

Spatial versus Temporal Structure: Implications of Inter-haul Variation and Relatedness in the North East Atlantic Spurdog *Squalus acanthias*.

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1 Abstract:

2 1) Micro-population processes, such as gene flow, operating within geographic regions
3 are often poorly understood despite their potential to impact stock structure and
4 sustainability. This is especially true for highly mobile species, such as elasmobranchs,
5 where the potential for spatial overlap of regional populations is increased due to
6 higher movement capabilities. A lack of information on these processes means
7 management plans rarely consider spatio-temporal structure.

8 2) Spurdog (*Squalus acanthias*) are globally distributed throughout temperate regions
9 yet there is an apparent lack of gene flow between ocean basins. In the North-east
10 Atlantic, there is little work on gene flow within the region which is currently managed
11 as a single stock that is estimated to be at 19% compared to 1905. Some evidence from
12 this region suggests population processes which have the potential to cause
13 structuring.

14 3) Population structure of NE Atlantic spurdog was investigated using an 828-bp
15 fragment of the mitochondrial DNA control region and seven focal polymorphic
16 microsatellite markers. Samples from 295 individuals from eight locations throughout
17 UK waters were used in this study.

18 4) Overall, mitochondrial sequences suggested some regional differentiation. Genetic
19 diversity was comparable with that reported in previous studies of spurdog. Haplotype
20 diversity (0.782 - 1) is amongst the highest observed for an elasmobranch.
21 Microsatellite markers suggested a high level of relatedness was responsible for
22 regional population structuring. There was no apparent spatial structure after removal
23 of 'full sibling' relationships.

24 5) Inter-haul variation from Celtic Sea samples is suggestive of sub-populations and
25 aggregation events which may have important implications for fisheries conservation
26 of this, and other, elasmobranch species.

27 Key words: coastal, ocean, distribution, fish, fishing, elasmobranch management,
28 genetic structure, relatedness, social interactions

29

30 **1.Introduction**

31 A fundamental challenge to the conservation of marine organisms is defining an
32 appropriate spatial scale at which to manage a species, a conundrum which has led to
33 the grouping of exploited marine organisms into stocks. As a general rule, stocks are
34 defined as populations that encounter no genetic or demographic overlap with each
35 other (Waples, 1998). The idealised concept of a genetically isolated stock arises when
36 a population becomes divided and gene flow ceases. Having achieved demographic
37 independence, the two populations will then begin to gradually diverge, until each is
38 characterized by a distinctive genetic signature (Palsbøll, Bérubé, & Allendorf, 2007;
39 Waples & Gaggiotti, 2006). In the aquatic environment, demographic independence
40 does not necessarily equate to spatial isolation and two genetically distinct populations
41 may be sympatric with spatial overlap, as has been shown in freshwater fish (Verspoor
42 & Cole, 1989) and marine mammals (Hoelzel & Dover, 1991). In both cases, the genetic
43 differentiation was caused by different behaviours, either migratory vs residency
44 (Verspoor & Cole, 1989) or foraging strategies (Hoelzel & Dover, 1991).

45 Complete genetic isolation in vagile marine species is rare as they experience few
46 physical barriers to gene flow (Palumbi, 2003; Waples, 1998). This often results in
47 species with high dispersal potential showing only slight genetic differentiation
48 throughout their range (Palumbi, 2003). Due to the need to define stocks for

49 management purposes, various threshold levels of gene flow have been proposed to
50 define a population and/or a management unit (Reiss, Hoarau, Dickey-Collas, & Wolff,
51 2009), one of which has been to identify separate stocks if a significant and
52 reproducible genetic differentiation can be detected (Reiss et al., 2009). In some cases,
53 this significant differentiation may be very small and the results of combined genetic
54 and tagging studies suggest that in teleost fish, small F_{ST} values of 0.0037 can
55 represent effective regional isolation with a dispersal rate of less than 1% (Knutsen et
56 al., 2011).

57 Such considerations may be especially important in interpreting genetic
58 differentiation in elasmobranchs that, due to slow rates of evolution (Martin et al.,
59 1992), can have even lower genetic variability than widespread teleost fish (Heist &
60 Gold, 1999). Genetic differentiation in elasmobranch species appears to be highly
61 correlated with dispersal ability (Veríssimo, McDowell, & Graves, 2010) with some
62 cosmopolitan species displaying very little global genetic differentiation (Schmidt et
63 al., 2009). This may suggest that genetic investigations into regional stocks would
64 yield little in the way of spatial resolution. There are however certain behaviours that
65 have been documented in elasmobranch populations which may promote genetic
66 differentiation, even in wide-ranging species.

67 Population segregation based on age or sex, as is common in many elasmobranch
68 species (Alonso et al., 2002; Hurst, Bagley, McGregor, & Francis, 1999), may allow one
69 of the sexes, more commonly females (Pardini et al., 2001; Portnoy, McDowell, Heist,
70 Musick & Graves, 2010; Daly-Engel et al., 2012), to maintain site fidelity. This,
71 especially when in conjunction with reproductive behaviour (i.e. natal philopatry -
72 (Hueter, Heupel, Heist, & Keeney, 2005)), can create genetic differentiation between
73 regions that are not separated by physical barriers to gene flow (Dudgeon et al., 2012;

74 Feldheim et al., 2002; Jorgensen et al., 2010; Pratt & Carrier, 2001). Hence, there is
75 the potential to create genetically distinct sympatric populations, highlighting a
76 difference between spatially and genetically distinct stocks. Anthropogenic
77 exploitation also has the potential to impact the genetic composition of a species
78 within a region; a significant population decline caused by overexploitation can cause
79 range contraction and population fragmentation (Kenchington, 2003), which may
80 encourage the formation of small, isolated sub-populations.

81 Spurdog (*Squalus acanthias*) are generally considered to be highly mobile (Gauld and
82 Macdonald, 1982; Templeman, 1976; Templeman, 1984) and are distributed
83 worldwide throughout temperate continental shelf seas (Camhi, Valenti, Fordham,
84 Fowler, & Gibson, 2009). No regional genetic differentiation has been found to date
85 (Hauser, Franks, Vega, & Gallucci, 2007) and it appears that oceanic water depths do
86 not act as a migratory barrier for this species as no differentiation has been found
87 between the southern Atlantic and Pacific, nor between the eastern and western North
88 Atlantic; a concept supported by tagging evidence indicating transoceanic movements
89 (Holden, 1967; Templeman, 1976). However, taking into account that just one
90 breeding migrant per generation may be enough to prevent, or greatly reduce, genetic
91 differentiation between typically discrete geographic populations (Slatkin, 1987;
92 Spieth, 1974), this is perhaps not surprising. Gene flow does, however, appear to be
93 restricted across equatorial waters (Hauser et al., 2007). This barrier to gene flow has
94 caused divergence to the point whereby the North-eastern Pacific spurdog has been
95 re-classified as *S. suckleyi* (Ebert et al., 2010). *Squalus suckleyi* has markedly different
96 population dynamics to *S. acanthias*, with a later age of maturity, larger maximum
97 size and larger length at maturity (Hauser et al., 2007; Ketchen, 1972; Saunders &
98 McFarlane, 1993).

