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## Distribution of the Lake Eacham Rainbowfish in the Wet Tropics Region, North Queensland

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### Abstract

The Lake Eacham rainbowfish, *Melanotaenia eachamensis* Allen & Cross, 1982, was thought to be extinct in the wild until recent research demonstrated the presence of wild populations in a few tributaries of the upper Johnstone River and the upper Barron River, north Queensland, by using the technique of DNA sequencing. We present the results of a multivariate analysis of a range of morphological and meristic characters of rainbowfish collected from rivers of the Wet Tropics region, particularly the Johnstone River, that demonstrate that *M. eachamensis* is widespread in the upper and lower reaches of the North and South Johnstone rivers and tributaries of the upper Tully River. *M. eachamensis* was most often the dominant species in those locations where sympatry with *M. splendida splendida* was observed. *M. eachamensis* should be considered a stream-dwelling species rather than a lacustrine species although a significant lacustrine population (Koombooloomba Dam) was detected.

### Introduction

The Lake Eacham rainbowfish, *Melanotaenia eachamensis* Allen & Cross, 1982, had the dubious distinction of being listed as the first freshwater fish to become extinct in the wild during the period of European occupation of the Australian continent (Wager 1993; Wager and Jackson 1993). The species' decline in abundance and eventual presumed extinction in Lake Eacham, its type locality, was documented by Barlow *et al.* (1987) and suggested to be due to predation by translocated indigenous fishes. Some debate about the specific status of this rainbowfish has occurred (Crowley and Ivanstovff 1991; Wager 1993) and was not resolved until research utilising DNA sequencing conclusively demonstrated that *M. eachamensis* was a valid species and distinct from the common and widely distributed eastern rainbowfish, *M. splendida splendida* (Peters, 1866) (Zhu *et al.* 1994).

Allen (1989, 1995) increased the distribution of *M. eachamensis* to include Dirran Creek, a tributary of the North Johnstone River and another volcanic crater lake, Lake Euramoo. Zhu *et al.* (1997) confirmed its presence in Dirran Creek and other tributaries of the North Johnstone River located on the Atherton Tablelands and in the Barron River and its impoundment, Lake Tinaroo (and associated irrigation supply system). The species was therefore not extinct in the wild but only from its type locality. Zhu *et al.* (1997) also reported the existence of *M. eachamensis*–*M. splendida splendida* hybrids occurring in the wild. Hybridisation has long been known to occur between rainbowfishes when kept together in captivity (Caughey *et al.* 1990) but is suggested to occur rarely in the wild (Allen and Cross 1982). The previous failure of electrophoretic methods to distinguish between the two species (Crowley and Ivanstovff 1991) may have been due to misidentification or by contamination of the samples by phenotypically cryptic hybrids (Zhu *et al.* 1997).

Rainbowfishes are morphologically variable (Allen and Cross 1982). In a survey of the freshwater fish fauna of the Wet Tropics region, all melanotaeniids other than *M. maccullochi* Ogilby, 1915 were assigned to *M. splendida splendida* (Pusey and Kennard 1996), although the extensive morphological variation within the samples was noted (unpublished data). Allen and Cross (1982) distinguished *M. eachamensis* from the related *M. splendida splendida* on the basis

of its more slender shape, lower anal fin ray count and less well-developed vomerine teeth. Zhu *et al.* (1997) further distinguished between *M. splendida splendida* and *M. eachamensis* (species allocated on the basis of prior analysis of DNA sequence data) by multivariate analysis of a range of additional meristic and morphological characters. The aim of the present study was to provide a preliminary distribution for *M. eachamensis* within the Johnstone River drainage and some other rivers of the Wet Tropics region based on a multivariate analysis of meristic and morphological characters as proposed by Zhu *et al.* (1997).

