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Genetic diversity and population structure of the threatened Bliss Rapids snail (*Taylorconcha serpenticola*)

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SUMMARY

1. The Bliss Rapids snail is a federally listed yet poorly known small caenogastropod which lives in the Snake River drainage (main stem river and spring-fed tributaries) of south-central Idaho. The construction of three large dams along this portion of the Snake River during the 20th century is thought to have fragmented a single, ancestral population of this species into genetically isolated subunits that are vulnerable to extinction. We assessed variation of 11 microsatellite loci within and among 29 samples (820 snails) from across the entire range of the Bliss Rapids snail to assess genetic structure and test whether habitat fragmentation resulting from dam construction has impacted population connectivity.
2. The overall F_{ST} (0.15133, $P < 0.05$) and pairwise comparisons among samples (384/406 significant) indicated extensive population subdivision in general. A consistent trend of isolation by distance trend was not detected by Mantel tests. We found no evidence of reduced genetic diversity attributable to segmentation of the Snake River, and genetic variation among portions of drainage separated by the dams was not significant. Population structuring in spring–tributary habitats was considerably greater than in the main stem river as evidenced by differences in F_{ST} (0.18370, 0.06492) and the number of private alleles detected (16, 4), and by the results of an assignment test (69.4%, 58.7% correctly classified to sample of origin) and Bayesian genetic clustering algorithm.
3. Our results provide no evidence that dam construction has genetically impacted extant populations of the Bliss Rapids snail. We speculate that the generally weaker genetic structuring of riverine populations of this species is a result of passive dispersal within the water column, which may enable occasional passage through the dams. The somewhat stronger structuring observed in a portion of the river (Shoshone reach) which receives discharge from many springs may be due to local mixing of main stem and more highly differentiated tributary populations. Our findings parallel recent, genetically based studies of other western North American freshwater gastropods that also demonstrate complex population structure that conflicts with traditional concepts of dispersal ability and sensitivity to putative barriers.

Keywords: dams, microsatellites, population structure, Snake River, *Taylorconcha serpenticola*

Introduction

The caenogastropod genus *Taylorconcha* is composed of two small, lotic species which live in the Snake River basin in the northwestern United States (Hershler *et al.*, 1994, 2006). One of these species, the Bliss Rapids snail (*T. serpenticola*, Hershler *et al.*, 1994), is endemic to a short (*c.* 105 km, USFWS, 2007) reach of

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the Snake River and various spring-fed tributaries to this master stream in south-central Idaho. This snail typically lives on cobbles and boulders, occurring in densities up to *c.* 3000 m^{-2} (Richards, Falter & Steinhorst, 2006). The portion of the Snake River catchment inhabited by the Bliss Rapids snail has been highly modified by human activities and in 1992 this species and four other local gastropods were added to the Federal List of Endangered and Threatened Wildlife because of the impacts of or threats posed by existing and proposed hydropower dams, water pollution, water withdrawal and diversions, inadequate regulatory mechanisms and the introduced New Zealand mudsnail, *Potamopyrgus antipodarum* (Gray, 1853) (USFWS, 1992).

The United States Fish and Wildlife Service is currently conducting a status review to determine whether delisting of the Bliss Rapids snail is warranted based on the implementation of additional mechanisms to regulate water quality and development, withdrawal of proposals to construct new hydropower facilities, and evidence that this species has a wider, more continuous geographic range and is less threatened by flow fluctuations caused by the existing dams (e.g. peak loading) than previously thought (USFWS, 2007). One threat discussed in the original listing determination (USFWS, 1992) for the Bliss Rapids snail which has been little investigated is the possible loss of population connectivity due to three major Snake River dams (Upper Salmon Falls, Lower Salmon Falls, Bliss) that were constructed between 1910 and 1957 (IPC, 2008) and flooded a substantial fraction of the fluvial habitat formerly available to this species (27.98/105 river km, 26.7%; USFWS, 2004). The Bliss Rapids snail has not been found in the large reservoirs behind these dams despite an intensive sampling effort (Richards *et al*., 2006), although it persists in the intervening free flowing reaches of the river.

Although there have been many studies of the effect of dams (and their associated impoundments) on the genetic structure of fishes, few such investigations have focused on benthic invertebrates (but see Berettoni, Mathieu & Hervant, 1998; Kelly & Rhymer, 2005). The construction of the Snake River dams is assumed to have fragmented a single, large, ancestral population of the Bliss Rapids snail (Taylor, 1982) into smaller, isolated subunits which are potentially vulnerable to loss of genetic variation and extinction (USFWS, 2004, 2005, Richards *et al*., 2006). It has also been suggested that present-day populations have been further subdivided by the diversion and pollution of the lower reaches of tributary streams (USFWS, 2004, 2005). However, the putatively causal relationship between dam construction and genetic fragmentation is based on a generalization that freshwater gastropods readily spread within their preferred habitats yet are unable to traverse terrestrial barriers or patches of unsuitable aquatic environments (Taylor & Bright, 1987). Given that nothing is actually known of the dispersal ability of the Bliss Rapids snail aside from the limited tolerance of this gill-breathing species to desiccation (Richards & Arrington, 2006), additional scenarios regarding the possible impact of the dams on genetic structure may be plausible. For example, this apparently specialized snail might be highly sedentary (Richards, 2004) and 'naturally' subdivided into localized populations, in which case dam construction may not have resulted in further genetic subdivision. Alternatively, it is possible that individuals survive passage through the Snake River impoundments and dams frequently enough to maintain unidirectional gene flow between seemingly isolated colonies, again implying that habitat segmentation may have had less effect on the genetic diversity of the Bliss Rapids snail than currently thought.

We recently published the first genetic study of the Bliss Rapids snail, which described shallow phylogeographic structure (using sequences from the first internal transcribed spacer region of nuclear ribosomal DNA and the mitochondrial cytochrome *c* oxidase gene) consistent with Taylor's (1982) hypothesis that this species was composed of a single continuous population prior to recent habitat fragmentation (Hershler *et al*., 2006). Here, we further examine the genetic characteristics of the Bliss Rapids snail using 11 polymorphic microsatellite loci that we recently developed for this species (Liu & Hershler, 2008). Rapidly evolving microsatellite markers have been frequently utilized for studies of imperilled species, fine-scale population structuring and contemporary evolutionary processes, but have been little applied to freshwater gastropods (but see Weetman, Hauser & Carcalho, 2002; Worthington Wilmer & Wilcox, 2007; Worthington Wilmer *et al*., 2008). Our goals were to evaluate genetic diversity and extent of population subdivision across the geographical range

of the Bliss Rapids snail, and to test whether the fragmentation of riverine habitat resulting from construction of Snake River dams has significantly impacted population connectivity.

Methods

Sampling

This study is based on 820 specimens that were collected from 29 sites during 2006–07. Our survey spanned almost the entire geographical range of the Bliss Rapid snail and encompassed both main stem river (10 samples) and spring-fed tributary (19 samples) habitats (Fig. 1). Six separate tributary systems (Niagara Springs, Banbury Springs, Sand Springs, Thousand Springs, Billingsley Creek, Malad River; Fig. 1) were sampled. Although the majority (20/29) of our samples was from the Shoshone reach (where we sampled several spring complexes in detail), we also obtained collections from drainage segments above, between and below the three Snake River dams which are thought to have fragmented the ancestral population of this species (Fig. 1; Table 1). We were only able to sample three of the four segmented reaches of the main stem river because of the paucity of suitable habitat in the almost entirely impounded segment between the lower and upper Salmon Falls Dams, although we did collect one sample from a tributary of this reach. Specimens were collected from small (*c.* 30 m^2) shallow water areas by hand and preserved in 90% ethanol in the field. Coordinates were determined for collection localities using a global positioning system in the field (Table 1). Additional locality and collection data, and museum voucher numbers for samples are available from the corresponding author upon request. Note that throughout this study, we reserve the use of the term 'population' for genetically differentiated subunits of the Bliss Rapids snail and do not assume that our 29 samples correspond to these entities.

