ICES Journal of Marine Science, 2023, **80**, 766–774
DOI: 10.1093/icesjms/fsad009
Advance access publication date: 2 February 2023
Original Article

Genetic population structure in Norway lobster (*Nephrops norvegicus*): management regime under panmixia

Jon-Ivar Westgaard[1], Guldborg Søvik[2,*], and Torild Johansen[1]

[1]Institute of Marine Research, Framsenteret, Tromsø, N-9007 Tromsø, Norway
[2]Institute of Marine Research, Bergen, N-5005 Bergen, Norway
[*] *Corresponding author: tel: +0047 94860985*; e-mail: guldborg.soevik@hi.no.

Investigations of genetic stock structure sometimes reveal a mismatch between management units and biological units. In Scandinavian waters, Norway lobster (*Nephrops norvegicus*) is divided into two management units (the Skagerrak–Kattegat and the Norwegian Deep). We have tested the population genetic structure of *Nephrops* within this region using microsatellite DNA markers, and compared the structure with the present management units. Our study suggests no population genetic structure of *Nephrops* within the Skagerrak, Kattegat, and Norwegian Deep region, whereas a shallow genetic structure was detected on a larger geographical scale when comparing outgroup samples from Scotland and Iceland. We found indications of sex-biased dispersal as the overall genetic differences were larger for females. Ocean current patterns suggest that *Nephrops* stocks in the region may be connected by larval drift. The two areas differ in fishing pressure, monitoring, assessment, and regulations, which is an argument for maintaining the present two-areas management regime despite the evidence for one biological population.

Keywords: genetic stock structure, management units, microsatellites, Norway lobster, sex-dependent dispersal.

Introduction

Boundaries of management units of commercially exploited marine species are often based on economic units and geographical separation, without considering genetic structure or gene-flow patterns. Investigations of genetic population structure sometimes reveal a mismatch between management units and biological units (Reiss *et al.*, 2009). Correctly identifying biological populations is, however, of crucial importance in fishery management. Most assessment models assume a closed population with negligible migration and that a single number with no spatial component suffices to describe and forecast population abundance (Begg *et al.*, 1999; Cadrin and Friedland, 1999). Jorde *et al.* (2014) noted that assessing only a portion of a biological population may lead to biased analyses of growth, recruitment, and mortality, which are key parameters when making forecasts and estimating yields. Additionally, assessing what is taken to be a whole biological population and making inferences about stock status of its components may also give biased results when sub-groups are demographically independent. Finally, assessing a management unit defined by economic or political boundaries without considering the possibility of it consisting of several genetic subpopulations might result in overexploitation of local populations (Fu and Fanning, 2004; Saha *et al.*, 2015). This may lead to the loss of intraspecific genetic variation (Hauser and Carvalho, 2008) and impair the species' ability to adapt to environmental changes.

Commercially important Norway lobster (*Nephrops norvegicus*) (Ungfors *et al.*, 2013) provides an example of the challenges in the assessment of marine species with an incomplete knowledge of genetic structure and demographic connectivity. *Nephrops* is found in the Mediterranean Sea and the Northeast Atlantic (Johnson *et al.*, 2013). Catches are often dominated by males (ICES, 2021), as berried females tend to remain within their burrows (Chapman, 1980; Eiriksson, 2014). The species has a patchy distribution in suitable muddy substrates, in which the protective burrows are excavated (Johnson *et al.*, 2013), and thus may be divided into isolated subpopulations. In the North Sea, Skagerrak, and Kattegat region, *Nephrops* is divided into eleven functional units (FU), for which separate quota advice is provided by the International Council for the Exploration of the Sea (ICES) (ICES, 2021). Management is, however, implemented on a larger geographical scale, with three management units with separate quotas, based on geographical separation and political borders (the Skagerrak and Kattegat, and respectively, Norwegian and EU/UK waters of the North Sea). A continuous, large area of *Nephrops* habitat stretching from the Kattegat into the Norwegian waters of the North Sea has been divided into several FUs. The Skagerrak and Kattegat (respectively, FUs 3 and 4) (Figure 1) are nevertheless assessed together due to the continuous distribution and a likely exchange of pelagic larvae (ICES, 2021). *Nephrops* in the Norwegian waters of the North Sea (Norwegian Deep, FU 32) is assessed as a separate stock.

Despite the economic importance of the North Sea and the Skagerrak–Kattegat *Nephrops* fisheries (Ungfors *et al.*, 2013), it is not known whether *Nephrops* in the eleven FUs constitute several genetic subpopulations, or one large, panmictic population. Earlier studies on the species revealed weak, but significant levels of genetic differentiation in the Northeast Atlantic and the Mediterranean Sea (Stamatis *et al.*, 2004; Stamatis *et al.*, 2006; Gallagher *et al.*, 2019). Stamatis *et al.* (2004) did not detect any significant differences between populations along the east and northeast UK coasts, whereas Stamatis *et al.*

Received: 12 August 2022; **Revised:** 11 January 2023; **Accepted:** 12 January 2023

