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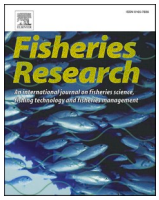

Population genomics reveals a single semi-continuous population of a commercially exploited marine gastropod

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ABSTRACT

Buccinum undatum is a commercially important marine gastropod with limited dispersal capabilities. Previous genetic studies utilising microsatellites and Double-digest Restriction-site Associated DNA sequencing (ddRAD-seq) provided evidence that *B. undatum* exhibits fine-scale genetic structure. Using ddRADseq, 128 individuals from the southern North Sea, English Channel, and the Irish Sea were genotyped using 7015 filtered single nucleotide polymorphisms (SNPs), 19 of which were identified as being under putative selection. Multiple genetic clustering methods – Discriminant analysis of principal components, Principal component analysis, and Sparse non-negative matrix factorisation,– were used to investigate population structure. Spatially explicit genetic structure was investigated using an Estimated Effective Migration Surface analysis and a Mantel correlogram. A single genetic population was found using neutral SNPs, with weak within-population structuring. Global F_{ST} was low (0.0046, $p < 0.001$), and pairwise F_{ST} estimates between sampling locations were between 0.0004 and 0.0224. There was a significant trend of isolation-by-distance across all sampling locations ($r = 0.743$, $p < 0.001$). Positive spatial autocorrelation indicated whelks located $\leq$ 50 km of one another were significantly more related than by chance ($r = 0.12$, $p = 0.003$), further emphasising the low dispersal capabilities of *B. undatum*. Finally, two barriers of lower-than-average dispersal were discovered; the Thames estuary and across the English Channel. Management implications are discussed for the sustainability of whelks from inshore fisheries.

1. Introduction

It is commonly assumed that the life-history strategy of marine organisms is strongly correlated with predicted genetic structure. Species with short or no pelagic larval stages typically exhibit more population structure than species that release gametes or young into the water column, which theoretically facilitates long-distance dispersal (Waples, 1987; Bohonak, 1999 and references within). However, recent studies suggest that genetic structuring in marine species does not always reflect this assumption (Kyle and Boulding, 2000; Sponer and Roy, 2002; Wilson et al., 2007; Hunter and Halanych, 2008), leading to growing calls for a species-by-species approach to investigating gene flow (Selkoe and Toonen, 2011, and references within). Genetic techniques have also refuted the concept that most marine species have panmictic populations due to the lack of obvious barriers to dispersal in the ocean (Hauser and Carvalho, 2008; Thornhill et al., 2008).

Buccinum undatum is the largest edible marine gastropod in the North Atlantic and represents a rapidly growing commercial fishery in the United Kingdom. The fishery nearly tripled in size between 2003 and 2016 when landings increased from 8.4 to 22.7 thousand tonnes (Blue Marine Foundation, 2018). In 2017, 20 800 tonnes of whelk were landed, which generated over £ 40 m in export value, 87 % of which are exported to South Korea (Sea Fish Industry Authority, 2019). *B. undatum* stocks are not regulated with quotas by the European Union, and are considered a displacement fishery as fishers move away from more tightly regulated stocks (McIntyre et al., 2015). In 1997, concerns were raised over unsustainable exploitation of *B. undatum*, especially in southeast England (Nicholson and Evans, 1997), and with recent and continued increases in landings and values from developing overseas markets, these concerns have led to increased scrutiny of stock

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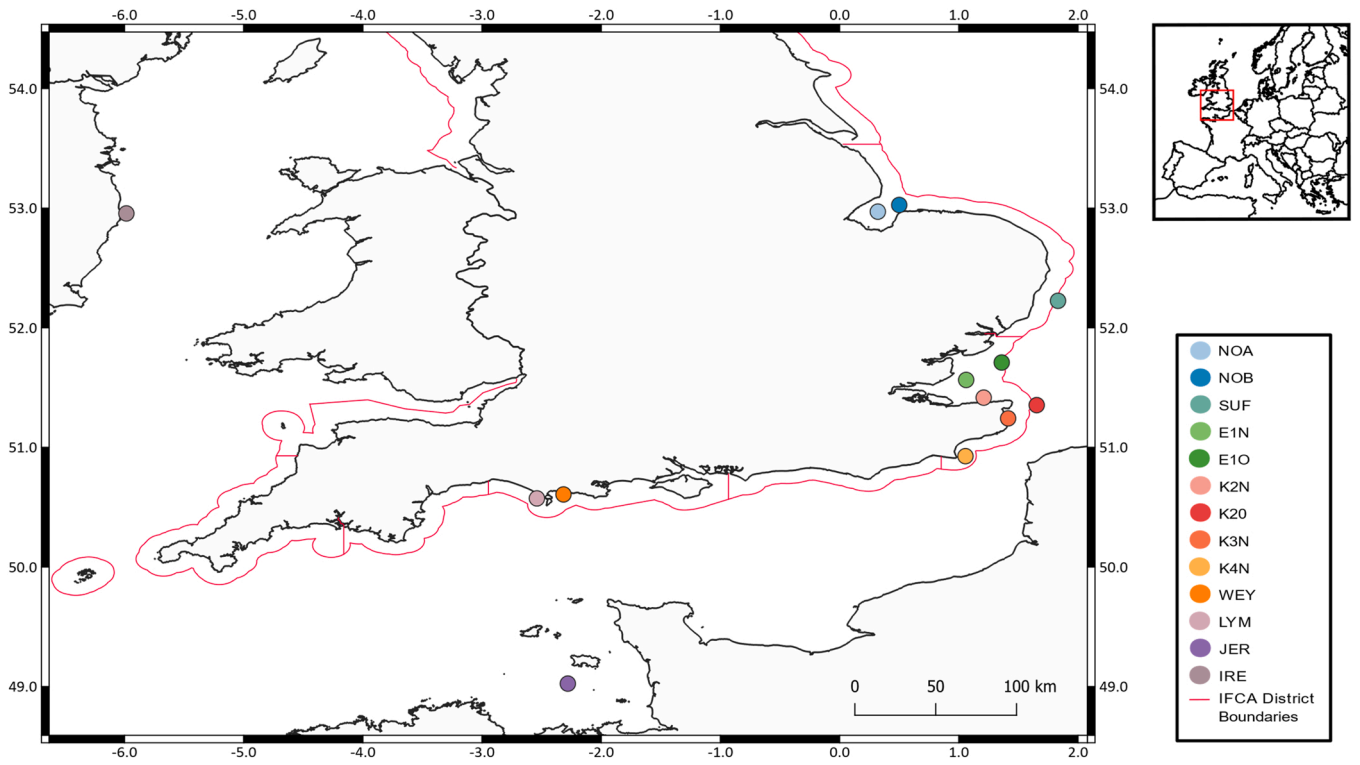