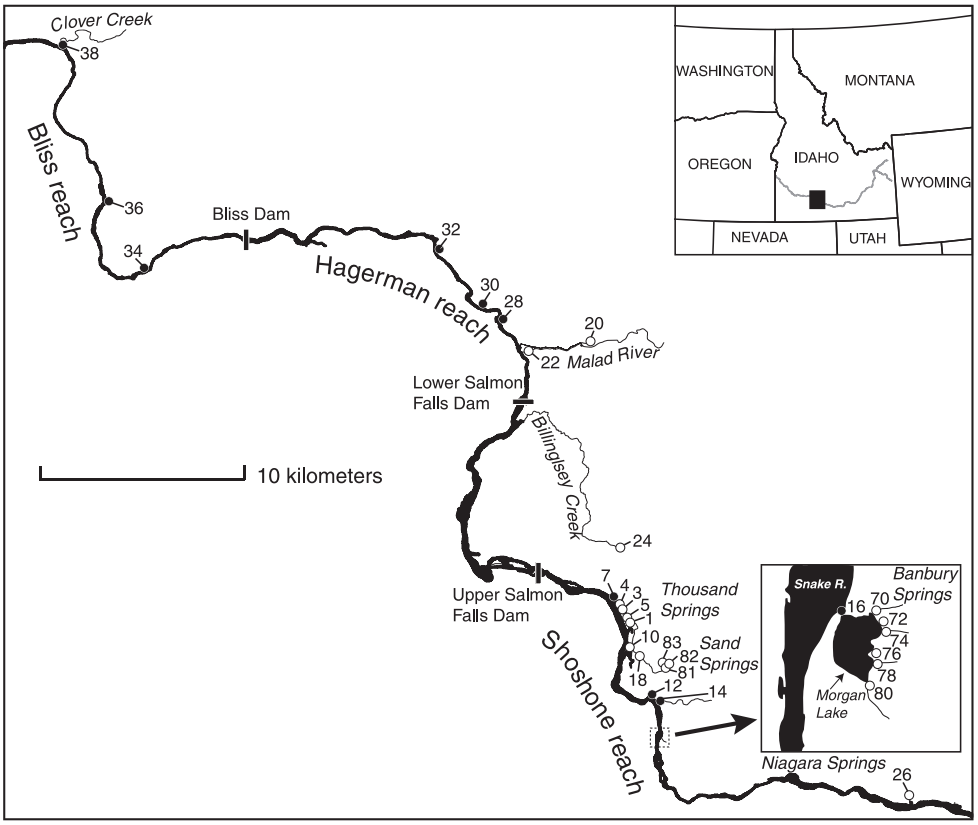

Fig. 1 Location of sampling sites within the Snake River basin in south-central Idaho. Numbers refer to samples listed in Table 1. Mainstem river sites are indicated by filled circles and spring–tributary sites by open circles. Note that only relevant tributaries are shown.

Table 1 Sample number, sample location, UTM NAD83 coordinates, N, N_A, N_R, H_O and H_E per locus

Sample no.	Location	Coordinates	N	N_A	N_R	H_O	H_E
	Shoshone reach						
26	Niagara Springs	690558, 4726111	29	2.1	2.0	0.434	0.419
80	Banbury Springs (G)	678444, 4728606	29	4.0	3.8	0.552	0.594
78	Banbury Springs (F)	678476, 4728681	28	3.9	3.7	0.531	0.578
76	Banbury Springs (E)	678469, 4728752	28	3.6	3.5	0.464	0.493
74	Banbury Springs (C)	678501, 4728816	27	3.5	3.3	0.482	0.507
72	Banbury Springs (B)	678500, 4728860	28	3.7	3.5	0.449	0.465
70	Banbury Springs (A)	678484, 4728888	28	3.4	3.2	0.464	0.503
16*	Snake River at outflow of Morgan Lake	678343, 4728909	28	3.6	3.5	0.451	0.488
14*	Snake River at mouth of Box Canyon	678181, 4730523	28	3.7	3.5	0.413	0.492
12*	Snake River at Blue Springs	677748, 4730990	28	3.7	3.6	0.411	0.481
82	Sand Springs, ca 27.5 m upflow from 81	678664, 4732492	28	3.8	3.7	0.375	0.497
81	Sand Springs, headspring area	678638, 4732485	28	4.1	3.9	0.403	0.480
83	Sand Springs, 30-40 m below source	678660, 4732527	28	3.7	3.6	0.470	0.509
18	Sand Springs, middle reach	677238, 4732800	28	3.8	3.6	0.444	0.508
10	Sand Springs, lower reach	676615, 4733083	28	4.5	4.3	0.406	0.442
1	Thousand Springs, south inlet (Lemon Falls)	676793, 4734195	28	4.2	3.9	0.429	0.420
5	Thousand Springs, south of Minnie Miller	676594, 4734783	30	4.3	4.0	0.412	0.459
3	Thousand Springs, Minnie Miller site	676462, 4734967	28	4.1	3.9	0.541	0.557
4	Thousand Springs, north inlet	676367, 4735060	30	4.1	3.8	0.356	0.419
7*	Snake River at outflow of spring south of Bickel Spring	675670, 4735798	29	4.1	3.9	0.419	0.503
	Between Upper and Lower Salmon Falls Dams						
24	Spring along Billingsley Creek	676028, 4738221	28	2.9	2.9	0.657	0.675
	Hagerman reach						
20	Cove Creek, headspring area	674449, 4748298	28	4.2	4.0	0.365	0.374
22	Malad River, near Snake River confluence	671367, 4747703	30	4.5	4.2	0.282	0.317
28*	Snake River, Sidewinder site	670017, 4749202	28	4.6	4.4	0.525	0.518
30*	Snake River, unnamed point	669108, 4749775	28	4.5	4.3	0.485	0.531
32*	Snake River, at outflow of large spring	667304, 4752162	28	3.8	3.7	0.679	0.716

Table 1 (*Continued*)

Sample no.	Location	Coordinates	N	N_A	N_R	H_O	H_E
	Bliss reach						
34*	Snake River at Pilgrim Springs	652668, 4751411	28	3.8	3.7	0.657	0.682
36*	Snake River at outflow of Bancroft Springs	650470, 4755099	28	3.8	3.6	0.454	0.507
38*	Snake River at mouth of Clover Creek	648244, 4762313	28	4.1	3.9	0.455	0.443

Sample numbers correspond to those used in Fig. 1.
N, sample size; N_A, mean number of alleles; N_R, mean allelic richness; H_O, mean observed heterozygosity diversity; H_E, mean expected heterozygosity.
*Sample from mainstem Snake River.

Laboratory methods

Genomic DNA was isolated from individual snails using a CTAB protocol (Bucklin, 1992). DNA was extracted from 27 to 30 snails per sample. All samples were screened with a panel of 11 microsatellite markers (BRSCA4, BRSM3, BRSM4-1, BRSM4-2, BRSM6, BRSM16, BRSM18, BRSM30, BRSM37, BRSM56, BRSM57) following protocols described in Liu & Hershler (2008).

Data analysis

Descriptive statistics consisting of the number of alleles (N_A) and allelic richness (N_R) adjusted for differences in sample size were compiled using FSTAT 2.9.3.2 (Goudet, 2001). Wilcoxon matched-pairs signed-ranks tests were used to evaluate possible differences in allelic richness among samples. Observed and expected heterozygosity, and deviation from Hardy–Weinberg equilibrium (HWE) for each locus-sample combination were calculated using ARLEQUIN 3.01 (Excoffier, Laval & Schneider, 2005). Linkage disequilibrium was tested using GENEPOP 3.4 (Raymond & Rousset, 1995) default values for all combinations of locus pairs within samples. We applied the modified false discovery rate (Benjamini & Yekutieli, 2001; referred to herein as the B–Y method following Narum, 2006) to correct the results of the latter two analyses for multiple testing.

