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Historical interdrainage dispersal of eastern rainbowfish from the Atherton Tableland, north-eastern Australia

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The widespread distribution of the eastern rainbowfish *Melanotaenia splendida splendida* throughout the isolated headwaters of the rivers on the Atherton Tableland, north-eastern Australia, suggests multiple colonization events from the eastern lowlands *via* each respective river channel, or a single colonization event on to the tableland with subsequent dispersal between the headwaters. To explore the likely processes that resulted in the current distribution on the tableland, two models of gene flow were tested: (a) the hierarchical gene flow model that tests the hypothesis for contemporary gene flow *via* stream channels and (b) the stepping stone model that tests for dispersal between streams. Neither of these models explained the observed genetic structure, adequately. However, there is support for extensive historical dispersal across the headwaters of the isolated drainages. If this dispersal followed a single colonization event, the subsequent range expansion could have facilitated a rapid rise in population size due to an increase in suitable habitat. The genetic data indicates an eight-fold increase in population size *c*. 100 thousand years ago.

Key words: rainbowfish; *Melanotaenia splendida*; mitochondrial DNA; gene flow; mismatch distribution.

INTRODUCTION

Rainbowfish, *Melanotaenia* spp. are common and distributed widely throughout much of Australia and New Guinea. They have a high profile, as they are popular aquarium fish (Allen, 1995), yet their biogeography and taxonomy from north-eastern Australia remains problematic (Zhu *et al*., 1994; Pusey *et al*., 1997; McGuigan *et al*., 2000). The current study focuses on populations of the eastern rainbowfish *Melanotaenia splendida splendida* Peters (1866), a widespread, obligate freshwater species from the Atherton Tableland (Fig. 1).

The eastern rainbowfish is a small-bodied (<14 cm) ornate species distributed throughout the eastern drainages of tropical north-eastern Australia as well as in the headwaters of some western flowing rivers. It is predominantly stream dwelling but is found also in lotic systems (Allen, 1995). The fish reach sexual maturity at *c*. 4 cm (Beumer, 1979) and attaining a length of 5–6 cm at 1 year (Allen, 1995) suggests a generation time of 6–7 months. The eastern rainbowfish breeds continuously with peak activity immediately before and during flood time (Merrick & Schmida, 1984) when up to 200 eggs are deposited on submerged vegetation over 2 weeks (Allen, 1995).

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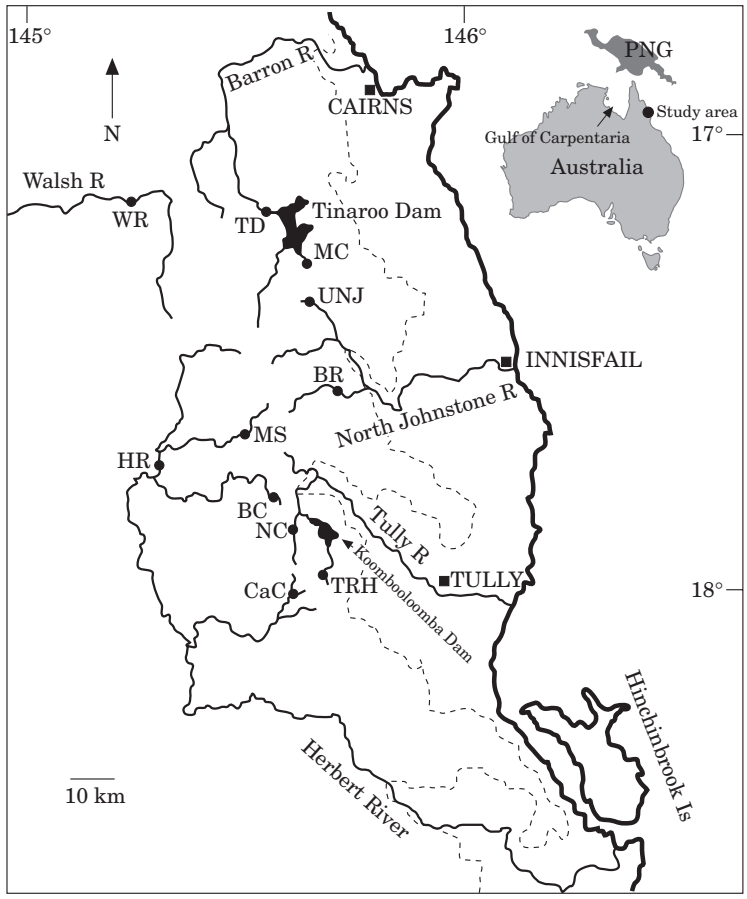