Fig. 1. Sampling locations of *Buccinum undatum*. NOA = Norfolk inside the bay. NOB = Norfolk outside the bay. E1O = KEIFCA outside zone 1. E1N = KEIFCA inside zone 1. K2N = KEIFCA inside zone 2. K2O = KEIFCA outside zone 2. K3N = KEIFCA inside zone 3. K4N = KEIFCA inside zone 4. WEY= Weymouth. LYM =Lyme Bay. JER = Jersey Island. IRE = Southeast of Ireland.

management (Blue Marine Foundation, 2018). Current whelk fisheries in England are managed by ten regional bodies of the Association of Inshore Fisheries and Conservation Authority (IFCA). Each regional IFCA regulates the whelks within six nautical miles by both technical and biological measures, but as stated, not with a quota. Technical measures include limits to baited pot numbers, escape mesh, and riddle sizes, e.g., Kent and Essex Inshore Fisheries and Conservation Authority (2013). Biological measures, include setting minimum landing sizes defined by region-specific size-at-maturation standards (Hollyman and Richardson, 2018). Differences in observed size-at-maturation, and growth rates, between geographical management areas have been observed (Haig et al., 2015; Borsetti et al., 2018), however the causal mechanisms underlying this phenomenon remain unknown, particularly when inshore habitats are structurally similar – emphasising the need for increased research into the relative role of environmental or genetic differentiation between regions.

Despite *B. undatum's* commercial importance, only three studies have investigated gene flow within the Northeast Atlantic using microsatellites (Weetman et al., 2006; Mariani et al., 2012; Pálsson et al., 2014). Those three studies used the five microsatellite markers discovered by Weetman et al. (2005). A geographically extensive investigation into the population structure of whelks was carried out by Weetman et al. (2006) that extended from the Bay of Biscay to Iceland, including the Swedish Skagerrak and Canada. Mariani et al. (2012) and Pálsson et al. (2014) also carried out regional studies on gene flow around Ireland and Iceland, respectively. More recently, Goodall et al. (2021) investigated genetic population structure using single nucleotide polymorphisms (SNPs) generated from Restriction site Associated DNA sequencing (RADseq) across the Northeast Atlantic and fine-scale gene flow within Iceland. All studies provided evidence that *B. undatum* exhibits fine-scale genetic structure over small spatial scales (tens of kilometres) and strong isolation-by-distance. It is hypothesised that the low genetic divergence is maintained by a stepping-stone model of dispersal that forms a semi-continuous population (Weetman et al., 2006; Mariani et al., 2012; Pálsson et al., 2014). The low dispersal potential – an inference based on *B. undatum*'s life-history strategy and low fecundity, where fertilisation is internal, and females deposit large egg masses on floating objects or hard substrates – is thought to contribute to the observed genetic structure (Kideys et al., 1993).

Reduced representation sequencing techniques have revolutionised population studies by providing a cheap and quick way to produce a high abundance of genetic markers from across the genome. A popular method is Restriction site-associated DNA sequencing (RADSeq) which does not require species-specific primers to be developed nor need a reference genome and instead uses restriction enzymes to cut across the whole genome to discover SNPs (Baird et al., 2008; Davey and Blaxter, 2010). Individual microsatellites provide more insight into population structure than a single SNP. Still, the hundreds to thousands of SNPs generated by RADseq provide more genomic resolution than the comparatively much smaller number of microsatellites commonly used in population genetic studies (Liu et al., 2005). SNPs have detected subtle population structure in benthic marine organisms, e.g., the American lobster (*Homarus americanus*, Benestan et al., 2015), the European lobster (*Homarus gammarus*, Jenkins et al., 2019), and the blacklip abalone *(Haliotis rubra*, Miller et al., 2016). Often RADSeq reveals previously masked population structure, e.g., the King Scallop (*Pecten maximus*, Vendrami et al., 2017) and the Northern Pike (*Esox lucius,* Sunde et al., 2020) due to the large increase in genomic resolution. Local adaption in the presence of high gene flow can reveal fine-scale population structuring, e.g., three-spined stickleback (*Gasterosteus aculeatus,* Guo et al., 2015), the Cape urchin *(Parechinus angulosus*, Nielsen et al., 2018), the Granular limpet (*Scutellastra granularis*, Nielsen et al., 2018), and European Hake (*Merluccius merluccius*, Milano et al., 2014).

Fisheries genomics combines genetic theory with fisheries management. It is not a new concept and has been used in fisheries biology for the last 50 years. However, fisheries genomics has rarely been applied to encompass a scale relevant to management units of smaller inshore

Table 1
Sampling information, coordinates, depth, and the number of individuals sequenced and retained. KEIFCA is the Kent and Essex Inshore Fisheries and Conservation Authority.

Location	County	Code	Longitude (D.DDD)	Latitude (D.DDD)	Depth (m)	Individuals sequenced	Individuals Retained
Norfolk Inside the wash	Norfolk	NOA	0.321	52.971	-4	15	15
Norfolk Outside the wash	Norfolk	NOB	0.501	53.026	-14	15	11
Suffolk	Suffolk	SUF	1.833	52.225	-26	15	10
KEIFCA Outside Zone 1	Essex	E1O	1.361	51.709	-13	15	6
KEIFCA Inside Zone 1	Essex	E1N	1.063	51.563	-7	15	9
KEIFCA Inside Zone 2	Kent	K2N	1.210	51.415	-3	15	12
KEIFCA Outside Zone 2	Kent	K2O	1.655	51.353	-28	14	10
KEIFCA Inside Zone 3	Kent	K3N	1.415	51.242	-10	15	11
KEIFCA Inside Zone 4	Kent	K4N	1.057	50.926	-32	15	13
Weymouth	Dorset	WEY	-2.317	50.606	-15	13	13
Lyme Bay	Dorset	LYM	-2.540	50.573	-21	15	5
Jersey Island	Jersey	JER	-2.280	49.024	-17	15	8
Southeast Ireland▲	Ireland	IRE	-5.985	52.956	-6	14	5

▲The exact coordinates and depth are unknown. These were obtained within ICES VIIa inside the Irish territorial sea. The given location is adjacent to the port where the whelks were landed, and depth was taken from that point.

fisheries and instead focuses more on national or large geographic range studies concerned with political boundaries to fishing instead of ecological concerns of the population. Many inshore fisheries are managed on sub-regional scales, most often determined by the terrestrial county or local government council boundaries.