Genetic differentiation was investigated by calculation of an overall estimate and pairwise comparison of F_{ST} values among samples (Weir & Cockerham, 1984) using ARLEQUIN 3.11 (Excoffier *et al.*, 2005). The results of these comparisons were adjusted using the B–Y correction. Isolation by distance (based on all of our samples) was assessed using a Mantel test implemented in the program IBD version 3.1.5 (Bohonak, 2002), which correlates genetic and geographical distance based on pairwise comparisons. We also tested for isolation by distance using only main stem river samples, tributary samples and samples from within individual tributary systems (Banbury, Sand, Thousand Springs). Rousset's (1997) measure of genetic distance $[F_{ST}/(1 - F_{ST})]$ was used for these tests. Pairwise geographical distances between sampling localities were measured as stream distances, which were modelled using ESRI ARCGIS software with the Network Analyst extension (http://www.esri.com/software/arcgis/extensions/networkanalyst/index.html). Stream network data were from the National Hydro Dataset (http://nhd.usgs.gov/). Partitioning of genetic variation was assessed by an analysis of molecular variance (AMOVA; Excoffier, Smouse & Quattro, 1992) performed in ARLEQUIN. We tested for genetic divisions between the main stem river and tributaries, and between tributaries. We also evaluated partitions between portions of Snake River drainage that are separated by dams, with separate analyses conducted based on all samples and main stem river samples only.

As an additional means of examining the genetic similarity among samples we calculated chord distance (D_{CE}, Cavalli-Sforza & Edwards, 1967) values with GENEDIST and used the resulting distance matrix to construct an unrooted neighbour-joining network with NEIGHBOR (PHYLIP, version 3.57c; Felsenstein, 1995). D_{CE} was used instead of other distance measures because of its greater accuracy in identifying the correct tree topology and because it has a low sampling error and makes no assumptions about population size and loci mutation rates (Takezaki &

Nei, 1996). Topological confidence was evaluated with 1000 bootstrap replicates using SEQBOOT and CONSENSE in the PHYLIP package.

Population structure was further evaluated using individual-based programs. We used the Bayesian algorithm in STRUCTURE 2.2 (Pritchard, Stephens & Donnelly, 2000) to infer the number of genetic clusters (K) represented in our data set. This program assigns specimens to clusters based on their genotypes without consideration of geographic information (e.g. sample origin) and consequently is a potentially tool for inferring cryptic genetic structure. However, given that this program works best for small numbers of samples (Pritchard, Wen & Falush, 2007) and the resulting clusters do not necessarily correspond to 'real' populations (Pritchard *et al.*, 2000) we used it to complement our other analyses of genetic differentiation. Ten independent runs of K = 1–29 were first performed with 100 000 burn-in and 100 000 Markov chain Monte Carlo (MCMC) repetitions without prior locality information and assuming correlated allele frequencies and an admixture model. Ten additional, independent runs of K = 6–16 were performed with 250 000 burn-in and 250 000 MCMC repetitions using the above model. The most probable value of K was estimated by inspection of ΔK (Evanno, Regnaut & Goudet, 2005) and log-likelihood [log $\Pr(X|K)$] (Pritchard *et al.*, 2000) statistics, and a final run using this number of clusters was conducted with 1 000 000 burn-in and 1 000 000 iterations. We also assessed the accuracy with which individual snails could be assigned to their sample of origin using the Bayesian method of Rannala & Mountain (1997) that is implemented in GENECLASS2 (Piry *et al.*, 2004).

Results

The number of observed alleles (per locus) across all samples ranged from three (BRSM4-1) to 20 (BRSM3) (Liu & Hershler, 2008; Table 1) and the mean ranged from 2.1 (sample 26; Niagara Springs, the most up flow main stem river locality) to 4.6 (28; Snake River, Sidewinder site) (Table 1). Private alleles were observed in eight loci (BRSM3, BRSM4-1, BRSM6, BRSM18, BRSM30, BRSM37, BRSM56 and BRSM57). The number of private alleles ranged from one (BRSM4-1, BRSM6, BRSM30) to four (BRSM18, BRSM56 and BRSM57). Sixteen of the 20 private alleles were observed in tributary samples. Levels of allelic richness were similar among samples with Niagara Springs having the lowest (2.0) and the Snake River Sidewinder site having the highest (4.4; Table 1). Only one sample (from Niagara Springs) had significantly lower allelic richness when compared with all others using the Wilcoxon matched-pairs signed-ranks test. Expected heterozygosity ranged from 0.317 to 0.716 (Table 1).

There were 22 significant departures from HWE among the 319 possible combinations of sample and loci based on P = 5%. After applying the B–Y correction, 11 sample/locus comparisons were significant ($P \leq 0.007881$). Nine of these were at the BRSM3 locus (samples 5, 7, 10, 16, 32, 36, 81, 82, 83), one was at the BRSM18 locus (sample 14), and one was at the BRSM30 locus (sample 3). The presence of null alleles was the most probable explanation for heterozygote deficiency at the BRSM3 locus. The test for linkage equilibrium examined each pair of loci in each sample for a total of 1595 comparisons. After applying the B–Y correction ($P \leq 0.006288$), three were significant – BRSM3 and BRSM37 loci in sample 3, BRSM3 and BRSM16 in sample 14 and BRSM56 and BRSM37 in sample 18. The various microsatellite loci investigated appeared to segregate independently.

The overall F_{ST}, which provides a measure of genetic subdivision across all samples, was 0.15133 ($P < 0.05$). The overall F_{ST} for spring–tributary samples (0.18370, $P < 0.05$) was considerably larger than that of mainstem river samples (0.06492, $P < 0.05$). Pairwise comparisons of F_{ST} were significant in all but 21 cases (385/406) after adjusting for multiple comparisons ($P \leq 0.007593$) (Table 2). Eighteen of the 21 non-significant comparisons consisted of pairs of samples from the Hagerman/Bliss reach of the main stem Snake River, or from a single tributary system (Banbury, Sand, Thousand Springs). The other three consisted of comparisons between samples from Thousand Springs and Banbury Springs, or between one of these spring complexes and proximal mainstem river localities. Pairwise F_{ST} estimates ranged from −0.006 (samples 34–36) to 0.519 (20–26). The Niagara Springs (26) and Cove Creek (20) samples were the most differentiated; mean F_{ST} compared to all other samples = 0.383 and 0.280, respectively. The least differentiated samples were the six from the Hagerman/Bliss reach of the main stem river (mean F_{ST} = 0.018). We also calculated pairwise F_{ST} without the BRSM3 locus to explore the possible effects of

Table 2 Pairwise F_{ST} (below diagonal) and probability that allelic frequencies are identical (above diagonal)

