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Genetic homogeneity in the deep-sea grenadier *Macrourus berglax* across the North Atlantic Ocean

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ABSTRACT

Paucity of data on population structure and connectivity in deep sea species remains a major obstacle to their sustainable management and conservation in the face of ever increasing fisheries pressure and other forms of impacts on deep sea ecosystems. The roughhead grenadier *Macrourus berglax* presents all the classical characteristics of a deep sea species, such as slow growth and low fecundity, which make them particularly vulnerable to anthropogenic impact, due to their low resilience to change. In this study, the population structure of the roughhead grenadier is investigated throughout its geographic distribution using two sets of molecular markers: a partial sequence of the Control Region of mitochondrial DNA and species-specific microsatellites. No evidence of significant structure was found throughout the North Atlantic, with both sets of molecular markers yielding the same results of overall homogeneity. We posit two non-mutually exclusive scenarios that can explain such outcome: i) substantial high gene flow among locations, possibly maintained by larval stages, ii) very large effective size of post-glacially expanded populations. The results can inform management strategies in this by-caught species, and contribute to the broader issue of biological connectivity in the deep ocean.

1. Introduction

Over the last few decades, it has become routine to use genetic techniques to investigate population structure in marine fishes (Carvalho et al., 2016). The results have led to the widespread rejection of the commonly held view that marine species are mostly panmictic, due to the lack of visible barriers to larval and adult movements (Hauser and Carvalho, 2008). The action of ocean circulation can in fact be two-fold: superficial or deep-water currents can increase gene flow by aiding individual dispersal, especially at the larval stages, but they can also act as a barrier to it, hence favouring divergence between groups.

The vast majority of published studies on marine fish have dealt with coastal pelagic species, given their commercial value and/or the convenient sampling. Yet, the fishing pressure on deep-sea stocks has been steadily increasing since the 1970s (Roberts, 2002), and the depth at which fisheries operate has also been increasing at an average pace of 65.2 m per decade (Morato et al., 2006; Watson and Morato, 2013). Despite being increasingly exploited, deep-sea fish species still suffer from a paucity of data, compared to their coastal and shallow counterparts, which can have deleterious effects on their management (see Clarke et al., 2015 for a quantitative discussion). The assessment of the level and range of spatial structure of exploited species is pivotal for the sustainable harvest and management of species, and failure to identify population structure may result in population collapse (Reiss et al., 2009; Lowe and Allendorf, 2010). Given the typical life history traits of deep-sea species (discrete spawning aggregations, slow growth, late maturity), any fishing pressure might have serious consequences for the persistence of stocks (Baker et al., 2009). Thus, it is important to gather data in order to better understand the population structure and dynamics of these fish stocks, whether they are directly exploited or caught as by-catch. The most recent studies on the dynamics of deep sea fish species have reported lack or very low genetic structuring across wide geographical scales (*Centroscymnus crepidater* in Cunha et al.,

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Table 1
Sampling locations, population codes (*ID*), year of sampling (*Year*) and genetic diversity parameters inferred from mitochondrial DNA and microsatellites. *N*, number of individuals screened; N_H, number of haplotypes; *h*, haplotype diversity; π, nucleotide diversity; A_r, allelic richness; N_A, number of alleles; H_o, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient (in bold, values that are significant; $p < 0.05$).

Location	ID	Year	Mitochondrial DNA					Microsatellites					
			N	N_H	h	π	*Ar*	N	N_A	*Ar*	H_O	H_E	F_{IS}
East Greenland	EGree	2000	12	5	0.58	0.0014	2.73	95	9.86	5.14	0.668	0.665	−0.005
South Greenland	SGree	2003	25	6	0.30	0.0006	1.92	88	9.57	4.88	0.673	0.650	−0.020
George Bank	GEO	2004	12	3	0.32	0.0004	1.67	52	7.86	4.96	0.599	0.649	0.070
Svalbard	SVA	2002	20	3	0.19	0.0002	1.00	80	8.26	5.02	0.535	0.668	**0.200**
Hatton Bank	HAT	2000	14	7	0.76	0.0015	4.51	50	7.71	4.82	0.592	0.619	0.040
Flemish Cap	FLE	2002	11	7	0.82	0.0018	3.08	21	5.43	4.89	0.530	0.674	**0.210**
Baffin Sea	BAF	2001	17	10	0.79	0.0017	5.56	75	9.14	4.77	0.637	0.646	0.010
Norway	NOR	2007	13	5	0.54	0.0009	3.07	98	7.29	4.64	0.623	0.629	0.010

2011; *Coryphaenoides mediterraneus* in Catarino et al., 2013; *Hoplostethus atlanticus* in White et al., 2009) across their vast geographic ranges, and capable of transoceanic ontogenetic migrations (*Aphanopus carbo* in Longmore et al., 2014). Depth has been found to represent a barrier to gene flow and promote low but significant population structuring (*Haplostethus atlanticus* in Carlsson et al., 2011; *Etmopterus spinax* in Gubili et al., 2016; *Coryphaenoides rupestris* and *Brosme brosme* in Knutsen et al., 2012, 2009; *Sebastes mentella* in Shum et al., 2014, *Centroscymnus coelolepis* in Catarino et al., 2015). Although the extent of pelagic habits typically influences the expected levels of genetic heterogeneity, even at global scales (see Gaither et al., 2016), the deeper layers of the oceans remain less understood, and no robust life-history predictors of spatial structure currently exist.