99 In contradiction to the genetic data, there is evidence suggesting more limited regional
100 movements in some populations. Based on mark and recapture tagging, some spurdog
101 appear to maintain a certain level of site association, often within coastal areas, where
102 sub-units appear to restrict movements to the coastal shelf and partially enclosed
103 water bodies (Campana et al., 2009; Carlson et al., 2014; Ketchen, 1986; Templeman,
104 1984; Thorburn, Neat, Bailey, Noble, & Jones, 2015). In contrast, offshore units appear
105 highly migratory (Campana et al., 2009; Ketchen, 1986; McFarlane & King, 2003).
106 Such differentiation may be a consequence of populations partitioning by age or sex, a
107 feature of many other elasmobranch species (Alonso et al., 2002; Hurst et al., 1999).

108 Spurdog in the NE Atlantic are currently viewed as a single stock (Aasen, 1964; Gauld
109 & Macdonald, 1982; Vince, 1991), a designation based on mark and recapture tagging
110 data demonstrating wide-ranging movements throughout this region (Gauld &
111 Macdonald, 1982; Templeman, 1976, Templeman, 1984; Vince, 1991). In 2010 The NE
112 Atlantic spurdog biomass was estimated to be about 23% of 1955 numbers and 19%
113 compared to 1905 (Oliveira, Ellis, & Dobby, 2013), but appear to have stabilized over
114 the last decade (ICES, 2016). There is limited evidence suggesting that some spurdog
115 in this region display winter residency within semi-enclosed coastal regions (Thorburn
116 et al., 2015), however, it is unknown if these individuals represent an isolated group or
117 if the area is used by a proportion of the wider population. Historical exploitation and
118 the subsequent reduction in biomass of the NE Atlantic spurdog places importance on
119 the appropriate management of the remaining population. There are management
120 schemes, such as spatial and temporal measures, currently (2015 – 2019) under trial
121 in the Celtic Sea; the Spurdog By-catch Avoidance Programme (Hetherington,
122 Nicholson, & O'Brien, 2016). These schemes aim to actively avoid spurdog
123 aggregations and reduce spurdog by-catch and discards, reducing overall fishing

124 mortality using information supplied by the fishing industry in real time. However,
125 management also needs to be on a wider scale for which it is essential we understand
126 the full range of movements and connectivity in the species. Beyond this, it is vital to
127 understand the impact of commercial fisheries on elasmobranch populations as,
128 beyond direct population reduction, fisheries exploitation can have significant direct
129 and indirect effects on communities (Jennings & Kaiser, 1998) by targeting specific
130 age and sex classes. In elasmobranchs, these processes can lead to changes in the age
131 structure and size of individuals within a population (Hutchings, 2005; Stevens,
132 Bonfil, Dulvy, & Walker, 2000) as well as changes to the community structure of
133 elasmobranchs within a given area (Walker & Hislop, 1998).

134 A prerequisite for sustainable management is the matching of biological processes and
135 management action (Reiss et al., 2009). As recent studies have shown, some
136 individuals display strong site association in coastal regions (Thorburn et al., 2015),
137 suggesting investigation of population genetic structure in the spurdog population
138 around the UK may indicate if there is partitioning suggestive of site
139 fidelity/philopatric behaviours. This would have implications for population
140 management. To explore this, an 828-bp fragment of the mitochondrial DNA
141 (mtDNA) control region and seven focal polymorphic microsatellite markers (μ SAT)
142 were used to determine levels of gene flow and relatedness in spurdog around the UK.

143 **2. Methods**

144 **2.1 Tissue sample collection**

145 Samples from 295 individuals from eight locations throughout UK waters (Figure 1,
146 central Latitude and Longitude points for each sampling area is given in
147 Supplementary table 1) collected between 2010 and 2013 were used in this study.

148 Additional information on individuals sampled can be found in Supplementary table
149 1. Collections were from research trawls (North Scotland, Rockall, and Jura)
150 undertaken by Marine Scotland (MS), the offshore gill net fishery (also deploying long-
151 lines opportunistically) (Celtic Sea), inshore longline fishery (Southern North Sea,
152 Wales) and recreational fishery (rod and line) (Wales) with sampling undertaken by
153 the Centre for Environment, Fisheries & Aquaculture Science (CEFAS) and the
154 recreational fishing community (rod and line) (Loch Sunart, Loch Etive). All tissue
155 samples were collected from the trailing edge of the first dorsal fin and immediately
156 preserved in 70-95% ethanol. Additionally, total length (TL) (snout to the tip of the
157 terminal dorsal lobe on the tail fin), and girth for most, but not all, of the spurdog
158 (around the central thorax, in front of the first dorsal fin and behind the pectoral fins)
159 were recorded. All licensed scientific sampling was carried out under the Animals
160 (Scientific Procedures) Act 1986, using the appropriate project and personal licences
161 authorized by the United Kingdom Home Office. Genomic DNA was extracted from
162 352 tissue samples using phenol-chloroform protocols (Sambrook & Russell, 2006)
163 with 100% ethanol precipitation.

164 **2.2 Mitochondrial DNA Sequencing**

165 PCR amplification of an approximately 900 base pair (bp) section of the mitochondrial
166 control region (CR) was conducted using primers TMTF1 (5'-
167 CCCACATACCCTAATATACCA) and TMTR1 (5'-CATCTTCAGTGCCATACTCT)
168 designed using Primer Premier vers. 5 (Premier Biosoft International). A 50µL PCR
169 master mix was used which included approximately 25-50ng DNA, 0.5µM of each
170 primer, 10µl Bioline 5xMyTaq reaction buffer, 0.25µl Bioline MyTaqHS (Hotstart Taq)
171 and UV sterilized water. PCR conditions were: initial denaturation at 95°C for 8min
172 followed by 36 cycles of 95°C for 60sec, 53°C for 60sec and 72°C for 90sec with a final

173 extension step at 72°C for 8min using Biometra TGradient PCR machines. Products
174 were purified using Qiagen PCR purification kits (www.qiagen.com) prior to
175 commercial sequencing (Beckman Coulter Genomics).

