



A first look at the population structure of Loch Maree wild trout

By Vu H. Dang – an MScRes project

Director: Dr. Steve Kett | Supervisor: Dr. Martijn Timmermans

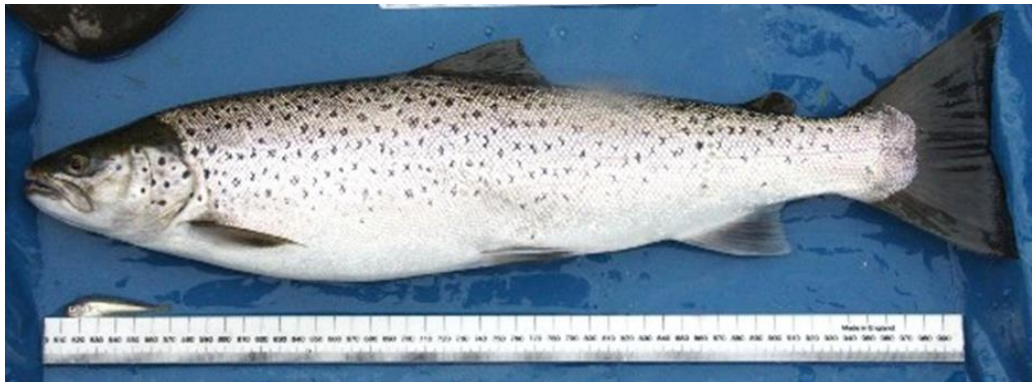
The Brown Trout (*Salmo trutta* L.1758) of Loch Maree



Mature brown trout (~35 cm fork length) caught and released in “Elf’s Loch”, July 2014.



Mature ferox trout (47.5 cm fork length) caught and released in Loch Kernsary, October 2013.



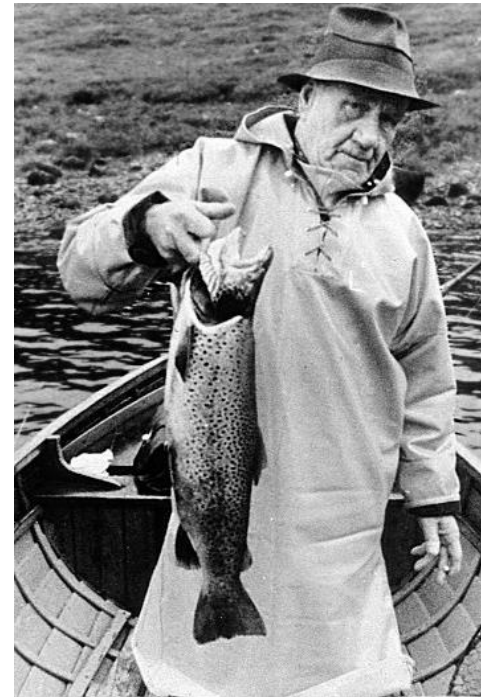
Mature sea trout (52 cm fork length, 1.6 kg weight) caught and released in Loch Ewe, June 2014.

Population collapse

- At the end of 1980s, the wild sea trout population collapsed, indicated by a 68% decline in the five-year mean catch between 1982 and 2000 (Walker, 2016; WRFT, no date).



Fishing boats outside the Loch Maree Hotel in the 1980s. Fishing effort was consistent on Loch Maree until the decline in catches (photos from the Gairloch Heritage Museum).



Project aims

- The project aims were to characterise the population genetic structure of the wild brown trout of Loch Maree - in an attempt to gain a better understanding of what environmental factors are influencing its genetic spatial distribution.



Sampling

- **Specimens genotyped:** 192
- **Sample sites:** 35 sites within Wester Ross and 1 site outside.
- **Pooling:** Sites were pooled into regional ranges.
- **Sampling dates:** 2006-2017 (85% sampled 2012-16)
- **Sampling methods:** Primarily fly rods with some fyke nets, electrofishing, and survey gill nets.

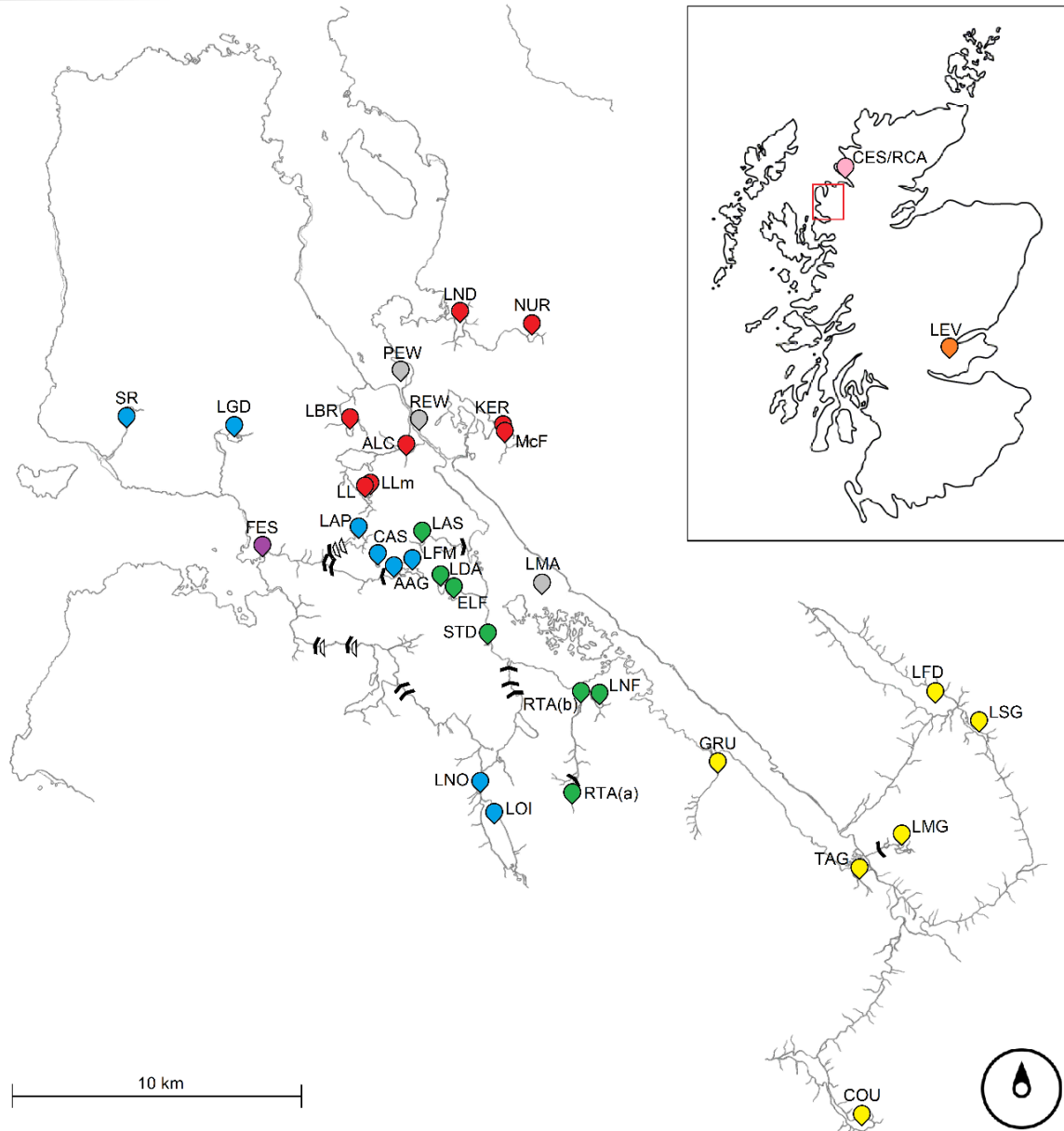
- **Genetic markers:** 9 BTMP microsatellite markers (Keenan *et al.*, 2013).

- **Loch Maree Ferox trout** – donated by Dr. Martin Hughes, PhD student (at the time), University of Glasgow.

- **Loch Leven brown trout** – donated by Dr. Ian J. Winfield, Freshwater Ecologist at the Centre for Ecology and Hydrology.

Study's sample range

Line-drawing of Wester Ross study area showing Loch Maree and neighbouring catchments' sample sites that drain into:



Resident trout were sampled:

- **NW Loch Maree** and **Poolewe**
- **CW Loch Maree**
- **SE Loch Maree**
- **Gairloch**
- **Loch Leven** (east coast of Scotland)

Sea trout were sampled in:

- **Poolewe**, the **Ewe river**, and **Loch Maree**
- **Flowerdale estuary**
- **Loch Canaird** and its outflow

Satellite map:

- **Loch Canaird** and its outflow
- **Loch Leven** (east coast of Scotland)

Barriers:

- Black chevrons mark *impassable waterfalls*
- Black and white trapezia mark the location of *man-made dams*

(Source map: Ordnance Survey acquired from

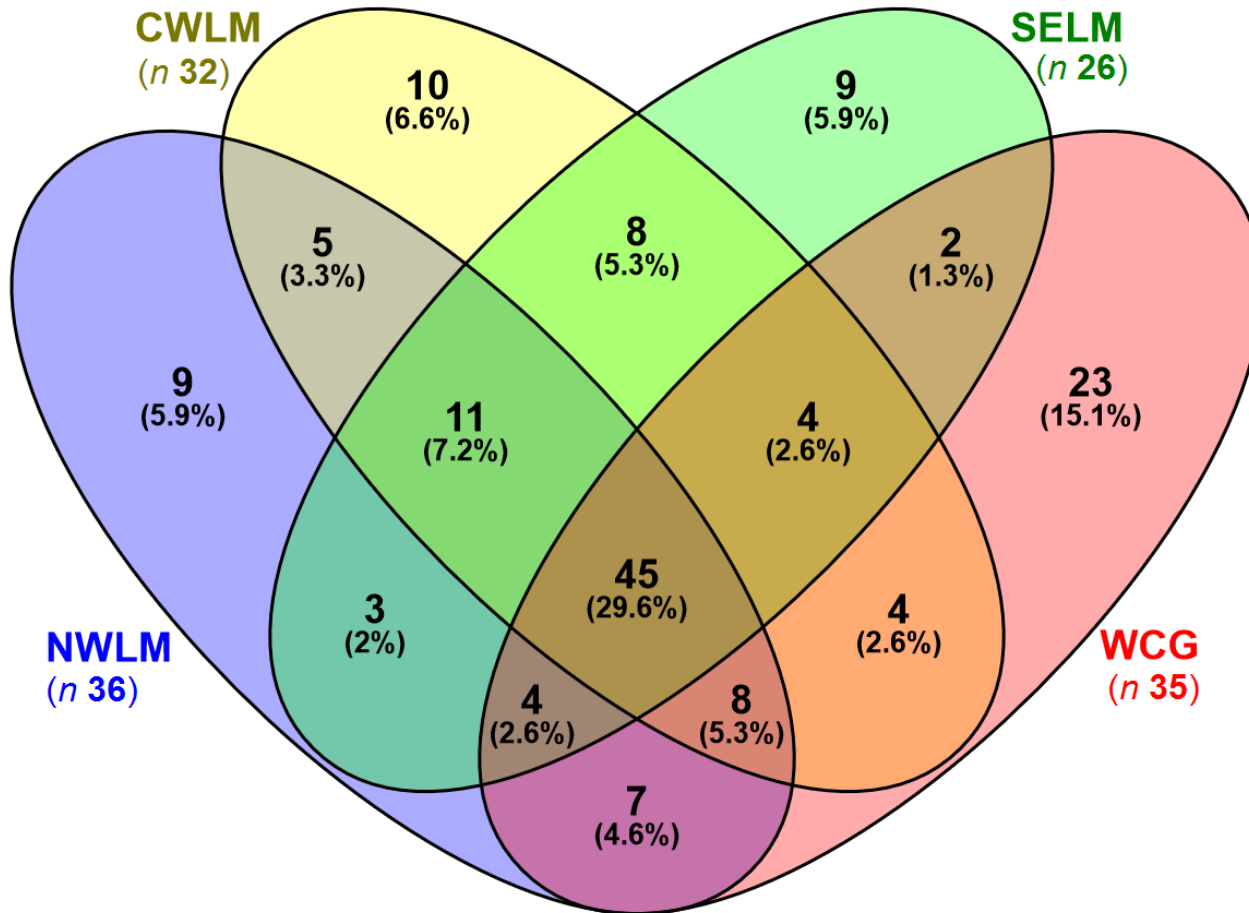
Intra-population genetic diversity

Within-population genetic diversity for resident and anadromous populations of *S. trutta* in sampled in this study at varying geographic ranges.