Sample no.	26	80	78	76	74	72	70	16	14	12	82	81	83	18	10	01
26	–	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
80	0.374	–	***	***	***	***	***	***	***	***	***	***	***	***	***	***
78	0.253	0.072	–	***	***	***	***	NS	***	***	***	***	***	***	***	***
76	0.292	0.164	0.051	–	NS	***	***	***	***	***	***	***	***	***	***	***
74	0.295	0.230	0.082	0.004	–	***	***	***	***	***	***	***	***	***	***	***
72	0.421	0.060	0.107	0.184	0.247	–	NS	***	***	***	***	***	***	***	***	***
70	0.495	0.085	0.139	0.220	0.288	0.010	–	***	***	***	***	***	***	***	***	***
16	0.279	0.038	0.006	0.075	0.110	0.080	0.115	–	***	***	***	***	***	***	***	***
14	0.327	0.116	0.074	0.103	0.150	0.159	0.188	0.071	–	***	***	***	***	***	***	***
12	0.422	0.119	0.134	0.176	0.237	0.161	0.181	0.126	0.169	–	***	***	***	***	***	***
82	0.518	0.109	0.148	0.243	0.313	0.114	0.126	0.131	0.205	0.182	–	NS	NS	***	***	***
81	0.466	0.087	0.120	0.202	0.269	0.089	0.112	0.107	0.186	0.161	0.006	–	NS	***	***	***
83	0.508	0.099	0.161	0.233	0.306	0.093	0.105	0.135	0.210	0.143	0.010	0.013	–	***	***	***
18	0.457	0.094	0.144	0.214	0.279	0.069	0.087	0.116	0.186	0.185	0.055	0.040	0.036	–	***	***
10	0.462	0.061	0.112	0.188	0.264	0.049	0.052	0.097	0.140	0.118	0.040	0.033	0.022	0.028	–	***
01	0.283	0.130	0.051	0.050	0.090	0.200	0.239	0.063	0.098	0.134	0.212	0.174	0.204	0.212	0.168	–
05	0.308	0.136	0.060	0.061	0.099	0.196	0.230	0.079	0.128	0.130	0.181	0.137	0.168	0.178	0.151	0.016
03	0.253	0.062	0.027	0.081	0.119	0.103	0.145	0.015	0.073	0.110	0.138	0.106	0.124	0.112	0.096	0.044
04	0.192	0.086	0.019	0.085	0.111	0.150	0.205	0.020	0.093	0.143	0.198	0.164	0.200	0.190	0.163	0.043
07	0.412	0.119	0.116	0.123	0.186	0.182	0.199	0.128	0.132	0.092	0.202	0.173	0.179	0.206	0.141	0.119
24	0.457	0.063	0.130	0.205	0.277	0.104	0.118	0.115	0.175	0.119	0.125	0.098	0.111	0.132	0.074	0.173
20	0.519	0.218	0.259	0.341	0.403	0.272	0.283	0.256	0.298	0.266	0.319	0.302	0.310	0.311	0.255	0.295
22	0.404	0.106	0.116	0.167	0.243	0.161	0.168	0.131	0.147	0.121	0.239	0.212	0.219	0.233	0.142	0.116
28	0.387	0.063	0.082	0.121	0.192	0.117	0.141	0.077	0.112	0.060	0.113	0.099	0.097	0.139	0.076	0.082
30	0.389	0.082	0.106	0.141	0.211	0.127	0.150	0.106	0.139	0.074	0.146	0.128	0.110	0.143	0.090	0.123
32	0.391	0.047	0.088	0.138	0.214	0.098	0.116	0.087	0.112	0.069	0.123	0.101	0.099	0.135	0.063	0.107
34	0.397	0.036	0.091	0.139	0.217	0.081	0.110	0.076	0.123	0.071	0.116	0.090	0.090	0.120	0.054	0.106
36	0.407	0.039	0.094	0.144	0.219	0.085	0.103	0.076	0.128	0.065	0.110	0.087	0.077	0.108	0.049	0.104
38	0.367	0.063	0.090	0.121	0.189	0.125	0.162	0.088	0.123	0.082	0.144	0.124	0.124	0.161	0.100	0.094

	05	03	04	07	24	20	22	28	30	32	34	36	38
26	***	***	***	***	***	***	***	***	***	***	***	***	***
80	***	***	***	***	***	***	***	***	***	***	***	***	***
78	***	***	NS	***	***	***	***	***	***	***	***	***	***
76	***	***	***	***	***	***	***	***	***	***	***	***	***
74	***	***	***	***	***	***	***	***	***	***	***	***	***
72	***	***	***	***	***	***	***	***	***	***	***	***	***
70	***	***	***	***	***	***	***	***	***	***	***	***	***
16	***	NS	NS	***	***	***	***	***	***	***	***	***	***
14	***	***	***	***	***	***	***	***	***	***	***	***	***
12	***	***	***	***	***	***	***	***	***	***	***	***	***
82	***	***	***	***	***	***	***	***	***	***	***	***	***
81	***	***	***	***	***	***	***	***	***	***	***	***	***
83	***	***	***	***	***	***	***	***	***	***	***	***	***
18	***	***	***	***	***	***	***	***	***	***	***	***	***
10	***	***	***	***	***	***	***	***	***	***	***	***	***
01	***	***	***	***	***	***	***	***	***	***	***	***	***
05	–	***	***	***	***	***	***	***	***	***	***	***	***
03	0.034	–	NS	***	***	***	***	***	***	***	***	***	***
04	0.062	0.018	–	***	***	***	***	***	***	***	***	***	***
07	0.126	0.124	0.144	–	***	***	***	***	***	***	***	***	***
24	0.179	0.131	0.165	0.118	–	***	***	***	***	***	***	***	***
20	0.314	0.270	0.282	0.264	0.247	–	***	***	***	***	***	***	***
22	0.152	0.128	0.141	0.094	0.123	0.186	–	***	***	***	***	***	***
28	0.096	0.073	0.097	0.027	0.071	0.229	0.066	–	NS	NS	NS	NS	NS

Table 2 (*Continued*)

	05	03	04	07	24	20	22	28	30	32	34	36	38
30	0.125	0.093	0.124	0.023	0.098	0.245	0.096	0.017	–	***	***	***	***
32	0.122	0.090	0.114	0.041	0.053	0.218	0.057	0.002	0.020	–	NS	NS	NS
34	0.125	0.087	0.112	0.063	0.040	0.223	0.068	0.008	0.038	0.003	–	NS	NS
36	0.112	0.069	0.115	0.057	0.048	0.221	0.065	0.005	0.030	0.004	−0.006	–	NS
38	0.110	0.082	0.093	0.038	0.089	0.240	0.082	0.001	0.026	0.008	0.012	0.016	–

NS, not significant; ***$P < 0.000123$.

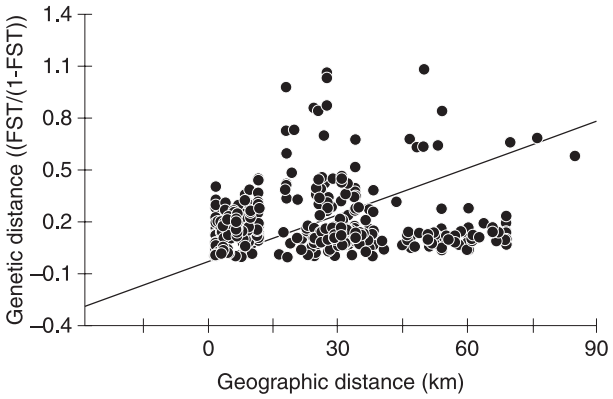

Fig. 2 Reduced major axis regression of genetic and geographical distances based on all pairwise combinations of samples.

possible null alleles. The results were closely similar to the above – only 24 of 406 comparisons were not significant and 17 of these involved pairs of samples from the Hagerman/Bliss main stem reach, or from a single tributary system. Genetic variation was not significantly correlated with stream distances based on pairwise comparisons of all samples using the Mantel test ($r = 0.1095$, $P = 0.1756$, Fig. 2). The correlation was also non-significant when only main stem river samples were analysed ($r = 0.1775$, $P = 0.1303$); however a weak, positive relationship was found in comparisons involving tributary samples ($r = 0.5$, $P = 0.0068$). The correlation was non-significant in separate analyses of the Banbury ($r = 0.188$, $P = 0.2353$, six samples), Sand Springs ($r = 0.6995$, $P = 0.0582$, five samples) and Thousand Springs ($r = 0.2009$, $P = 0.2870$, four samples) tributary systems.

In each of the four AMOVAs most of the variance was distributed within populations (80–93%) (Table 3). Only 1.41% of the total allelic frequency variation was explained by the grouping of tributary and main stem river samples while a larger (12.48%)

Table 3 Analysis of molecular variance (AMOVA) for four population structures

Source of variation	d.f.	Variance components	% of variation	Φ-Statistic
By tributary versus riverine habitat, two groups: (1,3,4,5,10,18,20,22,24,26,70,72,74,76,78,80,81,82,83), river (7,12,14,16,28,30,32,34,36,38)				
Among groups	1	0.02783	1.41	$\Phi_{CT} = 0.01408$
Among samples within groups	27	0.28389	14.36	$\Phi_{SC} = 0.14568$*
Within samples	1611	1.66490	84.23	$\Phi_{ST} = 0.15770$*
By tributary system, six groups: Niagara (26), Banbury (70,72,74,76,78,80), Sand (10,18,81,82,83), Thousand (1,3,4,5), Billingsley (24), Malad (20,22)				
Among groups	5	0.25331	12.48	$\Phi_{CT} = 0.12479$*
Among samples within groups	13	0.15784	7.78	$\Phi_{SC} = 0.08885$*
Within samples	1059	1.6187	79.74	$\Phi_{ST} = 0.20256$*
By river reach (all localities), four groups: Shoshone (1,3,4,5,7,10,12,14,16,18,26,70,72,74,76,78,80,81,82,83), between Upper and Lower Salmon Falls Dams (24), Hagerman (20,22,28,30,32), Bliss (34,36,38)				
Among groups	3	0.04531	2.28	$\Phi_{CT} = 0.02283$
Among samples within groups	25	0.27426	13.82	$\Phi_{SC} = 0.14143$*
Within samples	1611	1.66490	83.90	$\Phi_{ST} = 0.16103$*
By river reach (mainstem river localities only), three groups: Shoshone (7,12,14,16), Hagerman (28,30,32), Bliss (34,36,38)				
Among groups	2	0.00876	0.47	$\Phi_{CT} = 0.00467$
Among samples within groups	7	0.11530	6.14	$\Phi_{SC} = 0.06169$*
Within samples	552	1.75359	93.39	$\Phi_{ST} = 0.06607$*

*$P \leq 0.05$.