FIG. 1. Map of sampling sites from the Atherton Tableland. – – –, 330 m contour.

As it occurs in most streams and lakes across the Atherton Tableland it is assumed that it has excellent dispersal capabilities (Pusey & Kennard, 1996). As the initial uplift of the tableland at least 10 million years ago (Ollier, 1978) pre-dates significantly the speciation of the *M. splendida* group (Zhu *et al*., 1994; McGuigan *et al*., 2000), individuals would have had to negotiate significant waterfalls (commonly >100 m) in order to colonize these upland streams. The genetic structure of sub-populations on the Atherton Tableland can be analyzed to test whether their current distribution is a result of contemporary dispersal up the waterfalls in each of the respective river systems or a consequence of other processes.

The degree of dispersal between subpopulations can be inferred from levels of genetic differentiation (Slatkin, 1981). High rates of dispersal between sub-populations lead to genetic homogeneity, whereas restricted dispersal increases genetic differentiation. Although it is difficult to assign sub-population status *a priori* in riverine systems due to natural instream barriers, a high level of genetic structuring is expected for populations of obligate freshwater species (Gyllensten, 1985; Ward *et al*., 1994). Population genetic theory dictates that generally freshwater fishes will conform to a hierarchical pattern (Meffe &

Vrijenhoek, 1988). This is chiefly because natural barriers (including the sea) prevent dispersal between drainages. So if rainbowfish have dispersed up waterfalls within each system, genetic differentiation should be greater between rather than within drainages.

On the other hand, if waterfalls prevent dispersal but the drainage boundaries do not, a population genetic structure reflecting the stepping stone model of gene flow would be expected on the Atherton Tableland (Kimura & Weiss, 1964). This would result in a signature of isolation by distance (Slatkin, 1993) where populations geographically closer to each other should be more genetically similar regardless of the current drainage lines.

If these two models fail to explain the genetic pattern satisfactorily, it can be informative to examine the demographic history of the population. The analysis of mitochondrial DNA (mtDNA) is an effective means for investigating both contemporary and historical processes that underly biogeographic patterns of many taxa at the intraspecific level (Avise, 1994; Avise *et al*., 1987). Populations of obligate freshwater species existing in more than one river system implies that dispersal between systems has occurred or is still continuing. Analyses of nucleotide sequences from rapidly evolving regions of mtDNA can discriminate between contemporary and historical dispersal. Furthermore, the application of a molecular clock to mtDNA sequences from a region that has been characterized well for other freshwater fishes may help explain the processes involved.

MATERIALS AND METHODS

SAMPLING

A total of 83 samples of *M. s. splendida* was collected from 11 sites on the Atherton Tableland, northeastern Queensland (Fig. 1): four in the Herbert River (Blunder Creek, BC; Cameron Creek, CaC; The Millstream, MS and the main channel of the Herbert River, HR); two in the Tully River (Nitchaga Creek, NC and Tully River headwaters, TRH); two from the Barron River (Mobo Creek, MC and Tinaroo Dam, TD); two in North Johnstone River (Little Beatrice River, BR and upper North Johnstone River, UJR) and one in the Walsh River (WR). All these rivers flow over the escarpment towards the east coast except for the Walsh River, which flows north-west and drains into the Gulf of Carpentaria. Sampling was undertaken primarily in October, 1997. Fish were caught by seine and preserved in liquid nitrogen, 70% ethanol or a solution of NaCl saturated 20% dimethyl sulphoxide (DMSO).