Population	<i>n</i>	<i>A_R</i>		<i>H_E</i>		<i>H_O</i>	
		Mean	SE	Mean	SE	Mean	SE
NW Loch Maree	36	10	2.3	0.650	0.106	0.641	0.104
CW Loch Maree	32	10.4	2.4	0.622	0.105	0.612	0.104
SE Loch Maree	26	9.6	2.3	0.642	0.098	0.629	0.096
W Coast Gairloch	35	10.7	1.8	0.710	0.079	0.699	0.078
Ewe ST*	40	15	2.8	0.770	0.069	0.761	0.069
Flowerdale ST	12	6.7	1.2	0.672	0.095	0.644	0.091
Canaird ST**	6	5.2	1.1	0.655	0.116	0.600	0.107
E Coast Leven	5	4.7	0.6	0.734	0.094	0.658	0.084
Loch Maree residents*	94	14.1	3.5	0.669	0.103	0.666	0.103
Wester Ross residents**	129	16.6	3.7	0.696	0.098	0.693	0.097
Wester Ross sea trout***	58	16	3.2	0.752	0.076	0.745	0.075
All of Wester Ross****	187	19.4	4.2	0.717	0.090	0.715	0.09
All residents*****	134	17.1	3.7	0.701	0.097	0.698	0.097
All specimens	192	19.8	4.1	0.720	0.090	0.718	0.090

Abbreviations: *A_R*, allelic richness; *H_E*, multi-locus expected heterozygosity; *H_O*, multi-locus heterozygosity observed; SE, mean error.

Unique and shared alleles



The proportions of alleles found unique and shared within and between the Loch Maree and Gairloch resident populations.

Allele frequencies of shared alleles

Alleles and their frequencies found shared between the Loch Maree and Gairloch resident brown trout.

A(Locus)	NWLM	CWLM	SELM	WCG	A(Locus)	NWLM	CWLM	SELM	WCG
132(1)	0.319	0.031	0.038	0.443	471(5)	0.069	0.063	0.019	0.043
160(1)	0.542	0.688	0.635	0.414	174(6)	0.042	0.016	0.096	0.057
172(1)	0.125	0.203	0.231	0.071	178(6)	0.125	0.031	0.019	0.029
242(2)	0.097	0.047	0.077	0.086	182(6)	0.056	0.266	0.038	0.043
246(2)	0.028	0.094	0.115	0.071	186(6)	0.278	0.125	0.038	0.186
254(2)	0.014	0.016	0.038	0.014	190(6)	0.097	0.031	0.154	0.071
262(2)	0.042	0.063	0.115	0.057	194(6)	0.056	0.281	0.077	0.100
270(2)	0.083	0.031	0.019	0.071	198(6)	0.042	0.016	0.019	0.043
274(2)	0.194	0.016	0.019	0.029	202(6)	0.042	0.016	0.058	0.143
278(2)	0.111	0.016	0.019	0.014	206(6)	0.028	0.031	0.173	0.029
113(3)	1.000	0.953	1.000	0.871	210(6)	0.014	0.016	0.096	0.014
262(4)	0.292	0.391	0.154	0.143	292(7)	0.014	0.016	0.038	0.014
266(4)	0.125	0.078	0.058	0.171	296(7)	0.333	0.328	0.096	0.100
270(4)	0.306	0.188	0.635	0.129	306(7)	0.069	0.094	0.038	0.029
274(4)	0.125	0.016	0.077	0.243	307(7)	0.028	0.156	0.038	0.014
278(4)	0.028	0.188	0.019	0.086	309(7)	0.028	0.078	0.385	0.071
286(4)	0.056	0.016	0.019	0.029	169(8)	0.069	0.016	0.038	0.071
423(5)	0.069	0.016	0.077	0.043	177(8)	0.083	0.063	0.058	0.057
427(5)	0.042	0.094	0.019	0.014	181(8)	0.819	0.891	0.558	0.714
431(5)	0.056	0.016	0.019	0.014	230(9)	0.319	0.656	0.654	0.200
443(5)	0.111	0.063	0.077	0.100	233(9)	0.583	0.281	0.173	0.571
463(5)	0.042	0.016	0.038	0.014	260(9)	0.014	0.047	0.135	0.143
467(5)	0.014	0.031	0.077	0.014					

Frequencies ≥ 0.1 (or 10%) are shaded the same colour every 0.1 increment higher, frequencies < 0.1 are not shaded.

Departures from Hardy-Weinberg Equilibrium (HWE)

Proportions of loci found in Hardy-Weinberg equilibrium in resident and anadromous trout populations in this study.

Population	<i>n</i>	HWE	HWE %
NW Loch Maree	36	2/8*	<u>25.00%</u>
CW Loch Maree	32	5/9	55.60%
SE Loch Maree	26	4/8*	50.00%
Gairloch	35	1/9	<u>11.10%</u>
Ewe sea trout**	40	5/9	55.60%
Flowerdale sea trout	12	7/9	77.80%
Canaird sea trout***	6	7/8*	87.50%
Loch Leven	5	8/8*	100.00%

*Locus 3 monomorphic and is discounted.

**Ewe sea trout (EST) collate River Ewe (REW) & Poolewe (PEW) sea trout, and the lake trout caught in Loch Maree (LMA).

*** Canaird sea trout (CST) include the sea trout caught in Loch Canaird estuary (CES) and its outflowing river (RCA).

Population differentiation

Mean G_{ST} values for the trout populations sampled in this study at various geographic/population ranges.

Populations	$n\ pop'$	n	k	G_{ST}	SE
Loch Maree residents*	3	94	9	0.28	0.01
Wester Ross residents**	4	129	9	0.25	0.01
Wester Ross sea trout***	3	58	9	0.29	0.01
All of Wester Ross****	7	187	9	0.19	0.01
All residents*****	5	134	9	0.24	0.01
All specimens	8	192	9	0.19	0.01

Abbreviations: $n\ pop'$, number of populations included; n , number of specimens, k , number of loci; SE, standard error.

*Loch Maree residents are all the resident trout caught in NW, CW, and SE Loch Maree (NWLM, CWLM, SELM).

**Wester Ross residents are all the residents sampled in Wester Ross (all of Loch Maree and Gairloch).

***WR sea trout group the sea trout from Flowerdale (FES), Ewe (REW, PEW, and LMA) and Canaird (CES, RCA).

****All of Wester Ross collate all of its resident and sea trout.

*****All residents include Wester Ross and Leven residents.

Inter-population genetic divergence by distance

Mantel tests between inter-population geo-hydro distances (km) and population pairwise genetic distances.

Populations included	<i>n</i>	matrix <i>n</i>	<i>D_{ST}</i>	<i>p</i>	<i>r</i>
Loch Maree* & Gairloch	4	6	Observed	0.101	0.867
Loch Maree, Gairloch, & Canaird**	5	10	Observed	0.014	0.732
Loch Maree, Gairloch, & Loch Leven	5	10	Corrected	0.008	0.804
Loch Maree, Gairloch, Canaird, & Loch Leven	6	15	Corrected	0.002	0.713
Loch Maree, Gairloch, EST, & FST	6	15	Observed	0.135	0.324
Loch Maree, Gairloch, Canaird, EST, & FST	7	21	Corrected	0.238	0.208
Loch Maree, Gairloch, Loch Leven, EST, & FST	7	21	Corrected	0.019	0.772
Loch Maree, Gairloch, Canaird, Loch Leven, EST, & FST	8	28	Corrected	0.017	0.705

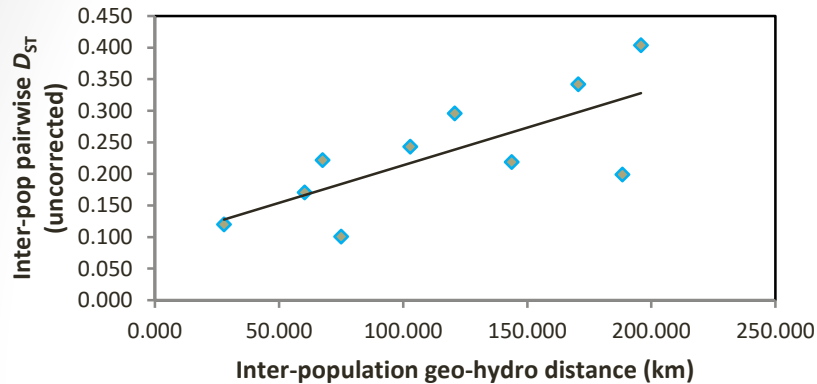
Abbreviations: *n*, number of populations included; matrix *n*, number of cells in matrices compared.

All mantel tests were run with 9999 permutations.

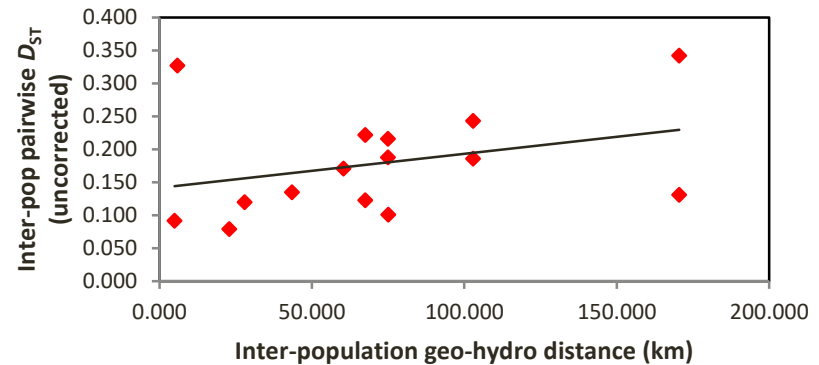
*Loch Maree includes the three NW, Central-W, and SE populations (NWLM, CWLM, SELM).

