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Norwegian fjords contain sub-populations of roundnose grenadier *Coryphaenoides rupestris*, a deep-water fish

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ABSTRACT: The roundnose grenadier *Coryphaenoides rupestris* is a benthopelagic fish distributed along the continental, island, and seamount slopes in the North Atlantic and along the Mid-Atlantic Ridge. Previous studies have indicated that *C. rupestris* consists of sub-populations across its distribution range, but no study has addressed small-scale population structuring at the scale of fjords. Here we study the population genetic structure of *C. rupestris* from fjords and coastal sites in south-western Norway using 8 microsatellite DNA markers. Genetic patterns were contrasted with environmental variables (geographic distance, bottom depth, sill depth, bottom salinity, bottom oxygen, and bottom temperature) and fish condition indices (length–weight, gonadosomatic index, and hepatosomatic index). We observed significant genetic heterogeneity across the study area (F_{ST} = 0.0297, p < 0.001), suggesting several populations occur at the scale of fjords or finer. The Skagerrak samples (2001, 2008, and 2016) did not differentiate and suggest that this area constitutes a temporally stable population unit. Population structuring in *C. rupestris* along the Norwegian coast seems to be influenced by geographic distance and Norway's complex bathymetry, such as fjord sills, appear to limit its dispersal and migration. We found a strong positive correlation between genetic distance and geographic distance (Mantel test, r = 0.702, p = 0.001), bottom depth (r = 0.555, p = 0.014), and a trend with bottom temperature (r = 0.639, p = 0.070). *C. rupestris* is an overfished species that has been Red-Listed as Critically Endangered. Based on these results, monitoring practices and conservation efforts should consider each of these population units independently.

KEY WORDS: Fjords · Roundnose grenadier · Connectivity · Population genetics

INTRODUCTION

Connectivity among oceanic fish populations was previously thought to be high because there are relatively few barriers to dispersal and migration in the marine environment (Ward et al. 1994). While population structure signals have been shown to be weak in most marine species, they still exist to varying degrees, depending on a species' biology and environment. Fishes with a long pelagic egg and larval duration are generally thought to disperse widely with ocean currents, but population structure is still evident in some of these species, such as Greenland halibut *Reinhardtius hippoglossoides* (Knutsen et al. 2007a), tusk *Brosme brosme* (Knutsen et al. 2009), and Atlantic cod *Gadus morhua* (Jorde et al. 2007, Knutsen et al. 2007b). In heterogeneous coastal regions, isolated sub-populations of fishes seem to be present within archipelagos and fjords, in fishes such as Atlantic cod (Jorde et al. 2007, Knutsen et al.

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2007b), sea perch *Helicolenus ercoides* (Lawton et al. 2010), mesopelagic fishes like *Maurolicus muelleri* and *Benthosema glaciale* (Suneetha & Nævdal 2001, Kristoffersen & Salvanes 2009), and Atlantic herring *Clupea harengus* (Aasen 1952). The complexity of Norway's heterogeneous coastal waters provides a unique environment to study population structuring in benthopelagic fishes that have pelagic early life stages and which are commonly found in deep fjords.

Studies of population structure have frequently contributed to the stock management of commercially important fishes like Atlantic cod (Wennevik et al. 2008, André et al. 2016) and Atlantic herring (Mariani et al. 2005). Declining shallow fish resources, increasing demand for these resources, and improved fishing technologies have led to the deepening of fishing grounds and the commercial harvest of deep-sea fishes since the 1950s (Morato et al. 2006, Watson & Morato 2013). Many deep-sea fishes have life-history characteristics that are not conducive to intensive exploitation, such as slow growth and late age at maturity, and have already experienced population declines (Devine et al. 2006, 2012). In order to improve the management of such species, research on their biology and population structure is required. Only a few studies have recently come to the fore in species like orange roughy *Hoplostethus atlanticus* (Varela et al. 2013), redfish (*Sebastes* spp., Valentin et al. 2014), and grenadiers (Knutsen et al. 2012, Catarino et al. 2017).

The roundnose grenadier *Coryphaenoides rupestris* is a benthopelagic fish occurring along the continental, island, and seamount slopes in the North Atlantic and along the Mid-Atlantic Ridge (MAR). The species has been recorded between 180 and 2200 m depth (Knutsen et al. 2012, FAO 2016). The combination of intensive commercial fishing and the slow life-history characteristics of *C. rupestris* has led to its depletion across the North Atlantic (Devine et al. 2006, COSEWIC 2008, Pawlowski & Lorance 2009, NAFO 2015, ICES 2016) and subsequent listing as Critically Endangered on IUCN's Red List (Iwamoto 2015). Previous studies on *C. rupestris* have suggested that sub-populations occur along the Canadian coast, the MAR, and to the west of the British Isles, as demonstrated using length-weight analyses (Atkinson 1989, Bergstad 1990, Vinnichenko & Khlivnoi 2007, O'Hea et al. 2013), otolith microchemistry (Longmore et al. 2010, 2011), and genetic studies (Logvinenko et al. 1983, Dushchenko & Savvatimskii 1987, White et al. 2010, Knutsen et al. 2012). In Norwegian waters, isolated sub-populations have been identified in the Skagerrak (Bergstad 1990, Longmore et al. 2010, 2011, Knutsen et al. 2012) and Trondheimsleia (Knutsen et al. 2012), both of which are deep basins surrounded by shallower sills. *C. rupestris* is also found in the deep fjords of southwestern Norway, but the grenadiers in these fjords have yet to be studied.

