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Description of the larval development of *Galaxies maculatus* in landlocked lentic and lotic systems in Western Australia

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Abstract

The larvae and larval development of *Galaxias maculatus* are described from a freshwater lake and a saline river in southwestern Western Australia. The size at hatching (7.0 mm total length) was similar to that recorded elsewhere for *G. maculatus* and the sequence of fin development (i.e., caudal, dorsal, anal, pectoral, and pelvic fins) was identical to that recorded for galaxiids generally. There were relative increases in the proportions of head length and body depth with larval growth and a decrease in proportion of pre-anal length. Larvae from river habitats were smaller throughout larval stages of development than those from the lake. Fins of riverine fish began and completed development at a smaller size of fish than the lacustrine population, presumably as a response to the need for great motility at a smaller fish size in lotic environments.

Keywords: common galaxias, prefiexion, flexion and postfiexion larvae, fin ray counts

Introduction

Of the native freshwater fishes in southwestern Australia, larvae have been described for three of the five galaxiids, i.e., *Galaxias occidentalis* Ogilby 1899, *Galaxiella munda* McDowall 1978 and *Ga. nigrostriata* (Shipway 1953) (Gill & Neira 1994), one of the three percichthyids, i.e., *Nannatherina balstoni* Regan 1906 (Gill & Morgan 1998), and the sole member of the Lepidogalaxiidae, *Lepidogalaxias salamandroides* Mees 1961 (Gill & Morgan 1999).

Galaxias maculatus (Jenyns 1842) is a widespread fish of considerable economic (Benzie 1968a) and biological (e.g., Berraetal. 1996) importance which has been studied extensively as an adult in Australia, New Zealand and South America (Berra et al. 1996), but little is known of its larval development (but see McKenzie 1933). Benzie (1968b) described the embryological development of New Zealand populations and compared New Zealand *G. maculatus* (as *G. m. attenuatus)* with its congener *G. vulgaris* Stokell 1949.

Mitchell (1989) described the larval development for laboratory cultured *G. maculatus* and provided illustrations of fish between 7 and 45 mm total length. Pollard's (1971) extensive research on Australian *G. maculatus*, and studies by Benzie (1968a,b,c) and Mitchell (1989), did not extend to detailed descriptions of larval development.

The aim of this study was to provide descriptions of larvae and the larval development of *G. maculatus* from a lake and a river system in southwestern Australia.

Materials and Methods

Galaxias maculatus larvae were collected from a permanent freshwater lake (Moates Lake) and an intermittently flowing brackish-hyper saline river (Jerdacuttup River) (Fig. 1). Moates Lake, located approximately 30 km east of Albany is fed by two small streams (Goodga River and Black Cat Creek) which have combined catchments of 2000 ha (Morgan 2003). The lake has a total area of 144 ha of which 62 ha are open water (halse et al. 1993). median rainfall of the goodga River catchment is 870 mm per year and mean annual flow is 4200 ml (Pen 1999). The river flows throughout the year and is periodically connected to the sea during winter each year via a series of swamps that connect to gardner Lake and then through a narrow entrance channel (Morgan 2003). A sandbar blocks the channel for most of the year, but is excavated each year in mid-late winter (Morgan 2003). despite this occasional contact with the ocean, the population is reproductively landlocked as larval fish are present in the lake throughout the year (Chapman et al. 2006).

Jerdacuttup River, 15 km east of Ravensthorpe, Western Australia (Fig. 1) has been landlocked for c. 6000 years (Hodgkin & Clark 1990). The collecting site pool is semi-permanent, measures 300 m by 15 m and is 1.5 m deep at bankful depth. median rainfall in the Jerdacuttup River catchment is 415 mm per year and mean annual flow is 8800 ML (Pen 1999). Flow is irregular and dependent upon sufficient winter rain or summer flooding following decaying tropical cyclones. For most of the year, this river is not flowing and is a chain of disconnected, shrinking pools (A. Chapman pers. obs.).