176 **2.3 PCR amplification of the microsatellite regions**

177 Seven focal nuclear microsatellite markers were used in this study, all of which have
178 been previously published; four loci from McCauley et al., (2004): DF T289, DF J451,
179 DF U285, DF J445 and three from Veríssimo et al., (2010): SACA GA11, SACA 3853
180 and SACA 6396. An 11 µL PCR master mix included approximately 1ng DNA, 0.2µL
181 0.5µM of each primer, 2µL Bioline 5x MyTaq reaction buffer solution, 0.15µL Bioline
182 MyTaq, and UV sterilized water. After testing, all seven loci were found to amplify well
183 under the same PCR conditions with an initial denaturation step at 94°C for 5min
184 followed by 35 cycles of 94°C for 60sec, 53°C for 30sec and 72°C for 30sec, with a final
185 extension step at 72°C for 7min. Samples were sent for commercial genotyping (MRC
186 PPU DNA Sequencing and Services, Dundee).

187 **2.4 Mitochondrial control region data analysis**

188 Sequences were aligned manually and edited using MEGA vs 6 (Tamura, Stecher,
189 Peterson, Filipinski, & Kumar, 2013), providing sequences of 828bp. Diversity indices
190 for mtDNA sequences (number of haplotypes (H), haplotype (h) and nucleotide (*n*)
191 diversity) were calculated in DNASP version 5 (Librado & Rozas, 2009). Regional
192 genetic differentiation was estimated in ARLEQUIN version 3.5.1.2 (Excoffier &
193 Lischer, 2010) using genetic-distance based pairwise Φ_{ST} , with 10,000 permutations
194 to estimate significance and the Kimura 2P model as selected by JModeltest (Darriba,
195 Taboada, Doallo, & Posada, 2012).

196 To examine genealogical relationships among haplotypes, a neighbour-joining
197 network was created in PHYLML 3.1 (Guindon, Delsuc, Dufayard, & Gascuel, 2009) and
198 visualized using HAPVIEW (Salzburger et al., 2011). Demographic history was
199 explored using neutrality tests (Tajima's D test (Tajima, 1989) and Fu's F_s test (Fu
200 1996)), implemented in ARLEQUIN with p-values generated from 10,000
201 simulations. Significant negative Tajima D or Fu's F values are indicative of recent
202 population expansion. A mismatch analysis was also undertaken in ARLEQUIN to
203 explore further demographic history; a smooth, unimodal peaked distribution with a
204 skew towards zero is suggestive of a historical population expansion event
205 (Harpending, 1994; Rogers & Harpending, 1992) while a ragged, erratic distribution
206 is suggestive of population stability (Harpending, 1994; Rogers & Harpending, 1992).

207 **2.5 Microsatellite data analysis**

208 The total number of alleles, observed heterozygosity (H_o), expected heterozygosity
209 (H_e), allelic richness (A), Wright's inbreeding coefficient (F_{IS} ; 10000 bootstrap
210 replicates), linkage disequilibrium and deviation from Hardy Weinberg Expectations
211 (HWE) (Monte Carlo replicates 10000) were estimated in the R package routine
212 `diveRsity` (Keenan, McGinnity, Cross, Crozier, & Prodöhl, 2013), and GENEPOP ver.
213 4.3 (Rousset, 2008). Regional genetic differentiation was estimated by pairwise F_{ST} in
214 ARLEQUIN. Significant F_{ST} differences after Bonferroni sequential correction were
215 visualized by a factorial correspondence plot, calculated in GENETIX ver. 4.05
216 (Belkhir, Borsa, Chikhi, Raufaste, & Bonhomme, 2004), and plotted using the R
217 package routine `GGplot2` (Wickham & Chang, 2009). Regional population
218 differentiation was also explored using STRUCTURE 2.3.4 (Pritchard, Stephens, &
219 Donnelly 2000). Maximum number of populations (K) 1-8 was tested based on the

220 number of sampling sites. Each run consisted of a 1,000,000 run burn-in period and
221 1,000,000 MCMC iterations, both with and without prior location information.

222 Levels of relatedness, both inter and intra regionally and between temporal sampling
223 episodes from the same site, were investigated using GENALEX (Peakall & Smouse,
224 2006) and MLRELATE (Kalinowski et al., 2006). Exploration of temporal variation
225 was only possible for Loch Etive, Loch Sunart, and the Celtic Sea due to the limited
226 number of temporal samples at other sites. In GENALEX, Lynch & Ritland (1999) and
227 Queller & Goodnight (1989) estimators of relatedness were used to investigate
228 pairwise relationships and mean levels of population relatedness; using 10000
229 permutations and 10000 bootstraps in each simulation. MLRELATE was used to
230 calculate the maximum likelihood estimates of relatedness and relationships taking
231 null alleles into account, using 10000 bootstraps. The significant number of full sibling
232 (FS values ≥ 0.5) relationships identified by MLrelate may have influenced estimates
233 of intra-regional structuring. Therefore, microsatellite regional differentiation tests
234 were re-rerun removing the individuals with the highest pairwise FS relationships
235 within the population. This ensured retention of the maximum number of individuals
236 per population. Related individuals were not removed for mtDNA analysis due to low
237 levels of haplotype differentiation in initial investigations.

238 Sex-biased dispersal was explored in FSTAT (Goudet, 2001) by comparing
239 microsatellite fixation index (F_{ST}), inbreeding coefficient (F_{IS}), levels of relatedness (r),
240 mean assignment indices (mAIc) and variance of assignment index (vAIc) between
241 males and females from each sampling site. Different levels of dispersal in each sex
242 will, in principle, lead to unequal levels of gene flow. This may create a Wahlund effect,
243 producing higher F_{IS} and vAIC values, lower F_{ST} and relatedness values, and negative
244 mAIc values in the dispersing sex; full descriptions of tests are given in Goudet et al.,

245 (2002). Only mature individuals were used for analysis as tests assume sampled
246 individuals have already had the opportunity to disperse (Goudet et al., 2002). Due to
247 the low numbers of mature spurdog of each sex from some sampling locations, only
248 five regions were used in these analyses (Celtic Sea, Loch Etive, Loch Sunart, North
249 Scotland and Southern North Sea).

250 **3. Results**

251 **3.1 Genetic Diversity**

252 Alignment of 828 bp mtDNA control region sequences from 228 individuals gave 49
253 haplotypes based on 25 polymorphic sites, 16 of which were parsimoniously
254 informative. Of the 49 haplotypes, 26 were singletons. As many singletons can imply
255 PCR and sequencing errors (Johnson & Slatkin, 2006), 10% of samples had PCR re-
256 run and were re-sequenced. Error rate was found to be <5% based on re-sequencing.
257 Haplotype diversities ranged from 0.782 (Wales) to 1.00 (North Scotland) (Table 1).
258 Nucleotide diversities ranged from 0.0015 (Wales) to 0.0035 (Rockall) (Table 1).