Fjords are long, narrow, and deep inlets that were carved out by glaciers and filled with seawater after the last glacial maximum around 17 000 yr ago. Fjords generally have an estuarine circulation pattern, with a low-salinity surface layer flowing towards the ocean, an intermediate layer flowing landwards, and static deep basin water. They often have a shallow sill at their entrance that limits the flushing of deep basin waters (Syvitsky et al. 1987). A large volume of water is exchanged between fjords and the Norwegian Coastal Current (NCC), driven by coastal winds and the characteristics of each fjord. These processes enable the transport of plankton in and out of fjords (Asplin et al. 1999). If pelagic early-life stages of fishes are present in the upper advective layers of fjords (above sill depth), they could disperse into, out of, and between fjords, depending on wind and ocean circulation patterns. Roundnose grenadiers spend considerable time high in the water column, which could put them into contact with different currents and increase their dispersal potential. They have a pelagic egg, larval, and juvenile phase that can last up to 7 mo, during which they have been found as shallow as 150 m (Bergstad & Gordon 1994, Knutsen et al. 2012). Their behaviour during these stages, however, is not well understood. In addition, they undergo vertical feeding migrations as adults (Haedrich 1974, Bergstad 1990, Bergstad & Gordon 1994), and we have collected them using both bottom and pelagic trawls (A. Delaval et al. pers. obs.). Roundnose grenadiers are also long-lived (Devine et al. 2012), but the effect of this greater longevity on dispersal is not known. Dispersal in Norwegian waters has been hypothesised to be limited by shallow bottom features such as sills (Bergstad 1990).

The present study investigates the connectivity of *C. rupestris* between 3 fjords and 2 coastal locations in Norway using 8 microsatellite DNA markers and has a 2-fold aim: (1) to determine the population genetic structure of *C. rupestris* across space and time, and (2) to identify the likely drivers of population sub-division. Based on population structuring patterns found in other fishes along Norway's coast and *C. rupestris'* benthopelagic habits, we predict that population structure will be found along Norway's coast because of bathymetric dispersal barriers like sills.

MATERIALS AND METHODS

Sampling

In total, 440 samples of *Coryphaenoides rupestris* were collected using bottom and pelagic trawls from 8 research cruises performed by the University of Bergen and the Institute of Marine Research (IMR). These were collected from 3 fjords (Lustrafjord, Masfjord, Korsfjord) and 2 coastal sites (Trondheimsleia, Skagerrak) in southwestern Norway (Table 1, Fig. 1). Lustrafjord samples were collected during 2 cruises (July and September 2016), and temporal replicates from 2001, 2008, and 2016 were available from the Skagerrak. Each of the sites is characterised by a deep basin and a bathymetric feature that separates each site from the others and the surrounding ocean. Four of these, Trondheimsleia, Masfjord, Korsfjord, and the Skagerrak, are separated from the ocean or connected fjords by shallow sills. Lustrafjord is a fjord arm located 170 km within Sognefjord, Norway's longest (200 km) and deepest (1308 m) fjord. Lustrafjord samples were collected from the inner (375 m) and outer (650 m) fjord basins, which are separated by a 320 m deep sill.

Position and depth were recorded at each site, and salinity, oxygen, and temperature data were available from most sites. All fish were either processed on board or frozen and later processed in the laboratory. Tissue samples for genetic analysis were taken as dorsal fin clips or muscle tissue and preserved in 96% ethanol, and the weights and pre-anal fin lengths (PAFL) of individual fish were measured. Grenadiers from the fjord sites also had their gonads and livers weighed; this information was used to calculate the gonadosomatic index (GSI) and hepatosomatic index (HSI). Data and tissue samples of Trondheimsleia and Skagerrak grenadiers were provided by IMR. These were the same samples used by Knutsen et al. (2012), but with additional Skagerrak 2016 samples. GSI and HSI were unavailable from Trondheimsleia and the Skagerrak, and environmental data were unavailable from Trondheimsleia and the Skagerrak in 2001. Korsfjord samples were collected aboard a small research vessel and environmental data could not be collected from this site.

Genetic analysis

Population genetics is a tool used to study the evolutionary history of a species and determine how and why individuals are grouped across space and time.

Table 1. Sample sites of *Coryphaenoides rupestris*. Table shows site name abbreviations, number of fish sampled (N), mean (SD) for fish weight, pre-anal fin length (PAFL), gonadosomatic index (GSI), and hepatosomatic index (HSI), bottom depth (BD), sill depth (Sill), bottom temperature (BT), bottom salinity (BS), and bottom oxygen (BO). NA: not available

Sample site (Date)	Abbr.	Lat, Long (°, decimal)	N	Weight (g)	PAFL (cm)	GSI	HSI	BD (m)	Sill (m)	BT (°C)	BS (PSU)	BO ($mg\ l^{-1}$)
Trondheimsleia (Aug 2004)[a]	TL	63.43360, 8.66080	93	919.2 (185.9)	17.5 (1.4)	NA	NA	270	100	NA	NA	NA
Inner Lustrafjord (Jul–Sep 2016)	Lus-In	61.36028, 7.38415	40	492.5 (495.0)	11.3 (5.6)	1.25 (1.21)	1.74 (1.29)	375	320[b]	7.6	35.0	3.5
Outer Lustrafjord (Jul–Sep 2016)	Lus-Out	61.23336, 7.37407	37	336.7 (285.3)	11.6 (3.2)	0.75 (1.30)	1.07 (0.78)	650	570[c]	7.4	35.0	3.7
Masfjord (Sep 2015)	Mas	60.88447, 5.45101	81	493.9 (401.8)	12.5 (4.0)	1.61 (2.30)	1.48 (0.82)	494	75	8.2	35.1	2.4
Korsfjord (Aug 2016)	Kor	60.18981, 5.23125	95	262.4 (163.8)	11.0 (2.4)	0.85 (1.03)	6.17 (2.50)	690	250	NA	NA	NA
Skagerrak (Oct 2001)[a]	SK01	58.00000, 9.00000	39	388.3 (176.0)	12.4 (1.8)	NA	NA	550	275	NA	NA	NA
Skagerrak (Feb 2008)[a]	SK08	58.22600, 9.54600	38	310.4 (118.4)	11.1 (1.5)	NA	NA	640	275	6.5	35.2	5.0
Skagerrak (Jan 2016)	SK16	58.37000, 9.90000	17	464.7 (328.5)	11.7 (4.0)	NA	NA	520	275	6.6	35.2	2.9