Larvae were collected using standard 100 m trawls with a conical plankton net (80 cm diam. with 500 μm mesh). Postflexion larvae (24-29 mm body length) and juveniles were occasionally collected with a 3 mm mesh seine net as part of sampling of juvenile and adult fish. Moates Lake was sampled monthly between April 1998 and July 1999 and Jerdacuttup River was sampled between April 2001 and october 2002. Larvae were euthanased with 25% benzocaine and preserved in 75% ethanol.

Identification of larvae

Larvae were identified as belonging to the genus *Galaxias* by their elongate form, relatively uniform depth and a dorsal fin that develops approximately above the anal fin (McDowall 1984; Gill & Neira 1994). At the river sampling site, the only sympatric species was *Pseudogobius olorum* (Sauvage 1880) whose larvae are cuneiform with a conspicuous swim bladder (Chapman 2003). In Moates Lake, sympatric species were *G. truttaceus* valenciennes 1846 and *P. olorum.* Juveniles and larger larvae of G. *maculatus* were distinguished from those of G. *truttaceus* by the following characteristics (see McDowall & Frankenberg 1981): trunk of G. *maculatus* had greenish-grey spots, with blotches or bands cf. large black spots surrounded by pale halo for G. *truttaceus;* no distinct markings on the head or around the pectoral fins of G. *maculatus* cf. an oblique stripe from the eye to the lower preoperculars and a pair of bars dorsal to the basal-most part of pectoral fins for G. *truttaceus.* The caudal fin of G. *maculatus* was distinctly forked and largely unpigmented cf. slightly forked and brown to orange for G. *truttaceus.* The anal fin of G. *maculatus* was angular with anterior rays longest cf. anal fin rounded with central rays longest for G. *truttaceus.* The anterior end of the G. *maculatus* mouth was small, extending only to the front of the eye cf. large mouth reaching to the anterior half of the eye for G. *truttaceus.*

The sequence of fin development and pigmentation patterns were used to link and identify successively smaller larvae of G. *maculatus,* i.e., using the series method of Leis & Trnski (1989).

Measurements, terminology and counts

Both body length and total length were measured. Total length was used for comparison with other studies, body length was used because of its greater precision.

Larvae <15 mm body length were measured to the nearest 0.1 mm using a stereomicroscope with an eye piece micrometer and those >15 mm body length with vernier calipers. As larval growth is a continuous process and precise stages are sometimes difficult to determine, Snyder's (1983) modification of the definitions of Ahlstrom et al. (1976) were followed: preflexion stage terminates with the appearance of the first caudal ray; the flexion stage terminates with the formation of all principal caudal rays and the postflexion stage terminates with the formation of all rays in all fins and the loss of median finfolds. Measurements of head length, body depth and pre-anal length are given as a percentage of body length. Body length refers to notochord length in preflexion and flexion larvae and standard length in postflexion larvae. Head length was measured as the horizontal distance from the tip of the snout to the posterior edge of the opercular membrane. Body depth was measured as the vertical distance between the dorsal and ventral midlines through the anterior margin of the pectoral fin base. Pre-anal length (PAL) was measured as the distance from the tip of the snout to a vertical line through the posterior edge of the anus. Myomere and fin ray counts were conducted on the left hand side of the body.

Results

Gross morphology of larvae

Larvae were typically elongate and had a large head and a long straight gut that became striated during flexion (Fig. 2). The smallest preflexion larva examined (7.0 mm total length) had a completely resorbed yolk sac, a well developed mouth with a wide gape, a well developed pectoral membrane and a narrow continuous fin fold surrounding the posterior margin of the body, only extending anterior of the anus on the ventral surface. The order of fin fold loss was dorsal, caudal, and pre-anal.

Head length and body depth for larvae from Moates Lake increased from approximately 7-10%

and 6-7% in preflexion larvae to 12-18% and 8-10% in postflexion larvae, respectively (Table 1). Pre-anal length decreased from approximately 75-88% in preflexion larvae to 72-78% in postflexion larvae.

Larvae from Jerdacuttup River showed a similar trend; head length and body depth increased from approximately 11-14% and 6-11% in preflexion larvae to 16-22% and 7-15% in postflexion larvae, respectively (Table 1). Pre-anal length decreased from approximately 76-87% in preflexion larvae to 74-80% in postflexion larvae.

