

26 among estuarine species along the north-eastern Iberian coast, in order to assess
27 community vulnerability to global change scenarios. To address this objective, two
28 connectivity proxy types have been used based upon genetic and ecological drift
29 processes: 1) DNA markers for the bivalve cockle (*Cerastoderma edule*) and seagrass
30 *Zostera noltei*, and 2) the decrease in the number of species shared between two sites
31 with geographic distance; neutral biodiversity theory predicts that dispersal limitation
32 modulates this decrease, and this has been explored in estuarine plants and
33 macroinvertebrates. Results indicate dispersal limitation for both saltmarsh plants and
34 seagrass beds community and *Z. noltei* populations; this suggests they are especially
35 vulnerable to expected climate changes on their habitats. In contrast, unstructured
36 spatial pattern found in macroinvertebrate communities and in *C. edule* genetic
37 populations in the area suggests that estuarine soft-bottom macroinvertebrates with
38 planktonic larval dispersal strategies may have a high resilience capacity to moderate
39 changes within their habitats. Our findings can help environmental managers to
40 prioritise the most vulnerable species and habitats to be restored.

41

42 1. INTRODUCTION

43

44 The most important direct drivers of global biodiversity loss and ecosystem service
45 changes are habitat change, climate change, invasive alien species, overexploitation, and
46 pollution (Millennium Ecosystem Assessment, 2005). The undergoing destruction and
47 degradation of natural habitats (Halpern et al., 2008) and, as a consequence, the
48 increasing number of threatened species (He and Hubbell, 2011), are particularly severe
49 at the coast, where human population is concentrated (Costanza et al., 1997;
50 McGranahan et al., 2007) and the artificialization and urbanization is increasing at a

51 greater rate than for inland areas (European Environment Agency, 2006). Climate
52 change is also considered as one of the major threats to coastal and estuarine ecosystems
53 for the 21st Century (FitzGerald et al., 2008; Defeo et al., 2009; Reid et al. 2009;
54 Philippart et al., 2011).

55

56 In this context, the conservation of estuarine biota is a priority. One of the main
57 adaptation strategies to global change scenarios to preserve ecosystem functioning and
58 biodiversity is to maximise ecosystem resilience (Mawdsley et al., 2009). The resilience
59 is the system's ability to absorb rapid environmental change (Heller and Zavaleta,
60 2009). The resilience of a species metapopulation can be improved by facilitating
61 connectivity among local populations, which will prevent demographic stochasticity
62 and inbreeding (Loew, 2000). Despite the fundamental role played by dispersal and
63 population connectivity in determining the resilience of populations (e.g. Hastings and
64 Botsford 2006; Cowen et al., 2007; Bradbury et al., 2008; Cowen and Sponaugle, 2009),
65 there is still a limited knowledge about the dispersal strategies of many marine species
66 due to the difficulty of tracking the trajectory and fate of propagules (e.g. Shanks, 2009;
67 Weersing and Toonen 2009; Selkoe and Toonen, 2011). In the seascape, the
68 connectivity among populations is mainly determined by the ocean currents and the
69 dispersal capacity of organisms (e.g. Gawarkiewicz et al., 2007; Alberto et al., 2011;
70 Coleman et al., 2011), as well as by the demographic prospects of reproduction,
71 mortality, and migration rate (Hubbell, 2001). In the particular case of ecotones such as
72 estuaries, the movement of organisms or propagules can be very different between
73 species depending on both habitat specificity and dispersal strategies (Boström et al.,
74 2010). Thus, it is difficult to anticipate, for a given spatial scale, whether estuarine
75 species circumvent habitat discontinuities, or on the contrary, are dispersal limited. The

76 analysis of highly polymorphic molecular markers is a powerful tool for the study of
77 connectivity among marine populations (e.g. Bradbury et al., 2008; Galindo et al., 2010;
78 Selkoe et al., 2010; Alberto et al., 2011). Although dispersal limitation factors has been
79 recognised to be a common process shaping both species and genetic diversity (Vellend
80 and Geber, 2005), the first empirical evidence has been recently proved in aquatic
81 beetles (Baselga et al., 2013).

82

83 The main objective of this contribution is to estimate the degree of connectivity among
84 the structural estuarine species (plants and macroinvertebrates) along the Basque coast
85 (south-eastern Bay of Biscay), in order to assess community vulnerability in the face of
86 global change scenarios. Basque estuaries have been radically transformed by
87 anthropogenic activities during the 20th century (Cearreta et al., 2004; Chust et al.,
88 2009), and they are expected to be impacted throughout the 21st century by a sea level
89 rise of 29 to 49 cm (Chust et al., 2010), storm surges (Marcos et al., 2012), warming of
90 surface air (especially heat wave episodes) and sea of 1.5 to 2.0 °C (Chust et al., 2011),
91 and the intensification of extreme daily rainfall of 10% (Chust et al., 2011). Thus, the
92 specific objectives are: 1) to determine and compare the connectivity between species
93 communities across two estuarine taxa groups (i.e. plants of saltmarshes and intertidal
94 seagrass meadows, and soft-bottom macroinvertebrates in intertidal and shallow
95 waters); 2) to determine and compare the genetic connectivity between estuarine
96 populations along the North Atlantic Iberian coast of two species with different
97 dispersal strategies and life traits: the seagrass *Zostera noltei* and the bivalve cockle
98 (*Cerastoderma edule*). Recent studies determining population genetic structure of
99 sympatric marine species (e.g. Kinlan & Gaines, 2003; Selkoe et al., 2010; Nikula et al.,
100 2011) has provided insightful information on gene flow through the seascape.

101 Estimating and understanding marine connectivity can also help environmental
102 managers to guide and prioritise local restoration plans for both species and habitats, as
103 well as to define strategies for climate change adaptation.

104

105 To address these objectives, two proxies of connectivity have been used, based upon
106 genetic and ecological drift processes and dispersal limitation factors (Vellend and
107 Geber, 2005). Under a ‘stepping stone model’ of dispersal, in which populations tend to
108 exchange migrants (or propagules) with nearest neighbours along the coastline, the
109 Isolation By Distance (IBD) theory suggested that pairwise genetic variation (for
110 instance the Wright’s fixations index F_{ST}) will increase with the geographic distance
111 between the pair of populations (Wright, 1943; Kimura, 1953; reviewed in Selkoe and
112 Toonen, 2011). IBD assumes neutral alleles (not affecting fitness) and populations at
113 equilibrium between dispersal and genetic drift (Hutchison and Templeton, 1999). In
114 contrast, in a metapopulation where all populations exchange migrants equally, F_{ST} is
115 not correlated with geographic distance. Therefore, the slope of IBD is commonly used
116 for estimating dispersal distance with genetic markers. The IBD theory is a central
117 concept of the neutral theory of molecular evolution (Kimura, 1983), which states that
118 most of evolutionary changes at the molecular level is the result of randomly genetic
119 drift acting on neutral alleles (not affecting fitness). In ecology, although disentangling
120 whether the regional distribution of species arises from dispersal limitation (MacArthur
121 and Wilson, 1967) or by niche adaptive processes (Hutchinson, 1957) have long
122 debated, the emergence of the concept of neutrality (Hubbell, 2001) appeared more
123 recently than in population genetics. The neutral theory of biodiversity developed by
124 Hubbell (1997, 2001) is *neutral* because all individuals are assumed to have the same
125 prospects for reproduction and death (Chave, 2004). Under a Hubbell’s model, where a

126 metacommunity is composed by a set of communities exchanging individuals of
127 different species with a migration rate, the variability in relative abundances across
128 species is solely due to demographic stochasticity or ‘ecological drift’. When migration
129 rate is low in such a model (i.e. species are dispersal limited), species cross-site
130 similarity (i.e. the opposite of β -diversity) is predicted to decline logarithmically with
131 increasing geographical distance (Hubbell, 2001; Chave and Leigh, 2002). This pattern,
132 named ‘distance decay’, has been observed for different taxonomic groups: rainforest
133 trees (e.g. Condit et al., 2002; Chust et al., 2006a), coral reefs (Hubbell, 2001), marine
134 bacteria (e.g., Martiny et al., 2011), and plankton (Irigoien et al., 2011; Chust et al.,
135 2013; but see Cermeño et al., 2010). The estimated correlation and rate of change (i.e.
136 slope) in species similarity with increasing geographic distance, hence, can be used to
137 compare the degree of dispersal limitation among different communities, (Chust et al.,
138 2006b). However, species distributions and environmental variables tend to be spatially
139 autocorrelated (Legendre, 1993), hence, distance decay might be a result from the
140 relation between species composition and environmental niche factors. In such case,
141 appropriate statistical techniques need to be applied in order to disentangle both effects
142 (e.g. Chust et al., 2013). Within this framework, our expectations in estuarine species is
143 that the group of species more limited by dispersal at the community level should also
144 have more fragmented genetic population structure, in accordance to recent findings in
145 aquatic beetles (Baselga et al., 2013).

146

147 2. MATERIAL AND METHODS

148

149 2.1 Study area

150

151 The study area is located within the Basque Country (Spain), in the southeastern part of
152 the Bay of Biscay (Fig. 1). The total length of this section of the coast is ca. 150 km,
153 with 13 main estuaries (Borja and Collins, 2004) (Fig. 1). The maritime climate along
154 the Basque coast is related mainly to its location within the Bay of Biscay and the NE
155 Atlantic (González et al., 2004). In relation to its location and orientation, this part of
156 the coast is exposed to large storms from the NW, produced by evolution of the North
157 Atlantic low pressure systems. Strong NW swell waves dominate and are the most
158 common sea state within the study area. The tidal wave is semi-diurnal in character
159 within the Bay of Biscay (Uriarte et al., 2004). Along the Basque coast, the mean tidal
160 range is approximately 1.65 m on neap tides and 4.01 m on springs (Chust et al., 2010).
161 Despite the importance of tidally-induced surface water fluctuations, the contribution of
162 the tides to the generation of currents is somewhat modest (except within the estuaries)
163 (Uriarte et al., 2004). The coast is dominated by rocky substrata with vertical cliffs
164 intercalated with small estuaries and sandy beaches. The continental shelf in the Basque
165 Country is characterised by its narrowness; it ranges from 7 km to 20 km (Galparsoro et
166 al., 2010). As a consequence of this coastal configuration, salt-marshes are few,
167 fragmentary and restricted to the inner parts of the estuarine areas (Cearreta et al.,
168 2002).