259 A total of 295 individuals were genotyped for seven microsatellite loci. To establish
260 PCR or genotyping errors, 10% of samples had PCRs re-run and were re-genotyped
261 establishing the error rate to be <5%. Prior to FS relationships being removed from
262 the full dataset, significant departures from HWE were detected at five loci, DF T289,
263 SACA 6396, DF J451, DF J445 and SACA 3853, within five populations, Loch Etive,
264 Sound of Jura, southern North Sea, Wales, and the Celtic Sea. The observed
265 heterozygosity ranged from 0.58 (Etive) – 0.7 (N.Sco) (Table 2; full population
266 summaries per locus in supplementary Table 2. With FS relationships removed, SACA
267 6396 in both the Celtic Sea and Southern North Sea and SACA 3853 in the Southern

268 North Sea population were out of HWE (Table 2; full population summaries per locus
269 in Supplementary Table 1;). All loci were in linkage equilibrium.

270 **3.2 Population differentiation**

271 **3.2.1 Spatial structure**

272 Of the 49 haplotypes identified the mtDNA haplotype network showed that six
273 common haplotypes are shared between most regions, indicating little evidence of
274 population structure around the UK as haplotypes did not appear to group by sample
275 location. A minor exception to this is Jura, which is not represented on several of the
276 multi-haplotype branches (Figure. 2). As expected, other less frequent haplotypes,
277 mainly singletons (33), branch from the common haplotypes.

278 Mitochondrial analyses showed evidence of weak spatial differentiation, with
279 significant ($p < 0.05$) pairwise Φ_{ST} differences detected between Rockall and the Celtic
280 Sea (Φ_{ST} 0.1551), Etive (Φ_{ST} 0.1727), Jura (Φ_{ST} 0.2681), Southern North Sea (Φ_{ST}
281 0.1587), North Scotland (Φ_{ST} 0.1917); and Jura and Sunart (Φ_{ST} 0.0617), Wales (Φ_{ST}
282 0.1138) and the Celtic Sea (Φ_{ST} 0.0605) following FDR correction (Table 3). After more
283 stringent Bonferroni sequential correction, however, only Jura and Rockall (Φ_{ST}
284 0.2681) remained significantly differentiated (Table 3).

285 Including all individuals, microsatellite evidence suggested there was some genetic
286 differentiation, with significant pairwise F_{ST} between Wales and Jura (F_{ST} 0.0305)
287 following FDR correction. After Bonferroni correction, F_{ST} remained significant
288 between Wales and the Celtic Sea (F_{ST} 0.029), Loch Etive (F_{ST} 0.038), Loch Sunart
289 (F_{ST} 0.041) and the southern North Sea (F_{ST} 0.034) (Table 3). Factorial
290 correspondence analysis shows that while the population mean of Wales is discrete
291 from those of other populations there is some overlap of individuals (Figure 3). After

292 removing full sibling (FS) relatives (as identified by MLrelate) from each sampling site
293 no significant genetic differentiation between regional populations was apparent (F_{ST}
294 range -0.01867 - 0.01113) (Table 3). Results from STRUCTURE both with and without
295 priors showed no regional differences, with $K= 1$ for both and no discernible pattern
296 in either case (data not shown).

297 **3.2.2 Temporal structure**

298 No temporal variation was observed in samples from Loch Etive or Loch Sunart,
299 however, it should be noted that samples from these regions comprised largely
300 individuals taken opportunistically from angling trips where typically low numbers of
301 fish are taken at a single spatiotemporal sampling point. Samples taken from
302 commercial fishing vessels in the Celtic Sea at four separate time points 2010, 2010a,
303 2011, 2011a (Table 4) showed significant ($p < 0.05$) differentiation after FS had been
304 removed between 2010 and 2010a (F_{ST} 0.028) following FDR, and between 2010a and
305 2011 (F_{ST} 0.037), following Bonferroni correction (Table 5). Factorial correspondence
306 analysis showed discrete population means, but admixture of individuals is evident
307 (Figure. 4). There was no significant variation in the number of FS relationships
308 between samples from each sampling occasion (Table 4). The ratio of full sibling
309 relationships was higher in the temporally split Celtic Sea groups (Table 4) than it was
310 for the Celtic Sea as a whole (Table 2). Sex ratios varied between the four commercial
311 fishing trips. In 2010a, only one male was caught out of 18 spurdog; in 2010 and 2011,
312 numbers of males and females were approximately equal; while in 2011a, there were
313 twice as many females caught as males (Table 4).

314 **3.3 Relatedness**

315 All regions had a similar proportion of FS relationships (relatedness values > 0.5)
316 between sampling sites (range 0.028 (N. Sco) – 0.034 (Rockall)) (Table 2). Samples

317 from Wales had a considerably higher number of intra-region FS relationships (0.368)
318 compared to other sampling sites which had similar, low levels of FS relationships
319 (mean = 0.033, range 0.000 (N.Sco) – 0.0071 (Rockall)) (Table 2). Further
320 investigation into relatedness using GenAlEx showed samples from Wales to have a
321 significantly higher mean relatedness ($r = 1.12$, $p < 0.05$) than expected (Figure. 5). No
322 other populations had significantly high or low levels of relatedness. All spurdog
323 caught in Wales were adult females, TL 94 – 111 cm.

324 **3.4 Sex biased dispersal**

325 There was limited evidence of male dispersal when comparing of male and female
326 microsatellite data, which showed that males had lower F_{IS} and F_{ST} values, a lower
327 level of relatedness, lower mAIC and higher vAIC values. However, only vAIC showed
328 a significant difference (Table 6).

329 **3.5 Demographic history**

330 All sites except Rockall displayed significant negative Fu's FS values (Table 1). No
331 sampling sites had significant Tajima's D values. The mismatch distribution showed a
332 smooth unimodal distribution with a heavy left skew towards zero (Figure. 6). Due to
333 the low number of samples sequenced, neutrality tests could not be performed on
334 sequences from North Scotland.

335

336 **4. Discussion**

337 **4.1 Genetic Diversity**

338 Haplotype diversity (0.782 – 1.0) was comparable to that found for *S. suckleyi* in the
339 NE Pacific (0.966; (Hauser et al., 2007)), but higher than that previously reported for
340 *S. acanthias* in the North-east Atlantic (0.56 – 0.71; Veríssimo et al., 2010). The

341 nucleotide diversities (0.0015 – 0.0035) compare to previously published values for
342 *S. acanthias* from sites within the NE Atlantic from the west of Ireland (0.0024) and
343 the Irish Sea (0.0016) (Veríssimo et al., 2010), yet lower than those reported for *S.*
344 *suckleyi* in the NE Pacific (0.0072; Hauser et al., 2007). The diversity values for *S.*
345 *suckleyi* in the NE Pacific only came from a small sample size (Hauser et al., 2007) so
346 may not be fully representative of the true genetic diversity of the NE Pacific spurdog
347 population.

