Heredity **86** (2001) 370–377 *Received 26 June 2000, accepted 22 November 2000*

Population structure and dispersal in the Canary Island caddisfly *Mesophylax aspersus* (Trichoptera, Limnephilidae)

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Population genetic structure of the circum-Mediterranean caddisfly *Mesophylax aspersus* (Trichoptera, Limnephilidae) on the Canary Islands was investigated by studying allozyme variation at nine putative loci in five populations. Genetic variability, population structure and gene flow were compared with data in the literature for continental taxa to assess the effect of isolation of island populations on the genetic structure. Larvae were collected from streams on the islands of Tenerife (one population), La Gomera (two populations in the same catchment) and La Palma (two populations in different catchments). Genetic variability within populations was high relative to that recorded previously for continental Trichoptera, e.g. mean heterozygosity was 0.119–0.336 (0.035–0.15 in continental taxa). Highly significant population structuring was observed (mean $F_{ST} = 0.250$), and there was significant within-population structuring (mean $F_{IS} = 0.098$). Populations from the same catchment or island were no more similar than populations from different islands, which suggests that occasional long-distance dispersal, both between and within islands, is the predominant influence on the population structure. This dispersal ability has contributed to the colonization of most permanent streams on the Canary Islands by *M. aspersus*.

Keywords: allozymes, dispersal, islands, population structure, Trichoptera.

Introduction

Drainage networks can be viewed as 'habitat islands' surrounded by a 'sea' of land inhospitable to freshwater invertebrates. Colonization of streams on oceanic islands is more problematic because of the dispersal barrier of the sea and, often, the scarcity of streams, resulting in aquatic taxa often being poorly represented on isolated islands (Wallace, 1880). The community present is strongly influenced by the dispersal abilities of the species in the archipelago species pool, their niche requirements and stochastic colonization processes (Bunn & Hughes, 1997; Belyea & Lancaster, 1999). The archipelago species pool, in turn, is influenced by the chance dispersal of suitable species from a continental source pool (MacArthur & Wilson, 1967). The isolation and age of the Canary Islands, situated off the coast of the western Sahara, have resulted in a high degree of endemism in their flora and fauna. This is due to both the presence of taxa of Tertiary origin, which have become extinct elsewhere in their range, and to post-colonization speciation (Juan *et al*., 2000).

Freshwater insects possess a wide variety of active and passive dispersal mechanisms. In-stream dispersal by active or passive drift, crawling and swimming typically takes place at the reach scale but, over longer time scales, may allow colonization of a whole stream system. Most freshwater insects can also disperse over land as actively flying adults, allowing colonization of other stream systems (Sheldon, 1984). Long-distance dispersal of winged adults can additionally occur by passive drift in air currents (e.g. Clarke, 1903; Ashmole & Ashmole, 1988). The freshwater taxa occurring on the Canary Islands exhibit a range of dispersal abilities, mechanisms and distributions from extremely localized to ubiquitous (Malmqvist *et al*., 1995). Widespread species may have greater dispersal ability than species with more restricted distributions, as patch occupancy is often related to dispersal ability (Plague & McArthur, 1998). The relative lack of single-island endemic species within the Canarian freshwater fauna, compared to terrestrial invertebrates, is an indication that inter-island dispersal is substantial in most freshwater taxa. In the Coleoptera,

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for example, 4% of Dytiscidae are single-island endemics, compared to 54% of Carabidae (Machado, 1992; Alarie & Bilton, in press).

The dispersal ability of individual taxa determines the geographical scale of recruitment and, in combination with historical factors, the scale of population genetic differentiation (Slatkin, 1985). Conversely, the degree of population differentiation observed at a particular scale can be used to infer the amount of dispersal (Bohonak, 1999). Interpopulation dispersal reduces the genetic differentiation of populations that would otherwise occur through founder events, genetic drift and natural selection (Wright, 1943).