Therefore, this study aimed to investigate the fine-scale population structure of *B. undatum* in the Southern North Sea across many management areas, including the English Channel and the Irish Sea, using SNPs generated from double digest RADSeq (ddRAD). We compare the results to previously published studies that employed microsatellites and SNPs and assess the results in light of the current spatial management structure for this species by the Association of Inshore Fisheries and Conservation Authority, UK.

2. Methods

A total of 195 individuals were collected from 13 sampling locations across the Southern North Sea, English Channel, and the Irish Sea between December 2018 and February 2019 (Fig. 1). The study was initially focused on the connectivity of whelks within the Kent and Essex Inshore Fisheries and Conservation Authority (KEIFCA) district before it was expanded to include whelks from other districts; leading to a high density of whelks within the KEIFCA area. Subsamples of tissue were taken from the foot and stored in either 100 % ethanol at − 20 °C or frozen at − 20 °C.

2.1. Double digest RAD library preparation and sequencing

Genomic DNA (gDNA) was extracted from 195 individuals using: (i) a modified CTAB and proteinase-K digest followed by phenol-chloroform purification and ethanol precipitation (Herrera et al., 2015) from frozen tissue or tissue stored in 100 % ethanol; or, (ii) using the Omega Biotek E.N.Z.A Mollusc extraction kit as per the manufacturer's instructions. A total of 191 gDNA samples were selected from both methods based on the level of high molecular weight gDNA to proceed to amplicon library preparation. The ddRADSeq libraries were constructed using 800 ng of gDNA from each individual and following the protocol of Peterson et al. (2012), using the restriction enzymes *ApeKI* and high fidelity *BamHI*. Each individual was dual indexed with a 5 bp forward and 6 bp reverse barcode. DNA fragments were size selected to target fragments between 360 and 440 bp using a Pippin Prep Marker L Cassette. The libraries were sequenced using four lanes of Illumina HiSeq X Ten (paired-end, 2 ×150 bp) by Beijing Genomics Institution with the addition of 10 % PHIX to each library. PHIX was added as previous sequencing runs from our collaborators found that its addition improved the overall read quality obtained. PHIX is a small viral genome that can help mitigate sequencing errors in unbalanced and low diversity libraries (Table 1).

2.2. De novo assembly and data filtering

Raw reads were processed using STACKS v 2.4 (Catchen et al., 2011, 2013). Reads were demultiplexed and quality filtered using the *process_radtags.pl* pipeline in STACKS. Any individual read with a Phred score below 33, ambiguous barcodes, or an unrecognised cut site were removed. Demultiplexed reads were assessed in FastQC (Andrews et al., 2015), and reads were truncated to 140 bp using TRIMMOMATIC (Bolger et al., 2014) due to the low Phred scores observed in the last 10 bases of the reads. All retained bases had a Phred score above 20.

De novo assembly was done using the *de_novo_map.pl*. The three main de novo parameters M, m, and n were tested using the *r80 method* (Paris et al., 2017). This sequentially tested the three main parameters, m, M, and n. While testing one of these parameters the other two were fixed e.g. when testing m, M, and n were fixed. m parameter is the minimum number of reads required to make a putative allele and is implemented in the *ustacks* component. M is the number of mismatches allowed between putative alleles to form a putative locus in *ustacks*. Finally, n is the number of mismatches allowed between putative loci during the construction of the catalogue in *cstacks*. After testing, the optimum parameters that maximised the number of *r80* polymorphic loci were m= 4, M= 3, and n = 3.

The *populations* script was run to filter loci present in 80 % of individuals (r = 0.8). Only individuals with coverage greater than 20x were used in the population script to ensure accurate genotyping. SNPs were filtered in PLINK v 1.9 (Purcell et al., 2007) to remove SNPs that were not called in 90 % of genotypes and remove individuals with greater than 10 % missing data. Alleles with minor frequencies of less than 1 % were removed. File conversions were either done directly in STACKS, PLINK, or using PGDSpider v. 2.1.1.5 (Lischer and Excoffier, 2012).

2.3. Genetic clustering

Multiple methodologies were employed to determine the number of genetic clusters (K) in the data. Sparse non-negative matrix factorization (sNMF) clustering was implemented in the R package *LEA* (Frichot and François, 2015) in R v 3.6 (R Core Team, 2019). sNMF is a least-squares approach where the most likely K is selected based on the lowest mean cross-entropy. Each value of K was run 10 times, and the lowest cross-entropy for each run (for each K) was extracted and plotted. The optimal K was determined as the value with the lowest cross-entropy.

Multivariate methods, Principle Component Analysis (PCA), and

Discriminant Analysis of Principal Components (DAPC) were carried out using the R package *adegenet* v 2.1.1 (Jombart, 2008; Jombart and Ahmed, 2011). These methods were used as they are free from assumptions of Hardy-Weinberg equilibrium and Linkage Disequilibrium. Optimum K was chosen using the lowest Bayesian Information Criteria (BIC) in the DAPC and visually in the PCA. DAPC was also run with sampling locations as defined prior groups with the optimal number of principal components for the analysis decided using the α-score method (Jombart et al., 2010) to investigate if there was any structure between sampling locations that could be visualised.

To explore genetic variation between sampling locations, pairwise F_{ST} (Weir and Cockerham, 1984), population-specific F_{IS} (Weir and Cockerham, 1984), expected (H_E) and observed heterozygosity (H_O), and an Analysis of Molecular Variance (AMOVA) were calculated in ARLEQUIN v 3.5 (Excoffier and Lischer, 2010). Global F_{ST}, F_{IT}, and F_{IS} were determined via AMOVA with 999 permutations to test for significance. Pairwise F_{ST} matrices were used to construct a neighbour-joining tree in the R package *ape* (Paradis et al., 2004).

2.4. Detection of loci under putative selection

Loci under putative selection were detected using a genome-scan method implemented using BayeScan v 2.1 (Foll and Gaggiotti, 2008), employing a Bayesian approach to estimate the posterior probability of selection acting on each locus using a reversible-jump Monte Carlo Markov Chain process. BayeScan allows F_{ST} coefficients to differ between populations, accommodating the different demographic histories that may be present. A False Discovery Rate (FDR, Storey, 2003) of 0.1 was used. An FDR is the number of expected false positive hypotheses that are expected when conducting multiple hypothesis testing. Prior odds of 100 were used in BayeScan, implying that the neutral model for each locus was 100 times more likely than the selective model. Twenty pilot runs were run with 10,000 iterations each, followed by a burn-in of 50,000 followed by another 50,000 iterations.

