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Regional genetic population structure and fine scale genetic cohesion in the Southern blue whiting *Micromesistius australis*

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Abstract

Southern blue whiting *Micromesistus australis* support a substantial commercial fishery in South America. There is growing evidence of a high level of demographic independence between stocks associated with the two main spawning grounds, one in the SW Atlantic (SWA) and one in the SE Pacific (SEP), but the potential genetic structuring of these stocks is unknown. In this study adults collected from sites throughout SWA and SEP waters were genotyped at hypervariable microsatellite markers to investigate genetic structuring between and within regions. Allele frequency-based analyses reported highly significant genetic differentiation between regions, indicating low levels of allo-recruitment. Ancillary data on migratory behaviours support natal homing as a prominent stock isolating mechanism. Genetic differentiation was also detected among samples from around the Falkland Islands: kinship analyses indicated that this was due to non-random genetic relatedness within samples. Despite a general pattern of genetic homogeneity among SEP samples, the northernmost sample exhibited significantly high mean relatedness. The data indicate the

occurrence of a further level of structuring within both regions that prevents complete mixing, specifically that schools may be hierarchically structured (from putative subpopulations down to kin-containing groups) and exhibit some degree of ontogenetic cohesion, which may also be a component of homing. The importance of homing and group cohesion as factors influencing resilience to, and recovery from, overexploitation is discussed. This study represents an important baseline for future genetic monitoring and assessment of *M. australis*. The need for such studies is emphasised by the observation of significantly lower levels of genetic variation among SWA samples, which may reflect genetic erosion, and the subsequent collapse of the SWA stock.

Keywords: population genetics; homing; fisheries; food security; conservation; management; overexploitation; sustainability

1. Introduction

The worldwide depletion of fish communities (Myers & Worm 2005) with evidence of fishery induced economic (Botsford et al. 1997) and biological extinctions (Jackson et al. 2001) highlights the importance of identifying biologically distinct components within marine fishes for both sustainable management and conservation of marine biodiversity (Ruzzante 2006). The ability to monitor dynamics of such components that may differ in life history and/or genetic composition within systems involving seasonal migration and potential spatial overlap is also beneficial as more easily exploited and/or less productive units may be susceptible to overharvesting, contributing to loss of diversity, adaptive potential (Iles & Sinclair 1982) and negative effects on recruitment potential and population/fishery viability (Ryman et al. 1995). Such threats may be particularly acute for schooling fish (Pitcher 1995; Hauser et al. 1998) examples of which include the two species in the genus *Micromesistus*:

blue whiting *M. poutassou* (Risso 1826) which inhabits the North Atlantic Ocean and Mediterranean; and Southern blue whiting *M. australis* (Norman 1937) found in the southern hemisphere. The *M. poutassou* fishery is currently regarded as an example of mismatch between biological and management stocks that threatens sustainability (Reiss et al. 2009).

Micromesistius australis sustains important southern hemisphere fisheries in New Zealand, Chilean, Argentinean, Falkland Islands and International waters (Niklitschek et al. 2010). The species is also considered a vital prey species for many predators in sub-Antarctic ecosystems (Paya 1992; Cherel et al. 1999; Nyegaard et al. 2004). The species is continuously distributed throughout the Falkland-Patagonia region and southern Chile, wherein two main spawning grounds and distinct migration circuits are known (Fig.1). In the Southwest Atlantic (SWA) spawning occurs southwest of the Falkland Islands from September to October (Shubnikov et al. 1969; Agnew 2002). After spawning adults migrate into feeding grounds along the Patagonian shelf NE of the Falklands (Agnew 2002) and in Antarctic waters of the Scotia Sea (Wöhler et al. 2001; Agnew et al. 2003). In the Southeast Pacific (SEP) spawning is reported to occur off the southern coast of Chile between Golfo de Penas and Peninsula de Tres montes (47S and 51S) (Céspedes et al. 1998). Acoustic surveys have shown dense aggregations of *M. australis* to migrate from SW Atlantic waters in June-July and move north along the Chilean coast towards the SEP spawning ground where spawning takes place in August. After spawning, SEP *M australis* move back to the Atlantic feeding grounds (Céspedes et al. 1998). While early life history stages are predicted to develop in the proximity of the spawning grounds (Agnew 2002; Balbontin et al. 2004; Arkhipkin et al. 2009) adults from both SWA and SEP spawning grounds may overlap in the more southern feeding areas (Cespedes et al. 1998). The potential for such mixing initially contributed support for the hypothesis of a single population throughout the region (Lillo et al. 1999). Morphometric analysis also provided no support for stock segregation (reviewed by

Arkhipkin et al. 2009), but more recent studies have provided compelling evidence of some degree of demographic independence between SWA and SEP stocks. Roa-Ureta (2009) reported significant differences in exploitation trajectories, growth patterns, size structure and age at first maturity. The otolith chemistry study of Arkhipkin et al. (2009) indicated that the majority (>80%) of individuals sampled at SWA and SEP spawning sites were locally spawned, while a later study combining otolith chemistry and parasite assemblage data indicated even lower proportions of non-regional-natives at such sites (Niklitschek et al. 2010).