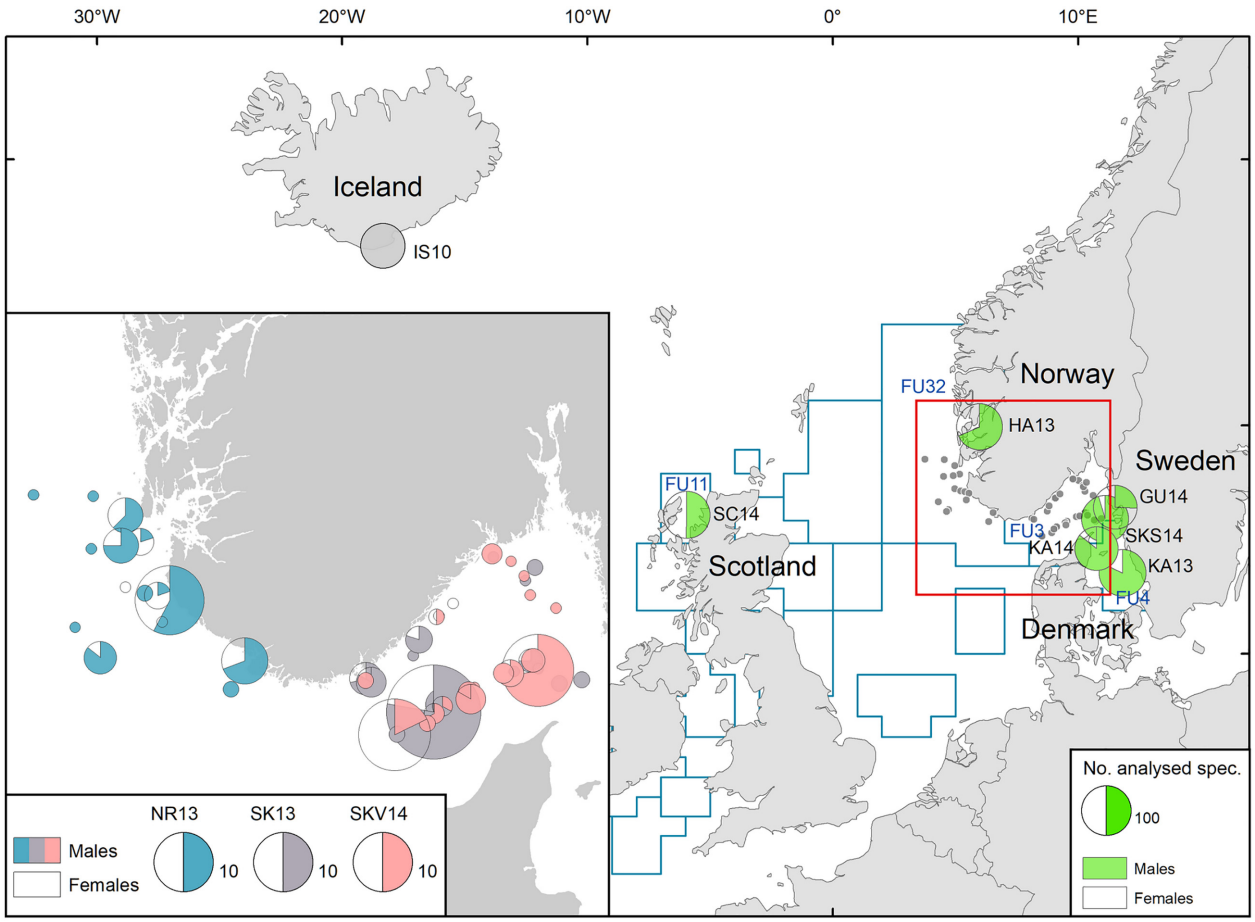

Figure 1. Map of the sampling localities of *Nephrops norvegicus*, where the size of the bubbles indicates sample size (size of bubble in legend corresponds to 100 specimens) and the colour coding indicates percentage of males in the samples. The inset map shows details for the three samples (NR13, SK13, and SKV14) consisting of specimens from several trawl catches (size of bubble in legend corresponds to 10 specimens). The red square shows the placement of the inserted map. The blue grid shows the functional units (FU) in the Greater North Sea, where, FUs 3 and 4 comprise one management unit, FU 32 one management unit, and the remaining FUs in the North Sea one management unit. Sample names are given in Table 1.

(2006) did find significant differences between samples from the northeast UK. Studies along the Portuguese coast (Streiff *et al.*, 2001) and on *Nephrops* grounds south of Iceland (Pampoulie *et al.*, 2011) did not find any significant genetic differences between populations within these areas. Gallagher *et al.* (2019) did not find significant differences between *Nephrops* in the North Sea and Skagerrak.

In the marine environment, gene flow typically takes place through dispersal of pelagic eggs or larvae, and/or by adult migration. Tagging experiments show that adult *Nephrops* undertake only small-scale movements (Farmer, 1975; Aguzzi and Sarda, 2008 and references therein; Merder *et al.*, 2020), and distances travelled do not seem to depend on sex or size (Merder *et al.*, 2020). The duration of the pelagic larval stage may last 50–60 days at 7°C–10°C (Farmer, 1975; Hill, 1990). No information is available on the extent of larval mixing between the Norwegian Deep, Skagerrak, and Kattegat, but modelling results from other regions show that *Nephrops* larvae may drift up to 300–650 km (Marta-Almeida *et al.*, 2008; O'Sullivan *et al.*, 2015). Prevailing currents into the Skagerrak from the North Sea and the Kattegat, and a strong northward current out of the Skagerrak [the Norwegian Coastal Current (NCC)] (Albretsen *et al.*, 2012) suggest that *Nephrops* in FUs 3, 4, and 32 may be connected by larval drift. However, large-scale cyclonic circulation in the surface layer of the Skagerrak (Gustafsson and Stigebrandt, 1996) may contribute to larval retention in this basin.

The *Nephrops* fisheries in the Norwegian Deep and the Skagerrak–Kattegat differ greatly. In the Kattegat and the Swedish and Danish waters of the Skagerrak, an economically important *Nephrops* fishery exists with annual landings of 3000–7000 tonnes, mainly from *Nephrops* trawls with minimum mesh size of 70–90 mm in the codend (ICES, 2021). The stock is annually monitored by underwater TV surveys (UWTV) and annual quota advice is provided by ICES (ICES, 2022a). A quota is set for the Danish and Swedish fisheries. *Nephrops* in the Norwegian Deep, on the other hand, is caught as bycatch in a mixed bottom trawl fishery and a shrimp fishery with minimum mesh sizes of 120 and 35 mm, respectively (Søvik *et al.*, 2016; ICES, 2021), as well as in a directed, Norwegian coastal trap fishery (Zimmermann *et al.*, 2022). Total landings have declined from 1000–1200 tonnes in the first half of the 2000s to a minimum of 137 tonnes in 2018 (ICES, 2021). Landings have been well below both the advice and the quota for many years. No UWTV survey is implemented for this data-poor stock, with biennial quota advice (ICES, 2022a). A quota is allocated to EU-vessels, whereas Norwegian vessels are not subject to quotas.

The objective of the present study was to investigate the genetic population structure of *Nephrops* within the Skagerrak, Kattegat, and Norwegian Deep region, including two fjord sites, and to discuss the results in light of the present within-region differences in fisheries, monitoring, assessment, and management. Samples were collected over two years to test for temporal variation, and data from Iceland and Scotland were included as outgroups for comparison with earlier results on genetic structuring in Iceland and the North Sea.

Materials and methods

Samples

Tissue samples for genetic analyses were collected onboard research and fishing vessels (Figure 1, Table 1). *Nephrops* in the Skagerrak and Kattegat were sampled over two years (2013 and 2014) for temporal analyses. The dataset included two fjord samples from the Norwegian and Swedish west coast. Outgroup samples from Iceland and Scotland were collected in 2010 and 2014, respectively. The NR13, SK13, and SKV14 (Table 1) samples were collected during a bottom-trawl survey (Søvik and Thangstad, 2021). Due to few *Nephrops* in individual catches, samples consisted of specimens from several hauls. Samples NR13 and SK13 consisted of *Nephrops* from 24 and 18 trawl stations, respectively. In 2014, the nine *Nephrops* caught in the Norwegian Deep were not included in the analyses, whereas the SKV14 sample came from 20 stations. For all specimens, except from Iceland, sex and carapace length were recorded. Muscle samples were stored in ethanol (2 ml tubes) at −20°C until analyzed.