The larval stage was completed when there was a full complement of fin rays in all fins; i.e., when there were 6-7 pelvic fin rays and fish had a total length of approximately 31-32 mm (body length equivalent was 26-27 mm). For the development of each fin for postflexion larvae with their adult complement of 6-7 pelvic fins, the size range was consistently less in Jerdacuttup River than in moates Lake (Table 2).

Development of pigmentation

In preflexion larvae, pigmentation was limited to 1-4 melanophores on the top of the head and 9-25 melanophores in a single line along the upper lateral surface of the gut (Fig. 2). On some larger preflexion larvae, there were also a variable number of minute melanophores dorsally and ventrally at the end of the notochord.

In flexion larvae, the number of melanophores on the head and the upper lateral surface of the gut had increased to 6 or 7 and 27-37, respectively, and some of the latter had coalesced to form larger blotches. In addition, flexion larvae had a single line of 17-37 internal melanophores under their dorsal surface and another line of 4-6 external melanophores on their ventral surface and pigmentation developing behind the outer edge of the opercular membrane.

In postflexion larvae, numerous punctate and dendritic melanophores were developed on the trunk with the density increasing dorsally, the melanophores on the upper lateral gut surface were internalised and the pre-maxillae were pigmented whilst distinct pigmented lines developed on the ventral margin of the operculum.

Development of dentition

dental development was not apparent until the late postflexion larval stage when erupting tubercles were visible as precursors to caniniform tooth rows in both upper and lower jaws. For moates Lake fish, between 34.0 and 37.5 mm total length, rows of 24 and 22 short and sharply pointed caniniform teeth were present in the upper and lower jaws, respectively. Fish from Jerdacuttup River, between 27.0 and 29.0 mm total length, were exhibiting variable numbers (between 12 and 20) of erupting caniniform teeth in both upper and lower jaws.

Discussion

The size at hatching for western Australian G. *maculatus* appears to be similar to that reported for laboratory cultured fish, i.e., 7.0-8.0 mm total length (Mitchell 1989), and catadromous fish in New Zealand rivers, i.e., 6.0-7.5 mm total length (Benzie 1968b). The smallest larva from moates Lake was 7.0 mm total length; all that remained of the yolk sac was a small oil globule. Benzie (1968c) recorded that in warm water conditions the yolk sac can be fully used before hatching occurs.

The sequence of fin development for G. *maculatus* at moates Lake and Jerdacuttup River was identical and is the same as that recorded for G. *maculatus* and G. *vulgaris* from New Zealand (Benzie 1968b,c; mitchell 1989), G. *occidentalis* from Collie River in southwestern Australia (gill & Neira 1994), and *Galaxiella munda* and *Ga. nigrostriata* from the streams and ephemeral pools of the peat flats of southwestern Australia (gill & Neira 1994). The onset of caudal, dorsal, anal, pectoral and pelvic ray development occurred at a larger size than in *G. occidentalis* in Western Australia and *G. vulgaris* in New Zealand (Gill & Neira 1994). The earlier development of fins in *G. occidentalis* and *G. vulgaris* larvae would help maintain position in upstream freshwater habitats in situations of downstream river flow. In contrast, for *G. maculatus* downstream dispersal of larvae is part of its reproductive and re-distribution strategy (Chapman 2003). This circumstance is also consistent with the observation from this study that the median finfold is greatly reduced in *G. maculatus* compared with that in *G. occidentalis* as indicated by Gill & Neira (1994).

Benzie (1968b) indicates that for catadromous *G. maculatus* in New Zealand, fish are larval from hatching until re-entry into fresh water at 5-6 months and 42-50 mm total length. These fish do not gain their adult pigmentation nor does their fore- and mid-gut region fully develop until they re-enter fresh water, at which point there is a reduction in total length without a change in head length and an increase in body depth (Benzie 1968a). Thus, these catadromous fish have assumed adult size but retained some juvenile characteristics. For catadromous fish that spend their larval and juvenile stages at sea, there may be survival advantages in rapid growth but curtailed development. Predator evasion and access to an abundant oceanic food supply are possibly the two selection pressures.

