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### *Population connectivity of an overexploited coastal fish, *Argyrosomus coronus* (Sciaenidae), in an ocean-warming hotspot*

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1 **Title:** Population connectivity of an overexploited coastal fish (*Argyrosomus coronus*  
2 Griffiths and Hecht, 1995) in an ocean warming hotspot

3

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24

25 **Abstract**

26 *Argyrosomus coronus* is a commercially exploited fish with a distribution confined to the  
27 Angola-Benguela Frontal Zone (ABFZ), in the southeastern Atlantic. A previous study  
28 revealed that during a recent period of local warming the species has extended its distribution  
29 into Namibian waters, where it hybridized with resident and congeneric *A. inodorus*.  
30 Environmental changes are one of the major threats to marine biodiversity, and when  
31 combined with over-fishing have the potential to accelerate the decline of species. However,  
32 little is known regarding the evolutionary history and population structure of *A. coronus*  
33 across the ABFZ. We investigated genetic diversity, population structure and historical  
34 demographic changes using mtDNA Control Region sequences and genotypes at six nuclear  
35 microsatellite loci for 180 individuals. A single, genetically homogeneous population was  
36 indicated across *A. coronus* distribution range ( $\phi_{ST} = 0.041$ ,  $F_{ST} = 0.000$ ,  $D = 0.000$ ;  $p > 0.05$ ).  
37 These results imply that the oceanographic features within the ABFZ do not appear to  
38 influence population connectivity in *A. coronus*, simplifying the management of the species.  
39 However, reconstruction of demographic history points to a close link between the  
40 evolutionary history of *A. coronus* and the characteristics of the ABFZ. This finding  
41 highlights the vulnerability of this species to the rapid environmental changes being observed  
42 across this region, and indicates a pressing need for transboundary management to mitigate  
43 potential impacts of climate change in this global hotspot of seawater temperature changes.

44

45 **Keywords:** Angola-Benguela Frontal Zone, climate change, demographic history, fisheries,  
46 population structure, Sciaenidae

47

48

## 49 **Introduction**

50 Anthropogenic activities are recognized to have significant impacts in marine systems  
51 at multiple levels, ranging from habitat disturbance (Pauly et al. 2005) to overfishing (Sala  
52 and Knowlton 2006) and loss of genetic diversity (Pinsky and Palumbi 2014). Exploitation  
53 and harvesting in particular are known to strongly influence fish populations and their  
54 associated ecosystems (Pauly et al. 2005), which in combination with on-going climate  
55 change can have compound effects on the viability and long-term survival of marine fishes  
56 (Last et al. 2011). Species can react to the impacts of climate change either by shifting their  
57 distributional range or by adapting to changing conditions through individual ecological  
58 plasticity and/or local population adaptation (Briggs 2011; Last et al. 2011). However, since  
59 ecological plasticity and local adaptation have strong genetic components, over-harvesting  
60 has the potential to impact the long-term adaptive ability of marine fishes by decreasing  
61 extant genetic diversity (Allendorf et al. 2014). Therefore, understanding the impact of  
62 exploitation on genetic diversity and population sub-structuring is critical for predicting the  
63 likely consequences of continued exploitation and climate change.

64 Global warming hotspots are defined as regions with above average increases in ocean  
65 temperature (Hobday and Pecl 2014). A number of ocean warming hotspots have been  
66 identified throughout the world, including one in the coastal waters off southern Angola  
67 (Hobday and Pecl 2014). From an oceanographic perspective, this region is dominated by the  
68 Angola-Benguela Frontal Zone (ABFZ) off the coast of central Angola (~16°S), which results  
69 from the convergence of the warm-tropical Angola Current and the cold, upwelling  
70 dominated Benguela Current (Kirkman et al. 2016). This is a highly dynamic environment,  
71 with the position and strength of the ABFZ varying throughout the year in response to  
72 changes in the Southern Atlantic Anticyclone (SAA) and the upwelling regime of the  
73 Benguela Current (Jahn et al. 2003). During summer, the ABFZ is displaced southwards due

74 to the expansion of the SAA (up to 18°S), while in winter the contraction of the SAA and  
75 increased upwelling off Namibia results in a northward movement of the front (to 13°S; Jahn  
76 et al. 2003). Despite the environmental and biological complexity of this area, few studies  
77 have investigated the impact of contemporary environmental changes at a regional level  
78 (Monteiro et al. 2008; Potts et al. 2009; 2010; 2014), with the region remaining largely  
79 understudied.

80 In the last two decades, the ABFZ region has experienced a rapid increase in sea surface  
81 temperatures (SSTs; Monteiro et al. 2008), which has already impacted distribution ranges of  
82 local species such as the sciaenid fish *Argyrosmus coronus* Griffiths & Hecht, 1995 (Potts et  
83 al. 2014). This coastal, migratory species has a distribution range extending from northern  
84 Angola to northern Namibia (Griffiths and Heemstra 1995; Potts et al. 2010), and is a  
85 valuable fishery resource targeted by recreational, artisanal and subsistence fisheries (Potts et  
86 al. 2009; 2010). Despite sustaining a multi-user fishery, there are currently no specific fishing  
87 regulations for *A. coronus* in Angola. The Angolan Presidential Decree 11/2016 (available  
88 upon request) groups it into “Sciaenid” fishes, which are managed as a quota. In particular,  
89 subsistence and recreational catches, which constitute the main fishing effort in the region,  
90 are not regularly monitored nor included in the yearly total capture allowance. Therefore, the  
91 species is effectively not managed at present and increasing fishing efforts in the region  
92 (Potts et al. 2009) have resulted in population collapse (Beckensteiner et al. 2016).