[a]Also analysed by Knutsen et al. (2012); [b]Depth of sill between inner and outer Lustrafjord basins; [c]Depth at the entrance of outer Lustrafjord from Sognefjord

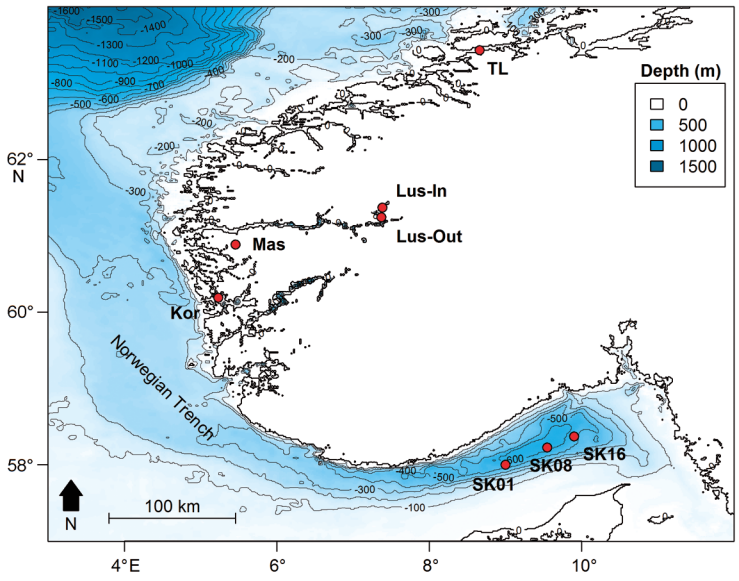

Fig. 1. Bathymetric map of southwestern Norway showing the sampling sites for *Coryphaenoides rupestris*. Site name abbreviations are in Table 1

Measurable differences in allele frequencies indicate the level of genetic differentiation between groups of individuals and hence how much gene flow occurs between these groups (population connectivity). Sufficiently differentiated groups might be considered as distinct populations. Microsatellites, which are short sequences of repeating DNA, are one of several molecular markers used to infer population structure.

Individuals from each location (Table 1) were analysed using 10 microsatellites (Table S1 in the Supplement at www.int-res.com/articles/supp/m586p181_supp.pdf) developed by Knutsen et al. (2008) and White et al. (2009). DNA was extracted from the ethanol-preserved fin clips or muscle tissue using hot sodium hydroxide and tris (HotSHOT, Truett et al. 2000). PCR were performed using a standard TaKaRa Ex HS kit, where each 25 µl reaction contained 2.5 µl of 10× buffer, 2 µl of dNTP (2.5 mmol), 0.15 µl of *Taq* polymerase (5 U μl^{-1}), 1 µl of forward primer (100 µmol, labelled with different fluorescent tags), 1 µl of reverse primer (100 µmol), 1 µl of DNA extract, and ddH_2O to reach the final volume. After optimizing the PCR conditions, 3 primers were run as a multiplex (Crup6, CorRu11, and CorRu33), 2 primers were run as a duplex (CorRu2 and CorRu3), and 3 primers were run in single PCR (Crup1, CorRu4, and CorRu12). For CorRu12, we needed to increase the primer concentration from 1 to 3 µl of each primer. Each set of PCR reactions had different annealing temperatures and number of cycles, and each ended with a 30 min period of 60°C to strengthen the A-plus peaks (Table S2 in the Supplement). All PCR products were analysed on an ABI 3730 Sequencer (Applied Biosystems), and binning and allele scoring was performed in GeneMapper Software 5. For samples with weak or no peaks, PCR and sequencing were repeated, and for some individuals, the protocol was repeated from DNA extraction. Two loci (Crup8 and CorRu7) had consistently poor screening outputs and were dropped early in the study. We tested for the occurrence of null alleles, large allele dropout, and stuttering using MicroChecker (v.2.2.3; Van Oosterhout et al. 2004). Potential null alleles resulting from an excess of homozygotes were detected at 4 loci across several samples (CorRu3, CorRu11, Crup1, and CorRu2). Statistical tests were performed with and without these 4 loci 'flagged' by Micro-Checker.

Statistical analysis

The overall scoring success ranged from 80 to 95%. Individuals with >3 non-scored loci were excluded from the analysis, resulting in the sample sizes in Table 1. The number of alleles and observed and expected heterozygosities were computed in GenAlEx v.6.5 (Peakall & Smouse 2006, Peakall & Smouse 2012). Allelic richness was calculated in FSTAT (Goudet 1995). Deviations from Hardy-Weinberg equilibrium were tested for each site at each locus using a Hardy-Weinberg exact probability test in Genepop, using Genepop's default settings (v.4.6; Rousset 2008), which calculated their inbreeding coefficients (F_{IS}; Weir & Cockerham 1984) and associated p-values. The false discovery rate (FDR) method of Benjamini & Hochberg (1995) was applied to control for Type I errors that may arise from multiple testing. The FDR method orders and ranks p-values from smallest to largest, and significant p-values are accepted if they fulfil equation $P_i \leq \frac{i}{m} \times 0.05$, where i is the rank, and m is the number of significance tests performed. The Hardy-Weinberg test was performed again after removing rare homozygotes (homozygotes for alleles with <5% frequency) to test for any influence of rare genotypes. A LOSITAN-selection workbench (Beaumont & Nichols 1996, Antao et al. 2008) was used to test for selection at each locus, using the default parameters and 50 000 simulations.

