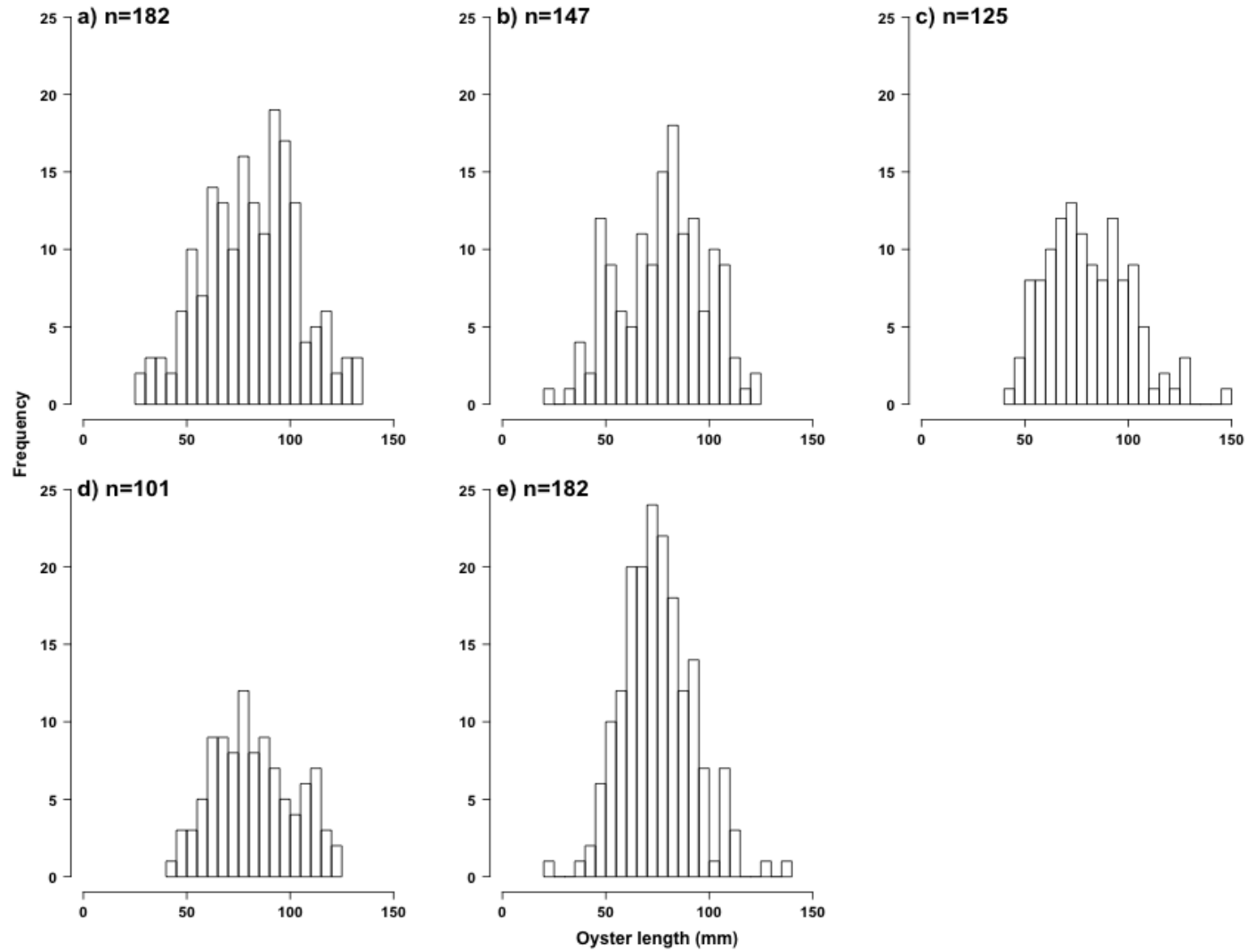838 n = number of oysters
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840 **Fig.3** Visualized results of estimated types of substratum from all collected habitats with and without
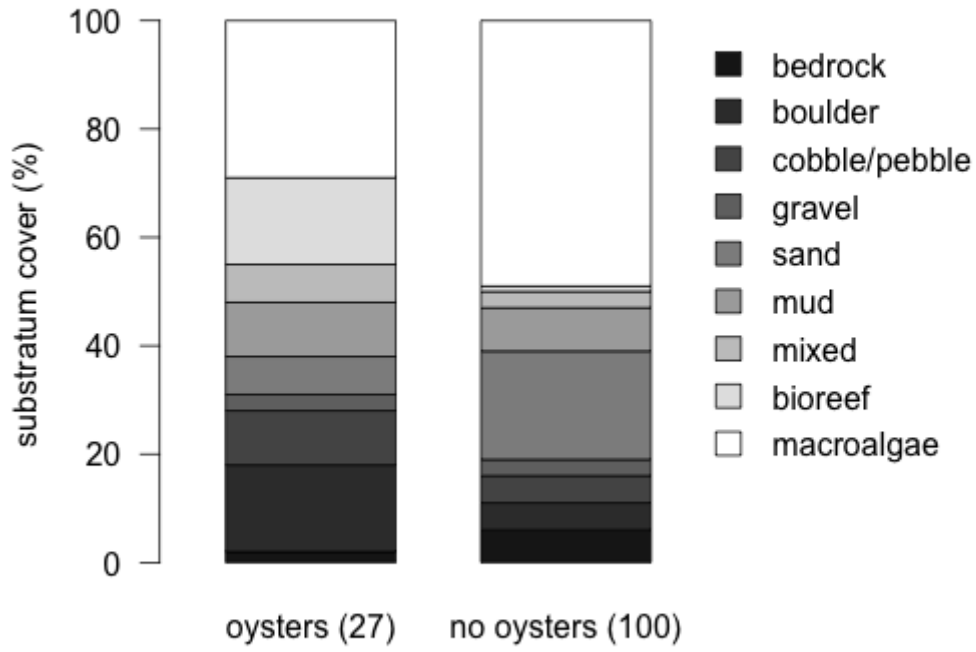841 oysters. The number of habitats with and without oysters is given in brackets