93 A previous life history study suggested that the distribution range of *A. coronus* is closely  
94 linked with the seasonal displacement of the ABFZ, with adults undertaking a seasonal  
95 alongshore migration, and spawning thought to occur in the southern region of its range  
96 during late spring and summer (Potts et al. 2010). Recent findings, however, seem to dispute  
97 this hypothesis, with ripe and running females observed on an offshore reef in 10 m of water  
98 near the Kwanza Estuary (northern Angola) during the austral winter months (Potts,

99 unpublished data). Therefore, the full extent of the spawning locations of the species remains  
100 unknown. The duration of the pelagic egg and larval stage is also unknown, although it is  
101 expected to be similar (~26 days) to that of the sister species, *Argyrosomus japonicus*  
102 (Edworthy et al. submitted). Juveniles (300 – 600 mm Total Length - TL) and subadults (601  
103 – 870 mm TL) are thought to be resident, with maturation (~870 mm TL) heralding the  
104 migratory phase (Potts et al. 2010). Growth is rapid, with fish attaining maturity at just four  
105 years of age (Potts et al. 2010).

106 The rapidly increasing SSTs in the region have coincided with a southwards distributional  
107 shift of *A. coronus* into central Namibia, where it now overlaps and has begun hybridizing  
108 with the congeneric *A. inodorus* (Potts et al. 2014). Anthropogenic-mediated hybridization  
109 increasingly has been reported in the marine environment, either due to habitat degradation  
110 (Mullen et al. 2012), species introduction (Coleman et al. 2014) or environmental changes  
111 (Potts et al. 2014), and has the potential to erode genetic diversity and change the  
112 evolutionary history of species (Roberts et al. 2009; 2010).

113 The aim of this study was to examine genetic diversity and population sub-structure of  
114 exploited *A. coronus* in order to gain an understanding of the distribution of the species in  
115 relation to the ABFZ. To do this, we employed both mitochondrial DNA (mtDNA) and  
116 nuclear microsatellite DNA markers to assess: i) levels of genetic diversity in *A. coronus*  
117 throughout its present range; ii) the influence of the oceanographic features of the ABFZ in  
118 population sub-structuring; and iii) the demographic and evolutionary history of the species  
119 in the region.

120

## 121 **Methods**

### 122 *Sampling and laboratory analyses*

123           Sampling was conducted during the austral winter month of June from 2007 to 2010,  
124 at five locations spanning the ABFZ region (Figure 1). Although spawning grounds and  
125 nursery areas remain mainly undescribed, previous work on species biology suggests that  
126 spawning occurs in the south of Angola from late austral spring to early summer (Potts et al.  
127 2010) and in the north during the austral winter (Potts, unpublished data). Therefore,  
128 sampling during the same season throughout the distribution range will likely maximize the  
129 possibility of capturing individuals representing the full diversity of the species. A fin clip  
130 was removed immediately after capture and preserved in 95% ethanol. Total genomic DNA  
131 was extracted using a standard phenol : chloroform method (Sambrook et al. 1989).

132           Assessment of genetic variation within and between sampling sites was performed  
133 using both mitochondrial (mtDNA) and nuclear (nDNA) markers. The mtDNA Control  
134 Region (CR) was amplified by Polymerase Chain Reaction (PCR) and sequenced for a sub-  
135 set of samples (12 per sampling site), using a universal primer pair following the original  
136 protocol (Apte and Gardner 2002). Obtained sequences were visually inspected and aligned  
137 in BIOEDIT 7.0.5 (Hall 1999) using CLUSTAL X (Thompson et al. 1997). To test for  
138 deviations to the expectation of neutrality we calculated Tajima's  $D$  (Tajima 1989) and Fu's  
139  $F_S$  (Fu 1997) summary statistics in ARLEQUIN 3.5 (Excoffier et al. 2005). The most suitable  
140 nucleotide substitution model was estimated in jMODELTEST 0.1 (Posada 2008), under the  
141 AIC approach, and used in subsequent analyses.

142           Six cross-specific nDNA microsatellite primer pairs developed for the sister species  
143 *Argyrosomus japonicus* (UBA5, UBA40, UBA50, UBA91, UBA853 and UBA854 –  
144 Archangi et al. 2009) were amplified following the original protocol. Microsatellite  
145 amplicons were genotyped in an ABI 3500 (Applied Biosystems, UK) using LIZ-600<sup>®</sup> as an  
146 internal size marker, and scored based on size in GENEMAPPER 4.0 (ABIPrism). In order to  
147 ensure accurate allele size scoring, we scored the same reference individuals across multiple

148 runs. The quality of the microsatellite dataset was evaluated by estimating the occurrence of  
149 stuttering and large allele dropout in MICROCHECKER (van Oosterhout et al. 2006), and  
150 null allele frequencies in FREENA (Chapuis and Estoup, 2007). Obtained genotypic  
151 frequencies were tested for deviations from Hardy-Weinberg and linkage expectations in  
152 GENEPOP 4.2 (Raymond and Rousset 1995).