To test for population differentiation among all samples, a *G*-test was performed with the software Genepop (*G*-test and default settings). The *G*-test

was also applied for all pairs of sites, and a FDR correction by Benjamini & Yekutieli (2001) was applied on p-values, which accounts for correlation among tests such that the number of significant p-values satisfies the equation $P_i \leq \frac{i}{m} \times \frac{0.05}{\sum_{i=1}^{m} \frac{1}{i}}$. The fixation index ($F_{ST}$), another measure of population differentiation, was also calculated for each locus and pairwise F_{ST} (Theta as in Weir & Cockerham 1984) between sites in Genepop. An analysis of molecular variance (AMOVA) was performed on pairwise F_{ST} in GenAlEx (999 permutations), and the FDR method was applied to p-values (Benjamini & Yekutieli 2001). Pairwise F_{ST} values were visualised in a multidimensional scaling (MDS) plot generated using XLSTAT (v.18.07, Addinsoft). The number of migrants per generation (M) between pairs of sites was estimated by the formula $M = \frac{1}{4}\left(\frac{1}{F_{ST}} - 1\right)$. To convert this to number migrants per year, M was divided by 9, the age at 50% maturity between that of females (10 yr) and males (8 yr) determined by Bergstad (1990).

We tested for correlations between genetic distance (pairwise linearized F_{ST}, $F_{ST}/(1-F_{ST})$, Rousset 1997) and pairwise differences in abiotic variables (geographic distance, bottom depth, sill depth, bottom salinity, bottom oxygen, bottom temperature) and fish condition indices (length–weight regression slopes, mean HSI, mean GSI) between sites, using Mantel correlation tests in GenAlEx (999 permutations). Length–weight regression slopes were calculated using log-transformed PAFL rounded down to cm) and log-transformed weights (rounded down to g) of the sampled grenadiers.

RESULTS

Gene diversity varied across loci, with the number of alleles ranging from 6 (Crup1) to 24 (CorRu3; Table 2). The number of observed heterozygotes was generally lower than expected across loci (Table 2) and populations (Table 3), which is reflected in some of the high inbreeding coefficients (F_{IS}) observed (average 0.1464 across all loci and populations; Table 2). Allele richness was highest in Trondheimsleia (8.116) and was lower at the other sites (between 6.087 and 6.886; Table 3). After FDR correction, 19 out of 64 locus–site combinations were not in Hardy-Weinberg equilibrium; this value was reduced to 14 after removing rare homozygotes. Deviations from Hardy-Weinberg were found at Crup1, CorRu2, CorRu3, and CorRu11, the same loci flagged by Micro-Checker at ≥4 sites. CorRu3 was also a candidate for positive selection in LOSITAN. The 4 flagged loci displayed the highest values of F_{IS} (Table 2); F_{IS} was low for the other 4 loci (Crup6, CorRu4, CorRu12 and CorRu33). Removing the 4 flagged loci meant no deviations from Hardy-Weinberg were found. Their removal resulted in reduced statistical power in tests of genetic distance (*G*-test and AMOVA). While p-values were larger, significant differences were still found between most pairs of sites; only a few comparisons became non-significant after removing the 4 flagged loci, and these are described in the following section. Therefore, the genetic structure patterns observed were similar after rare homozygotes and flagged loci were taken into account.

Table 2. Summary statistics for each microsatellite locus for *Coryphaenoides rupestris*, indicating the mean number of alleles (N), observed (H_O) and expected heterozygosity (H_E), deviation from Hardy-Weinberg equilibrium (F_{IS}), genetic differentiation among samples (F_{ST}) across sites, p-values for exact tests of genetic differentiation across sites (*G*-test; p < 0.001 reported as '0' in GenePop), and the grand mean across all loci and populations. *Loci flagged by Micro-Checker and Hardy-Weinberg tests

Locus	N	H_O	H_E	F_{IS}	F_{ST}	p
Crup1*	6	0.152	0.256	0.3682	0.0033	<0.001
Crup6	12	0.761	0.775	0.0200	0.0152	<0.001
CorRu2*	21	0.614	0.751	0.1779	0.0444	<0.001
CorRu3*	24	0.418	0.710	0.4449	0.0703	<0.001
CorRu4	13	0.572	0.570	0.0040	0.0303	<0.001
CorRu11*	18	0.657	0.869	0.2923	0.0173	<0.001
CorRu12	15	0.828	0.815	−0.0196	0.0255	<0.001
CorRu33	17	0.730	0.704	0.0207	0.0194	<0.001
Grand mean	8.875	0.592	0.681	0.1464	0.0297	<0.001

Table 3. Summary statistics for the 8 sampling sites of *Coryphaenoides rupestris*, showing average allele richness (R), observed (H_O) and expected (H_E) heterozygosity

Population	R	H_O	H_E
Korsfjorden	6.886	0.614	0.677
Inner Lustrafjorden	6.778	0.578	0.678
Outer Lustrafjorden	6.660	0.556	0.698
Masfjorden	6.087	0.609	0.699
Skagerrak 2001	6.159	0.553	0.640
Skagerrak 2008	6.574	0.600	0.648
Skagerrak 2016	6.280	0.633	0.655
Trondheimsleia	8.116	0.590	0.757