Genetic analysis

DNA was extracted using the commercial kit Omega E-Z 96 Tissue DNA kit (Omega Bio-Tek Inc., USA) following the manufacturer's protocol. A total of 13 microsatellite DNA markers (Streiff *et al.*, 2001; Skirnisdottir *et al.*, 2010) were organised into three multiplexes (Supplementary Table S1). The alleles were scored using GeneMapper 4.0 (Applied Biosystems, Foster City, CA, USA). All profiles of alleles were visually inspected. Further details are provided in Supplementary Materials.

Statistical analyses

The microsatellite loci were screened with Microchecker (van Oosterhout *et al.*, 2006) to account for null alleles and scoring error due to stuttering. Sample and locus observed and expected heterozygosity, linkage disequilibrium, and conformity to Hardy–Weinberg expectations were calculated with Genepop 4.1.4 (Rousset, 2008). Pairwise F_{ST} were estimated with θ (Weir and Cockerham, 1984) and tested for population differentiation with the exact *G*-test in Genepop.

Barrier 2.2 (Manni *et al.*, 2004) was used to reveal potential areas of reduced gene flow between populations. This approach uses Delaunay triangulation to connect the samples on a plane using triangles, thus creating a network of interconnecting sample localities. The (Monmonier, 1973) maximum difference algorithm identified genetic barriers. To estimate statistical support for genetic barriers, we applied multiple regressions on distance matrices (MRM) (Legendre *et al.*, 1994), in which a single dependent distance matrix (*Y*) of linearized F_{ST} was expressed as a function of several independent matrices (*Xi*), represented by putative barriers. Putative barriers

Table 1. Characterization of the samples of *Nephrops norvegicus* included in this study based on eleven microsatellite DNA loci.

Population	Sample ID	Latitude	Longitude	Depth (*m*)	Gir	Year	Date	*N*	% females	N_a	H_o	H_e
Hardangerfjord	HA13	59 58 N	005 59 E	159–165	traps	2013	May, 21	87	31.4	23.8	0.819	0.847
Norwegian Deep	NR13	several trawl stations*		145–333	trawl	2013	January, 13–17	83	37.3	22.3	0.814	0.851
Skagerrak	SK13	several trawl stations#		140–361	trawl	2013	January, 18–24	90	18.9	23.6	0.826	0.849
	SKV14[1]	several trawl stations&		126–272	trawl	2014	January, 12–22	94	37.8	24.1	0.824	0.844
	SKS14[2]	58 02 N	011 06 E	120	traps	2014	June, 18	85	4.5	23.6	0.831	0.849
Kattegat	KA13	56 51 N	011 49 E	45	traps	2013	February, 21	89	18.0	22.7	0.821	0.841
	KA14	57 23 N	010 45 E	30	traps	2014	June, 18	77	14.3	21.5	0.811	0.844
Gullmarsfjord	GU14	NA	NA	40	traps	2014	July, 7	79	74.4	24.6	0.805	0.841
Iceland	IS10	63 22 N	020 00 W	180–183	trawl	2010	May, 6	79	NA	23.0	0.845	0.849
Scotland, North Minch	SC14	58 07 N	005 37 W	150	trawl	2014	June, 20	89	49.4	24.1	0.824	0.843

[1]SKV denotes Skagerrak west.
[2]SKS denotes Skagerrak south.
*NR13 (57 58 N–59 18 N, 003 46 E–006 32 E).
#SK13 (57 39 N–58 53 N, 008 08 E–010 57 E).
&SKV14 (57 39 N–58 54 N, 008 08 E–010 42 E).
N is the number of individuals, N_a is the number of alleles, H_O is observed heterozygosity, and H_e is the expected heterozygosity. *NA*: not available.

Table 2. Analysis of the statistical power under varying levels of differentiation.

Expected F_{ST}	Average F_{ST}	x^2-test	Fischer's test	N_e	Generation (t)	Runs
0.0000	0.0000	0.0379	0.0749	1 000	0	10 000
0.0005	0.0005	0.9059	0.8401	1 000	1	10 000
0.0010	0.0010	1.0000	0.9998	1 000	2	10 000
0.0015	0.0015	1.0000	1.0000	1 000	3	10 000

were constructed as binary matrices where populations on the same side of a barrier were denoted as 0, whereas populations on the opposite side of the barrier were denoted as 1. In addition to putative barriers, a geographical distance matrix was included in the regression model to account for isolation by distance. Significance on the regression coefficients was determined with 10 000 permutations of the dependent distance matrix. We estimated the significance for the highest ranked barrier first, then proceeded to the next highest ranked barrier, until we approached non-significant values.

We used molecular variance (AMOVA; Excoffier *et al.*, 1992) to quantify and test the statistical significance of the differentiation within and among all populations and among selected groups representing proposed management units. We also partitioned genetic variation in a hierarchy of population groups. Initially the groups were based on the results of the Barrier analysis. However, alternative groupings were also explored. We tested for temporal stability in the genetic structure with samples from two consecutive years for the localities in the Skagerrak and Kattegat with AMOVA in Arlequin 3.5 (Excoffier and Lischer, 2010). Samples were pooled by year creating two groups between which the variance was estimated.

We performed a power analysis with POWSIM 4.1 (Ryman and Palm, 2006) to ensure that sample sizes provided enough statistical power to detect differences at the observed level (details in Supplementary Materials).

Sex-biased dispersal

We used FSTAT 2.9.3 (Goudet, 2001) to test for sex-biased dispersal (details in Supplementary Materials). The F_{ST}, mean assignment percentage (*mAlc*), and assignment variance (*vAlc*) were assessed for differences between the sexes. We used a one-sided test, as we had an a priori idea based on the F_{ST} values that females were the sex likely to disperse the most. Comparisons between males and females were made among samples within the Kattegat–Skagerrak area (Table 1).

Results

Microchecker indicated null alleles at two of the 13 microsatellite loci. These two loci showed heterozygote deficits in all samples and were removed from further analysis. Individual locus heterozygosities and F_{IS} for all sample/locus combinations appear in Supplementary Table S1. Observed heterozygosities at the remaining 11 loci ranged from 0.30 (locus C12, HA13) to 0.94 (locus PLH15, SC14). Randomization tests showed that genotypes for most samples were consistent with Hardy–Weinberg expectations. A total of 110 tests were made, of which eight deviated from expectations (Supplementary Table S1). Linkage disequilibrium between any pair of loci was not found.

The assessment of the statistical power based on the 11 microsatellite loci enabled the detection of F_{ST} values as low as 0.0005 in 90% (Chi2) or 84% (Fisher) of the cases for the simulated sampling of an effective population size of 1000 into 10 populations (Table 2). Thus, the possibility of a type 2 error was considered to be minor.

