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

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The West Coast dusky kob *Argyrosomus coronus* is a commercially exploited fish with a distribution confined to the Angola–Benguela Frontal Zone (ABFZ) of the southeastern Atlantic Ocean. A previous study revealed that during a recent period of local warming the species extended its distribution into Namibian waters, where it hybridised with the resident and congeneric *Argyrosomus inodorus*. Environmental changes are a major threat to marine biodiversity and when combined with overfishing have the potential to accelerate the decline of species. However, little is known regarding the evolutionary history and population structure of *A. coronus* across the ABFZ. We investigated genetic diversity, population structure and historical demographic changes using mtDNA control region sequences and genotypes at six nuclear microsatellite loci, from 180 individuals. A single, genetically homogeneous population was indicated across the distributional range of *A. coronus* (ϕ_{ST} = 0.041, F_{ST} = 0.000, D = 0.000; p > 0.05). These findings imply that the oceanographic features within the ABFZ do not appear to significantly influence population connectivity in *A. coronus*, which simplifies management of the species. However, reconstruction of the demographic history points to a close link between the evolutionary history of *A. coronus* and the environmental characteristics of the ABFZ. This outcome suggests the species' vulnerability to the rapid environmental changes being observed across this region, and highlights a pressing need for transboundary management to mitigate the impacts of climate change in this global hotspot of seawater temperature changes.

Keywords: Angola–Benguela Frontal Zone, climate change, demographic history, marine fisheries, molecular ecology, population structure

Online supplementary material: Supplementary data on allelic distributions per loci and the population sampled, as well as all STRUCTURE results for population substructuring, are available at https://doi.org/10.2989/1814232X.2018.1434090.

Introduction

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

Global-warming hotspots are defined as regions with above-average increases in ocean temperature (Hobday and Pecl 2014). A number of ocean-warming hotspots have been identified throughout the world, including one in the coastal waters off southern Angola (Hobday and Pecl 2014). From an oceanographic perspective, this region is dominated by the Angola–Benguela Frontal Zone (ABFZ) off the coast of central Angola (~16° S), which results from the convergence of the warm-tropical Angola Current and the cold, upwelling-dominated Benguela Current (Kirkman et al. 2016). This is a highly dynamic environment, with the position and strength of the ABFZ varying throughout the year in response to changes in the Southern Atlantic Anticyclone (SAA) and the upwelling regime of the Benguela Current (Jahn et al. 2003). During summer, the ABFZ is displaced southwards due to the expansion of the SAA (up to 18° S), while in winter the contraction of the SAA and increased upwelling off Namibia results in a northward movement of the front (to 13° S; Jahn et al. 2003). Despite the environmental and biological complexity of this area, few studies have investigated the impact of contemporary environmental changes at a regional

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level (Monteiro et al. 2008; Potts et al. 2009, 2010, 2014), with the region remaining largely understudied.

In recent decades, the ABFZ region has experienced a rapid increase in sea surface temperatures (SSTs) (Monteiro et al. 2008), which has already impacted the distributional ranges of local species such as the west coast dusky kob *Argyrosomus coronus* Griffiths and Heemstra 1995 (Potts et al. 2014). This coastal, migratory species ranges from northern Angola to northern Namibia (Griffiths and Heemstra 1995; Potts et al. 2010), and is a valuable fishery resource targeted by recreational, artisanal and subsistence fisheries (Potts et al. 2009, 2010). Despite sustaining a multiuser fishery, there are currently no specific fishing regulations for *A. coronus* in Angola. The Angolan Presidential Decree 11/2016 (available upon request from RH) groups it with 'sciaenid' fishes, which are managed as a quota. However, subsistence and recreational catches, which constitute the main fishing effort in the region, are not regularly monitored nor included in the yearly total capture allowance. Therefore, the species is essentially not managed at present and increasing fishing efforts in the region (Potts et al. 2009) have resulted in a population collapse (Beckensteiner et al. 2016).

A previous life-history study suggested that the distributional range of *A. coronus* is closely linked with the seasonal displacement of the ABFZ, with adults undertaking a seasonal alongshore migration, and with spawning thought to occur in the southern region of its range during late spring and summer (Potts et al. 2010). Recent findings, however, seem to dispute this hypothesis, with ripe and running females observed on an offshore reef in 10 m of water near the Kwanza Estuary (northern Angola) during the austral winter months (WMP, unpublished data). Therefore, the full extent of the spawning locations of the species remains unknown. The duration of the pelagic egg and larval stages is also unknown, although it is expected to be similar (~26 days) to that of its sister species *Argyrosomus japonicus* (Edworthy et al. 2018). Juveniles (300–600 mm total length [TL]) and subadults (601–870 mm TL) are thought to be resident, with maturation (at approximately 870 mm TL) heralding the migratory phase (Potts et al. 2010). Growth is rapid, with fish attaining maturity at just four years of age (Potts et al. 2010).

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

The aim of this study was to examine genetic diversity and population substructuring in exploited *A. coronus* to gain an understanding of the distribution of the species in relation to the ABFZ. To achieve this, we employed both mitochondrial DNA (mtDNA) sequences and nuclear DNA (nDNA) microsatellite markers to assess: (i) levels of genetic diversity in *A. coronus* throughout its present range; (ii) the influence of the oceanographic features of the ABFZ in population substructuring; and (iii) the demographic and evolutionary history of the species in the region.