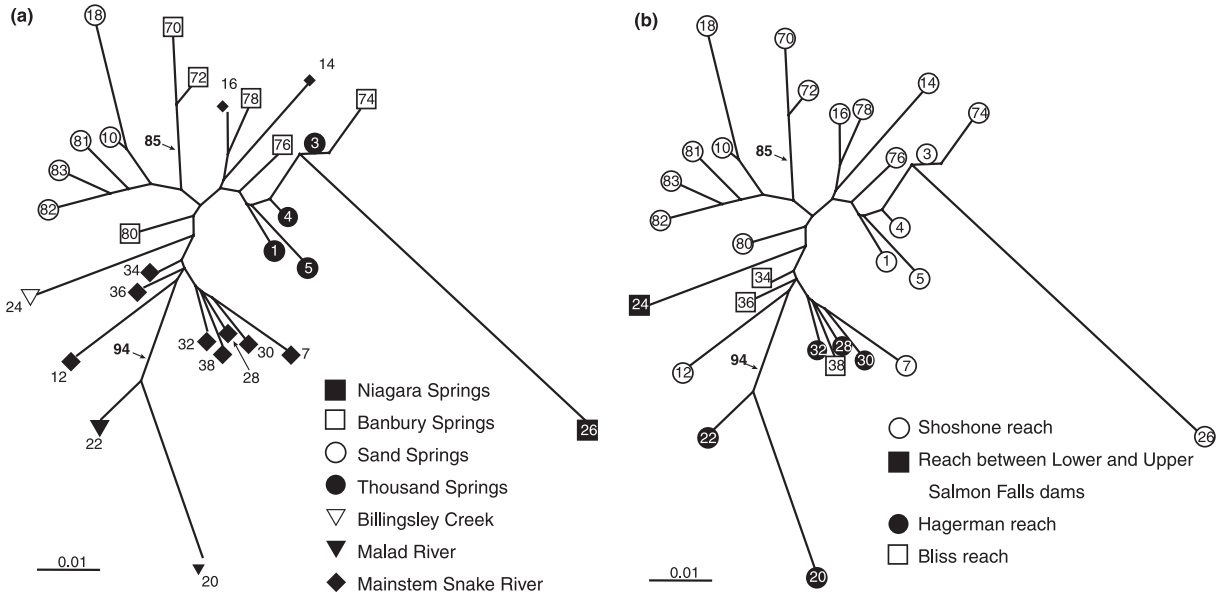

Fig. 3 Neighbour-joining network based on chord distances for 29 samples coded by habitat (a) and river reach (b). Bootstrap values (small, bold-faced font) are shown for nodes when ≥85%.

and significant amount of variation was explained by differences among the six tributary systems (Table 3). Variation among the reaches of drainage segmented by Snake River dams was very small and non-significant in analyses that included all samples (2.28%) and main stem river samples only (0.47%). Closely similar results were obtained when we performed the same set of analyses without the BRSM3 locus.

Relationships based on Cavalli-Sforza & Edwards (1967) chord distance with samples coded by habitat, and by river reaches separated by dams are shown in Fig. 3a,b, respectively. Samples from the Malad system and Sand Springs formed distinct groups and the single samples from Billingsley Creek and Niagara Springs were differentiated by long branches (Fig. 3a). Samples from the other two tributary systems (Banbury and Thousand Springs) were spread among multiple clusters. All but two (14, 16) of the main stem river samples were clustered in the portion of the network that also contained the Malad system samples. When samples are coded by reaches (Fig. 3b), the resulting groupings clearly were non-random with respect to this category (e.g. 18 of the 21 samples from the Shoshone reach formed a cluster), although none of the three drainage segments from which more than one sample was collected formed an exclusive group (Fig. 3b).

The Bayesian assignment analysis (Table 4) correctly assigned about two-thirds (539/820, 65.7%) of the snails to their sample of origin. The proportion of correctly assigned individuals was considerably lower for main stem river samples (46.4–85.7%, 58.7% average) than for those from spring to tributary habitats (64.3–100%, 69.4%). This disparity was even more pronounced in the assignment of snails to the correct river reach or spring complex (Table 4).

The most appropriate number of genetic clusters (K) was estimated to be nine using both the Pritchard *et al.* (2000) and Evanno *et al.* (2005) methods. The proportional membership of the 29 samples in each of the nine clusters is given in Table 5 and portrayed using pie diagrams on a map in Fig. 4. Although the proportional membership for a given sample assigned to a particular cluster was rarely >50% (Table 5), the genetic structure delineated by this analysis nonetheless suggests several patterns relating to habitat and drainage that are relevant to our study (Fig. 4).

One of the discernable patterns is the genetic distinctiveness of samples collected from the spring-fed tributaries. For example, 93% of specimens from Niagara Springs, 71% from Billingsley Creek and 55–85% from the Malad system (two samples) were assigned to clusters 9, 8 and 2, respectively. The cluster analysis also suggests a varying amount of population subdivision within the tributary systems.

Table 4 Results of the assignment test based on genotype frequencies at 11 microsatellite loci

Sample no.	Sample (*A*)	River reach (*B*)	Tributary (*C*)	*A* + *B*/*C*
16*	46.4	–	–	46.4
14*	85.7	–	–	85.7
12*	78.6	–	–	78.6
7*	58.6	6.9	–	65.5
28*	53.6	3.6	–	57.1
30*	53.6	14.3	–	67.0
32*	53.6	10.7	–	64.3
34*	39.3	17.9	–	57.1
36*	53.6	7.1	–	60.7
38*	64.3	10.7	–	75.0
26	100.0	–	–	100.0
80	58.6	–	10.3	69.0
78	60.7	–	17.9	78.6
76	50.0	–	28.6	78.6
74	77.8	–	11.1	88.9
72	57.1	–	21.4	78.6
70	85.7	–	7.1	92.9
82	64.3	–	28.6	92.9
81	50.0	–	28.6	78.6
83	57.1	–	32.1	89.3
18	85.7	–	10.7	96.4
10	50.0	–	14.3	64.3
1	71.4	–	7.1	78.6
5	80.0	–	10.0	90.0
3	50.0	–	28.6	78.6
4	56.7	–	20.0	76.7
24	89.3	–		89.3
20	96.4	–	3.6	100.0
22	76.7	–	3.3	80.0

Values indicate the percentage of individuals correctly assigned to the sample of origin and river reach/tributary of origin.
*Sample from mainstem Snake River.

Specimens from the six springs that we sampled in the Banbury complex (Fig. 4, insert) were most frequently assigned to clusters 2–8 (sample 80), 2–6 (78), 6 (76), 6 (74), 5 (72) and 5 (70), which suggests that they may represent as many as four genetically distinct populations. In contrast, the four samples from Thousand Springs (1, 3, 4, 5) were closely similar in genetic structure, each having relatively high membership in cluster 2. A different pattern was evident in the Sand Springs samples. Although these formed a distinct group with relatively high membership in clusters 3 and 5, they are clearly differentiated into separate headspring (81, 82, 83) and down flow (10, 18) subunits based on higher membership in clusters 3 (32–52%) and 5 (31–49%), respectively. Similarly, the two samples from the Malad system (20, 22) formed a distinctive group based on their large representation in cluster 7, but are readily distinguished from each other by the proportions of specimens assigned to this (85, 55%, respectively) and several other clusters. The other pattern revealed by STRUCTURE is the striking similarity of seven of the 10 samples from the main stem river (7, 28, 30, 32, 34, 36, 38) which, although highly mixed in membership, are nonetheless united by the relatively large proportion of specimens assigned to clusters 1 and 4. Note that these samples are spread among three reaches of river separated by dams (Shoshone, Hagerman, Bliss). The other three main stem river samples (12, 14, 16), which are in the Shoshone reach, are clearly differentiated from each other.