Genetic differentiation

The *G*-test revealed significant population structuring across all loci and populations, with an average F_{ST} of 0.0297 ($p < 0.001$, Table 2). Pairwise *G*-tests revealed significant differences between all but 6 pairs of sites after FDR correction ($p \leq 0.001$; Table 4); non-significant differences were between the temporal Skagerrak samples and between each of those and Korsfjord. The AMOVA generated from pairwise F_{ST} values calculated in GenAlEx revealed the same pattern, with an added significant difference between Korsfjord and Skagerrak 2008 ($p \leq 0.001$; Table 5). Excluding the flagged loci (Crup1, CorRu2, CorRu3, and CorRu11) resulted in a loss of significance in 7 pairwise comparisons in the *G*-test (Table 4) and 1 pairwise comparison in the AMOVA (Table 5). Temporal samples from the Skagerrak were homogeneous in both the *G*-test and the AMOVA. Temporal homogeneity was also found when performing a *G*-test and AMOVA on only the Skagerrak samples. Temporal Skagerrak samples were therefore pooled, increasing the sample size to 94, and a *G*-test and AMOVA were performed again. The *G*-test still revealed significant genetic structuring overall ($p < 0.001$) and for each locus ($p < 0.001$ for all 8 loci). A pairwise *G*-test revealed highly significant differences between all pairs of sites after FDR correction ($p < 0.001$), except between Skagerrak and Korsfjord ($p = 0.029$). The AMOVA revealed significant differences between all pairs of sites after FDR correction ($p \leq 0.002$). Excluding the flagged loci had no effect on the results; all significant pairwise differences were maintained in the *G*-test and the AMOVA. A multi-dimensional scaling (MDS) plot summarises the patterns observed (Fig. 2): Trondheimsleia grenadiers are the most genetically distant, Skagerrak and Korsfjord grenadiers are more closely related, and inner and outer Lustrafjord are genetically distant with inner Lustrafjord clustering closer to Masfjord. F_{ST} translated to a low number of migrants between sites, with the highest migratory movement occurring between the Skagerrak and Korsfjord and the lowest in migrations to and from Trondheimsleia (Table 6).

Table 4. Pairwise differentiation between sites (see Table 1) and years for *Coryphaenoides rupestris*, showing p-values from a *G*-test. Significant p-values after correction using Benjamini-Yekutieli's false discovery rate (FDR) are in **bold**. Values in *italics* remained significant when removing 4 loci flagged in Micro-Checker, Hardy-Weinberg tests, and LOSITAN (Crup1, CorRu2, CorRu3, CorRu11)

	Kor	Lus-In	Lus-Out	Mas	SK01	SK08	SK16	TL
Kor	–							
Lus-In	**<0.001**	–						
Lus-Out	***<0.001***	***<0.001***	–					
Mas	***<0.001***	***<0.001***	***<0.001***	–				
SK01	0.129	**<0.001**	**<0.001**	***<0.001***	–			
SK08	0.141	***<0.001***	**<0.001**	***<0.001***	0.229	–		
SK16	0.284	**<0.001**	**<0.001**	**<0.001**	0.540	0.540	–	
TL	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	***<0.001***	–

Table 5. Pairwise differentiation between sites (see Table 1) and years for *Coryphaenoides rupestris*. F_{ST} values (below diagonal) and p-values from an AMOVA (above diagonal) are shown. Significant p-values after correction using Benjamini-Yekutieli's false discovery rate (FDR) are in **bold**. Values in *italics* remained significant after removing 4 flagged in Micro-Checker, Hardy-Weinberg tests, and LOSITAN (Crup1, CorRu2, CorRu3, CorRu11)

	Kor	Lus-In	Lus-Out	Mas	SK01	SK08	SK16	TL
Kor	–	***0.001***	***0.001***	***0.001***	0.011	***0.001***	0.112	***0.001***
Lus-In	0.0165	–	***0.001***	***0.001***	**0.001**	***0.001***	***0.001***	***0.001***
Lus-Out	0.0203	0.0228	–	***0.001***	***0.001***	***0.001***	***0.001***	***0.001***
Mas	0.0203	0.0087	0.0338	–	***0.001***	***0.001***	***0.001***	***0.001***
SK01	0.0038	0.0299	0.0248	0.0308	–	0.015	0.110	***0.001***
SK08	0.0062	0.0341	0.0238	0.0332	−0.0009	–	0.434	***0.001***
SK16	−0.0027	0.0253	0.0248	0.0235	−0.0021	−0.0034	–	***0.001***
TL	0.0467	0.0363	0.0331	0.0393	0.0525	0.0535	0.0577	–

Relation to environmental variables and condition indices

Results of the Mantel tests showed a significant effect of isolation by distance ($r = 0.702$, $p = 0.001$; Fig. 3), with genetic distance increasing with geographic distance between sites. A positive correlation was also found with differences in bottom depth between sites ($r = 0.555$, $p = 0.014$), indicating genetic distance increases with larger differences in bottom depth between sites. A positive trend between genetic distance and differences in bottom temperature between sites was found; however, this was not significant ($r = 0.639$, $p = 0.070$). The Skagerrak had the coldest bottom temperature of all the sites (Table 1); between-site differences of 0.9°C or greater were observed for all

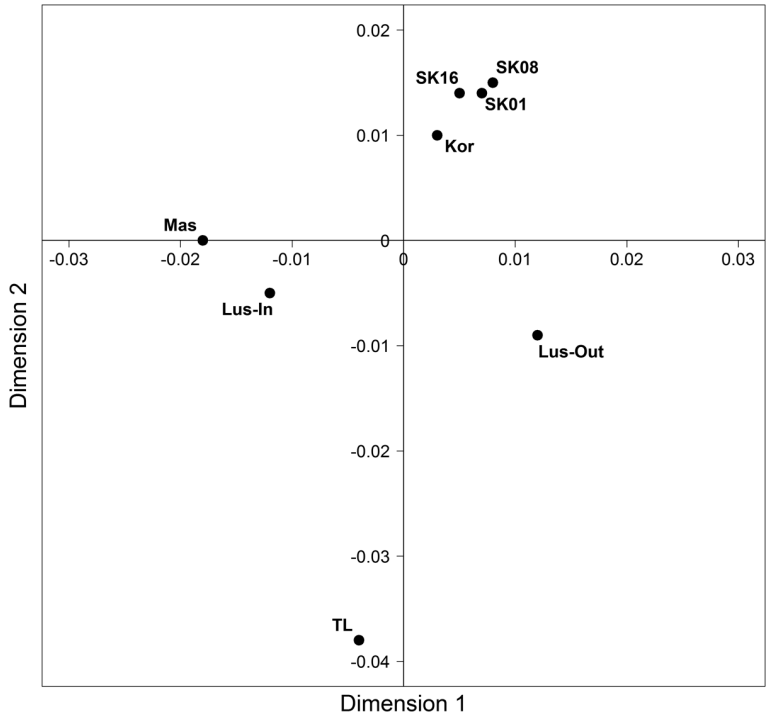

Fig. 2. Multi-dimensional scaling plot showing the genetic distance of *Coryphaenoides rupestris* between 8 Norwegian sites (see Table 1) based on pairwise F_{ST} (GenePop, Table 5). Kruskal's stress = 0.086

