

Abstract—Morphological development of the larvae and small juveniles of estuary perch (*Macquaria colonorum*) (17 specimens, 4.8–13.5 mm body length) and Australian bass (*M. novemaculeata*) (38 specimens, 3.3–14.1 mm) (Family Percichthyidae) is described from channel-net and beach-seine collections of both species, and from reared larvae of *M. novemaculeata*. The larvae of both are characterized by having 24–25 myomeres, a large triangular gut (54–67% of BL) in postflexion larvae, small spines on the preopercle and interopercle, a smooth supraocular ridge, a small to moderate gap between the anus and the origin of the anal fin, and distinctive pigment patterns. The two species can be distinguished most easily by the different distribution of their melanophores. The adults spawn in estuaries and larvae are presumed to remain in estuaries before migrating to adult freshwater habitat. However, larvae of both species were collected as they entered a central New South Wales estuary from the ocean on flood tides; such transport may have consequences for the dispersal of larvae among estuaries. Larval morphology and published genetic evidence supports a reconsideration of the generic arrangement of the four species currently placed in the genus *Macquaria*.

Larval development of estuary perch (*Macquaria colonorum*) and Australian bass (*M. novemaculeata*) (Perciformes: Percichthyidae), and comments on their life history

Thomas Trnski

Amanda C. Hay

Ichthyology, Australian Museum
6 College Street
Sydney, New South Wales 2010, Australia

E-mail address (for T. Trnski, senior author): tomt@austmus.gov.au

D. Stewart Fielder

New South Wales Fisheries
Port Stephens Fisheries Centre
Private Bag 1
Nelson Bay, New South Wales 2315, Australia

The Percichthyidae is a family of freshwater fishes restricted to Australia (8 genera, 17 species) and South America (2 genera, 7 species) (Johnson, 1984; Nelson, 1994; Allen et al., 2002; Paxton et al., in press). There is continuing debate regarding the monophyly of the family; several genera are variously allocated to separate families: *Gadopsis* is allocated to Gadopsidae (Allen et al., 2002; see Johnson, 1984 for a history of the systematic placement of the genus) and *Edelia*, *Nannatherina*, and *Nannoperca* are allocated to Nannopercidae (Allen et al., 2002). Other Australian genera of Percichthyidae include *Bostockia*, *Guyu*, *Maccullochella*, and *Macquaria* (Pusey and Kennard, 2001; Allen et al., 2002; Paxton et al., in press). The genera *Percalates* and *Plectroplites* were synonymized with *Macquaria*, based on morphological and biochemical characters (MacDonald, 1978), and although this arrangement was accepted by Paxton and Hanley (1989), Paxton et al. (in press), Eschmeyer (1998), Johnson (1984), and Nelson (1994) recognized both *Percalates* and *Plectroplites* as valid genera.

There are four described species in the genus *Macquaria*, all confined to southeastern Australia. *Macquaria ambigua* occurs naturally in freshwaters of the Murray-Darling river

system and has been translocated outside of its natural range (Kailola et al., 1993; Allen et al., 2002). There is genetic evidence for an additional undescribed freshwater species closely related to *M. ambigua* from central Australian drainages (Musyl and Keenan, 1992). *Macquaria australasica* is also confined to freshwater of the Murray-Darling river system, and an isolated population exists from the Shoalhaven and Hawkesbury Rivers, New South Wales (Allen et al., 2002) that may be a separate species (Dufty, 1986). The other two species (*M. colonorum* and *M. novemaculeata*) are catadromous and occur in coastal southeastern Australian drainages between southern Queensland and eastern South Australia (Paxton et al., in press). They are sympatric from northern New South Wales (NSW) to eastern Victoria. Adults of *M. novemaculeata* occur in freshwater, whereas *M. colonorum* prefers brackish water of estuaries (Williams, 1970). Both species migrate to estuarine areas to breed in winter (Allen et al., 2002). Both species are protected from commercial fishing but are highly prized by recreational fishermen (Harris and Rowland, 1996; Allen et al., 2002) and *M. novemaculeata* is an important aquaculture species.

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Of the 17 Australian percichthyids, larvae of only *Maccullochella macquariensis*, *M. peelii peelii*, and *Macquaria ambigua* have been described (Dakin and Kesteven, 1938; Lake, 1967; Brown and Neira, 1998). Larval and early juvenile development of the estuary perch (*Macquaria colonorum*) and the Australian bass (*Macquaria novemaculeata*) is described from specimens collected from the central and southern coast of NSW, and from reared larvae of the latter species obtained from brood stock from central NSW. This is the first description of the morphological development of the early life history of these two species.

Materials and methods

Morphological definitions, measurements, and abbreviations follow Neira et al. (1998) and Leis and Carson-Ewart (2000). Larvae and juveniles were examined and measured under a dissecting microscope at magnifications from 6 to 50 \times . Precision of the measurements varied with magnification but ranged from 0.02 to 0.16 mm. Where morphometric values are given as a percentage, they are as a proportion of body length (BL) unless otherwise indicated. All pigment described is external unless otherwise specified. The juveniles collected are in transition from larvae to juveniles because they retain some of their larval characters and squamation is incomplete; these are called "transitional juveniles" (Vigliola and Harmelin-Vivien, 2001). Illustrations were prepared with a Zeiss SR with an adjustable drawing tube.

Field-caught larvae were collected in a fixed 2-m² channel net with about 1-mm mesh in Swansea Channel, Lake Macquarie, central NSW. The net filtered surface waters to 1 m depth during night flood tides (Trnski, 2002). Small juveniles were collected in a 30-m beach seine dragged over sand, mud, and *Zostera* seagrass in the Clyde River, southern NSW. Reared larvae of *M. novemaculeata* were obtained from rearing tanks at the Port Stephens Fisheries Centre, an aquaculture research facility of NSW Fisheries. Brood stock came from the Williams River, central NSW. All specimens were initially fixed in 10% formalin and subsequently transferred to 70% ethanol.