DNA EXTRACTION AND SEQUENCING

Total genomic DNA was extracted from muscle tissue as described in Hurwood & Hughes (1998). The mitochondrial protein coding genes ATP*ase* 6 (partial) and ATP*ase* 8 (complete) were amplified using the primers ATP8·2 (supplied by E. Bermingham) and ME-ATP6 (5′>GGA ACA TAA GTG TAA ATA CGG C<3′). PCR conditions were as Hurwood & Hughes (1998) which produced a fragment of *c*. 700 bp. PCR product was cleaned using Qiaquick columns (Qiagen) following the manufacturer's specifications. Sequencing reactions were carried out using big dye terminator cycle sequencing reactions (Perkin Elmer) as per manufacturer's instructions with *c*. 30 ng of clean DNA template and 3·2 pmol of primer on an Applied Biosystems 377 automated sequencer. Both the heavy and light strands were sequenced using the PCR primers.

ANALYSIS

Sequences were aligned and edited using the program SEQED (ABI) from which 670 base pairs were used for further analysis. Genetic variation was calculated using the

ARLEQUIN package (version 1.0, Schneider *et al.*, 1997). The relationship between haplotypes was determined using the program MINSPNET (Excoffier, 1993) on the basis of the minimum number of base pair differences between all haplotypes.

To test the hierarchical gene flow hypothesis, genetic variation within and between sub-populations or drainages was determined using the AMOVA procedure (Excoffier *et al.*, 1992) also in ARLEQUIN. This procedure partitions genetic variation hierarchically based on evolutionary divergence between haplotypes, estimated using the Kimura 2-parameter distance method (Kimura, 1980). The resulting Φ statistics and corresponding variance components were tested for significance using a nonparametric permutation procedure (Excoffier *et al.*, 1992) incorporating 1000 permutations. Conformity to the stepping stone model was tested by comparing the level of gene flow ($\log N_e m$) between all sub-populations to the geographic distances (log km) among sites (Slatkin, 1993). The pairwise matrix of number of migrants was generated using ARLEQUIN. The relationship between gene flow and distance was tested for significance using the Mantel (1967) test in the PATN software package (Belbin, 1995).

The demographic history of *M. s. splendida* on the tableland was investigated by analysing the distribution of pairwise differences (mismatch distribution) between all individuals using the DnaSP software package (version 3.00.0; Rozas & Rozas, 1993). Analysis of the mismatch distribution can discriminate between a population that has remained stable over time and one that has undergone a rapid population expansion (Rogers & Harpending, 1992). A stable population is likely to produce a multi-modal distribution as the rise of new mutations is offset by the loss of variation due to random genetic drift. In contrast, the pairwise differences in a population that has expanded in the past will fit a Poisson distribution due to the rate of the accumulation of new mutations being greater than the loss of variation through drift. To test whether the observed distribution differed significantly from that expected for a stable population, a measure of raggedness, r (Harpending, 1994), was calculated and tested for significance using a coalescent simulation test (Hudson, 1990) in DnaSP with 1000 replicates. The time and magnitude of an inferred population expansion was determined by calculating the expected mean pairwise differences (θ), and units of mutational time (τ), where $\tau = 2ut$, (u = the mutation rate over the fragment assayed; t = time in generations), and $\theta = 2nu$ (n = effective population size).

RESULTS

GENETIC VARIATION

From the 670 bp assayed in the mtDNA sequence analysis, 23 haplotypes were identified with 23 variable sites (Table I) (sequences submitted to GenBank with accession nos. AY008723-AY008745). The resulting nucleotide diversity over all samples was relatively low ($0{\cdot}0044 \pm 0{\cdot}003$) as was the mean number of pairwise differences ($2{\cdot}94 \pm 1{\cdot}56$). The transition (TS) : transversion (TV) ratio was 7·6 : 1 which is lower than the typical value for fish mtDNA of 10 : 1 (Meyer, 1994), yet is similar to the TS : TV ratio found for the ATP*ase* genes for another freshwater fish species (Hurwood & Hughes, 1998). The ratio of 3 : 1 : 9 for 1st, 2nd and 3rd codon position substitutions is typical for a mitochondrial coding region (Meyer, 1994). Of the 23 substitutions observed, 15 were silent, being either two- or four-fold degenerate sites, while the other eight substitutions altered the amino acid coding.