Materials and methods

Sampling and laboratory analyses

Sampling of *Argyrosomus coronus* was conducted during the austral winter month of June, from 2007 to 2010, at five locations spanning the ABFZ region: Luanda (LUA), Lucira (LUC), Flamingo River (FLA), Cunene River mouth (CUN), and Henties Bay (HEN) (Figure 1). Although the spawning grounds and nursery areas remain mainly undescribed, previous work on the species' biology suggests that spawning occurs in the south of Angola from late austral spring to early summer (Potts et al. 2010) and in the north during the austral winter (WMP, unpublished data). Therefore, sampling during the same season throughout the distributional range will likely maximise the possibility of capturing individuals representing the full diversity of the species. A fin clip was removed immediately after capture and preserved in 95% ethanol. Total genomic DNA was extracted using a standard phenol:chloroform method (Sambrook et al. 1989).

Assessment of genetic variation within and between sampling sites was performed using both mtDNA and nDNA markers. The mtDNA control region (CR) was amplified by polymerase chain reaction (PCR) and sequenced for a subset of samples (12 per sampling site), using a universal primer pair following the original protocol (Apte and Gardner 2002). Obtained sequences were visually inspected and aligned in BIOEDIT 7.0.5 (Hall 1999) using CLUSTAL X (Thompson et al. 1997). To test for deviations to the expectation of neutrality we calculated Tajima's D (Tajima 1989) and Fu's F_S (Fu 1997) summary statistics in ARLEQUIN 3.5 (Excoffier et al. 2005), with statistical significance assessed after 10 000 permutations. The most suitable nucleotide substitution model was estimated in jMODELTEST 0.1 (Posada 2008) under the Akaike information criterion, and then used in subsequent analyses.

Six cross-specific nDNA microsatellite primer pairs, developed for the sister species *A. japonicus* (i.e. UBA5, UBA40, UBA50, UBA91, UBA853 and UBA854; Archangi et al. 2009), were amplified following the original protocol. Microsatellite amplicons were genotyped in an ABI 3500 genetic analyser (Applied Biosystems, UK), using 600 LIZ® as an internal size marker, and scored based on size in GENEMAPPER 4.0 (ABIPrism). To ensure accurate allele size scoring, we scored the same reference individuals across multiple runs. The quality of the microsatellite dataset was evaluated by estimating the occurrence of stuttering and large allele dropout in MICROCHECKER (van Oosterhout et al. 2006), and null allele frequencies in FREENA (Chapuis and Estoup 2007). Obtained genotypic frequencies were tested for deviations from Hardy–Weinberg and linkage expectations in GENEPOP 4.2 (Raymond and Rousset 1995).

Genetic diversity and population substructuring of **A. coronus** *across the ABFZ region*

The overall and intra-sample levels of genetic diversity were estimated as the number of haplotypes (H), number

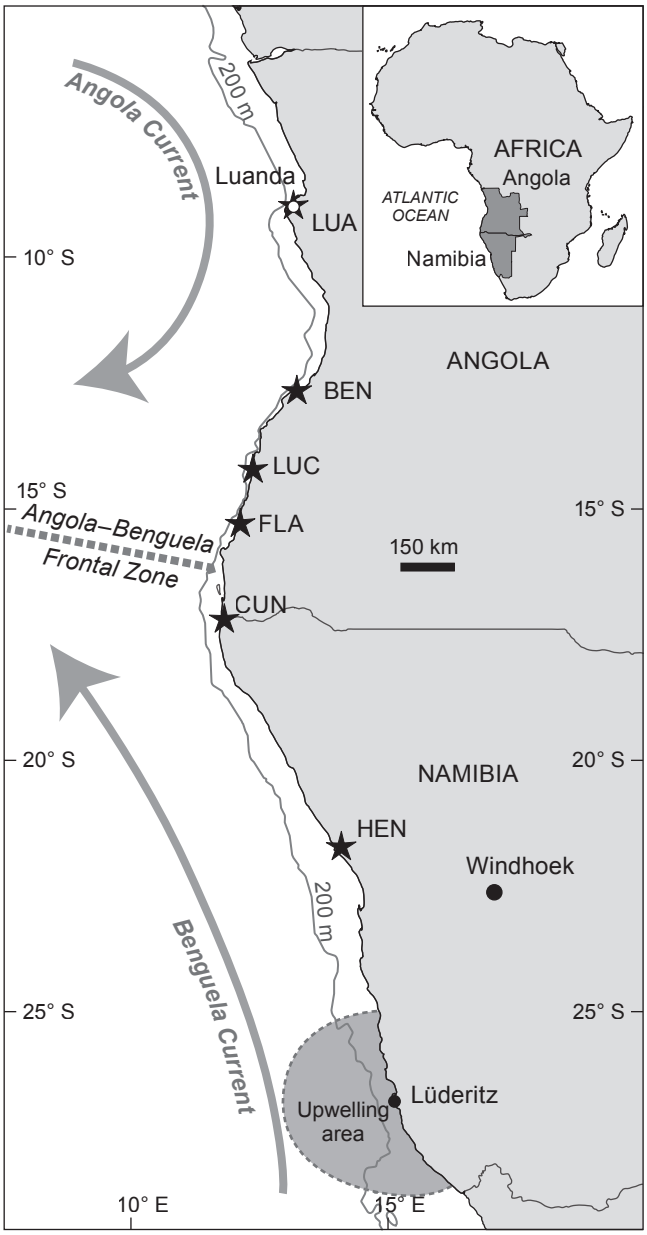

Figure 1: Sampling strategy for *Argyrosomus coronus* across the northern Benguela subsystem, highlighting locations of the five sampling sites: Luanda (LUA, n = 40), Lucira (LUC, n = 40), Flamingo River (FLA, n = 40), Cunene River mouth (CUN, n = 28), and Henties Bay (HEN, n = 40). Major oceanographic features of the system include the Benguela and Angola currents, position of the Angola–Benguela Frontal Zone, and continental shelf width (200-m isobath)