The roughhead grenadier *Macrourus berglax* Lacepède 1801, family Macrouridae, is a benthopelagic species occurring across the northern Atlantic Ocean, between the Georges Bank to the west, all the way to the Barents Sea as the easternmost edge. It dwells between a depth of 100 and 1000 m, although it is especially common at depths of 300–500 m (Cohen, 1990). Data about its biology, population structure and dynamics are scarce, even though it is an important part of the bycatch in the red fish and the Greenland halibut fisheries (Garabana et al., 2016; Gonzales Costas and Murua, 2005; Gonzales costas, 2010). Life history traits of this species are similar to those of other deep sea fishes: it lives long (up to 25 years according to Lorance et al., 2008 and Drazen and Haedrich, 2012), grows slowly and has low fecundity, between 14,000 and 80,000 eggs (Devine et al., 2012; Fossen et al., 2003; Murua, 2003; Drazen and Haedrich, 2012). Spawning has been documented across the species' geographic distribution in late Winter/early Spring (Magnússon and Magnússon, 1995; Savvatimsky, 1989), although geographical differences in time of spawning might exist (Lorance et al., 2008; Garabana et al., 2016). Very little is known about the dispersal ability at different life stages of *M. berglax:* spawning migration has been hypothesised (Garabana et al., 2016), but not demonstrated. The other four species of the genus *Macrourus* (*M. carinatus, M. whitsoni, M. caml* and *M. holotrachys)*, are all present exclusively in the southern hemisphere and have well-documented extended adult migration (Laptikhovsky, 2011; Münster et al., 2016), while more distantly related macrourids, such as the roundnose grenadier *Coryphaenoides rupestris,* have been found to have a very long pelagic phase, which can last for almost a year (Lorance et al., 2008).

The population structure of *M. berglax* across its geographic range is also poorly investigated. The only published genetic study finds low differentiation, but advocates the existence of at least three units or stocks: East Greenland, West Greenland and Norwegian Sea (Katsarou and Naevdal, 2001). This investigation used allozyme markers, which, due to their nature of being expressed by coding regions may poorly reflect patterns of neutral gene flow (O'Sullivan et al., 2003).

Concerns regarding the lack of data and the status of the stock of the roughhead grenadiers in the North Atlantic were recently raised by NAFO (Northwest Atlantic Fisheries Organization) and ICES (International Council for the Exploration of the Sea), given the decrease in landings of grenadiers in the North Atlantic (Gonzales Costas, 2010; ICES, 2015). In the NAFO Regulated Area (western Atlantic), this species is mainly caught in subareas 3LMN, just around Flemish Cap, where it is becoming a commercially important fish despite the fishery being unregulated (Gonzales Costas and Murua, 2005). In the eastern Atlantic (ICES Area), it is by-caught with the roundnose grenadier *Coryphenoides rupestris*, and its stock status is unknown and unmanaged (ICES, 2015).

In this study, our aim was to fill some of these knowledge gaps by investigating the population structure of the roughhead grenadier across its geographic range and over multiple years, using species-specific microsatellite markers (Helyar et al., 2010) and the mitochondrial DNA control region (CR). In particular, we tested whether spatial genetic heterogeneity exists in *M. berglax,* and whether the three stocks suggested by Katsarou and Naevdal (2001) are upheld by our data. The findings significantly enhance our understanding of past and present population structure and diversification in *M. berglax*, and lay the foundation for improved conservation and management of the species.

2. Materials and methods

2.1. Sampling

A total of 638 individuals were sampled at eight locations across the entire species' geographic distribution, between 2000 and 2007 (Table 1), by research and commercial vessels. The sampling localities are northern Norway (Bear Island), Svalbard, East and South Greenland, Baffin Bay, Flemish Cap, Georges Bank and Hatton Bank (Fig. 1). Tissue samples were collected and stored in absolute ethanol. Fork length was measured for each individual at all except one location (Georges Bank). Finally, for all populations excluding Georges Bank, anal fin length data was collected, and for Flemish Cap and South Greenland individuals were sexed.

2.2. Genetic analysis

DNA was extracted from muscle tissue using a standard salting-out protocol (Miller et al., 1988). A 1100 bp long fragment of the mtDNA Control Region (CR) was PCR amplified from 124 individuals (Table 1) using primers L-Pro1 (Ostellari et al., 1996) and 12Sar-H (Palumbi et al., 1991). All PCRs were carried out in a final volume of 25 µl, containing 1× PCR buffer (*Buffer BD Advantage 2 PCR* with $MgCl_2$), 0.2 mM of each dNTP, 0.2 µM of each primer, 1 µl of template DNA, and Taq DNA polymerase (1 unit, *Taq BD Advantage™ 2 Polymerase Mix;* CLONTECH-Takara). The following PCR profile was used for the amplification: one cycle of 1 min at 95 °C, 35 cycles of 30 s at 95 °C, 30 s at 52 °C, and 70 s at 68 °C, and finally, one cycle of 5 min at 68 °C. PCR products were purified with an ethanol/sodium acetate precipitation,

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