Discussion

One of our goals was to document genetic diversity and population subdivision of the Bliss Rapids snail. Our previous study (Hershler *et al.*, 2006) had depicted shallow phylogeographical structure (based on sequences from the first internal transcribed spacer region of nuclear ribosomal DNA and the mitochondrial cytochrome *c* oxidase gene), suggesting that this species may be composed of a single continuous population. In contrast, in this study we found significant differentiation among most samples, with levels of divergence (pairwise F_{ST} = −0.006–0.519) comparable to those obtained in a recent study of microsatellite variation in a related Australian species that lives in a poorly integrated desert spring system (pairwise F_{ST} = −0.016–0.326; Worthington Wilmer & Wilcox, 2007). We are not aware of any studies of microsatellite variation in other dioecious, freshwater gastropods. We documented significant genetic divergence among samples from a single spring complex separated by as little as 300 m (e.g, samples 70, 74; F_{ST} = 0.288), among samples from separate spring to tributary systems (e.g. sample 26 compared to all others, F_{ST} = 0.192–0.519), and among samples collected within continuous habitat (e.g. samples 7, 12, 14, 16, F_{ST} = 0.071–0.169). These findings, together with the assignment test and STRUCTURE results, provide strong evidence that the Bliss Rapids snail is a generally sedentary species which is structured into a large number of genetically differentiated populations.

Our other goal was to test whether the large dams, which have fragmented the portion of the Snake River inhabited by the Bliss Rapids snail and impounded a

Table 5 Proportional membership of samples in each of the nine genetic clusters inferred by STRUCTURE 2.2

	Clusters								
Sample no.	1	2	3	4	5	6	7	8	9
26	0.009	0.011	0.007	0.008	0.008	0.015	0.007	0.008	**0.925**
80	0.133	0.237	0.062	0.057	0.092	0.035	0.142	0.211	0.032
78	0.052	0.248	0.085	0.049	0.089	0.219	0.074	0.076	0.112
76	0.077	0.068	0.024	0.029	0.059	**0.597**	0.022	0.025	0.099
74	0.063	0.054	0.019	0.031	0.032	**0.676**	0.016	0.019	0.090
72	0.070	0.057	0.049	0.060	0.474	0.085	0.059	0.101	0.045
70	0.061	0.044	0.052	0.042	**0.566**	0.081	0.050	0.089	0.016
16	0.074	0.219	0.047	0.074	0.125	0.241	0.043	0.092	0.085
14	0.048	0.054	0.204	0.033	0.124	0.411	0.027	0.029	0.070
12	0.082	0.083	0.040	**0.629**	0.030	0.020	0.041	0.058	0.017
82	0.026	0.101	**0.524**	0.036	0.085	0.021	0.019	0.175	0.013
81	0.079	0.181	0.316	0.058	0.106	0.053	0.019	0.167	0.020
83	0.065	0.102	0.419	0.058	0.163	0.021	0.019	0.138	0.014
18	0.024	0.141	0.158	0.023	0.490	0.027	0.025	0.098	0.014
10	0.064	0.104	0.237	0.076	0.305	0.036	0.042	0.121	0.014
01	0.107	0.250	0.049	0.105	0.066	0.178	0.055	0.077	0.113
05	0.064	0.435	0.055	0.116	0.026	0.104	0.055	0.071	0.074
03	0.047	0.298	0.114	0.068	0.100	0.096	0.048	0.093	0.135
04	0.082	0.224	0.043	0.124	0.043	0.109	0.048	0.089	0.239
07	0.283	0.033	0.120	0.187	0.033	0.168	0.102	0.054	0.020
24	0.051	0.029	0.028	0.074	0.026	0.022	0.047	**0.709**	0.013
20	0.024	0.020	0.017	0.022	0.013	0.011	**0.851**	0.031	0.011
22	0.126	0.041	0.019	0.125	0.030	0.040	**0.551**	0.046	0.022
28	0.241	0.072	0.140	0.262	0.039	0.044	0.074	0.080	0.047
30	0.303	0.041	0.127	0.190	0.102	0.045	0.069	0.093	0.030
32	0.280	0.036	0.104	0.239	0.062	0.064	0.077	0.114	0.024
34	0.289	0.059	0.053	0.181	0.058	0.053	0.098	0.178	0.030
36	0.248	0.100	0.060	0.186	0.087	0.037	0.113	0.148	0.021
38	0.390	0.067	0.094	0.201	0.031	0.054	0.051	0.075	0.036

Values given in bold are >50%.

substantial amount of fluvial habitat, have had an effect on genetic variation within this species. Our data do not support this hypothesis. Genetic diversity is rather uniform across all samples (excepting that from Niagara Springs) and we found no evidence of reduced allelic richness and expected heterozygosity consistent with population fragmentation by dams. Nor did we find significant genetic differences among the portions of the catchment separated by these structures, regardless of whether all 29 samples or only the 10 from the main stem river were included in the AMOVA. These results parallel several studies of unionid mussels (Kelly & Rhymer, 2005) and fishes (e.g. Burridge & Gold, 2003; Reid *et al*., 2008) that also found no significant impact of dams on microsatellite variation.

One possible explanation for this somewhat surprising finding is that not enough time has passed since the construction of the Snake River dams in the early–middle part of the last century to detect any resulting genetic changes in this snail. Other studies have documented a significant genetic impact of recently constructed dams on fishes (e.g. Laroche *et al*., 1999; Taylor, Stamford & Baxter, 2003; Stamford & Taylor, 2005; Heggenes & Røed, 2006; Bessert & Ortí, 2008) that have much longer generation times than the Bliss Rapids snail, which is an annual species (Hershler *et al*., 1994). However, this comparison is constrained by the likelihood that the effective population sizes within these two groups are quite different. If the Bliss Rapids snail is structured into large populations, then it may well be too early to discern a genetic impact from dam construction. Unfortunately, we cannot further explore this possibility because there are no data on the population sizes of this species (USFWS, 2008). Another