GEOGRAPHIC STRUCTURE

Haplotype MS5 was the most common and widespread, being detected in three of the five river drainages (Table II). There was a relatively low level of genetic divergence between haplotypes with only *c.* 1·3% sequence divergence

TABLE I. Variable sites of the 23 haplotypes detected for *M.s. splendida*. Dots indicate homology to MS1

	21	45	97	109	121	126	192	195	198	240	246	253	306	312	327	356	396	530	531	606	630	664	669
MS1	A	C	T	T	G	C	G	C	G	G	T	G	C	A	T	G	C	A	A	A	T	A	G
MS2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.
MS3	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.
MS4	G	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MS5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.
MS6	.	T	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.
MS7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	T	.	.	.	.	.	.
MS8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	A
MS9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	G	.	.	.	.	.
MS10	.	.	.	.	.	.	.	.	.	A	.	.	.	.	C	A	.	.	.	.	.	.	.
MS11	.	.	.	.	.	.	.	.	.	A	.	.	.	.	C	A	.	.	.	.	.	G	.
MS12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.
MS13	.	.	.	.	.	.	.	.	.	A	.	.	.	.	C	A	.	.	.	.	.	.	A
MS14	.	.	.	.	.	T	.	.	.	A	C	.	.	.	C	A	.	.	.	G	.	.	.
MS15	.	.	.	.	.	.	.	.	.	.	.	.	.	T	C	.	.	.	.	.	.	.	.
MS16	.	.	.	.	A	.	.	.	.	A	.	A	.	.	C	A	.	.	.	.	.	.	A
MS17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.
MS18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.
MS19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	A	.	.	.	.	.	.	.
MS20	.	.	.	C	.	.	.	.	C	A	.	.	.	.	C	A	.	.	.	.	.	.	.
MS21	.	.	C	.	A	.	.	.	.	A	.	A	.	.	C	A	.	.	.	.	.	.	A
MS22	.	.	.	.	.	.	A	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.
MS23	.	.	.	.	.	.	.	T	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.

between the most differentiated haplotypes (MS4-MS21). Nineteen of the detected haplotypes were site specific which may be a function of the relatively low sample size. However, the most common and widespread haplotypes tended to be the internal nodes (ancestral haplotypes) of the minimum spanning network (Fig. 2) which is consistent with coalescent theory (Crandell & Templeton, 1996).

A highly significant Φ_{ST} between sub-populations (Table III) supported strong subdivision as is expected for obligate freshwater species. However, the geographic distribution of haplotypes (Table II) infers that there was little genetic structure by drainages. For example, the Tully River contained two of the most divergent haplotypes creating a high degree of among-populations-within-drainage variation. These data were supported by the analysis of molecular variance (Table III) which demonstrated that the observed partitioning of total genetic variation did not reflect the expected hierarchical model. The among-populations-within-drainage variation was 50% greater than the among-drainage variation. Furthermore the associated Φ_{CT} for among-drainage variation was not significant. Although a larger sample size could well have made this value significant, it was the relationship between Φ_{SC} and Φ_{CT} which clearly did not follow hierarchical expectations. The Mantel test implied that there was no

TABLE II. Haplotype frequencies per site for *M.s. splendida*. Drainage of origin and sample size is indicated. Nucleotide diversity (π) is given for each site