2.5. Spatial analysis of genetic variation

Isolation-by-distance (IBD) tests were carried out in ARLEQUIN v 3.5 using a linearized F_{ST} (F_{ST}/ 1-F_{ST}) matrix with the shortest distance by sea (km) matrix created using the R package *marmap* (Pante and Simon-Bouhet, 2013). A Mantel test (Mantel and Valand, 1970) was used to test for a significant correlation between the matrices with 1000 permutations.

Spatial autocorrelation was tested using a Mantel correlogram created and visualised in the R package *ecodist* (Goslee and Urban, 2007). A Mantel correlogram is used to test for the correlation between two matrices by defined size classes. This analysis is often used as a supplementary test to the standard Mantel test to delineate further the structure underpinning any observed trend seen in the Mantel test. Since there was no a priori assumption of step size for *B. undatum*, multiple-step sizes (distance classes) were examined; 5 km, 10 km, 20 km, and 50 km.

Spatial variation in gene flow was investigated using Estimated Effective Migrations Surfaces (EEMS) analysis using 128 individuals, two million MCMC iterations, a burn-in of one million iterations, and a thinning iteration of 9999 for each run (Petkova et al., 2016). Three runs of 300, 400, 500, 600, 700, 800, 900, and 1000 demes were carried out and an average of all runs was plotted using *rEEMSplots* as recommended by Petkova et al. (2016). This method assumes IBD as the null model and reveals geographic deviations from the null. This method reveals possible corridors (high effective migration; represented in blue) or barriers (low effective migration; represented in red). The habitat map required by EEMS was created by broadly following the SE coast of England around to SW Ireland using QGIS Desktop 3.10.4. The individual genetic dissimilarity matrix was created using the *bed2diffs* function of EEMS.

Table 2
The number of individuals and SNPs retained at each of the processing and filtering stages.

Step	Individuals remaining	SNPs
Stacks		
Process RADtags	191	N/A
De novo assembly (m4M3n3)	191	N/A
Populations (*r80 method*) – removed individuals with < 20x coverage	150	34290
Quality Filtering (PLINK)		
Loci missing in > 10 % of genotypes	150	12817
Genotypes missing > 10 % of loci	128	10400
Minor allele frequency > 1 %	128	7015
Total	128	7015
Putatively Neutral SNPs	128	6996
Putatively Outlier SNPs	128	19

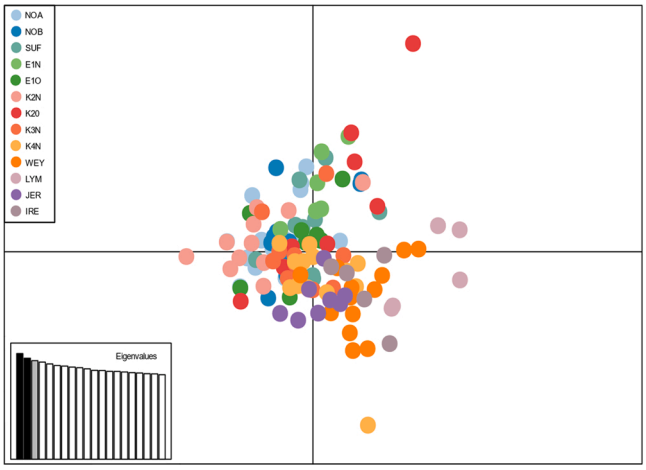

Fig. 2. Principal component analysis of all individuals using the neutral dataset of 6996 SNPs. NOA = Norfolk inside the bay. NOB = Norfolk outside the bay. E1O = KEIFCA outside zone 1. E1N = KEIFCA inside zone 1. K2N = KEIFCA inside zone 2. K2O = KEIFCA outside zone 2. K3N = KEIFCA inside zone 3. K4N = KEIFCA inside zone 4. WEY= Weymouth. LYM =Lyme Bay. JER = Jersey Island. IRE = Southeast of Ireland.

3. Results

In total, 1 427 813 991 paired-end reads were generated across 191 samples. 4.19 % had no barcode, 0.08 % were removed due to low quality, and 4.4 % had no RAD cut site. 1 303 931 081 high-quality paired-end reads and 7015 polymorphic SNPs from 128 individuals remained after the filtering process (Table 2). Coverage varied from 20.6x to 116.5x (mean = 69.3x, S.D. = 25x). Outlier analysis identified 19 SNPs (0.27 % of retained SNPs) as being under putative positive selection.

To gain further insight into the role of neutral and putative selective forces in structuring populations, the data was split into two. The first was the 6996 SNPs, the full dataset minus the SNPs identified as being under putative selection, hereafter referred to as the neutral dataset, and (ii) the 19 SNPs identified as being under putative selection by BayeScan, hereafter referred to as the outlier dataset. The results of the outlier analysis are presented in the Supplementary material. We present the results of Pairwise F_{ST} comparisons, location-specific H_E, H_O, and F_{IS}, and DAPC and sNMF clustering using the outlier dataset in the Supplementary material A. However, the results of the analyses should be interpreted with caution due to the low genomic resolution. All analyses presented in text hereafter are derived from the neutral dataset.

Table 3
Below the diagonal: pairwise F_{ST} estimates between sampling locations derived from the neutral data. Values in bold refer to comparisons that are significant after Bonferroni correction. Above the diagonal: p values. NOA = Norfolk inside the bay. NOB = Norfolk outside the bay. E1O = KEIFCA outside zone 1. E1N = KEIFCA inside zone 1. K2N = KEIFCA inside zone 2. K2O = KEIFCA outside zone 2. K3N = KEIFCA inside zone 3. K4N = KEIFCA inside zone 4. WEY= Weymouth. LYM =Lyme Bay. JER = Jersey Island. IRE = Southeast of Ireland.