of private haplotypes (PH), and haplotype (h) and nucleotide diversity (π) for the mtDNA dataset in ARLEQUIN 3.5 (Excoffier et al. 2005), and the number of alleles (*Na*), allelic richness (AR), observed (H_O) and expected (H_E) heterozygosity, and Wright's inbreeding coefficient (F_{IS}), for the microsatellite dataset in FSTAT 2.9.3 (Goudet 1995). In addition, the distribution of microsatellite allelic frequencies per locus and sampling region were calculated in the R environment using the gstudio package. Due to sampling restrictions, resulting in limited sample sizes, and the cross-specific nature of the microsatellite loci, we conducted a preliminary analysis to investigate the statistical power of marker variability to infer population structure. Simulations were performed in POWSIM 4.1 (Ryman and Palm 2006) for six loci and two populations representing minimum and maximum sample sizes (n = 26 and n = 40), for five levels of postulated genetic differentiation (F_{ST} = 0.002, F_{ST} = 0.005, F_{ST} = 0.01, F_{ST} = 0.02 and F_{ST} = 0.05), using a combination of effective population size (Ne = 3 000) and time since divergence (t = 10, t = 30, t = 70, t = 125 and t = 310 generations since isolation). Each simulation ran for 10 000 replicates, and power was estimated as the proportion of exact tests that indicated significant differentiation.

Haplotype networks were constructed in NETWORK 5.0.0.0 (Bandelt et al. 1999) to investigate the geographical distribution of mtDNA haplotypes, using the Median–Joining spanning network algorithm with the maximum parsimony post-processing option enforced to help solve ambiguous connections. The shortest tree was chosen using a coalescent theory approach (Grant and Bowen 2006).

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

Argyrosomus coronus *demography*

As no significant between-sample differentiation was observed (see Results), assessment of *A. coronus* demographic history was performed using all samples pooled to generate a more representative sample size. Summary statistics (h, π, Tajima's D and Fu's F_S) and mismatch distribution analyses were performed in ARLEQUIN 3.5 (Excoffier

et al. 2005) for the CR dataset. Significant deviations from the hypothesis of past demographic expansion were assessed using the sum-of-squared differences (SSD) test, after 10 000 permutations. Estimates of time since expansion (τ) were obtained using the mismatch distribution parameters, after $\tau = 2$ μt. Given the uncertainty regarding mutation rates (μ), we used three different values to estimate demographic parameters: (i) μ = 3.6% per million years (MY, conservative mutation rate derived from an ancient speciation event in marine fishes due to the closure of the Isthmus of Panama; Donaldson and Wilson 1999); (ii) μ = 5% per MY (a mid-point estimate); and (iii) μ = 10% per MY (a faster mutation rate derived from a shallower and more recent divergence event in Atlantic pygmy angelfishes of genus *Centropyge*; Bowen et al. 2006) with generation time (*t*) estimated at 4.3 years for females (Potts et al. 2010). In addition, a Bayesian skyline plot (BSP) was performed in BEAST 1.8 (Drummond and Rambaut 2007) to examine historical changes in the female effective population size (N_{ef}). We performed three independent runs, using the piece-wise constant method for population expansion, for 50 million MCMC (Markov Chain Monte Carlo) steps, sampling every 5 000 steps, under a strict molecular clock. Convergence of runs, BSP estimates and intervals of 95% highest posterior density (HPD) were assessed in TRACER 1.6 (Rambaut et al. 2014).

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

Results

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

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

There was no evidence of amplification errors, and the microsatellite genotype frequencies conformed to Hardy–Weinberg and linkage equilibrium expectations of random-mating across loci and samples (Table 2). Overall, nDNA genetic diversity was high ($H_O = 0.716$, $H_E = 0.734$), and ranged between $H_E = 0.718$ and 0.731 (FLA and CUN, respectively; Table 2). The number of alleles and allelic richness did not vary between samples (*N*a = 10, AR ~9), with the exception of LUA which exhibited the lowest values (Table 2). The distribution of allelic frequencies per locus and population did not reveal obvious differences between sampling sites (Supplementary Figure S1). Assessment of the power of the dataset to detect genetic differentiation between samples indicated that the six cross-specific loci used in this study could potentially detect differentiation as low as $F_{ST} = 0.01$ for population samples of $n = 26$–40 in 85.5% of tests (100% of tests for $F_{ST} = 0.05$ and $F_{ST} = 0.02$), suggesting that these markers provided acceptable power for detecting relevant levels of differentiation within the *A. coronus* population.

The null hypothesis of genetic homogeneity within the *A. coronus* population across the ABFZ region could not be rejected, regardless of the dataset and analysis used. Network analyses did not indicate obvious geographical substructuring, either by frequency or ancestral relatedness of mtDNA haplotypes in *A. coronus*: the majority of individuals were represented by unique haplotypes, with a high frequency of private haplotypes within samples, but which were mostly singletons with no association of related singletons within particular samples, while more abundant shared haplotypes were equally frequent among sites (Figure 2). Overall levels of genetic differentiation among samples were low and non-significant (mtDNA $\phi_{ST} = 0.041$, nDNA $F_{ST} = 0.000$, nDNA $D = 0.000$; $p > 0.05$), with pairwise values between samples all very low and not significantly different from zero (Table 3). Similarly, the hierarchical analyses of

Table 1: Mitochondrial genetic diversity and neutrality tests for *Argyrosomus coronus* control region (CR accession numbers JX191938-97): *N* = number of individuals; *n* = number of haplotypes; PH = number of private haplotypes; *h* = haplotype diversity; π = nucleotide diversity; *D* = Tajima neutrality test; F_S = Fu neutrality test. See Figure 1 for the five sampling locations. Bold font indicates statistically significant values ($p < 0.05$)