Genetic structure

The overall spatial genetic structure was weak, but statistically significant ($F_{ST} = 0.0005$, $p = 0.01$). However, pairwise F_{ST} was significant only before false discovery rate corrections for multiple tests (Table 3).

The additive approach for the assessment of barriers to gene flow resulted in two significant barriers (Figure 2). The first barrier occurred between the populations in Scotland (SC14) and Iceland (IS10) (Barrier a, $p = 0.04$). The second barrier occurred between populations in Scotland and the Norwegian Deep and Hardangerfjord (NO13, HA13) (Barrier b, $p = 0.02$). The MRM analysis showed a slightly significant ($p = 0.05$) relationship between genetic and geographical distance.

Assessing the hierarchical structure through AMOVA by defining groups based on the Barrier analysis showed a non-significant result ($F_{CT} = 0.0007$, $p = 0.07$). However, an alternative analysis of four, instead of three groups, with the Gullmarsfjord (GU14) sample as a separate group (otherwise as above) was significant ($F_{CT} = 0.0009$, $p = 0.02$). We found temporal stability in the Skagerrak and Kattegat area between two years of sampling ($F_{CT} = 0.00006$, $p = 0.51$).

Sex-biased dispersal

Evidence of sex-related genetic differences was found in the contrast between overall F_{ST}'s for males and females. We found significant differences ($F_{ST} = 0.001$, $p = 0.001$) between samples of males, but not for females ($F_{ST} = -0.010$, $p = 0.45$). The pairwise comparison between samples also showed that male samples were more differentiated than female samples (Table 3b and c). The mean assignment indices (*mAlc*) indicated a female-biased dispersal for both years within the Skagerrak and Kattegat area (Table 4). Values were negative for females in both comparisons, which indicate a lower assignment rate. However, the assignment variance (*vAlc*) was larger for females in 2014, but not in 2013 (Table 4), where *vAlc* is expected to be largest for the most dispersing sex. Global population F_{ST}, however, showed no clear difference between the sexes.

Discussion

Our study indicates no population genetic structure of *Nephrops* within a large region that included the Skagerrak, Kattegat, and Norwegian Deep ($F_{ST} = 0.0002$), whereas a shallow genetic structure was observed on a larger geographical scale when comparing with Scotland and Iceland ($F_{ST} = 0.0005$, $p = 0.01$). These results are supported by two significant barriers to gene flow located (1) between Scot-

Table 3. Pairwise comparison of the genetic difference among each pair of samples of *Nephrops norvegicus* measured as F_{ST} (above diagonal) and the exact test for genetic differentiation (*p*-values) below the diagonal for (a) combined for both sexes, (b) females, and (c) males.

(a)

	IS10	HA13	SC14	NR13	SK13	SKV14	SKS14	KA13	KA14	GU14
IS10	–	0.2956	**0.0190**	0.6086	0.1522	0.0748	0.3692	0.2523	0.3808	0.0946
HA13	0.0055	–	0.0444	0.3068	0.2840	0.1098	0.3818	0.1915	0.3214	0.3936
SC14	0.0022	0.0017	–	0.1194	**0.0228**	0.0636	0.2266	**0.0197**	0.2281	0.0967
NR13	−0.0001	0.0006	0.0013	–	0.1776	0.6698	0.6407	0.9406	0.7854	0.2046
SK13	0.0010	0.0006	0.0020	0.0010	–	0.3040	0.2179	0.0941	0.1740	0.1898
SKV14	0.0015	0.0012	0.0015	−0.0002	0.0005	–	0.8058	0.6759	0.6281	0.1138
SKS14	0.0003	0.0004	0.0007	−0.0002	0.0008	−0.0006	–	0.3612	0.8375	0.1298
KA13	0.0007	0.0009	0.0022	−0.0010	0.0013	−0.0003	0.0004	–	0.8736	0.1298
KA14	0.0004	0.0006	0.0008	−0.0005	0.0011	−0.0001	−0.0007	−0.0010	–	0.1054
GU14	0.0015	0.0004	0.0015	0.0011	0.0010	0.0013	0.0013	0.0013	0.0015	–

(b)

	HA13	SC14	NR13	SK13	SKV14	SKS14	KA13	KA14	GU14
HA13 ($n = 27$)	–	0.6012	0.6486	0.3849	0.4283	0.5311	0.5223	0.9591	0.2695
SC14 ($n = 44$)	−0.0003	–	0.5548	0.8070	0.6229	0.5763	0.2474	0.9750	0.4378
NR13 ($n = 31$)	−0.0005	0.0006	–	0.5919	0.6861	0.6567	0.7522	0.9422	0.7011
SK13 ($n = 17$)	0.0012	−0.0020	−0.0003	–	0.1733	0.3788	0.0714	0.7856	0.6828
SKV14 ($n = 37$)	0.0006	−0.0003	−0.0006	0.0033	–	0.5842	0.2761	0.9630	0.6163
SKS14 ($n = 4$)	−0.0002	−0.0003	−0.0015	0.0041	−0.0008	–	0.4152	0.8107	0.4122
KA13 ($n = 16$)	0.0000	0.0027	−0.0014	0.0076	0.0024	0.0040	–	0.8913	0.3226
KA14 ($n = 11$)	−0.0066	−0.0062	−0.0049	−0.0032	−0.0061	−0.0076	−0.0056	–	0.9751
GU14 ($n = 58$)	0.0015	0.0005	−0.0005	−0.0009	−0.0002	0.0038	0.0020	−0.0058	–

(c)

	HA13	SC14	NR13	SK13	SKV14	SKS14	KA13	KA14	GU14
HA13 ($n = 59$)	–	0.0729	0.2020	0.1444	0.1454	0.1761	0.0086	0.4054	0.1646
SC14 ($n = 45$)	0.0026	–	0.0540	**0.0018**	0.0629	**0.0177**	**0.0270**	**0.0398**	0.2578
NR13 ($n = 52$)	0.0016	0.0031	–	**0.0475**	0.7172	0.2401	0.4783	0.5722	0.2587
SK13 ($n = 73$)	0.0015	0.0051	0.0026	–	0.2672	0.1082	**0.0060**	**0.0330**	0.1151
SKV14 ($n = 61$)	0.0018	0.0026	−0.0005	0.0009	–	0.7628	0.3945	0.7713	0.1278
SKS14 ($n = 85$)	0.0012	0.0032	0.0011	0.0013	−0.0006	–	0.3060	0.6382	0.1485
KA13 ($n = 73$)	0.0037	0.0031	0.0003	0.0032	0.0005	0.0006	–	0.2359	0.0519
KA14 ($n = 66$)	0.0005	0.0029	0.0001	0.0024	−0.0006	−0.0002	0.0010	–	**0.0289**
GU14 ($n = 20$)	0.0034	0.0018	0.0023	0.0034	0.0037	0.0028	0.0048	0.0059	–

Significant values are indicated in bold. None of the *p*-values remained significant after correction for multiple tests by the false discovery rate approach.