Drainage	Herbert River				Tully River		North Johnstone River		Barron River		Walsh River
Site Haplotype	BC $n=10$	CaC $n=10$	HR $n=10$	MS $n=10$	NC $n=10$	TRH $n=10$	MJR $n=3$	BR $n=5$	MC $n=5$	TD $n=5$	WR $n=5$
MS1	0·7	0·1	0·1		0·5						
MS2	0·1										
MS3	0·1										
MS4	0·1										
MS5		0·4	0·4	0·4			0·67	0·4			1·0
MS6		0·1									
MS7		0·1									
MS8		0·1									
MS9		0·1									
MS10			0·1	0·3			0·33				
MS11			0·1								
MS12			0·2								
MS13			0·1						1·0		
MS14				0·1							
MS15				0·2							
MS16					0·3	0·9					
MS17					0·1						
MS18					0·1						
MS19										0·8	
MS20										0·2	
MS21						0·1					
MS22								0·4			
MS23								0·2			
π	0·001	0·002	0·003	0·003	0·005	0·000	0·002	0·002	0·000	0·002	0·000

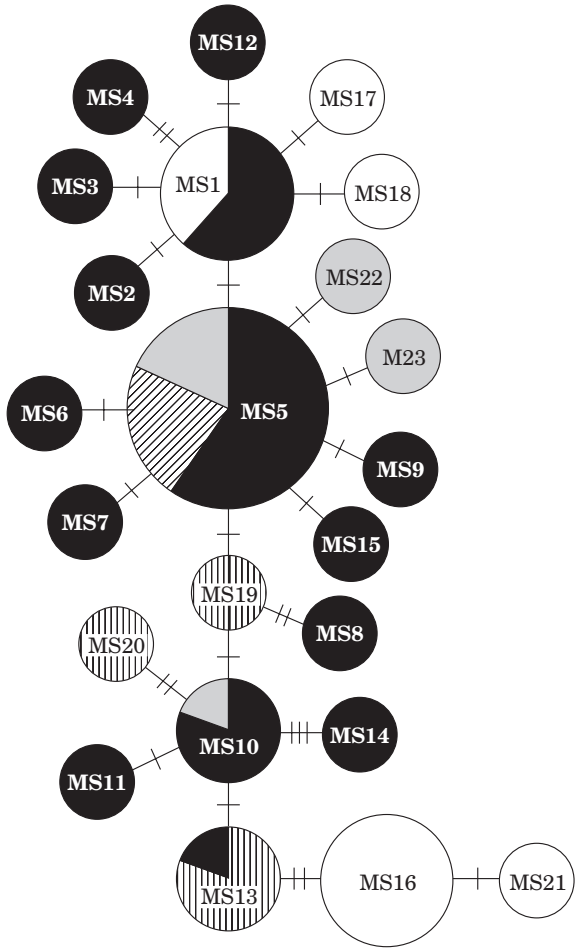

FIG. 2. One of several minimum spanning networks showing the number of base pair differences between haplotypes (alternative minimum distances include 2 bp between MS4 and MS6; 2 bp between MS1 and MS8; 2 bp between MS8 and MS13). Hash marks between nodes indicate the number of differences. The size of the circles represent relative frequency of haplotypes (smallest, <5; 2nd smallest, 6–10; 2nd largest, 11–20; largest, >20). Shading indicates the relative frequency of each haplotype by river drainage. □, Tully; ■, Herbert; ▨, North Johnstone; ▥, Barron; ▨, Walsh.

relationship between geographic distance and genetic divergence ($P=0{\cdot}38$) indicating that there was little support for the stepping stone model.

DEMOGRAPHIC HISTORY

There was a maximum of three base pair differences between any two adjacent nodes in the minimum spanning network (Fig. 2). The short internodal distances were consistent with a star phylogeny that is indicative of a rapid population expansion (Avise *et al.*, 1984). As a population expands, the effects of random genetic drift are reduced, thereby increasing the probability of retaining new mutations. These results were supported by the mismatch distribution (Fig. 3) with a very low raggedness index ($r<0{\cdot}02$). The probability of obtaining by chance a lower raggedness value than the one observed was relatively low

TABLE III. Φ statistics and the hierarchical partitioning of genetic variation within and among drainages. *P* values are the probability under the null distribution of having a more extreme Φ value than observed by chance