The island-like nature of stream habitats can potentially lead to genetic structuring of populations, which is likely to be enhanced by the distribution of the species across real islands. Several studies have used population genetic structure estimates to infer dispersal patterns from allozyme variation in stream invertebrates. Some workers have found no evidence for isolation-by-distance and conclude that stochastic processes such as founder events and fluctuating population sizes are sufficient to explain the population genetic structure (e.g. Jackson & Resh, 1992; Bunn & Hughes, 1997). Others have demonstrated isolation-by-distance, suggesting an additional influence of ongoing distance-dependent dispersal (e.g. Varvio-Aho & Pamilo, 1979; Dillon & Wethington, 1995; Hughes *et al*., 1996).

In the present study we made a survey of allozyme variation in *Mesophylax aspersus* Rambur 1842 (Trichoptera, Limnephilidae) from five populations on three islands in the Canary archipelago. We tested three hypotheses about genetic variability, population structure and gene flow in *M. aspersus*. We hypothesized that genetic variability would be lower than in continental Trichoptera, as island populations are likely to have undergone more marked founder events, and as the sea may be a significant barrier to long-distance gene flow (Pashley *et al*., 1985). The second hypothesis predicted that genetic structure would be significant, because of the patchy nature of the stream habitat and the effect of the islands in isolating populations (e.g. Schug *et al*., 1998; Thomas *et al*., 1998). It was expected that populations would be nested by island and within island by watershed (e.g. Jackson & Resh, 1992; Hughes *et al*., 1996; Bunn & Hughes, 1997). In addition we expected that interpopulation gene flow would be lower than in continental species, because of the greater difficulty of trans-oceanic dispersal (e.g. Mulvey *et al*., 1988). Our final hypothesis predicted that genetic differentiation of populations would increase with geographical distance regardless of island boundaries (e.g. Varvio-Aho & Pamilo, 1979; Dillon & Wethington, 1995).

Materials and methods

Study species

Mesophylax aspersus has a circum-Mediterranean distribution, occurring from the Canary Islands to the Near East (e.g. Schmid, 1957; Botosaneanu, 1974; Dakki, 1987). The species is common on the western Canary Islands of Tenerife (Nybom, 1948; Malmqvist *et al*., 1993), La Gomera (Nybom, 1954; L.C.K., unpublished data) and La Palma (L.C.K., unpublished data). *M. aspersus* is found in most first and second order streams at altitudes of 200–2150 m in a range of habitats including dense *laurisilva* woodland, open pine forest and agricultural land (Malmqvist *et al*., 1995).

Localities and sampling

In April 1999 late-instar larvae of *Mesophylax aspersus* were collected from shallow pools in a set of five streams on three islands (Tenerife, La Gomera and La Palma), chosen to allow comparisons within and between catchments and islands (Fig. 1). The study streams are referred to as P1, P2, T, G1 and G2. They are located in Barranco Taburiente, La Palma, Barranco del Rio, La Palma, Barranco del Rio, Tenerife, and a tributary and the main channel at El Cedro, La Gomera, respectively. In an attempt to sample from a single population individuals were collected from two to three shallow pools in a 5–10 m stretch of stream (minimum sample size 24). Specimens were kept alive in insulated flasks of stream water then transferred to individual cryotubes within 2–3 h, for storage at −196°C until analysis.

Electrophoretic analysis

Fourteen enzyme systems were successfully screened using cellulose acetate gel electrophoresis (protocol modified from Hebert & Beaton, 1991), revealing nine putative loci (eight enzyme systems) which could be scored reliably in all five populations. The eight enzymes, the abbreviations used and their Enzyme Commission numbers (International Union of Biochemistry Nomenclature Committee, 1984) were: esterase, EST (E.C. 3.1.1._) with α-naphthyl acetate substrate; fumarate hydratase, FUM (E.C. 4.2.1.2); glucose-6-phosphate isomerase, GPI (E.C. 5.3.1.9); isocitrate dehydrogenase, IDH (E.C. 1.1.1.42); leucine aminopeptidase, LAP (E.C. 3.4._._); glycyl-L-leucine peptidase, PEP C (E.C. 3.4._._); proline dipeptidase, *PEP D* (E.C. 3.4._._); and phosphoglucomutase, PGM (E.C. 5.4.2.2).