153

#### 154 ***Genetic diversity and population sub-structuring of A. coronus across the ABFZ region***

155 Overall and intra-sample levels of genetic diversity were estimated as number of  
156 haplotypes (H), number of private haplotypes (PH), and haplotype ( $h$ ) and nucleotide  
157 diversity ( $\pi$ ) for the mtDNA dataset in ARLEQUIN 3.5 (Excoffier et al. 2005), and number  
158 of alleles (Na), allelic richness (AR), observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosity and  
159 Wright's inbreeding coefficient ( $F_{IS}$ ), for the microsatellite dataset in FSTAT 2.9.3 (Goudet  
160 1995). In addition, the distribution of microsatellite allelic frequencies per locus and sampling  
161 region were calculated in the R package gstudio. Due to sampling restrictions, resulting in  
162 limited sample sizes, and the cross-specific nature of the microsatellite loci, we conducted a  
163 preliminary analysis to investigate statistical power of marker variability to infer population  
164 structure. Simulations were performed in POWSIM 4.1 (Ryman and Palm 2006) for six loci  
165 and two populations representing minimum and maximum sample sizes ( $N = 26$  and  $N = 40$ ),  
166 for five levels of postulated genetic differentiation ( $F_{ST} = 0.002$ ,  $F_{ST} = 0.005$ ,  $F_{ST} = 0.01$ ,  $F_{ST}$   
167  $= 0.02$  and  $F_{ST} = 0.05$ ), using a combination of effective population size ( $N_e = 3000$ ) and time  
168 since divergence ( $t = 10$ ;  $t = 30$ ,  $t = 70$ ,  $t = 125$ ,  $t = 310$  generations since isolation). Each  
169 simulation ran for 10 000 replicates, and power was estimated as the proportion of exact tests  
170 that indicated significant differentiation.

171 Haplotype networks were constructed in NETWORK 5.0.0.0 (Bandelt et al. 1999) to  
172 investigate the geographical distribution of mtDNA haplotypes, using the Median-Joining



173 spanning network algorithm with the maximum parsimony post-processing option enforced  
174 to help solve ambiguous connections. The shortest tree was chosen using a coalescent theory  
175 approach (Grant and Bowen 2006).

176 Levels of pairwise genetic differentiation between samples and across the whole dataset  
177 were estimated using  $\phi_{ST}$  in ARLEQUIN 3.5 (Excoffier et al. 2005) for mtDNA, and Weir &  
178 Cockerham's  $F_{ST}$  estimator (Weir and Cockerham 1984) in FSTAT 2.9.3 (Goudet 1995) and  
179 Jost's D (Jost 2008) in SMOGD (Crawford 2010) for nDNA, with statistical significance  
180 assessed after 10 000 permutations. In addition, a hierarchical analysis of molecular variance  
181 (AMOVA) was performed for both datasets to test two hypotheses: i) population  
182 differentiation in *A. coronus* is associated with the position of the ABFZ at the time of  
183 sampling (LUA, LUC, FLA vs. CUN, HEN); ii) population differentiation is associated with  
184 the temporal nature of the sampling strategy: (2007 FLA & CUN vs. 2009 LUC & HEN vs.  
185 2010 LUA). All AMOVA tests were performed in ARLEQUIN 3.5 (Excoffier et al. 2005),  
186 and statistical significance was assessed after 10 000 permutations. Furthermore, we  
187 investigated the potential for the presence within the dataset of mixtures of individuals from  
188 differentiated sub-populations of *A. coronus* by testing the spatial distribution and clustering  
189 of genotypes using a factorial component analysis in GENETIX 4.0.5 (FCA – Belkhir et al.  
190 2000), and by employing the approach of STRUCTURE 2.3.4 (Pritchard et al. 2000).  
191 Simulations were performed under the admixture model, with correlated allele frequencies,  
192 and allowing the number of clusters to vary between 1 and 5 ( $K = 1$  to 5). Five independent  
193 runs were performed for each  $K$  to ensure convergence, and estimation of the most likely  $K$   
194 followed the method of Evanno et al. (2005), in STRUCTURE HARVESTER 0.6.94 (Earl et  
195 al. 2012).

196

197 ***Demographic history of A. coronus***

198 As no significant between-sample differentiation was observed (see Results), assessment  
199 of *A. coronus* demographic history was performed using all samples pooled to generate a  
200 more representative sample size. Summary statistics ( $h$ ,  $\pi$ , Tajima's  $D$  and Fu's  $F_S$ ) and  
201 mismatch distribution analyses were performed in ARLEQUIN 3.5 (Excoffier et al. 2005) for  
202 the CR dataset. Significant deviations from the hypothesis of past demographic expansion  
203 were assessed using the sum of squared differences (SSD) test, after 10 000 permutations.  
204 Estimates of time since expansion ( $\tau$ ) were obtained using the mismatch distribution  
205 parameters, after  $\tau = 2\mu t$ . Given the uncertainty regarding mutation rates ( $\mu$ ), we used three  
206 different values to estimate demographic parameters: i)  $\mu = 3.6\%$  per million years (MY,  
207 conservative mutation rate derived from an ancient speciation event in marine fishes due to  
208 the closure of the Isthmus of Panama – Donaldson and Wilson 1999); ii)  $\mu = 5\%$  per MY (a  
209 mid-point estimate); and iii)  $\mu = 10\%$  per MY (a faster mutation rate derived from a shallow  
210 and more recent divergence event in Atlantic pygmy angelfishes – Bowen et al. 2006) with  
211 generation time ( $t$ ) estimated at 4.3 years for females (Potts et al. 2010). In addition, a  
212 Bayesian Skyline Plot (BSP) was performed in BEAST 1.8 (Drummond and Rambaut 2007)  
213 to examine historical changes in the female effective population size ( $N_{ef}$ ). We performed  
214 three independent runs, using the piece-wise constant method for population expansion, for  
215 50 million MCMC steps, sampling every 5 000 steps, under a strict molecular clock.  
216 Convergence of runs, BSP estimates and 95% highest posterior density (HPD) intervals were  
217 assessed in TRACER 1.6 (Rambaut and Drummond 2007).