348 The genetic variation observed in the mtDNA in this study is among the highest
349 recorded of any elasmobranch (e.g. Blower, Pandolfi, Bruce, GomezCabrera, &
350 Ovenden, 2012; Keeney, Heupel, Hueter, & Heist, 2005; Stow et al., 2006; Tavares et
351 al., 2013; Valsecchi, Vacchi, & Di Sciara, 2005). This is surprising as spurdog in the
352 NE Atlantic are known to have undergone a severe decline in biomass (Oliveira et al.,
353 2013) which might be expected to erode much of the genetic diversity (Kenchington,
354 2003). While this may be indicative of a mutational hotspot in the Control Region, as
355 observed in other elasmobranch species (Tavares et al., 2013), this cannot be shown
356 by this data and should be explored further by sequencing the entire mitogenome.

357 Another possibility for the observed haplotype diversity would be some form of
358 aggregating behaviour. Aggregations may occur in response to high levels of
359 exploitation, as previously observed in both teleost's (Rose & Kulka, 1999) and
360 elasmobranchs (Ellis et al., 2008). Spurdog are known to be an aggregating species
361 (Fordham, Fowler, Coelho, Goldman, & Francis, 2006) and if aggregations are formed
362 following exploitation, these would represent convergence of several different sub-
363 populations thus increasing genetic diversity. As the UK lies at the junction of several
364 biogeographic zones (e.g. Johnson et al., 2014) where spurdog are known to occur, it
365 is possible that following population reduction, individuals from these different zones

366 have come together. These would, potentially, bring unique haplotypes with them and
367 produce the high haplotype diversity observed. However regional genetic distinction
368 was not observed in this study so cannot support this theory. Increased diversity may
369 also come from the NW Atlantic. No genetic differentiation has been found between
370 these two regions (Veríssimo et al., 2010), yet as only one migrant per generation can
371 prevent populations becoming genetically differentiated (Slatkin, 1987; Spieth, 1974),
372 this does not necessarily prove regular admixture. The initial evidence of weak
373 differentiation between Rockall and the rest of the sampling sites observed in the
374 mtDNA does tentatively offer the possibility that this offshore region is slightly
375 different from the rest of the UK, potentially influenced by spurdog from the NW
376 Atlantic. However, small sample sizes and weak differentiation, that is removed with
377 multiple analysis corrections, does not support this hypothesis. Tagging studies have
378 shown some connectivity between the NE and NW Atlantic (Templeman, 1976), yet
379 not in great numbers. If connectivity is low, this could be a means of introducing new
380 haplotypes to the NE Atlantic from the NW Atlantic, increasing diversity while
381 maintaining heterogeneity. The level of connectivity between the NE and NW Atlantic,
382 is worthy of further investigation as this has important implications for spurdog stock
383 maintenance and management, because their observed decline in the NE Atlantic may
384 be buffered by numbers and genetic admixture from the NW Atlantic.

385 Some aggregations are attributed to life history events (Carlson et al., 2014; Pawson,
386 1995) including mating (Carlson et al., 2014) and may not be a result of
387 overexploitation, but a population strategy to allow for genetic mixing helping to
388 retard inbreeding and increase overall genetic diversity (Newby, Darden, Bassos-Hull,
389 & Shedlock, 2014). Significant spurdog by-catch events of approximately 10 tonnes in

390 Celtic Sea fisheries (Hetherington et al., 2016) are not uncommon and demonstrates
391 the aggregative tendency of spurdog in the UK.

392 Identification of aggregation behaviour, is important because it can lead to an over
393 estimation of population numbers, as Catch Per Unit Effort remains high and stable at
394 aggregation sites while overall abundance declines (Erisman et al., 2011; Rose & Kulka,
395 1999).

396

397 **4.2 Population differentiation**

398 Overall, no structuring was observed in the mtDNA haplotype network, and while
399 significant Φ_{ST} values were observed between Rockall and other regions, sample
400 numbers for Rockall were too low to draw firm conclusions regarding genetic
401 differentiation with other regions. The mtDNA also offered no evidence of natal
402 philopatry in spurdog (Hueter et al., 2005). Microsatellite analysis initially showed
403 some significant differentiation between Wales and other regions. This appeared to be
404 caused by high numbers of individuals with above-average levels of relatedness in
405 samples from Wales; with these individuals removed there was spatial homogeneity
406 across all sampling locations. However, further intra-regional investigations using
407 trawls taken on different dates in the same area did reveal temporal heterogeneity in
408 the Celtic Sea. This may be attributed to genetically distinct sympatric populations
409 using the same region (McPherson, Stephenson, & Taggart, 2003) which has been
410 shown to create similar levels of genetic variation at the same location between
411 samples collected at different times as that across widely separated geographic points
412 (Reiss et al., 2009). As spurdog are known to aggregate, it may be that, following such
413 an event, spurdog split into genetically distinct sub-units, as shown in teleosts

414 (Hutchinson, Carvalho, & Rogers, 2001) and suggested by the discrete trawls in the
415 Celtic Sea.

416 It may be that sub-groups are associated with geographic regions. The British Isles can
417 be considered to lie near the intersection of several biogeographic provinces (e.g.
418 Johnson et al., 2014) as discussed in the diversity section of this paper, the lack of natal
419 philopatry and unambiguous spatial genetic differentiation found in this study does
420 not support the suggestion of geographically separate stocks associated with these
421 regions, despite initial weak differentiation between Rockall and other sites.
422 Furthermore, such geographic separation has not been shown in previous tagging
423 studies which show spatial homogeneity in the NE Atlantic with spurdog being wide
424 ranging and cosmopolitan (Gauld & Macdonald, 1982; McFarlane & King, 2003;
425 Templeman, 1976; Templeman, 1984).

426 Sub-grouping may be a consequence of social structuring. Social relationships have
427 been shown in other free-ranging species of shark which form communities based on
428 individual preference to other individuals (Mourier, Vercelloni, & Planes, 2012; Newby
429 et al., 2014). There is evidence of this in some elasmobranch species within spatially
430 limited nursery areas where juveniles and sub-adults appear to remain in brood
431 groups within these areas (Larson et al., 2010). Similarly, some teleosts display a
432 preference for remaining in kin groups (Olsén, Petersson, Ragnarsson, Lundqvist, &
433 Järvi, 2004; Selkoe, Gaines, Caselle, & Warner, 2006; Sikkel & Fuller, 2010), showing
434 aggression towards unrelated individuals (Sikkel & Fuller, 2010), suggesting both
435 recognition of siblings and an active choice to maintain brood relationships.