Source of Variation	% Total variation	Φ statistics	*P*
Among-drainages	21·86	Φ_{CT}=0·219	0·240 ± 0·015
Among-populations-within-drainages	33·87	Φ_{SC}=0·433	<0·00001
Within-populations	44·27	Φ_{ST}=0·557	<0·00001

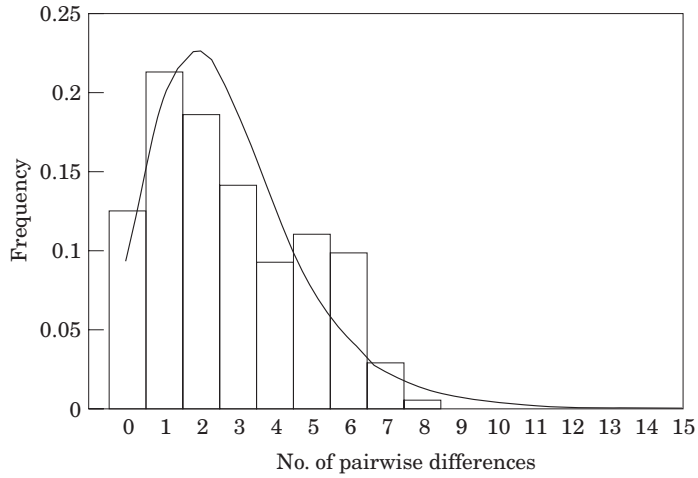

FIG. 3. Mismatch distribution of the number of pairwise differences for *M. s. splendida*. □, Observed frequency of pairwise differences; ——, expected frequency of pairwise differences under the population expansion model. θ_0=1·171; θ_1=9·708; τ=1·603; r=0·0187.

(*P*=0·07) suggesting that the observed distribution of pairwise differences did not differ significantly from that expected under the expansion model. The calculated θ parameters (θ_0=1·171; θ_1=9·708) indicate that *M. s. splendida* on the Atherton Tableland underwent a rapid expansion in effective population size from about 135 000–1·1 million individuals (*c*. eight-fold). Based on the divergence rate of the assayed mtDNA fragment of 1·3% per million years (E. Bermingham, unpubl. data) and the calculated units of mutational time (τ=1·603), the expansion event is estimated to have occurred 90–110 thousand years ago.

DISCUSSION

GENETIC STRUCTURE OF THE EASTERN RAINBOWFISH

The AMOVA showed that the Atherton population of *M. s. splendida* did not conform to the hierarchical model typical of obligate freshwater species. Contrary to prediction there was a higher percentage of genetic variation among sub-populations within drainages than between populations from different river drainages. Therefore, delineating sub-populations based on the current drainage

pattern can be considered artificial and current gene flow along the stream channel was not the dominant force that influenced the present population genetic structure. Also as there was no uniform pattern of isolation by distance, the stepping stone model was not supported.

Although these two gene flow models can be rejected, these data may be explained by a combination of the models. However, there is evidence that isolated interdrainage dispersal events have occurred relatively recently between Nitchaga Creek (NC) and subpopulations in the Herbert River (BC and/or CaC).

The highest nucleotide diversity was found at Nitchaga Creek (Table II) principally through two divergent haplotypes (MS1 and MS16; Fig. 2). This could reflect retention of both ancestral haplotypes since recruitment to Nitchaga Creek during the initial radiation onto the tableland. The coalescence time for haplotypes MS1 and MS16 is *c.* 345 thousand years ago, which pre-dates the population expansion event significantly. Due to the lack of MS1 in the upper Tully River (TRH) a more plausible hypothesis is that the diversity in Nitchaga Creek is the result of recent secondary contact suggesting interdrainage dispersal.