**Canaird includes the sea trout and brown trout caught in river Canaird (RCA) and its estuary Loch Canaird (CES).

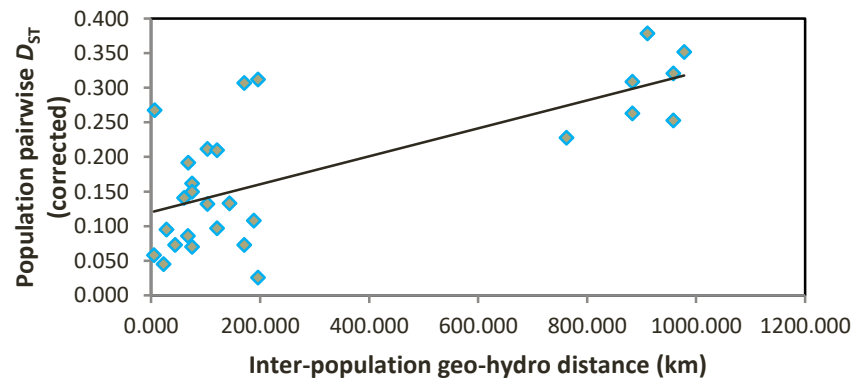
Inter-population genetic divergence by distance (continued)



Mantel scatterplot of pairwise distances between Loch Maree, Gairloch and Canaird trout, ($n = 5$), p 0.014, r 0.732.

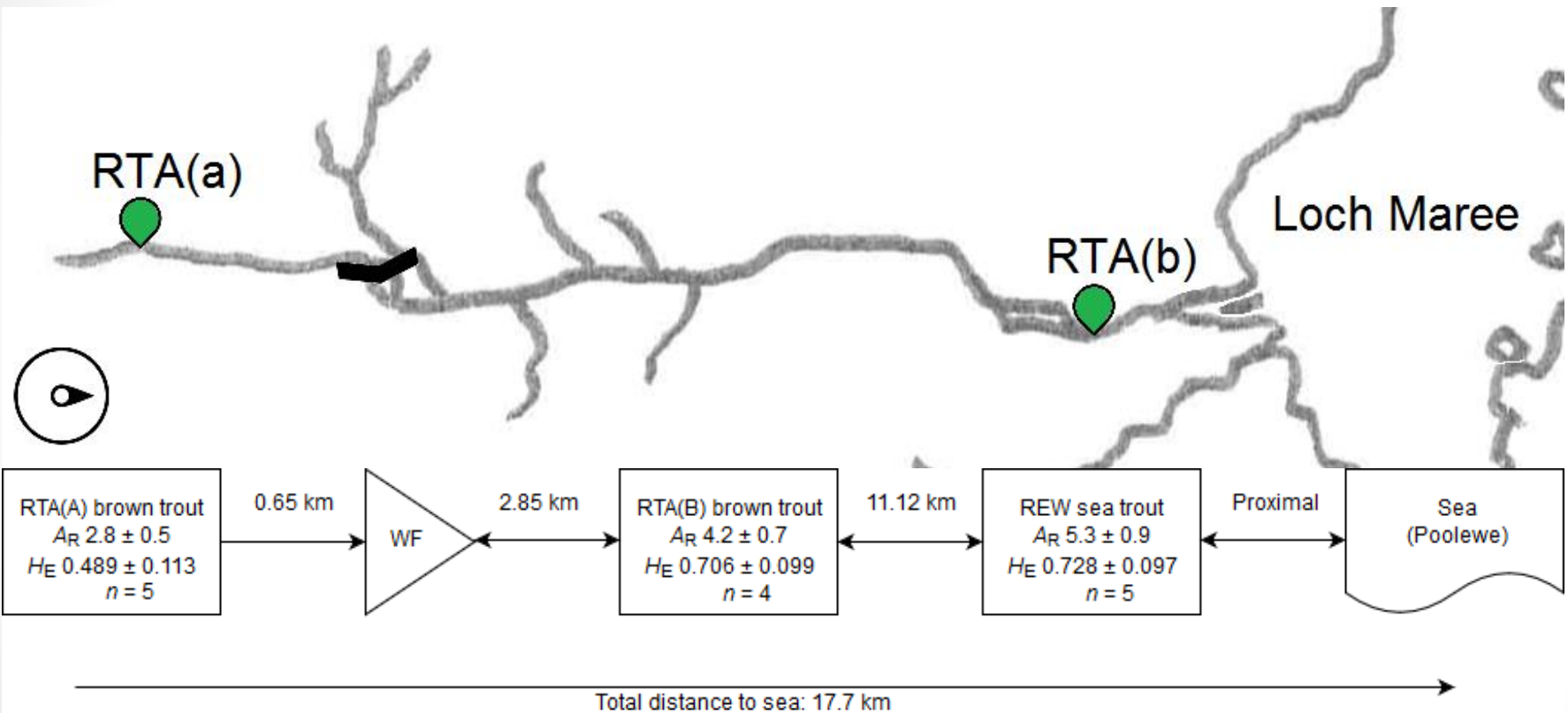


Mantel scatterplot of pairwise distances between the WR resident trout, and sea trout populations ($n = 6$), p 0.135, r 0.324.



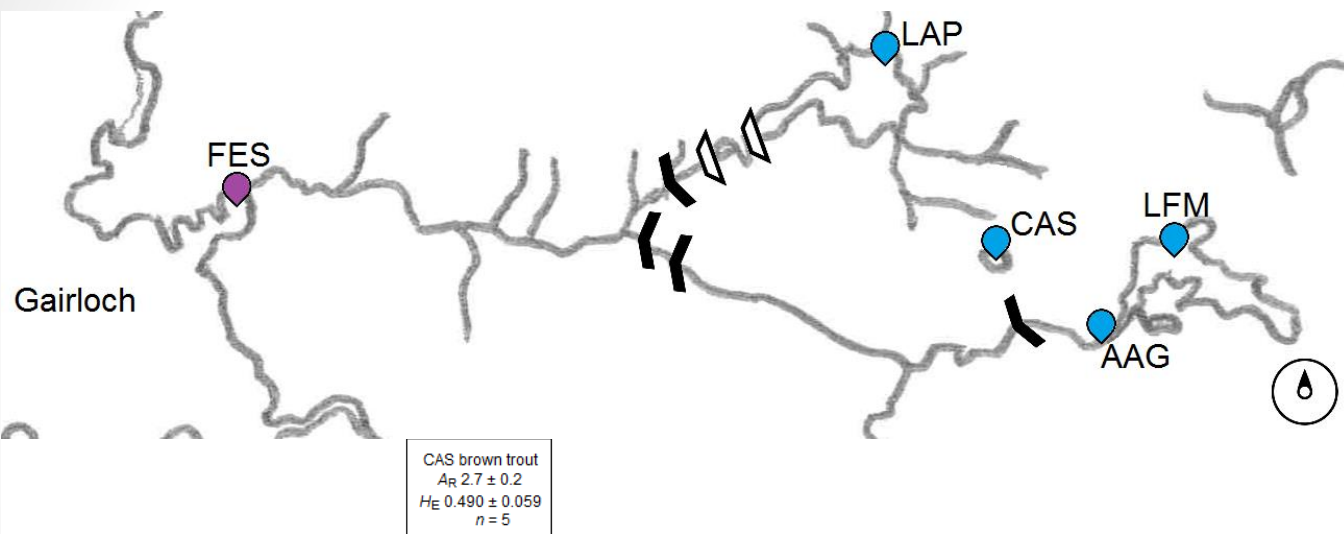
Mantel scatterplot of pairwise distances between all populations sampled ($n = 8$), p 0.017, r 0.705.

Headwater populations & barriers to movement



River Talladale headwater population (RTA[a]) and post-barrier comparison with resident downstream population (RTA[b]) and River Ewe sea trout (REW).

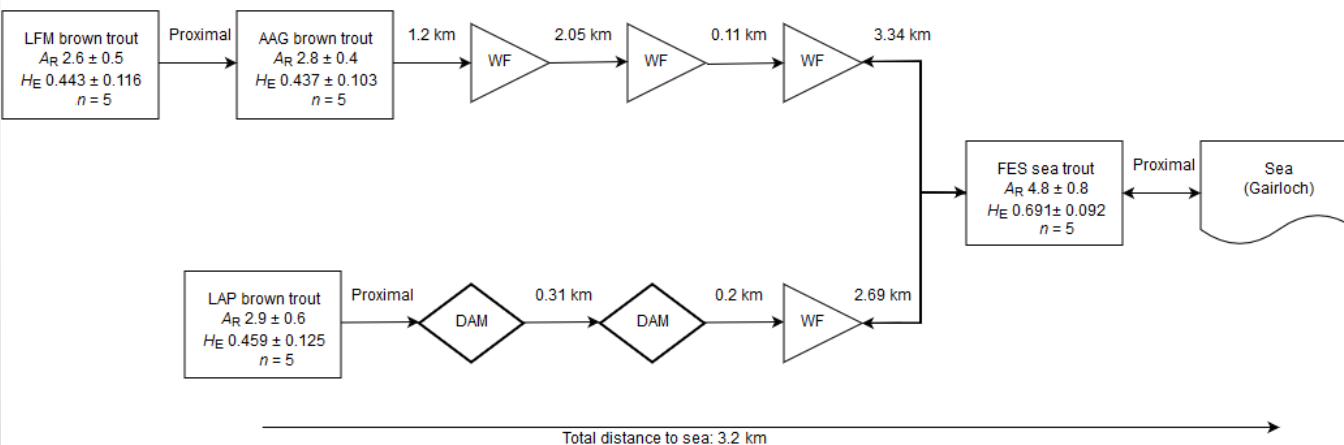
Headwater populations & barriers to movement (continued)



Loch na Feithe Mugaig (LFM), its outflow river (AAG), Loch Airigh a' Phuill (LAP) and "Cassius lochan" (CAS) headwater populations and post barrier comparison with downstream Flowerdale sea trout (FES).