Larvae were removed from their cases and homogenized in 200 μL of grinding buffer (Peakall & Beattie,

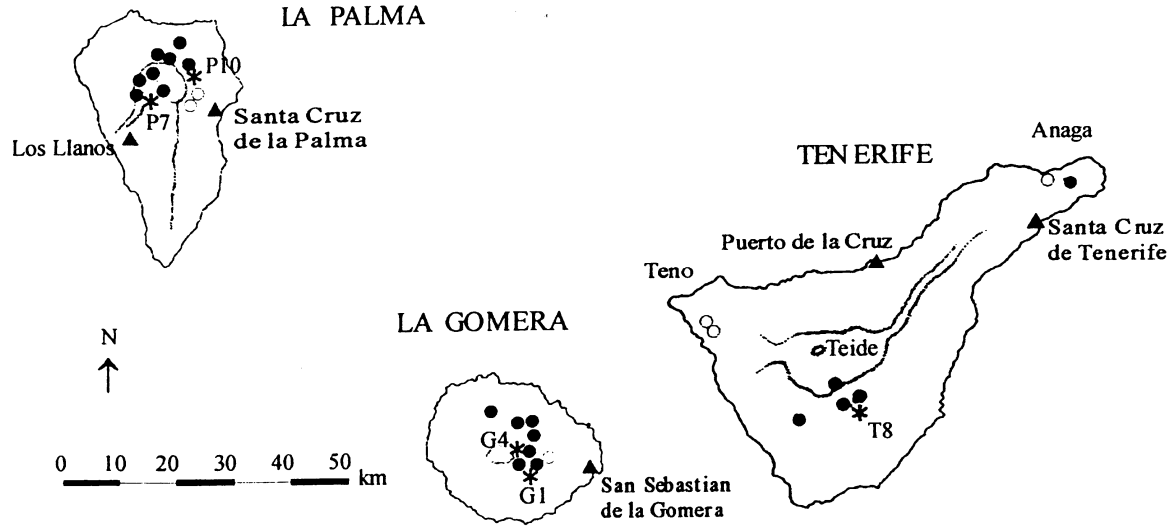

Fig. 1 The distribution of *Mesophylax aspersus* in permanent streams on the western Canary Islands. ●, species present; ○, species absent; ∗, species present and population sampled; ▲, major town or city.

1991). Running buffers and stains were adapted from Richardson *et al.* (1986), Easteal & Boussy (1987), Hillis & Moritz (1990) and Hebert & Beaton (1991). 0.025 M tris-glycine buffer, pH 8.5, was used for running the EST enzyme system; 0.01 M citrate-phosphate, pH 6.4, was used for running FUM and PEP C; the other enzyme systems were run with 0.04 M tris-citrate, pH 7.6. Specific methods are available from D.T.B. on request. Rat liver tissue (adult male Sprague–Dewley rats) was run in one lane on each gel as a positive control. Loci and alleles were labelled numerically and alphabetically, respectively, in ascending order from the least to the most mobile.

Statistical analysis

The data were summarized as allele frequencies at each locus in each population with the BIOSYS-1 package (Swofford & Selander, 1989). As measures of genetic variability, the mean number of alleles (*MNA*) per locus, the percentage of polymorphic loci (*P*) at the 95% levels and expected heterozygosity (*H*) (Nei's 1978 unbiased estimate) were calculated with BIOSYS-1.

Population differentiation and structure was investigated with *F*-statistics (Wright, 1943) estimated by the formulae of Weir & Cockerham (1984) with the GENETIX package (Université de Montpellier II, 1999). Standard deviations of the multilocus *F* statistic estimates were obtained by jack-knifing over loci. Comparing the observed means to the outcomes generated from permutation tests estimated significance: to test F_{IS}, alleles were randomized within populations; to test F_{ST}, individual genotypes were randomly allocated to populations. A sequential Bonferroni correction for the analysis of multiple tests was used (Rice, 1989), calculated by hand. Multilocus F_{ST} was calculated for each pair of sites. Pairwise site comparisons were also performed using Rogers' (1972) genetic distance, calculated with GENETIX. Significance was estimated by comparing the observed distances with a null distribution generated by recalculating the distance matrix after 1000 random reassignments of individuals to sites. A dendrogram showing the relationships between the sites was constructed by the distance Wagner (Farris, 1972) procedure with BIOSYS-1.