	NOA	NOB	SUF	E1O	E1N	K2N	K2O	K3N	K4N	WEY	LYM	JER	IRE
NOA	–	0.3643	0.0215	0.1084	0.0039	0.0244	0.0147	0.0273	0.0176	< 0.0001	< 0.0001	< 0.0001	< 0.0001
NOB	0.0023	–	0.8086	0.0449	0.2432	0.0068	0.5869	0.2900	0.0898	< 0.0001	< 0.0001	0.0010	0.0010
SUF	0.0051	0.0012	–	0.4736	0.4463	0.0391	0.8682	0.2012	0.6240	0.0254	0.0010	0.0010	< 0.0001
E1O	0.0058	0.0088	0.0042	–	0.3613	0.1406	0.4141	0.3125	0.1152	0.0029	0.0078	0.0010	0.0049
E1N	0.0062	0.0037	0.0026	0.0036	–	0.2285	0.1367	0.1904	0.1426	0.0137	0.0029	< 0.0001	< 0.0001
K2N	0.0046	0.0071	0.0060	0.0061	0.0037	–	0.0137	0.1807	0.0039	< 0.0001	< 0.0001	< 0.0001	< 0.0001
K2O	0.0057	0.0019	0.0005	0.0034	0.0039	0.0068	–	0.6426	0.8047	0.1826	0.0039	0.0420	0.0029
K3N	0.0045	0.0031	0.0038	0.0038	0.0035	0.0036	0.0011	–	0.8779	0.0420	< 0.0001	0.0039	< 0.0001
K4N	0.0046	0.0046	0.0023	0.0065	0.0039	0.0066	0.0011	0.0004	–	0.8828	0.0039	0.0010	< 0.0001
WEY	**0.0118**	**0.0075**	0.0062	0.0102	0.0059	**0.009**	0.0039	0.0048	0.0009	–	0.0215	0.0010	0.0117
LYM	**0.0217**	**0.0192**	0.0124	0.0134	0.0126	**0.0232**	0.0124	**0.0177**	0.0120	0.0091	–	0.0049	0.0137
JER	**0.0143**	0.0101	0.0115	0.0145	**0.0120**	**0.0144**	0.0074	0.0092	0.0094	0.0085	0.0159	–	< 0.0001
IRE	**0.0153**	0.0158	**0.0156**	0.0214	**0.0167**	**0.0236**	0.0170	**0.0168**	**0.0126**	0.0113	0.0224	**0.0224**	–

Table 4
Sampling site-specific H_O, H_E, F_{IS}, Pi, and the number of polymorphic SNPs for the neutral data. SD is one standard deviation. Values in bold are significant at $\alpha = 0.05$. NOA = Norfolk inside the bay. NOB = Norfolk outside the bay. E1O = KEIFCA outside zone 1. E1N = KEIFCA inside zone 1. K2N = KEIFCA inside zone 2. K2O = KEIFCA outside zone 2. K3N = KEIFCA inside zone 3. K4N = KEIFCA inside zone 4. WEY= Weymouth. LYM =Lyme Bay. JER = Jersey Island. IRE = Southeast of Ireland.

Sampling site	H_O (± SD)	H_E (± SD)	F_{IS}	Nucleotide diversity (± SD)	Polymorphic SNPs
NOA	0.1878 ± 0.1491	0.2024 ± 0.1409	0.0397	0.1301 ± 0.0635	4836
NOB	0.2082 ± 0.1564	0.2296 ± 0.1396	0.0551	0.1273 ± 0.0630	4250
SUF	0.2152 ± 0.1560	0.2350 ± 0.1386	0.0597	0.1325 ± 0.0660	4190
E1O	0.2789 ± 0.1770	0.3014 ± 0.1339	0.0500	0.1317 ± 0.0682	3262
E1N	0.2304 ± 0.1609	0.2450 ± 0.1360	0.0284	0.1293 ± 0.0648	3964
K2N	0.2031 ± 0.1545	0.2252 ± 0.1424	**0.0583**	0.1261 ± 0.0622	4307
K2O	0.2176 ± 0.1546	0.2378 ± 0.1408	0.0386	0.1260 ± 0.0627	4116
K3N	0.2114 ± 0.1568	0.2292 ± 0.1418	0.0359	0.1255 ± 0.0621	4204
K4N	0.1926 ± 0.1466	0.2118 ± 0.1391	**0.0599**	0.1298 ± 0.0638	4615
WEY	0.1939 ± 0.1493	0.2116 ± 0.1393	0.0566	0.1314 ± 0.0646	4629
LYM	0.2973 ± 0.1780	0.3209 ± 0.1291	0.0497	0.1321 ± 0.0699	3076
JER	0.2337 ± 0.1610	0.2618 ± 0.1378	**0.0770**	0.1276 ± 0.0644	3698
IRE	0.3000 ± 0.1906	0.3298 ± 0.1318	0.0591	0.1252 ± 0.0662	2907

3.1. Genetic structure

Population clustering methods did not identify multiple genetic clusters (sMNF Figure B.1 A, and DAPC Figure B.1B). All individuals are grouped within a single cluster, with individuals across all sampling locations having considerable overlap in the PCA plot (Fig. 2).

Overall, Global F_{ST} was 0.0046 and significant ($p < 0.001$), indicating that individuals are not panmictic across the sampled range. F_{IS} (0.0508, $p < 0.001$; variation held within individuals within populations) and F_{it} (0.0552, $p < 0.001$) variation held within/among individuals) accounted for 5.06 % and 94.48 % of all observed genetic variation, consistent with a lack of major geographic genetic structure (Table B.1). Pairwise F_{ST} was low across the range (0.0004 – 0.0224, Table 3), with 17 out of 78 pairwise comparisons significant after Bonferroni correction. Location-specific F_{IS} ranged from 0.02841 to 0.077.

Location-specific H_O and H_E varied between 0.188 and 0.298 and 0.203–0.328, respectively. Location-specific F_{IS} ranged from 0.02841 to 0.077. Information on location-specific H_E, H_O, F_{IS}, nucleotide diversity, and polymorphic loci can be found in (Table 4).

Pairwise F_{ST} comparisons (Table 3) indicate weak, but evident within-population structure hereafter referred to as population substructure. This weak substructure broadly separates locations into four groups: Southern North Sea, English Channel, Jersey Island, and Ireland. These results are further seen in the unrooted neighbour-joining tree (Fig. 3 A), and within the DAPC analysis where sampling locations were used as predefined groups (Fig. 3B and C). Within the Southern North Sea, only K2N is significantly different from K4N. Both of these locations have low but significant F_{IS} values, 0.0583 and 0.0599, respectively.

3.2. Spatially explicit population substructure

There was a significant trend of IBD across all sampling sites ($r = 0.743$, $p < 0.001$; Fig. 4A). Further interrogation of this trend through a Mantel correlogram revealed a strong spatial autocorrelation; using a step size of 10 km, whelks up to 50 km were more likely to be more genetically similar than by chance ($r = 0.12$, $p = 0.003$; Fig. 4B). After this distance, whelks are no more related than at random. Regardless of the step size used, there were no autocorrelations at distances larger than 50 km.

The EEMS analysis revealed deviations from the null IBD model as a divergent scale between lower-than-average gene flow (red) to higher-than-average gene flow (blue; Fig. 5). EEMS revealed two clusters where there was lower than average gene flow; The Thames estuary and across the English Channel between JER and the Southern English coast. The Thames cluster included samples from Essex (E1O, E1N) and Kent (K2N, K2O, K3N), and the English Channel cluster included LYM, WEY, and JER.