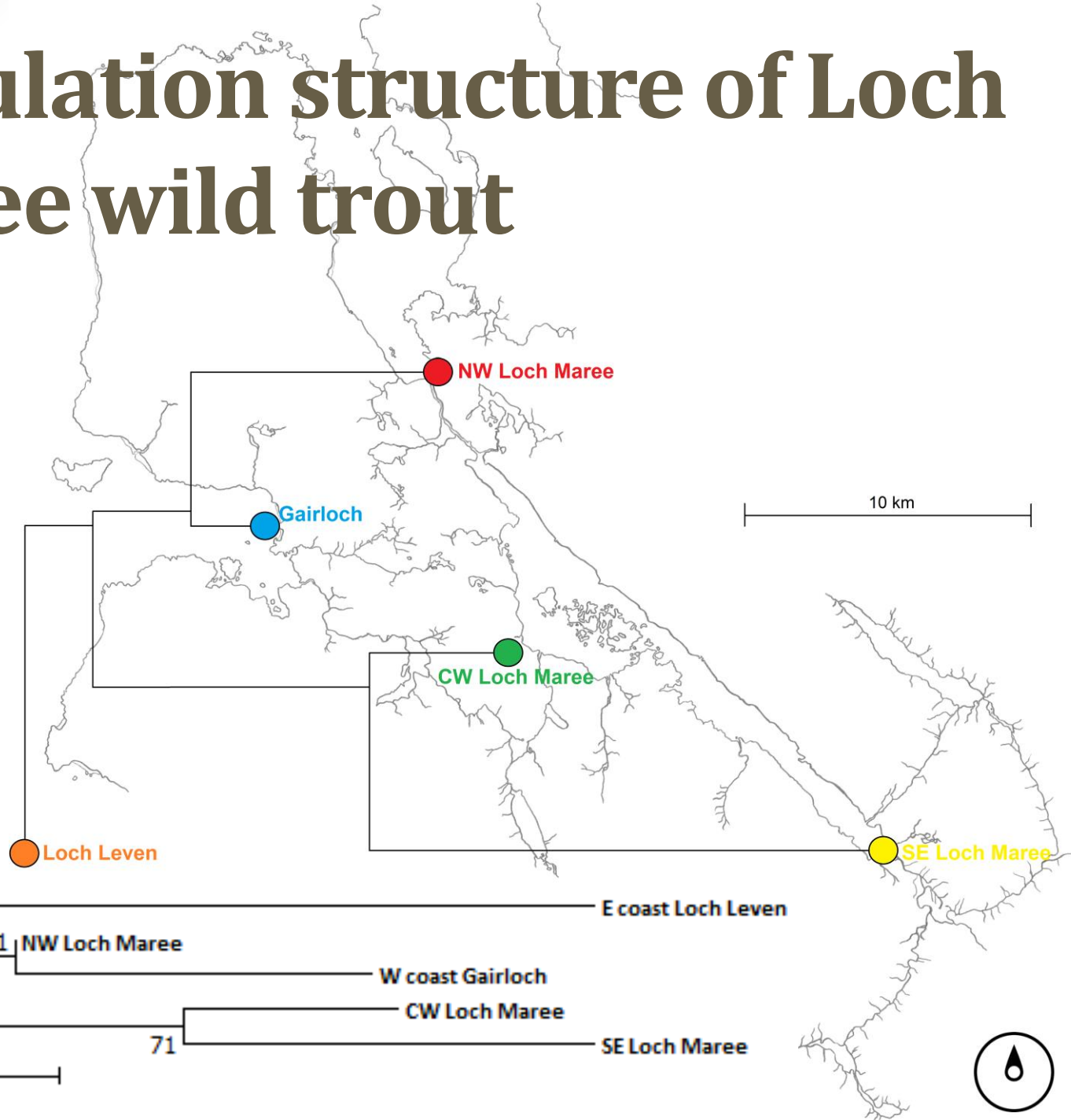
CAS brown trout
 $A_R 2.7 \pm 0.2$
 $H_E 0.490 \pm 0.059$
 $n = 5$

Total distance to sea: 6.7 km

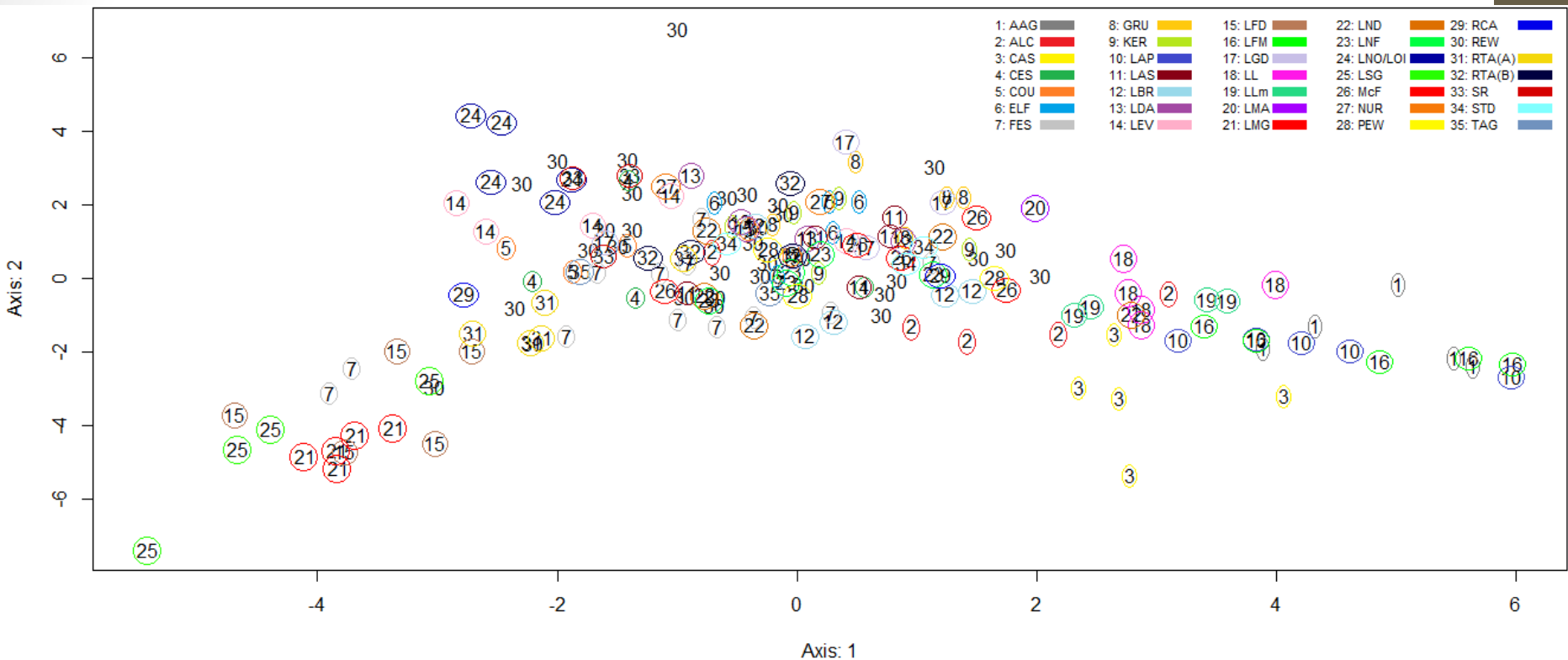


Population structure of Loch Maree wild trout

NJ tree depicting the Wester Ross brown trout population genetic structure, based on D_{ST} (corrected) values generated in this study, with an overlay on the study range map.

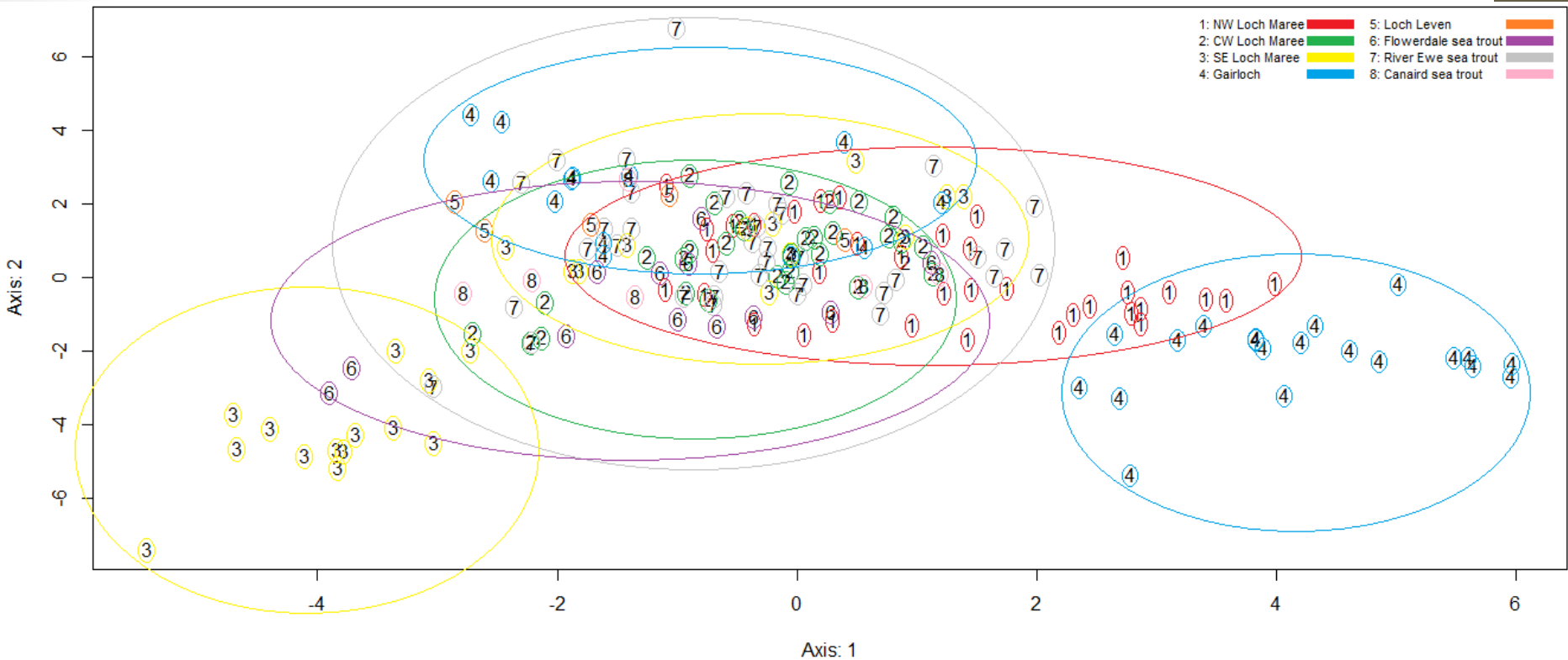


Principle Component Analysis (PCA)



PCA two-axis plot of Wester Ross brown trout and sea trout at individual sample site range.

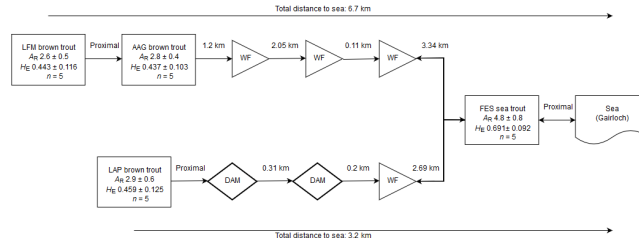
PCA (continued)



PCA two-axis plot of Wester Ross brown trout and sea trout at pooled regional groups.

