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A TASMANIAN LANDLOCKED POPULATION OF THE NORMALLY DIADROMOUS FISH GALAXIAS MACULATUS (JENYNS)

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(with two tables and one text-figure)

ABSTRACT

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A landlocked population of the normally diadromous fish *Galaxias maculatus* is recorded for the first time from Tasmania. The differences between the landlocked population and normal diadromous *G. maculatus* are examined and discussed. The association with other species together with the probable mode of origin of the landlocked population are considered.

INTRODUCTION

The taxonomy of *G. maculatus*, both at the generic and specific levels, has been in a state of confusion virtually since its description. From material collected during the voyage of Darwin's "Beagle" Jenyns (1842) described *Mesites maculatus* and *M. alpinus* from South America and *M. attenuatus* from New Zealand. All three species were included in *Galaxias* by Valenciennes (1846) but later Ogilby (1899) proposed a new genus *Austrocobitis* for *G. attenuatus* and an additional Australian species. *Austrocobitis* was intended as a substitute for *Mesites*, which was found to be preoccupied by a genus of beetles, and has been rejected by most recent writers (see Scott 1966) but retained by Whitley (1933) although in a different sense from that originally proposed.

Stokell (1966) considered the *G. attenuatus* of Australia and New Zealand and the *G. maculatus* and *G. alpinus* of South America, concluded that they were only subspecifically distinct and applied the name *G. maculatus* on the grounds of page precedence. Stokell's less than fortunate choice of name has been criticised by McDowall (1967a) and Scott (1968) but as McDowall (1967a) has pointed out Stokell is first revisor and the name *G. maculatus* must now be used. However some recent writers (Green 1969; Scott 1971, 1974; Maclean 1974; Thomson 1977) have retained *G. attenuatus*.

Further confusion exists in that G. maculatus has been recorded from Australia, New Zealand, Lord Howe Island, Chatham Islands, Chile, Argentina, Tierra del Fuego and the Falkland Islands (McDowall and Frankenberg 1981) with both diadromous and lake isolated populations having been recorded from mainland Australia, New Zealand and South America (McDowall 1972). The existence of such widely dispersed populations together with lacustrine variates, has led to populations in various areas being repeatedly redescribed as new species. McDowall and Frankenberg (1981) listed a total of thirty-five names which at one time or another have been applied to populations of G. maculatus. Even after much recent study there is still not a general consensus among taxonomists as to whether G. maculatus represents one species (McDowall 1972), more than one species (Scott 1968; Campos 1974) or more than one subspecies (Stokell 1966). Some lacustrine populations have also been regarded as distinct. Stokell (1964) described G. parrishi from Victoria, McDowall (1967b) described G. gracilis and G. usitatus from New Zealand and Campos (1974) applied the name G. alpinus to freshwater limited populations in Chile. Pollard (1971b) examined a number of landlocked Australian populations and concluded that they were best regarded as "ecological races" rather than distinct species.

This conclusion was supported by McDowall (1972) who concluded that the only valid lacustrine species was $G.\ gracilis$ of New Zealand. The results of the present study appear to support this conclusion.

MATERIALS AND METHODS

In a previous study (Andrews 1976) it was stated that no Tasmanian populations of *G. maculatus* were encountered which could be regarded as landlocked. Subsequently a sample of twenty-one specimens were obtained from Bowlers Lagoon, an isolated sand dune lake in northeastern Tasmania (map reference EQ780760) located some 2 km from the coast and 1 km east of the Ringarooma River (fig. 1). All specimens were recovered from fyke nets set by a commercial eel fisherman and were fixed in the field in 10% formalin and subsequently transferred to 70% ethanol. Seven of the specimens were cleared and stained for osteological study.





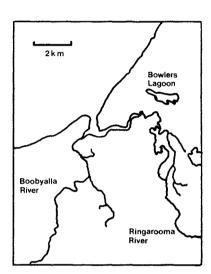


FIG. 1.- Locality map.

Methods of measurement and counts followed those adopted by Andrews (1976) except that segmented fin rays only were counted whether branched or unbranched. For meristic and morphometric comparison a group of twelve G. maculatus was selected from samples of diadromous Tasmanian populations, chosen largely at random, to form a group of comparable standard length range to the Bowlers Lagoon material which varied from 99.6 mm to 147.0 mm standard length.