Dispersal and gene flow, due to their respective influences on population structuring, are key processes affecting both short-term population dynamics and long-term evolutionary change. Dispersal mediates the abundance and exchange of individuals among subpopulations and the extent to which local populations may fluctuate independently. Gene flow, through dispersal and subsequent interbreeding, determines how populations are bound together as evolutionarily cohesive units. Despite supporting separation of stocks the differential proportions of dispersal indicated by the studies of Arkhipkin et al. (2009) and Niklitschek et al. (2010) highlights the uncertainty regarding the extent of demographic independence, in terms of both rates of dispersal and gene flow between SWA and SEP spawning stocks, as well as the potential existence of additional stock components. Addressing such knowledge gaps has been recognised as vital for sustainable management of the resource by local researchers (Paya et al. 2002; Wöhler et al. 2007).

Genetic markers are the only tools that can describe gene flow, and can also be applied to describe 'real time' dispersal (Castric & Bernatchez 2004). Microsatellite markers have provided insight into population genetic structuring in *M. poutassou* (Ryan et al. 2005; Was et al. 2008), and so were used here to genotype *M. australis* adults collected from multiple sites throughout the SWA and SEP. While population genetic analyses have played a vital

role in characterising patterns of connectivity and population structure in marine systems, a recognised weakness of standard analyses is that, particularly for large populations, they can struggle to detect contemporary demographic independence due to historical gene flow (Lowe & Allendorf 2010). Therefore, in this study, standard population genetic analyses (allele frequency based) were complemented with kinship-based analyses (allele sharing based) that have been shown to be effective at detecting contemporary recruitment processes in other marine systems (Iacchei et al. 2013; Christie et al. 2010). The data were then used to test the null hypothesis of panmixia throughout SEP-SWA for *M. australis* , and in doing so address several key questions:

(i) Do genetic patterns support the differentiation of SEP and SWA stocks and provide information on the degree of isolation and isolating mechanism(s)?

(ii) Is there evidence of further complexity within regions?

(iii) What behavioural and/or environmental features may be shaping recruitment patterns?

2. Materials and methods

2.1 Sample collection and microsatellite genotyping

Samples of adults were collected by pelagic trawls during September 2002 from areas of maximum *M. australis* abundance south of the Falkland Islands, across the Patagonian shelf and along the coast of Chile to 45^{o}S (see Fig. 1). Three samples from Falkland Islands waters were collected: Falk-1 (East Falkland); Falk-2 from the main spawning ground south of West Falkland; Falk-3 from SW of West Falkland. Falkland samples were provided by the Falkland Islands Government Fisheries Department. Samples from Chilean waters were collected at 11 (Chile-1 - Chile-11) positions from the southern tip of the continent up to

45°C, with each sample obtained from a single trawl by a commercial trawler. A further sample (Chile-12) comprised individuals from two trawls on the same day by a fisheries research vessel at ~48°S. All samples are presumed to contain multiple age classes. Individual tissue samples (finclip) were preserved in absolute ethanol. Genomic DNA was extracted using a standard CTAB-chlorofrom/isoamylalcohol method (Winnepenninckx *et al*. 1993).

A number of primer pairs for previously developed microsatellite loci were tested for their utility as genetic markers in *M. australis*: four developed from blue whiting (MpouBW7, MpouBW8, MpouBW9, and MpouBW13 – Moran et al. (1999)); one developed from whiting (*Merlangius merlangus*) and shown to work in southern blue whiting (MmerUEA W01 – Rico et al. (1997), Ryan et al. (2002)); and seven developed from walleye pollock and shown to work in blue whiting (Tch3, Tch5, Tch8, Tch10, Tch11, Tch21, Tch22 – O'Reilly et al. (2000)). Only the four blue whiting loci and Tch10 were found to amplify consistently in the present samples. The loci were individually amplified by PCR in 10 ul reactions containing ~50ng of DNA, 3pmol of each primer (forward primer labelled with a Cy5 fluoresent dye group), 0.1 U of *Taq* DNA polymerase (Bioline, UK), 1X supplied PCR Buffer, 2.0 mM MgCl2, and 0.2 mM dNTPs. The PCR thermoprofile involved an initial denaturation step (95 C for 3 min) followed by 35 cycles of 30 s at 95, 30s at 52 and 30s at 72. Single locus PCR products were separated on a Pharmacia ALF*Express*II automated DNA sequencer and alleles scored using FRAGMENT MANAGER Software. Hansen et al. (2001) demonstrated that misclassification of 4% of genotypes could produce an apparent F_{ST} of 0.001 to 0.003 when true $F_{ST} = 0$. Given that low F_{ST} might be expected between samples a number of steps (following McKeown et al. 2015) were taken to maximise accuracy of genotyping: (i) PCR products of four individuals with known genotypes were run for every locus in every gel; (ii) all genotyping was performed independently by two experienced

individuals with any mismatching genotypes being included in the repeat analysis (step iii); (iii) ~10% of all individuals were re-assayed (i.e. PCR, electrophoresis and genotyping) to assess/minimise rates of genotyping error.