Field-caught larvae were restricted to a narrow size range: 4.8–7.1 mm body length (BL) for *M. colonorum* ($n=12$), and 4.6–7.6 mm BL for *M. novemaculeata* ($n=15$). Juveniles of both species ranged from 10.3 to 13.5 ($n=5$) and from 10.1 to 14.1 mm BL ($n=5$), respectively. Reared larvae of *M. novemaculeata* were available to confirm the identification of the larvae and to extend the developmental series for this species to 3.3–10.2 mm BL ($n=18$).

All material examined is registered in the fish collection at the Australian Museum. Registration numbers of *M. colonorum* larvae are AMS I.20052-010, I.41690-005 to -008, I.41691-002, I.41692-001, I.41693-001; *M. novemaculeata* are AMS I.20052-012, I.27051-013, I.41561-001 to -008, I.41590-001, I.41641-001, I.41661-

001 and -002, I.41662-001, I.41668-001, I.41690-001 to -0004, I.41691-001, I.41694-001.

Identification

Field-caught larvae and juveniles were identified as percichthyids by using the characters in Brown and Neira (1998), particularly the combination of a relatively large gut, the small to moderate gap between the anus and origin of the anal fin prior to complete formation of the anal-fin, continuous dorsal fin, fin-ray, and vertebral counts, and head spination including small preopercular spines, a small interopercular spine, and a smooth supra-ocular ridge. The larvae and juveniles described here were confirmed as being *Macquaria colonorum* and *M. novemaculeata* because of their coastal distribution and meristics; all other species in the family are restricted to freshwater. The overlap in meristics between *M. colonorum* and *M. novemaculeata* made separation of the species difficult. The availability of reared *M. novemaculeata* from positively identified adults determined the species allocations.

Results

Development of *Macquaria colonorum*

Adult meristic data Dorsal (D) IX–X, 8–11; Anal (A) III, 7–9; Pectoral (P_1) 12–16; Pelvic (P_2) I, 5; Vertebrae 25
17 specimens: 4.8–7.1 and 10.3–13.5 mm BL

General morphology (Tables 1 and 2, Fig. 1) Larvae and transitional juveniles are moderately deep bodied (body depth, BD 30–35%). The body and head are laterally compressed. There are 24–25 myomeres (12–14 preanal and 11–13 postanal). The large, triangular gut is fully coiled in the smallest larva examined. The pre-anal length ranges from 60% to 67%. The conspicuous gas bladder located over the midgut is small to moderate in size but difficult to distinguish in transitional juveniles. The round to slightly elongate head is large (head length, HL 32–41%). The snout is slightly concave to straight. The snout is approximately the same length as the eye diameter but becomes shorter from 7 mm. The eye is round and moderate in size (27–32% of HL) in larvae but becomes moderate to large in transitional juveniles (32–36% of HL). The large mouth reaches to the middle of the pupil. Small canine teeth are present in both jaws in all larvae examined. The nasal pit closes shortly after settlement, by 12.5 mm.

Head spination is weak. Three short spines are present on the posterior preopercular border in the smallest larva examined; a fourth spine is present in some postflexion larvae from 6.3 mm and in all transitional juveniles. The spine at the angle of the preopercle is longest but remains shorter than the pupil diameter. A minute interopercular spine is present from 6.0 mm and persists in all transitional juveniles. A low, smooth

Table 1

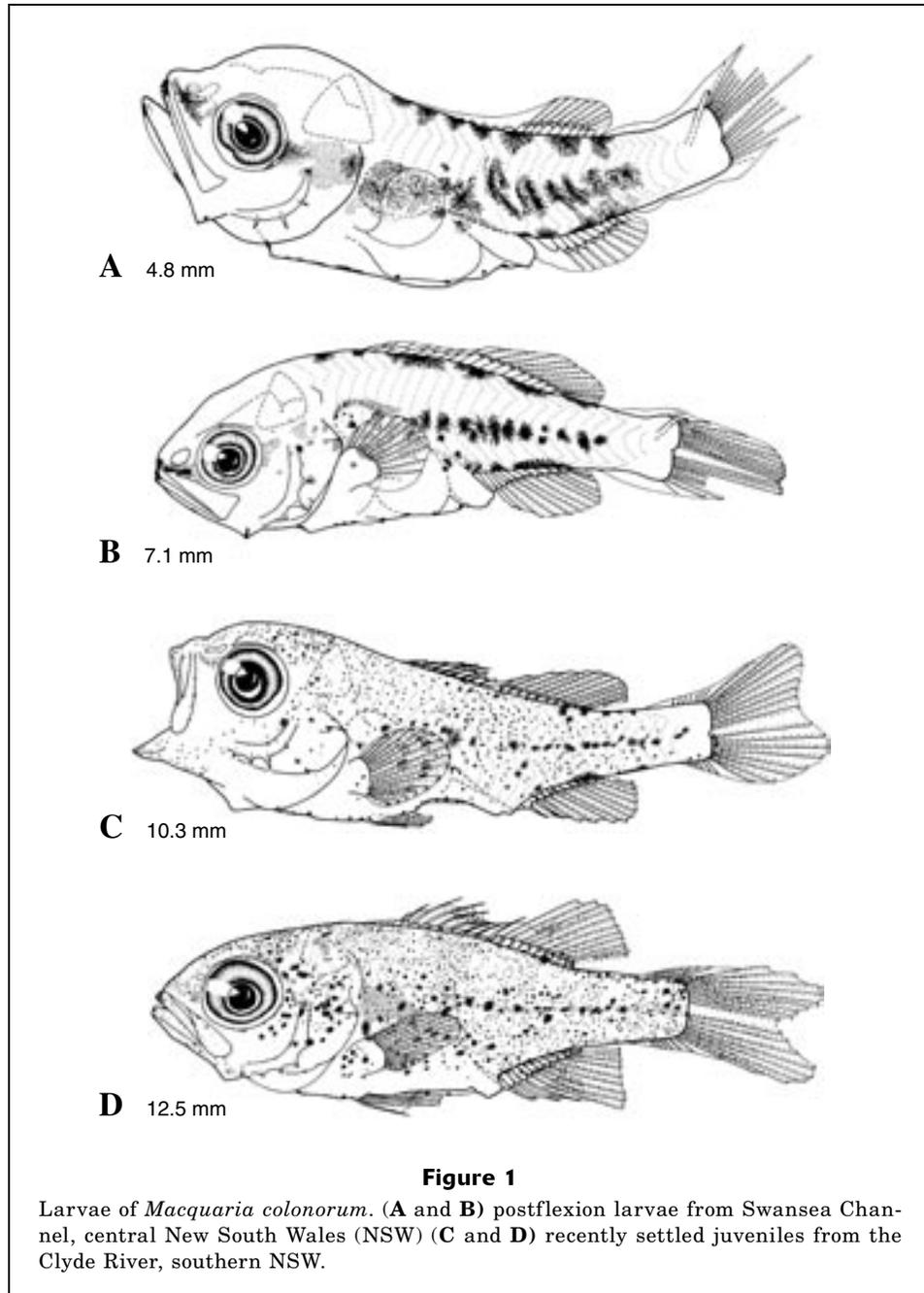
Morphometric data for *Macquaria colonorum* larvae from channel-net samples and juveniles from beach-seine samples. Measurements are in mm. VAFL = vent to anal-fin length.