For each pair of sites, multilocus F_{ST} and Rogers' genetic distance were regressed against geographical distance between sites and minimum inter-island distances, both directly and with log transformations, using Microsoft Excel. Distances were defined as the shortest measurements on the map. The relationships between the genetic and geographical distances were tested formally with Mantel tests (Mantel, 1967) in the GENETIX package.

Results

Genetic variability measures

All loci but *FUM* were polymorphic in at least one population, and *EST*, *LAP-1* and *PEP C* were polymorphic in every population (Table 1). There was large variation in allele frequencies between populations, and at only two loci was the most common allele constant across populations. However there were only one site-specific (allele *B* of *FUM* locus at P1) and no island-specific alleles. Populations at the five sites showed different amounts of variability, with the Tenerife sample

Table 1 Allele frequencies (alleles labelled *A* to *D*) at each locus studied in *Mesophylax aspersus*. (*N*) is the number of individuals for which the locus was scored. *MNA* is the mean number of alleles scored per locus. *P* is the percentage of polymorphic loci at the 95% criterion. *H* is the unbiased estimate of expected heterozygosity

Locus	Allele	P1	P2	T1	G1	G2
EST	(*N*)	55	36	21	40	32
	A	0.064	0.194	0.024	0.013	0.047
	B	0.273	0.403	0.238	0.538	0.594
	C	0.445	0.306	0.5	0.3	0.266
	D	0.218	0.097	0.238	0.15	0.094
FUM	(*N*)	48	37	24	40	20
	A	0.979	1	1	1	1
	B	0.021	0	0	0	0
GPI	(*N*)	53	40	20	40	31
	A	0.66	0.1	1	0.325	0.355
	B	0.34	0.9	0	0.675	0.645
IDH	(*N*)	46	28	18	35	32
	A	1	0.982	1	0.843	1
	B	0	0.018	0	0.157	0
LAP-1	(*N*)	54	34	17	37	32
	A	0.704	0.559	0.088	0.446	0.531
	B	0.296	0.441	0.912	0.554	0.469
LAP-2	(*N*)	52	29	15	32	28
	A	0.077	0.379	0	0	0.714
	B	0.923	0.621	1	1	0.286
PEP C	(*N*)	56	37	22	39	28
	A	0.054	0	0.023	0.013	0
	B	0.946	0.878	0.841	0.91	0.964
	C	0	0.122	0.136	0.077	0.036
PEP D	(*N*)	30	38	22	40	30
	A	1	0.289	1	0.85	0.567
	B	0	0.711	0	0.15	0.433
PGM	(*N*)	50	35	19	28	23
	A	0.14	0.257	0	0.018	0.109
	B	0.86	0.629	1	0.714	0.196
	C	0	0.114	0	0.268	0.696
MNA		2	2.222	1.667	2.222	2.111
SD (*MNA*)		0.87	0.83	1.1	0.97	0.93
P (95%)		66.67	77.78	33.33	77.78	66.67
H		0.230	0.336	0.119	0.293	0.328
SD (*H*)		0.236	0.239	0.217	0.212	0.234

showing particularly little: *MNA*, *P* and mean *H* were all lowest at T, however, *H* was not significantly lower.