169

170 2.2 Population genetics: sampling and genotyping

171

172 2.2.1 *Zostera noltei*

173

174 The seagrass *Zostera noltei* (Hornemann, 1832) is an estuarine flowering plant which
175 forms meadows at the muddy and sandy flats within the intertidal zone. The seagrass

176 colonisation mainly proceeds through clonal growth through rhizomes. It is distributed
177 widely within the coastal zones from the southern coasts of Norway to the
178 Mediterranean Sea, the Black Sea, the Canary Islands, with the southern limit on the
179 Mauritanian coast (Valle et al., 2011). *Z. noltei* has been reported to occur along most
180 northern Spanish estuaries, and there are also historical references about its presence
181 along the Basque Country estuaries, but nowadays is present only in three (Oka, Lea
182 and Bidasoa) of them (Valle et al., 2011; Fig. 1). The general degradation in quality of
183 Basque estuaries over the last two centuries, due to human pressures (Borja et al.,
184 2006a), might explain the decline (from 6 to 3 vegetated estuaries) of this species within
185 the region (Valle et al., 2011).

186

187 *Zostera noltei* samples were collected from nine estuaries in Northern Spain and
188 Western France: three in the Basque Country region (Oka, Lea and Bidasoa) (Fig. 1) in
189 which the plant is still present (Valle et al., 2011), three estuaries in Cantabria (St.
190 Vicente de la Barquera, Santoña, Santander) and one in Asturias (Ribadesella) regions,
191 one estuary in France (Arcachon), and one population from Galicia region, Ria de Vigo
192 estuary (42°21'2.95"N and 8°36'57.76"W) as a distant reference population. Shoots
193 (between 17 and 70 per estuary) were collected randomly with at least 2 meter distant
194 between samples.

195

196 Genomic DNA was extracted from silica dried plant material by a CTAB (2%
197 hexadecyl trimethylammonium bromide) method. Seven microsatellite loci (Genbank
198 accession codes: ZnB1, ZnB8, ZnD6, ZnF11, ZnF8, ZnH10, ZnH8) were PCR amplified
199 using fluorescently labeled primers (Coyer et al., 2004). PCR products were visualized
200 using an ABI-3130XL automated sequencer (Applied Biosystems). Raw allele sizes

201 were scored with STRAND (<http://www.vgl.ucdavis.edu/informatics/STRand/>), binned
202 using the R package MsatAllele (Alberto, 2009) in R software (R Development Core
203 Team, 2011), and manually reviewed for ambiguities.

204

205 2.2.2 *Cerastoderma edule*

206

207 The common cockle, *Cerastoderma edule* (Linnaeus 1758), is a bivalve with a north
208 Atlantic distribution. This species inhabits in estuaries and sandy bays and its
209 development include a planktonic larval phase (Young et al., 1996). Planktonic larvae
210 dispersal has been reported to last up to 3-6 weeks in the water column (Marine Life
211 Information Network; available at: <http://www.marlin.ac.uk>). A total of 479 individuals
212 of *C. edule* were sampled at the estuaries of Butron, Bidasoa, Deba, Lea and Oka
213 (Basque Country, Fig. 1) and at Carril (Ria de Arousa, Galicia, NW Spain, 42° 21' 57"
214 N, 8° 27' 46" W). Cockles were sampled at intertidal sandy areas by sieving, and froze
215 in a freezer until analyses.

216

217 Genomic DNA was extracted from 25 mg of muscle tissue for each individual using
218 Nucleospin® 96 Tissue Kit (Macherey-Nagel). The amount and quality of DNA from
219 each sample was subsequently quantified in a NanoDrop ND-8000 spectrophotometer
220 (Thermo Fisher Scientific). The 12 polymorphic microsatellites developed by Martinez
221 et al. (2009) were genotyped for the 479 *C. edule* individuals as to account for genetic
222 diversity and relatedness. These markers were amplified in two independent multiplex
223 polymerase chain reactions (PCR). The two multiplexed reactions, namely COCKLE1
224 and COCKLE2, included, respectively, 8 and 4 markers. While COCKLE1 included
225 CeATC1-5, CeATC1-36, CeATC1-52, CeATC2-4, CeATC2-11, CeATC2-34,

226 CeATC2-44 and CeATC2-46, microsatellite loci, COCKLE2 consisted of CeATC1-22,
227 CeATC1-54, CeATC2-12 and CeATC2-51 ones. All PCR reactions were carried out in
228 a final volume of 12.5 μ l in a Veriti™ Thermal Cycler (Applied Biosystems). Each
229 multiplex PCR reaction contained 5-10 ng DNA. While COCKLE1 reaction contained 1
230 μ l $MgCl_2$ (25 mM), 0.30 μ l of each primer (10 μ M), except for 0.50 μ l of CeATC2-46
231 ones, 1.25 μ l GeneAmp® PCR Buffer II (Applied Biosystems), 1 μ l dNTPs (2.5 mM
232 each), 0.48 μ l AmpliTaq Gold DNA Polymerase (5 U/ μ l ;Applied Biosystems) and 2.07
233 μ l ultrapure H_2O , COCKLE2 reaction included 1.25 μ l $MgCl_2$, 0.30 μ l of each primer,
234 except for 0.50 μ l of CeATC2-51 ones, 1.25 μ l PCR Buffer, 1 μ l dNTPs (2.5 mM each),
235 0.24 μ l DNA Polymerase and 4.46 μ l ultrapure H_2O . Both multiplex PCRs were
236 performed using the following conditions: 5 min initial denaturation at 95°C, followed
237 by 34 cycles of denaturation for 30 s at 95 °C, 30 s at annealing temperature (T_a = 60
238 °C), and 30 s at 72 °C for extension. An extra final extension for 10 min at 72 °C was
239 included after the last cycle. PCR products were analysed in two independent
240 electrophoresis runs with an ABI Prism 3100 Avant Genetic Analyzer (Applied
241 Biosystems). Raw data were processed with GENESCAN 3.7.1 and allele calling was
242 performed with GENOTYPER 3.7 software (Applied Biosystems). Only the nine, out of
243 twelve, microsatellite loci that were successfully genotyped, meaning that were
244 polymorphic and reliably scored, were considered for further analysis (CeATC1-5,
245 CeATC1-36, CeATC2-4, CeATC2-11, CeATC2-34, CeATC2-44, CeATC1-22,
246 CeATC1-54 and CeATC2-12).

247

248 2.3 Statistical analysis: Genetic diversity and divergence

249

250 In *Zostera noltei*, after removal of duplicate multilocus genotypes (ramets, i.e. shoots,
251 belonging to the same genet, which is a group of genetically identical individuals),
252 heterozygosity (H_e and H_o) and inbreeding coefficient (F_{IS}) were calculated using
253 Genetix version 4.05 software (Belkhir et al., 2004). Genotypic diversity, the proportion
254 of different genets in each sample, was estimated as R following Dorken and Eckert
255 (2001): $R = (G-1)/(N-1)$, where N corresponds to the number of collected individuals
256 and G to the number of genets (i.e. clonal colony). R ranges from 0 (all samples belong
257 to the same genet) to 1 (all samples are unique genetic individuals). Also, the genetic
258 variation was calculated as the allelic richness (\hat{A}) standardized for sample size
259 (standArich package for R language, see Alberto et al. 2006). In *Cerastoderma edule*,
260 FSTAT v.2.9.3 software (Goudet, 2001) was used to estimate allelic richness (AR),
261 heterozygosity (H_e and H_o) and inbreeding coefficient (F_{IS}).

262

263 The presence and frequency of null alleles was tested for both species using the
264 expectation maximization algorithm of Dempster et al. (1977) implemented in FreeNA
265 (Chapuis and Estoup, 2007). Genetic divergence between populations was assessed by
266 means of calculating two differentiation measures: 1) fixation index (F_{ST} ; Weir and
267 Cockerham, 1984) using FreeNA software (Goudet, 1995; 2001) that provides null
268 allele corrected F_{ST} values, and 2) D (Jost, 2008). Statistical significance of F_{ST} was
269 obtained bootstrapping over loci; probability was $p < 0.05$ when the 95% confidence
270 interval did not include 0 (F_{ST} statistically different from zero).

271

272 2.4 Genetic metrics of dispersal

273

274 Interconnectivity of populations was examined through use of cluster analysis and by
275 calculation of isolation by distance. Isolation by distance was tested for both *Z. noltei*
276 and *C. edule* species by searching for correlation between genetic and geographic
277 distance matrices with Mantel approach (Legendre and Legendre, 1998). This test
278 computes a statistic r_M which measures the correlation between two matrices and is
279 tested by a non-parametric permutation test. Geographic distance was measured as the
280 minimum path distance between two estuaries along the coastline, i.e. circumventing
281 the terrestrial zone, using geographic information system tools (Fig. 1b). Genetic
282 distance was estimated by $F_{ST}/1-F_{ST}$ (Rousset, 1997).

283

284 Population structure was analysed using the Bayesian clustering techniques
285 implemented in the software STRUCTURE 2.3.1 (Pritchard et al., 2000). STRUCTURE
286 uses individual multilocus genotype data to cluster individuals into K groups while
287 minimising Hardy-Weinberg disequilibrium and gametic phase disequilibrium between
288 loci within groups. First we calculated the mode of ΔK (Evanno, 2005) which is a good
289 predictor for the real number of clusters in the data. Then STRUCTURE was run for the
290 modal value with 100000 burnin and 1000000 Markov Chain Monte Carlo (MCMC)
291 iterations.

292

293 2.5 Floristic and faunal β -diversity across estuaries

294

295 The floristic (flowering plants) inventory of mudflats and saltmarshes, and soft-bottom
296 macroinvertebrates have been analysed in order to test whether population isolation
297 among estuarine communities takes place at the geographic scale of the study area
298 (Basque coast). To this end, the correlation strength and slope between species

299 similarity among estuaries and the oceanographic distance is interpreted as a surrogate
300 of dispersal limitation (Chust et al., 2006b). Thus, the greater the isolation the lower the
301 capacity of the community species, in average, to adapt to new conditions. Dataset on
302 these species, together with information on dispersal modes, are given below.

303

304 Plant (angiosperms) inventory of saltmarshes and seagrass beds was obtained from
305 Silván & Campos (2002). The sampling considered all plant species found in
306 saltmarshes, exclusive of halophytic wetlands and intertidal seagrass meadows, and
307 excluded exotic species and those associated to inland habitats. The sampling was
308 undertaken in 2001 over 9 estuaries (Barbadun, Butron, Oka, Lea, Deba, Urola,
309 Iñurritza, Oria, Bidasoa) since Nervion, Urumea and Oiartzun did not present saltmarsh
310 habitats. Overall dataset presented 31 plant species (Table S1). The estuarine occurrence
311 of *Zostera noltei* seagrass was updated from Valle et al. (2011). The flowering plants
312 have different dispersal modes (Table S1): 13 species (41%) are dispersed by water
313 exclusively or also by other modes, 5 by wind only, 4 by animals only, and 9 are
314 unassisted (i.e. seeds drop to the ground close to or beneath the parent plant). In terms
315 of dispersal efficiency, it is also important to take into account the pollinization modes
316 (Friess et al., 2011) (Table S1): 20 species (65%) by wind only, 7 by insects only, 2 by
317 water only, and 2 species use multiple modes.

