Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

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

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ARTICLE INFO

Article history: Received 30 March 2016 Received in revised form 31 August 2016 Accepted 8 September 2016 Handled by Prof. George A. Rose Available online 19 September 2016

Keywords: Population genetics Homing Fisheries Food security Conservation Management Overexploitation Sustainability

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.

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1. Introduction

The worldwide depletion of fish communities (Myers and 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 et al., 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 diver-

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http://dx.doi.org/10.1016/j.fishres.2016.09.006 0165-7836/© 2016 Elsevier B.V. All rights reserved. sity, adaptive potential (Iles and 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 (Payá 1992; Cherel et al., 1999; Nyegaard et al., 2004). The species is continuously distributed throughout









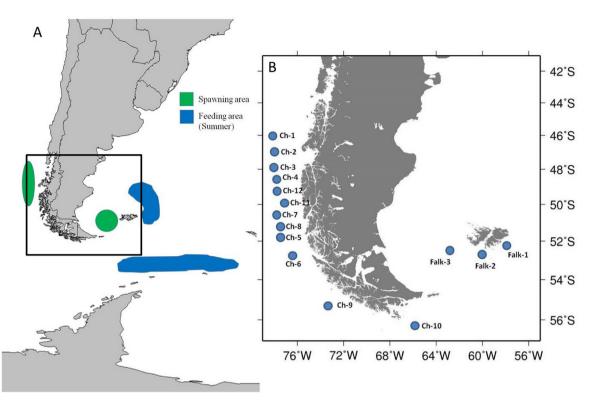


Fig. 1. (A) Overview of approximate locations of spawning and feeding grounds and sampled area (in box). (B) Specific locations of sample sites.

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. aus*tralis 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., 2002). 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 nonregional-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 (Payá 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 and 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 and 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 (lacchei 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:

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