2.2 Statistical analysis

Genetic variation within samples was characterised using numbers of alleles (N_A), allelic richness (A_R; El Mousadik & Petit 1996), observed heterozygosity (H_O), and expected heterozygosity (H_E), calculated using FSTAT 2.9.3 (Goudet, 1995). Genotype frequency conformance to Hardy-Weinberg equilibrium (HWE) expectations and genotypic linkage equilibrium between pairs of loci were tested using exact tests (10,000 batches, 5000 iterations) in GENEPOP 3.3 (Raymond & Rousset 1995). Deviations from HWE were measured using F_{IS}, calculated according to Weir & Cockerham (1984) and tested for significance by 10,000 permutations in FSTAT 2.9.3. As mentioned, the dataset was carefully assessed for human error, however, in order to evaluate the additional potential of technical artefacts the data was analysed with MICROCHECKER v. 2.2.3 (van Oosterhout et al. (2004).

Mean pairwise relatedness within samples was calculated using the relatedness estimator, r_{qg}, of Queller & Goodnight (1989) in GENALEX (Peakall & Smouse 2006) with associated 95% confidence intervals determined by 1000 bootstraps. Permutation of genotypes among all samples (999 times) was used to calculate the upper and lower 95% confidence intervals for the expected range of r_{qg} under a panmictic model. The maximum likelihood method implemented in ML-RELATE (Kalinowski et al. 2006), was used to infer the relationships among pairs of individuals, specifically to categorise them as unrelated (U), half-sib (HS) ,full-sib (FS) or parent-offspring (PO). Since every method of kinship analysis includes a level of uncertainty, COLONY (Jones & Wang 2010) was also used to identify HS/FS dyads

Following suggestions by Wang (2012) the full likelihood model was used with run length and precision set to medium. Genotyping error rate was set to 0.005 for each locus and polygamy and polyandry assumed. Since COLONY associates a probability with each result, only those with a probability of > 0.99 were taken into account.

Genetic structuring was investigated using the Bayesian clustering method implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000). Briefly, the analysis identifies the most probable number of genetically distinct groups (*K*) represented by the data and estimates assignment probabilities (*Q*) for each individual (specifically their genomic components) to these groups. The analysis can be run without any prior information, however, incorporating prior information using the LOCPRIOR model that allows the clustering algorithm to assume that the probability of assignment varies among samples, has been shown to increase power while not biasing results (Hubisz et al. 2009). The analysis was performed with and without the LOCPRIOR model. When the LOCPRIOR model was used the priors consisted of sample membership and not geographical location. Analyses with and without LOCPRIOR were then performed with multiple parameter sets (i.e. with and without admixture, and with and without correlated allele frequencies).. Each run had a burn-in of 100,000 Markov Chain Monte Carlo samples followed by 1,000,000 MCMC repetitions. Simulations were run 10 times for each proposed value of K (1-5) to assess convergence. Optimal models were assessed using L(K) following Pritchard et al. (2000) and where there was support for K >1, Δ*K* (Evanno et al. 2005) was also assessed. Genetic clustering was also assessed using BAPS 6.0 (Corander et al. 2004) for models of K=1-5 (10 runs per K).

Genetic differentiation was quantified by global and pairwise F_{ST} values, with associated significance evaluated by 10,000 permutations (exact F_{ST} estimator test (Goudet et al. 1996)), using FSTAT. Hierarchical analysis of molecular variance (AMOVA; Excoffier et al. 1992) was performed in ARLEQUIN to partition genetic variance among groups of samples (F_{CT})

and among samples within groups (F_{SC}) with significance levels of F_{CT} and F_{SC} tested using 1000 permutations. To complement *F*–statistics global and pairwise exact *G*-tests were performed in GENEPOP (10,000 batches 5000 iterations). The simulation method implemented in POWSIM (Ryman & Palm 2006) was used to estimate the sample size dependent Type I and Type II error probabilities of the *G*-tests. Genetic relationships among samples were also assessed using a factorial correspondence analysis (FCA) in GENETIX (Belkhir et al. 2004). Randomisation procedures in FSTAT were used to detect significant differences in heterozygosity, A_R, F_{IS}, F_{ST} and relatedness among user defined groups of samples following 10,000 permutations.

The assumption of selective neutrality of the microsatellite loci was assessed using the FDIST outlier identification test (Beaumont & Nichols 1996) implemented in LOSITAN (Antao et al. 2008) performed (i) globally (i.e. across groups of samples) and (ii) between pairs of samples. Simulations were run for 10 000 replications, 95% confidence intervals estimated using the options for neutral and forced mean F_{ST} and analyses replicated for infinite allele and stepwise mutation models.