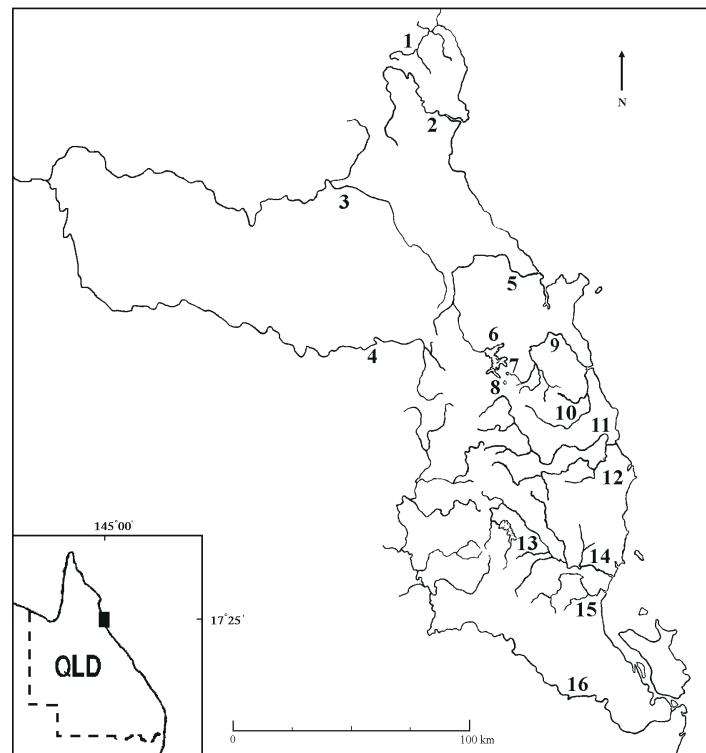
## Methods

### *Specimen Collection*

Specimens intended for morphological analysis were mainly collected from the Johnstone River in 1994 and 1995 (Fig. 1). Specimens from the Bloomfield, Daintree, Tully and Murray rivers were collected in 1993 (see Pusey and Kennard 1996) and additional specimens from the Tully River and tributary streams of the Herbert River were collected in October 1996. Fish were collected by electrofishing and seine netting and immediately fixed in 4% buffered formal saline.

### *Analysis of Meristic and Morphological Variation*

The following characters were counted or measured for each of the 569 specimens; standard length (S.L.), first dorsal fin rays, second dorsal soft fin rays, pectoral fin rays, anal fin rays, horizontal scale count, vertical



**Fig. 1.** Major drainages of the Wet Tropics region of north Queensland. Geographical locations mentioned in the text are depicted and given codes for clarity. 1, Bloomfield River; 2, Daintree River; 3, Mitchell River; 4, Walsh River; 5, Barron River; 6, Lake Tinaroo; 7, Lake Euramoo; 8, Lake Eacham; 9, Mulgrave River; 10, Russell River; 11, North Johnstone River; 12, South Johnstone River; 13, Koombooloomba Dam; 14, Tully River; 15, Murray River; 16, Herbert River.

scale count, predorsal scale count, cheek scale count, head length, head depth, predorsal length, body depth at origin of first dorsal fin, body depth at the origin of the pelvic fin, snout length, eye diameter, mouth length and length and depth of the caudal peduncle. Most of these characters are diagnostic for the melanotaeniids in general and formally described in Allen and Cross (1982) or Zhu *et al.* (1997). Morphological characters are shown in Fig. 2. All of the characters listed above, with the exception of head depth, dorsal depth, pelvic depth, mouth length and caudal depth and length, were used in Zhu *et al.* (1997).

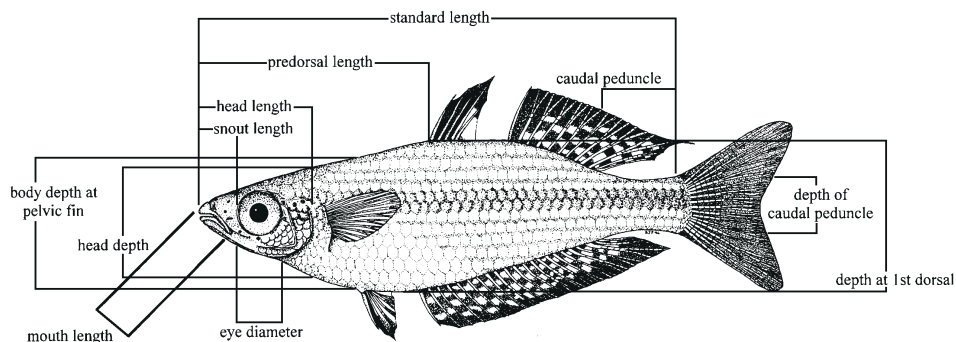


Fig. 2. External anatomy of *Melanotaenia* with all measured morphological traits labelled.