For episodes of contemporary gene flow to explain the observed genetic structure, a plausible explanation for interdrainage dispersal must be found. Individuals could have been translocated inadvertently through the restocking of fish (e.g. barramundi) for recreational purposes in Koombooloomba and Tinaroo Dams or *via* passive dispersal by animals, however improbable (McDowall, 1981). Alternatively dispersal may be possible during times of high flooding. For example the watershed between the Barron and North Johnstone River is not highly pronounced (Jardine, 1925) and may be breached during times of flood. While each situation is theoretically possible, neither is likely to occur frequently enough to explain the observed distribution of haplotypes across the Atherton Tableland.

As a high level of contemporary gene flow appears unlikely, past dispersal may have been widespread. If present genetic variation in *M. s. splendida* is a consequence of historical gene flow, then that pattern is a function of not only dispersal but also the geomorphological evolution of the drainage lines on the Atherton Tableland. It is generally accepted that widespread drainage rearrangement has occurred on the highlands of north-eastern Australia (Ollier, 1978). The rearrangement of stream channels has been invoked to explain the genetic structure of other freshwater species on the Atherton Tableland (Hughes *et al.*, 1996; Hurwood & Hughes, 1998; McGlashan & Hughes, 2000).

A major geomorphological process affecting drainage patterns is volcanism (Bishop, 1995). Considerable volcanism occurred in north-eastern Australia up to 10 thousand years ago (Stephenson *et al.*, 1980). Evidence suggests that larval flow dammed several drainages in this region (Ollier, 1978), and could have facilitated widespread dispersal between the Herbert, North Johnstone, Barron and possibly Walsh Rivers. If there was a single invasion of *M. s. splendida* on to the Atherton Tableland, presumably *via* a single river, then the dispersal into other drainages would open up significantly more suitable habitat for this species allowing for a rapid population expansion. If this was the case, the expansion event could correspond with the conclusions from the mismatch distribution suggesting a population increase *c.* 100 thousand years ago. Furthermore,

rainfall was significantly higher than present day levels just prior to and after the inferred expansion date (Kershaw, 1978), and may have promoted the relatively recent invasion on to, and dispersal across the tableland.

There is strong evidence to suggest that the *M. splendida* group itself is the result of a recent and rapid speciation event in the Gulf of Carpentaria (McGuigan *et al*., 2000) [existing as the brackish to freshwater Lake Carpentaria, several times during the late Quaternary due to considerably lower sea levels (Torgersen *et al*., 1985)]. Hence *M. s. splendida* can only be a relatively recent migrant to the Atherton Tablelands. It is noteworthy that the estimate of population expansion is consistent with one episode of the disappearance of Lake Carpentaria <120 thousand years ago (Torgersen *et al*., 1985).

Widespread historical dispersal of *M. s. splendida* across the Atherton Tableland due to localized volcanism and the associated change in drainage lines would have a homogenizing effect on the genetic structure among subpopulations. As the headwaters gradually became isolated with the drainage lines evolving to their current pattern, it may be expected that representatives of each haplotype would be evident in each river system, which is not the case. However, this does not allow for the effects of random lineage sorting through genetic drift. As discussed previously, lineage sorting is expected to be relatively rapid in headwater streams, but it is doubtful that there has been sufficient time for reciprocal monophyly to have been attained even in the absence of interdrainage gene flow.

Although the Herbert River was sampled more intensively, the haplotypes detected were the most widely distributed with nearly all ancestral haplotypes detected (Fig. 2), suggesting that this river may be representative of an ancestral distribution. Whether the eastern rainbowfish arrived by dispersing up the eastern rivers such as the Herbert River or *via* the Walsh River to the west, is unclear. The relationship between *M. s. splendida* and other parapatric subspecies of the *M. splendida* group from northern Australia and New Guinea remains unresolved (McGuigan *et al*., 2000) and the lowland coastal drainages were not sampled here. However, taking into account the fact that the sample from the Walsh River was fixed for the most ancestral haplotype (MS5) and coupled with a significantly more accessible gradient on the western side of the tableland, it is plausible that migration was from the west. Once on the Atherton Tableland, subsequent interdrainage dispersal across the tableland, possibly over *c*. 100 thousand years ago, resulted in the present distribution of genetic variation.

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