218 As effective population size is a good estimator of relative recruitment levels in marine  
219 species (Carvalho and Hauser 1994), we used the microsatellite dataset to assess current  $N_e$ .  
220 Point estimates of  $N_e$  were performed using the linkage disequilibrium approach implemented  
221 in NeEstimator (Do et al. 2014), at the 0.05 critical allele frequency. Confidence intervals  
222 were assessed using a pairwise jack-knife approach.

223

## 224 **Results**

### 225 *Genetic diversity and population differentiation in A. coronus across the ABFZ region*

226         Given the hypervariability of the mtDNA CR marker, a 524bp fragment was amplified  
227 for a subset of 60 individuals (12 per sampling site), displaying 46 variable sites resulting in  
228 47 haplotypes (Table 1). The Tamura-Nei nucleotide substitution model (Tamura and Nei  
229 1993), with variable rates among lineages ( $\alpha = 0.613$ ), was identified as the most suitable  
230 model of sequence evolution and used in subsequent analyses. Significant deviations from the  
231 expectation of neutrality were detected for all sampling sites with Fu's  $F_S$ , but not with  
232 Tajima's  $D$  (Table 1). However, both metrics were significantly different from zero when the  
233 entire dataset was combined (Table 1). Overall, haplotype and nucleotide diversity were high  
234 ( $h = 0.990$ ,  $\pi = 0.010$ ; Table 1), and varied between  $h = 0.970$  and  $h = 1.000$  (LUC and  
235 CUN), and  $\pi = 0.008$  and  $\pi = 0.014$  (LUA and CUN).

236         There was no evidence of amplification errors and the microsatellite genotype  
237 frequencies conformed to Hardy-Weinberg and linkage equilibrium expectations of random-  
238 mating across loci and samples (Table 2). Overall, nDNA genetic diversity was high ( $H_O =$   
239  $0.716$ ,  $H_E = 0.734$ ), and ranged between  $H_E = 0.718$  and  $H_E = 0.731$  (FLA and CUN,  
240 respectively; Table 2). The number of alleles and allelic richness did not vary between  
241 samples ( $N_a = 10$ , AR  $\sim 9$ ), with the exception of LUA which exhibited the lowest values  
242 (Table 2). Distribution of allelic frequencies per locus and population did not reveal obvious  
243 differences between sampling sites (Supplementary Figure S1). Assessment of the power of  
244 the dataset to detect genetic differentiation between samples indicated that the six cross-  
245 specific loci used in this study could potentially detect differentiation as low as  $F_{ST} = 0.01$  for  
246 populations samples of  $N = 26 - 40$  in 85.5% of tests (100% of tests for  $F_{ST} = 0.05$  and  $F_{ST} =$

247 0.02), suggesting that these markers provided acceptable power for detecting relevant levels  
248 of differentiation within the *A. coronus* population.

249 The null hypothesis of genetic homogeneity within the *A. coronus* population across the  
250 ABFZ region could not be rejected, regardless of the dataset and analysis used. Network  
251 analyses did not indicate obvious geographical sub-structuring either by frequency or  
252 ancestral relatedness of mtDNA haplotypes in *A. coronus*: the majority of individuals were  
253 represented by unique haplotypes, with a high frequency of private haplotypes within  
254 samples but which were mostly singletons with no association of related singletons within  
255 particular samples, while more abundant shared haplotypes were equally frequent among  
256 sites (Figure 2). Overall levels of genetic differentiation among samples were low and non-  
257 significant (mtDNA  $\phi_{ST} = 0.041$ , nDNA  $F_{ST} = 0.000$ , nDNA  $D = 0.000$ ;  $p > 0.05$ ), with  
258 pairwise values between samples all very low and not significantly different from zero (Table  
259 3). Similarly, the hierarchical analyses of molecular variance (AMOVA) did not detect  
260 distinct sub-structuring for either hypothesis tested, with the majority of variance found  
261 within samples and not between groups (Table 4). Assessment of cryptic genetic structuring  
262 (clustering of genotypes) within the microsatellite dataset did not reveal any hidden patterns  
263 of genetic differentiation across the ABFZ region: the FCA displayed a single cluster of  
264 genotypes, despite some outlier individuals (Figure 3). Although the method of Evanno et al.  
265 (2005) suggested  $K=2$  as the most likely number of clusters ( $\Delta K = 15.987$  – see  
266 Supplementary material S1, Table S1), STRUCTURE plots for  $K=2$  were admixed, with the  
267 probability of belonging to each cluster being roughly 50% for every individual  
268 (Supplementary material S1, Figure S1). The most likely explanation for this resides in the  
269 inability to calculate  $\Delta K$  for  $K=1$  (Supplementary material S1, Table S1). Therefore,  
270 STRUCTURE analyses suggest the presence of one population, as this hypothesis had the

271 highest likelihood of all K tested ( $K=1$ ,  $\text{LnP}(D) = -3910.70$ , Supplementary material S1 –  
272 Figure S2).

273

#### 274 ***Demographic history***

275 The negative and significant results from sequence evolution neutrality tests (Fu's  $F_S$ ),  
276 combined with the inability to reject the null hypothesis of a sudden population expansion  
277 using mismatch distribution analyses (Figure 4) and the retrieved Skyline Plots (Figure 5), all  
278 point to the occurrence of a past population expansion in *A. coronus*. Estimates of time since  
279 expansion based on mismatch distribution parameters put expansion date between 11 and 31  
280 thousand years ago (KY – Figure 4), depending on the mutation rate used. Similarly, the  
281 Skyline Plot approach revealed the occurrence of a steep increase in female effective  
282 population size circa ~25-70 KY (Figure 5), depending on the mutation rate used and despite  
283 the broad 95% HPD.

284 Assessment of current effective population size, based on the microsatellite dataset,  
285 revealed that *A. coronus* exhibits moderately large long-term effective population sizes ( $N_e =$   
286 3 307; 95% CI: 322 -  $\infty$ ).