We recognise that many of these characters may be allometrically related to body size. In order to reduce the influence that such allometry might have in influencing the conclusions drawn from our analysis we restricted the analysis to fish between 30 and 60 mm S.L. In addition, rather than standardising morphological characters (head length to depth of the caudal peduncle inclusive) by dividing by standard length, we standardised by dividing by standard length raised to whatever power best described the relationship between length and the character in question for the entire data set (i.e.  $n = 569$ ). Preliminary analyses revealed that a power fit explained more variation in all characters than did a linear fit with standard length. However, in no case did a power fit result in more than a 2.5% better explanation of the observed variance than did a linear fit.

A canonical discriminant functions analysis (DFA) (SPSS for Windows™) was used to discriminate between rainbowfish specimens. Prior to analysis, 62 specimens collected from the main river channel of the South Johnstone River and from Mena Creek, a tributary of the South Johnstone River, were assigned to *M. splendida splendida*. These specimens closely matched the specific description of *M. splendida splendida* and were accordingly designated as this species in the analysis (a decision fully supported *a posteriori* by the results of our analyses). In all, 39 specimens from Dirran Creek, North Johnstone River, were assigned to *M. eachamensis*. Zhu *et al.* (1997) identified the rainbowfish population present in Dirran Creek (bridge crossing on the Palmerston Highway) as being a pure stock of *M. eachamensis*. All other fishes collected from the Wet Tropics region ( $n = 468$ ) were not given specific status and allowed into the analysis without group allocation. On the basis of position on the resultant discriminant function, specimens without specific assignment were allocated with a given probability to either two species by DFA. All proportional data were arcsin transformed prior to analysis. Mean values for each morphological character given in Table 1 are standardised by division by standard length rather than S.L. raised to some power for three reasons. First, specific diagnoses and descriptions (Allen and Cross 1982; Allen 1989; Allen 1995) are presented as ratios of standard length; second, linear ratios were only very slightly different from ratios derived from power functions; and, third, researchers in the field may be better able to conceptualise linear ratios rather than ratios derived from power functions. This third point may seem trivial; however, the failure by many researchers to identify *M. eachamensis* in the field since it was suggested to have become extinct would suggest otherwise.

## Results

### Morphological Variation

Highly significant discrimination between the two rainbowfish species was revealed by DFA ( $\chi^2 = 210.9$ , d.f. = 18, eigenvalue = 9.413) and significant between-species differences in all but

**Table 1. Means ( $\pm$  s.d.) of meristic and morphometric characters for *M. splendida splendida* and *M. eachamensis* used in the DFA to define species-groups**

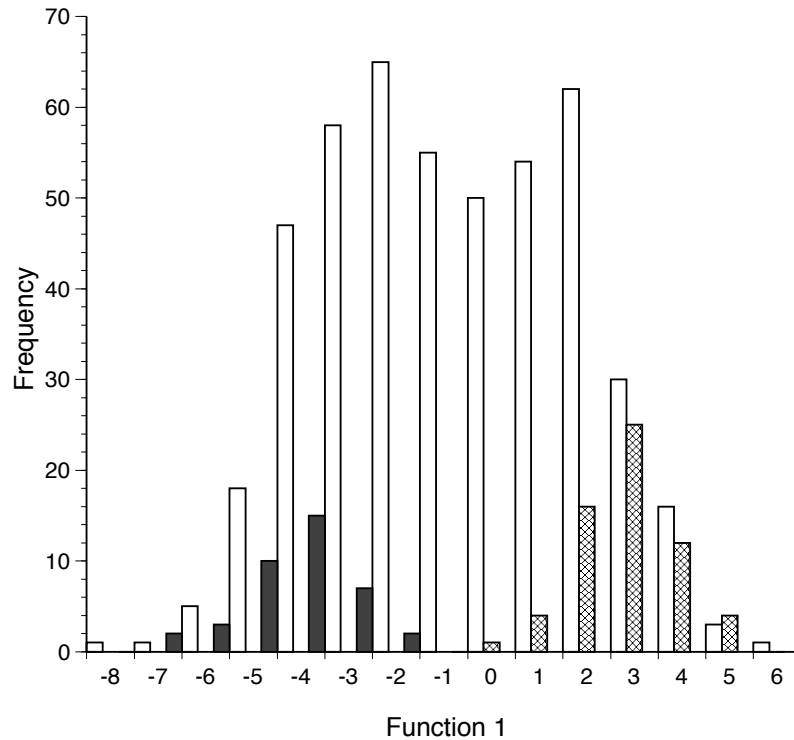
Means of morphometric characters are expressed as a proportion of S.L. *F*-values of univariate ANOVAs and their associated levels of significance for each variable are also shown. n.s.,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ . The exponent relating each parameter to S.L. used in the standardisations and  $r^2$  are shown. Standardised canonical discriminant function coefficients for each character are listed as loadings on Discriminant Function 1