Body length	Preanal length	Predorsal length	Body depth	Head length	Snout length	Eye diameter	VAFL
Flexion							
4.80	3.40	2.48	1.49	1.96	0.58	0.58	0.04
5.10	3.40	3.00	1.60	1.88	0.60	0.56	0
5.40	3.40	2.80	1.60	1.72	0.50	0.50	0
5.48	3.32	2.91	1.74	1.80	0.56	0.56	0
Postflexion							
5.73	3.49	2.80	1.99	2.08	0.56	0.60	0
5.98	3.68	3.24	1.99	2.04	0.60	0.60	0
6.00	3.72	2.60	1.92	2.00	0.50	0.60	0
6.31	3.98	2.57	2.16	2.20	0.60	0.68	0
6.60	4.00	3.00	2.20	2.40	0.64	0.64	0
6.81	4.15	3.07	2.16	2.32	0.66	0.66	0
7.00	4.32	3.32	2.08	2.24	0.60	0.72	0
7.10	4.36	2.91	2.32	2.28	0.60	0.72	0
Settled							
10.29	6.81	4.81	3.15	3.74	0.91	1.25	0
10.62	6.81	4.98	3.24	3.90	0.95	1.25	0
11.29	7.47	5.56	3.74	4.48	1.00	1.58	0
12.45	7.97	5.64	4.15	4.57	1.00	1.66	0
13.45	8.70	6.64	4.48	5.23	1.41	1.83	0

Table 2

Meristic data for *Macquaria colonorum* larvae and juveniles. () indicates only fin bases present, [] incipient rays or spines, { } ray transforming to a spine, d = damaged.

Body length	Dorsal	Anal	Pectoral	Pelvic	Caudal	Myomeres
Flexion						
4.80	(V), 9	(I), 8[1]			9+7[1]	14+11=25
5.10	d, (10)	(I), 9			[1]8+7[1]	13+11=24
5.40	d, (9)	(II), 9	[2]		9+8	13+12=25
5.48	(III), 9	(II), 8	3		9+8	12+12=25
Postflexion						
5.73	(IV), 11	(II), 8	5		9+8	13+12=25
5.98	(V), 10	(II), 8	2		9+8	13+12=25
6.00	(IV), 10	(II), 8	3		9+8	13+12=25
6.31	(IV)I, 11	[III], 9	9	buds	9+8	13+12=25
6.60	IV, 11	II, 9	5	buds	9+8	13+12=25
6.81	VII, 11	II, 10	9	buds	9+8	13+12=25
7.00	VII, 11	II, 10	5 (d)	buds	9+8	12+13=25
7.10	VIII, 10	II(I), 9	11[1]	buds	9+8	14+11=25
Settled						
10.29	VIII (I), 10	II(I), 8	15	I,5	7+9+8+6	13+12=25
10.62	VIII (I), 10	II(I), 8	13	I,5	7+9+8+4	12+13=25
11.29	IX, 10	III, 8	15	I,5	7+9+8+8	12+13=25
12.45	IX, 10	III, 8	14	I,5	12+9+8+7	12+13=25
13.45	IX, 10	III, 9	14	I,5	9+9+8+8	12+13=25



supraocular and supracleithral ridge form by the time notochord flexion is complete. A weak posttemporal ridge is present from 7 mm, and a small spine develops in transitional juveniles from 11.3 mm. A small spine develops on the supracleithrum from 10.6 mm. An opercular spine is present in transitional juveniles.