318

319 The soft-bottom macroinvertebrate data were obtained from the abovementioned water
320 monitoring network (see Borja et al., 2009b; Pascual et al., 2011). The sampling
321 considered all macroinvertebrates taxa found in 3 replicates of 0.25 m² within the lower
322 to mid intertidal zone (*circa* 1-2 m above minimum astronomic low tide), except for
323 Nervion and Oiartzun, where the subtidal was sampled, using a van Veen grab of 0.07

324 m² (for details, see Borja et al., 2009b). Data considered here corresponded to the period
325 from 2002 to 2008, with samples taken once a year, in winter, over 12 estuaries
326 (Barbadun, Nervion, Butron, Oka, Lea, Artibai, Deba, Urola, Oria, Urumea, Oiartzun,
327 Bidasoa). The number of sampling sites per estuary was different (from 2 to 5 sites),
328 depending on the size of the estuary. For the analysis, species presence was counted
329 over all sites of an estuary. Only species taxonomically identified at, at least, the genus
330 level were considered. Overall dataset presented 321 species (Table S2). Among all
331 species found in Basque estuaries, 49 of them had information available on dispersion
332 mode of their larvae (Table S2): 39 species (80%) are planktonic, 4 planktonic and
333 benthic, 3 benthic only, 2 with no larvae phase, and 1 reptant.

334

335 The correlation between species similarity and oceanographic distance across estuaries
336 was estimated using Mantel test (Legendre and Legendre, 1998). In our case, the
337 number of species of each estuary greatly differs mainly because of different sampling
338 effort, as a consequence of different estuary size. This is due to the well-known species-
339 area relationship (e.g. Rosenzweig, 1995; Rumohr et al., 2001; Ricotta et al., 2002;
340 Sabetta et al., 2007). Hence, the quantification of similarity (i.e. β -diversity) is
341 problematic (Koleff et al., 2003). One of the most used similarity measure in equal
342 sampling areas is the Jaccard index (Koleff et al., 2003), which is the number of species
343 shared between the two sites (a), divided by the total number of species observed ($a + b$
344 + c), where b is the total number of species that occur in site 1 and c is the total number
345 of species that occur in site 1. If there is a large difference in richness between sites
346 (here, estuaries), Jaccard index will always be small. To address this problem, we used
347 two “narrow sense” dissimilarity indices that focus on compositional differences

348 independent of species richness gradients (Koleff et al., 2003): β_{sim} (Lennon et al.,
349 2001), and β_{-3} (Williams, 1996):

350
$$\beta_{sim} = 1 - \frac{a}{\min(b, c) + a}$$
 (Lennon et al., 2001)

351 which express the proportion of shared species with respect to the minimum number of
352 species of the two sites; and

353
$$\beta_{-3} = \frac{\min(b, c)}{a + b + c}$$
 (William, 1996, re-expressed by Koleff et al., 2003)

354 which was proposed to map species turnover adjusting for sites with different sizes.
355 Dissimilarity measures were converted to similarity indices (= 1 - dissimilarity).

356

357 Oceanographic distance was measured as in the case of *Z. noltei* and *C. edule*
358 populations. We also used Mantel tests to determine the correlation between species
359 similarity matrices and geographic distance. The rate of change (i.e. slope) in species
360 similarity with increasing geographic distance (i.e. distance decay) was calculated
361 fitting a linear model.

362

363 Since distance decay may also result from the relation between species composition and
364 environmental niche factors (Chust et al., 2013) of the estuary, partial Mantel tests were
365 undertaken to determine the relative contribution of geographic distance and
366 environmental distance in accounting for species composition similarity. Environmental
367 features comprised eight geomorphological and hydrological variables of the estuary
368 extracted from Uriarte et al. (2004): drainage area, mean river flow, estuary length,
369 estuary volume, subtidal volume, estuary area, intertidal area, and tidal prism. Pairwise
370 environmental distances was computed using Euclidean distance.

371

372 3. RESULTS

373

374 3.1 Genetic analysis of *Zostera noltei*

375

376 The number of alleles per marker showed values ranging from 11 to 18, H_e values
377 varied from a minimum of 0.29 to a maximum of 0.81 (meaning 1 total absence of
378 homozygotes). All loci show significant positive F_{IS} except for ZnF8 (Table 1). Null
379 allele frequencies estimated for *Z. noltei* loci were negligible ($r < 0.05$, according to
380 Chapuis and Estoup (2007)) or nearly negligible (0.06-0.07). Genotypic diversity (R)
381 ranged from a low (0.20) in Lea to a high value (1.00) in Arcachon and Santoña (Table
382 2). *Z. noltei* patches in Lea were dominated by a single clone, while in Ria de Vigo
383 almost each collected shoot was a genetically an unique individual. Observed
384 heterozygosity ranged from 0.26 to 0.62. There was significant deviation from Hardy-
385 Weinberg equilibrium as shown by positive F_{IS} values in all estuaries except for Lea,
386 Ribadesella and San Vicente de la Barquera, resulting in heterozygote deficiency.
387 Allelic richness, when standardized for the minimum genet number (Lea, $G=10$), was
388 2.65 in Bidasoa but much higher in Oka, Ria de Vigo and Lea.

389

390 Although no correlation was observed between geographic distance and genetic distance
391 ($r_M = 0.12$ and $p < 0.223$ for F_{ST} , $r_M = 0.04$ and $p = 0.294$ for D , see Fig. 2), populations
392 of *Zostera noltei* in the studied estuaries were highly differentiated as estimated by high
393 pairwise F_{ST} and D , indicating distinct and dynamically independent populations (Table
394 3). Moreover, estuaries closer than 65 km had F_{ST} and D lower than those separated
395 farther than that distance (t-test p-value = 0.0011, and 0.0002, respectively; see Fig. 2).
396 These results indicate low connectivity. Regarding patterns within estuaries, we

397 detected large clones in all three Basque estuaries (results not shown). Each site
398 contained at least one dominant clone covering an area of *ca.* 3 hectares (i.e. shoots
399 collected across the sampling area in different patches belonged to the same multilocus
400 genotype).

401

402 In STRUCTURE analysis, the most probable number of clusters (ΔK) when considering
403 all populations resulted in $K=2$ and a less supported solution of $K=3$ and $K=8$ (Fig. 3a).
404 The $K=2$ plot (Fig. 3b) shows clustering between Vigo and Bidasoa separated from the
405 others. However, after repeating the STRUCTURE analysis with only those two
406 populations resulted also in $K=2$ and clearly show that Bidasoa and Vigo are different.
407 With $K=8$, all populations are separated from each other, except Lea that is clustered
408 with Ribadesella (Fig. 3b). The $K=3$ plot, which has a similar $L(K)$ than $K=8$, shows
409 Vigo and Bidasoa together and also Santander and Santoña are clustered.

410

411 3.2 Genetic analysis of *Cerastoderma edule*

412

413 As stated previously, only nine microsatellites (out of the twelve that were genotyped)
414 were considered for *C. edule* population genetics. While the number of alleles per
415 marker showed values ranging from 11 to 51 (Table 4), H_e values varied from a
416 minimum of 0.418 to a maximum of 0.902 (meaning 1 total absence of homozygotes).
417 Non-negligible null allele frequencies were reported for seven of the microsatellite
418 markers (Table 4).

419

420 When comparing within genetic diversity among the different estuaries, sample from
421 Ria de Arousa showed the highest values of H_e and AR (Table 5). Nevertheless, only 3

422 out of 30 pairwise comparisons were statistically significant using Wilcoxon test:
423 Arousa vs. Deba for both H_e ($p = 0.028$) and AR ($p = 0.021$), and Arousa vs. Lea for AR
424 ($p = 0.028$).

425

426 Regarding genetic differentiation among estuaries, the pairwise comparison of fixation
427 index (F_{ST}) values showed significant values only when comparing Butron estuary
428 against both Deba and Arousa estuaries, and when comparing Arousa against Lea. This
429 last comparison became non-significant when applying null allele correction (Table 6).
430 The geographically farthest estuaries (Arousa and Bidasoa, Fig. 1) showed a F_{ST} value
431 of 0.0030 (non-significant; null allele corrected).

432

433 In the estuaries where more than one sampling point was surveyed, a pairwise F_{ST} test
434 was performed without obtaining any significant value. While regarding Oka estuary,
435 F_{ST} values among sampling locations ranged between 0.000 and 0.009 (11 sample
436 points), a range of 0.000-0.011 corresponded to Deba estuary (3 sample points) and a
437 sole value of 0.008, corresponding to the presence of two sampling points, was found
438 within Butron estuary. No correlation was found when comparing genetic and
439 geographical distances (for F_{ST} : $r_M = 0.017$; $p = 0.553$; for D : $r_M = -0.14$, $p = 0.627$).
440 STRUCTURE analysis was not performed since it has been described that the
441 performance in STRUCTURE to detect the correct clusters number within a given
442 dataset increases with F_{ST} , and that the test fails at F_{ST} values of 0.01-0.02 (Latch et al.
443 2006).

444

445 3.3 Floristic and faunal β -diversity across estuaries

446

447 The Mantel correlations between species similarity (for the two measures used: $1-\beta_{sim}$,
448 $1-\beta_{.3}$) and the oceanographic distance was statistically significant in plants, whilst in
449 macroinvertebrates were not statistically significant (Fig. 4, Table 7). Environmental
450 distances were not statistically correlated with species similarity in any of the taxa
451 group. The partial Mantel correlations between plant species similarity and the
452 oceanographic distance, partialling out environmental distance, were statistically
453 significant. This indicates that plants were dispersal limited. In contrast,
454 macroinvertebrates did not present a patchy structure, suggesting that species did not
455 have important movement barriers and populations (in average) were highly connected.

456

457 4. DISCUSSION

458

459 Results indicate that similarity of plant assemblages of saltmarshes and seagrass beds
460 decreases with oceanographic distance among estuaries, while is unrelated with
461 environmental niche factors. This is interpreted as plants are more isolated between
462 estuaries than soft-bottom macroinvertebrates. As it has been seen, 59% of salt-marsh
463 species are dispersed by modes other than water (i.e. wind, animals or unassisted) and
464 23% of species are pollinated by insects. Given the steep geomorphological
465 configuration of the Basque coast, with few and fragmentary salt-marshes restricted to
466 inner parts of the estuaries, and separated apart by hilly reliefs and seacliffs, it is
467 possible that most of these plant species (especially those having wind, animal or
468 unassisted modes of seed dispersal, and those pollinated by insects) are constrained to
469 spread (Friess et al., 2011). In contrast, most of the soft-bottom macroinvertebrates
470 (80%) spread through the planktonic larvae; this could explain the unstructured spatial
471 distribution of those communities, suggesting no dispersal barriers at this regional scale.