	HEN	CUN	FLA	LUC	LUA	Overall
N	12	12	12	12	12	60
n	11	12	11	10	11	47
PH	7	11	7	8	7	41
h	0.985	1.000	0.985	0.970	0.985	0.990
π	0.011	0.014	0.010	0.012	0.008	0.010
D	−0.437	−0.976	−0.823	−0.504	−0.917	**−1.501**
F_s	**−5.206**	**−6.652**	**−5.957**	**−3.065**	**−8.853**	**−25.445**

molecular variance (AMOVA) did not detect distinct population substructuring for either hypothesis tested, with the majority of variance found within samples and not between groups (Table 4). Assessment of cryptic genetic structuring (clustering of genotypes) within the microsatellite dataset did not reveal any hidden patterns of genetic differentiation across the ABFZ region: the FCA displayed a single cluster of genotypes, despite some outlier individuals (Figure 3). Although the method of Evanno et al. (2005) suggested K = 2 as the most likely number of clusters (DeltaK = 15.971; Supplementary Table S1), STRUCTURE plots for K = 2 were admixed, with the probability of belonging to each cluster being roughly 50% for every individual (Supplementary Figure S2). The most likely explanation for this resides in the inability to calculate DeltaK for K = 1 (Supplementary Table S1). Therefore, the STRUCTURE analyses suggest the presence of one population, as this hypothesis had the highest likelihood of all K tested (K = 1, LnP(D) = −3910.70; Supplementary Figure S3).

Demographic history

The negative and significant results from sequence evolution neutrality tests (Fu's F_S), combined with the inability to reject the null hypothesis of a sudden population expansion using mismatch distribution analyses (Figure 4) and the retrieved skyline plots (Figure 5), all point to the occurrence of a past

Table 2: Genetic diversity in *Argyrosomus coronus* at six cross-specific microsatellite loci. See Figure 1 for the five sampling locations; N = number of individuals genotyped; *Na* = number of alleles; AR = allelic richness (minimum of 16 individuals); H_E = expected heterozygosity; H_O = observed heterozygosity; F_{IS} = inbreeding coefficient. No significant deviations from Hardy–Weinberg equilibrium were detected (after correction for multiple tests)

Locus	Measure	HEN	CUN	FLA	LUC	LUA	Overall
UBA5	*N*	40	26	40	34	40	180
	Na	6	6	7	6	5	9
	AR	5.610	6.000	6.529	5.945	4.999	8.933
	H_E	0.721	0.761	0.724	0.747	0.732	0.743
	H_O	0.775	0.615	0.700	0.853	0.925	0.783
	F_{IS}	−0.063	0.210	0.045	−0.127	−0.252	−0.054
UBA40	*N*	40	26	40	34	40	180
	Na	15	16	14	15	14	22
	AR	13.457	16.000	12.433	14.030	12.264	21.833
	H_E	0.865	0.880	0.842	0.892	0.835	0.879
	H_O	0.825	0.808	0.825	0.971	0.950	0.872
	F_{IS}	0.059	0.102	0.033	−0.073	−0.125	0.008
UBA50	*N*	40	26	39	34	39	178
	Na	16	13	15	15	17	22
	AR	14.585	13.000	13.929	13.755	15.478	21.887
	H_E	0.884	0.875	0.882	0.888	0.894	0.903
	H_O	0.875	0.846	0.821	0.794	0.846	0.843
	F_{IS}	0.024	0.053	0.083	0.121	0.066	0.067
UBA91	*N*	40	26	40	33	34	179
	Na	5	4	4	3	3	6
	AR	4.260	4.000	3.530	2.958	2.650	5.999
	H_E	0.287	0.270	0.282	0.219	0.258	0.293
	H_O	0.275	0.308	0.325	0.182	0.226	0.263
	F_{IS}	0.054	−0.120	−0.139	0.183	0.142	0.105
UBA853	*N*	39	26	35	34	40	174
	Na	9	13	9	11	11	16
	AR	8.323	13.00	8.929	10.465	10.352	16.000
	H_E	0.870	0.878	0.849	0.848	0.830	0.858
	H_O	0.795	0.962	0.943	0.735	0.800	0.822
	F_{IS}	0.028	−0.076	−0.096	0.148	0.049	0.043
UBA854	*N*	40	26	40	34	40	180
	Na	9	7	8	8	6	13
	AR	7.790	7.000	7.167	7.516	5.867	12.833
	H_E	0.717	0.719	0.734	0.742	0.704	0.738
	H_O	0.700	0.654	0.625	0.706	0.900	0.711
	F_{IS}	0.039	0.146	0.161	0.064	−0.267	0.036
Average of all loci	*N*	40	26	39	34	39	178
	Na	10	10	10	10	9	15
	AR	9.004	9.833	8.753	9.112	6.768	14.581
	H_E	0.724	0.731	0.718	0.728	0.709	0.734
	H_O	0.698	0.699	0.707	0.697	0.778	0.716
	F_{IS}	0.022	0.069	0.030	0.037	−0.080	0.028