Conclusions: Population structure

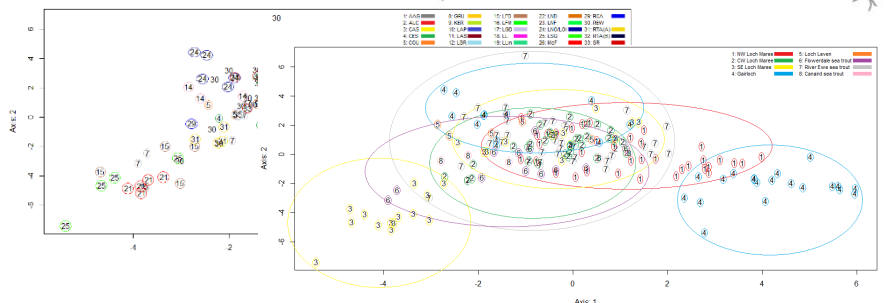
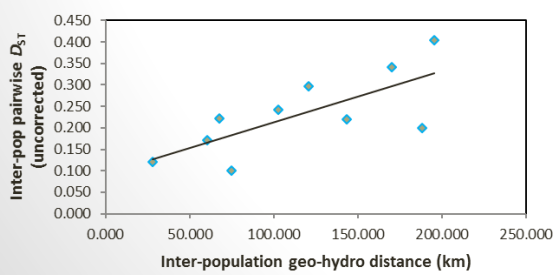
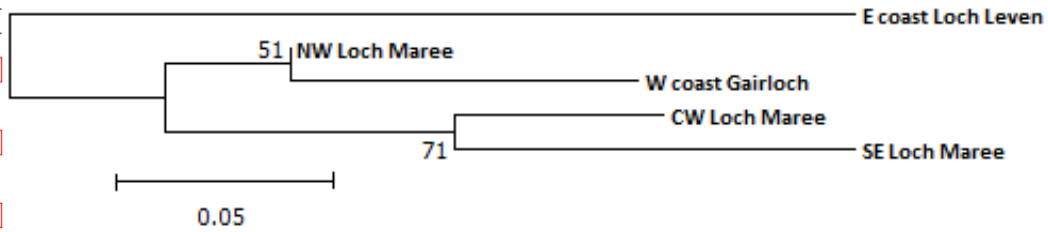
AL(locks)	NWLM	CWLM	SELM	WGO	A(locks)	NWLM	CWLM	SELM	WGO
132(1)	0.319	0.031	0.038	0.443	47(15)	0.069	0.063	0.019	0.043
160(1)	0.542	0.688	0.635	0.414	174(6)	0.042	0.016	0.096	0.057
172(1)	0.125	0.203	0.231	0.071	179(6)	0.125	0.031	0.019	0.029
242(2)	0.097	0.047	0.077	0.086	183(6)	0.056	0.296	0.038	0.043
246(2)	0.028	0.094	0.115	0.071	186(6)	0.278	0.125	0.038	0.196
254(2)	0.014	0.016	0.038	0.014	190(9)	0.097	0.031	0.154	0.071
262(2)	0.042	0.063	0.115	0.057	194(9)	0.056	0.281	0.077	0.190
270(2)	0.083	0.031	0.019	0.071	198(6)	0.042	0.016	0.019	0.043
274(2)	0.194	0.016	0.019	0.029	202(6)	0.042	0.016	0.058	0.143
276(2)	0.111	0.016	0.019	0.014	206(6)	0.028	0.031	0.173	0.029
113(3)	1.000	0.000	1.000	0.671	210(6)	0.014	0.016	0.096	0.014
262(4)	0.292	0.391	0.154	0.143	262(7)	0.014	0.016	0.038	0.014
266(4)	0.125	0.078	0.058	0.171	296(7)	0.333	0.368	0.096	0.160
270(4)	0.306	0.188	0.635	0.129	306(7)	0.069	0.094	0.038	0.029
274(4)	0.125	0.016	0.077	0.243	307(7)	0.028	0.156	0.038	0.014
278(4)	0.028	0.188	0.019	0.086	309(7)	0.028	0.019	0.345	0.011
286(4)	0.058	0.016	0.019	0.029	169(6)	0.069	0.016	0.038	0.071
423(5)	0.069	0.016	0.077	0.043	177(8)	0.083	0.083	0.058	0.057
427(5)	0.042	0.094	0.019	0.014	181(8)	0.816	0.841	0.558	0.714
431(5)	0.058	0.016	0.019	0.014	233(9)	0.319	0.605	0.654	0.290
443(5)	0.111	0.063	0.077	0.100	233(9)	0.583	0.281	0.173	0.571
483(5)	0.042	0.016	0.038	0.014	260(9)	0.014	0.047	0.135	0.143
487(5)	0.014	0.031	0.077	0.014					



Population	n	HWE	HWE %
NW Loch Maree	36	2/8*	25.00%
CW Loch Maree	32	5/9	55.60%
SE Loch Maree	26	4/8*	50.00%
Gairloch	35	1/9	11.10%
Ewe sea trout**	40	5/9	55.60%
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Canaird sea trout***	6	7/8*	87.50%
Loch Leven	5	8/8*	100.00%

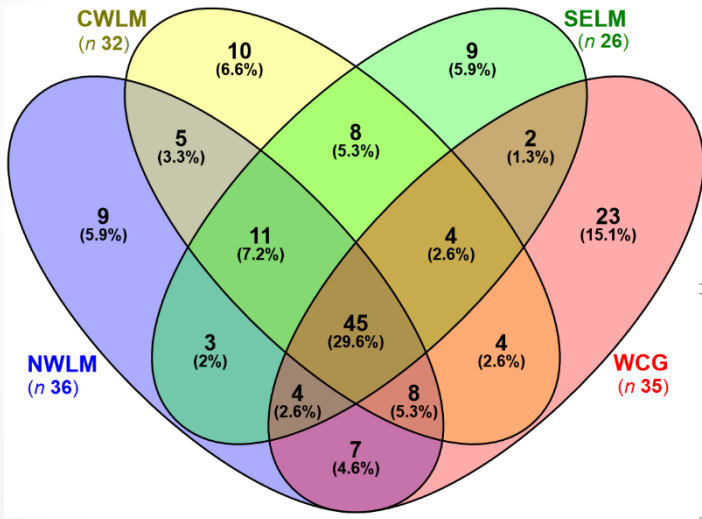
Population genetic structure is present in the Loch Maree wild trout, suggesting a non-panmictic population exists in Wester Ross (allele frequencies, HWE, mantel tests, headwaters & barriers statistics, NJ tree, PCA).

Populations included	n	matrix	n	D _{ST}	p	r
Loch Maree* & Gairloch	4	6	Observed	0.101	0.867	
Loch Maree, Gairloch, & Canaird**	5	10	Observed	0.014	0.732	
Loch Maree, Gairloch, & Loch Leven	5	10	Corrected	0.008	0.804	
Loch Maree, Gairloch, Canaird, & Loch Leven	6	15	Corrected	0.002	0.713	
Loch Maree, Gairloch, EST, & FST	6	15	Observed	0.135	0.324	
Loch Maree, Gairloch, Canaird, EST, & FST	7	21	Corrected	0.238	0.208	
Loch Maree, Gairloch, Loch Leven, EST, & FST	7	21	Corrected	0.019	0.772	
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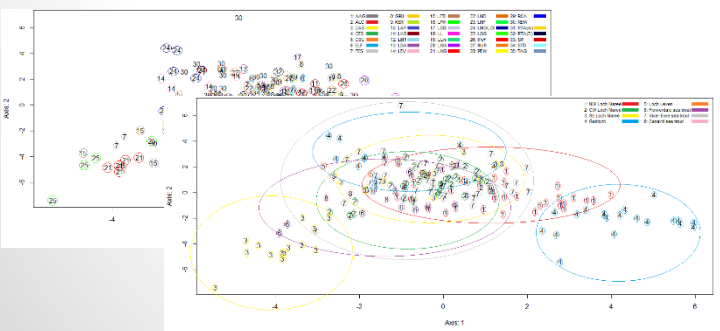
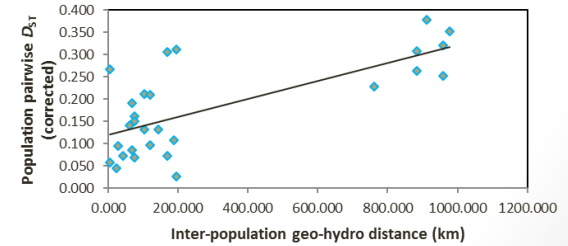
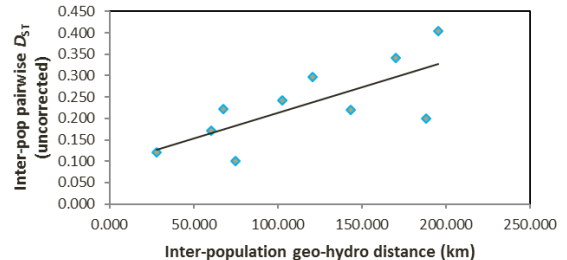
Conclusion: Genetic distance x hydro-distance correlation and introgression

Genetic diversity between populations is positively correlated with hydrological distances between them, however despite this, gene flow appears evident in all populations that are hydrologically connected (*Unique/shared alleles, mantel tests, PCA*).

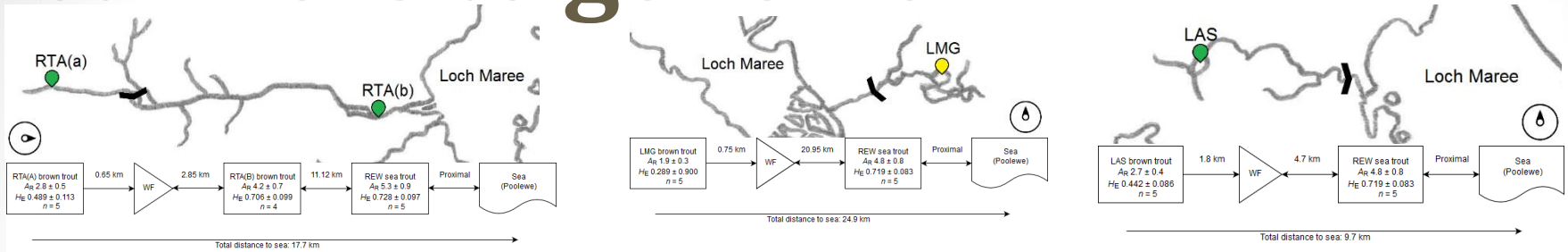


Alleles	NWLM	CWLM	SELM	WCG	Alleles	NWLM	CWLM	SELM	WCG
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274(4)	0.125	0.016	0.077	0.248	307(7)	0.028	0.156	0.038	0.014
278(4)	0.028	0.188	0.019	0.086	309(7)	0.028	0.078	0.383	0.071
288(4)	0.058	0.016	0.019	0.029	186(8)	0.069	0.016	0.058	0.071
423(5)	0.069	0.016	0.077	0.043	177(8)	0.083	0.063	0.058	0.057
427(5)	0.042	0.064	0.019	0.014	181(8)	0.019	0.007	0.058	0.216
431(5)	0.058	0.016	0.019	0.014	230(9)	0.378	0.058	0.066	0.200
443(5)	0.111	0.063	0.077	0.100	233(9)	0.683	0.281	0.173	0.571
485(5)	0.042	0.016	0.038	0.014	260(9)	0.014	0.047	0.135	0.143
487(5)	0.014	0.031	0.077	0.014					