472 Chang et al. (2007) also concluded that medium to long distance diaspore dispersal is
473 rare in saltmarsh systems except in extreme weather events.

474

475 *Z. noltei* had highly population differentiation in north Iberian estuaries as estimated by
476 high pairwise F_{ST} and D values and clustering techniques. Although no correlation was
477 observed between geographic distance and seagrass genetic distance, estuaries closer
478 than 65 km had F_{ST} and D lower than those separated farther than that distance. Highly-
479 structured populations of this seagrass could be attributed to 1) small effective
480 population size (the resulting genetic drift may be higher than migration rates), and 2)
481 founder effects (*Z. noltei* is a clonal plant with potential long-lived generations). This
482 suggests a low recolonization rate in agreement with Thayer et al. (1975) and Diekmann
483 et al. (2005). In particular, Diekmann et al. (2005) found genetic population
484 differentiation in the West Iberian coast, as a result of habitat isolation, small
485 populations and near-shore currents. Friess et al. (2012) also pointed out that large-scale
486 exchange of genetic material is potentially constrained by distance between saltmarsh
487 populations due to poor diaspore buoyancy and flotation. The combination of limited
488 dispersal capacity of *Z. noltei*, its clonal strategy and the genetic drift, might be
489 problematic for long-term conservation perspective in the face of habitat changes, which
490 might exacerbate its declining situation (from 6 to 3 vegetated estuaries through the 20th
491 Century) within the Basque Country (Valle et al., 2011). At the community level, salt-
492 marshes and seagrass beds, and especially those species with low occurrence, and those
493 with animal-based dispersal mode or unassisted, can be also considered as vulnerable to
494 habitat changes because of dispersal limitation.

495

496 Pairwise F_{ST} and D results for *C. edule* individuals collected from five different Basque
497 estuaries and a NW Spain location showed a lack of genetic structure for this species in
498 the studied area. Therefore, *C. edule* in the Northern coast of the Iberian Peninsula
499 would conform a panmictic population. The high degree of polymorphism (denoted by
500 allelic richness and observed heterozygosity values) of the molecular markers applied in
501 this study implies a high discriminatory power when identifying sub-populations and
502 thus gives further support to the reported pattern. Moreover, present results point to a
503 high degree of connectivity among *C. edule* assemblies along the north Iberian estuaries
504 and suggest cockle being a highly mobile species, through the planktonic larvae
505 dispersal, that has been reported to last up to 3-6 weeks in the water column (Marine
506 Life Information Network; available at: <http://www.marlin.ac.uk>). On the other hand,
507 large effective population size may also explain the lack of significant structure. The
508 genetic analysis of *C. edule* coincides with the community analysis in terms of high
509 connectivity at population and community levels, respectively, suggesting no dispersal
510 barriers at this regional scale for the soft-bottom macroinvertebrates, most of them
511 spreading through planktonic larvae. Within this panmictic population of *C. edule* along
512 the north Iberian coast, all estuarine populations would contribute a certain percentage
513 of offspring to a larval pool with homogeneous redistribution to all populations (Selkoe
514 and Toonen, 2011). Lack of population structure applying a similar number of
515 microsatellites over long coastal areas has been also reported for other mollusc species
516 (e.g. Bester-van der Merwe et al., 2011; Donald et al., 2011; but see Coscia et al., 2013).
517 High connectivity would imply a high resilience and, therefore, a low vulnerability to
518 moderate environmental change and the putative loss of intertidal habitat. On the other
519 hand, high connectivity can also impede local adaptation (e.g., Lenormand, 2002; but
520 see Clarke et al., 2010 and Sanford and Kelly, 2011). On the contrary, warming of the

521 sea of 1.5 to 2.0 °C within the area (Chust et al., 2011) might trigger a reduction in the
522 dispersion period of planktonic bivalve larvae such as *C. edule*. Moreover, bivalves are
523 not able to regulate osmotic pressure and the intensification of extreme daily rainfall of
524 10%, would provoke punctual changes in salinity and intense mortality of the post-
525 larvae.

526

527 Our findings suggest that populations of species dwelling exclusively within the
528 estuarine soft-bottom intertidal zone, such as the seagrass *Z. noltei* and most of salt-
529 marsh plants, can be separated apart by large functional distances along the coastline. In
530 contrast, other estuarine sessile species but with planktonic larval dispersal and dwelling
531 different habitats, such as *C. edule* and other soft-bottom macroinvertebrates, could
532 exchange migrants from the metapopulation pool without strong barriers to gene flow.
533 In comparison with other ecosystems, the role played by dispersal limitation in
534 saltmarsh plants is similar to the one reported for inland plants (e.g. Condit et al. 2002,
535 Chust et al. 2006a,b), whilst the gene flow in intertidal soft-bottom macroinvertebrates
536 seems to move almost with no barriers as in most of the pelagic organisms (e.g., Kinlan
537 and Gaines, 2003; Cermeño and Falkowski, 2009).

538

539 The projected scenario of sea level rise induced by climate change (Chust et al., 2010),
540 could threaten the smallest populations of some of saltmarsh species. Although the
541 morphodynamic evolution of mudflats with sea level rise in the estuaries is site specific,
542 and saltmarshes are capable of responding to sea level rise being near equilibrium in
543 relation to sea level (e.g. Friedrichs and Perry, 2001; Friess et al., 2012; Leorri et al.,
544 2013), the suitable habitat for vegetation could be reduced in some cases. This is the
545 case, for instance, where the coastal margin is squeezed between the fixed landward

546 boundary (artificial or natural) and the sea level rise, i.e. the so-called ‘coastal squeeze’
547 effect (Schleupner, 2008). In the Basque estuaries, habitat squeeze induced by present
548 artificial barriers is expected to be more severe in the upper tidal zone than in the mid or
549 lower intertidal zone (Chust et al., 2011).

550

551 As commented, Basque estuaries have been dramatically transformed by anthropogenic
552 activities during the 20th Century (Cearreta et al., 2004), supporting many human
553 pressures (Borja et al., 2006a). However, in recent times, these estuaries have
554 experienced some recovery, due to water treatment (Borja et al., 2009a; 2010). Hence,
555 some habitat restoration experiments have been undertaken, after recovery of the
556 aquatic quality (Marquiegui and Aguirrezabalaga, 2009). Since genetic connectivity of
557 some species is very low, it may affect recovery and restoration success, as shown in
558 other areas for *Zostera* species (Campanella et al., 2010a; Tanaka et al., 2011).
559 Moreover, the low genetic diversity in *Z. noltei* at the estuary level weakens the
560 population’s ability to overcome physical disturbances (Campanella et al., 2010b),
561 including also habitat loss due to sea-level rise. In contrast, the connectivity of soft-
562 bottom macroinvertebrate communities indicate high recolonization capacity, in
563 agreement with that reported in azoic parts of some Basque estuaries after 10-15 years
564 (Borja et al., 2006b; 2009b; 2010). Hence, the proxies of connectivity used and
565 compared in the present study, based on genetic and ecological drift processes and
566 dispersal limitation factors, can be applied to assess the vulnerability of species to
567 global change; likewise, to help environmental managers to prioritise local restoration
568 plans for the most vulnerable species and habitats. Further research should focus on
569 applying the genetic analysis to a large number of species enough to represent the
570 diversity of estuarine communities, thus, in order to test if species dispersal limitation

571 drives similarly both genetic population structure and community patterns, as recently
572 shown in aquatic beetles (Baselga et al., 2013).

573

574 5. CONCLUSIONS

575

576 Two proxies of connectivity at community and species levels, based on genetic and
577 ecological neutral theories, respectively, provided similar results in estuarine biota.

578 Although salt-marsh and seagrass plants share a sedentary life history with soft-bottom
579 macroinvertebrates and they inhabit in a similar environment, the latter disperse at

580 larger scales and this is attributed to differences in biological dispersal modes between
581 these two taxa. The proxy at community level indicates that plant populations of

582 saltmarshes and seagrass beds are partially isolated among estuaries, as a result of
583 dispersal limitation. One of these species is the seagrass *Z. noltei*; their populations

584 within the Basque estuaries were found genetically differentiated. This suggests that
585 main processes operating to the seagrass populations are genetic drift and low gene

586 flow, especially for the most distant populations, probably because seagrass
587 colonisation mainly proceeds locally through clonal growth. The chances that

588 recolonization would occur naturally if populations get extinct would be highly
589 unlikely. In contrast, estuarine soft-bottom macroinvertebrates did not present a spatial

590 structure, suggesting that species do not have strong movement barriers and
591 populations, in average, are highly connected. Accordingly, the cockle (*C. edule*)

592 assemblages within the Basque estuaries were found genetically undifferentiated,
593 indicating they own to a unique panmictic population. Thus, *C. edule* seemed to be a

594 highly mobile species, probably throughout the planktonic larvae dispersed by ocean
595 currents, with a high recolonization capacity.

596

597 Overall, our findings suggest that *C. edule*, and other similar estuarine soft-bottom
598 macroinvertebrates, with planktonic larval dispersal strategies, would have a high
599 resilience capacity in the face of moderate changes within their habitats. In contrast,
600 saltmarsh plants and seagrass beds are especially vulnerable to these changes because of
601 their dispersal limitation, in particular those changes reducing species habitat extent
602 such as those induced by anthropogenic impacts and sea level rise. As shown, the
603 seagrass *Z. noltei* is a particularly threatened species within the Basque estuaries
604 because of fragmented, few and genetically low diverse populations. These findings can
605 help environmental managers to guide species and habitat restoration plans as well as
606 climate change adaptation strategies.

607

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609

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Figure legends

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1030

1031 Fig. 1. A) Estuaries of the Basque coast, C) Galician (Ria de Vigo and Ria de Arousa),
1032 Asturian (Rib.: Ribadesella), and Cantabrian (Barq: Sant Vicente de la Barquera, Santa.:
1033 Santander, Santo.: Santoña) sampling stations, in the northwestern Spain, and Arcachon
1034 (France) station. B) Detail of the minimum path distances (d) between adjacent
1035 estuaries. Stars: genetic sampling stations for *Z. noltei*. Circles: genetic sampling
1036 stations for *C. edule*.

1037

1038 Fig. 2. Pairwise genetic distance (F_{ST} and D) of *Z. noltei* and *C. edule* against the
1039 oceanographic distance. Estuaries closer than 65 km (discontinuous line) had F_{ST} and D
1040 for *Z. noltei* lower than those separated farther than that distance.