287

#### 288 **Discussion**

##### 289 ***Genetic diversity, population structure and phylogeographic patterns of A. coronus across*** 290 ***the ABFZ***

291 In recent years, intense fishing pressure has been linked in several marine fishes to  
292 reduced population sizes (Briggs 2011), shifts in size ranges and age structures (Miethe et al.  
293 2010), and perhaps most importantly to loss of genetic diversity (Pinsky and Palumbi 2014;  
294 Henriques et al. 2016). In a changing environment, the loss of genetic diversity is of great  
295 concern, as it will influence the ability of a species to adapt to future changes (Briggs 2011).

296 Despite the previously reported high levels of exploitation and reduced population size of *A.*  
297 *coronus*, where the Egg-per-Recruit measure of abundance was estimated at less than 10% of  
298 the value in the absence of fishing for the period 2005-2013 (Beckensteiner et al. 2016), the  
299 historical and present levels of genetic diversity in this species were found to be high and  
300 similar in range to those reported for other sciaenid species not only from the same region  
301 (Henriques et al. 2014; 2015) but also to those occurring in more stable environments  
302 (Silberschneider and Gray 2008; Diaz-Jaimes et al. 2010). The results presented here suggest  
303 that overfishing does not appear to have had (yet) a strong impact on contemporary levels of  
304 genetic diversity in *A. coronus*.

305 Patterns of population genetic diversity and phylogeography indicated by both  
306 mitochondrial and nuclear microsatellite DNA markers could not reject the hypothesis that *A.*  
307 *coronus* comprises a single genetically homogeneous population across its complete range  
308 within the ABFZ region, suggesting that there are no barriers to dispersal or interbreeding  
309 (i.e. panmixia) of this species across this region. However, due to difficulties in accessing  
310 large samples of the study species from such an inaccessible area, sample sizes were below  
311 the recommended 50 individuals per sampling site (Cornuet et al. 1999): therefore it is  
312 possible that small sample sizes and hypervariability of the markers used could have  
313 decreased resolution power for detecting subtle population sub-structuring if present. For  
314 example, the high haplotype diversity observed for the mtDNA dataset might reduce power to  
315 statistically test differentiation as the majority of individual possessed unique haplotypes.  
316 However, phylogeographic theory predicts that sub-structuring of populations would result in  
317 non-random geographical clustering of related haplotypes (Avice 2000). In contrast, our  
318 results show haplotypes private to individual samples are most closely related to haplotypes  
319 private to other samples, interconnected throughout the phylogeographic network without an  
320 obvious geographical clustering pattern, consistent with random dispersion of *A. coronus*

321 throughout the entire distribution range and similar to patterns observed in other abundant  
322 marine fish species with high gene flow (e.g. McKeown et al. 2015).

323 For the nDNA microsatellite allelic distributions, POWSIM analyses indicated that the  
324 dataset had suitable power to detect genetic differentiation as low as  $F_{ST} = 0.01$  in 85.5% of  
325 the tests, with power decreasing to 41% for  $F_{ST} = 0.005$ . The combination of the observed  
326 results does not allow to reject the null hypothesis of genetic homogeneity in this species. In  
327 fact, several lines of evidence support potential panmixia, as the microsatellite loci had the  
328 ability to detect even weak genetic sub-structuring ( $F_{ST} > 0.01$ ), and revealed very low levels  
329 of population divergence (global  $F_{ST} = 0.000$ , inter-sample  $F_{ST} = 0.000 - 0.005$ ).  
330 Furthermore, there was no evidence of cryptic genetic structuring within samples, as no  
331 deviations to Hardy-Weinberg or linkage equilibrium were observed, which might have  
332 indicated the presence of a Wahlund effect (Nei and Li 1973; Pusack et al. 2014; Henriques  
333 et al. 2017). Finally, both FCA and STRUCTURE clustering analyses supported the presence  
334 of one gene pool, even though STRUCTURE may have less power to detect sub-structuring  
335 if  $F_{ST} < 0.02$  (Latch et al. 2006). Therefore, the most likely scenario is that *A. coronus* is  
336 composed by one population throughout its distribution range. Resolution of spatial stock  
337 structure at a finer scale may be beyond the level of neutral genetic markers and benefit from  
338 complementary analysis of markers under selection (Canino et al. 2005).

339 Major oceanographic features across the wider Benguela Current region have been shown  
340 as barriers to effective dispersal of marine taxa, with many species exhibiting distinct genetic  
341 divergence between populations indicating breakdown of interbreeding and gene flow  
342 (Henriques et al. 2012; 2016; von der Heyden et al. 2008; 2011). However, the potential of an  
343 oceanographic feature to be a barrier to gene flow is closely linked to the biological features  
344 of the species itself (Galarza et al. 2009; Luiz et al. 2012). *Argyrosomus coronus* is a  
345 relatively long-lived (max = 13 years), benthopelagic sciaenid that appears to undertake