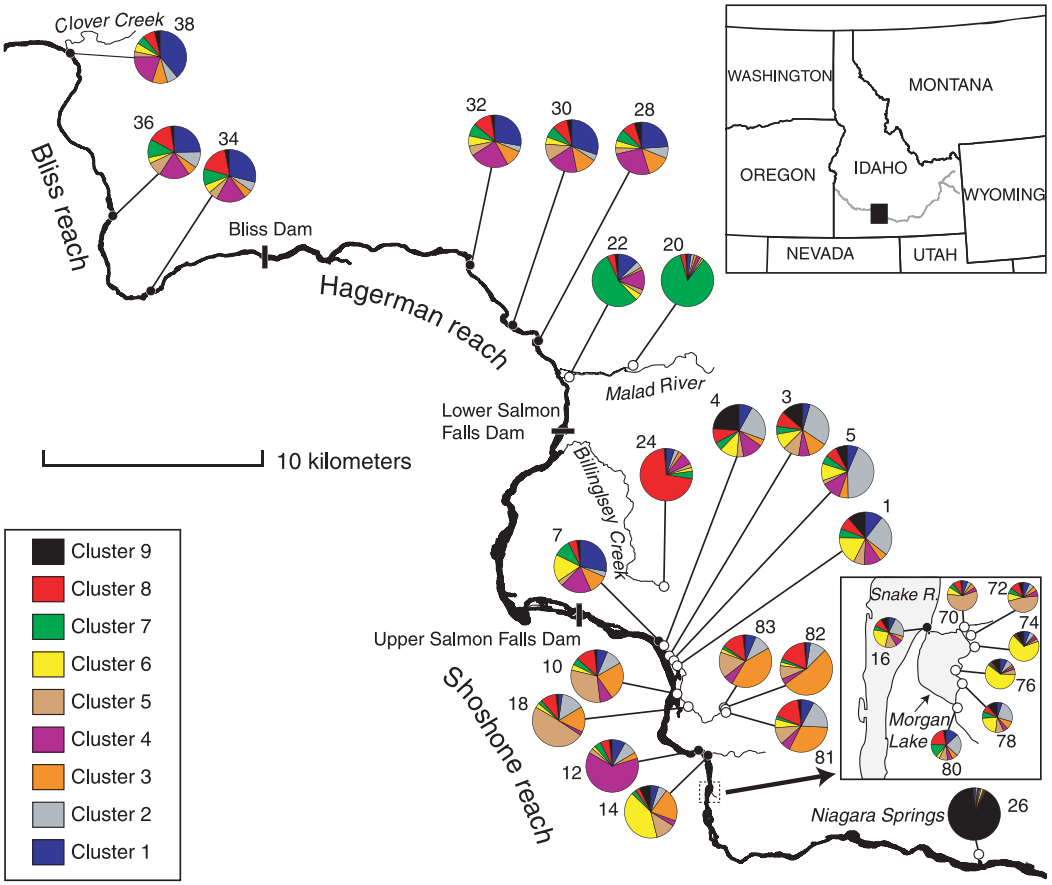

Fig. 4 Pie charts for 29 collection localities showing proportional membership in each of nine clusters identified by STRUCTURE (data from Table 5). Sample numbers correspond to those in Fig. 1 and Table 1. Mainstem river sites are indicated by filled circles and spring–tributary sites by open circles.

possibility is that snails are passing through or across the dams frequently enough to prevent detection of a genetic structuring effect. The strongest evidence for this comes from the westernmost portion of this snail's range where we sampled along a 37 km reach of the river that is subdivided by the Bliss Dam. Pairwise F_{ST} values between samples from either side of the dam (28, 30, 32, Hagerman reach; 34, 36, 38, Bliss reach) were very small (0.003–0.038), and non-significant in six of nine comparisons. The absence of significant differentiation was also suggested by STRUCTURE, which depicted closely similar memberships of these samples to the nine clusters (Fig. 4).

Our results suggest that spring–tributary populations are more strongly structured (e.g. overall F_{ST} = 0.18370, 16 private alleles detected, 69.4% of specimens correctly assigned) than those of the main stem Snake River (F_{ST} = 0.06492, four private alleles, 58.7% correct assignment). Based on these findings we speculate that the Bliss Rapids snail, while apparently sedentary in general, may be subject to passive transport in the main stem river and occasionally pass through the Snake River dams by this mechanism. The latter may be most likely during periods of large discharge, such as when the river is augmented by snow melt in the spring and early summer (Stanford *et al.*, 2005). Note that this form of dispersal may be largely independent of distance (Knutsen *et al.*, 2003) and its occurrence may thus contribute to the absence of a correlation between stream and genetic distance in our data set. We suggest that weak structuring and relatively elevated gene flow may be typical of main stem populations of the Bliss Rapids snail, but was not observed in the Shoshone reach because of the strongly spring-influenced character of this portion of the Snake River.

This reach receives discharge from a large number of springs (Thomas, 1968) and we suspect that some of the main stem samples that we collected may be composed, at least in part, of individuals from the typically well differentiated populations that live in these tributary habitats, thus obscuring the local genetic structuring of 'true riverine' populations. Note in this regard that 66.6% of the misclassified snails from one of these samples (16) were assigned to samples from the closely proximal Banbury Springs complex. The scant differentiation of another sample from this reach (7) relative to those from the Hagerman/Bliss reach (pairwise F_{ST} = 0.023–0.063; also see Figs 3b & 4) suggests that the weak structuring of riverine populations observed in the latter portion of the Snake River may extend at least this far up flow.

Current assessments of the conservation status of the Bliss Rapids snail assume that this species readily disperses throughout continuous reaches of suitable aquatic habitat, yet is unable to traverse the series of dams and impoundments which have fragmented its geographical range and consequently has been negatively impacted genetically by these putative barriers. Our findings do not support these hypotheses, although it is possible that not enough time has passed since the construction of these barriers to detect a resulting genetic impact (e.g. if effective population sizes are quite large). We suggest that, although the Bliss Rapids snail appears to be highly sedentary in general, its pattern of genetic variation has been rendered complex by apparently substantial differences in gene flow related to geography and/or habitat. These findings parallel recent, genetically-based studies of other western North American freshwater gastropods (e.g. Liu, Hershler & Clift, 2003; Hershler, Mulvey & Liu, 2005; Miller, Weigel & Mock, 2006) which also demonstrated complex population structure that conflicts with traditional, monolithic concepts of the dispersal ability of these animals and their sensitivity to putative barriers (Taylor, 1985; Taylor & Bright, 1987).

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References

Benjamini Y. & Yekutieli D. (2001) The control of the false discovery rate in multiple testing under dependency. *The Annals of Statistics*, **29**, 1165–1188.

Berettoni S., Mathieu J. & Hervant F. (1998) Genetic variation in the stygobite amphipod *Niphargus rhenorhadanensis*: comparison of four hyporheic populations of the Rhône and the Ain Rivers (France). *Archiv für Hydrobiologie*, **142**, 484–492.

Bessert M.L. & Ortí G. (2008) Genetic effects of habitat fragmentation on blue sucker populations in the upper Missouri River (*Cycleptus elongates* Lesueur, 1918). *Conservation Genetics*, **9**, 821–832.

Bohonak A.J. (2002) IBD (isolation by distance): a program for analyses of isolation by distance. *Journal of Heredity*, **93**, 153–154. Available at: http://ibdws.sdsu.edu/~ibdws (last accessed on 29 January 2009).

Bucklin A. (1992) Use of formalin-preserved samples for molecular analysis. *Newsletter of Crustacean Molecular Techniques*, **2**, 3.

Burridge C.P. & Gold J.R. (2003) Conservation genetic studies of the endangered Cape Fear Shiner, *Notropis mekistocholas* (Teleostei: Cyprinidae). *Conservation Genetics*, **4**, 219–225.

Cavalli-Sforza L.L. & Edwards A.W.F. (1967) Phylogenetic analysis: models and estimation procedures. *Evolution*, **21**, 550–570.

Evanno G., Regnaut S. & Goudet J. (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, **14**, 2611–2620.

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

Excoffier L., Laval G. & Schneider S. (2005) Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics*, **1**, 47–50.

Felsenstein J. (1995) *PHYLIP (Phylogeny Inference Package), Version 3.57c*. Distributed by the author. University of Washington, Seattle, WA.

Goudet J. (2001) *FSTAT, a Program to Estimate and Test Gene Diversities and Fixation Indices (Version 2.9.3)*. Distributed by the author. University of Lausanne, Lausanne. Available at: http://www2.unil.ch/popgen/softwares/fstat.htm (last accessed on 29 January 2009).

Heggenes J. & Røed K.H. (2006) Do dams increase genetic diversity in brown trout (*Salmo trutta*)? Microgeographic differentiation in a fragmented river. *Ecology of Freshwater Fish*, **15**, 366–375.

Hershler R., Frest T.J., Johannes E.J., Bowler P.A. & Thompson F.G. (1994) Two new genera of hydrobiid snails (Prosobranchia: Rissooidea) from the northwestern United States. *Veliger*, **37**, 221–243.

Hershler R., Mulvey M. & Liu H.-P. (2005) Genetic variation in the Desert Springsnail (*Tryonia porrecta*): implications for reproductive mode and dispersal. *Molecular Ecology*, **14**, 1755–1765.

Hershler R., Liu H.-P., Frest T.J., Johannes E.J. & Clark W.H. (2006) Genetic structure of the western North American aquatic gastropod genus *Taylorconcha* and description of a second species. *Journal of Molluscan Studies*, **72**, 167–177.

Idaho Power Company (IPC) (2008) *Hydroelectric*. Available at: http://www.idahopower.com/energycenter/electricitybasics/generation/hydroelectric.htm (last accessed on 29 January 2009).