3. Results

All loci produced unambiguous products that were readily scored with no incongruence between replicates indicating a very low degree of human genotyping error. There was a low level of missing data per sample (Table S1) and all individuals were genotyped for a minimum of four loci (i.e. maximum of one missing locus). The total number of alleles per locus ranged from 14 to 39 (average = 22.2). Global observed and expected heterozygosity per locus ranged from 0.748 to 0.900 (overall 0.806) and 0.760 to 0.956 (overall 0.827) respectively. Indices of genetic variability for each sample are reported in Table 1. Of 75 locus/sample tests of HWE 17 yielded significant results (at critical $P = 0.05$) (Table S1), in

all cases due to heterozygote deficits, of which 7 occurred among Falkland samples (4 for Falk-1, 1 for Falk-2, 2 for Falk-3). Across all samples (n = 15) no locus exhibited more than 5 significant departures from HWE suggesting no consistent effect of null alleles. MICROCHECKER found no evidence of scoring error due to stuttering, or large allele drop out but suggested the possible occurrence of null alleles in 7 locus/sample combinations (out of 75) (Table S1). These potential null allele occurrences were not associated with a specific locus. Furthermore, three of the potential cases of null alleles were found for Falk-1 sample suggesting biological rather than technical factors (see discussion). Employing the van Oosterhout algorithm did not change results of subsequent tests of differentiation (F_{ST} and G) and so results are reported for unedited data. There was no evidence of linkage disequilibrium between loci for any sample or across all samples. The three Falkland samples and sample Chile-1 exhibited mean kinship values that exceeded predictions of a panmictic model and were significantly higher than most of the other samples (Fig. 2). ML-relate analysis identified 3 full-sib dyads within samples (two full-sib dyads in the Falk_1 sample and 1 full-sib dyad in the Falk_ 3 sample). These dyads were also supported by results from COLONY (all at P =1). One member from each dyad was excluded from subsequent analyses. Across, all 269745 comparisons between individual pairs ML-relate identified 5650 pairs as being unrelated but could not categorise the remaining pairs unambiguously as being unrelated or related highlighting the limited power of the data..

Both BAPS and STRUCTURE (without LOCPRIOR) failed to detect more than one genetic group (probability = 1 for model of K = 1). However distinct genetic clusters were detected with STRUCTURE analysis using LOCPRIOR with identical patterns across the different parameter permutations. ΔK supported a model of K = 2 (Fig. S1) wherein there was a clear separation of SEP and SWA samples. However, L(K) indicated the optimum model to be K = 3 wherein there was separation of SEP and SWA samples but the SWA samples were further

split into two groups, with Falk-2 partitioned from Falk-1 and Falk-3. With the exception of those from Chile-4, individuals were strongly assigned to their groups as evident from their respective *Q* values (Fig.3). To further investigate clustering for Chile-4, the STRUCTURE analysis with LOCPRIOR was repeated for the SEP samples only and revealed no signs of substructuring (i.e. probability of 1 that $K = 1$). This clustering of Chile 4 with the other SEP samples is further observed in subsequent analyses. Across all samples differentiation was highly significant ($F_{ST} = 0.006$, $P < 0.0001$; *G*-test $P < 0.0001$). AMOVA revealed significant ($P < 0.00001$) and similar proportions of variation due to differences between regional groupings ($F_{CT} = 0.00439$) and among samples within regional groupings ($F_{SC} = 0.00472$). F_{ST} and exact tests yielded concordant patterns and indicated that the within-region variation revealed by the AMOVA was largely due to differentiation among the SWA samples (global $F_{ST} = 0.022$, $P < 0.001$; global *G*-test $P < 0.0001$; all pairwise tests significant – Table 2), with much less differentiation among the SEP samples (global $F_{ST} = 0.002$, $P = 0.011$; global *G*-test $P = 0.001$; F_{ST} significant for 11 out of 66 pairwise comparisons; *G*-tests significant in 16 out of 66 pairwise tests). Out of 39 pairwise comparisons between regions 35 displayed significant F_{ST} and 37 significant *G*-tests results. FCA results clearly illustrated the overall patterns described wherein there was aclear separation between SEP and SWA samples, as well as overall similarity among SEP samples and differentiation among SWA samples (Fig.4). POWSIM analysis indicated that the average sample size (n=49) conferred *G*-tests with a high level of statistical power. Specifically, the simulation indicated a high probability ($P = 0.989$) that true differentiation at the level of $F_{ST} = 0.01$ would be detected while Type I error probability was low ($P = 0.058$). Global and pairwise outlier analysis provided no support for divergent or balancing selection effects at any locus (Fig S2). Comparison of genetic variability between regions using randomisation tests reported significantly lower

allelic richness (P = 0.0013) and heterozygosity (P = 0.037), but higher F_{ST} (P = 0.0202) and relatedness (P = 0.0227), for the SWA samples compared to SEP samples (Table S2).

4. Discussion

Population genetic analyses (Bayesian clustering; FCA, pairwise F_{ST} and G tests, AMOVA) reported concordant patterns of structuring, with the salient feature being the significant differentiation between the Falkland Islands (SWA) and Chilean (SEP) samples, as well as among SWA samples. Although structuring was not detected by the BAPS and STRUCTURE (without LOCPRIOR) analyses, the associated F_{ST} values indicate that underlying structuring was beyond the resolution threshold of these analyses (Latch et al. 2006). In contrast, STRUCTURE analyses incorporating the LOCPRIOR model robustly partitioned individuals in fitting with the reported enhanced resolution for with LOCPRIOR (Hubisz et al. 2009). The differing optimal models reported by ΔK (K = 2 separating SEP and SWA) and L(K) (K = 3 further splitting SWA samples) also reflect the reported tendency for ΔK to preferentially identify the first level of hierarchical structuring (Waples & Gaggiotti 2006). In addition kinship analyses estimated significantly higher mean intra-sample relatedness for the three Falkland samples and the Chile-1 sample. Furthermore, a number of full-sib dyads (technically first order relatives as putative parents/offspring were not separated in the analysis) were identified within the Falkland samples, providing further evidence for non-random mixing of individuals. Collectively, the data confirm that despite considerable dispersal potential *M. australis* does not maintain a single homogenous population and clearly rejects the hypothesis of panmixia in this region.