Character	Exp.	$r^2$	<i>M. splendida splendida</i> ( <i>n</i> = 62)	<i>M. eachamensis</i> ( <i>n</i> = 39)	<i>F</i> -value	Loading on DF1
Meristics						
Fin rays						
1st Dorsal			5.84 (0.55)	5.92 (0.62)	0.51 <sup>n.s.</sup>	0.084
2nd Dorsal			10.63 (0.87)	12.66 (0.77)	36.91***	-0.438
Pectoral			13.77 (0.68)	13.00 (0.95)	22.61***	0.129
Anal			20.82 (0.69)	19.41 (0.95)	48.99***	0.339
Scale counts						
Horizontal			11.47 (0.74)	10.94 (0.51)	14.73***	0.233
Vertical			35.08 (1.06)	36.12 (1.23)	20.48***	-0.089
Predorsal			16.04 (0.77)	15.67 (0.77)	5.80*	0.097
Cheek			12.46 (1.50)	11.05 (1.39)	22.47***	0.074
Morphometrics						
Head length	0.827	0.921	0.274 (0.012)	0.269 (0.015)	3.40 <sup>n.s.</sup>	-0.391
Head depth	0.896	0.778	0.220 (0.019)	0.231 (0.023)	6.86*	-0.362
Predorsal length	0.942	0.925	0.477 (0.012)	0.445 (0.017)	152.15***	0.797
Depth at 1st dorsal fin	1.036	0.777	0.282 (0.033)	0.265 (0.023)	9.39**	2.636
Depth at pelvic fin	0.990	0.783	0.257 (0.024)	0.255 (0.018)	0.17 <sup>n.s.</sup>	-2.103
Snout length	1.021	0.856	0.082 (0.005)	0.076 (0.005)	28.86***	0.309
Eye diameter	0.666	0.814	0.094 (0.006)	0.097 (0.006)	9.62**	0.057
Mouth length	0.814	0.806	0.112 (0.006)	0.119 (0.007)	41.35***	-0.416
Peduncle length	0.880	0.728	0.175 (0.012)	0.182 (0.014)	7.90**	-0.330
Peduncle depth	1.055	0.887	0.108 (0.006)	0.110 (0.006)	4.98*	-0.307

three of the meristic and morphological characters used in the analysis were detected by ANOVA (Table 1). None of the 101 *a priori* allocated specimens was allocated to another species by the analysis, resulting in an overall classification success of 100%. Both species showed considerable morphological variation but there was no overlap in species distributions on Discriminant Function 1 (Fig. 3). *M. eachamensis* and *M. splendida splendida* were clearly morphologically distinct. *M. eachamensis* had a narrower body but deeper head than *M. splendida splendida*, had a slightly larger mouth and eye and the eye was positioned more anteriorly, and the dorsal fins were positioned more anteriorly thus leading to a longer caudal peduncle. Fin ray counts and scale counts also differed significantly. Despite the clear separation between *M. eachamensis* from Dirran Creek and *M. splendida splendida* from the South Johnstone River and Mena Creek, many specimens included in the analysis, but without specific assignment, were distributed between these two extremes on Function 1 (Fig. 3), indicating that either both species were more morphologically variable than previously thought or that hybrids were common in our samples.

