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

James Thorburn[1*], Rosie Jones[2], Francis Neat[3], Cecilia Pinto[2], Victoria Bendall[4], Stuart Hetherington[4], David Mark Bailey [5], Noble Leslie[2+], Cath Jones[2+**]

[1]Scottish Oceans Institute, University of St. Andrews, Gatty Marine Laboratory, East Sands, St Andrews, KY16 8LB

[2]School of Biological Sciences, College of Life Sciences & Medicine, University of Aberdeen, Aberdeen, AB24 2TZ, UK

[3]Marine Scotland Science

[4] Centre for Environment, Fisheries and Aquaculture Science

[5]Institute of Biodiversity Animal Health and Comparative Medicine, University of Glasgow

*Author for all correspondence during publication: James Thorburn, 07793950325, jat21@st-andrews.ac.uk

**Author for all correspondence following publication: Cath Jones c.s.jones@abdn.ac.uk

+ joint last authors

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Abstract:

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

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

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

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

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

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

1.Introduction

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

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

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

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

Population segregation based on age or sex, as is common in many elasmobranch species (Alonso et al., 2002; Hurst, Bagley, McGregor, & Francis, 1999), may allow one of the sexes, more commonly females (Pardini et al., 2001; Portnoy, McDowell, Heist, Musick & Graves, 2010; Daly-Engel et al., 2012), to maintain site fidelity. This, especially when in conjunction with reproductive behaviour (i.e. natal philopatry - (Hueter, Heupel, Heist, & Keeney, 2005)), can create genetic differentiation between 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).

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

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

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

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

2. Methods

2.1 Tissue sample collection

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

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

2.2 Mitochondrial DNA Sequencing

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

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

2.3 PCR amplification of the microsatellite regions

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

2.4 Mitochondrial control region data analysis

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

196 To examine genealogical relationships among haplotypes, a neighbour-joining
197 network was created in PHYML 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

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

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

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

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

3. Results

3.1 Genetic Diversity

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

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

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

3.2 Population differentiation

3.2.1 Spatial structure

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

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

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

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

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

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

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

Some aggregations are attributed to life history events (Carlson et al., 2014; Pawson, 1995) including mating (Carlson et al., 2014) and may not be a result of overexploitation, but a population strategy to allow for genetic mixing helping to retard inbreeding and increase overall genetic diversity (Newby, Darden, Bassos-Hull, & 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 ΦST 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

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

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

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

4.3 The Origin of NE Atlantic Spurdog

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

5. Conclusions

We suggest there is genetic mixing of spurdog in UK waters, supporting the notion that, for management purposes, spurdog should be treated as a single large stock unit. However, we suggest this assumption is treated with some caution as, while unambiguous spatial evidence to the contrary is unavailable, there are indications of 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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563

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

Table 2: Nuclear microsatellite (averaged over all loci) genetic diversity indices and summary of the regional proportions of full sibling (FS) pairwise relationships between individuals for all samples from each population of *Squalus acanthias*. Microsatellite diversity values with FS relationships (as identified by MLrelate) removed are also shown (italic). Sampling locations as seen in Figure. 3.1: CELTIC = Celtic Sea, ETIVE = Loch Etive, JURA = Sound of Jura, S. N. SEA = Southern North Sea, N.SCO = North Scotland, ROCKALL = Rockall, SUNART = Loch Sunart, WALES = Wales. N = number of individuals, H_o = observed heterozygosity, H_e = expected heterozygosity, *A* = mean allelic richness, HWE = Hardy Weinberg Expectation *P* values, F_{IS} = Wright's inbreeding coefficient. Proportion of FS relationships between different sampling regions (B), and between individuals from the same sampling region (W). Relationships where estimated using the Maximum likelihood method in 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	**16**	*10*	**0.69**	*0.64*	**0.62**	*0.66*	**3.8**	*4.1*	**0.000***	*0.147*	**-0.11**	*0.024*	**0.030**	**0.368**

Table 3: Mitochondrial ΦST (top panel, below the diagonal), nuclear microsatellite FST (middle panel, below the diagonal) and nuclear microsatellite FST with 'FS' relationships (as identified by MLrelate) removed (bottom panel, below the diagonal) of genetic differentiation between areas removed among 8 sampling localities of spurdog Squalus acanthias from around the UK. Associated p-values are above the diagonal in all panels. **significant after Bonferroni sequential correction. *significant after fdr correction. Significant FST values and related p-valeus are highlighted in bold text. Sample regions legend: JURA = Sound of Jura; CELTIC = Celtic Sea; SUNART = Loch Sunart; ROCKALL = Rockall; ETIVE = Loch Etive; N.SCO = North Scotland; 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	-0.0068	-0.0012		0.6538	0.8695	0.7202	0.8662	0.7263
S.N.SEA	0.0013	-0.0029	-0.0013		0.8028	0.6215	0.9075	0.5714
N.SCO	-0.0076	-0.0011	-0.0081	-0.0048		0.9315	0.7706	0.8116
ROCKALL	-0.0035	0.0111	-0.0064	-0.0011	-0.0187		0.5527	0.4510
SUNART	-0.0061	-0.0107	-0.0056	-0.0057	-0.0054	-0.0020		0.4471
WALES	-0.0023	0.0051	-0.0054	0.0004	-0.0103	0.0034	0.0020	

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

Group	*Date*	*Males*	*Females*	*Size range (cm)*	*FS*	*HS*	*PO*	*U*
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

Table 5: FST value (below diagonal) and associated P-values of genetic differentiation between the temporal sampling occasions within the Celtic sea with FS relationships removed. **Significant after Bonferroni sequential correction, *significant after fdr correction. For details of samples from each group, refer to Table 4.

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

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

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

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

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

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

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

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

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

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

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