436 Small genetic differences have been observed between interannual cohorts of
437 elasmobranchs at the same nursery site as well as between nursery sites within the
438 same year (Sampio, 2014). There have been observations of neonatal spurdog in

439 partially enclosed loch systems in Scotland (Thorburn et al., 2015) suggesting multiple
440 pupping sites throughout the UK. The small genetic differentiation observed in the
441 samples from Jura, which comprised of a high level of juvenile individuals, may be
442 indicative of this in spurdog, although it was not observed in other areas where
443 juveniles were sampled. If social cohesion occurs and lends structure to sub-groups of
444 spurdog based on nursery site and these bonds are maintained throughout life, then
445 this could create genetically distinct sub-units within a population.

446 Due to the high level of relatedness observed in the samples from Wales, such bonds
447 may be formed with related individuals. Yet, as spurdog aggregate, it is likely some
448 females give birth in the same locale, therefore any social drivers for maintenance of
449 relationships would occur between unrelated individuals as well as within broods,
450 which may explain why relatedness was within expected ranges for all other sampling
451 locations including the temporally split Celtic Sea samples. The difference in sizes
452 between the groups samples in the Celtic Sea do suggest that they may be formed from
453 interannual cohorts, which may be causative of the differentiation between groups
454 observed.

455 It is worth noting that the markers used in this study are unlikely to be powerful
456 enough to definitively detect siblings, whilst the lack of a common haplotype amongst
457 samples identified as FS negates them all being full siblings. However, the above
458 average level of relatedness does suggest some level of genetic relationship.

459 Suggested drivers for segregation in elasmobranch populations refer to differences
460 between either the sexes (Economakis & Lobel, 1998; Hanchet, 1991; Klimley, 1987)
461 or life stages (Lucifora, García, Menni, & Escalante, 2006); (Wearmouth & Sims,
462 2010). There is, therefore, no physiological reason why same sex individuals cannot
463 remain associated throughout life from birth, assuming they are born at the same
464 spatial-temporal point, an opportunity increased in live bearing species like spurdog

465 (Hanchet, 1988), as drivers of segregation will act on these individuals concurrently.
466 The limited evidence of male-biased dispersal, a common feature of elasmobranch
467 populations (Daly-Engel et al., 2012; Pardini et al., 2001; Portnoy et al., 2010),
468 observed in the microsatellite data may give further opportunities for females to
469 maintain social groups.

470 The overall spatial homogeneity does suggest that even if spurdog do exist as
471 genetically distinct sub-populations, these groups are highly mobile, moving
472 throughout much of their range. Furthermore, it does not appear that the NE Atlantic
473 population experience behavioural separation, as sites where there is evidence of site
474 fidelity in spurdog are not genetically distinct. In fact, Loch Etive, a site where there is
475 limited evidence of site fidelity (Thorburn et al., 2015) had the highest number of
476 observed haplotypes, including all major UK haplotypes and the second highest
477 haplotype diversity and allelic richness, increasing the conservation potential of such
478 sites for the species.

479 What is unclear is if this spatial homogeneity is caused by complete admixture within
480 the spurdog population, or sub-groups of the population moving throughout the
481 entirety of the species NE Atlantic range and a factor of the sampling regime. A lack of
482 temporal sampling, while the only option available over most of the area covered in
483 this study, may have led to a perception of homogeneity, as temporal genetic variation
484 can promote spatial homogeneity across sampling sites (Hedgecock, 1994).
485 Consequently a comprehensive understanding of spatial differentiation is contingent
486 upon a more extensive and intensive sampling regime with synoptic sampling
487 throughout the region may produce more spatial heterogeneity to clarify this. A wider
488 sampling area may also help investigations into Biogeographic regionality.

489

490 **4.3 The Origin of NE Atlantic Spurdog**

491 The presence of several common haplotypes suggests the contemporary population of
492 spurdog around the UK was derived from several populations, while the low levels of
493 sequence divergence suggest historical population expansion from a small effective
494 population size following a bottleneck, with no long-term geographic separation
495 (Awise, 2000). This contention is further supported by negative Tajima D and Fu's FS
496 values for each region (Fu 1997; Joshi, Salar, Banerjee, & others, 2013; Okello,
497 Nyakaana, Masembe, Siegismund, & Arctander, 2005; Tajima, 1989) and a smooth,
498 unimodal mismatch distribution (Harpending, 1994; Rogers & Harpending, 1992).
499 Such population formation may have occurred during rapid recolonization of the NE
500 Atlantic shelf during the current interglacial period. Interestingly, the weak genetic
501 differentiation observed between Rockall and other areas, coupled with a non-
502 significant FS value tentatively suggest that there may have been a historically stable
503 offshore population of spurdog (or again, one buffered by the NW Atlantic). However,
504 the small samples size from Rockall does prevent any firm conclusions being drawn.
505 The geographic location of Rockall and the small irregularities observed in the genetic
506 data from this study suggest it is an area worthy of further investigation.

507

508 **5. Conclusions**

509 We suggest there is genetic mixing of spurdog in UK waters, supporting the notion
510 that, for management purposes, spurdog should be treated as a single large stock unit.
511 However, we suggest this assumption is treated with some caution as, while
512 unambiguous spatial evidence to the contrary is unavailable, there are indications of
513 population processes at a temporal and regional level that cause some smaller

514 genetically distinct groups. This suggests local management may be additionally
515 beneficial to the population rather than a single blanket management strategy. Local
516 spatial management at apparent key habitats could contribute towards the
517 conservation of the species as it would eliminate any bycatch of the species in that area.
518 It may also be important for contributing to the conservation of the species on a much
519 wider spatial scale as it appears some locations would offer protection to a
520 considerable proportion of the apparent NE Atlantic spurdog genetic resource. On a
521 more local scale, spatial closures could provide an opportunity to conserve all age
522 classes of both sexes (Thorburn et al., 2015) which is key to ensuring population
523 survival in this late maturing species (Kinney & Simpfendorfer, 2009).

524 Tools such as temporal closures may disproportionality affect some genetic sub-
525 populations due to the type of temporal variation observed in the Celtic Sea and could
526 have significant implications for the region's genetic diversity. The effect of genetic
527 variation over time may be of importance to temporary closures and should be further
528 investigated in line with temporal management strategies, with special focus on the
529 effect of seasonality which, might indicate times when temporal management may be
530 most effective. Future genetic investigation should be conducted sampling locations at
531 multiple synoptic temporal points to clarify regional temporal genetic variation of
532 spurdog and the occurrence of groups of high relatedness. Identifying the times of
533 greatest stock integrity.