The genetic partitioning of Falkland and non-Falkland samples readily aligns with the evidence from non-genetic based studies of restricted connectivity on ecological time scales between SEP and SWA stocks (Arkhipkin et al. 2009; Roa-Ureta 2009; Niklitschek et al.

2010). Based on analysis of otolith core microchemistry, formed during the larval and juvenile stages, Arkhipkin et al. (2009) estimated that approximately 20% of individuals at SEP and SWA spawning sites were non-natives (i.e. were born in the other region). Similar proportions of inter-region migrants were estimated from otolith core microchemistry by Niklitschek et al. (2010), however they suggest that such non-native proportions are inflated due to lack of marker resolution and obtained complete assignment to region when otolith core data and parasite assemblage data were combined. Deriving quantitative estimates of contemporary dispersal and gene flow from genetic data in abundant species like *M. australis* can be problematic (Whitlock & McCauley 1999; Palsboll et al. 2007; Hellberg 2009), however, as gene flow is measured as the product of effective population size and migration rate, significant genetic differentiation, even if numerically small, implies a very small proportion of migrants in the recipient population (Palumbi 2003; Hellberg 2006; Hauser & Carvalho 2008). While this study and those of Arkhipkin et al. (2009) and Niklitschek et al. (2010) represent limited temporal snapshots of *M. australis* dispersal, genetic patterns retain signatures of gene flow over multiple generations, and so significant genetic differentiation between SEP and SWA samples indicates levels of inter-population recruitment so low that the respective populations/stocks are essentially self-recruiting on timescales of interest to fishery managers (Hauser & Carvalho 2008).

The identification of isolating mechanisms is a crucial facet of the analysis of demographic independence, with a central topic in fisheries genetics being the relative roles of environmental forcing or behaviour (Heath et al. 2008). The potential for active dispersal by adult *M. australis* emphasises the potential importance of homing behaviours in shaping population connectivity. Homing, where adults repeatedly return to spawning grounds irrespective of whether they were hatched there has been widely reported in a number of species (e.g. Lundy et al. 2000) and may not promote population differentiation if there is

opportunistic and non-philopatric recruitment of adults (Heath et al. 2008). As an example, McKeown et al., (2015) report high connectivity between SWA and SEP spawning stocks of the Patagonian Grenadier (*Macruronus magellanicus*) by non-natal homing. In contrast natal homing, where adults return to and spawn at the site they were born, is predicted to promote population differentiation. The detection of significant genetic differentiation along with evidence of natal region spawning fidelity indicated by ontogenetic studies, are jointly compatible with natal homing as a governing factor limiting regional stock allo-recruitment in *M. australis*. Recognition of such a slow-changing stock isolating mechanism is important as it may lead to resistance to mixing, expansion and colonization of new habitats (Secor 2005; Svendang et al. 2007), as illustrated by the slow and unpredictable recovery of many northern hemisphere cod stocks (Svendang 2003, Bundy & Fanning 2005; Svdenag & Svenson 2006).

Levels of genetic differentiation among the Falkland Islands samples, as measured by F_{ST}, were high and comparable to inter-regional comparisons. As such the microgeographical differentiation among the Falkland samples fits with a pattern of chaotic genetic patchiness that has been widely reported among marine taxa (Selkoe et al. 2010; Toonen & Grosberg 2011). While otolith data provides ancillary information supporting restricted gene flow between both regions, direct interpretation of the microgeographic differentiation in the context of gene flow is complicated due to both the nature of such summary statistics (reviewed by Lowe & Allendorf 2010; Hart & Marko 2010)) and the potential for temporal genetic fluctuations among highly fecund marine taxa (Eldon & Wakeley 2009; Toonen & Grosberg 2011) such as *M. australis*.

For all three Falkland samples, as well as for sample Chile-1, mean relatedness estimates were significantly higher than values reported for most other samples, and in all cases exceeded values expected under a model of random mixing. This indicates that the

differentiation among Falkland samples, and for Chile-1 from most other SEP samples, is driven by non-random genetic relatedness among individuals in those samples. Moreover, among two of the Falkland samples a number of dyads exhibiting first-order level relationships were identified. This is a striking feature as previous studies that have looked at kin relationships among adults, rather than among cohorts of recruits, have found no evidence of kin aggregation in marine species (Avise & Shapiro 1986; Kolm et al. 2005; Buston et al. 2007; Palm et al. 2008; Andrews et al. 2010; Berry et al. 2012; but see Iacchei et al. 2013 for a study documenting kin among sedentary adults of *Panulirus interruptus*). Collectively these results indicate that schools may exhibit non-random genetic relatedness, including kin associations, and individuals stay together within schools over extended periods.