Table 6. The estimated number of migrants (M) of *Coryphaenoides rupestris* between pairs of sites (see Table 1) per generation ($M = \frac{1}{4}(\frac{1}{F_{ST}} - 1)$, above diagonal) and per year ($\frac{M}{9\ \text{years}}$, below diagonal

	Kor	Lus-In	Lus-Out	Mas	SK	TL
Kor	–	14.9	12.1	12.1	57.9	5.1
Lus-In	1.7	–	10.7	28.1	8.1	6.6
Lus-Out	1.3	1.2	–	7.1	9.1	7.3
Mas	1.3	3.2	0.8	–	7.6	6.1
SK	6.4	0.9	1.0	0.8	–	4.1
TL	0.6	0.7	0.8	0.7	0.5	–

pairwise site comparisons that included the Skagerrak. No significant correlations were found between genetic distance and other environmental variables, or with the fish condition indices (Fig. 3).

DISCUSSION

Population genetic structure of roundnose grenadier in the North Atlantic and along the Norwegian coast has been previously investigated (Logvinenko et al. 1983, Dushchenko & Savvatimskii 1987, White et al. 2010, Knutsen et al. 2012), but this was the first study to investigate population genetic structure among and within Norwegian fjords and coastal areas. Our analysis of 8 microsatellite DNA loci revealed strong evidence for spatial population genetic structure in southwestern Norway, characterised by limited gene flow between sites, high inbreeding coefficients (F_{IS}) in half of the loci examined, and a large proportion of homozygotes at each site. We found that allele richness and diversity were low relative to North Atlantic populations (White et al. 2010, Knutsen et al. 2012), and these were lower in the fjords and the Skagerrak relative to Trondheimsleia. This indicates a post-glacial (re)colonization to these marine areas after the last glacial period, marked by a genetic bottleneck or founder effect, a pattern that has been observed in other species in Northern Europe (Francisco et al. 2009, Gonzalez et al. 2016). The data suggest isolation by geographic distance and bathymetric barriers are the likely forces of spatial population structuring of roundnose grenadier in southwestern Norway.

Highly significant structure among samples indicates that each of the study sites represented highly isolated sub-populations of roundnose grenadier. Trondheimsleia grenadiers were the most isolated, supporting the results of Knutsen et al. (2012), who used the same material. Average allele richness was highest in Trondheimsleia, suggesting that this population may have been established before the fjord and Skagerrak sub-populations. Its closer proximity to the Norwegian continental slope and the North Atlantic may allow for greater gene flow between Trondheimsleia and North Atlantic grenadier populations, maintaining a higher genetic diversity than in the fjords and in the Skagerrak. Such a pattern is also seen in corkwing wrasse *Symphodus melops* (Gonzalez et al. 2016) when comparing European samples with samples from western and southern Norway. Sub-populations that have high genetic diversity, high heterozygosity, and high gene flow are often more resilient to environmental change (Allendorf et al. 2007). Norwegian sub-populations of roundnose grenadier, in particular those in the fjords and Skagerrak, may therefore be at greater risk to environmental changes and increased fishing activity.

The isolation of Lustrafjord can be explained by its position 170 km within Norway's longest and deepest