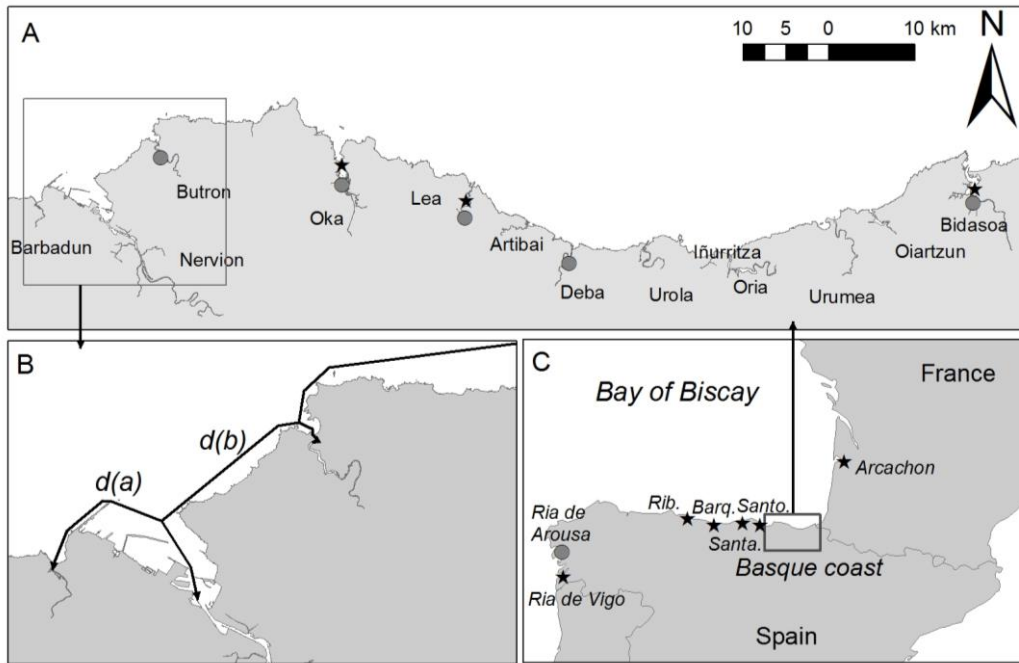
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1042 Fig. 3. A) $\Delta(K)$ as a function of K groups in STRUCTURE analysis. B) Barplot
1043 showing results from STRUCTURE with K groups (colors) for *Zostera noltei*. On the y -
1044 axis is the individual membership proportion.

1045

1046 Fig. 4. Pairwise species similarity ($1-\beta_{sim}$) of plants (saltmarshes and seagrass meadows)
1047 and benthic macroinvertebrates against the oceanographic distance. The Mantel
1048 correlation between species similarity and geographic distance are given in Table 7.

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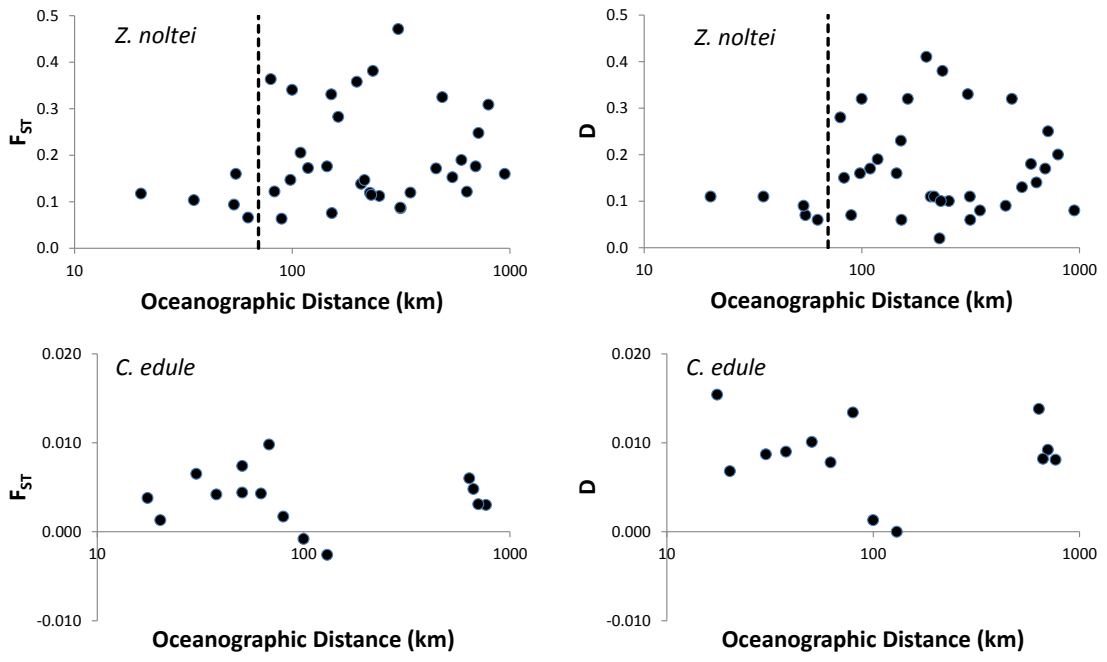


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1051 Fig. 1.

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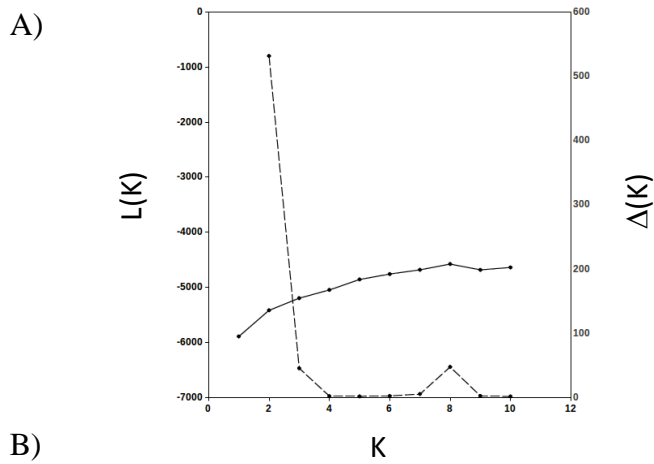
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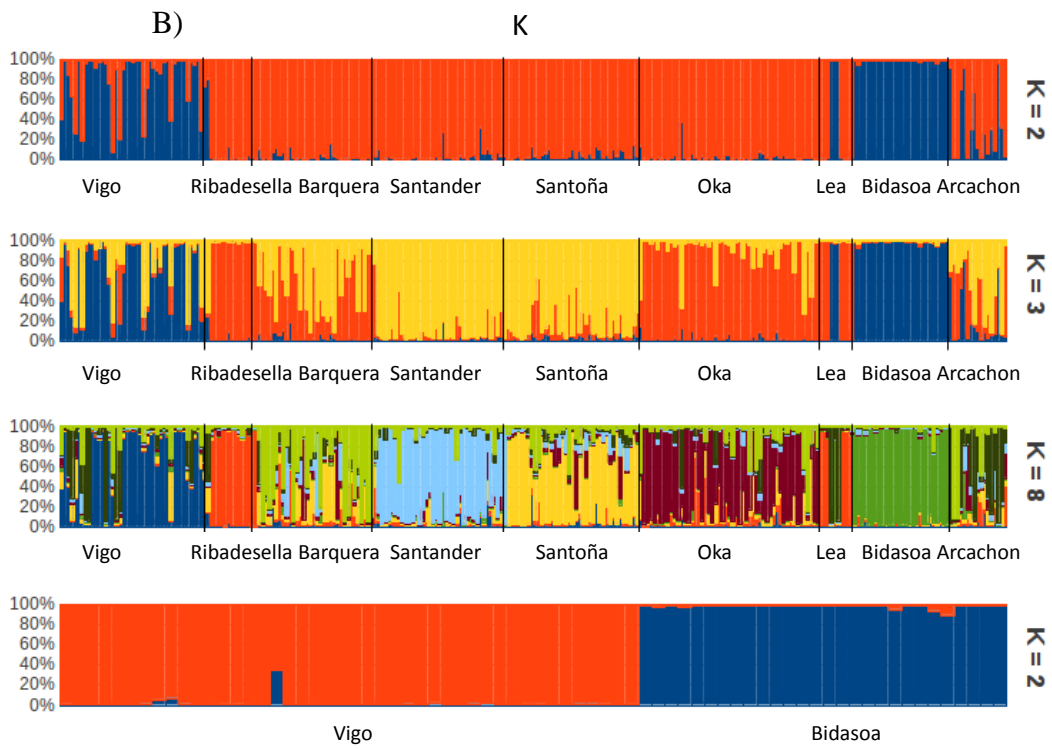
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1055 Fig. 2

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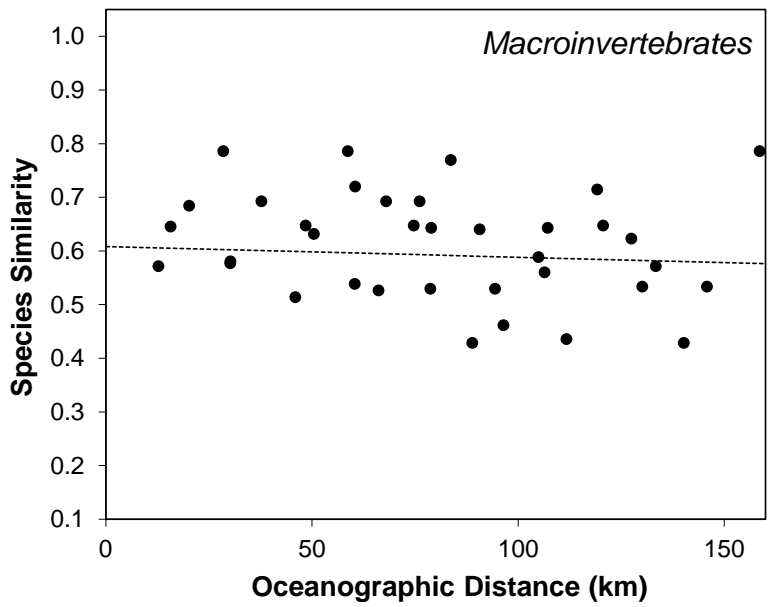
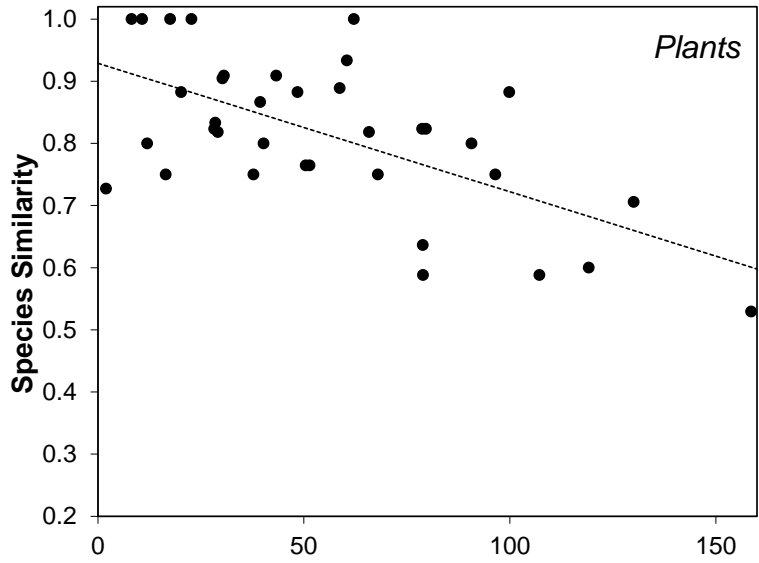
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1059 Fig. 3.