Dorsal-fin soft rays are ossified by the completion of notochord flexion, the posteriormost rays being the last to ossify. The pterygiophores of the spinous rays of the dorsal fin develop from posterior to anterior and begin to form during notochord flexion. Spines begin to ossify in postflexion larvae by 6.3 mm, and the full comple-

ment of dorsal-fin elements is present by 7.1 mm. All soft rays of the anal fin are ossified by the completion of notochord flexion, by which time 1–2 pterygiophores of the spinous rays are present. The first two anal-fin spines are ossified by 6.6 mm. The last spinous soft ray of the dorsal and the third spinous ray of the anal fin transforms from a soft ray after settlement and they are fully transformed by 11.3 mm. Incipient rays begin to form in the pectoral fin during notochord flexion, and the rays ossify from dorsal to ventral in postflexion larvae. A few pectoral-fin rays remain unossified at 7.1 mm and are fully ossified prior to settlement.

Pelvic-fin buds appear in postflexion larvae from 6.3 mm, but no elements have formed in the largest specimen; they are all ossified in the transitional juveniles. All primary caudal-fin rays are ossified by the end of notochord flexion. Procurent caudal rays are present in the transitional juveniles. Notochord flexion commences before 4.8 mm, and is complete by 5.7 mm. Scales have not begun to develop in the largest transitional juvenile examined (13.5 mm).

Pigment (Fig. 1, A–D) Larvae are moderately to heavily pigmented; melanophores are concentrated on the dorsal and ventral midlines, and midlateral surface of the trunk and tail. Small expanded melanophores are present at the tips of the upper and lower jaws, and there are one or two melanophores ventral to the nasal pit. Additional internal melanophores are present along the roof of the mouth, and posterior to the eye below the mid- and hindbrain. External melanophores may be present on the operculum in line with the eye. One or two melanophores are present on the ventral midline of the lower jaw, and there is one at the angle of the lower jaw.

Four to seven large, expanded melanophores are present along the dorsal midline of the trunk and tail, from the nape to just posterior to the dorsal-fin base. There are one or two melanophores on the nape and four or five along the dorsal-fin base. A series of large, expanded melanophores is present along the lateral midline of the trunk and tail, commencing at the gas bladder and extending to the posterior end of the dorsal and anal fins. In postflexion larvae, this series extends onto the anterior third of the caudal peduncle. Internal melanophores are present over the gas bladder, the mid- and hindgut, and may be present along the notochord. The external and internal pigment series thus give the impression of a line of heavy pigment from the tip of the snout, across the head and trunk, to the tail.

Small melanophores are present along the ventral midline of the gut; one melanophore on the isthmus immediately anterior to the cleithral symphysis, usually three (range: 2–4) melanophores between the cleithral symphysis and pelvic-fin base, and usually three (range: 1–4) melanophores between the pelvic-fin base and the anus. Expanded melanophores are present along the ventral midline of the tail, from above the anus to the posterior end of the anal-fin base. Between one and three melanophores occur along the anal-fin base. A small melanophore is occasionally present in early postflexion larvae at the base of ventral primary caudal-fin rays 1–2.

In transitional juveniles, the expanded melanophores are relatively smaller, and are most prominent midlaterally along the trunk and tail. The expanded melanophores along the dorsal and ventral midlines become small to absent during the juvenile stage. Additional expanded melanophores develop laterally on the head and body, and the dorsal and anal fins become pigmented. Small melanophores cover the head and body—coverage lightest ventrally on the head and gut. Three broad

vertical bands become apparent dorsally on the nape, below the center of the spinous dorsal fin and below the center of the soft dorsal fin by 13.5 mm.

Development of *Macquaria novemaculeata* larvae

Adult meristic data D VIII–X,8–11; A III,7–9; P₁ 12–16; P₂ I,5; Vertebrae 25; 38 specimens: 3.3–14.1 mm BL

Eggs and hatching Eggs are approximately 900 μ m in diameter and have multiple oil globules. Larvae are 3.3 mm SL at time of hatching.

General morphology (Tables 3 and 4, Fig. 2) Yolksac and early preflexion larvae are elongate (BD 15–18%), but in late preflexion and flexion larvae, body depth becomes moderate (BD 26–34%). Body depth of field-caught postflexion larvae ranges from 29% to 35%, and in transitional juveniles from 33% to 34%. Reared postflexion larvae and transitional juveniles are deeper than wild larvae, ranging from 32% to 44%, which is an artifact of the extremely full guts in the reared larvae. Body depth decreases abruptly posterior to the anus, although this becomes less marked with development. The head and body are laterally compressed. There are 25 myomeres (10–13 preanal+12–15 postanal). In general, there are 10–12 preanal myomeres in preflexion and flexion larvae, and 12–13 preanal myomeres in postflexion larvae and transitional juveniles. The gut is initially straight in yolksac larvae but is coiled by 3.9 mm. The gut is oval to triangular in shape; preanal length reaches 44–56% of BL in yolksac and preflexion larvae, 54–60% in flexion stage larvae, and 54–66% in postflexion larvae and transitional juveniles. The gut mass is large, particularly in reared postflexion larvae and transitional juveniles. The conspicuous gas bladder, which is located over the midgut, is moderate to large in size, except in the yolksac larvae where it is small and inconspicuous. The head is round and small in yolksac larvae (HL 15–16%), moderate in preflexion larvae (HL 22–31%), and becomes moderate to large in flexion (29–35%) and postflexion larvae and transitional juveniles (32–38%). The snout is always shorter than the eye diameter and is initially concave, but becomes convex to straight in postflexion larvae. The eye is moderate to large (27–36% of HL) but is relatively larger in yolksac larvae (42–45% of HL). The eye is initially unpigmented, but is fully pigmented by 3.6–3.8 mm, prior to the complete absorption of the yolk. The moderate mouth reaches to the middle of the pupil. Small canine teeth appear in both jaws in late preflexion larvae by 4.4 mm. The number of teeth increases with development. The nasal pit begins to close by 8.6 mm, and both nostrils are developed by 10.3 mm.