Population differentiation and structure

A summary of *F*-statistics is provided in Table 2. F_{IS} was found to be very variable. P1 and G1 showed a significant excess of heterozygotes whilst P2 and G2 showed a significant deficiency. T had a nonsignificant deficiency. *LAP-1* had a particular excess of heterozygotes, whilst for *PEP D* there was an excess of heterozygotes at site G1 but a deficiency at P2 and none at all at G2. The multilocus estimates of F_{IS} and F_{IT} were significantly positive. The multilocus F_{ST} was 0.250, which implies substantial population structuring ($P < 0.001$). All the pairwise genetic distances (both F_{ST} and Rogers' distance) were significant ($P < 0.001$). The most distant pair of sites was T–G2, and the closest P1–G1 (Table 3). The branching order and relative branch lengths of the distance Wagner network showed that sites within an island were not more similar than sites on different islands.

Table 2 F_{IS} over all alleles at polymorphic loci in each population of *Mesophylax aspersus*, and *F*-statistics for each locus over all populations

Locus	P1	P2	T1	G1	G2	F_{IS}	F_{IT}	F_{ST}
EST	0.338*	0.417	0.438	0.055	0.196	0.307	0.338	0.045
FUM	−0.011					−0.006	−0.002	0.004
GPI	−0.338	0.179		0.214	0.030	−0.039	0.333	0.358
IDH		0.000		−0.172		−0.155	−0.008	0.127
LAP-1	−0.413*	−0.662*	−0.067	−0.800*	−0.750*	−0.618	−0.382	0.145
LAP-2	0.917	0.858*			−0.032	0.398	0.671	0.453
PEP C	−0.048		−0.143	−0.074*		−0.094	−0.065	0.026
PEP D		0.875*		−0.164*	1.000*	0.664	0.806	0.422
PGM	−0.153	0.072		0.132	0.836*	0.277	0.496	0.302
All loci	−0.151	0.264*	0.110	−0.172	0.166	0.098***	0.323***	0.250***
Resampling mean						0.099	0.323	0.247
SE						0.179	0.152	0.069

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 3 Interpopulation genetic distance (all $P < 0.05$). Above the diagonal: θ, an estimator of F_{ST} (Weir & Cockerham, 1984); below the diagonal: Rogers' genetic distance (Rogers, 1972)

	P1	P2	T1	G1	G2
P1	0	0.280	0.216	0.118	0.330
P2	0.250	0	0.426	0.165	0.142
T1	0.152	0.342	0	0.259	0.460
G1	0.169	0.203	0.216	0	0.224
G2	0.286	0.188	0.380	0.207	0

Genetic distance and geographical isolation

Regressions of pairwise F_{ST} and Rogers' genetic distance against geographical distances were nonsignificant. Mantel tests on each pair of matrices confirmed that there was no significant pattern of isolation by distance.

Discussion

Genetic variability compared to continental species

Levels of genetic variability in *Mesophylax aspersus* were generally high, except at site T (Table 1). The mean *H* and *P* were higher than any previously recorded in Trichoptera (Plague & MacArthur, 1988; Jackson & Resh, 1992; Guinand, 1994), falsifying the first stated hypothesis. *MNA* of *M. aspersus* was more typical of Trichoptera. The lack of site- or island-specific alleles suggests that the populations are not of independent origin.

The most likely cause of the high genetic variability in *M. aspersus* is occasional interpopulation dispersal of individuals between populations with different genetic composition, despite their geographical isolation and the dispersal barrier of the sea. If populations are of reasonable size and longevity then genetic variability can accumulate. It is also possible that balancing selection and temporal and spatial variation in selection pressures may maintain some of the genetic diversity. The genetic variability estimates are likely to be inflated by the lack of monomorphic loci in the data set; however, further work (L.C.K., unpublished data) found that of an additional 10 loci none were monomorphic.

The lower heterozygosity found in other studies of Trichoptera might also be due in part to the sampling methods employed. Attracting adults to a light trap may inadvertently sample individuals from more than one population, leading to the Wahlund effect (e.g. Plague & McArthur, 1998). On the other hand, larvae collected from a small area of a stream may represent only one or a few sibling groups (e.g. Jackson & Resh, 1992; Guinand, 1994; Bunn & Hughes, 1997).