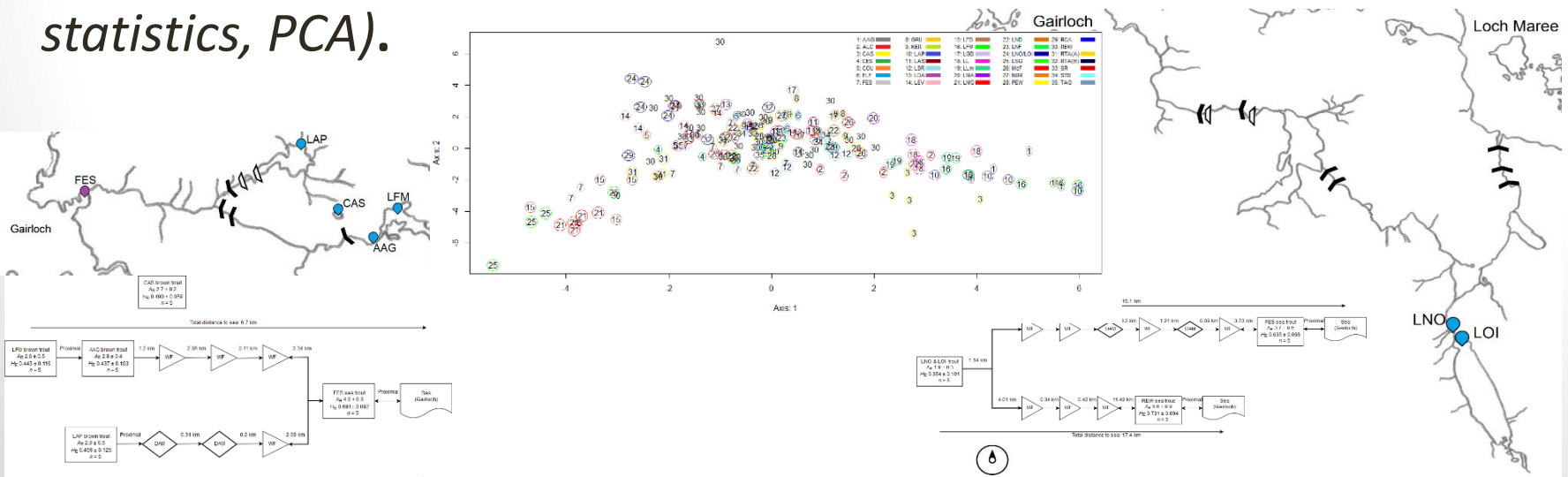
Populations included	n	matrix n	D _{ST}	p	r
Loch Maree* & Gairloch	4	6	Observed	0.101	0.867
Loch Maree, Gairloch, & Canaird**	5	10	Observed	0.014	0.732
Loch Maree, Gairloch, & Loch Leven	5	10	Corrected	0.008	0.804
Loch Maree, Gairloch, Canaird, & Loch Leven	6	15	Corrected	0.002	0.713
Loch Maree, Gairloch, EST, & FST	6	15	Observed	0.135	0.324
Loch Maree, Gairloch, Canaird, EST, & FST	7	21	Corrected	0.238	0.208
Loch Maree, Gairloch, Loch Leven, EST, & FST	7	21	Corrected	0.019	0.772
Loch Maree, Gairloch, Canaird, Loch Leven, EST, & FST	8	28	Corrected	0.017	0.705



Conclusions: Headwaters & barriers to gene flow



Headwater populations above barriers have reduced genetic diversity than downstream populations and seem to be genetically diverging from their neighbouring populations (*allelic richness & heterozygosities - headwaters & barriers statistics, PCA*).



Conclusions: Intra-population genetic diversity

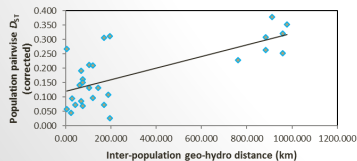
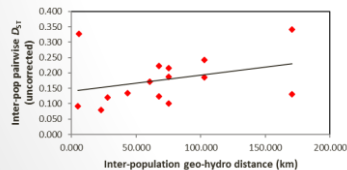
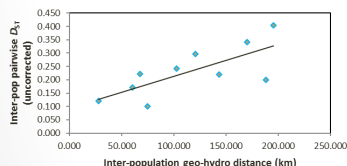
Within-population genetic diversity appears similar between the regional resident populations sampled in this study, while the sea trout appear to be a more genetically diverse group (*allelic richness and heterozygosities*).

Population	<i>n</i>	<i>A_R</i>		<i>H_E</i>		<i>H_O</i>	
		Mean	SE	Mean	SE	Mean	SE
NW Loch Maree	36	10	2.3	0.650	0.106	0.641	0.104
CW Loch Maree	32	10.4	2.4	0.622	0.105	0.612	0.104
SE Loch Maree	26	9.6	2.3	0.642	0.098	0.629	0.096
W Coast Gairloch	35	10.7	1.8	0.710	0.079	0.699	0.078
Ewe ST*	40	15	2.8	0.770	0.069	0.761	0.069
Flowerdale ST	12	6.7	1.2	0.672	0.095	0.644	0.091
Canaird ST**	6	5.2	1.1	0.655	0.116	0.600	0.107
E Coast Leven	5	4.7	0.6	0.734	0.094	0.658	0.084
Loch Maree residents*	94	14.1	3.5	0.669	0.103	0.666	0.103
Wester Ross residents**	129	16.6	3.7	0.696	0.098	0.693	0.097
Wester Ross sea trout***	58	16	3.2	0.752	0.076	0.745	0.075
All of Wester Ross****	187	19.4	4.2	0.717	0.090	0.715	0.09
All residents*****	134	17.1	3.7	0.701	0.097	0.698	0.097
All specimens	192	19.8	4.1	0.720	0.090	0.718	0.090

Conclusions: Sea trout origins and coastal influences

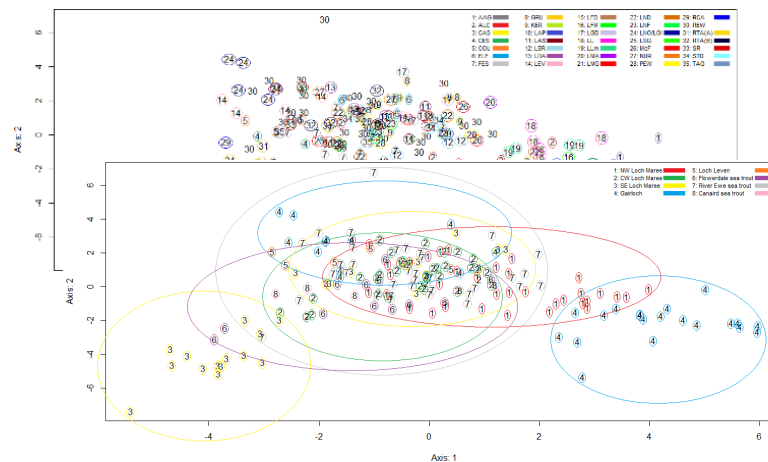
The sea trout sampled in this study appear to originate from within Wester Ross, mostly from Loch Maree, as well as Gairloch, suggesting they may occupy large coastal ranges (*population differential* – G_{ST} , mantel tests, *PCA*).

Furthermore, resident populations beside the sea appear to be under greater environmental influence, which may suggest they are more reliant on sea trout returns (*allele frequencies* – *HWE*).

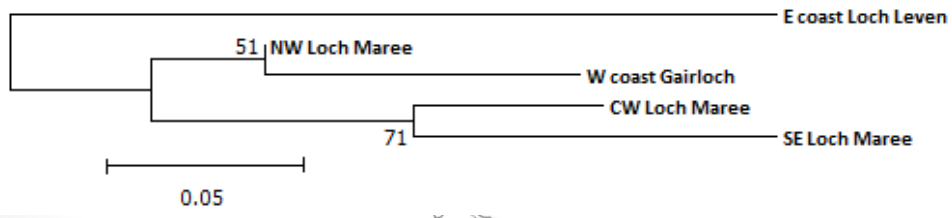
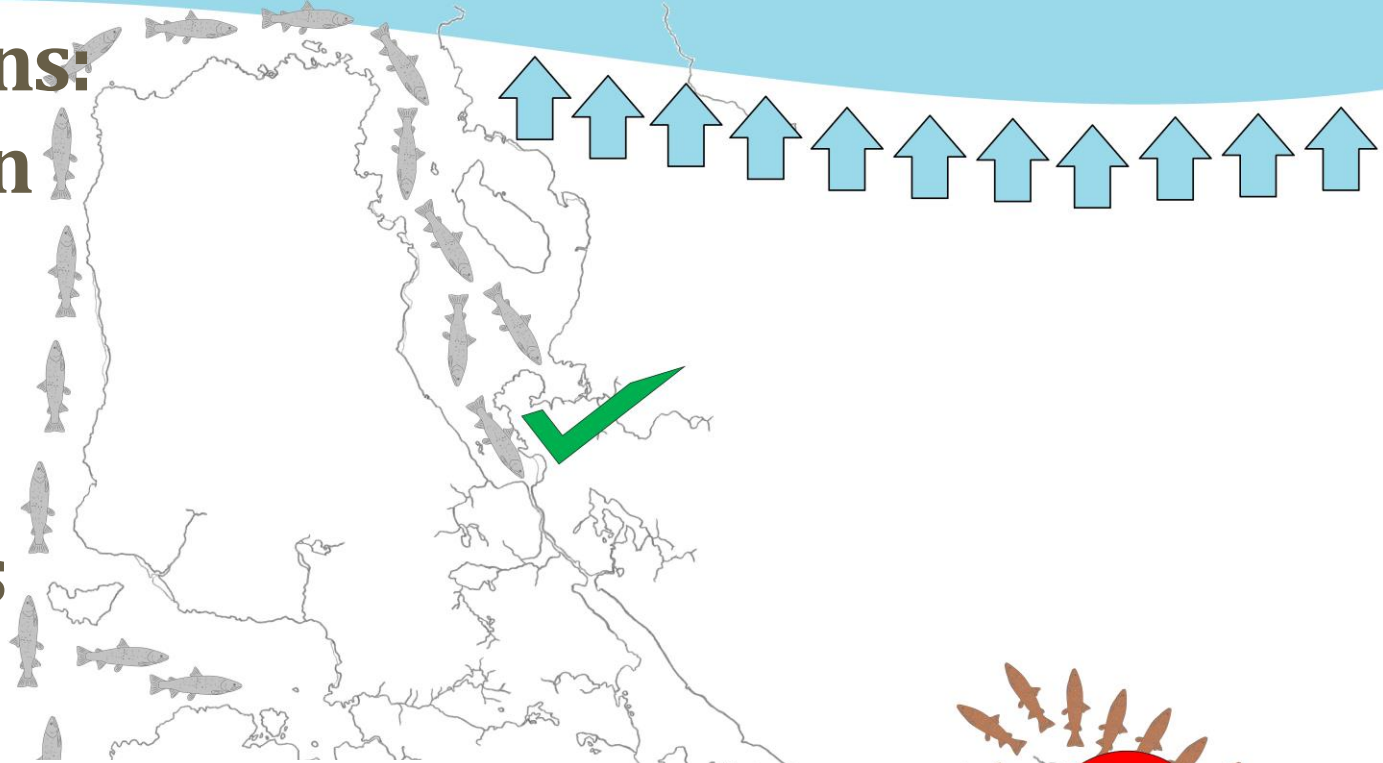


Populations	n pop'	n	k	G_{ST}	SE
Loch Maree residents*	3	94	9	0.28	0.01
Wester Ross residents**	4	129	9	0.25	0.01
Wester Ross sea trout***	3	58	9	0.29	0.01
All of Wester Ross****	7	187	9	0.19	0.01
All residents*****	5	134	9	0.24	0.01
All specimens	8	192	9	0.19	0.01

Population	n	HWE	HWE %
NW Loch Maree	36	2/8*	25.00%
CW Loch Maree	32	5/9	55.60%
SE Loch Maree	26	4/8*	50.00%
Gairloch	35	1/9	11.10%
Ewe sea trout**	40	5/9	55.60%
Flowerdale sea trout	12	7/9	77.80%
Canaird sea trout***	6	7/8*	87.50%
Loch Leven	5	8/8*	100.00%