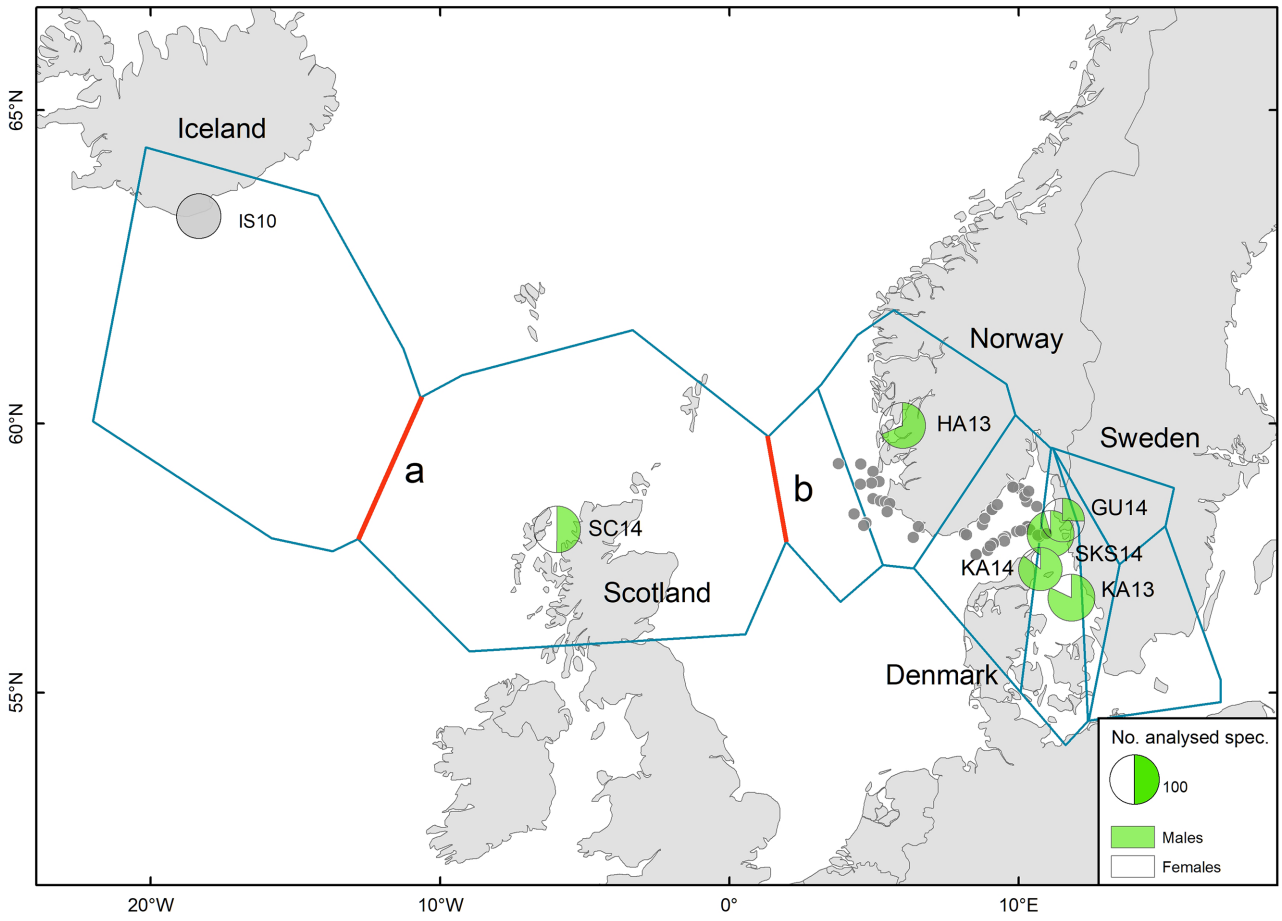

Figure 2. Results from the Barrier analysis overlaid the map of sampling localities of *Nephrops norvegicus*, where the rank of the barriers (red lines) to gene flow is indicated by letters (a being the strongest barrier). The size of the bubbles indicates sample size (size of bubble in legend corresponds to 100 specimens) and the colour coding indicates percentage of males in the samples. Sample names are given in Table 1.

Table 4. Results from sex-biased dispersal test in samples of *Nephrops norvegicus* as estimated by F_{ST} (Weir and Cockerham, 1984), the mean assignment indix (*mAlc*), and the assignment variance (*vAlc*).

	mAlc		*vAlc*		F_{ST}	
	Female	Male	Female	Male	Female	Male
KASK2013	−4.60	1.05	11.62	14.65	−0.006	0.001
KASK2014	−3.15	0.77	24.40	14.41	−0.007	0.001
Overall	−1.82	0.84	20.18	13.71	−0.010	0.001

KASK2013 and KASK2014 denote all samples from the Skagerrak and Kattegat area in 2013 and 2014, respectively.

land and Iceland, and (2) between Scotland and Scandinavia (Norway and the Skagerrak and Kattegat) (Figure 2). Finally, AMOVA indicated weak population structure within the Skagerrak and Kattegat that was strengthened by separating the Gullmarsfjord sample into another group. Temporal differences within the Skagerrak and Kattegat area were not found.

The results are consistent with earlier genetic studies from the North Sea and the Mediterranean (Stamatis *et al.*, 2004; Stamatis *et al.*, 2006; Pampoulie *et al.*, 2011; Gallagher *et al.*, 2019) showing weak, but significant genetic differentiation among *Nephrops* populations. A borderline significant isolation by distance pattern indicated that geographic distance between populations had only a slight influence on the genetic structure. As in our study, Pampoulie *et al.* (2011) found significant pairwise microsatellite-allele differences (F_{ST}) between Icelandic and Scottish populations that became non-significant after correction for multiple tests. Also similar to our results, Gallagher *et al.* (2019) did not detect significant differences between *Nephrops* in the northern part of the North Sea and the Skagerrak.

Larval drift can facilitate gene flow. The current system in the Skagerrak and Kattegat and the NCC may transport larvae as far as to the Hardangerfjord, since this fjord is subject to influx of water masses from the NCC (Asplin *et al.*, 2014). Thus, we suggest that *Nephrops* from the Skagerrak, Kattegat, Norwegian Deep, and Hardangerfjord constitute one large, panmictic population. Alternatively, the pattern can be due to large population size and too little time for the population to genetically diverge. A similar pattern was found by Knutsen *et al.* (2015) that suggested a common biological population of northern shrimp (*Pandalus borealis*) in the Skagerrak and Norwegian Deep, which supported the present management

regime where the whole area is regarded as a single unit (ICES, 2022b). The two species are both found in muddy habitats and are partially overlapping in distribution in the North Sea and the Skagerrak and Norwegian Deep region (ICES, 2021; Søvik and Thangstad, 2021), and the duration of the larval stage of northern shrimp is like that of *Nephrops* (45–60 days at 7°C–10°C; Shumway *et al.*, 1985).