4. Discussion

This study was the first study to genotype *B. undatum* using SNPs generated from ddRAD at a relevant spatial scale for management uses in the Southern North Sea, English Chanel, and South East Ireland. This

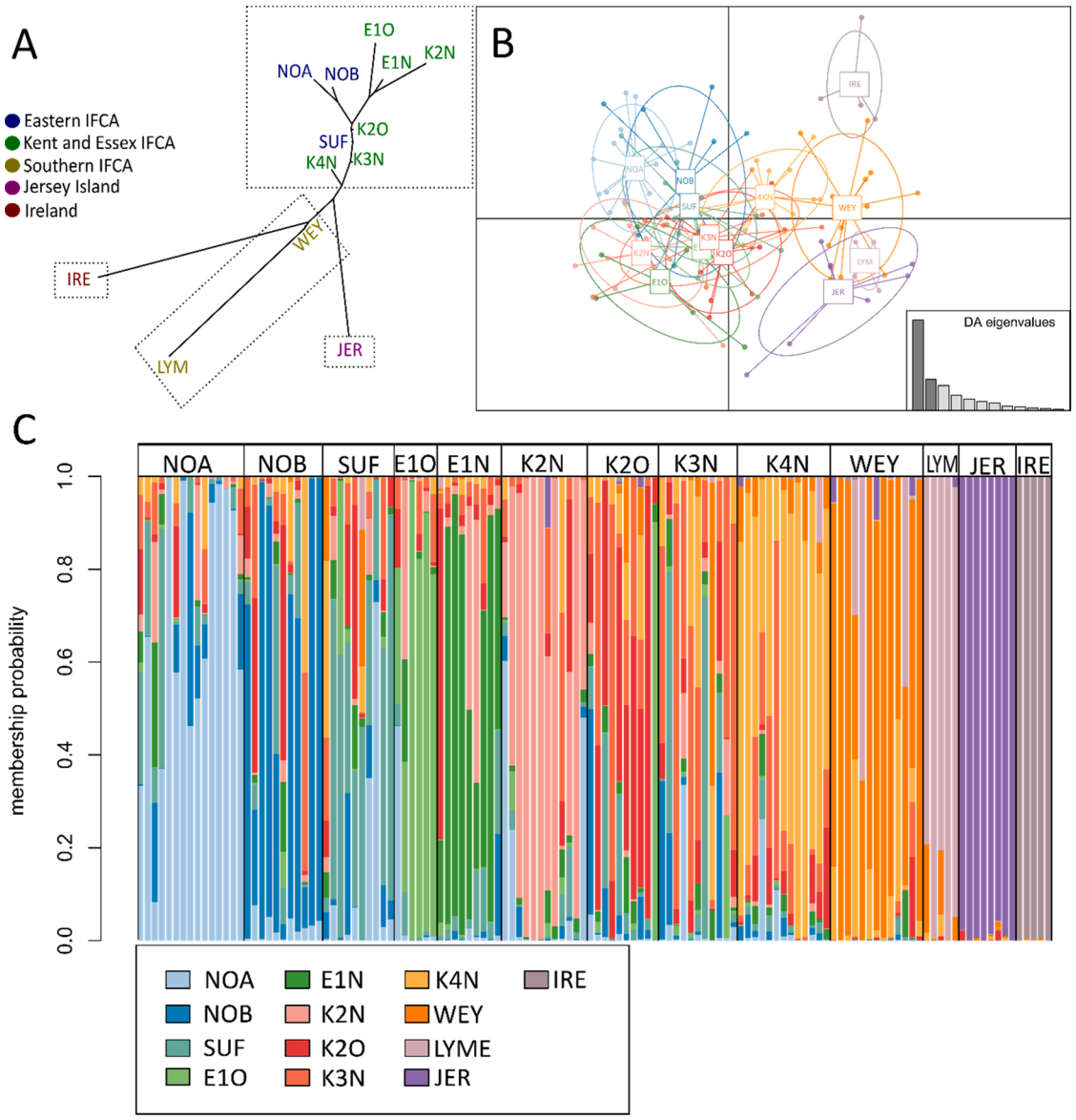

Fig. 3. A) Neighbour-joining clustering method based on pairwise F_{ST} comparisons. Dashed lines represent the four identified groupings. Text colour represents the local management body. B) DAPC analysis using sampling locations as prior defined groups. C) Membership probability of each individual to the pre-defined groups. Each column represents one individual. IFCA = Inshore Fisheries and Conservation Authority. NOA = Norfolk inside the bay. NOB = Norfolk outside the bay. E1O = KEIFCA outside zone 1. E1N = KEIFCA inside zone 1. K2N = KEIFCA inside zone 2. K2O = KEIFCA outside zone 2. K3N = KEIFCA inside zone 3. K4N = KEIFCA inside zone 4. WEY= Weymouth. LYM =Lyme Bay. JER = Jersey Island. IRE = Southeast of Ireland.

study genotyped 128 individuals using 7015 robust SNPs (6996 were putatively neutral, and 19 were identified to be under putative selection). Using the neutral SNPs, multiple clustering methods, sNMF, DAPC, and PCA revealed a single population of *B. undatum* across the 1165 km sampling range, and pairwise F_{ST} comparisons showed that there is significant within-population structure present.

4.1. Genetic substructure of Buccinum undatum

This current study represents a much higher genomic resolution and finer spatial scale analyses of population structure than previous studies of *B. undatum* utilising microsatellites (Weetman et al., 2006; Mariani et al., 2012; Pálsson et al., 2014). Comparisons with those studies that used microsatellites are not recommended as F_{ST} values derived from microsatellites are generally higher than those produced from SNPs (Fischer et al., 2017). Indeed, previous studies reported much higher Global F_{ST} due to the difference in Irish (F_{ST} = 0.019, Mariani et al., 2012) andEnglish (F_{ST} = 0.014, Weetman et al., 2006) based regional studies. Our Global F_{ST} in this study (0.0046) is similar to F_{ST} values reported within the single population of whelks from Iceland (F_{ST} = 0.003 – 0.068, Goodall et al., 2021) that used SNPs.

This study found evidence to indicate the presence of a single population across the sampling area. Due to the direct development life history strategy of *B. undatum*, the lack of multiple distinct populations over the sampling area was unexpected. Our result of a single population was concordant among the three different clustering methods used in this study. Within the population, there are significant intrapopulation barriers to gene flow, such as distance ($r = 0.743$, $p < 0.001$).