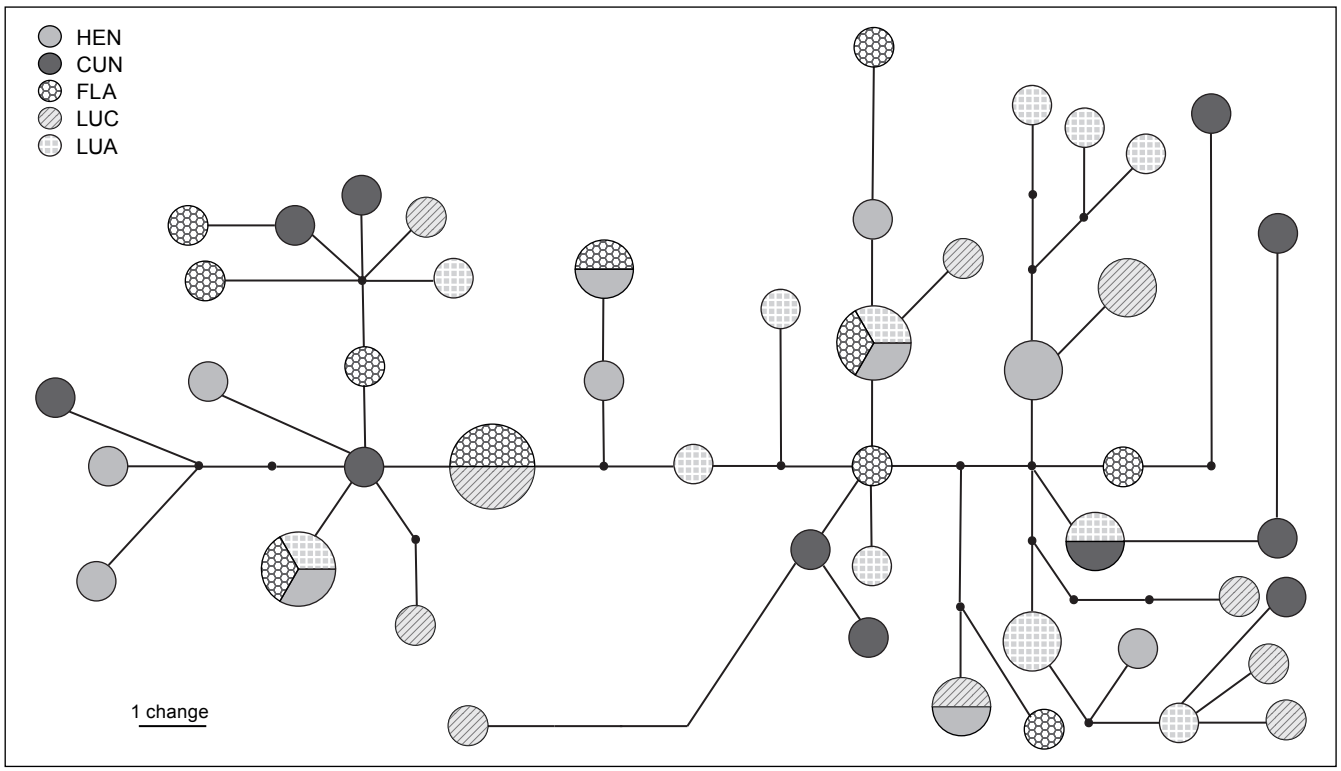

Figure 2: Reconstructed haplotype network for *Argyrosomus coronus* across the northern Benguela subsystem, based on 524 bp of mtDNA control region sequence. Branch lengths are proportional to mutational changes; black dots represent missing haplotypes. Sampling site abbreviations as per Figure 1

Table 3: Pairwise genetic differentiation between samples of *Argyrosomus coronus*: mtDNA control region ϕ_{ST} below the diagonal, microsatellite F_{ST}/D above the diagonal. No values were significantly greater than zero ($p > 0.05$). Sampling sites: HEN = Henties Bay; CUN = Cunene River mouth; FLA = Flamingo River; LUC = Lucira; LUA = Luanda

	HEN	CUN	FLA	LUC	LUA
HEN	–	–	−0.003/0.000	0.005/0.007	−0.001/0.000
CUN	0.017	–	–	–	–
FLA	−0.039	0.018	–	0.002/0.008	−0.001/0.001
LUC	0.013	0.028	0.028	–	0.001/0.001
LUA	0.032	0.015	−0.024	0.021	–

Table 4: Hierarchical analysis of molecular variance (AMOVA), based on frequencies of mtDNA control region haplotypes and nuclear microsatellite multi-locus genotypes, for two hypotheses of population substructuring in *Argyrosomus coronus*: the position of the Angola–Benguela Frontal Zone (ABFZ), and the time of sampling (Year). *F* = fixation index

Hypothesis		mtDNA			Microsatellites		
	Source of variation	% of variation	*F*	*p*-value	% of variation	*F*	*p*-value
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