In contrast, landlocked populations are probably subject to different environmental variables, food availability, and predator/prey regimes. For example, landlocked fish in Western Australia consume terrestrial as well as aquatic invertebrates including spiders, winged ants and orthopterans, and predation is by piscivorous waterbirds rather than other fish (Chapman 2003). In these situations, growth and development appear to be more or less synchronous and larval stages are completed earlier.

The reasons for the small size of *G. maculatus* in Jerdacuttup River relative to other populations (see Chapman et al. 2006) and its attainment of comparable stages of larval development at smaller size are likely to be complex. Jerdacuttup River has been barred from the sea for approximately 6000 years (Hodgkin & Clark 1990), which is a longer period than that for other rivers in its range in Western Australia. In New Zealand, landlocking can reduce body size of derived species compared with their diadromous founder stock (e.g., McDowall 1967). In the semi-arid environment on the south coast of Western Australia, it is possible that size reduction of populations that have been landlocked for an extended period of time is a response to environmental conditions. There might be selection pressure for size reduction to maintain contact with food supply, or to evade predation by piscivorous waterfowl in small, confined river pools.

In conclusion, the size at hatching and the sequence of fin development for *G. maculatus* in southwestern Australia was identical to that of fish from New Zealand. The sequence of fin development was also identical to that reported for other galaxiids in southwestern Australia. Finray development occurred at longer body lengths than in *G. occidentalis* and the median finfolds were greatly reduced in *G. maculatus.* A limitation of the present study was that the sampling periods were not contemporaneous at the sites, but these differences were interpreted as adaptations to the local environments, particularly whether development took place in lentic or lotic situations.

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Fig. 1 Larval collecting localities for *Galaxias maculatus* in southwestern Australia.