#### Distribution

Discriminant functions analysis indicated that *M. eachamensis* was present in the Johnstone, Tully and Herbert River drainages and that *M. splendida splendida* was present in all the drainages examined (Table 2). Fourteen of the 25 sites examined in the Johnstone River drainage contained *M. eachamensis* although all but two of these sites contained *M. splendida*



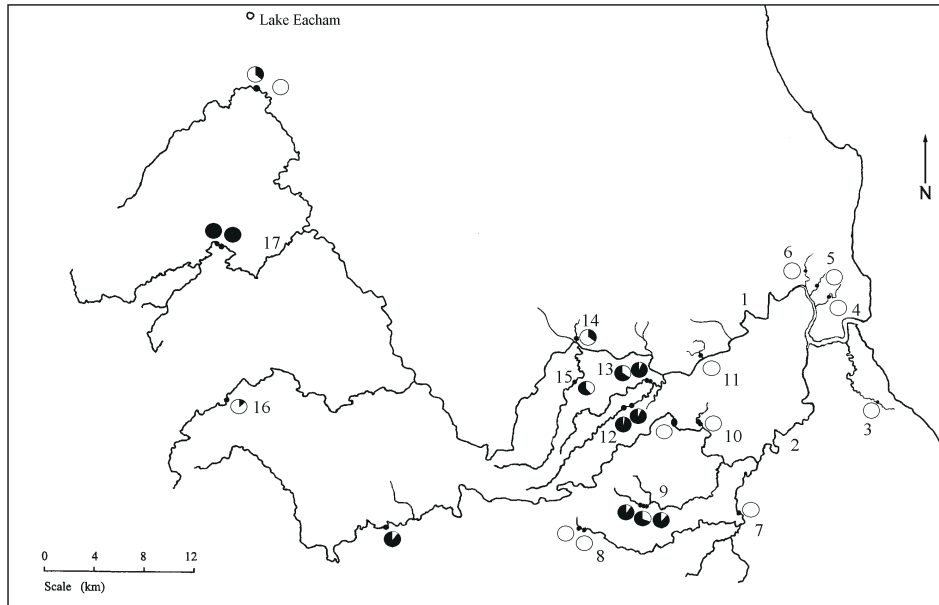
**Fig. 3.** The distribution of *M. eachamensis* (solid bars) and *M. splendida splendida* (hatched bars) on Function 1 resulting from discriminant functions analysis of meristic and morphometric characters. Specimens included in the analysis but without species assignment are shown as open bars.

*splendida* also (Fig. 4). These two sites were located on Dirran Creek: we designated these sites as containing pure populations of *M. eachamensis* following Zhu *et al.* (1997). It therefore appears that sympatry is common within this drainage basin, although in most of these sites (12 of 14) *M. eachamensis* was the numerically dominant rainbowfish. *M. eachamensis* only occurred above an elevation of 80 m above sea level within the Johnstone River drainage.

**Table 2.** The composition of rainbowfish populations in various drainages of the Wet Tropics region of northern Queensland

Species assignment was based on the results of DFA of meristic and morphological characters. The number of specimens from each river is given as *N*. The relative composition of the fauna is given as a percentage of the entire sample. The Johnstone River sample contains both specimens that were included in the DFA without species assignment and specimens that were assigned *a priori* to either *M. splendida splendida* or *M. eachamensis*