842   Figure 1.
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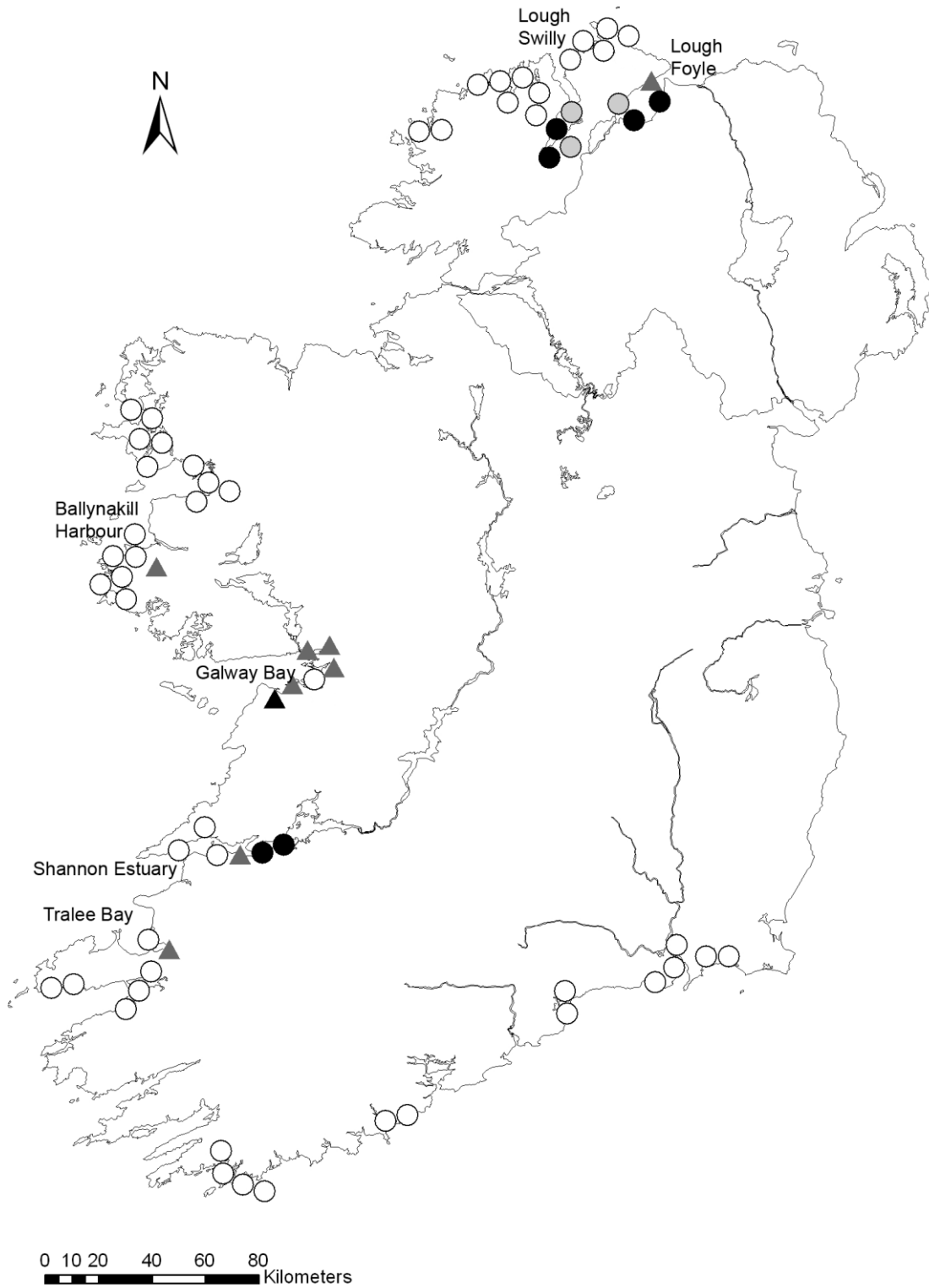
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846   Figure 2.

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848   Figure 3.
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