Constraints, however, on the extent of larval drift are suggested by the presence of the large-scale surface gyre in the Skagerrak (Gustafsson and Stigebrandt, 1996) and may explain why most 1-year old juvenile northern shrimp are found here, compared to low abundances farther west (Søvik and Thangstad, 2021). Lack of genetic structure does not necessarily mean ecologically connected populations (Kritzer and Sale, 2004), but without knowledge on larval dynamics it is difficult to determine the demographic connectivity of the *Nephrops* populations in the Skagerrak and the Norwegian Deep. Discards have been minor in the Norwegian Deep for several years. As direct estimates of recruitment are lacking for *Nephrops* populations, discards of small specimens (2–3 years old; Farmer, 1975) are used as a proxy for recruitment, assuming that fishery effort and gear selectivity remain stable over years. Recruitment therefore might be less in the Norwegian Deep than in the Skagerrak (ICES, 2021). This suggests at least partly independent demographic units. Juvenile *Nephrops* are sedentary and rarely emerge from their burrows during the first year (Chapman, 1980), implying that larvae settling in the Skagerrak in general will remain there, reinforcing larval settlement patterns.

The Barrier analysis showed that the Scottish and Icelandic populations are weakly genetically different from the Skagerrak, Kattegat, and Norwegian Deep populations, whereas pairwise differences (F_{ST}) became non-significant after correction for multiple tests. This shows that the difference is weak and not detectable by all methods. As *Nephrops* in Scottish and Icelandic waters do not reside within the same oceanic current system as *Nephrops* in the Skagerrak, Kattegat, and Norwegian Deep region, they are not affected by these homogenizing forces. The cause for the shallow genetic structure may be found in a common glacial refugium for the species, which has been postulated by previous studies on *Nephrops* (Stamatis *et al.*, 2004; Stamatis *et al.*, 2006; Pampoulie *et al.*, 2011). During the last glacial maximum, conditions in the northern Atlantic may have been too cold for *Nephrops*, presently found at temperatures between 6°C and 17°C (Johnson *et al.*, 2013). A southern common glacial refugium may have harbored a panmictic population, and the warming of the ocean led to a population expansion from this common gene pool. The interpretation of the low level of genetic structuring observed both in our study as well as in the previous studies (Stamatis *et al.*, 2004; Stamatis *et al.*, 2006; Pampoulie *et al.*, 2011; Gallagher *et al.*, 2019) is that the heterogeneity among habitats along the expansion routes has not been sufficient for natural selection to create differences between localities.

Sex-biased dispersal

We found indications of female-biased dispersal in the Skagerrak and Kattegat area as the overall genetic differences were larger for males than for females. This was also supported by smaller mean assignment indices (*mAlc*) in females than in males (Table 4). The F_{ST} values, however, showed no clear difference between the sexes, which corresponds well to a scenario of high gene flow, in which individual-based assignment tests are expected to have greater power than summary statistics such as F_{ST}. Rather, they provide a qualitative and quantitative idea of the scale of dispersal because they do not average over samples (Cannas *et al.*, 2012).

Most of our current understanding of sex-biased dispersal comes from birds and mammals, where mammals are skewed towards male-biased dispersal (MBD) and birds show greater female-biased dispersal (FBD) (Prugnolle and de Meeus, 2002). Trochet *et al.* (2016) found that most publications referred to MBD. Tagging studies show that *Nephrops* is a territorial species with limited adult dispersal (Farmer, 1975; Aguzzi and Sarda, 2008; Merder *et al.*, 2020). Furthermore, berried females keep close to, or stay within their burrows (Chapman, 1980; Aguzzi and Sarda, 2008; Eiriksson, 2014), which might make them even more territorial than males. These observations contradict our findings, which indicate that females are the dispersing sex. A sex bias in discarding could be a potential factor in explaining our findings. As commercial catches are sorted when steaming between hauls this would cause some dispersal, and as females grow more slowly than males, they might form a larger part of the discards and therefore have wider dispersal.

It is worth noting that the biparental markers used here (microsatellites) convey information on short-term dispersal. Therefore, the sex-biased migration signal will disappear after one generation of random mating due to Mendelian segregation if the dispersal is no longer sex-biased (Goudet *et al.*, 2002; Prugnolle and de Meeus, 2002). However, a significant proportion of the migrants may disperse, but not reproduce in the new population. This would maintain allele-frequency differences between the populations and allow the detection of immigrants within every generation.

Relevance for management

Nephrops in the Skagerrak, Kattegat, and Norwegian Deep region is currently assessed and managed as two separate units (ICES, 2021). The two functional units in the Skagerrak (FU 3) and the Kattegat (FU 4) are presently assessed together, whereas the Norwegian Deep (FU 32) is assessed separately. Our results indicate one genetic population in the whole region, which may extend northward along the Norwegian coast, as larvae may drift with the NCC and settle outside the region. The lack of genetic structure within the Skagerrak and Kattegat area is in agreement with the current management regime of treating the two FUs as one biological stock. However, without knowledge of larval dynamics, it is difficult to determine whether one large, panmictic population in the region exists, or a biological (genetic) population consisting of at least two discrete subpopulations with their own internal dynamics, but with some demographic influence from the other(s). The temporal scale of exchange is a question relevant for management. If one subpopulation were to suffer a population decline (e.g. over-fished or poor local recruitment), it is important to consider how long it might take for sufficient larval import from another subpopulation to re-establish commercial quantities. On a larger geographical scale, (Gallagher *et al.*, 2019) similarly noted that current management practices in the Northeast Atlantic of several separate *Nephrops* FUs are not in line with their findings of no significant differentiation between sampled areas.

It seems advisable to continue the current practice of two separate management units in view of the differences between the Skagerrak–Kattegat stock and the Norwegian Deep stock

and the uncertainty related to the demographic connectivity of these stocks. Fishing pressure is important in this respect. As a data-poor stock, the assessment of the Norwegian Deep stock is based on the precautionary principle, whereas the data-rich Skagerrak–Kattegat stock is assessed according to the MSY approach (ICES, 2022a). A single area management unit would fail to recognize different rates of stock productivity or fleet dynamics and would increase the risk of overexploitation in one or the other area. For the North Sea, ICES consider the different FUs to be independent stocks with low larval interchange and therefore provide separate advice. In spite of this, management is being carried out for the North Sea as a whole. The fisheries in the majority of the FUs in the North Sea surpassed catch or landings recommendations in some years between 2010 and 2019 (Letschert *et al.*, 2021). Overexploitation has been taking place in FUs 9, 33, and 34 during the 2–3 most recent years, while hardly any fishing takes place in Noup (FU 10), west of the Orkney Islands (ICES, 2022a).