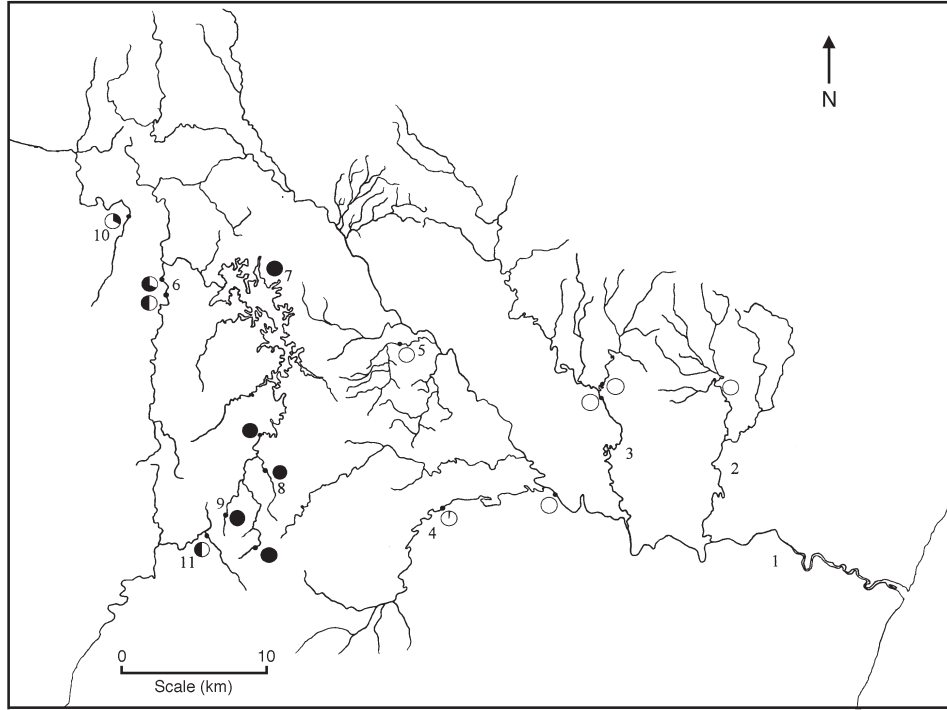
River	<i>N</i>	Proportion of sample	
		<i>M. s. splendida</i>	<i>M. eachamensis</i>
Bloomfield	7	100.0	
Daintree	11	100.0	
Johnstone	403	52.6	47.4
Tully	119	49.6	50.4
Murray	8	100.0	
Herbert	21	81.0	19.0



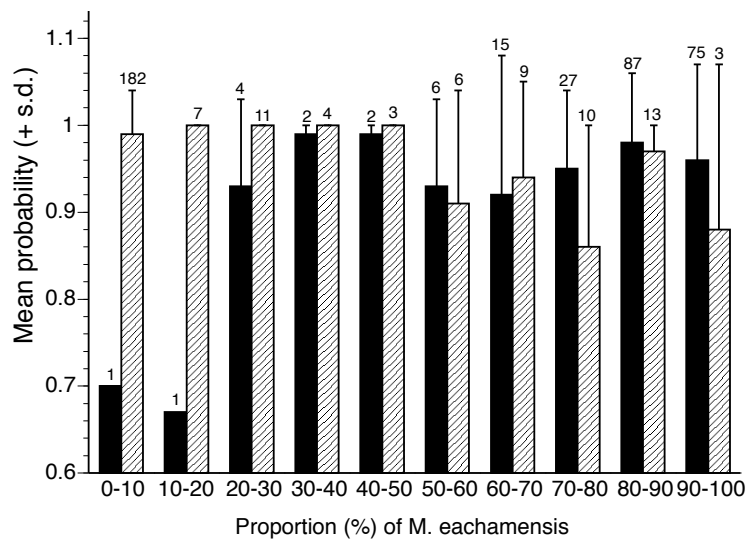
**Fig. 4.** The distribution of *M. eachamensis* and *M. splendida splendida* in the Johnstone River drainage. Each pie represents a sampling location and the proportion of the sample represented by *M. eachamensis* is given as the solid component. Tributary names are as follows: 1, North Johnstone River; 2, South Johnstone River; 3, Ninds Creek; 4 and 5, un-named tributary; 6, Polly Creek; 7, Stewart Creek; 8, Mena Creek; 9, Utchee Creek; 10, un-named tributary; 11, Wharrapa Creek; 12, Fishers Creek; 13 and 14, un-named tributaries; 15, Rankin Creek; 16, Beatrice River; 17, Dirran Creek.

*Melanotaenia eachamensis* was almost entirely restricted to upstream reaches of the Tully River drainage (Fig. 5) in streams located at over 700 m elevation in the Tully River (i.e. above the Tully Falls). One specimen out of a total of 23 fish collected from Davidson Creek (elevation of 20–40 m) was identified as *M. eachamensis* although the probability that it was correctly assigned to this species was not high (0.701). Although apparently widely distributed in the lower reaches of the Tully River, *M. splendida splendida* was very uncommon above the Tully Falls with only one specimen being collected from Nitchaga Creek ( $n = 7$  for this site). This specimen was assigned to *M. splendida splendida* with weak probability (0.664). All 28 specimens collected from Koombaloo Dam were identified as *M. eachamensis*; two of these were assigned to this species with very low probability (<0.60) whereas the remainder were assigned with very high probability (>0.975). Collections made in Blunder Creek, Cameron Creek and Millstream, within the Herbert River drainage, were dominated by *M. splendida splendida* although the specimens assigned to *M. eachamensis* from these sites were assigned with high probability (>0.95).