RESULTS

Morphometric and meristic data are summarized in tables 1 and 2. Morphometric comparison indicated that the landlocked population differed little from typical *G. maculatus* apart from a slight tendency towards smaller paired fins, a narrower caudal peduncle and a wider head. Values of Student's "t" were calculated using a pooled estimate of the variance in both the diadromous and landlocked populations and in only one proportion was the 5% level of significance exceeded. Meristic data tended to indicate fewer vertebrae, fewer dorsal, anal and caudal fin rays and an increase in pectoral and ventral fin rays and gill rakers in the landlocked population. However these differences were small and in only one case, anal fin rays, was the 1% level of significance exceeded. With the exception of vertebrae, the landlocked population exhibited a greater range of variation in

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almost all characters examined. The reduction in caudal and increase in ventral fin rays is unusual in that *G. maculatus* normally exhibits high stability in both these characters (McDowal 1 1972, Pollard 1971b), so much so that they were not tabulated by Andrews (1976). The Tasmanian *G. maculatus* examined by McDowall and Frankenberg (1981) exhibited eight rayed ventrals in 5% of cases, considerably less than the 10.5% of occurrences in the Bowlers Lagoon material.

TABLE 1 MORPHOMETRIC VARIATION BETWEEN THE LANDLOCKED AND DIADROMOUS G. MACULATUS. Numerator written as a percentage of the denominator. (\bar{x} = sample mean, S.D. = standard deviation, t = Student's t).

		Landlocked			Diadromous				
	min.	max.	x	S.D.	min.	max.	$\bar{\mathbf{x}}$	S.D.	t
Head length/standard length	16.6	20.4	18.6	0.95	17.4	20.3	18.6	0.84	0.11
Snout-dorsal origin/standard length	73.5	78.2	76.3	1.30	74.9	79.1	76.6	1.10	0.63
Snout-ventral origin/standard length	48.7	51.2	49.9	0.75	47.1	50.7	49.4	1.03	1.47
Pectoral length/pectoral base- ventral origin	30.7	47.5	38.0	4.10	36.6	43.2	39.7	2.05	1.31
Ventral length/ventral base- anal origin	31.8	45.3	37.5	3.52	36.5	42.1	38.7	1.90	1.06
Depth caudal peduncle/length caudal peduncle	40.4	53.0	45.7	4.17	41.3	50.0	46.5	3.06	0.56
Length caudal peduncle/ standard length	13.7	15.0	14.3	0.53	13.7	15.3	14.5	0.57	0.95
Eye diameter/head length	17.3	22.3	20.2	1.29	19.1	23.5	20.7	1.20	1.04
Upper jaw length/head length	24.0	35.9	29.3	2.61	26.7	32.0	29.3	1.54	0.01
Lower jaw length/head length	21.0	30.8	25.9	2.46	23.4	30.0	26.5	1.72	0.72
Gape width/head length	31.5	42.8	35.2	2.65	27.5	37.4	32.3	2.69	2.84
Interorbital width/head length	38.2	45.2	41.2	2.18	37.6	42.7	40.6	1.53	0.81

LIFE HISTORY AND ASSOCIATION WITH OTHER SPECIES

Pollard's (1971a) studies on landlocked *G. maculatus* indicated that spawning took place during late winter and early spring in contrast to diadromous populations which normally spawn during autumn and early winter (Burnet 1965; McDowall 1968). The Tasmanian landlocked material was collected in autumn (II.IV.1979) and females were found to contain partially developed eggs 0.5 mm diameter which would seem to indicate a late winter or early spring spawning presumably when water levels are at a maximum following winter rains.

Two other species were recorded in association with the landlocked population, a commercial species of eel (Anguilla sp.) and the southern pygmy perch Nannoperca australis Günther, a species not recorded in association with G. maculatus in a previous study (Andrews 1976). However as all populations previously studied were diadromous and as N. australis favours a stagnant weedy habitat (Llewellyn 1980) this is hardly surprising.

TABLE 2

MERISTIC VARIATION BETWEEN THE LANDLOCKED AND DIADROMOUS G. MACULATUS. Bracketed numbers indicate frequency of occurrence. (\bar{x} = sample mean, S.D. = standard deviation, t = Student's t)

	Landlocked	x̄	S.D.	t
Dorsal rays	8(4), 9(6), 10(10), 11(1)	9.4	0.84	
Anal rays	13(3), 14(11), 15(7)	14.2	0.66	
Caudal rays	15(1), 16(20)	15.9	0.22	
Pectoral rays	12(9), 13(22), 14(9), 15(1)*	13.0	0.73	
Ventral rays	7(38), 8(4)	7.1	0.50	
Gill rakers	14(3), $15(2)$, $16(4)$, $17(3)$, $18(2)$, $19(1)$, $20(1)$	16.4	1.70	
Vertebrae	57(1), 58(3), 59(2), 60(1)	58.4	0.90	
	Diadromous			
Dorsal rays	9(4), 10(8)	9.6	0.48	0.81
Anal rays	14(2), 15(7), 16(3)	15.1	0.64	3.75
Candal mara				
Caudal rays	16(12)	16.0	-	0.17
Pectoral rays	16(12) 12(10), 13(11), 14(3)	16.0 12.7	- 0.68	$0.17 \\ 1.15$
•	· ·			
Pectoral rays	12(10), 13(11), 14(3)	12.7	0.68	1.15