We see a need for our genetic study to be extended with larval drift modelling in the Skagerrak, Kattegat, and Norwegian Deep region to elucidate the degree of demographic connectivity between sub-stocks of *Nephrops* and thereby determine whether the species has a patchy distribution, a metapopulation structure, or a system of discrete, closed subpopulations (Kritzer and Sale, 2004). This knowledge gap pertains to *Nephrops* in the whole North Sea region as well. The use of only neutral genetic markers to resolve the genetic population structure has shown its limitations in species with large population sizes and high gene flow, as in this study. Therefore, including a larger panel of genetic markers subjected to natural selection (e.g. SNPs) might better resolve the genetic population structure in *Nephrops*, if present, as well as improving our understanding of the genetic structure of this species.

Acknowledgements

The authors would like to thank the following for collecting samples for this study: Sarah Helyar (Iceland), Rikke P. Frandsen (KA14, SKS14), Mats Ulmestrand (Gullmarsfjord, KA13), Adrian Weetman (Scotland), Tore Hartvik Kristensen (F/V 'Stauper'), and Merete Vik Ottesen (Hardangerfjord). We are grateful for the help of Silje Kristin Jensen and Neil Aldridge with the logistics of bringing the Scottish sample to Norway. Trude H. Thangstad kindly made the map in Figures 1 and 2. The manuscript was greatly improved by comments from three reviewers.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest statement

The authors have no conflicts of interest to declare.

Funding

The work was funded through Interreg IVA, Öresund–Kattegat–Skagerrak, European Regional Development Fund (https://interreg-oks.eu), project ØBJ-FISK—Economically sustainable growth in the *Nephrops* fishery in the KASK region (2012–2014), and by the Norwegian Ministry of Trade, Industry and Fisheries through the Norwegian Institute of Marine Research project 'Economically sustainable *Nephrops* fishery' in the research programme 'The North Sea'.

Data Availability statement

The data underlying this article are available on https://hdl.handle.net/11250/3036954.

Author contributions statement

JIW: conceptualization, methodology, analyses, visualization, and writing. GS: conceptualization, methodology, resources, and writing. TJ: conceptualization, methodology, and writing.

References

Aguzzi, J., and Sarda, F. 2008. A history of recent advancements on *Nephrops norvegicus* behavioral and physiological rhythms. Reviews in Fish Biology and Fisheries, 18: 235–248.

Albretsen, J., Aure, J., Saetre, R., and Danielssen, D. S. 2012. Climatic variability in the Skagerrak and coastal waters of Norway. ICES Journal of Marine Science, 69: 758–763.

Asplin, L., Johnsen, I. A., Sandvik, A. D., Albretsen, J., Sundfjord, V., Aure, J., and Boxaspen, K. K. 2014. Dispersion of salmon lice in the Hardangerfjord. Marine Biology Research, 10: 216–225.

Begg, G. A., Friedland, K. D., and Pearce, J. B. 1999. Stock identification and its role in stock assessment and fisheries management: an overview. Fisheries Research, 43: 1–8.

Cadrin, S. X., and Friedland, K. D. 1999. The utility of image processing techniques for morphometric analysis and stock identification. Fisheries Research, 43: 129–139.

Cannas, R., Sacco, F., Follesa, M. C., Sabatini, A., Arculeo, M., Lo Brutto, S., Maggio, T. *et al.* 2012. Genetic variability of the blue and red shrimp *Aristeus antennatus* in the Western Mediterranean Sea inferred by DNA microsatellite loci. Marine Ecology, 33: 350–363.

Chapman, C. J. 1980. Ecology of juvenile and adult *Nephrops*. In The biology and management of lobsters: Ecology and Management, 2, pp. 143–179. Ed. by J. Cobband and B. Phillips Academic Press, Inc, New York.

Eiriksson, H. 2014. Reproductive biology of female Norway Lobster, *Nephrops norvegicus* (Linnaeus, 1758) Leach, in Icelandic waters during the period 1960–2010: comparative overview of distribution areas in the Northeast Atlantic and the Mediterranean. Advances in Marine Biology, 68: 65–210.

Excoffier, L., and Lischer, H. E. L. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Molecular Ecology Resources, 10: 564–567.

Excoffier, L., Smouse, P. E., and Quattro, J. M. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics, 131: 479–491.

Farmer, A. S. D. 1975. Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). FAO Fisheries Synopsis No. 112: 108.

Fu, C. H., and Fanning, L. P. 2004. Spatial considerations in the management of Atlantic cod off Nova Scotia, North American Journal of Fisheries Management, 24: 775–784.

Gallagher, J., Finarelli, J. A., Jonasson, J. P., and Carlsson, J. 2019. Mitochondrial D-loop DNA analyses of Norway lobster (*Nephrops norvegicus*) reveals genetic isolation between Atlantic and East Mediterranean populations. Journal of the Marine Biological Association of the United Kingdom, 99: 933–940.

Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). http://www./unil. ch/izea/softwares/fstat (last accessed 19 November 2014).
Goudet, J., Perrin, N., and Waser, P. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. Molecular Ecology, 11: 1103–1114.
Gustafsson, B., and Stigebrandt, A. 1996. Dynamics of the freshwater-influenced surface layers in the Skagerrak. Journal of Sea Research, 35: 39–53.
Hauser, L., and Carvalho, G. R. 2008. Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. Fish and Fisheries, 9: 333–362.
Hill, A. E. 1990. Pelagic dispersal of Norway lobster *Nephrops norvegicus* larvae examined using an advection-diffusion-mortality model. Marine Ecology Progress Series, 64: 217–226.
ICES. 2021. Working group for the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports, 3:66. https://doi.org/10.17895/ices.pub.8211
ICES. 2022a. ICES Advice Publications. Collection. https://doi.org/10.17895/ices.pub.c.5796935.v82
ICES. 2022b. Joint NAFO\ICES *Pandalus* Assessment Working Group (NIPAG). ICES Scientific Reports. 4:38. 25 pp. https://doi.org/10.17895/ices.pub.19692181
Johnson, M. P., Lordan, C., and Power, A. M. 2013. The Ecology and Biology of *Nephrops norvegicus*. Advances in Marine Biology, 64: 27–63.
Jorde, P. E., Søvik, G., Westgaard, J.-I., Orr, D., Han, G., Stansbury, D., and Jørstad, K. E. 2014. Genetic population structure of northern shrimp, *Pandalus borealis*, in the Northwest Atlantic. Canadian Technical Report of Fisheries and Aquatic Sciences, 3046: iv + 27.
Knutsen, H., Jorde, P. E., Gonzalez, E. B., Eigaard, O. R., Pereyra, R. T., Sannaes, H., Dahl, M. *et al.* 2015. Does population genetic structure support present management regulations of the northern shrimp (*Pandalus borealis*) in Skagerrak and the North Sea? Ices Journal of Marine Science, 72: 863–871.
Kritzer, J. P., and Sale, P. F. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries, 5: 131–140.
Legendre, P., Lapointe, F. J., and Casgrain, P. 1994. Modeling brain evolution from behavior: a permutational regression approach. Evolution; Internation Journal of Organic Evolution 48: 1487–1499.
Letschert, J., Stollberg, N., Rambo, H., Kempf, A., Berkenhagen, J., and Stelzenmuller, V. 2008. The uncertain future of the Norway lobster fisheries in the North Sea calls for new management strategies. Canadian Journal of Fisheries and Aquatic Sciences, 65: 2253–2268.
Manni, F., Guerard, E., and Heyer, E. 2020. Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by using Monmonier's algorithm. Ambio, 49: 107–117.
Marta-Almeida, M., Dubert, J., Peliz, A., dos Santos, A., and Queiroga, H. 2008. A modelling study of Norway lobster (*Nephrops norvegicus*) larval dispersal in southern Portugal: predictions of larval wastage and self-recruitment in the Algarve stock. Canadian Journal of Fisheries and Aquatic Sciences, 65: 2253–2268.
Merder, J., Browne, P., Freund, J. A., Fullbrook, L., Graham, C., Johnson, M. P., Wieczorek, A. *et al.* 2020. Density-dependent growth in 'catch-and-wait' fisheries has implications for fisheries management and Marine Protected Areas. Ambio, 49: 107–117.
Monmonier, M. 1973. Maximum-difference barriers - an alternative numerical regionalization method. Geographical Analysis, 5: 245–261.
O'Sullivan, D., Lordan, C., Doyle, J., Berry, A., and Lyons, K. 2015. Metapopulation connectivity via larval transport of the Norway lobster *Nephrops norvegicus* in waters around Ireland: a modelled approach. Marine Ecology Progress Series, 534: 95–106.
Pampoulie, C., Skirnisdottir, S., Hauksdottir, S., Olafsson, K., Eiriksson, H., Chosson, V., Hreggvidsson, G. O. *et al.* 2011. A pilot genetic study reveals the absence of spatial genetic structure in Norway lobster (*Nephrops norvegicus*) on fishing grounds in Icelandic waters. Ices Journal of Marine Science, 68: 20–25.
Prugnolle, F., and de Meeus, T. 2002. Inferring sex-biased dispersal from population genetic tools: a review. Heredity, 88: 161–165.
Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W. J. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. Fish and Fisheries, 10.
Rousset, F. 2008. GENEPOP' 007: a complete re-implementation of the GENEPOP software for Windows and Linux. Molecular Ecology Resources, 8: 103–106.
Ryman, N., and Palm, S. 2006. POWSIM: a computer program for assessing statistical power when testing for genetic differentiation. Molecular Ecology Notes, 6: 600–602.
Saha, A., Hauser, L., Kent, M., Planque, B., Neat, F., Kirubakaran, T. G., Huse, I. *et al.* 2015. Seascape genetics of saithe (*Pollachius virens*) across the North Atlantic using single nucleotide polymorphisms. Ices Journal of Marine Science, 72: 2732–2741.
Shumway, S. E., Perkins, H. C., Schick, D. F., and Stickney, A. P. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Krøyer, 1838.
Skirnisdottir, S., Olafsson, K., Hauksdottir, S., Pampoulie, C., Hreggvidsson, G., Gunnarsson, G., and Hjorleifsdottir, S. 2010. Isolation and characterisation of eight new microsatellite loci in the Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758). Molecular Ecology Resources Database, http://tomato. bio. trinity. edu/manuscripts/10-4/mer-10-0048. pdf(accessed 26 October 2010).
Søvik, G., Furevik, D., Jørgensen, T., Bakke, S., Larssen, W., Thangstad, T., and Woll, A. 2016. The Norwegian *Nephrops* fishery—history, exploitation and management. In Sustainable bio-resources. Management, product development and raw material quality, pp.89–112. A.C. Gundersenand and B.J. Thu Orkana Akademisk, Stamsund.
Søvik, G., and Thangstad, T. H. 2021. Results of the Norwegian Bottom Trawl Survey for Northern Shrimp (*Pandalus borealis*) in Skagerrak and the Norwegian Deep (ICES Divisions 3.a and 4.a east) . 38 pp. https://doi.org/10.17895/ices.advice.19453658.
Stamatis, C., Triantafyllidis, A., Moutou, K. A., and Mamuris, Z. 2004. Mitochondrial DNA variation in northeast atlantic and mediterranean populations of Norway lobster, *Nephrops norvegicus*. Molecular Ecology, 13: 1377–1390.
Stamatis, C., Triantafyllidis, A., Moutou, K. A., and Mamuris, Z. 2006. Allozymic variation in Northeast Atlantic and Mediterranean populations of Norway lobster, *Nephrops norvegicus*. ICES Journal of Marine Science, 63: 875–882.
Streiff, R., Guillemaud, T., Alberto, F., Magalhaes, J., Castro, M., and Cancela, M. L. 2001. Isolation and characterization of microsatellite loci in the Norway lobster (*Nephrops norvegicus*). Molecular Ecology Notes, 1: 71–72.
Trochet, A., Courtois, E. A., Stevens, V. M., and Baguette, M. 2016. Evolution of sex-biased dispersal. The Quarterly Review of Biology, 91: 297–320.
Ungfors, A., Bell, E., Johnson, M. L., Cowing, D., Dobson, N. C., Bublitz, R., and Sandell, J. 2013. Advances in Marine Biology, 64. In: The Ecology and Biology of *Nephrops norvegicus*, 247–314. Ed. by M.L. Johnsonand and M.P. Johnson Elsevier Ltd., London.
van Oosterhout, C., Weetman, D., and Hutchinson, W. F. 2006. Estimation and adjustment of microsatellite null alleles in nonequilibrium populations. Molecular Ecology Notes, 6: 255–256.
Weir, B. S., and Cockerham, C. C. 1984. Estimating F-statistics for the analysis of population-structure. Evolution; Internation Journal of Organic Evolution, 38: 1358–1370.
Zimmermann, F., Kleiven, A. R., Ottesen, M. V., and Søvik, G. 2022. Inclusion of recreational fishing in data-limited stocks: a case study on Norway lobster (*Nephrops norvegicus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences, 79: 969–978.

Handling Editor: W. Stewart Grant