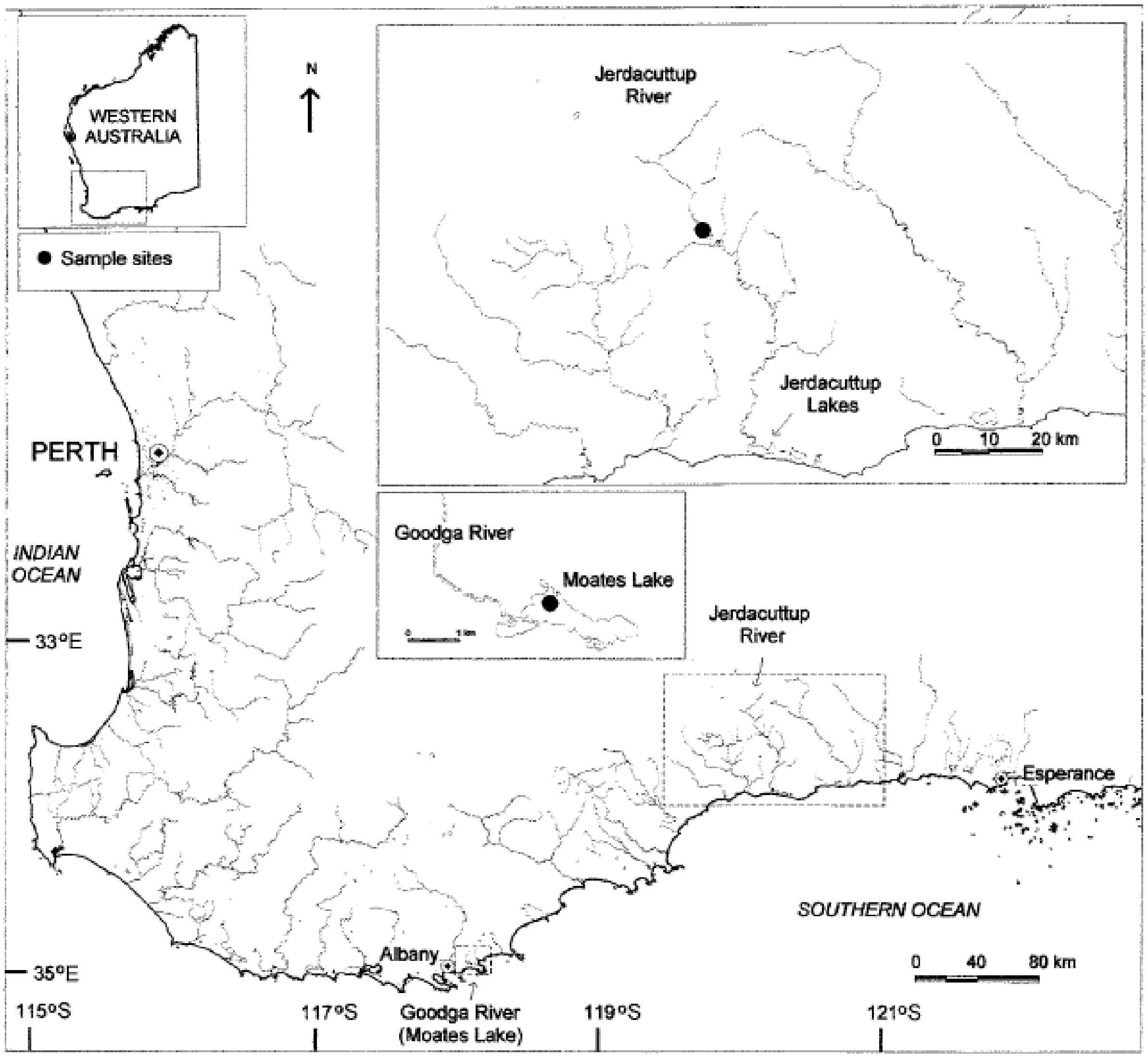

Fig. 2 Larval to juvenile developmental stages of *Galaxias maculatus* from moates Lake, Western Australia. All lengths are body lengths.