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Fig. 4

1072 Table 1. Allele number, observed heterozygosity (H_o), expected heterozygosity (H_e),
 1073 and inbreeding coefficient (F_{IS} ; *: $p < 0.05$, NS = Not Significant) for three sampling
 1074 locations of *Zostera noltei* from the Basque estuaries and one from a distant location in
 1075 the Galicia region (Ria de Vigo, NW Spain).

Locus	Number of Alleles/locus	H_e	H_o	F_{IS}	Null allele frequency
ZnB1	18	0.81	0.71	0.13*	0.02
ZnB8	18	0.71	0.47	0.35*	0.06
ZnD6	15	0.68	0.44	0.35*	0.07
ZnF11	15	0.64	0.46	0.27*	0.05
ZnF8	10	0.29	0.27	0.07 ^{NS}	0.01
ZnH10	15	0.74	0.60	0.20*	0.02
ZnH8	12	0.64	0.55	0.14*	0.06

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1079 Table 2. Number of collected individuals (N), number of genets (G), genotypic diversity
 1080 (R) and standardized genetic diversity or allelic richness (AR), inbreeding coefficient,
 1081 and observed (H_o) and expected (H_e) heterozygosities for three sampling locations of
 1082 *Zostera noltei* from the Basque estuaries and one from a distant location in the Galicia
 1083 region (Ria de Vigo, NW Spain).

Location	N	G	R	AR (G=10)	H_e	H_o	F_{IS}
Vigo	48	44	0.91	4.343 ± 0.485	0.557	0.508	0.0993*
Ribadesella	40	14	0.33	2.654 ± 0.112	0.350	0.415	-0.1496*
San Vicente de la Barquera	50	35	0.69	4.463 ± 0.335	0.537	0.548	-0.0076
Santander	40	38	0.95	4.623 ± 0.305	0.587	0.544	0.0867
Santoña	40	40	1.00	5.209 ± 0.404	0.646	0.615	0.0605
Oka	70	52	0.74	4.263 ± 0.422	0.537	0.492	0.0934*
Lea	47	10	0.20	3.857 ± 0.000	0.487	0.582	-0.1379
Bidasoa	54	28	0.51	2.651 ± 0.181	0.310	0.263	0.1716
Arcachon	17	17	1.00	5.08 ± 0.336	0.569	0.424	0.2864

1084 * Significant F_{IS} ($p < 0.05$)

1085

1086 Table 3. Pairwise F_{ST} and D values for *Zostera noltei*. Significant F_{ST} (at $p < 0.05$) are in
 1087 bold (see Materials and Methods for null allele correction and significance testing).

F_{ST}	Vigo	Ribadesella	Barquera	Santander	Santoña	Oka	Lea	Bidasoa	Arcachon
Vigo	-	0.32	0.15	0.19	0.12	0.18	0.25	0.31	0.16
Ribadesella		-	0.16	0.21	0.18	0.14	0.12	0.47	0.17
Barquera			-	0.09	0.06	0.08	0.15	0.38	0.09
Santander				-	0.10	0.15	0.17	0.36	0.12
Santoña					-	0.07	0.12	0.28	0.09
Oka						-	0.12	0.34	0.11
Lea							-	0.36	0.11
Bidasoa								-	0.33
Arcachon									-

D	Vigo	Ribadesella	Barquera	Santander	Santoña	Oka	Lea	Bidasoa	Arcachon
Vigo	-	0.32	0.13	0.18	0.14	0.17	0.25	0.20	0.08
Ribadesella		-	0.07	0.17	0.16	0.11	0.02	0.33	0.09
Barquera			-	0.09	0.07	0.06	0.11	0.38	0.06
Santander				-	0.11	0.16	0.19	0.41	0.08
Santoña					-	0.06	0.15	0.32	0.11
Oka						-	0.11	0.32	0.10
Lea							-	0.28	0.10
Bidasoa								-	0.23
Arcachon									-

1088

1089 Table 4. Allele number, observed heterozygosity (H_o), expected heterozygosity (H_e),
 1090 inbreeding coefficient (F_{IS} ; *: $p < 0.001$, NS: Not Significant) and estimated null allele
 1091 frequency values for each of the markers considered for population genetics analysis in
 1092 *C. edule* (see Material and Methods for further information). According to Chapuis and
 1093 Estoup (2007) non-negligible null allele frequencies (in bold) are categorized as
 1094 moderate ($0.05 \leq r < 0.20$) or large ($r \geq 0.20$).

Microsatellite	Allele number	H_o	H_e	F_{IS}	Null allele frequency
CeATC1-5	26	0.445	0.902	0.507*	0.240
CeATC1-36	11	0.346	0.418	0.171*	0.075
CeATC2-4	15	0.400	0.682	0.413*	0.171
CeATC2-11	51	0.658	0.887	0.259*	0.122
CeATC2-34	15	0.620	0.790	0.215*	0.095
CeATC2-44	11	0.600	0.633	0.051 ^{NS}	0.030
CeATC1-22	11	0.710	0.797	0.109*	0.049
CeATC1-54	31	0.426	0.794	0.464*	0.202
CeATC2-12	13	0.221	0.666	0.668*	0.274

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1096

1097 Table 5. Expected heterozygosity (H_e) and allelic richness (AR) when pooling
1098 individuals per estuary in *C. edule*.

Estuary	H_e	AR
Bidasoa	0.722 ± 0.160	6.21 ± 2.37
Deba	0.729 ± 0.154	6.51 ± 2.30
Lea	0.711 ± 0.152	5.91 ± 2.28
Oka	0.725 ± 0.155	6.43 ± 2.38
Butron	0.725 ± 0.152	6.66 ± 2.41
Ria de Arousa	0.748 ± 0.142	7.15 ± 2.73

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1100

1101 Table 6. Pairwise F_{ST} values with (below diagonal) and without (above diagonal)
 1102 applying null allele correction in *C. edule* (see Material and Methods; significant values
 1103 in bold). Matrix below show pairwise D values in *C. edule*.

F_{ST}	Bidasoa	Deba	Lea	Oka	Butron	Arousa
Bidasoa	-	0.0040	0.0017	-0.0006	-0.0044	0.0024
Deba	0.0043	-	0.0065	0.004	0.0096	0.0038
Lea	0.0017	0.0038	-	0.0023	0.0039	0.0121
Oka	-0.0008	0.0042	0.0013	-	0.0053	0.0055
Butron	-0.0026	0.0098	0.0044	0.0065	-	0.0057
Arousa	0.0030	0.0031	0.0074	0.0048	0.006	-

D	Bidasoa	Deba	Lea	Oka	Butron	Arousa
Bidasoa	-	0.0078	0.0134	0.0013	0.0000	0.0081
Deba		-	0.0154	0.0090	0.0218	0.0092
Lea			-	0.0068	0.0101	0.0301
Oka				-	0.0087	0.0082
Butron					-	0.0138
Arousa						-

1104

1105 Table 7. Mantel and partial Mantel tests between species similarity indices ($1-\beta_{sim}$,
 1106 $1-\beta_{.3}$), oceanographic distance and environmental variables. r_M : Mantel correlation; p :
 1107 probability of significance.

		$1-\beta_{sim}$		$1-\beta_{.3}$	
		r_M	p	r_M	p
Plants (saltmarshes and seagrass beds)	Species × Distance	-0.63	<0.001	-0.58	0.001
	Species × Environ.	-0.15	0.176	-0.14	0.259
	Species × Distance (Environ. partially out)	-0.62	0.002	-0.57	0.002
Macroinvertebrates	Species × Distance	-0.06	0.323	-0.01	0.519
	Species × Environ.	-0.08	0.673	-0.29	0.937
	Species × Distance (Environ. partially out)	na	na	na	na

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1111 Supplementary material

1112

1113 Table S1. Flowering plants in Basque estuaries, polinization and dispersal modes, and
 1114 reproduction type.

1115

Species	Number of estuaries	Polinization modes	Dispersal modes	Vegetative reproduction	References and/or source
<i>Apium butronensis</i>	1	Insects	Water	No	Tela Botanica ¹
<i>Apium graveolens</i>	5	Insects	Water	No	Bañares <i>et al.</i> (2004)
<i>Aster tripolium</i>	9	Insects	Wind	No	Tela Botanica ¹
<i>Carex extensa</i>	9	Wind	Unassisted	NA	Tela Botanica ¹
<i>Carex punctata</i>	2	Wind	Unassisted	NA	Tela Botanica ¹
<i>Cochlearia aestuaria</i>	4	Insects	Unassisted	NA	Tela Botanica ¹
<i>Festuca littoralis</i>	7	Wind	Unassisted	NA	Tela Botanica ¹
<i>Glaux maritima</i>	5	Wind	Unassisted	NA	Tela Botanica ¹
<i>Halimione portulacoides</i>	8	Wind	Wind Water	Yes	Tela Botanica ¹
<i>Inula crithmoides</i>	7	Insects	Wind	NA	Tela Botanica ¹
<i>Juncus gerardi</i>	5	Wind	Animal	NA	Tela Botanica ¹
<i>Juncus maritimus</i>	9	Wind	Animal	NA	Tela Botanica ¹
<i>Limonium humile</i>	2	Insects Wind	Animal	Yes	Tela Botanica ¹
<i>Limonium ovalifolium</i>	1	Insects	Wind	Yes	Tela Botanica ¹
<i>Limonium vulgare</i>	4	Insects Wind	Unassisted	NA	Tela Botanica ¹
<i>Parapholis strigosa</i>	2	Wind	Unassisted	NA	Tela Botanica ¹
<i>Puccinellia maritima</i>	8	Wind	Unassisted	Yes	Tela Botanica ¹
<i>Ruppia maritima</i>	3	Water	Water Wind Animal	Yes	Tela Botanica ¹
<i>Salicornia dolichostachya</i>	5	Wind	Water	NA	Tela Botanica ¹
<i>Salicornia lutescens</i>	4	Wind	Water	NA	Tela Botanica ¹
<i>Salicornia obscura</i>	2	Wind	Water	NA	Tela Botanica ¹
<i>Salicornia ramosissima</i>	2	Wind	Water	NA	Tela Botanica ¹
<i>Sarcocornia fruticosa</i>	4	Wind	Water	NA	Tela Botanica ¹
<i>Sarcocornia perennis</i>	3	Wind	Water	NA	Tela Botanica ¹
<i>Scirpus compactus</i>	8	Wind	Wind	NA	Tela Botanica ¹
<i>Spartina maritima</i>	3	Wind	Unassisted	Yes	Tela Botanica ¹
<i>Spergularia media</i>	7	Insects	Wind	NA	Tela Botanica ¹
<i>Suaeda albescens</i>	2	Wind	Water Animal	NA	Tela Botanica ¹

Species	Number of estuaries	Polinization modes	Dispersal modes	Vegetative reproduction	References and/or source
<i>Suaeda maritima</i>	3	Wind	Water Animal	NA	Tela Botanica ¹
<i>Triglochin maritima</i>	8	Wind	Animal	Yes	Tela Botanica ¹
<i>Zostera noltei</i>	3	Water	Water Animal	Yes	BIOTIC ²

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¹ Tela Botanica – Le réseau de la botanique francophone. Available from: <http://www.tela-botanica.org/site:botanique>; searched on January 2012.

² BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. [Cited insert date] Available from: www.marlin.ac.uk/biotic; searched on January 2012.

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Table S2. Macroinvertebrate species in Basque estuaries, dispersal modes and dispersion distance.

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Abarenicola claparedi</i>	2			
<i>Abludomelita obtusata</i>	1			Marine Life Information Network ¹
<i>Abra alba</i>	2	Planktonic	>10 km	Marine Life Information Network ¹
<i>Abra prismatica</i>	3			
<i>Abyssoninoe hibernica</i>	2			
<i>Acanthocardia paucicostata</i>	2			
<i>Acanthocardia tuberculata</i>	1			
<i>Achelia</i> sp.	1			
<i>Alkmaria romijni</i>	9	Benthic	10-100 m	Marine Life Information Network ¹
<i>Allomelita pellucida</i>	2			Marine Life Information Network ¹
<i>Ampelisca brevicornis</i>	1			
<i>Ampelisca tenuicornis</i>	1			
<i>Ampharete finmarchica</i>	2			
<i>Amphiglena mediterranea</i>	1			
<i>Amphipholis squamata</i>	2			
<i>Amphiura filiformis</i>	1	Planktonic	>10 km	Marine Life Information Network ¹
<i>Anapagurus hyndmanni</i>	2			
<i>Anapagurus laevis</i>	1			
<i>Antalis novemcostata</i>	1			
<i>Anurida maritima</i>	11			
<i>Aonides oxycephala</i>	3			
<i>Aonides paucibranchiata</i>	2	Planktonic		Rodriguez (2003)
<i>Aphelochaeta marioni</i>	1			Marine Life Information Network ¹
<i>Aponuphis bilineata</i>	1			
<i>Aricidea (Acmira) cerrutii</i>	1			
<i>Aricidea suecica meridionalis</i>	1			
<i>Armandia cirrhosa</i>	1	Planktonic		Marine Life Information Network ¹
<i>Balanus</i> sp.	1	Planktonic	>10 km	Marine Life Information Network ¹
<i>Bathyporeia elegans</i>	2			
<i>Bathyporeia Pelagica</i>	1		10-100 m	Marine Life Information Network ¹
<i>Bathyporeia pilosa</i>	1			
<i>Bathyporeia sarsi</i>	2			Marine Life Information Network ¹
<i>Bela nebula</i>	1			
<i>Bittium reticulatum</i>	2			
<i>Bledius</i> sp.	1			
<i>Boccardia polybranchia</i>	1			
<i>Boccardia proboscidea</i>	1	Planktonic and/or Benthic		Marine Life Information Network ¹
<i>Boccardia semibranchiata</i>	5			
<i>Boccardiella ligerica</i>	1			
<i>Bodotria scorpioides</i>	1			Marine Life Information Network ¹

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Branchiomaldane sp.</i>	1			
<i>Brania pusilla</i>	1			
<i>Brissopsis lyrifera</i>	1	Planktonic	>10 km	Marine Life Information Network ¹
<i>Callianassa subterranea</i>	1	Planktonic and/or Benthic		Marine Life Information Network ¹
<i>Capitella capitata</i>	11	Planktonic and/or Benthic		Marine Life Information Network ¹
<i>Caprella acanthifera</i>	1			Marine Life Information Network ¹
<i>Caprella penantis</i>	1			Marine Life Information Network ¹
<i>Carcinus maenas</i>	8	Planktonic	>10 km	Marine Life Information Network ¹
<i>Caulleriella alata</i>	3			
<i>Caulleriella bioculata</i>	1			
<i>Caulleriella killariensis</i>	2			
<i>Caulleriella zetlandica</i>	1			
<i>Cavernularia pusilla</i>	1			
<i>Cerastoderma edule</i>	8	Planktonic		Marine Life Information Network ¹
<i>Cerastoderma glaucum</i>	4	Planktonic		Marine Life Information Network ¹
<i>Cerebratulus marginatus</i>	1			
<i>Cerianthus sp.</i>	2		>10 km	Langmead <i>et al.</i> (2010)
<i>Chaetozone gibber</i>	2			
<i>Chaetozone setosa</i>	1			
<i>Chamelea gallina</i>	1			
<i>Chartella papyracea</i>	1			
<i>Chone sp.</i>	1	Planktonic		Rodriguez (2003)
<i>Chrysallida terebellum</i>	1			
<i>Chthamalus montagui</i>	1		>10 km	Marine Life Information Network ¹
<i>Cirriiformia tentaculata</i>	2			
<i>Cirrophorus furcatus</i>	1			
<i>Corbula gibba</i>	2	Planktonic		Marine Life Information Network ¹
<i>Corophium multisetosum</i>	10			Günter (1992)
<i>Corophium urdaibaiense</i>	1			Günter (1992)
<i>Corophium volutator</i>	2		<10 m	Marine Life Information Network ¹
<i>Cossura sp.</i>	2			
<i>Crassostrea gigas</i>	3	Planktonic		Marine Life Information Network ¹
<i>Cumopsis fagei</i>	2			Marine Life Information Network ¹
<i>Cumopsis longipes</i>	1			Marine Life Information Network ¹
<i>Cyathura carinata</i>	11			Reise (2003)
<i>Cyclope neritea</i>	2			Minelli (2009)
<i>Cylichna cylindracea</i>	2			
<i>Desdemona ornata</i>	5			
<i>Diastylis bradyi</i>	1			Marine Life Information Network ¹
<i>Diogenes pugilator</i>	1			
<i>Diopatra neapolitana</i>	2			
<i>Diplocirrus glaucus</i>	1			
<i>Dipolydora flava</i>	2			

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Dispio uncinata</i>	1			
<i>Dorvillea sp.</i>	1			
<i>Dosinia lupinus</i>	4			
<i>Echinocardium cordatum</i>	1	Planktonic		Marine Life Information Network ¹
<i>Echinogammarus stoerensis</i>	1			Marine Life Information Network ¹
<i>Edwardsia sp.</i>	2			
<i>Ensis siliqua</i>	1			
<i>Epitonium clathrus</i>	1			
<i>Epizoanthus sp.</i>	1			
<i>Eteone foliosa</i>	1			
<i>Euclymene oerstedii</i>	1			
<i>Eudorella truncatula</i>	1			Marine Life Information Network ¹
<i>Eumida bahusiensis</i>	2			
<i>Eumida ockelmanni</i>	1			
<i>Eumida sanguinea</i>	1			
<i>Eurydice affinis</i>	2			Marine Life Information Network ¹
<i>Eurydice pulchra</i>	11		100-1000 m	Marine Life Information Network ¹
<i>Eurydice spinigera</i>	1			Marine Life Information Network ¹
<i>Euspira pulchella</i>	2			
<i>Ficopomatus enigmaticus</i>	3	Planktonic		Marine Life Information Network ¹
<i>Gammarella fucicola</i>	1			Marine Life Information Network ¹
<i>Gammarus chevreuxi</i>	1		100-1000 m	Marine Life Information Network ¹
<i>Gari depressa</i>	1			
<i>Gastrosaccus spinifer</i>	2			Marine Life Information Network ¹
<i>Glycera alba</i>	1			
<i>Glycera convoluta</i>	5			
<i>Glycera dayi</i>	1			
<i>Glycera gigantea</i>	1			
<i>Glycera lapidum</i>	1			
<i>Glycera rouxi</i>	2			
<i>Glycera unicornis</i>	3			
<i>Glycymeris glycymeris</i>	1			
<i>Gnathia sp.</i>	1			Marine Life Information Network ¹
<i>Goniada maculata</i>	1			
<i>Grania sp.</i>	1			
<i>Harpinia pectinata</i>	1			Marine Life Information Network ¹
<i>Haustorius arenarius</i>	11			Marine Life Information Network ¹
<i>Hediste diversicolor</i>	11		0-10 km	Marine Life Information Network ¹
<i>Hemigrapsus penicillatus</i>	8	Planktonic		Dauvin <i>et al.</i> (2009)
<i>Hemilepton nitidum</i>	2			
<i>Hesionura elongata</i>	1			
<i>Heteromastus filiformis</i>	7			Günter (1992)
<i>Heterotanais oerstedii</i>	1			Marine Life Information Network ¹