534 Our findings have implications for all elasmobranch fisheries, as the presence of
535 related groups and temporal variability in spurdog may be indicative of population
536 processes creating sub-structuring in other species. Therefore, until movement and
537 genetic studies including temporal samples can be integrated to define population
538 processes, a precautionary approach to management measures should address the

539 possibility of temporal stock variability and temporal differentiation should be
540 considered equally important as regional differentiation in management decisions.

541 One such measure could, theoretically, be, if commercial catch limits are reinstated,
542 the addition of a temporal element to the catch limit that spreads numbers taken over
543 a certain time to take individuals from several different genetic sub-units in an effort
544 maintain the high genetic diversity observed around the UK. This may, upon further
545 investigation, prove to be more beneficial to many other species of elasmobranch that
546 display similar genetic sub-grouping. There is also the suggestion that there may be
547 benefits from reassessment of historical tagging studies, with each spatial area looked
548 at on a temporal level.

549

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562

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865 Table 1: Mitochondrial control region genetic diversity indices and results of neutrality
 866 test (Tajima's D and Fu's FS) for all samples from each population of *Squalus*
 867 *acanthias* (no neutrality test results for North Scotland due to low sample numbers).
 868 Sampling locations as seen in Figure. 3.1: CELTIC = Celtic Sea, ETIVE = Loch Etive,
 869 JURA = Sound of Jura, S. N. SEA = Southern North Sea, N.SCO = North Scotland,
 870 ROCKALL = Rockall, SUNART = Loch Sunart, WALES = Wales. N = number of
 871 individuals, H = number of haplotypes, h = haplotype diversity, n = nucleotide
 872 diversity. Tajima's D = Tajima value with associated P-value in column to the left, Fu's
 873 FS = Fu's FS value with associated P-value in the column to the left.

	N	H	h	n	Tajima's D	P-value	Fu's FS	P-value
CELTIC	48	13	0.838	0.0022	-1.171	0.115	-5.64	0.006
ETIVE	65	23	0.936	0.0028	-0.745	0.249	-15.505	0
JURA	22	11	0.909	0.0024	-0.625	0.295	-5.551	0.001
S. N. SEA	33	17	0.917	0.0030	-0.738	0.252	-10.785	0
N.SCO	7	7	1	0.0026	-	-	-	-
ROCKALL	7	5	0.905	0.0035	0	0.519	-0.803	0.239
SUNART	33	17	0.939	0.0029	-0.414	0.385	-9.747	0
WALES	13	6	0.782	0.0015	-1.244	0.111	-2.375	0.021

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876 Table 2: Nuclear microsatellite (averaged over all loci) genetic diversity indices and
 877 summary of the regional proportions of full sibling (FS) pairwise relationships
 878 between individuals for all samples from each population of *Squalus acanthias*.
 879 Microsatellite diversity values with FS relationships (as identified by MLrelate)
 880 removed are also shown (italic). Sampling locations as seen in Figure. 3.1: CELTIC =
 881 Celtic Sea, ETIVE = Loch Etive, JURA = Sound of Jura, S. N. SEA = Southern North
 882 Sea, N.SCO = North Scotland, ROCKALL = Rockall, SUNART = Loch Sunart, WALES
 883 = Wales. N = number of individuals, H_o = observed heterozygosity, H_e = expected
 884 heterozygosity, A = mean allelic richness, HWE = Hardy Weinberg Expectation P
 885 values, F_{IS} = Wright's inbreeding coefficient. Proportion of FS relationships between
 886 different sampling regions (B), and between individuals from the same sampling
 887 region (W). Relationships where estimated using the Maximum likelihood method in
 888 MLRelate.

	N		H_o		H_e		A		HWE		FIS		B	W
Celtic	76	64	0.59	0.6	0.64	0.65	4.35	4.5	0.01	0.091	0.088	0.073	0.030	0.032
Etive	69	40	0.58	0.57	0.64	0.66	4.46	4.6	0.000*	0.287	0.1	0.141	0.029	0.030
Jura	31	24	0.63	0.61	0.65	0.65	4.36	4.4	0.025	0.362	0.032	0.07	0.029	0.026
S. N. Sea	48	29	0.6	0.59	0.66	0.68	4.36	4.5	0.000*	0.000*	0.083	0.133	0.029	0.048
N.Sco	13	13	0.7	0.7	0.68	0.68	4.78	4.8	0.519	0.519	-0.03	-0.03	0.028	0
Rockall	8	7	0.65	0.65	0.62	0.62	3.91	3.9	0.697	0.697	-0.03	-0.03	0.034	0.071
Sunart	33	26	0.6	0.62	0.64	0.65	4.2	4.3	0.017	0.206	0.06	0.047	0.029	0.025
Wales	166	100	0.69	0.64	0.62	0.66	3.8	4.1	0.000*	0.147	-0.11	0.024	0.030	0.368

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890 Table 3: Mitochondrial Φ ST (top panel, below the diagonal), nuclear microsatellite
 891 FST (middle panel, below the diagonal) and nuclear microsatellite FST with 'FS'
 892 relationships (as identified by MLrelate) removed (bottom panel, below the diagonal)
 893 of genetic differentiation between areas removed among 8 sampling localities of
 894 spurdog *Squalus acanthias* from around the UK. Associated p-values are above the
 895 diagonal in all panels. **significant after Bonferroni sequential correction. *significant
 896 after fdr correction. Significant FST values and related p-values are highlighted in bold
 897 text. Sample regions legend: JURA = Sound of Jura; CELTIC = Celtic Sea; SUNART =
 898 Loch Sunart; ROCKALL = Rockall; ETIVE = Loch Etive; N.SCO = North Scotland;
 899 WALES = Wales; S.N.SEA = Southern North Sea.