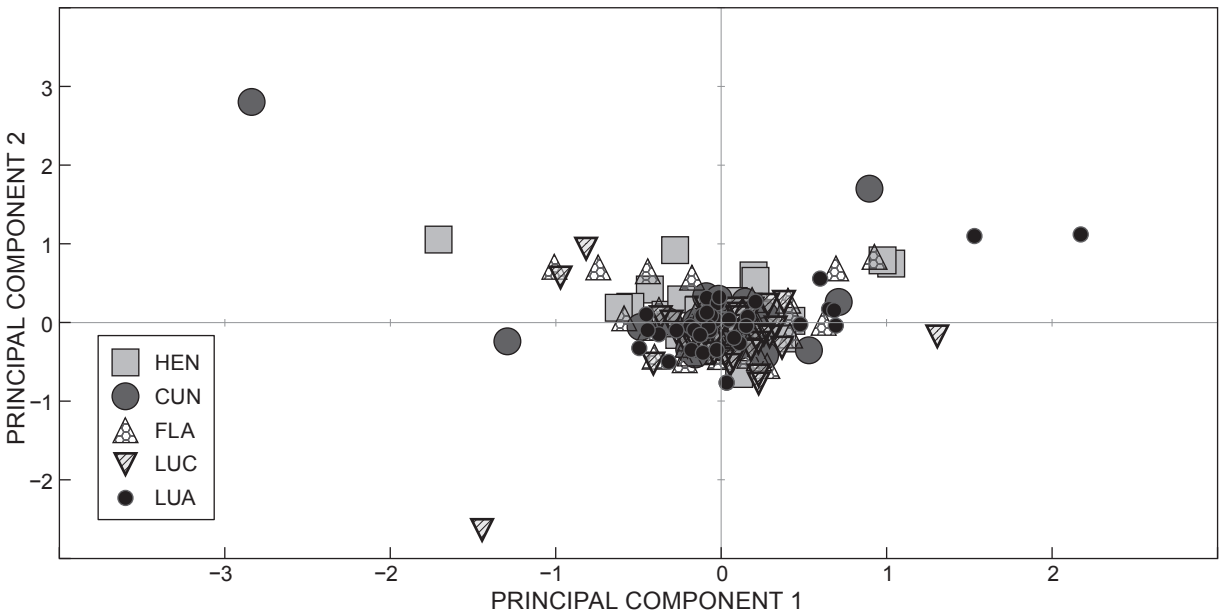

Figure 3: Factorial component analysis for *Argyrosomus coronus* microsatellite genotypes. The first two axes explained 11.28% of the variation. Sampling site abbreviations as per Figure 1

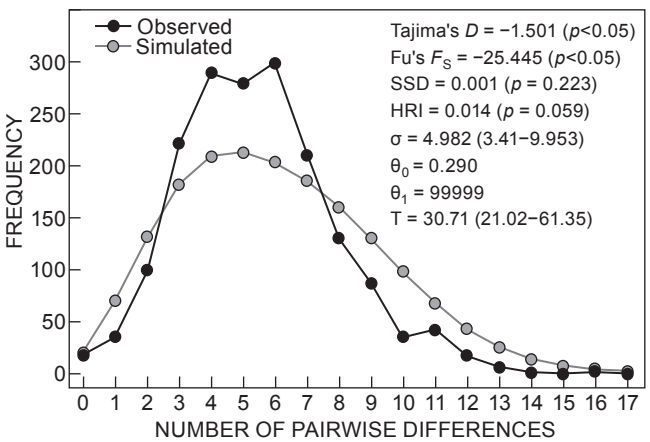

Figure 4: Mismatch distribution analyses for *Argyrosomus coronus*, based on 524 bp of mtDNA control region sequence, including neutrality tests (Tajima's *D* and Fu's F_S) and mismatch distribution parameters (σ = time since expansion, in mutation units; θ_0 = population size before expansion; θ_1 = population size after expansion; *T* = time since expansion [thousands of years, ky])

population expansion in *A. coronus*. Estimates of time since expansion based on mismatch distribution parameters put the expansion date between 11 and 31 thousand years ago (kya) (Figure 4), depending on the mutation rate used. Similarly, the skyline plot approach revealed the occurrence of a steep increase in female effective population size at about 25–70 kya (Figure 5), depending on the mutation rate used and despite the broad intervals of 95% HPD.

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

Discussion

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

In recent years, intense fishing pressure on several marine fishes has been linked to reduced population sizes (Briggs 2011), shifts in size ranges and age structures (Miethe et al. 2010), and perhaps most importantly to loss of genetic diversity (Pinsky and Palumbi 2014; Henriques et al. 2016). In a changing environment, the loss of genetic diversity is of great concern, as it will influence the ability of a species to adapt to future changes (Briggs 2011). Despite the previously reported high levels of exploitation and reduced population size of *Argyrosomus coronus*, where the egg-per-recruit measure of abundance was estimated at <10% of the value in the absence of fishing for the period 2005–2013 (Beckensteiner et al. 2016), the historical and present levels of genetic diversity in this species were found to be high and similar in range to those reported for other sciaenid species not only from the same region (Henriques et al. 2014, 2015) but also to those occurring in more stable environments (Silberschneider and Gray 2008; Diaz-Jaimes et al. 2010). The results presented here suggest that overfishing does not appear to have had (yet) a strong impact on contemporary levels of genetic diversity in *A. coronus*.

Patterns of population genetic diversity and phylogeography indicated by both mitochondrial and nuclear microsatellite DNA markers could not reject the hypothesis that *A. coronus* comprises a single genetically homogeneous population across its complete range