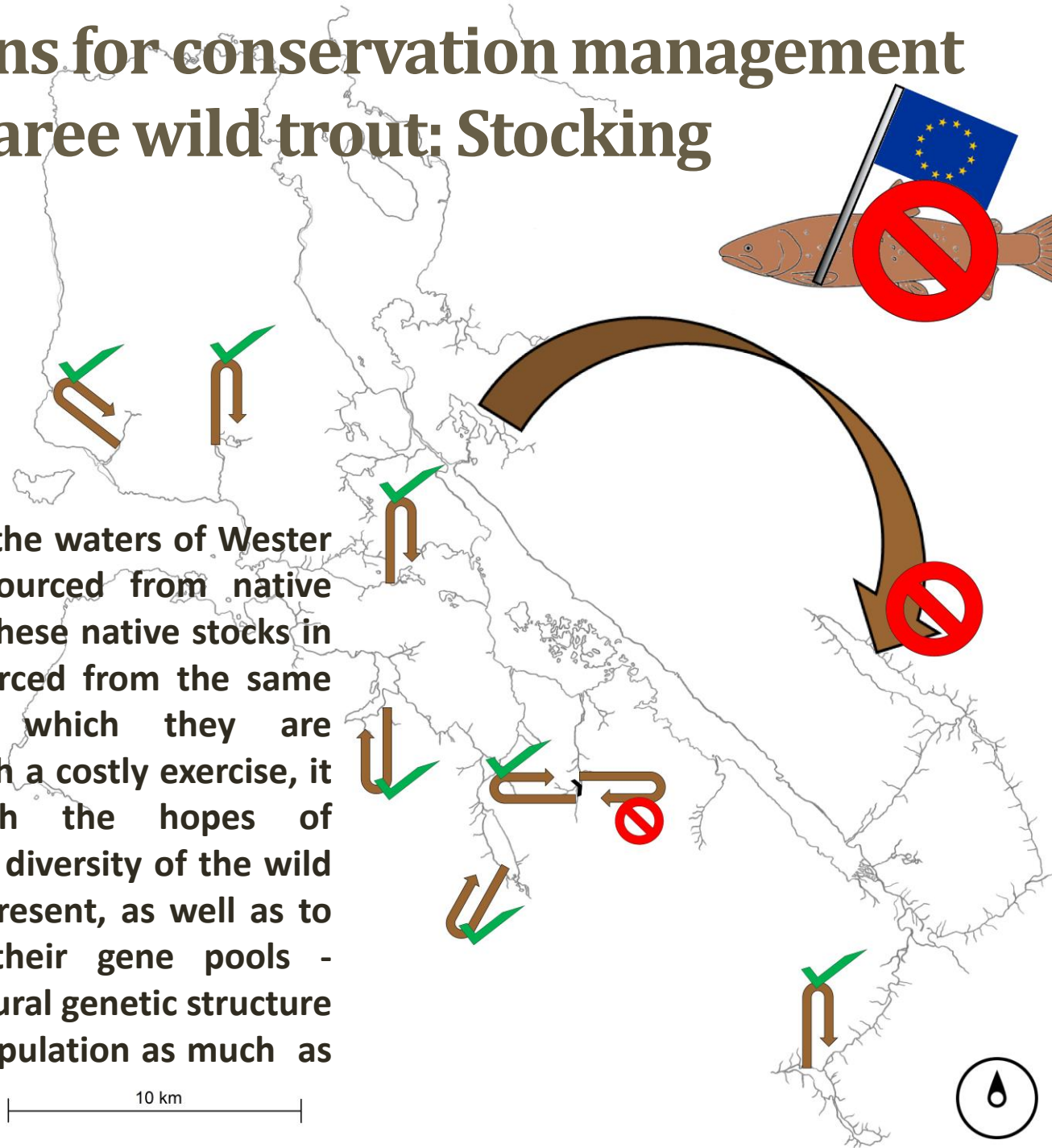
Conclusions: Population structure and historical colonisers



The population structure observed at regional level suggest brown trout colonised Loch Maree at the NW point initially, suggesting colonisation by ancient migrant sea trout is more likely than a freshwater radiation from an inland glacial refuge since the retreat of the last glacial maximum (*NJ tree*).



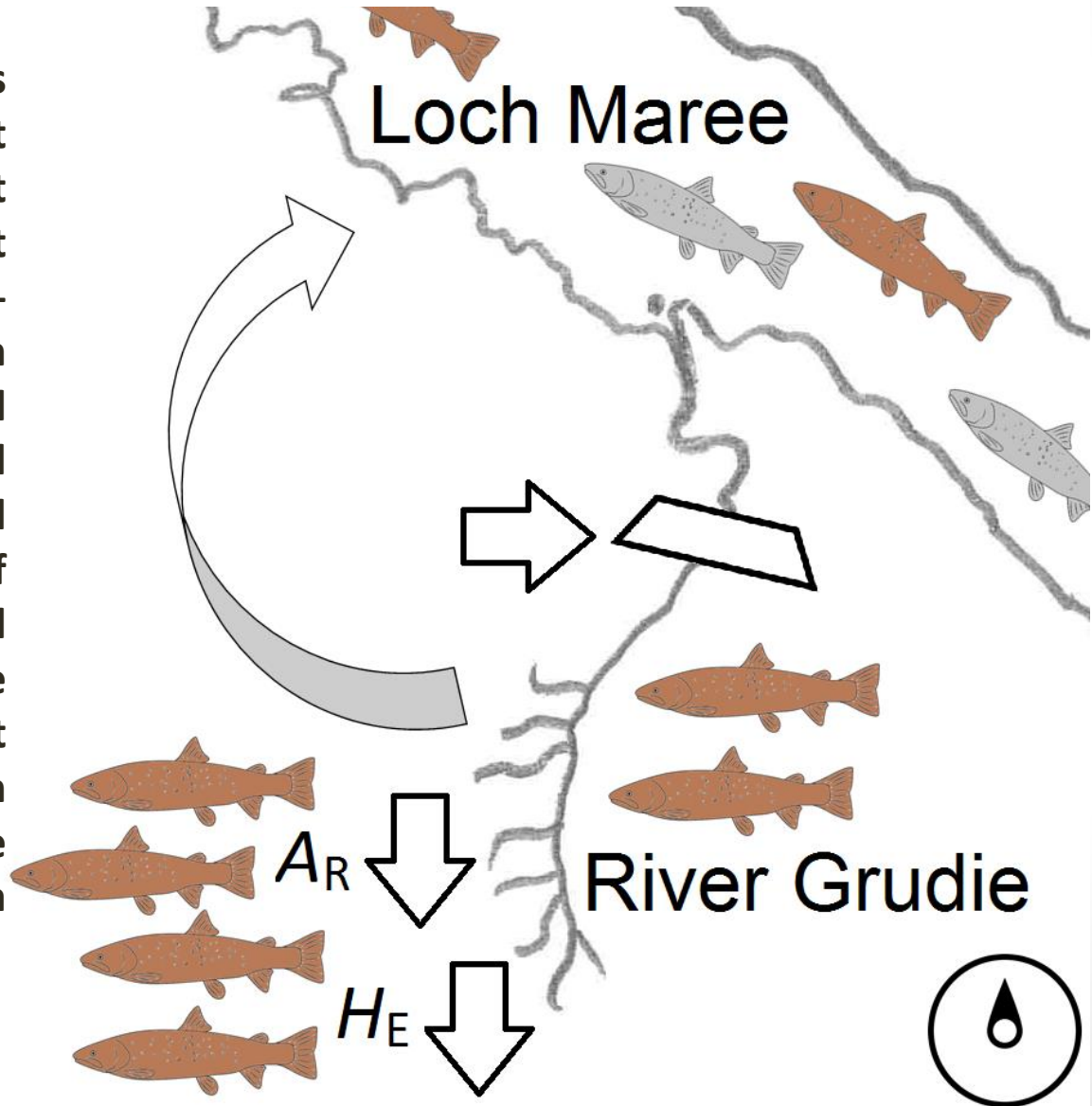
Suggestions for conservation management of Loch Maree wild trout: Stocking



Stocking trout into the waters of Wester Ross, should be sourced from native trout populations; these native stocks in turn should be sourced from the same watercourses for which they are intended for. Though a costly exercise, it is suggested with the hopes of maintaining genetic diversity of the wild trout populations present, as well as to not contaminate their gene pools - maintaining the natural genetic structure of the wild trout population as much as possible.

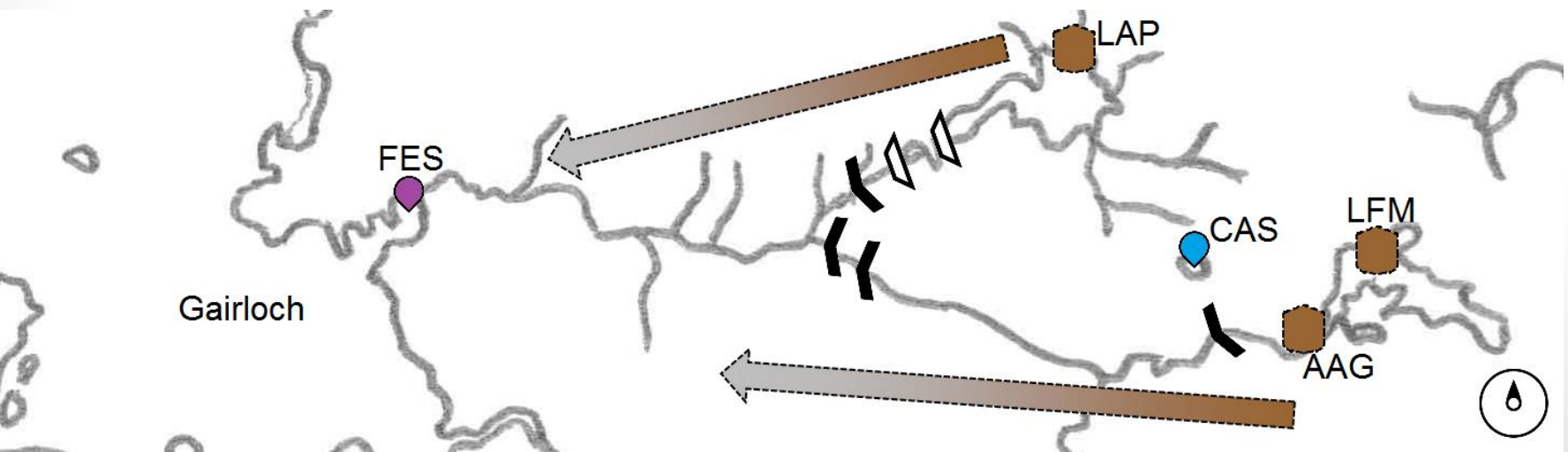
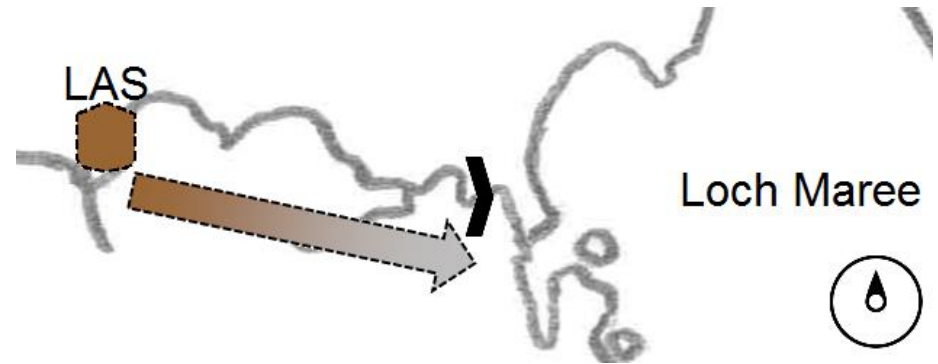
Suggestions for conservation management of Loch Maree wild trout: Barriers & connectivity

Since the regional populations in this study appear to exhibit gene flow between them, it would suggest that maintaining hydro-connectivity is influential in maintaining the overall genetic diversity in the wild trout of Loch Maree and Wester Ross. The advent of impassable or unidirectional barriers will likely reduce the genetic diversity of trout populations upstream, which in turn could have cascade effects for downstream populations as well.