Over the range of sites examined by us, few contained both species in roughly equal proportions and where this occurred, sample sizes were not large (Fig. 6). When one species dominated, however, there was a general tendency for the other species to have an intermediate morphology (meristic and morphometric characters) but this was not a symmetrical relationship. For example, when *M. splendida splendida* was the dominant species (>70%), specimens allocated to *M. eachamensis* were done so with reduced probability. When *M. eachamensis* was dominant, however, both species were allocated with lower probabilities and the samples were more variable in allocation.



**Fig. 5.** The distribution of *M. eachamensis* and *M. splendida splendida* in the Tully and Herbert Rivers. Each pie represents a sampling location and the proportion of the sample represented by *M. eachamensis* is given as the solid component. Tributary names are as follows: 1, Tully River; 2, Banyan Creek; 3, Jarra Creek; 4, Davidson Creek; 5, Stony Creek; 6, Nitchaga Creek; 7, Koombooloomba Dam; 8, O’Leary Creek; 9, Luft Creek; 10, Blunder Creek; 11, Cameron Creek.



**Fig. 6.** Changes in the mean probability of species assignment ( $\pm$  s.d.) of unassigned specimens into either *M. eachamensis* (solid bar) or *M. splendida splendida* (hatched bar) with increasing proportion of *M. eachamensis* in the samples. Specimens were assigned to either species by a discriminant functions analysis of meristic and morphometric characters.



## Discussion

The observation by Zhu *et al.* (1997) that *Melanotaenia eachamensis* is not extinct in the wild but only from its type locality is corroborated by the results of the present study. Furthermore, the distribution of this species of rainbowfish can be extended to include many streams, other than Dirran Creek, within the Johnstone River catchment and can now also be extended to include the upper reaches of the Tully River and its tributaries and the Koombaloo Dam. Four specimens (out of 21) collected from the upper reaches of the Herbert River were identified as *M. eachamensis* by DFA and these data suggest that it also occurs in the Herbert River catchment. We did not detect *M. eachamensis* in the Daintree River; however, all of the sites from which these fish were collected were at low elevation (Pusey and Kennard 1996) and sample sizes were small. Given that *M. eachamensis* appears to be most common at elevations above 100 m, then we suggest that further collection in small, upland, forested streams of the Wet Tropics region, particularly streams draining the Windsor and Mt Carbine Tablelands, may reveal an even more widespread distribution.

The presence of *M. eachamensis* in the Koombaloo Dam is interesting particularly since this impoundment contains two species of large piscivorous fish, *Hephaestus fuliginosus* (Mcleay) and *Lates calcarifer* (Bloch) (A. Hogan, personal communication). Predation by translocated fishes, notably by *Glossamia aprion* (Richardson) was suggested to be the primary cause of the extinction of *M. eachamensis* from its type locality, Lake Eacham (Barlow *et al.* 1987). Rainbowfish in Utchee Creek, a tributary of the South Johnstone River, have long been recognised as being phenotypically distinctive (Allen and Cross 1982). This study has shown that most of the specimens recorded from this stream are phenotypically indistinguishable from *M. eachamensis*. Further research focused particularly on the genetic distinctiveness of separate rainbowfish populations (i.e. by DNA sequencing) throughout the Wet Tropics region is needed.