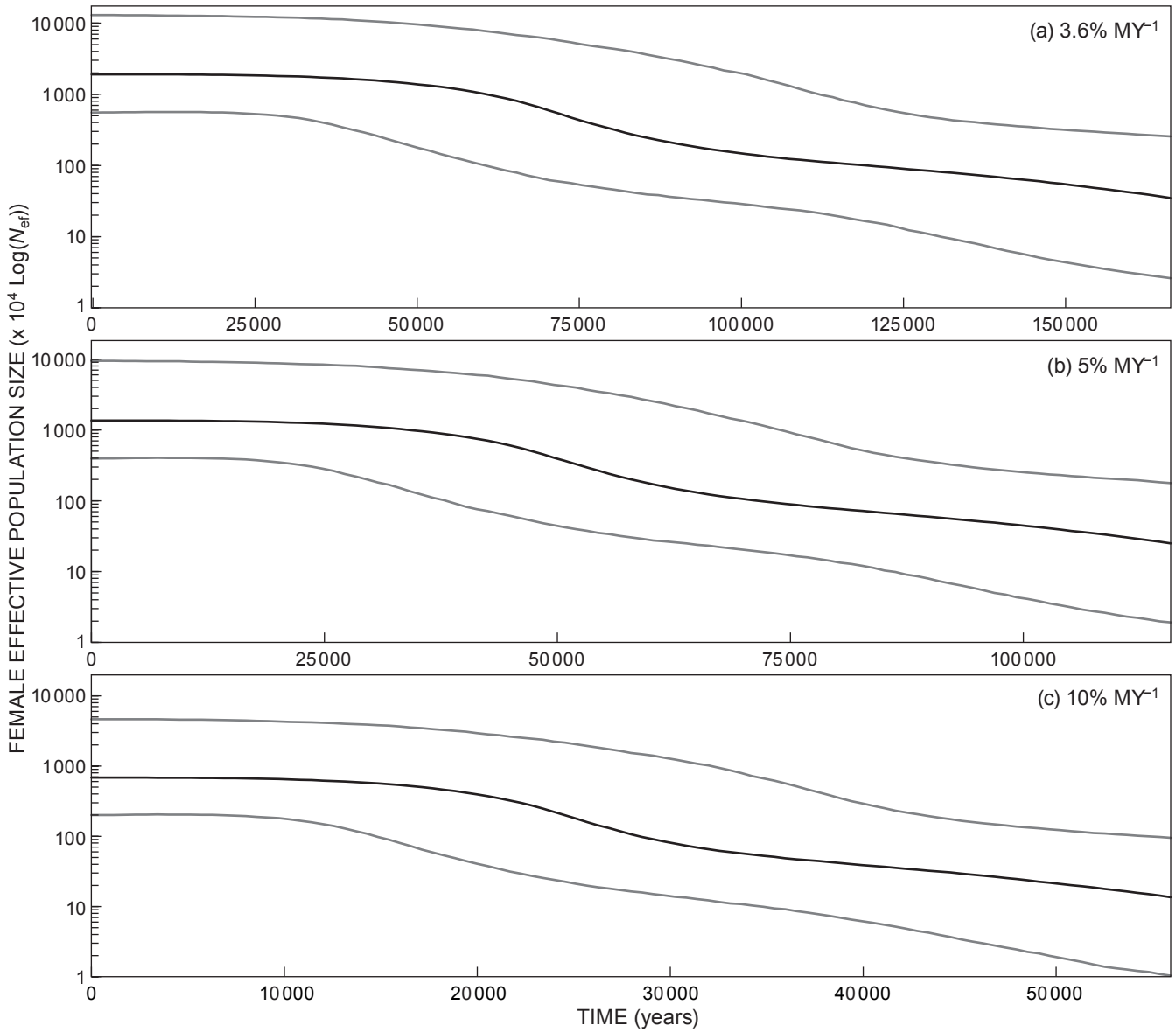

Figure 5: Bayesian skyline plot showing changes in modelled female effective population size (N_{ef}) over time (thousands of years [ky]) in modelled population size for *Argyrosomus coronus* in the Angola–Benguela Frontal Zone region, per mutation rate used: (a) = 3.6% per million years (MY), (b) = 5% per MY, and (c) = 10% per MY. Black line indicates the median estimate; grey lines depict intervals of 95% highest posterior density (HPD)

within the ABFZ region, suggesting that there are no barriers to dispersal or interbreeding (i.e. panmixia) of this species across this region. However, due to difficulties in accessing large samples of the study species from such an inaccessible area, the sample sizes here were below the recommended 50 individuals per sampling site (Cornuet et al. 1999). Therefore, it is possible that small sample sizes and hypervariability of the genetic markers used could have decreased resolution power for detecting subtle population substructuring, if present. For example, the high haplotype diversity observed for the mtDNA dataset might reduce power to statistically test differentiation because the majority of individuals possessed unique haplotypes. However, phylogeographic theory predicts that substructuring of populations would result in non-random geographical clustering of related haplotypes (Avise 2000). In contrast, the results show haplotypes private to individual samples are most closely related to haplotypes private to other samples, interconnected throughout the phylogeographic network without an obvious geographical clustering pattern, consistent with random dispersion of *A. coronus* throughout the entire distributional range and similar to patterns observed in other abundant marine fish species with high gene flow (cf. McKeown et al. 2015).

For the nDNA microsatellite allelic distributions, POWSIM analyses indicated that the dataset had suitable power to detect genetic differentiation as low as F_{ST} = 0.01 in 85.5% of the tests, with power decreasing to 41% for F_{ST} = 0.005.

The combination of the observed results does not allow rejection of the null hypothesis of genetic homogeneity in this species. In fact, several lines of evidence support potential panmixia, because the microsatellite loci had the ability to detect even weak genetic substructuring (F_{ST} > 0.01), and revealed very low levels of population divergence (global F_{ST} = 0.000, intersample F_{ST} = 0.000–0.005). Furthermore, there was no evidence of cryptic genetic structuring within samples, as no deviations to Hardy–Weinberg or linkage equilibrium were observed, which might have indicated the presence of a Wahlund effect (Nei and Li 1973; Pusack et al. 2014; Henriques et al. 2017). Finally, both FCA and STRUCTURE clustering analyses supported the presence of one gene pool, even though STRUCTURE may have less power to detect substructuring if F_{ST} is <0.02 (Latch et al. 2006). Therefore, the most likely scenario is that *A. coronus* is composed of one population throughout its distributional range. Resolution of spatial stock structure at a finer scale may be beyond the level of neutral genetic markers and benefit from complementary analysis of markers under selection (Canino et al. 2005).