Population structure: genetic and geographical isolation

Mesophylax aspersus has substantial population structuring on the Canary Islands (Table 2), as predicted. F_{IS} was significantly positive overall but varied in sign from locus to locus. Possible explanations for the variability in F_{IS} are that null alleles confounded the scoring of gels, or that selection is acting upon some loci (e.g. against homozygotes at *LAP-1*) whilst others are subject to genetic drift (e.g. Giles *et al*., 1998). The Wahlund effect

may have produced significant F_{IS} in the study by Plague & McArthur (1998) but is not likely to have operated alone in the present study, as heterozygote excess as well as deficiency was found.

The hypothesis of hierarchical population structure in *M. aspersus* was not supported, as population subdivision was as significant within as between islands, and same-island pairs had genetic distances in the mid-range of the pairwise distances (Table 3). The patchy nature of suitable stream habitat may make dispersal between streams on the same island as unlikely as dispersal over the sea. In contrast, Jackson & Resh (1992) found that genetic variation in *Helicopsyche* was hierarchically structured, with smaller differences in allele frequencies observed among sites within a stream and larger differences between catchments and regions.

Similar values of multilocus F_{ST} are reported for *M. aspersus* and the continental species, when populations are separated by comparable geographical distances: $F_{ST} = 0.425$ over 200 km in *Helicopsyche borealis* (Jackson & Resh, 1992); $F_{ST} = 0.015$ over 25 km in *Hydropsyche exocellata* (Guinand, 1994). Thus the prediction that interpopulation gene flow would be lower in *M. aspersus* was not supported. However single-locus F_{ST} in *M. aspersus* varied by two orders of magnitude, and this heterogeneity means that the multilocus estimator should be interpreted with caution (Guinand, 1994).

The final hypothesis was that F_{ST} would increase with geographical distance, whether within or between islands. This was not supported. This implies that streams will not necessarily be colonized by the nearest neighbouring population. Dispersal between sites in close proximity could be prevented by: prevailing wind direction; topography, particularly when streams are in deep gorges (as are P1, P2, and T); dense forest (as surrounds P2, G1, and G2); and low stream density (as on Tenerife). Passive dispersal over longer distances could occur if an airborne insect became caught in a wind current, as studies of insect fallout on the snowfields of Mount Teide, Tenerife (Ashmole & Ashmole, 1988), on ships and over the sea (Clarke, 1903) have demonstrated. A number of similar studies have failed to find isolation-by-distance (e.g. Jackson & Resh, 1992; Bunn & Hughes, 1997), and the stochastic effect of recruitment, random dispersal, population history and environmental structure are invoked. In this case we have shown that the division of the species' range into an archipelago of islands does not determine its genetic structure, and the genetic variability within populations suggests that the stochastic effect of recruitment is also not the cause of the population structure.

Conclusion: genetic differentiation and dispersal

Bohonak (1999) found that there is a robust relationship between population structure and dispersal ability: genetic distance estimates are informative and patterns of dispersal do, in the majority of comparisons, make a measurable contribution to observed population genetic structure. This study makes use of this paradigm to infer dispersal ability from genetic differentiation in order to investigate the relationship between dispersal ability and distribution of *Mesophylax aspersus*. It is likely that *M. aspersus* is the strongest flier of the Canarian trichopteran fauna (Gothberg, 1973; Svensson, 1974), and adult flight is the principal mechanism of dispersal in Trichoptera (Bunn & Hughes, 1997). We conclude that a small amount of distance-independent dispersal of individuals between populations occurs, which has allowed *M. aspersus* to colonize almost all the permanent streams in the archipelago. Whilst the paucity of streams on the Canary Islands leaves freshwater fauna isolated in an otherwise arid environment, populations of *M. aspersus* appear to be large and persistent enough, and receive enough genetically distinct immigrants, to maintain high levels of genetic variability within them.

Acknowledgements

This study was financially supported by a studentship from the University of Plymouth. Marcos Baez, University of La Laguna, Tenerife, and Björn Malmqvist, University of Umeå, Sweden, are thanked for their kind assistance in the field. The manuscript was improved by the comments of two anonymous referees.

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