Head spination is weak. A small spine appears at the preopercular angle by the end of the preflexion stage. By the time notochord flexion is complete, there are three spines on the posterior preopercular border, and the spine at the angle is the longest. All spines are shorter than the pupil diameter. Additional spines

Table 3

Morphometric data for *Macquaria novemaculeata* larvae from channel net samples and reared in aquaria (body length preceded by "R"), and juveniles from beach-seine samples. Measurements are in mm. VAFL = vent to anal-fin length.

Body length	Preanal length	Predorsal length	Body depth	Head length	Snout length	Eye diameter	VAFL
Yolksac							
R 3.32	1.48		0.52	0.53	0.16	0.24	
R 3.60	1.60		0.58	0.53	0.16	0.22	
Preflexion							
R 3.60	2.00		0.92	0.96	0.24	0.34	
R 3.80	2.00		1.00	1.04	0.30	0.38	
R 3.90	1.76		0.64	0.84	0.18	0.30	
R 4.20	2.00		0.64	0.93	0.20	0.33	
R 4.40	2.00		0.78	1.06	0.26	0.34	
4.57	2.36	2.16	1.20	1.40	0.28	0.40	0.22
Flexion							
5.00	2.72	2.40	1.52	1.48	0.32	0.48	0.12
5.14	2.90	2.32	1.48	1.76	0.44	0.48	0.10
R 5.31	2.84	2.60	1.40	1.60	0.48	0.56	0.20
5.39	2.74	2.66	1.58	1.60	0.40	0.48	0.12
R 5.39	2.90	2.66	1.36	1.56	0.40	0.56	0.20
5.47	2.80	2.74	1.60	1.72	0.44	0.48	0.12
R 5.47	3.00	2.60	1.56	1.76	0.52	0.60	0.12
5.70	3.40	2.92	1.96	2.00	0.52	0.56	0.06
5.90	3.32	2.90	1.80	1.88	0.52	0.56	0.04
Postflexion							
5.64	3.07	2.41	1.66	2.00	0.52	0.60	0.08
5.89	3.52	2.64	2.00	2.00	0.52	0.60	0.06
6.06	3.32	2.81	1.99	2.00	0.52	0.56	0.10
6.30	3.40	2.57	1.91	1.99	0.50	0.60	0.20
6.60	3.73	2.91	2.24	2.08	0.50	0.66	0
6.72	3.74	2.82	2.24	2.16	0.60	0.64	0.08
R 6.72	3.74	2.60	2.16	2.16	0.52	0.76	0.08
R 7.20	3.98	3.00	2.32	2.28	0.52	0.68	0.08
7.40	4.15	3.02	2.49	2.32	0.66	0.72	0
R 7.47	4.15	3.04	2.49	2.48	0.64	0.72	0.08
7.55	4.30	3.15	2.66	2.57	0.66	0.72	0
R 8.18	5.31	3.49	3.07	2.91	0.75	0.91	0
R 8.60	5.56	4.15	3.24	3.24	0.83	1.08	0
R 9.20	5.56	3.98	3.75	3.50	0.75	1.21	0
Settled							
10.13	6.64	4.81	3.49	3.65	0.83	1.33	0
R 10.20	6.64	4.57	3.74	3.74	0.83	1.33	0
R 10.30	6.64	4.57	3.99	3.82	1.05	1.33	0
11.62	7.55	5.56	3.82	4.23	1.00	1.49	0
11.62	7.55	5.47	3.98	4.39	1.07	1.49	0
13.28	8.30	5.98	4.56	4.98	1.41	1.66	0
14.10	8.63	6.47	4.65	5.15	1.41	1.74	0

Table 4

Meristic data of *Macquaria novemaculeata* larvae and juveniles. Body length preceded by "R" indicates larvae reared in aquarium. () indicates only fin bases present, [] incipient rays or spines, { } ray transforming to a spine.

Body length	Dorsal	Anal	Pectoral	Pelvic	Caudal	Myomeres
Yolksac						
R 3.32						10+15=25
R 3.60						11+14=25
Preflexion						
R 3.60						12+13=25
R 3.80						11+14=25
R 3.90						11+14=25
R 4.20						10+15=25
R 4.40						10+15=25
4.57	(9)	(8)			[2+3]	10+15=25
Flexion						
5.00	(VI), (6)	(8)			7+6	10+15=25
5.14	(VI), (8)	(9)			8+7	10+15=25
R 5.31	(III), (9)	(8)			[7+6]	12+13=25
5.39	(IV), [9]	(I), [9]			8+7	11+14=25
R 5.39	(III), (9)	(9)			6+6	12+13=25
5.47	(V), [8]	[I], [7]			[1]7+7[1]	11+14=25
R 5.47	(VI), [10]	(I), [8](1)			[1]8+7[1]	12+13=25
5.70	VI, 10	(I), 8	6		9+8	13+13=26
5.90	[I]V, 10	(I), 8	6		9+8	12+13=25
Postflexion						
5.64	VI, 10	(I), 9	5		9+8	10+15=25
5.89	[VI], 10	(I), 9	5		9+8	12+13=25
6.06	VI, 10	(I), 9	6		9+8	12+13=25
6.30	VI, 11	I, 9	6		9+8	11+14=25
6.60	VI, 11	I, 9	8		9+8	12+13=25
6.72	VI, 11	I, 9	8	buds	9+8	12+13=25
R 6.72	VI, 10	I, 9	12	buds	9+8	12+13=25
R 7.20	VII, 11	II, 9	10	buds	9+8	12+13=25
7.40	VII, 11	II, 9	12	buds	9+8	13+12=25
R 7.47	VII, 11	II, 9	13	buds	9+8	12+13=25
7.55	VII, 11	II, 9	12	buds	9+8	12+13=25
R 8.18	VIII, 11	II, 9	13	I, 5	9+8	13+12=25
R 8.60	VIII, 11	II, 8	13	I, 5	9+8	13+12=25
R 9.20	IX, 10	II(I), 7	15	I, 5	9+8	13+12=25
Settled						
10.13	IX, 10	II(1), 8	14	I,5	7+9+8+7	12+13=25
R 10.20	IX, 10	II(1), 8	14	I, 5	9+8	13+12=25
R 10.30	IX, 10	II(1), 8	14	I, 5	9+8	13+12=25
11.62	VIII (1),10	II (1), 8	14	I,5	9+9+8+8	13+12=25
11.62	IX, 9	II (1), 8	14	I,5	8+9+8+7	13+12=25
13.28	IX, 10	III, 8	14	I,5	7+9+8+9	12+13=25
14.1	IX, 10	III, 8	14	I,5	9+9+8+7	12+13=25