Major oceanographic features across the wider Benguela Current region have been shown as barriers to effective dispersal of marine taxa, with many species exhibiting distinct genetic divergence between populations, indicating a breakdown of interbreeding and gene flow (Henriques et al. 2012, 2016; von der Heyden et al. 2008, 2011). However, the potential of an oceanographic feature to be a barrier to gene flow is closely linked to the biological features of the species itself (Galarza et al. 2009; Luiz et al. 2012). *Argyrosomus coronus* is a relatively long-lived (maximum 13 years), benthopelagic sciaenid that appears to undertake seasonal alongshore migrations (Potts et al. 2010). Catch-per-effort data indicate that this species is predominantly found in a temperature range of 16–22 °C, similar to the SST range around the ABFZ, and that the seasonal movement patterns of this frontal zone are thought to be the driver of *A. coronus* migratory behaviour (Potts et al. 2010, 2014). Recent biological findings suggest that spawning may occur throughout the distributional range, with ripe and running females found in northern Angolan waters during the austral winter (June) (WMP unpublished data), and a protracted spawning period documented for the southern region, extending from late spring to summer (Potts et al. 2010). Based on these findings and the seasonal shifts of the ABFZ, it is possible that spawning only occurs during a narrow thermal window. Indeed, spawning in the sister species *A. japonicus* off South Africa occurs only when temperatures are within a narrow range (20–24 °C; Griffiths 1996). These findings may suggest that *A. coronus* has multiple spawning grounds distributed throughout the system, with spawning regulated by the marked seasonal and regional SST patterns (Jahn et al. 2003). Besides the appropriate thermal range, the timing and location of spawning may also have evolved to maximise the dispersal of pelagic eggs and larvae in this highly unstable habitat (Potts et al. 2010). Thus, *A. coronus*, like *A. japonicus*, is thought to use estuaries as nursery grounds (Griffiths 1996; Potts et al. 2010). By migrating and reproducing in the southern part of their distribution during spring–summer, pelagic eggs and larvae can be passively transported to the Cunene Estuary through the seasonal displacement of the ABFZ. Similarly, by reproducing in the northern part of their distribution during winter, when SSTs are cooler, eggs and larvae can be passively dispersed northwards towards nursery grounds in the large estuaries (e.g. Kwanza and Congo) to the north. Indeed, juveniles (185–285 mm TL) have been observed as far north as Gabon (Poll 1954). Interestingly, an ongoing conventional tagging study has revealed that movement may occur during the late juvenile stage (400–600 mm TL), with individuals dispersing up to 210 km, and during the adult stage, with individuals migrating up to 750 km (M Parkinson et al., Rhodes University, unpublished data). The tagging studies thus suggest that *A. coronus* is capable of dispersal throughout much of its life cycle, which may explain the observed genetic homogeneity of the species across the ABFZ region.

Demographic history of A. coronus

The demographic history of *A. coronus* provides evidence of past population-size changes that appear to be linked with historical climate shifts in the region. Results from the mtDNA analyses revealed evidence for a past population expansion approximately 11–75 kya (depending on the mutation rate used), around or just pre-dating the last glacial maximum (LGM) (Clark et al. 2009). Although estimates of time since expansion should be regarded with caution, because of the assumptions required for calibration of the molecular clock, both the mismatch distribution and the coalescent-based analyses depicted a clear population increase in the last 25–75 thousand years (ky). The expansion in *A. coronus* appears to have occurred earlier in time than those reported for other fishes (Grant and Bowen 2006) yet is similar in range to those suggested for geelbek *Atractoscion aequidens* and Cape hake *Merluccius capensis* in the same region (Henriques et al. 2014, 2016).

During the Quaternary, the Benguela Current experienced increased upwelling events and colder SSTs, particularly around 60 kya and 18 kya (Kirst et al. 1999). Climatic changes in the Pleistocene are thought to have influenced the genetic signatures of the populations of several marine fishes, particularly in the southeastern Atlantic, with several population expansions dating from the Holocene (8–6 kya) (Matthee et al. 2007; von der Heyden et al. 2007, 2010). In the case of *A. coronus*, it appears that the population survived the LGM (in possible glacial refugia), after which expansion began early in the warming process. Similar refugial hypotheses are suggested to have contributed to an earlier population expansion of *A. aequidens* in the northern Benguela (Henriques et al. 2014), and in other temperate species from the Atlantic Ocean (Francisco et al. 2011; Faria et al. 2012). With temperature requirements that overlap with those found in the ABFZ (Potts et al. 2010), it is likely that changes in the range of the frontal system would be mirrored by changes in the distribution and abundance of *A. coronus*. Indeed, recent rapid warming in the southern Angola region has coincided with a decrease in the abundance of this species in the region, and an increase (when compared with *A. inodorus*) in the cooler waters off central and northern Namibia (Potts et al. 2014). Such distributional shifts associated with changing

average temperatures are thought to be one of the first consequences of climate change for multiple species (Grant and Bowen 2006; Garroway et al. 2011; Hill et al. 2011).

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

Conclusions and implications for understanding climate-change effects and sustainable harvesting

The results from this study combined with the findings of Potts et al. (2010, 2014) suggest that the evolutionary history of *A. coronus* is strongly linked with the characteristics of the ABFZ. The inability to reject the null hypothesis of genetic homogeneity, leading to a conclusion of widespread panmixia, may be a consequence of the adaptation to, and colonisation of, the frontal system itself by *A. coronus*. The observed spawning behaviour and possible annual return migration appear to correlate to the shifts of the ABFZ; thus, climate changes that affect the front's oscillatory pattern may have a direct impact on the distributional range and population dynamics of *A. coronus*. Future studies should be conducted using not only neutral but also adaptive markers to investigate the possibility of cryptic genetic differentiation linked to local adaptation. Furthermore, the recent hybridisation and introgression with *A. inodorus* in Namibia (Potts et al. 2014) deserves further research attention, while continuous genetic surveys are required to understand the impacts of such hybridisation events in the genomic architecture of both species.

The observed poleward range shift by *A. coronus* may also impact the fishing industry of the region. Fishing policies differ between Angola and Namibia, and because both species of *Argyrosomus* found there have significantly different life-history traits (Holtzhausen et al. 2001; Potts et al. 2010), a transboundary fishing policy is urgently required. The Benguela Current Convention (BCC) has the mandate to coordinate fishing management policies across the Benguela Current region, aided in this endeavour through the Convention signed by South Africa, Namibia and Angola, which seeks to promote a coordinated regional approach to the long-term conservation, protection, rehabilitation, enhancement and sustainable use of the Benguela Current Large Marine Ecosystem. The BCC should thus initiate and participate in future management plans for *A. coronus*.

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