346 seasonal alongshore migrations (Potts et al. 2010). Catch-per-effort data indicate that this  
347 species is predominantly found in a temperature range of 16 – 22°C, similar to the SST range  
348 around the ABFZ, and that the seasonal movement patterns of this frontal zone are thought to  
349 be the driver of *A. coronus* migratory behaviour (Potts et al. 2010; 2014). Recent biological  
350 findings suggest that spawning may occur throughout the distribution range, with ripe and  
351 running females found off northern Angolan waters during the austral winter (June – Potts,  
352 unpublished data), and a protracted spawning period documented for the southern region,  
353 extending from late spring to summer (Potts et al. 2010). Based on these findings and the  
354 seasonal shifts of the ABFZ, it is possible that spawning only occurs during a narrow thermal  
355 window. Indeed, spawning in the sister species *A. japonicus* off South Africa occurs only  
356 when temperatures are within a narrow range (20 – 24°C; Griffiths, 1996). These findings  
357 may suggest that *A. coronus* has multiple spawning grounds distributed throughout the  
358 system, with spawning regulated by the marked seasonal and regional SST patterns (Jahn et  
359 al. 2003). Besides the appropriated thermal range, the timing and location of spawning may  
360 also have evolved to maximize the dispersal of pelagic eggs and larvae in this highly unstable  
361 habitat (Potts et al. 2010). *Arygyrosomus coronus*, like *A. japonicus*, is thought to use  
362 estuaries as nursery grounds (Griffiths 1996; Potts et al. 2010). By migrating and reproducing  
363 in the south of their distribution during the spring-summer, pelagic eggs and larvae can be  
364 passively transported to the Cunene Estuary, through the seasonal displacement of the ABFZ.  
365 Similarly, by reproducing in the northern region during winter when SSTs are cooler, eggs  
366 and larvae can be passively dispersed northwards towards nursery grounds in the large  
367 estuaries (e.g. Kwanza, Congo) to the north. Indeed, juvenile specimens (185 – 285 mm TL)  
368 have been observed as far north as Gabon (Poll 1954). Interestingly, an on-going  
369 conventional tagging study has revealed that movement may occur during the late juvenile  
370 stage (400 – 600 mm TL), with individuals dispersing up to 210km, and during the adult



371 stage with individuals migrating 750 km (Parkinson et al., unpublished data). The tagging  
372 studies thus suggest that *A. coronus* is capable of dispersal throughout much of its life cycle,  
373 which may explain the observed genetic homogeneity of the species across the ABFZ region.

374

#### 375 ***Demographic history of A. coronus***

376 The demographic history of *A. coronus* shows evidence for past population size changes  
377 that appear to be linked with historical climatic shifts in the region. Results from the mtDNA  
378 analyses revealed evidence for a past population expansion approximately 11-75 KY  
379 (depending on the mutation rate used) around or just pre-dating the Last Glacial Maximum  
380 (LGM; Clark et al. 2009). Although estimates of time since expansion should be regarded  
381 with caution due to the assumptions required for calibration of the molecular clock, both the  
382 mismatch distribution and the coalescent-based analyses depicted a clear population increase  
383 in the last 25-75 KY. The expansion in *A. coronus* appears to have occurred earlier in time  
384 than those reported for other fishes (Grant and Bowen 2006), but is similar in range to those  
385 suggested for *Atractoscion aequidens* (currently *A. microlepis*) and *Merluccius capensis* in  
386 the same region (Henriques et al. 2014; 2016).

387 During the Quaternary, the Benguela Current experienced increased upwelling events and  
388 colder SSTs, particular around 60 KY and 18 KY (Kirst et al. 1999). Climatic changes in the  
389 Pleistocene are thought to have influenced the genetic signatures of the populations of several  
390 marine fishes, particularly in the southeastern Atlantic, with several population expansions  
391 dating from the Holocene (8-6 KY; e.g. Matthee et al. 2007; von der Heyden et al. 2007;  
392 2010). In the case of *A. coronus*, it appears that the population survived the LGM (in possible  
393 glacial refugia) after which expansion began from early during the warming process. Similar  
394 refugial hypotheses have been suggested to have contributed to an earlier population  
395 expansion of *A. aequidens* in the northern Benguela (Henriques et al. 2014), and in other

396 temperate species from the Atlantic Ocean (Francisco et al. 2011; Faria et al. 2012). With  
397 temperature requirements that overlap with those found in the ABFZ (Potts et al. 2010), it is  
398 likely that changes in the range of the frontal system would be mirrored by changes in the  
399 distribution and abundance of *A. coronus*. Indeed, recent rapid warming in the southern  
400 Angola region has coincided with a decrease in the abundance of this species in the region,  
401 and an increase (when compared with *A. inodorus*) in the cooler waters off central and  
402 northern Namibia (Potts et al. 2014). Such distributional shifts associated with changing  
403 temperatures are thought to be one of the first consequences of climate changes in multiple  
404 species (Grant and Bowen 2006; Garroway et al. 2011; Hill et al. 2011).

405 Estimates of long-term effective population sizes, based on the microsatellite dataset,  
406 showed values well above the minimum threshold for maintenance of a species' evolutionary  
407 potential ( $N_e > 500$ , Frankham 2005), and with no evidence for recent population contraction.  
408 This implies that exploitation has not impacted the genetic diversity of *A. coronus*, despite a  
409 recent study suggesting that the population is at 5-10% of its pristine biomass (Beckensteiner  
410 et al. 2016). Such findings are likely to result from historically high effective population sizes  
411 and diversity levels, where only severe and long-term population crashes would result in a  
412 large and detectable loss (Riccioni et al. 2010). However, these results should only be  
413 interpreted as exploratory, as the observed upper bound of the 95% confidence interval was  
414 infinity, suggesting that the dataset had limited power to define  $N_e$  accurately (Waples and  
415 Do 2010), and further studies should be performed employing a higher number of markers  
416 and larger sample sizes to investigate contemporary changes in  $N_e$ .