The non-random genetic relatedness among individuals within samples could be generated by recruitment pulses of related individuals wherein larvae released together stay together (larval cohesion), with such cohesion then persisting throughout the ontogeny of fish. Such recruitment pulses could be associated with extreme reproductive success among individuals (sweepstakes recruitment, Hedgecock 1994). The batch spawning (spawning frequency of 4 days during peak season) and high fecundity (35,000 to 245,000 eggs per batch) of *M australis* (Macchi et al. 2005) are both features conducive to recruitment pulses/skews, that have also been linked to heterozygote deficits like that reported for the Falk-1 sample (Harvey et al. 2016). Kinship analysis have reported high levels of relatedness within cohorts of larval recruits in a number of fish taxa (Planes et al. 2002; Pujolar et al. 2006; Selkoe et al. 2006; Buston et al. 2009; Bernardi et al. 2012; Selwyn et al. 2016), compatible with both larval cohesion and sweepstakes recruitment effects. Environmental heterogeneity may also contribute to such recruitment fluctuations (Banks et al. 2007) and it is perhaps notable that the Atlantic spawning grounds are known to vary in size and location depending on the intensity of the Falkland current (Arkhipkin et al. 2009). Alternatively, the high levels of

kinship could reflect temporally stable self-recruitment and ontogenetic cohesion. In the same marine region McKeown et al. (2015) described a self- recruiting SWA sub-stock of Patagonian hoki and proposed both behavioural and environmental factors maintaining genetic integrity. The large number of dyads that could not be unanimously classified to a single relationship category (i.e. unrelated or related) indicates that the available data has insufficient power to infer the exact kin patterns within samples. Hence, distinguishing between the alternative scenarios will require more sensitive genetic assays as well as analysis of age-segregated samples (Burford et al. 2011), however the results indicate the occurrence of a further level of structuring within both regions that prevents complete mixing.

There has been extensive research into the nature of schooling, with documented cases of associations among fish persisting through time (Tamdrari et al. 2012). However, an important question is whether such cohesions are maintained during migrations or whether schools visit specific locations with precise timing for feeding or spawning. As the Falkland and Chile-1 samples represent the geographically closest to spawning areas the genetic patterns may reflect re-associations of individuals homing to spawning sites, i.e. individuals from different genetic groups may mix randomly in other areas. At the regional level Niklitschek et al. (2010) interpreted parasite data as supporting limited mixing between SEP and SWA individuals, but both these authors and Arkhipkin et al (2009) highlight the importance of assessing mixing in key fishery areas such as Tierra del Fuego and Staten island shelfs. The dynamics of mixing among various regional and intra-regional stock components has important implications for mixed stock fishery management, in particular concerning the detection of early warning signs of overexploitation (Mackinson et al. 1997; Hauser et al. 1998).

In summary, the data support a high level of self-recruitment and demographic independence for the SEP and SWA stocks, and identify natal-region-homing as a possible stock isolating mechanism. The data also indicate that within regions, schools may be hierarchically structured (from putative subpopulations down to groups containing related individuals) and exhibit some degree of permanence, which may also be a component of homing effects. The hierarchical structuring of *M. australis* may predispose the species to genetic erosion if entire schools are harvested (Fraser et al. 2005) but may also buffer species against genetic erosion if schools are only partially depleted (Hauser et al. 1998). Homing may also promote recovery at local levels (Tamdrari et al. 2012), but not at regional levels meaning that natural recovery of depleted regional stocks will be unpredictable, and on a timescale unacceptable to fishers and resource managers (Svendang et al. 2007). Homing behaviour and cohesion are thus important features influencing resilience to, and recovery from, overexploitation that will need to be characterised. Such research would benefit from improved understanding of species ecology, and additional genetic and ontogenetic marker analysis of short interval time-series samples of spawning and feeding grounds. Schooling fish are particularly vulnerable to exploitation as modern fishing technologies are able to detect schools at large range and so catchability (the proportion of the stock caught per unit effort) may increase as abundance declines (Mackinson et al. 1997) meaning that stocks may collapse even if effort is reduced (Pitcher & Parrish 1993). Genetic data here indicated a lower level of genetic variation among the SWA samples. As the analysed samples were collected shortly before the SWA stock collapsed between 2004 and 2007 (Laptikhovsky et al. 2013) the lower variation may reflect genetic erosion. Interestingly, another study analysing samples collected after the collapse reported no genetic structuring (Galleguillos et al. 2009). Although there are a number of technical differences with our study, one potential biological reason for the different results could be that the collapse of the SWA stock meant that SWA fish were

largely unrepresented/unsampled. Therefore, the lack of detected structure by Galleguillos et al. (2009) could simply reflect the reduced abundance of the SWA population. This study thus provides an important baseline for vital future genetic monitoring and assessment of *M. australis*.