It is well documented that isolation-by-distance is characteristic of *B. undatum* (Weetman et al., 2006; Mariani et al., 2012; Pálsson et al., 2014; Goodall et al., 2021, this study). Previous studies have used Mantel tests to examine the correlation between geographic and genetic distance; this study further scrutinised the observed spatial genetic variation with an EEMS analysis and a mantel correlogram. The EEMS

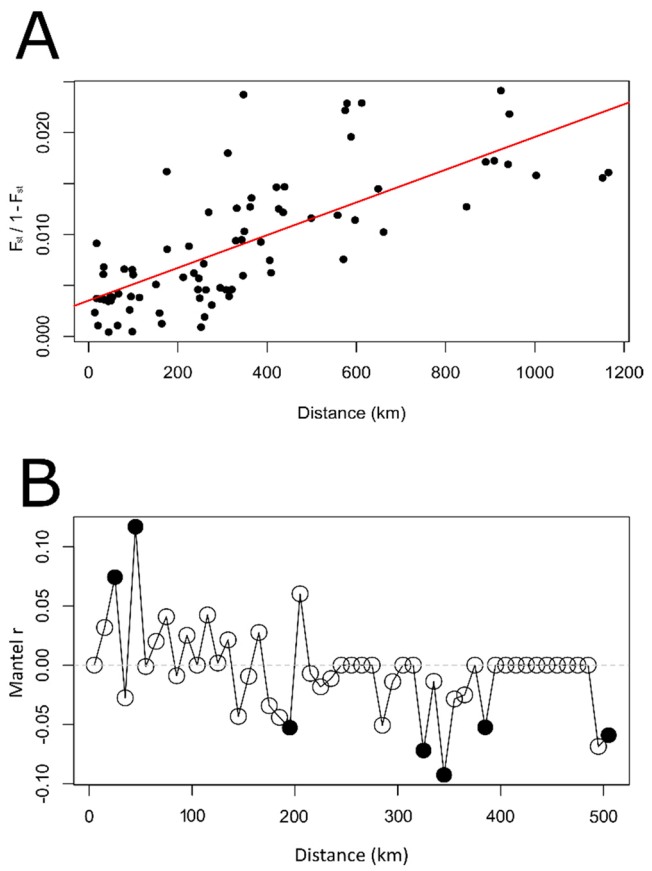

Fig. 4. (A) A scatterplot of the Mantel correlation test between linearized F_{ST} (genetic distance) and geographic distance to test for isolation by distance ($r = 0.732$ $p < 0.001$). (B) Mantel correlogram visualising the relationships between genetic and geographic distance within each 10 km size class. Each circle represents a 10 km size class with the black circle representing significant correlations. Whelks are more related within 50 km of each other than by chance alone ($r = 0.12$, $p = 0.003$).

analysis identified two distinct barriers where gene flow was lower than average. There was reduced gene flow across the English Channel in the southern barrier, from LYM and WEY to JER. Cold and fast-moving Atlantic water enters the English Channel from the east, which could create a barrier between the south coast of England and the Channel Islands, and France (Salomon and Breton, 1993). This large water mass may also promote a continuous network along the southern English coast east until it reaches the influence of the tidal Thames estuary (which was the second lower than average gene flow barrier identified). The Thames is a very shallow warm muddy estuary, fished heavily for common whelks by several neighbouring ports, and there is a legacy of historical and recent pollution. One or all of these factors may contribute to the estuary acting as a local barrier to dispersal. However, this would need to be validated with further sampling across these barriers. Using a step size of 10 km, the mantel correlogram revealed whelks up to 50 km were more likely to be more genetically similar than by chance alone ($r = 0.12$, $p = 0.003$). Thus, there is evidence that gene flow is variable over the sampling range where large distances may restrict breeding between individuals. However, only one genetic cluster is present in our data and so genetic continuity at distances greater than 50 km may be maintained by a stepping-stone model. *Buccinum undatum* eggs can be laid on macroalgae which may become detached due to grazing or storm damage. This can lead to a phenomenon known as egg rafting where individuals are transported large distances beyond their normal dispersal range (Kyle and Boulding, 2000; Marko, 2004). It is not known how common this phenomenon is or the survival rates of rafted juveniles.

Spatially explicit population analysis has revealed fine-scale population structuring in terrestrial species where clustering analysis determined only one population was present (Richmond et al., 2017; Rick et al., 2017; Combs et al., 2018; Carlen and Munshi-South, 2020). This method has been applied to marine species of conservation concern (Antoniou et al., 2017; O'Connell et al., 2019) where barriers to dispersal are not immediately obvious. This study is the first to show its usefulness as a tool for fisheries management.

4.2. Management implications and recommendations

With increased landings – growing 63 % since 2003 (8.4–22.7 thousand tonnes in 2017; Blue Marine Foundation, 2018), determining what is required to achieve the sustainable exploitation of *B. undatum* by England's IFCAs is a priority. The IFCAs responsible for monitoring coastal fisheries were created as part of the Marine and Coastal Access Act 2009 (U.K. Parliament, 2009) to monitor the exploitation of coastal stocks.

Pairwise F_{ST} comparisons revealed weak population substructure, which broadly corresponds to four groups outlined in the neighbour-joining tree and DAPC: Southern North Sea, English Channel, Jersey Island, and South East Ireland. Presently, these whelks are managed under their respective IFCAs; Southern IFCA (LYM, WEY), Kent and Essex IFCA (E1O, E1N, K2N, K2O, K3N, K4N), and the Eastern IFCA (NOA, NOB, SUF). The Jersey Island whelks are managed by local governmental bodies, and the stock in Ireland is unmanaged; however, port sampling is conducted by the Marine Institute of Ireland. While accepting that more samples at a higher spatial resolution in the Channel from both UK and mainland Europe ports are required, the lower-than-average gene flow clusters identified by EEMS indicate that there should be collaboration between IFCAs in managing what might be a semi-continuous whelk population. This is certainly the case west of the Thames through the Channel and north from the Thames into the southern North Sea. Our results have also identified the greater Thames estuary as a potential barrier to gene flow, requiring further scrutiny. Limited dispersal and the stepping-stone model of connectivity means that care must be taken not to overfish large portions of this network of whelks to ensure population resilience. This study demonstrates the application of population genomics to further inform relevant management bodies, in this case, the IFCAs, about the long-term sustainable exploitation of fisheries.