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Hiatella arctica</i>	1			
<i>Hippomedon denticulatus</i>	1			Marine Life Information Network ¹
<i>Hyalia vitrea</i>	3			
<i>Hydractinia carnea</i>	1	Benthic		Marine Life Information Network ¹
<i>Hydrobia ulvae</i>	11	Planktonic and/or benthic	>10 km	Marine Life Information Network ¹
<i>Idotea sp.</i>	1	No larval phase		Marine Life Information Network ¹
<i>Iphinoe serrata</i>	1			Marine Life Information Network ¹
<i>Iphinoe tenella</i>	3			Marine Life Information Network ¹
<i>Jaera (Jaera) albifrons</i>	1			Marine Life Information Network ¹
<i>Jassa marmorata</i>	2	No larval phase		Marine Life Information Network ¹
<i>Kellia suborbicularis</i>	2			
<i>Kurtiella bidentata</i>	3			
<i>Labidoplax digitata</i>	1			
<i>Lagis koreni</i>	2	Planktonic		Rodriguez (2003)
<i>Laonice cirrata</i>	1	Planktonic		Rodriguez (2003)
<i>Lekanesphaera hookeri</i>	6			Marine Life Information Network ¹
<i>Lekanesphaera levii</i>	1			Marine Life Information Network ¹
<i>Lekanesphaera rugicauda</i>	4			Marine Life Information Network ¹
<i>Lepidochitona (Lepidochitona) cinerea</i>	1			
<i>Leptocheirus pilosus</i>	2			
<i>Leptognathiidae sp.</i>	1			
<i>Lepton squamosum</i>	1			
<i>Leptopentacta elongata</i>	1			
<i>Leptosynapta inhaerens</i>	1			
<i>Leucothoe incisa</i>	1			Marine Life Information Network ¹
<i>Levinsenia gracilis</i>	1			
<i>Liocarcinus sp.</i>	1	Planktonic		Marine Life Information Network ¹
<i>Loripes lacteus</i>	2			
<i>Lucinella divaricata</i>	1			
<i>Lumbrineris cingulata</i>	2			
<i>Lumbrineris latreilli</i>	1			
<i>Lumbrineris sp.</i>	2			
<i>Lysidice ninetta</i>	1			
<i>Magelona alleni</i>	1		>10 km	Marine Life Information Network ¹
<i>Magelona johnstoni</i>	2		>10 km	Marine Life Information Network ¹
<i>Malacoceros fuliginosus</i>	10	Planktonic		Rodriguez (2003)
<i>Malmgreniella andreaopolis</i>	1			
<i>Manayunkia aestuarina</i>	10			Reise (2003)
<i>Mangelia costulata</i>	1			
<i>Marenzelleria sp.</i>	2			
<i>Marphysa bellii</i>	1			
<i>Mediomastus fragilis</i>	5			Marine Life Information Network ¹
<i>Melarhaphe neritoides</i>	1			

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Melinna palmata</i>	2			
<i>Melita hergensis</i>	1			Marine Life Information Network ¹
<i>Melita palmata</i>	7			Marine Life Information Network ¹
<i>Micromaldane ornithochaeta</i>	1			
<i>Microphthalmus pseudoaberrans</i>	2	Planktonic		Rodriguez (2003)
<i>Microspio atlantica</i>	3			
<i>Mitrella sp.</i>	1			
<i>Modiolus adriaticus</i>	1		>10 km	Marine Life Information Network ¹
<i>Monocorophium ascherusicum</i>	3			Marine Life Information Network
<i>Monocorophium insidiosum</i>	1			Marine Life Information Network ¹
<i>Monticellina dorsobranchialis</i>	1			
<i>Musculus costulatus</i>	1			
<i>Musculus discors</i>	1	Reptant		Marine Life Information Network ¹
<i>Myosotella myosotis</i>	1			
<i>Myrianida sp.</i>	1			
<i>Mysta picta</i>	1			
<i>Mytilaster minimus</i>	1			
<i>Mytilus galloprovincialis</i>	1	Planktonic	>10 km	Marine Life Information Network ¹
<i>Nassarius incrassatus</i>	1			
<i>Nassarius nitidus</i>	2			
<i>Nassarius pygmaeus</i>	3			
<i>Nassarius reticulatus</i>	4			Marine Life Information Network ¹
<i>Neanthes caudata</i>	3			
<i>Nematonereis hebes</i>	1			
<i>Neoamphitrite edwardsi</i>	1			
<i>Nephtys cirrosa</i>	6			
<i>Nephtys cuvieri</i>	5			
<i>Nephtys hombergii</i>	4	Planktonic		Marine Life Information Network ¹
<i>Nephtys incisa</i>	1			
<i>Nephtys kersivalensis</i>	3			
<i>Nereis lamellosa</i>	1	Planktonic		Rodriguez (2003)
<i>Notocirrus scoticus</i>	1			
<i>Notomastus latericeus</i>	4			Marine Life Information Network ¹
<i>Nototropis falcatus</i>	1			Marine Life Information Network ¹
<i>Nucula sulcata</i>	2			
<i>Obelia dichotoma</i>	1	Planktonic	>10 km	Marine Life Information Network ¹
<i>Ocenebra erinaceus</i>	1			
<i>Ophelia limacina</i>	1			
<i>Ophiodromus flexuosus</i>	2			
<i>Ophryotrocha baccii</i>	1			
<i>Orbinia latreillii</i>	1			
<i>Oriopsis armandi</i>	1			
<i>Owenia fusiformis</i>	2		>10 km	Marine Life Information Network ¹

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Pachygrapsus marmoratus</i>	3			
<i>Pagurus prideaux</i>	1			
<i>Paradoneis armata</i>	3			
<i>Paradoneis ilvana</i>	1			
<i>Paradoneis lyra</i>	3			
<i>Paragnathia formica</i>	7	Planktonic		Tinsley and Reilly (2002)
<i>Paramphitrite tetrabanchia</i>	3			
<i>Parapionosyllis brevicirra</i>	1			
<i>Parapionosyllis cabezali</i>	1			
<i>Parapionosyllis elegans</i>	1			
<i>Parapionosyllis gestans</i>	1			
<i>Parapionosyllis minuta</i>	1			
<i>Parasinelobus chevreuxi</i>	1			Marine Life Information Network ¹
<i>Pariambus typicus</i>	2			Marine Life Information Network ¹
<i>Parvicardium pinnulatum</i>	1			
<i>Parvicardium scabrum</i>	11			
<i>Pectinaria (Amphictene) auricoma</i>	1			
<i>Perinereis cultrifera</i>	1			
<i>Pestarella tyrrhena</i>	1			
<i>Petricolaria pholadiformis</i>	1			
<i>Phascolion (Phascolion) strombus strombus</i>	2			
<i>Philine sp.</i>	1		>10 km	Marine Life Information Network ¹
<i>Pholas dactylus</i>	1			
<i>Phtisica marina</i>	1			Marine Life Information Network ¹
<i>Phyllodoce (Anaitides) groenlandica</i>	1			
<i>Phyllodoce lineata</i>	2			
<i>Phyllodoce maculata</i>	2			
<i>Phyllodoce mucosa</i>	2	Planktonic		Rodriguez (2003)
<i>Phylo foetida</i>	1			
<i>Pilumnus hirtellus</i>	1			
<i>Pinnotheres pisum</i>	1			
<i>Pionosyllis sp.</i>	1			
<i>Pisione remota</i>	1			
<i>Pista cristata</i>	1			
<i>Plakosyllis brevipes</i>	1			
<i>Podarkeopsis capensis</i>	2			
<i>Polycirrus aurantiacus</i>	1			
<i>Polycirrus tenuisetis</i>	1			
<i>Polydora ciliata</i>	4	Planktonic	>10 km	Marine Life Information Network ¹
<i>Polydora cornuta</i>	8	Planktonic		Rodriguez (2003); Levin (1984)
<i>Polydora tentaculata</i>	1			
<i>Polyophthalmus pictus</i>	1			

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Prionospio fallax</i>	5			
<i>Prionospio multibranchiata</i>	3			
<i>Prionospio pulchra</i>	1			
<i>Prionospio steenstrupi</i>	4			
<i>Processa nouveli</i>	1			
<i>Prosphaerosyllis campoyi</i>	1			
<i>Protodorvillea kefersteini</i>	2			
<i>Protodrilus sp.</i>	1			
<i>Pseudocuma (Pseudocuma) longicorne</i>	1			Marine Life Information Network ¹
<i>Pseudomystides limbata</i>	1	Planktonic		Rodriguez (2003)
<i>Pseudopolydora paucibranchiata</i>	5	Planktonic		Levin (1983, 1984)
<i>Pseudopolydora pulchra</i>	2			
<i>Pseudopythina macandrewi</i>	1			
<i>Pygospio elegans</i>	4	Planktonic		Rodriguez (2003); Pedersen (2008)
<i>Ringicula auriculata</i>	1			
<i>Ruditapes decussatus</i>	10	Planktonic		Borsa <i>et al.</i> (1994)
<i>Ruditapes philippinarum</i>	4			
<i>Salmacina dysteri</i>	1			
<i>Schistomeringos rudolphii</i>	1			
<i>Schistomeringos sp.</i>	1			
<i>Scolaricia sp.</i>	5			
<i>Scolecipis (Scolecipis) squamata</i>	2	Planktonic		Rodriguez (2003)
<i>Scolecipis cantabra</i>	1	Planktonic		Rodriguez (2003)
<i>Scolecipis cirratulus</i>	1			
<i>Scrobicularia plana</i>	11	Planktonic		Santos <i>et al.</i> (2011)
<i>Semibalanus balanoides</i>	1	Planktonic	>10 km	Marine Life Information Network ¹
<i>Siphonoecetes (Centraloecetes) kroyeranus</i>	1			Marine Life Information Network ¹
<i>Solen capensis</i>	2			
<i>Sphaerosyllis bulbosa</i>	1			
<i>Sphaerosyllis hystrix</i>	1			
<i>Spio decoratus</i>	3	Planktonic	>10 km	Marine Life Information Network ¹
<i>Spio martinensis</i>	3	Planktonic	>10 km	Marine Life Information Network ¹
<i>Spiochaetopterus costarum</i>	3			
<i>Spiochaetopterus solitarius</i>	1			
<i>Spiophanes bombyx</i>	1	Planktonic		Rodriguez (2003)
<i>Spiophanes kroyeri</i>	2			
<i>Spisula elliptica</i>	1			
<i>Spisula subtruncata</i>	2			
<i>Sternaspis scutata</i>	1			
<i>Sthenelais boa</i>	1			
<i>Streblosoma bairdi</i>	1			
<i>Streblospio shrubsolii</i>	11	Benthic		Qian and Dahms (2005)
<i>Streptosyllis websteri</i>	1			

Species name	Number of estuaries	Dispersal modes	Distance	Reference and/or source
<i>Syllis amica</i>	1			
<i>Syllis gracilis</i>	2			
<i>Syllis parapari</i>	1			
<i>Syllis pontxioi</i>	1			
<i>Synchelidium maculatum</i>	1			Marine Life Information Network ¹
<i>Tapes (Tapes) rhomboides</i>	4			
<i>Tellinmya ferruginosa</i>	2			
<i>Tellina compressa</i>	4			
<i>Tellina donacina</i>	4			
<i>Tellina pygmaea</i>	1			
<i>Tellina tenuis</i>	3			
<i>Terebella lapidaria</i>	2			
<i>Terebellides stroemii</i>	1			
<i>Tetrastemma sp.</i>	1			
<i>Tharyx sp.</i>	2			
<i>Thyasira flexuosa</i>	1		<10 m	Marine Life Information Network ¹
<i>Timoclea ovata</i>	2			
<i>Tubulanus polymorphus</i>	4			
<i>Turbonilla acuta</i>	1			
<i>Upogebia deltaura</i>	1			
<i>Upogebia pusilla</i>	4			
<i>Urothoe brevicornis</i>	2			Marine Life Information Network ¹
<i>Urothoe pulchella</i>	1			Marine Life Information Network ¹
<i>Venus casina</i>	1			

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