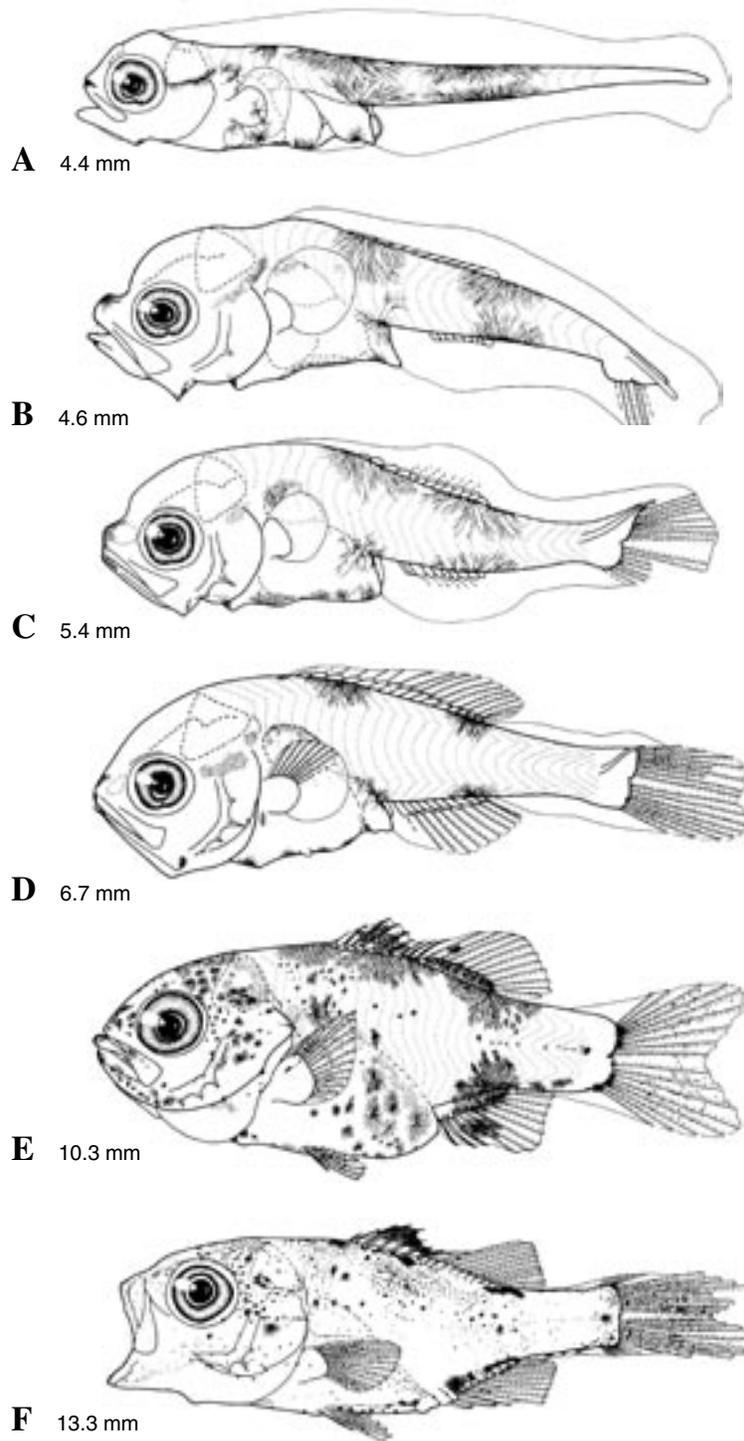


Figure 2

Larvae of *Macquaria novemaculeata*. (A) yolk sac larva, 10 days after hatching, note remnant of yolk below pectoral-fin base; (B) preflexion larva; (C) flexion stage larva; (D) postflexion larva; (E) postflexion larva, 57 days after hatching; (F) recently settled juvenile. Specimens A and E were reared at Port Stevens Fisheries Centre, New South Wales (NSW); B–D from Swansea Channel, central NSW; specimen F is a recently settled juvenile from the Clyde River, southern NSW.

form as larvae develop; four or five spines are present in larvae and transitional juveniles from 7.5–8.2 mm. A minute spine (rarely two) develops on the anterior preopercular border from 9 mm; a third spine develops in transitional juveniles from 13.3 mm. A small interopercular spine develops by the time notochord flexion is complete. Low posttemporal and supraocular ridges, but no spines, develop during notochord flexion; they both become inconspicuous in postflexion larvae from 8.2 and 8.6 mm, respectively. An opercular spine is present from 8.6 mm. A small supracleithral spine is present in transitional juveniles from 10.1 mm.