417

418 ***Conclusions and implications for understanding climate change effects and sustainable***  
419 ***harvesting***

420 The results from this study combined with the findings of Potts et al. (2010; 2014)  
421 suggest that the evolutionary history of *A. coronus* is strongly linked with the characteristics  
422 of the ABFZ. The inability to reject the null hypothesis of genetic homogeneity, leading to a  
423 conclusion of widespread panmixia may be a consequence of the adaptation to, and  
424 colonization of, the frontal system itself by *A. coronus*. The observed spawning behavior and  
425 possible annual return migration appear to correlate to the movement of the ABFZ and thus  
426 climatic changes that affect its oscillatory pattern may have a direct impact on the distribution  
427 range and population dynamics of *A. coronus*. Future studies should be conducted using not  
428 only neutral but also adaptive markers to investigate the possibility of cryptic genetic  
429 differentiation linked to local adaptation. Furthermore, the recent hybridization and  
430 introgression with *A. inodorus* in Namibia (Potts et al. 2014) deserves further research  
431 attention and continuous genetic surveys are required to understand the impacts of such  
432 hybridization events in the genomic architecture of both species.

433 The observed poleward range shift by *A. coronus* will also have a significant impact in  
434 the fishing industry of the region. Fishing policies differ between Angola and Namibia, and  
435 since both *Argyrosomus* species have significantly different life-history traits (Holtzhausen et  
436 al. 2001; Potts et al. 2010) a transboundary fishing policy is urgently required. The Benguela  
437 Current Convention (BCC) has the mandate to coordinate fishing management policies across  
438 the Benguela Current region, aided in this endeavor through the Convention signed by South  
439 Africa, Namibia and Angola, which seeks to promote a coordinate regional approach to the  
440 long-term conservation, protection, rehabilitation, enhancement and sustainable use of the  
441 Benguela Current Large Marine Ecosystem. The BCC should thus both initiate and be  
442 involved in the establishment of future management plans for *A. coronus*.

443

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450

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689

690 **Tables**

691 **Table 1:** Mitochondrial genetic diversity and neutrality tests for *A. coronus* CR: N – number  
 692 of individuals; n – number of haplotypes; PH – number of private haplotypes; *h* – haplotype  
 693 diversity;  $\pi$  - nucleotide diversity; D – Tajima neutrality test;  $F_S$  – Fu neutrality test.  
 694 Statistically significant results ( $p < 0.05$ ) in bold. See Figure 1 for sample site locations (CR  
 695 accession numbers JX191938-97).

	<b>HEN</b>	<b>CUN</b>	<b>FLA</b>	<b>LUC</b>	<b>LUA</b>	<b>Overall</b>
<b>N</b>	12	12	12	12	12	60
<b>n</b>	11	12	11	10	11	47
<b>PH</b>	7	11	7	8	7	41
<b><i>h</i></b>	0.985	1.000	0.985	0.970	0.985	0.990
<b><math>\pi</math></b>	0.011	0.014	0.010	0.012	0.008	0.010
<b><i>D</i></b>	-0.437	-0.976	-0.823	-0.504	-0.917	<b>-1.501</b>
<b><i>F<sub>S</sub></i></b>	<b>-5.206</b>	<b>-6.652</b>	<b>-5.957</b>	<b>-3.065</b>	<b>-8.853</b>	<b>-25.445</b>

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698 **Table 2:** Genetic diversity in *A. coronus* at six cross-specific microsatellite loci (see Figure 1  
 699 for site locations): N – number of individuals genotyped; Na – number of alleles; AR – allelic  
 700 richness (minimum of 16 individuals);  $H_E$  – expected heterozygosity;  $H_O$  – observed  
 701 heterozygosity;  $F_{IS}$  – inbreeding coefficient. No significant deviations to Hardy-Weinberg  
 702 were detected (after correction for multiple tests).

<b>Locus</b>	<b>Measure</b>	<b>HEN</b>	<b>CUN</b>	<b>FLA</b>	<b>LUC</b>	<b>LUA</b>	<b>Overall</b>
<b>UBA5</b>	<b>N</b>	40	26	40	34	40	180
	<b>Na</b>	6	6	7	6	5	9

	<b>AR</b>	5.610	6.000	6.529	5.945	4.999	8.933
	<b>H<sub>E</sub></b>	0.721	0.761	0.724	0.747	0.732	0.743
	<b>H<sub>O</sub></b>	0.775	0.615	0.700	0.853	0.925	0.783
	<b>F<sub>IS</sub></b>	-0.063	0.210	0.045	-0.127	-0.252	-0.054
<hr/>							
<b>UBA40</b>	<b>N</b>	40	26	40	34	40	180
	<b>Na</b>	15	16	14	15	14	22
	<b>AR</b>	13.457	16.000	12.433	14.030	12.264	21.833
	<b>H<sub>E</sub></b>	0.865	0.880	0.842	0.892	0.835	0.879
	<b>H<sub>O</sub></b>	0.825	0.808	0.825	0.971	0.950	0.872
	<b>F<sub>IS</sub></b>	0.059	0.102	0.033	-0.073	-0.125	0.008
<hr/>							
<b>UBA50</b>	<b>N</b>	40	26	39	34	39	178
	<b>Na</b>	16	13	15	15	17	22
	<b>AR</b>	14.585	13.000	13.929	13.755	15.478	21.887
	<b>H<sub>E</sub></b>	0.884	0.875	0.882	0.888	0.894	0.903
	<b>H<sub>O</sub></b>	0.875	0.846	0.821	0.794	0.846	0.843
	<b>F<sub>IS</sub></b>	0.024	0.053	0.083	0.121	0.066	0.067
<hr/>							
<b>UBA91</b>	<b>N</b>	40	26	40	33	34	179
	<b>Na</b>	5	4	4	3	3	6
	<b>AR</b>	4.260	4.000	3.530	2.958	2.650	5.999
	<b>H<sub>E</sub></b>	0.287	0.270	0.282	0.219	0.258	0.293
	<b>H<sub>O</sub></b>	0.275	0.308	0.325	0.182	0.226	0.263
	<b>F<sub>IS</sub></b>	0.054	-0.120	-0.139	0.183	0.142	0.105
<hr/>							
<b>UBA853</b>	<b>N</b>	39	26	35	34	40	174
	<b>Na</b>	9	13	9	11	11	16