The Johnstone River has a rich melanotaeniid fauna composed of *M. eachamensis*, *M. splendida splendida*, *M. maccullochi* (Ogilby), *M. trifasciata* (Rendahl) and *Cairnsichthys rhombosomoides* (Nichols & Raven) (Pusey and Kennard 1996). As such, it raises some interesting questions concerning historical biogeography and contemporary ecology. *Cairnsichthys* is clearly the most plesiomorphic of the rainbowfish genera (Allen 1980) and the monotypic status of the genus and its limited distribution (Pusey and Kennard 1996) suggest it is a paleoendemic and may have existed in the Wet Tropics region for an extensive period. Zhu *et al.* (1994) presented a phylogenetic tree for 10 species of Australian and New Guinean *Melanotaenia*, including *M. eachamensis* and five currently recognised subspecies of *M. splendida* and showed that *M. eachamensis* is widely divergent from *M. splendida splendida* and more closely allied to the subspecies *M. splendida australis* from Western Australia. We propose the following hypothesis to account for the observed biogeography. The *Melanotaenia splendida* group originated in the west and colonised eastward. As it progressed eastward, one or more populations colonised the Tablelands, possibly via river capture of the Walsh River or Mitchell River by the Barron River (Coventry *et al.* 1980; Willmott and Stephenson 1989) and differentiated into *M. eachamensis*. Other populations of *M. splendida* continued their eastward spread, north into New Guinea and then southward down the north-east coast of Australia, coincidentally differentiating into the various subspecies seen today. *M. splendida splendida* may have recently colonised the upper reaches of rivers of the Wet Tropics region by moving upstream in a east–west direction. Changes in river drainage are not uncommon for eastern Australia (Ollier 1982; Haworth and Ollier 1992; Fried and Smith 1992).

Of ecological interest are the interactions that may be currently occurring (or within recent history) between *M. eachamensis* and *M. splendida splendida* and between other rainbowfishes in the Johnstone River. Although sympatry between species of rainbowfish in the Wet Tropics region is occasionally observed (Russell and Hales 1993; Pusey *et al.* 1995; Pusey and Kennard 1996; this study) little is known of the strength of interaction between species or the degree to which such factors are responsible for the observed patterns of distribution. Similarly, little is known of the degree to which species-specific differences in physiological tolerance may

influence distribution. For example, frosts are not uncommon on the Tablelands during the period from May to August and the incidence of fungal infection in many species of freshwater fish is more common at this time (personal observations). Water temperature varies significantly according to season and altitude in the Wet Tropics region and this effect is discernible even when comparing streams located above and below 100 m elevation (mean June/July water temperatures of  $16.9 \pm 0.7$  (s.e.)°C and  $21.3 \pm 0.4$ °C respectively) (unpublished data). Low water temperatures are suggested to be responsible for determining the southern limit of the distribution of *M. fluviatilis* (Allen 1995) and may play some role in determining the altitudinal limits of *M. splendida splendida*.

The extent to which body morphology in rainbowfishes is influenced by habitat structure and dependent on genetic or developmental factors is unknown. *M. splendida splendida* is phenotypically very variable and '... it almost appears that each stream population has its own peculiarities'. (Allen and Cross 1982, p. 60). *M. eachamensis* and *M. splendida splendida* are clearly genetically, meristically and morphologically distinct (Zhu *et al.* (1997; this study) yet there were many specimens in our analysis that exhibited an intermediate set of characters. There is therefore the possibility that specimens accorded the identity of *M. eachamensis* were in fact *M. splendida splendida* with body shapes adapted to or influenced by the structure of small stream habitats. If so, we have overestimated the distribution of *M. eachamensis*; however, the generally high probability with which many specimens were allocated to *M. eachamensis* suggests otherwise. Zhu *et al.* (1997) clearly identified the existence of hybrids on the basis of DNA sequencing data and it may be that hybrids also show intermediate body forms. Similarly, the results of the present study suggest that hybridisation between these species may be common place if intermediate body morphologies are indicative of hybrids. Resolution of this problem requires further investigation if meaningful conservation strategies are to be put in place for *M. eachamensis*. Zhu *et al.* (1997) suggest that hybridisation between these two species is part of the evolutionary process and should be allowed to run its course. Anthropogenic facilitation of extensions in the distribution of *M. splendida splendida* may, however, result in a greater potential for hybridisation as may poor land use practices. For example, it would be instructive to know whether changes in flow regime (and hence in-stream habitat structure) or the extent and nature of riparian vegetation favour one species over another or increase the likelihood of hybridisation.

In conclusion, *M. eachamensis* is widespread throughout the Johnstone River and present in the upper reaches of the Tully River and in the Herbert River. The known distribution of *M. eachamensis* can now be extended to include the Barron, Johnstone, Tully and Herbert River drainages. *M. eachamensis* should more properly be considered a stream-dwelling rainbowfish, despite its type location being Lake Eacham, and this should be borne in mind when its conservation needs are considered.

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