Kelly M.W. & Rhymer J.M. (2005) Population genetic structure of a rare unionid (*Lampsilis cariosa*) in a recently glaciated landscape. *Conservation Genetics*, **6**, 789–802.

Knutsen H., Jorde P.E., Andre C. & Stenseth N.C. (2003) Fine-scale genetic population structuring in a highly mobile marine species: the Atlantic cod. *Molecular Ecology*, **12**, 385–394.

Laroche J., Durand J.D., Bouvet Y., Guinand B. & Brohon B. (1999) Genetic structure and differentiation among populations of two cyprinids, *Leuciscus cephalus* and *Rutilus rutilus*, in a large European river. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1659–1667.

Liu H.-P. & Hershler R. (2008) Microsatellite markers for the threatened Bliss Rapids snail (*Taylorconcha serpenticola*) and cross-amplification in its congener, *T. inspirata*. *Molecular Ecology Resources*, **8**, 418–420.

Liu H.-P., Hershler R. & Clift K. (2003) Mitochondrial DNA sequences reveal extensive cryptic diversity within a western American springsnail. *Molecular Ecology*, **12**, 2771–2782.

Miller M.P., Weigel D.E. & Mock K.E. (2006) Patterns of genetic structure in the endangered aquatic gastropod *Valvata utahensis* (Mollusca: Valvatidae) at small and large spatial scales. *Freshwater Biology*, **51**, 2362–2375.

Narum S.R. (2006) Beyond Bonferroni: less conservative analyses for conservation genetics. *Conservation Genetics*, **7**, 783–787.

Piry S., Alapetite A., Cornuet J.-M., Paetkau D., Baudouin L. & Estoep A. (2004) GENECLASS2: a software for genetic assignment and first-generation migrant detection. *Journal of Heredity*, **95**, 536–539.

Pritchard J.K., Stephens M. & Donnelly P. (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Pritchard J.K., Wen X. & Falush D. (2007) Documentation for *structure* software, version 2.2. In: *Structure*. Available at: http://pritch.bsd.uchicago.edu/software/structure22/readme.pdf(last accessed on 29 January 2009).

Rannala B. & Mountain J.L. (1997) Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences*, **94**, 9197–9201.

Raymond M. & Rousset F. (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.

Reid S.M., Wilson C.C., Mandrak N.E. & Carl L.M. (2008) Population structure and genetic diversity of black redhorse (*Moxostoma duquesnei*) in a highly fragmented watershed. *Conservation Genetics*, **9**, 531–546.

Richards D.C. (2004) *Competition Between the Threatened Bliss Rapids Snail, Taylorconcha serpenticola (Hershler et al.) and the Invasive, Aquatic Snail, Potamopyrgus antipodarum (Gray)*. Unpublished PhD Dissertation, Montana State University, Bozeman, MT, 156 pp.

Richards D.C. & Arrington T. (2006) *Evaluation of the Threatened Bliss Rapids Snail, Taylorconcha serpenticola Susceptibility to Exposure: Potential Impact of Water Level Fluctuations on the Mid-Snake River*. Report to the Idaho Power Company, Boise, 27 pp.

Richards D.C., Falter C.M. & Steinhorst K. (2006) *Status Review of the Bliss Rapids Snail, Taylorconcha serpenticola in the mid-Snake River, Idaho*. Report to the United States Fish and Wildlife Service, Boise, ID, 170 pp.

Rousset F. (1997) Genetic differentiation and estimation of gene flow from *F*-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

Stamford M.D. & Taylor E.B. (2005) Population subdivision and genetic signatures of demographic changes in Arctic grayling (*Thymallus arcticus*) from an impounded watershed. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2548–2559.

Stanford J.A., Hauer F.R., Gregory S.V. & Snyder E.B. (2005) Columbia River basin. In: *Rivers of North America*

(Eds A.C. Behnke & C.E. Cushing), pp. 591–653. Elsevier Academic Press, Burlington, MA.

Takezaki N. & Nei M. (1996) Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. *Genetics*, **144**, 389–399.

Taylor D.W. (1982) *Status Report on Bliss Rapids Snail*. Report to the United States Fish and Wildlife Service, Portland, OR, 8 pp.

Taylor D.W. (1985) Evolution of freshwater drainages and molluscs in western North America. In: *Late Cenozoic History of the Pacific Northwest: Interdisciplinary Studies on the Clarkia Fossil Beds of Northern Idaho* (Ed. C.J. Smiley), pp. 265–321. American Association for the Advancement of Science, San Francisco, CA.

Taylor D.W. & Bright R.C. (1987) Drainage history of the Bonneville Basin. In: *Cenozoic Geology of Western Utah. Sites for Precious Metal and Hydrocarbon Accumulations* (Eds R.S. Kopp & R.E. Cohenour). *Utah Geological Association Publication*, 16, 239–256.

Taylor E.B., Stamford M.D. & Baxter J.S. (2003) Population subdivision in westslope cutthroat trout (*Oncorhynchus clarki lewisi*) at the northern periphery of its range: evolutionary inferences and conservation implications. *Molecular Ecology*, **12**, 2609–2622.

Thomas C.A. (1968) Records of north-side springs and other inflow to Snake River between Milner and King Hill, Idaho, 1948–1967. *Idaho Department of Reclamation Water Information Bulletin*, **6**, 1–65.

United States Fish and Wildlife Service (USFWS) (1992) Endangered and threatened wildlife and plants; determination of endangered or threatened status for five aquatic snails in south central Idaho. *Federal Register*, **57**, 59244–59256.

United States Fish and Wildlife Service (USFWS) (2004) *Biological Opinion for the Federal Energy Regulatory Commission Proposed Relicensing of Five Hydroelectric Facilities on the Middle Snake River, Idaho: Shoshone Falls (FERC No. 2778), Upper Salmon Falls (FERC No. 2777), Lower Salmon Falls (FERC No. 2061), Bliss (FERC No. 1975), and C. J. Strike (FERC No. 2055), and their Impacts on Five Mollusc Species and Bald Eagles*. U.S. Fish and Wildlife Service, Boise, ID, 139 pp. Available at: http://www.fws.gov/idaho/publications/BOs/Relicense%20of%20MidSnake%20Hydropower%20Projects%20BO.pdf (last accessed on 29 January 2009).

United States Fish and Wildlife Service (USFWS) (2005) *Biological Opinion for Bureau of Reclamation Operations and Maintenance in the Snake River Basin Above Brownlee Reservoir*, 342 pp. Available at: http://www.fws.gov/idaho/publications/BOs/Final.pdf (last accessed on 29 January 2009).

United States Fish and Wildlife Service (USFWS) (2007) Endangered and threatened wildlife and plants; 90-day finding on a petition to remove the Bliss Rapids snail (*Taylorconcha serpenticola*) from the List of Endangered and Threatened Wildlife. *Federal Register*, **72**, 31250–31256.

United States Fish and Wildlife Service (USFWS) (2008) *Revised Draft Status Review for the Bliss Rapids Snail (Taylorconcha serpenticola), Version 2.0*, 66 pp. Available at: http://www.fws.gov/idaho/species/BRS/Status_Review/draft%20BRS%20status%20final%20science%20panel%20no%20track%20changes.pdf (last accessed on 29 January 2009).

Weetman D., Hauser L. & Carcalho G.R. (2002) Reconstruction of microsatellite mutation history reveals a strong and consistent detection bias in invasive clonal snails, *Potamopyrgus antipodarum*. *Genetics*, **162**, 813–822.

Weir B.S. & Cockerham C.C. (1984) Estimating *F*-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

Worthington Wilmer J.W. & Wilcox C. (2007) Fine scale patterns of migration and gene flow in the endangered mound spring snail, *Fonscochlea accepta* (Mollusca: Hydrobiidae) in arid Australia. *Conservation Genetics*, **8**, 617–628.

Worthington Wilmer J.W., Elkin C., Wilsox C., Murray L., Niejalkes D. & Possingham H. (2008) The influence of multiple dispersal mechanisms and landscape structure on population clustering and connectivity in fragmented artesian spring snail populations. *Molecular Ecology*, **17**, 3733–3751.

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