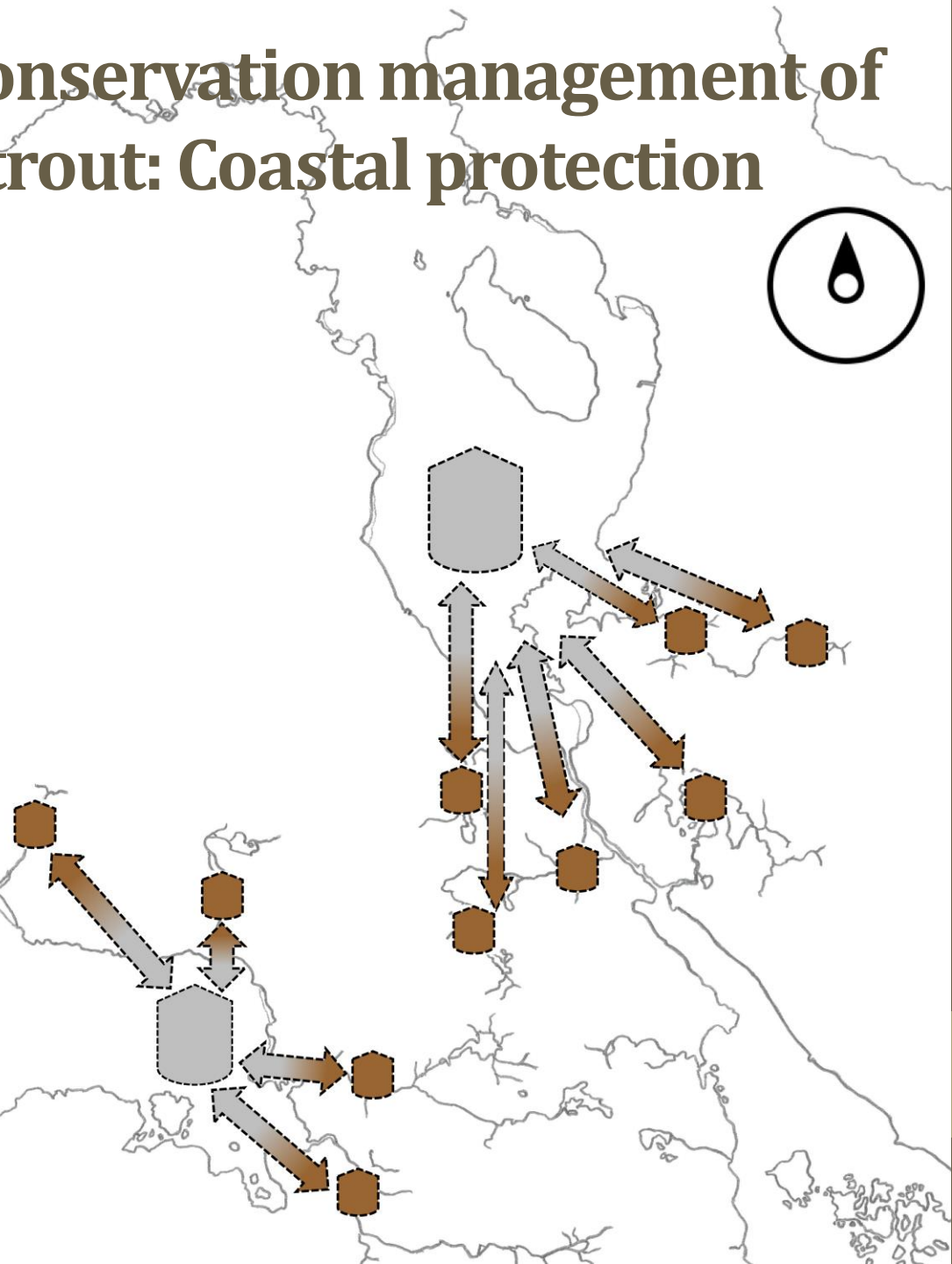
Suggestions for conservation management of Loch Maree wild trout: Headwater protection

Headwater populations would benefit from increased inland protection, since their isolation and reduced genetic diversity make them particularly vulnerable to population decline and inbreeding depression. They may also be important sources of local adaptations that are beneficial to populations downstream.



Suggestions for conservation management of Loch Maree wild trout: Coastal protection

Sea trout protection, with particular regards to coastal management may be very important, since the sea trout, which are more genetically diverse, may range significant coastal distances. Therefore, pinpoint coastal activities may in turn affect significant numbers of sea trout that may or may not return to their natal streams and resident siblings. Resident populations close to the sea are likely to also benefit from greater sea trout protection, which may well increase sea trout numbers in return.



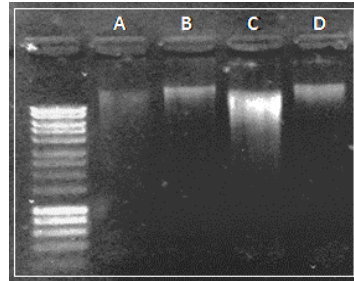
References

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- Wester Ross Fisheries Trust (no date) *Brown trout and sea trout (Salmo trutta)*. Available at: <http://www.wrft.org.uk/fishes/trout.cfm> (Accessed: 12/01/2017).

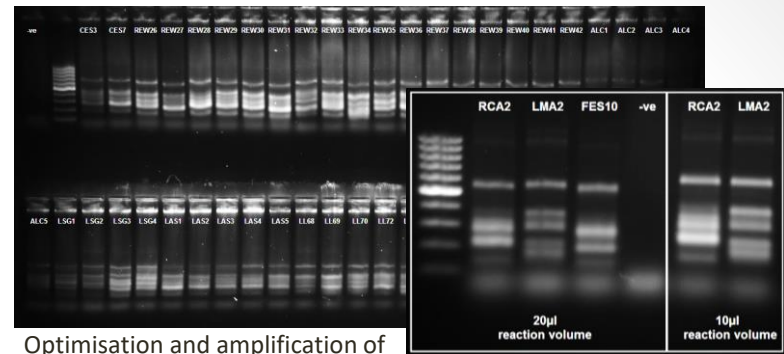
Project methods



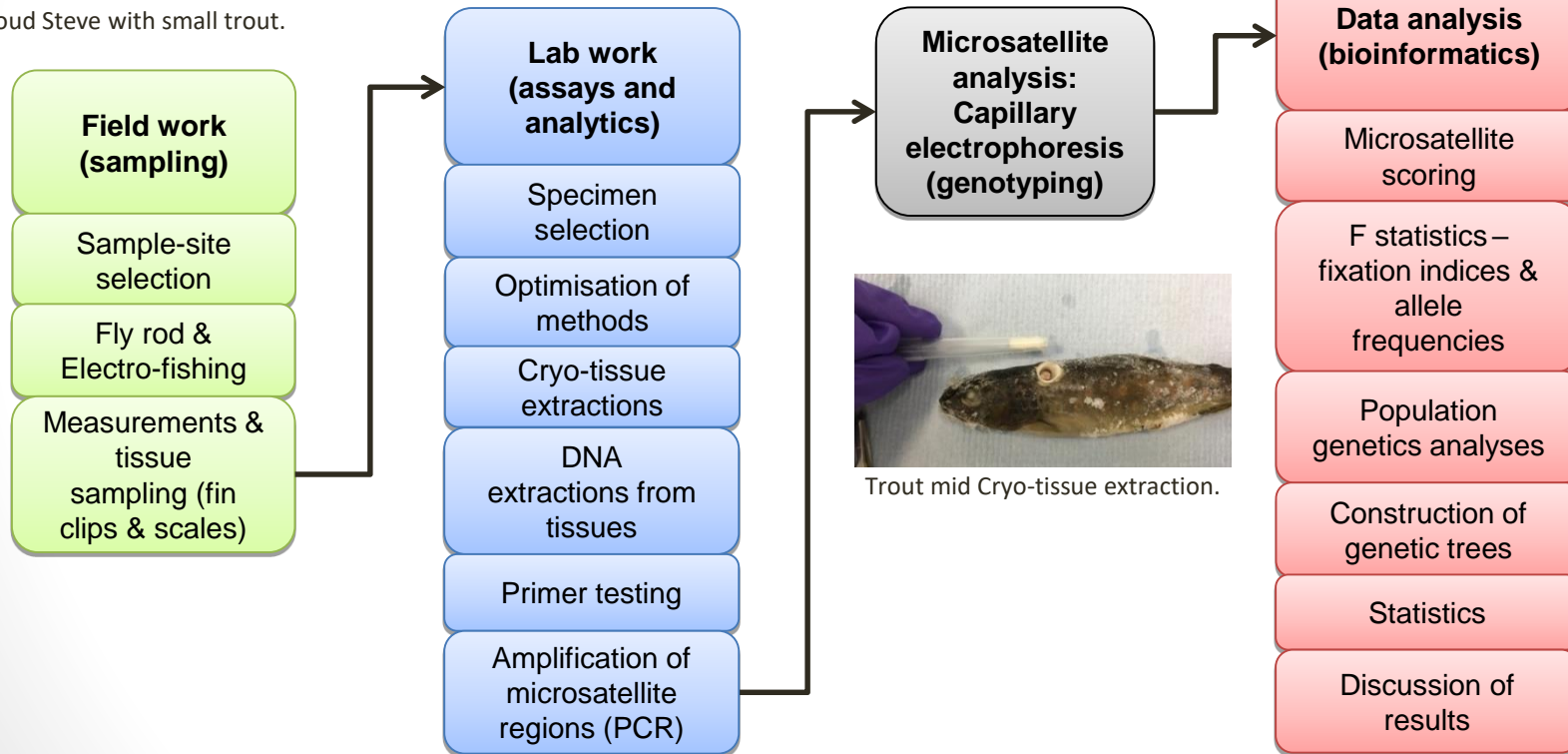
Proud Steve with small trout.



DNA quality by tissue/storage test.



Optimisation and amplification of microsatellite markers.



Flow chart of the study's methodology, briefly outlining what was done in an attempt to achieve the project's aims.

Project questions

- Is the Loch Maree wild trout population genetically structured?
- If there are structured subpopulations, what are their relative levels of genetic diversity?
- How much of the returning sea trout to Loch Maree originate from the Loch Maree catchment? Is there any contribution from neighbouring catchments?
- Are resident brown trout populations at the source of a unidirectional gene flow (above impassable waterfalls) genetically distinct to populations below the barrier?
- Are Ferox trout genetically distinguishable from brown/sea trout?