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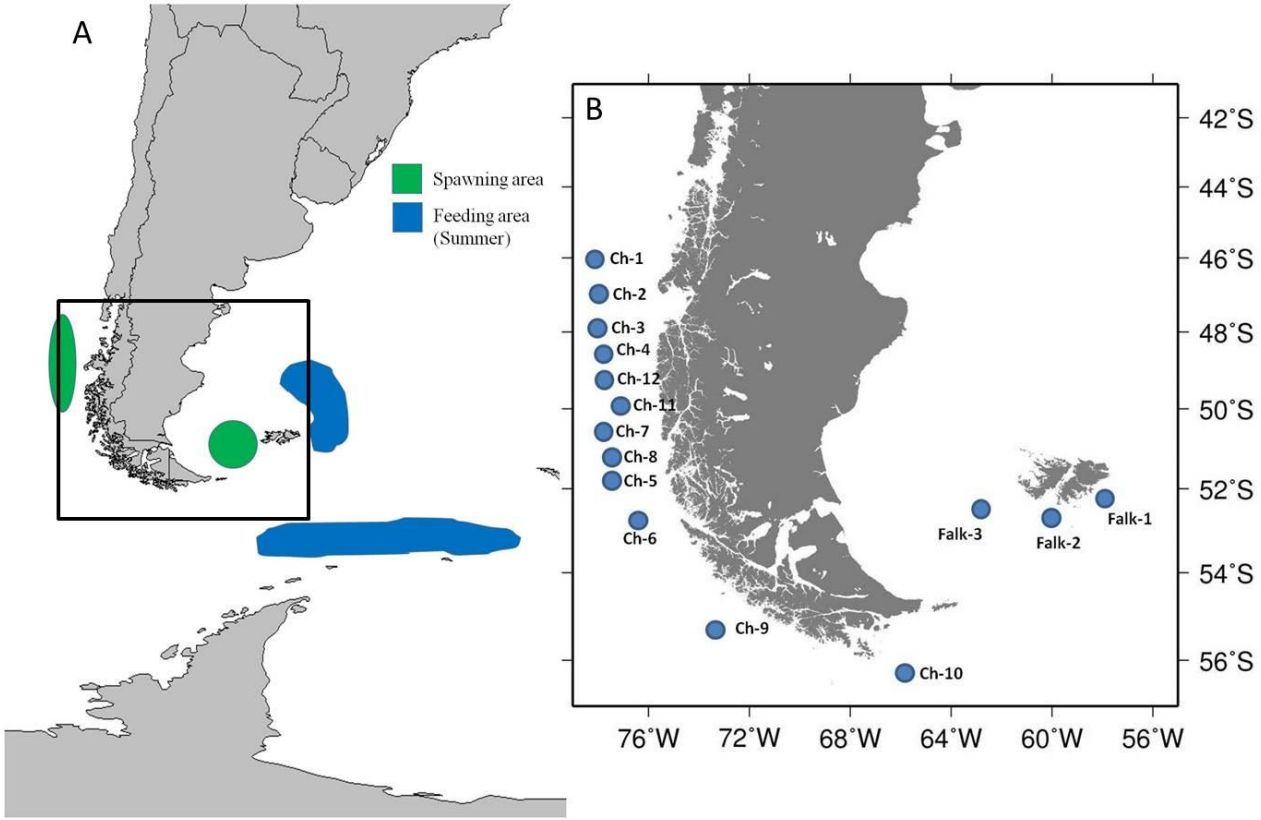

Figure 1. (A) Overview of approximate locations of spawning and feeding grounds and sampled area (in box) . (B) Specific locations of sample sites.