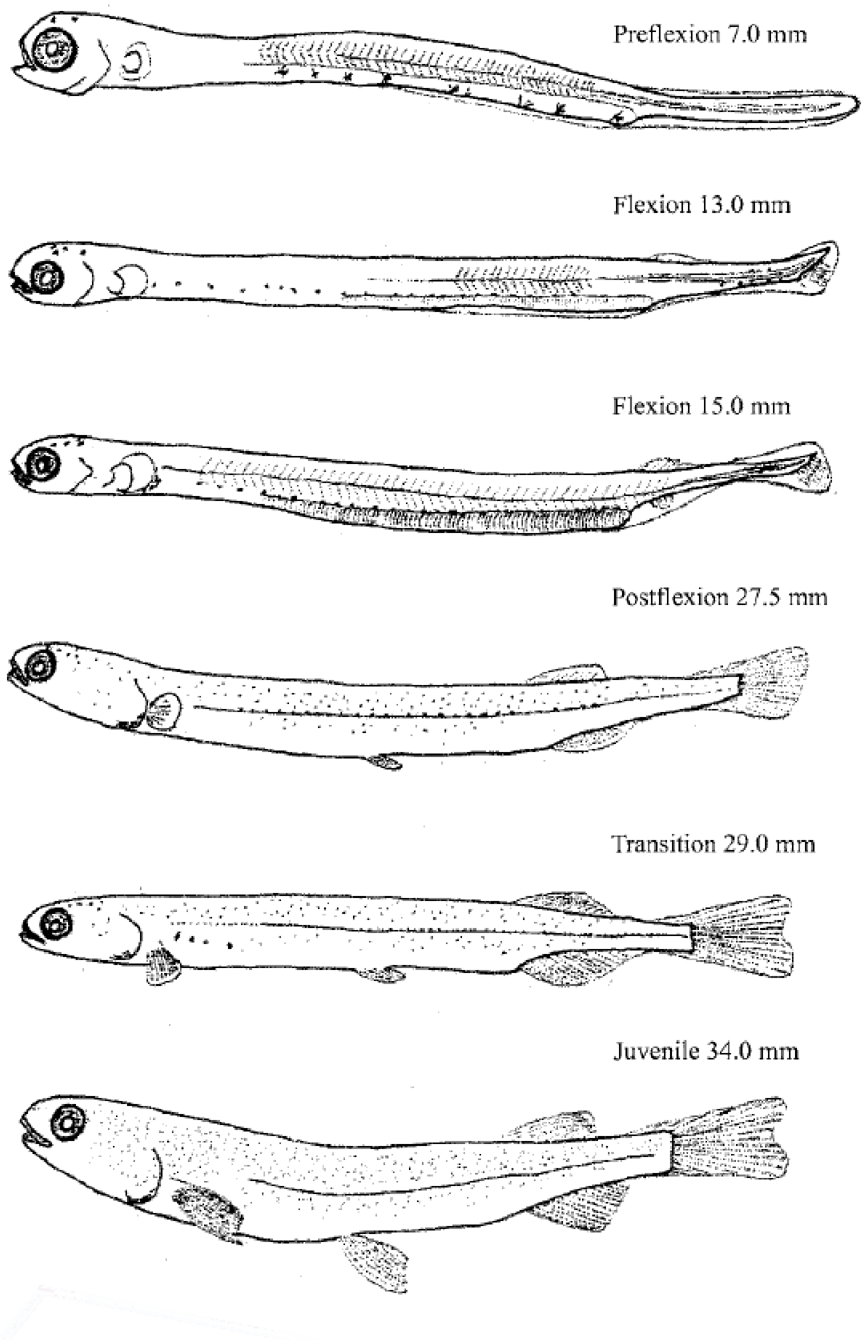

Table 1 Range and mean (± Se) of body proportions of *Galaxias maculatus* larvae from Moates Lake and Jerdacuttup River, Western Australia. (BL, body length; HL, head length; BD, body depth; PAL, pre-anal length.)

	Preflexion		Flexion		Postflexion	
Measurement	Moates Lake (n =10)	Jerdacuttup R. (n = 5)	Moates Lake (n = 10)	Jerdactttup R. (n = 8)	Moates Lake (n = 10)	Jerdacttup R. (n = 12)
BL (mm)	7.0 – 14.0	5.5 – 7.5	12.4 – 24.1	11.2 – 15.4	23.7 – 29.2	16.2 – 25.0
	11.5 ± 0.8	6.6 ± 0.4	18.5 ± 1.1	13.4 ± 0.4	25.9 ± 0.5	19.8 ± 0.8
HL (%BL)	6.9 – 10.0	11.1 – 13.9	6.8 – 15.7	15.0 – 20.1	11.8 – 18.1	16.1 – 22.0
	8.6 ± 0.4	12.7 ± 0.6	12.0 ± 0.9	17.3 ± 0.8	15.6 ± 0.8	19.1 ± 0.5
BD (%BL)	5.9 – 7.0	6.4 – 10.7	5.4 – 9.0	7.8 – 9.5	7.7 – 10.1	7.4 – 14.8
	6.6 ± 0.2	9.0 ± 0.8	7.2 ± 0.3	8.6 ± 0.3	8.8 ± 0.3	10.4 ± 0.6
PAL (%BL)	75.0 – 87.5	76.0 – 86.6	76.2 – 88.8	73.2 – 83.6	71.6 – 78.4	74.0 – 80.0
	81.3 ± 1.3	79.8 ± 2.1	80.0 ± 1.1	80.2 ± 1.6	74.0 ± 0.7	77.3 ± 0.7
Myomeres	NA	NA	49	NA	48 – 51	50

Table 2 Sequence of fin development (mm body length (BL)) and fin ray and myomere count for Galaxias maculatus larvae from Moates Lake and Jerdacuttup River, Western Australia. Lower values were for smallest larvae for which the primordium for fin rays were starting to form and for which the fin rays had their adult numerical complement. Fin ray counts are for postflexion larvae with their adult complement of 6-7 pelvic fin rays.

Measurement/count	Moates Lake BL range (mm)	Jerdacuttup R. BL range (mm)
Fin development	(*n* = 35)	(*n* = 28)
Caudal	12.4–24.1	11.0–18.2
Dorsal	12.9–24.0	11.0–19.5
Anal	13.0–24.0	11.0–21.6
Pectoral	22.6–25.5	12.0–21.6
Pelvic	24.1–26.3	17.8–26.5
Fin ray count	(*n* = 10)	(*n* = 3)
Caudal	16	16
Dorsal	9	9
Anal	13	13
Pectoral	12	12
Pelvic	7	6–7
Myomeres	46–50	45–49