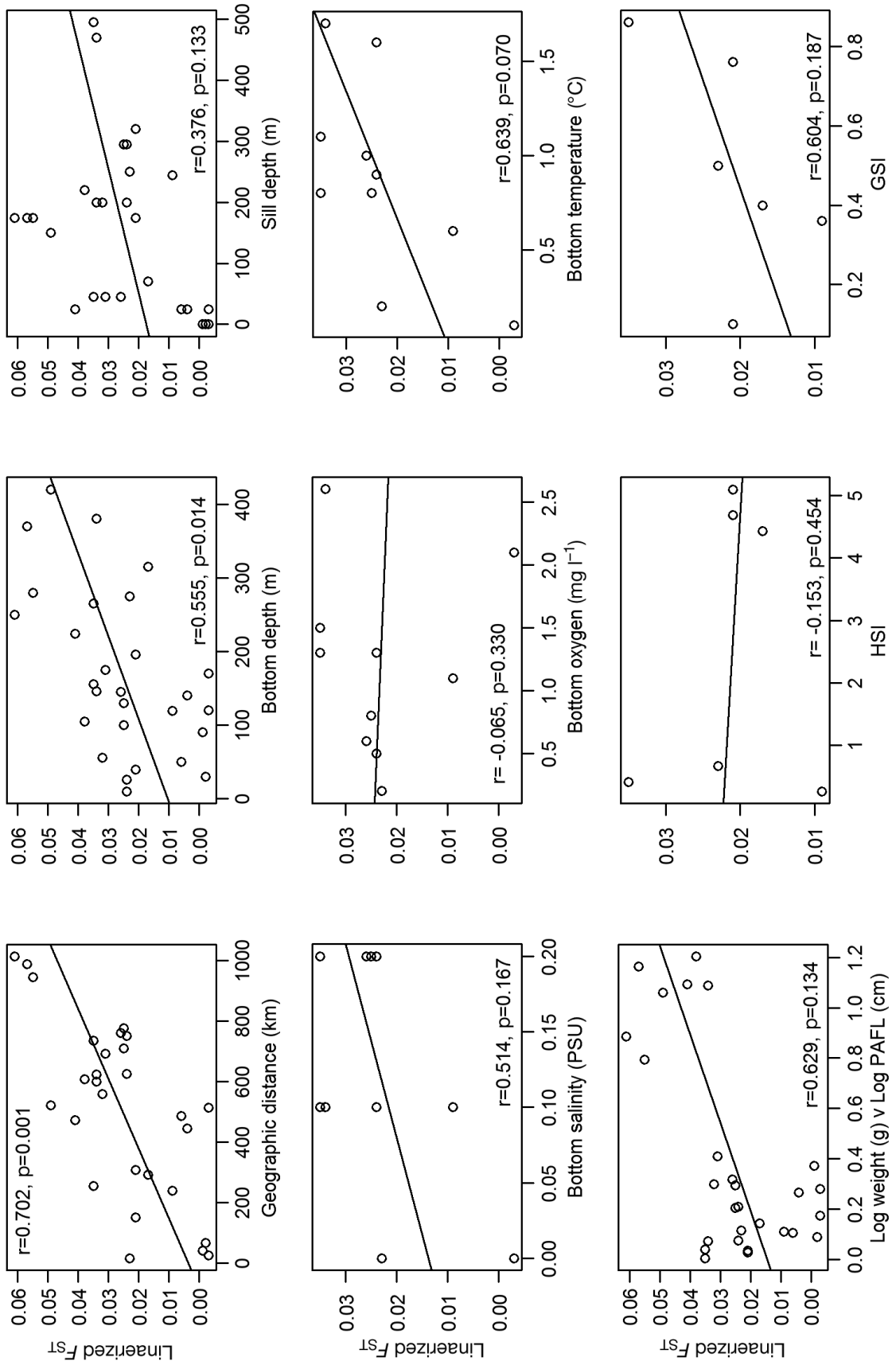

Fig. 3. Pairwise genetic distances (linearized F_{ST}) of *Coryphaenoides rupestris* plotted against pairwise differences between sites for geographic distance (N = 8 sites), bottom depth (N = 8 sites), sill depth (N = 8 sites), bottom salinity (N = 5 sites), bottom oxygen (N = 5 sites), bottom temperature (N = 5 sites), log-weight vs. log-PAFL (N = 8 sites), hepatosomatic index (HSI, N = 4 sites) and gonadosomatic index (GSI, N = 4 sites). Results of the Mantel test are shown by the correlation factor (r) and p-values (P(random correlation ≥ observed correlation)) following 999 permutations in GenAlEx. Three sites lacked salinity, oxygen and temperature data, resulting in 10 pairwise site comparisons. HSI and GSI were only collected at 4 fjord sites, resulting in 6 pairwise site comparisons. PAFL: pre-anal fin length; HSI: hepatosomatic index; GSI: gonadosomatic index

fjord. The deep Sognefjord might act as a dispersal barrier, a pattern that was also observed in herring (Aasen 1952). While the proximity of the inner and outer fjord basins (~16 km apart) goes against the observed trend of isolation by geographic distance, it complements the evidence of isolation by depth; the bottom depths of inner and outer Lustrafjord are 375 m and 650 m, respectively. Although Lustrafjord's bathymetry does not obstruct movement of pelagic herring within the fjord (Aasen 1952), the 320 m sill between the inner and outer fjord basins might be a barrier to grenadier movement. A preliminary inspection of water circulation within Lustrafjord revealed that the tidal flow over this sill might be limited (<10 cm s^{-1}; L. Asplin pers. comm.). The limited exchange of water masses between Lustrafjord's inner and outer basins might not be an important dispersal mechanism for grenadier offspring. Grenadiers from the inner Lustrafjord basin have higher condition indices than in the outer Lustrafjord basin, as shown by their heavier weight-for-length, HSI, and GSI (Table 1). This could reflect different environmental conditions between the 2 basins that might represent a barrier to dispersal and settlement. The reasons for population structuring within Lustrafjord are currently speculative and might be uncovered by further studies.

Similarly, the isolation of the Masfjord sub-population might be explained by its geographic position in a northward branch of the larger Fensfjord. In addition, at the entrance of Masfjord is the shallowest sill (75 m) among the sites studied. This sill is known to drive population structuring in mesopelagic fishes (Suneetha & Nævdal 2001, Suneetha & Salvanes 2001, Kristoffersen & Salvanes 2009) and may also prevent movement of early pelagic stages of grenadier. Less genetic differentiation was found with F_{ST} between Masfjord and inner Lustrafjord sub-populations than between inner and outer Lustrafjord. This may be due to chance with the genetic markers we used; incorporating other genetic markers may reveal greater differences between these populations. Alternatively, the similarity might have resulted from a single migration or recruitment event between these sites, or as an artefact of the smaller sample size from inner Lustrafjord.

Our results suggest that the Korsfjord grenadier sub-population could possibly be grouped with the Skagerrak sub-population. After the non-differentiated temporal Skagerrak samples were pooled, the *G*-test revealed large but non-significant differences with Korsfjord grenadiers, while AMOVA indicated these differences were significant. Although still isolated within Norway's coastline and by a sill, Korsfjord is situated much closer to the coast than the other fjords. Korsfjord's basin waters also undergo regular flushing by the NCC, maintaining oceanic conditions in these waters (Matthews & Sands 1973, Bakke & Sands 1977). Dispersal of pelagic eggs and larvae is therefore more likely to occur between Korsfjord and oceanic populations like the Skagerrak due to their proximity and the influence of the NCC.

Our results support the existing evidence of an isolated sub-population occurring in the Skagerrak (Bergstad 1990, Longmore et al. 2010, 2011, Knutsen et al. 2012). These studies propose this sub-population is isolated by the shallow sill surrounding the deep Skagerrak basin, creating a barrier to movement, and by egg and larvae retention by the Skagerrak's cyclonic circulation. Knutsen et al. (2012) found temporal stability between 2001 and 2008. Our results suggest temporal stability extends to 2016; however, our sample size was limited to 17 individuals and may therefore contain a large margin of error.