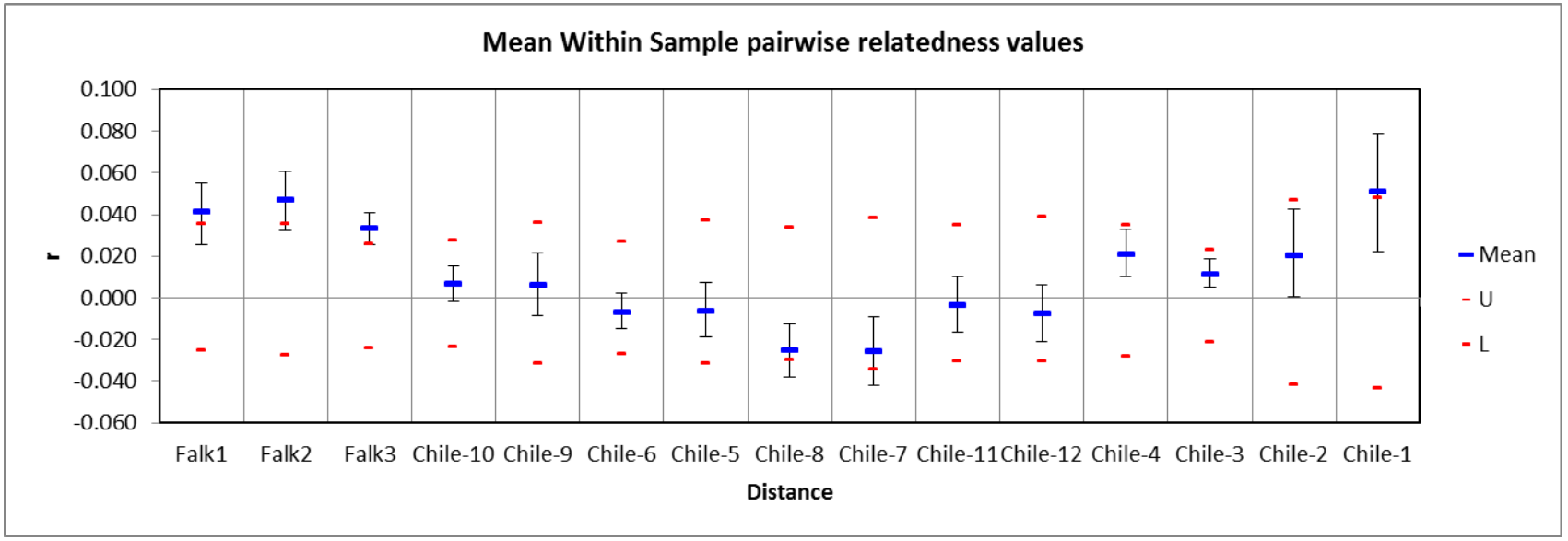

Figure 2. Mean within-sample pairwise relatedness, r_{qg}, and 95% confidence intervals determined by bootstrap resampling. Red bars are the 95% upper and lower expected values for a null distribution generated from 999 permutations of data among all samples, and enclose the values expected within a panmictic system.

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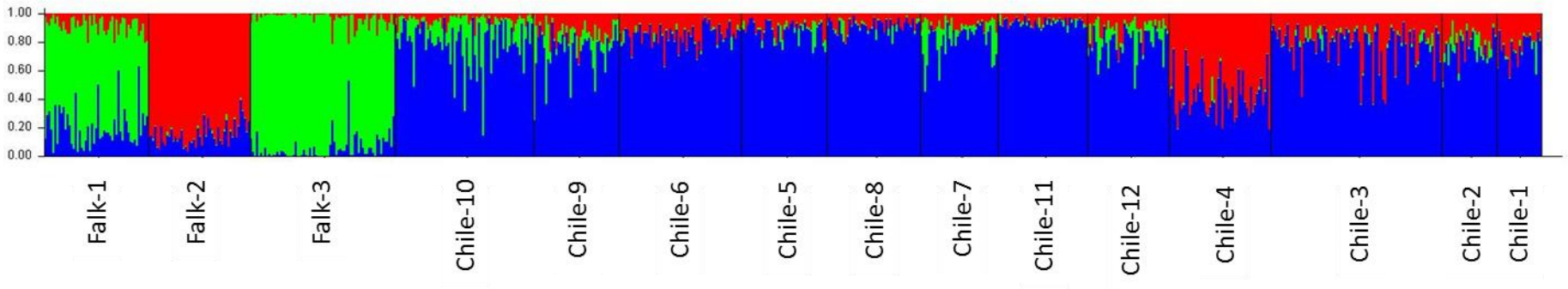
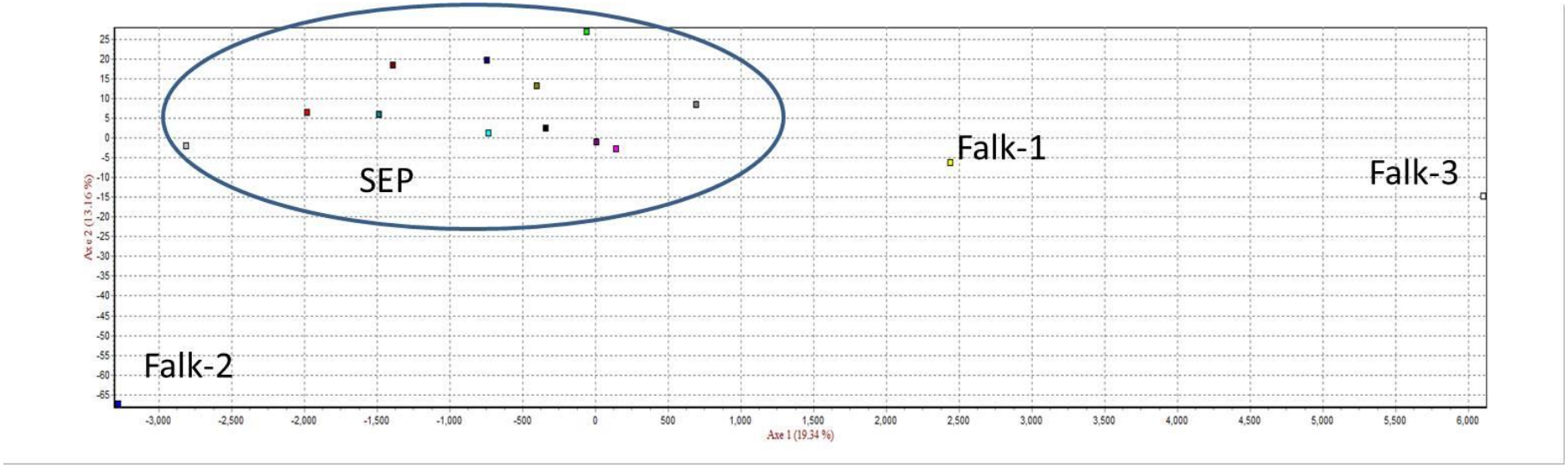


18

19 Figure 3. Plot of assignment probability (*Q*- values) of individuals to three genetic groups (resolved within the model of K =3) each represented by a
20 different colour.



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22 Figure 4. Factorial correspondence analysis among samples and percentage of total variation explained by each of the two axes.

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