^{*} absence of a fin in one specimen

Scott (1971), who had earlier (1935; date cited in error as 1936 in Scott 1971; and 1942) claimed he could detect no specific differences between N. australis Günther and N. tasmaniae Johnston, later (1971) proposed subspecific distinction for the Tasmanian population which became N. australis tasmaniae. Scott's proposals were accepted by Scott et al. (1974) and Frankenberg (1974) but were not accepted by Lake (1971, 1978). Llewellyn, who had earlier (1974) accepted Scott's subspecific divisions, later expressly rejected them (Llewellyn 1980).

DISCUSSIONS AND CONCLUSIONS

Although almost morphologically indistinguishable from diadromous *G. maculatus* the landlocked population exhibited differences in the form of meristic variation and instability in a number of characters and a change from the usual spawning period. The first observation of differences in populations of *G. maculatus* was by Jenyns (1842) who at the conclusion of his description of *G. maculatus* mentioned four other specimens from the upper regions of streams in Patagonia and drew attention to the differences exhibited by them. Jenyns then proceeded to describe *M. alpinus* from freshwater lakes in Peninsula Hardy, Tierra del Fuego as a distinct species on the basis of the larger eye and longer head although he admitted that it differed little from *G. maculatus*. Similarly he considered *M. attenuatus* from New Zealand to be distinct on the basis of the longer body, smaller head, mouth, eyes and teeth, and the more anterior insertion of the ventral fins.

Subsequent to Jenyns (1842) many nominal species have been described (see McDowall and Frankenberg 1981) largely on alleged morphometric differences. Stokell (1964) considered G. parrishi to be distinct on the basis of the low number of vertebrae and the presence of an abdominal keel. McDowall (1967b) described G. gracilis and G. usitatus largely on the basis of meristic variations. Pollard (1971b) considered G. parrishi, G. usitatus and G. gracilis differed from G. maculatus in having longer heads, larger eyes and fewer vertebrae and that the landlocked Lake Modewarre form studied by him was intermediate between these three forms and typical G. maculatus. He also concluded that the

[†] data from Andrews (1976)

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change from autumn to spring spawning in the Lake Modewarre form was due to environmental rather than genetic factors. McDowall (1972) again examined the problem and considered the effects of geographic and genetic isolation on the landlocked populations and the probable influence of environmental factors on the differences between them. That populations in different areas appeared to vary in different ways from each other was interpreted by McDowall as mosaic evolution. He concluded that biological species criteria failed to provide an adequate basis for taxonomic divisions and that morphological criteria had to be relied on instead. Thus he considered G. alpinus, G. parrishi and G. usitatus to be junior synonyms of G. maculatus although G. gracilis was retained as distinct on account of the disjunction between it and typical G. maculatus in a number of characters.

One aspect of the landlocked populations dealt with only in passing in recent studies is the length of time the various populations have been isolated. Pollard (1971a) indicated that Lake Modewarre had its origins during the Late Pleistocene or Holocene and McDowall (1972) in his discussion of South American landlocked populations commented, "their present isolation seems likely to ensure that with time they will continue to diverge from their parental stock and may ultimately attain a level of distinctness requiring taxonomic recognition, but this is not so at present." On the evidence presently available it would appear that the Tasmanian landlocked population is of fairly recent origin. The almost negligible morphological differences from typical *G. maculatus* and meristic instability, perhaps indicative of a reduced gene pool, all appear to indicate that the population has been recently derived from diadromous *G. maculatus*. The change in spawning period being probably due, as Pollard (1971a) has suggested, to environmental rather than genetic factors.

Bowlers Lagoon appears to have originated during the Holocene, some 6-8 000 years before present (A. Goede, pers. comm.), probably as an anabranch of the Ringarooma River, from which diadromous *G. maculatus* were recorded during the present study. Rising sea levels after the last glacial period apparently deflected the river mouth westwards resulting in the lagoon becoming isolated from the river by subsequent deposition.

If, as has been outlined above, the landlocked population is of recent origin then it seems reasonable to assume that those landlocked populations which show the greatest divergence from typical *G. maculatus* will be those isolated the longest. McDowall (1972) has pointed out that isolated populations tend to diverge ecologically and morphologically from each other as a result of genetic isolation, itself a product of geographic isolation, and sometimes genetic drift. If this is the case with the presently known landlocked *G. maculatus* then McDowall's (1972) conclusions are correct and taxonomic recognition is not required. The current exception, *G. gracilis* of New Zealand may in fact represent no more than the most divergent of the landlocked populations yet examined and as more such populations become known the taxonomic status of *G. gracilis* may require reappraisal.

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