Geographic distance between sites and bathymetric features appear to be the primary drivers of population sub-division in roundnose grenadier along the Norwegian coast. Our results suggest that genetic distance increases with increasing geographic distance between sites. In addition, larger differences in bottom depth between sites increase genetic distance in grenadiers. Depth has been identified as a possible source of speciation in the *Coryphaenoides* genus (Gaither et al. 2016) and sub-division in *C. rupestris* (White et al. 2010). Although the dividing boundaries were considerably deeper (4000 m and 1200 m in both studies, respectively) than the present study's depth range (270–700 m), our results show that depth differences in combination with shallow sills are important factors for structuring populations of roundnose grenadier, even at relatively shallow depth ranges.

Adult roundnose grenadiers are thought to be poor swimmers and relatively sedentary (Longmore et al. 2010). Although they are long-lived and may travel long distances over a lifetime, their migratory movements as adults are not well known. The distances and complex bathymetry separating the studied sites could present obstacles to adult grenadiers. Bathymetric barriers have been observed as possible dispersal barriers in grenadiers. For example, the Charlie-Gibbs Fracture Zone has been identified as a barrier between sub-populations of roundnose grenadier on either side of it along the MAR (White et al. 2010). In a related species, the Mediterranean grenadier *Coryphaenoides mediterraneus*, the Strait

of Gibraltar acts as a dispersal barrier for sub-populations in the Mediterranean and the Atlantic Ocean (Catarino et al. 2017). Our findings suggest similar patterns occur for roundnose grenadier along Norway's coast as a result of bathymetric features like fjord sills. Our results do not suggest a correlation between genetic distance and sill depth, but this might be a result of the small number of sites studied. Roundnose grenadiers are found deeper than 180 m (FAO 2016) and are not typically found at shallower depths. Being poor swimmers, it is unlikely for grenadiers to overcome bottom features located at depths shallower than their preferred range. Dispersal is more likely to occur via ocean currents during the long pelagic egg, larval, and juvenile phases of roundnose grenadiers. This should allow long-range dispersal along the NCC and for dispersal in and out of the fjords despite the sills. Nevertheless, these barriers appear to restrict movement of the pelagic life stages. Sills might cause the retention of offspring within fjords due to estuarine circulation patterns, as has been found in Atlantic cod (Knutsen et al. 2007b). Grenadiers appear to undergo short-range dispersal independent of ocean currents, rather than the common assumption of long-range dispersal via ocean currents (Knutsen et al. 2012). For dispersal between the fjords and the NCC, the timing of these early life stages may need to coincide with the advection of pelagic water layers above sill height in and out of the fjords, which depend on atmospheric circulation patterns along the Norwegian coast (Asplin et al. 1999). Dispersal might also depend on the flushing of deep fjord-basin waters, which occurs episodically when the density of water flowing over the sill exceeds that of deep basin water, the densest water in a fjord (Mann & Lazier 2006). The frequency of basin flushing varies between fjords; it occurs seasonally in Korsfjord (Bakke & Sands 1977) and approximately every 8 yr in Sognefjord (Svendsen 2006). Norway's coastal geography, bathymetry and circulation patterns might therefore limit gene flow during all life stages of roundnose grenadier. These processes are also drivers of population heterogeneity in tusk (Knutsen et al. 2009) and Greenland halibut (Knutsen et al. 2007a), 2 species with similar life stages to roundnose grenadier, marked by early pelagic stages and benthic adult stages. Our elementary understanding of roundnose grenadier life-history stresses the importance of studies on all life stages to better understand their biology and dispersal ability.

The results do not provide evidence of any correlation between genetic distance and environmental differences between sites, but this lack of an apparent relationship may be the result of poor seasonal coverage. No correlations were found with bottom oxygen or bottom salinity. There was a non-significant positive trend with bottom temperature resulting from temperature differences in comparisons with the Skagerrak where waters were colder. However, this trend might be a result of sampling design. Bottom temperatures generally vary by <1°C seasonally at the sampled depths (Syvitsky et al. 1987), corresponding approximately to the differences observed between the Skagerrak, sampled in winter, and the fjords, sampled in summer and autumn. No correlations were found with measures of fish condition either. The opportunistic nature of sampling, a lack of environmental data from Korsfjord and Trondheimsleia, and lack of gonad and liver weight data from Trondheimsleia and the Skagerrak may have resulted in correlations with these variables going undetected.

CONCLUSIONS

Roundnose grenadier occurs in highly isolated subpopulations among the western Norwegian fjords studied, and population sub-division might occur in other fjords and heterogeneous environments across its distribution range. The low level of genetic diversity of fjord and Skagerrak populations relative to Trondheimsleia and North Atlantic populations suggests grenadiers may have settled from the North Atlantic into the fjords and the Skagerrak relatively recently, sometime after glaciers began retreating at the last glacial maximum 17 000 yr ago (Syvitsky et al. 1987). A founder effect or bottleneck may have occurred, after which these groups became isolated by the complex bathymetry of the region, resulting in higher levels of inbreeding, lower genetic diversity, and high levels of homozygosity. The poor swimming ability of adult grenadiers means they are unlikely to migrate long distances, while their long pelagic early-life stages allow some, albeit limited, dispersal between these sites. Based on our results, roundnose grenadiers from each of the fjords should be considered as distinct biological populations, and neighbouring populations cannot be expected to replenish these areas in the short term.

Future research should incorporate other tools in the population biology toolkit; additional molecular markers, otolith microchemistry, morphometry and chronology, body morphometrics, and egg and larvae surveys would provide further insights into the population biology of roundnose grenadier. Incorpo-

rating samples of roundnose grenadier and other deep-dwelling species from other sites along Norway's coast, or within large fjord systems, could advance our understanding of the structuring mechanisms involved in deep Norwegian fjords.

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