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ARTICLE

Intraspecific mitogenomics of three marine species-at-risk: Atlantic, spotted, and northern wolffish (*Anarhichas* spp.)

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Abstract: High-resolution mitogenomics of within-species relationships can answer such phylogeographic questions as how species survived the most recent glaciation, as well as identify contemporary factors such as physical barriers, isolation, and gene flow. We examined the mitogenomic population structure of three at-risk species of wolffish: Atlantic (*Anarhichas lupus*), spotted (*A. minor*), and northern (*A. denticulatus*). These species are extensively sympatric across the North Atlantic but exhibit very different life history strategies, a combination that results in concordant and discordant patterns of genetic variation and structure. Wolffish haplogroups were not structured geographically: Atlantic and spotted wolffish each comprised three shallow clades, whereas northern wolffish comprised two deeper but unstructured lineages. We suggest that wolffish species survived in isolation in multiple glacial refugia, either refugia within refugia (Atlantic and spotted wolffish) or more distant refugia (northern wolffish), followed by secondary admixture upon post-glacial recolonisation of the North Atlantic.

Key words: phylogeography, conservation genetics, Pleistocene glaciations, population genetics, *Anarhichas*, species-at-risk.

Résumé : La mito-génomique à haute résolution des relations intraspécifiques permet de répondre à diverses questions en phylogéographie comme identifier les espèces qui ont survécu à la dernière glaciation ou identifier des facteurs contemporains tels que les barrières physiques, l'isolement et les flux géniques. Les auteurs ont examiné la structure de la population au sein des génomes mitochondriaux chez trois espèces menacées de poisson-loup : atlantique (*Anarhichas lupus*), tacheté (*A. minor*) et gélatineux (*A. denticulatus*). Ces espèces sont largement sympatriques dans l'Atlantique Nord, mais font appel à des stratégies de cycle de vie très différentes, une combinaison qui entraîne des schémas de variation génétique et de structure à la fois concordants et discordants. Les haplotypes de poissons-loup n'étaient pas structurés sur une base géographique; les poissons-loup atlantique et tachetés formaient trois clades peu profonds, tandis que le poisson-loup gélatineux comprenait deux lignages plus profonds mais non-structurés. Les auteurs suggèrent que ces espèces ont survécu en isolement dans de multiples refuges glaciaires, soit des refuges au sein de refuges (poissons-loup atlantique et tacheté) ou au sein de refuges plus distants (poisson-loup gélatineux), avant de connaître de l'admixture lors de la re-colonisation de l'Atlantique Nord. [Traduit par la Rédaction]

Mots-clés : phylogéographie, génétique de conservation, glaciations du pléistocène, génétique des populations, *Anarhichas*.

Introduction

The population genetic structure of marine species is often enigmatic. Many widely distributed fish species display little or no population structure (Ward 1995; Vis et al. 1997), which is attributed to large ranges, high dispersal capability, and few barriers to dispersal (Palumbi 1992). Although population connectivity and the presence or absence of physical barriers significantly affect population genetic structure, species in the Northern Hemisphere were also heavily influenced by the Quaternary glaciations, particularly those of the Pleistocene (ca. 200–10 kya; Hewitt 2000, 2004; Pflaumann et al. 2003; Shaw 2006). Understanding population genetic structure is particularly important for species of conservation concern. Lack of genetic diversity in a species limits their ability to effectively respond to, and recover from, environmental threats such as disease, pollution, parasites, and climate change (Frankham 1995; Amos and Harwood 1998); whereas maintenance or enhancement of variation can mitigate the effects of climatic extremes and environmental changes (Hilborn et al. 2003), and can affect the recovery of species.

The marine environment has been heavily impacted by overexploitation, habitat destruction, and climatic changes (Hutchings 2000). Three species heavily affected by the fisheries of the mid-20th century are the Atlantic wolffish *Anarhichas lupus* (Linnaeus, 1758), the spotted wolffish *Anarhichas minor* (Olafsen, 1772), and the northern wolffish *Anarhichas denticulatus* (Krøyer, 1845). Populations decreased by 91%, 96%, and 98%, respectively, due to a combination of overharvesting as bycatch and habitat destruction (Watling and Norse 1998; O'Dea and Haedrich 2002), leading to these three species being among the first marine fish species to be listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) under the *Canadian Species At Risk Act* (SARA): Atlantic wolffish as Special Concern (COSEWIC 2000, 2012*a*) and spotted and northern wolffish as Threatened (COSEWIC 2001*a*, 2001*b*, 2012*b*, 2012*c*).

The North Atlantic wolffish species are largely sympatric along the continental shelves of North America and Europe (Fig. 1), although they occur in somewhat different habitats, are stratified by depth, and have adopted different feeding strategies (Barsukov 1959;

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