The pterygiophores of all the soft rays and up to six of the pterygiophores of the first dorsal fin form during notochord flexion. Soft rays of the dorsal fin are ossified by the time notochord flexion is complete, whereas spinous rays ossify from posterior to anterior in late flexion and early postflexion larvae by 5.7–6.1 mm. The full complement of spines is present by 8.2 mm. Anal-fin pterygiophores form during notochord flexion, and all soft rays are ossified by the time notochord flexion is complete. Spinous rays of the anal fin begin to ossify in postflexion larvae by 6.3 mm, and all anal-fin elements are present by 7.2 mm. The last spinous ray of the dorsal fin and the third spinous ray of the anal fin transform from a soft ray between 7.6 and 9.2 mm. Pectoral-fin elements begin to ossify by the time notochord flexion is complete, and all rays are present in postflexion larvae by 7.5 mm. Pelvic-fin buds form in postflexion larvae by 6.7 mm, and all elements are ossified by 8.2 mm. Caudal-fin rays first appear in preflexion larvae from 4.6 mm, and all principal rays are ossified by the time notochord flexion is complete. Procurrent caudal rays are present in field-caught transitional juveniles. Notochord flexion commences between 4.6 and 5.0 mm, and is complete by 5.6–6.1 mm. There is a prominent gap between the anus and anal fin while the anal fin forms (vent to anal-fin length [VAFL] up to 5% of BL). The gap reduces in size as the anal fin develops, and it is absent by 7.6 mm. Scales have not developed in the largest specimen examined.

Pigment (Fig. 2, A–F) Larvae are moderately to heavily pigmented. An expanded melanophore is present on the tip of the snout and a small melanophore develops under the tip of the lower jaw in preflexion larvae from 3.6 mm. A second melanophore on the snout develops posterior to the first by the time notochord flexion is complete. A single melanophore is present at the angle of the lower jaw. A few small melanophores develop ventrally along the lower jaw in postflexion larvae from 7.2 mm. A series of internal melanophores underlie the mid- and hindbrain.

There are two very large expanded melanophores on the dorsal midline of the tail; the first is on the trunk centered over the hindgut, and the second is mid way along the tail. Once the dorsal fin forms they are centred under the middle of the spinous portion of the dorsal fin and under the posterior end of the soft dorsal fin, respectively. An additional smaller expanded

melanophore is present from 7.2 to 7.5 mm on the dorsal midline of the nape above the pectoral-fin base.

Two very large expanded melanophores occur ventrally, opposite the two large dorsal melanophores. The anteriormost of these melanophores reduces in prominence as larvae develop and is inconspicuous to absent by metamorphosis. Internal expanded melanophores over the gas bladder may have filaments that emerge externally, particularly in preflexion and flexion larvae. Internal melanophores along the notochord may be apparent on the caudal peduncle in postflexion larvae from 7 mm. There is an expanded melanophore on the midline of the isthmus, immediately anterior to the cleithral symphysis. A series of three to six small, expanded melanophores is present along the ventral midline of the gut. In postflexion larvae there is a bilaterally paired melanophore anterior to the pelvic-fin base, and two to four melanophores along the midline of the gut between the pelvic-fin base and the anus. A small contracted melanophore ventrally on the posterior margin of the caudal-fin base develops between 5.0 and 6.1 mm, and is located between ventral rays 1–5. This melanophore expands from 6.7 to 7.6 mm and spreads across up to four ray bases.

Pigment distribution spreads rapidly over most of the head from 7.2 to 7.5 mm, and laterally on the trunk, gut and tail from 8.2 mm. The expanded melanophores on the dorsal and ventral midlines of the trunk and tail remain large as the larvae develop; the posteriormost of these increases in intensity in reared larvae. The expanded melanophores on the dorsal and ventral midlines of the body become relatively smaller after settlement. By settlement, small melanophores develop on the membranes of the pectoral, pelvic, anal, and caudal fins, and the membrane of the spinous portion of the dorsal fin becomes heavily pigmented. After settlement, small melanophores cover most of the head and body, but the heaviest cover is seen dorsally. Three broad vertical bands become apparent dorsally on the nape, below the center of the spinous dorsal fin, and below the center of the soft dorsal fin in the largest specimen examined (14.1 mm).

Discussion

Adults of *M. colonorum* and *M. novemaculeata*, which have only minor morphological differences, such as the relative length of the snout, the profile of the head dorsally, postorbital head length, and gill-raker counts, are difficult to distinguish (Williams, 1970). None of these characters are useful for distinguishing larvae. The larvae of these two species could be positively identified only by comparison with reared larvae derived from positively identified brood stock.

Melanophore distribution is the most distinguishing character between the larvae of *M. colonorum* and *M. novemaculeata*. *Macquaria colonorum* has between four and seven expanded melanophores along the dorsal midline of the trunk and tail between 4.8 and 7.1 mm.

Macquaria novemaculeata has only two melanophores, and these are much larger; a third expanded melanophore develops on the nape from 7.2 mm. In addition, *M. novemaculeata* lacks a midlateral series of melanophores along the tail until settlement, and it is never as well developed as that in *M. colonorum*. On the other hand, *M. colonorum* has a prominent midlateral series until after settlement. One other morphological character that distinguishes the larvae is a snout length which is about equal to eye diameter in *M. colonorum* larvae until 7 mm, but snout length is always smaller than the eye diameter in *M. novemaculeata*.

Within the genus *Macquaria*, larval development of only *M. ambigua* has been described (Lake, 1967; Brown and Neira, 1998). There are several differences in the life history and development of the larvae of *M. ambigua* compared with *M. colonorum* and *M. novemaculeata*. *Macquaria ambigua* is restricted to freshwater, the eggs are large (3.3–4.2 mm in diameter, compared with 0.9 mm in reared *M. novemaculeata*) and the yolk sac in *M. ambigua* is large in small larvae and is not resorbed until the flexion stage (Brown and Neira, 1998). Compared with the larvae described in the present study, larvae of *M. ambigua* have more myomeres (24–28, but typically 26–27), and these larvae are relatively large by the time they complete notochord flexion (7.3 mm). They also lack an interopercular spine and supraocular ridge, and lack dorsal and lateral pigment on the tail until the postflexion stage.