	CELTIC	ETIVE	JURA	S.N.SEA	N.SCO	ROCKALL	SUNART	WALES
CELTIC		0.1265	0.0141*	0.1743	0.4809	0.0052*	0.4039	0.3434
ETIVE	0.0113		0.1479	0.1758	0.9780	0.0024*	0.2986	0.0435
JURA	0.0605	0.0162		0.2942	0.6400	0**	0.0132*	0.0125*
S.N.SEA	0.0108	0.0093	0.0062		0.6913	0.0049*	0.1014	0.1890
N.SCO	-	-0.0602	-0.0325	-0.0302		0.0127*	0.6545	0.0659
ROCKALL	0.1551	0.1727	0.2681	0.1587	0.1917		0.0296	0.0378
SUNART	-	0.0033	0.0617	0.0199	-0.0268	0.0987		0.2413
WALES	0.0044	0.0552	0.1138	0.0215	0.1048	0.1068	0.0145	

CELTIC		0.1622	0.9203	0.0844	0.7426	0.6495	0.7793	0.0015**
ETIVE	0.0029		0.1939	0.2719	0.2559	0.1328	0.8194	0.0003**
JURA	-	0.0041		0.1815	0.6878	0.4047	0.7989	0.0022*
S.N.SEA	0.0051	0.0023	0.0044		0.6023	0.5235	0.4570	0.0005**
N.SCO	-	0.0059	-0.0042	-0.0014		0.9311	0.5911	0.0826
ROCKALL	-	0.0162	0.0024	0.0001	-0.0187		0.5943	0.0350
SUNART	-	-0.0026	-0.0037	0.0007	-0.0015	-0.0029		0.0006**
WALES	0.0285	0.0378	0.0305	0.0340	0.0146	0.0323	0.0412	

CELTIC		0.7877	0.9740	0.4369	0.8997	0.6607	0.9710	0.6329
ETIVE	-		0.6774	0.841	0.6585	0.2686	0.9998	0.4115
JURA	-	-0.0012		0.6538	0.8695	0.7202	0.8662	0.7263
S.N.SEA	0.0068	-0.0029	-0.0013		0.8028	0.6215	0.9075	0.5714
N.SCO	-	-0.0011	-0.0081	-0.0048		0.9315	0.7706	0.8116
ROCKALL	0.0076							
SUNART	-	0.0111	-0.0064	-0.0011	-0.0187		0.5527	0.4510
WALES	0.0035	-0.0107	-0.0056	-0.0057	-0.0054	-0.0020		0.4471
	-	0.0061						
	-	0.0051	-0.0054	0.0004	-0.0103	0.0034	0.0020	
	0.0023							

901 Table 4: Temporal sampling details for the four hauls from the Celtic Sea. Including
 902 group name, Date of haul, sex ratio and size range of caught spurdog. Details from
 903 Celtic sea temporal sampling incidences. FS: Full sibling relationships, HS: Half
 904 sibling relationships, PO: Parental offspring and U: unrelated.

<i>Group</i>	<i>Date</i>	<i>Males</i>	<i>Females</i>	<i>Size range</i> (<i>cm</i>)	<i>FS</i>	<i>HS</i>	<i>PO</i>	<i>U</i>
2010	03 Oct 2010	10	8	75 - 109	0.046	0.177	0.052	0.725
2010a	12 Dec 2010	1	18	93 - 116	0.039	0.137	0.078	0.745
2011	21 Aug 2011	79	58	58 - 107	0.040	0.110	0.053	0.797
2011a	21 Sep 2011	5	10	64 - 108	0.038	0.124	0.067	0.777

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909 Table 5: FST value (below diagonal) and associated P-values of genetic differentiation
 910 between the temporal sampling occasions within the Celtic sea with FS relationships
 911 removed. **Significant after Bonferroni sequential correction, *significant after fdr
 912 correction. For details of samples from each group, refer to Table 7.

	<i>CEL2010</i>	<i>CEL2010a</i>	<i>CEL2011</i>	<i>CEL2011a</i>
<i>CEL2010</i>		0.0076**	0.3754	0.0599
<i>CEL2010a</i>	0.03722		0.0109*	0.7568
<i>CEL2011</i>	0.00353	0.02827		0.5429
<i>CEL2011a</i>	0.02073	-0.00629	-0.00029	

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916 Table 6: Comparisons of inbreeding coefficient (FIS), fixation index FST, relatedness (REL), =
 917 mean assignment indices (mAIC) and variance of assignment index (vAIC) between
 918 male (M) and female (F) spurdog from UK waters as indicators of sex biased dispersal.
 919 Significant differences are indicated by a p-value.

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	<i>FIS</i>	<i>FST</i>	<i>REL</i>	<i>mAIC</i>	<i>vAIC</i>
<i>M</i>	0.024	-0.01	-0.019	-0.15778	10.00471
<i>F</i>	0.1285	0.0045	0.0079	0.12335	5.15851
<i>P</i>	0.9818	0.1596	0.1512	0.3224	0.0185

924 Figure 1: Sampling locations for spurdog around the UK. Insert shows the three
 925 sampling sites from the west coast of Scotland. Total number of samples from which
 926 DNA was extracted from each sampling site: Celtic Sea = **48**, 76; Loch Etive = **65**, 69;
 927 Sound of Jura = **22**, 31; Southern North Sea = **33**, 48; North Scotland = 7, 13; Rockall
 928 = 7, 8; Loch Sunart = **33**, 33; Wales = **12**, 17. Total = **228**, 295. Bold numbers indicate
 929 samples sequenced for mitochondrial analysis, italics indicate number of samples
 930 genotyped for microsatellites.

931 Figure 2: Haplotype network of the mitochondrial DNA control region sequences for
 932 the spiny dogfish *Squalus acanthias* indicating lack of spatial population structure in
 933 the NE Atlantic. Haplotypes are represented by circles with sizes proportional to
 934 absolute frequency in the total sample. Colour codes are given of sample regions:
 935 JURA = Sound of Jura; CELTIC = Celtic Sea; SUNART = Loch Sunart; ROCKALL =
 936 Rockall; ETIVE = Loch Etive; N.SCO = North Scotland; WALES = Wales; S.N.SEA =
 937 Southern North Sea. All branches correspond to one nucleotide substitution between
 938 haplotypes. Blue dots represent missing haplotypes.

939 Figure 3: Factorial correspondence analysis plot of significant F_{ST} differences using
 940 all 7 μ SAT loci before related individuals were removed (Table 3). All samples are
 941 connected to the population mean. Sample regions legend: JURA = Sound of Jura;
 942 CELTIC = Celtic Sea; SUNART = Loch Sunart; ETIVE = Loch Etive; WALES = Wales;
 943 S.N.SEA = Southern North Sea.

944 Figure 4: Factorial correspondence analysis plot of spurdog μ SAT data from Table 5
 945 with FS relationships removed. All points are linked to the populations mean.

946 Figure 5: Mean relatedness (r) within 8 populations of spurdog from NE Atlantic based
 947 on pairwise comparisons. Mean values refer to the mean level of relatedness within

948 the population. U & L refer to the 95% confidence intervals around the null hypothesis
949 'No difference' across the populations. Sample regions legend: JURA = Sound of Jura;
950 CELTIC = Celtic Sea; SUNART = Loch Sunart; ROCKALL = Rockall; ETIVE = Loch
951 Etive; N.SCO = North Scotland; WALES = Wales; S.N.SEA = Southern North Sea.

952 Figure 2: Observed and expected mismatch distribution of mtDNA haplotypes from
953 samples of spurdog (*Squalus acanthias*) in UK waters.

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