Whelks have a low dispersal potential, and so we propose management units that reflect this. Currently, KEIFCA operates whelk management across four zones within their local government areas. Other IFCA also have sub-management units, and these smaller-scale units may be appropriate for management – but the semi-continuous nature of whelk populations across the Channel or in the Southern North Sea must be acknowledged. If research is suggesting different life-history strategies for whelks in different areas – e.g., variation in local size at maturation (Hollyman and Richardson, 2018) – it must be asked why that is given the very weak population substructure and suggestion from our results that this is largely a single population without much genetic differentiation. A greater understanding of how and why developmental growth rates differ between sites is now required – e.g., founder effects, habitat quality, or harvest mortality effects.

5. Conclusions

In summary, this study successfully genotyped *B. undatum* using 7015 robust filtered SNPs. Multiple clustering methods found evidence for a single genetic population over the sampled 1165 km. However, there was strong evidence that this population was not panmictic. Global F_{ST} was very low (0.0046) yet significant. There was a large correlation between genetic distance and geographic distance. Further spatial autocorrelation analyses revealed whelks located within 50 km of each

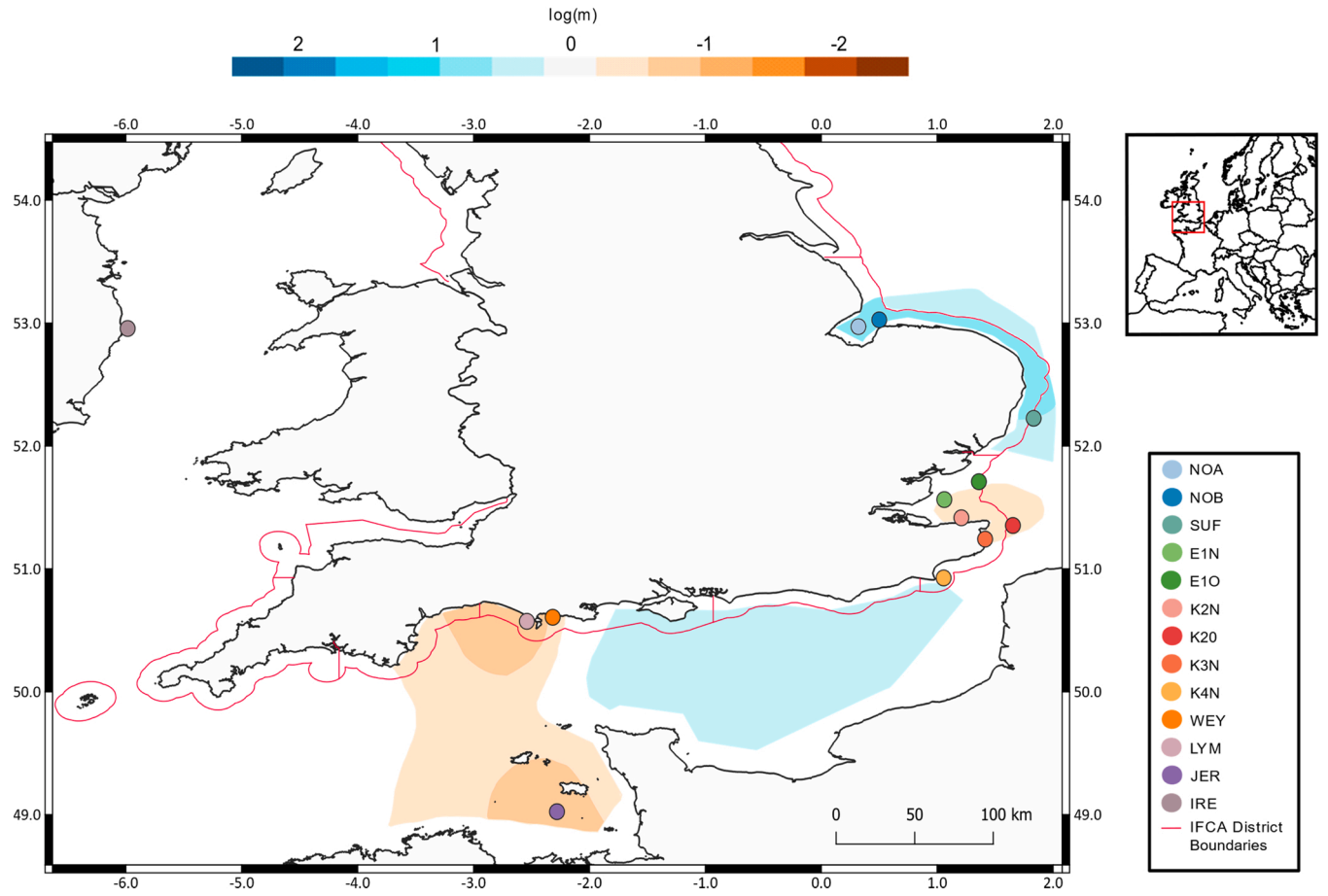

Fig. 5. Estimated Effective Migration Surfaces (EEMS) analysis. EEMS assumes isolation by distance as the null model and reports deviations from the null as lower-than-average (red) and higher-than-average (blue) geneflow. NOA = Norfolk inside the bay. NOB = Norfolk outside the bay. E1O = KEIFCA outside zone 1. E1N = KEIFCA inside zone 1. K2N = KEIFCA inside zone 2. K2O = KEIFCA outside zone 2. K3N = KEIFCA inside zone 3. K4N = KEIFCA inside zone 4. WEY= Weymouth. LYM =Lyme Bay. JER = Jersey Island. IRE = Southeast of Ireland.

other are more related than by chance. These results indicate a species with a low dispersal potential and that the genetic coherence of the semi-continuous population is maintained by stepping-stone dispersal of a very large population over time. An EEMS analysis showed two corridors of reduced gene flow. The first crossed the English Channel, where cold, fast-moving water may provide an oceanographic barrier. The other barrier was found at the Thames estuary, where pollution, overfishing, and the oceanographic and bathymetric setting may have reduced gene flow.

This study was the first to apply population genomic techniques to inform inshore fisheries of *B. undatum* at a relevant management scale and demonstrates the feasibility of using population genomics to aid in stock management where there is an absence of existing regulations controlling landings.

CRediT authorship contribution statement

Declan Morrissey: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Jake Goodall:** Methodology, Resources, Writing – original draft, Writing – review & editing, Supervision. **Rita Castilho:** Methodology, Writing – original draft, Writing – review & editing, Supervision. **Tom C. Cameron:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition. **Michelle L. Taylor:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Demultiplexed Illumina sequences are available from the European Nucleotide Archive (ENA) via study accession: PRJEB53993 (ERP138810)

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106418.

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