Larvae of several other generalized percoid families are morphologically similar to *Macquaria*, including Latidae (Trnski et al., 2000), Microcanthidae (Walker et al., 2000a), Kyphosidae (Walker et al., 2000b), and some Apogonidae (Leis and Rennis, 2000). The latid genus *Lates* is morphologically most similar to the *Macquaria* larvae described in the present study but is tropical and does not have an overlapping distribution with *Macquaria*. *Lates* can be distinguished by the small size at notochord flexion (3.0–3.8 mm), dorsal and pectoral fin-ray counts when complete, and heavier melanophore distribution at a given size. Microcanthid and kyphosid larvae can be distinguished from coastal percichthyid larvae by the higher number of fin elements in the dorsal and anal fins, and the presence of supracleithral spines that are absent in larval percichthyids until the juvenile stage. Some deep-bodied apogonids resemble *Macquaria* larvae but can be distinguished by having separate spinous and soft dorsal fins and a large, conspicuous gas bladder.

Larvae of *M. colonorum* and *M. novemaculeata* were collected in Swansea Channel from July to August. This collection period coincides with adults of *M. novemaculeata* spawning from June to September in central New South Wales (Harris, 1986). *Macquaria colonorum* probably spawns at a similar time (McCarragher and McKenzie, 1986), and eggs have been collected from June to November in western Victoria (Newton, 1996). Adults of both species are thought to spawn in the middle reaches of estuaries at salinities above 8–10 g/kg (Harris, 1986; McCarragher, 1986), but *M. novemaculeata* will spawn in

waters up to 35 g/kg in culture (Battaglione and Selosse, 1996). The optimal conditions for incubation and hatching of *M. novemaculeata* eggs are 18 [\pm 1] $^{\circ}$ C and salinity at 25 to 35‰ (van der Wal, 1985). Eggs are buoyant within this salinity range and hatch in 42 h at 18 $^{\circ}$ C.

The presence of field-caught larvae of both species on incoming tides in Swansea Channel indicates that the larvae have spent some time in the ocean and that the eggs were potentially spawned in the ocean rather than in an estuary if they were not carried out to sea by outgoing tides. *Macquaria novemaculeata* adults move downstream into estuaries to spawn in water of suitable salinity. In low rainfall years, the spawning location is further upstream than in wet years, when spawning can occur in shallow coastal waters adjacent to estuaries (Searle¹). Mature *M. novemaculeata* adults can be found outside of estuaries in wet years (Williams 1970). This is verified by the collection of mature adults by trawl in July 1995 in 11–17 m of water off Newcastle, NSW (AMS I.37358-001). *Macquaria colonorum* adults have also been collected on the continental shelf (McCarragher and McKenzie, 1986). In addition, larvae can tolerate waters of marine salinity in culture, and late in their larval phase wild larvae can tolerate marine salinity as shown from our field collections. The presence of larvae and adults in continental shelf waters may provide two modes of dispersal among estuaries. Thus, these two species of *Macquaria* may not be confined to freshwater and estuarine conditions as often assumed (Harris and Rowland, 1996; Allen et al., 2002).

The smallest juveniles of *M. colonorum* and *M. novemaculeata* collected in the wild are from the Clyde River estuary, southern NSW. These range in size from 10 to 14 mm SL, and were collected among *Zostera* seagrass. They are morphologically similar to the largest pelagic larvae collected in the channel net in Swansea Channel. Based on the largest larvae and smallest juveniles, settlement occurs between 7.1 and 10.3 mm SL in *M. colonorum* and between 9.2 and 10.1 mm in *M. novemaculeata*. Transition to the juvenile stage is gradual, because scales are not present and juvenile pigmentation is still forming at about 15 mm. Juveniles of both species have been collected in estuarine waters until at least 100 mm SL (AMS fish collection). Juveniles of *M. novemaculeata* would be expected to migrate to freshwater because this is the nominal adult habitat (Williams, 1970), but the size at which this migration occurs is unclear.

The two species described in the present study were the only members of the genus *Percalates*, until this genus (along with *Plectroplites*) was synonymized with *Macquaria* by MacDonald (1978). Analyzing morphological and biochemical similarities of the three genera, MacDonald (1978) listed eight morphological differences that distinguished *Percalates* from *Macquaria* and *Plectroplites*. Protein electrophoresis similarities were stron-

¹ Searle, G. 2002. Personal commun. Searle Aquaculture, 255 School Rd, Palmers Island NSW 2463.

ger between *Pe.* (currently *Macquaria*) *colonorum* and *Pe. (Macquaria) novemaculeata* (similarity coefficient 0.95), and *M. australasica* and *Pl. (Macquaria) ambigua* (0.71) than between the *Percalates* and *Macquaria* + *Plectroplites* (0.63) (MacDonald, 1978). The species of *Percalates* are euryhaline, whereas *Macquaria* and *Plectroplites* are strictly freshwater. This fact, combined with the difference in larval morphological features between *Macquaria ambigua* (Brown and Neira, 1998) and *M. colonorum* and *M. novemaculeata*, provides evidence that the genus *Macquaria* as defined by MacDonald may be polyphyletic. Recent phylogenetic analysis of the Percichthyidae with the use of molecular data indicates that *M. colonorum* and *M. novemaculeata* are more closely related to *Maccullochella* species than to *Macquaria (sensu stricto)* (Jerry et al., 2001). Molecular and larval evidence indicates the two catadromous species (*M. colonorum* and *M. novemaculeata*) belong in a genus separate from the freshwater species (*M. ambigua* and *M. australasica*).

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