	<b>AR</b>	8.323	13.00	8.929	10.465	10.352	16.000
	<b>H<sub>E</sub></b>	0.870	0.878	0.849	0.848	0.830	0.858
	<b>H<sub>O</sub></b>	0.795	0.962	0.943	0.735	0.800	0.822
	<b>F<sub>IS</sub></b>	0.028	-0.076	-0.096	0.148	0.049	0.043
<hr/>							
<b>UBA854</b>	<b>N</b>	40	26	40	34	40	180
	<b>Na</b>	9	7	8	8	6	13
	<b>AR</b>	7.790	7.000	7.167	7.516	5.867	12.833
	<b>H<sub>E</sub></b>	0.717	0.719	0.734	0.742	0.704	0.738
	<b>H<sub>O</sub></b>	0.700	0.654	0.625	0.706	0.900	0.711
	<b>F<sub>IS</sub></b>	0.039	0.146	0.161	0.064	-0.267	0.036
<hr/>							
	<b>N</b>	40	26	39	34	39	178
	<b>Na</b>	10	10	10	10	9	15
<b>Average</b>	<b>AR</b>	9.004	9.833	8.753	9.112	6.768	14.581
<b>all loci</b>	<b>H<sub>E</sub></b>	0.724	0.731	0.718	0.728	0.709	0.734
	<b>H<sub>O</sub></b>	0.698	0.699	0.707	0.697	0.778	0.716
	<b>F<sub>IS</sub></b>	0.022	0.069	0.030	0.037	-0.080	0.028
<hr/>							

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705 **Table 3:** Pairwise genetic differentiation between samples of *A. coronus*: mtDNA CR  $\phi_{ST}$

706 below diagonal, microsatellite  $F_{ST}/D$  above diagonal. No values were significantly greater

707 than zero ( $p > 0.05$ ).

	<b>HEN</b>	<b>CUN</b>	<b>FLA</b>	<b>LUC</b>	<b>LUA</b>
<b>HEN</b>	-	-	-0.003 / 0.000	0.005 / 0.007	-0.001 / 0.000
<b>CUN</b>	0.017	-	-	-	-

<b>FLA</b>	-0.039	0.018	-	0.002 / 0.008	-0.001 / 0.001
<b>LUC</b>	0.013	0.028	0.028	-	0.001 / 0.001
<b>LUA</b>	0.032	0.015	-0.024	0.021	-

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709

710 **Table 4:** Hierarchical analyses of molecular variance (AMOVA) based on frequencies of  
711 mtDNA CR haplotypes and nuclear microsatellite multi-locus genotypes for two hypotheses  
712 of population sub-structuring: the position of the ABFZ (ABFZ) and the year of sampling  
713 (Year). F = fixation index; p = statistical significance.

<b>Hypothesis</b>	<b>Source of variation</b>	<b>mtDNA</b>			<b>Microsatellites</b>		
		<b>% of variation</b>	<b>F</b>	<b>p</b>	<b>% of variation</b>	<b>F</b>	<b>p</b>
ABFZ	Between groups	0.00	0.000	0.702	0.00	0.000	0.602
	Among sites	2.16	0.021	0.106	0.00	0.000	0.514
	Within sites	98.63	0.014	0.129	100	0.000	0.593
Year	Among groups	0.00	0.000	0.398	0.00	0.000	0.883
	Among sites	1.95	0.019	0.209	0.13	0.001	0.374
	Within sites	98.39	0.016	0.127	99.87	0.000	0.598

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717 **Figures**

718 **Figure 1:** Sampling strategy for *A. coronus* across the northern Benguela sub-system,  
719 highlighting sampling sites: Luanda (LUA, N = 40); Lucira (LUC, N = 40); Flamingo River  
720 (FLA, N = 40); Cunene River Mouth (CUN, N = 28); Henties Bay (HEN, N = 40). Major  
721 oceanographic features of the system: the Benguela and Angola Currents, position of the  
722 Angola-Benguela Frontal Zone, and continental shelf width (grey line = -200m contour).

723

724 **Figure 2:** Reconstructed haplotype network for *A. coronus* across the northern Benguela sub-  
725 system, based on 524bp of mtDNA CR sequence. Black dots represent missing haplotypes.  
726 Sample sites abbreviations as per Figure 1. Branch lengths are proportional to mutational  
727 changes.

728

729 **Figure 3:** Factorial Component Analysis for *A. coronus* microsatellite genotypes. The first  
730 two axes explained 11.28% of variation. Sample sites abbreviations as per Figure 1.

731

732 **Figure 4:** Mismatch distribution analyses for *A. coronus*, based on 524bp of mtDNA CR  
733 sequence, including neutrality tests (Tajima's  $D$  and Fu's  $F_S$ ) and mismatch distribution  
734 parameters ( $\sigma$  - time since expansion in mutation units;  $\theta_0$  - population size before  
735 expansion;  $\theta_1$  - population size after expansion,  $T$  - time since expansion, KY).

736

737 **Figure 5:** Bayesian Skyline Plot (BSP) showing changes in modelled female effective  
738 population size ( $N_{ef}$ ) over time (KY) in modeled population size for *A. coronus* in the ABFZ  
739 region per mutation rate used: A - 3.6% per MY; B - 5% per MY; C - 10% per MY. Solid  
740 black line indicates the median estimate, with the 95% HPD lines depicted in grey.

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