

Early Life History of the Nurseryfish, *Kurtus gulliveri* (Perciformes: Kurtidae), from Northern Australia

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Eggs and larvae of nurseryfish, *Kurtus gulliveri*, one of two known species of Kurtidae, are described and illustrated for the first time using material collected in two rivers of Australia's Northern Territory. Nurseryfish are unique among fishes in that males carry a cluster of fertilized eggs on a bony hook projecting from their foreheads. No brooding males were captured during this study, although one partial egg cluster was found adjacent to a male caught in a gill net. Three clusters found attached to gill nets without associated males had approximately 900–1300, slightly elliptical, 2.1–2.5 mm diameter, eggs, each with multiple oil droplets and a single, relatively thick chorionic filamentous strand at opposite poles. Larvae are pelagic and hatch at approximately 5-mm body length (BL) at the flexion stage possessing a large yolk sac, forming dorsal, caudal, and anal fins, and little pigment. Notochord flexion and yolk-sac resorption are complete by 6.9 mm. Post-yolk-sac larvae resemble adults in having a hatchet-shaped body that is almost transparent in life, including a large head with relatively small eyes, preopercular spines and a prominent, inflated gas bladder. Larval length data obtained fortnightly from August to November 2001 suggests that breeding occurs during northern Australia's dry season (May to November) and that larvae leave the pelagic environment at about 25 mm.

THE nurseryfish, *Kurtus gulliveri* Castelnau, is a hatchet-shaped, hump-headed fish found in estuarine and fresh waters of northern Australia and southern New Guinea (Berra, 2001). Maximum reported total length is 590 mm (Weber, 1913). Together with *Kurtus indicus* Bloch from southern Asia (India to Borneo), the two species constitute the sole known representatives of the family Kurtidae within the monotypic perciform suborder Kurtoidei (Nelson, 1994). The common name "nurseryfish" derives from the fact that males carry the egg mass on a bony hook projecting forward from the supraoccipital crest (Weber, 1910, 1913), a structure unique among teleosts (Fig. 1A–B inset).

Information on the early life-history stages of nurseryfish is limited to a few early studies describing an egg mass carried by a single captured male *K. gulliveri* (Weber, 1910) and a description of early-stage eggs from the same egg mass (Guitel, 1913). Hardenberg (1936) examined thousands of *K. indicus* and never found males carrying eggs. Since the latter paper, there have been no studies on this unique mode of parental care, termed forehead brooding by Balon (1975). It is not known how the egg mass becomes attached to the male's hook, and there is virtually no information on nurseryfish ecology, reproductive biology, breeding grounds or the development of their eggs and larvae. Recent research on this species in rivers of Australia's Northern Territory has provided informa-

tion on their arthropod and fish diet (Berra and Wedd, 2001) and on the anatomy and histology of the male's hook that exhibits modifications for the attachment of an egg mass (Berra and Humphrey, 2002).

This paper describes for the first time the late-stage eggs and larvae of *K. gulliveri* using field-caught material and provides information on the size and occurrence of larvae collected in two tropical rivers of northern Australia. We also briefly discuss the timing of the spawning season and possible adaptive significance of forehead brooding.

MATERIALS AND METHODS

Adult nurseryfish were captured in four tributaries of the Adelaide River (mouth = 12°13.4'S, 131°13.5'E, Adam Bay), a highly flushed, turbid and tidal river located east of Darwin, Northern Territory. The tributaries were No. 2 (or "C" Creek), 8.0 km upstream from the mouth of the Adelaide River; "F Creek," 19.5 km upstream; Scott's Creek, 70 km upstream; and Marrakai Creek, 82 km upstream and approximately 2 km up from the Arnhem Highway bridge (Messel et al., 1979). Salinity in the Adelaide River during the sampling period was measured with a refractometer and ranged from 28 ppt downstream to 0 ppt in Marrakai and Scott's Creeks. Streams up to 31.6 km from the mouth of the Adelaide River are considered "saltwater creeks," whereas those above 31.6 km

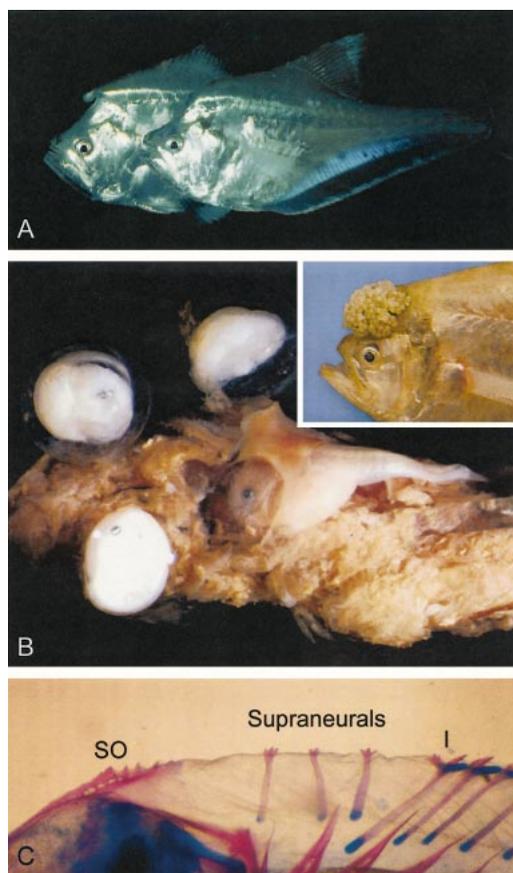


Fig. 1. (A) Male (behind) and female (front) *Kurtus gulliveri* photographed live in an aquarium at the Northern Territory Wildlife Park (photo by T. M. Berra); (B) partial egg mass obtained in a gill net immediately adjacent to a 224 mm SL male *K. gulliveri* in the Adelaide River on 20 June 2001; note yolk-sac larva almost dislodged from egg mass; top right inset: head of a 190-mm SL male with eggs captured from Ajkwa Estuary near Timika (Papua Province, Irian Jaya) in 2000 (photo by K. Hortle). (C) Antero-dorsal region of a cleared-and-stained 20-mm postflexion *K. gulliveri* larva from the Wildman River showing the serrated supraoccipital crest (SO), the three serrated supraneurals, and Y-shaped first spine-bearing pterygophore (I).

are designated as “freshwater creeks” (Messel et al., 1979). Salinity was undetectable at Marrakai Creek until late September when it was 2 ppt. By the end of the dry season in early November, salinity at Marrakai Creek was 4 ppt.

Collections of adults were made during daytime weekly between May and November 2001 using two 2–3 m deep, 10–13 cm mesh gill nets. Night-time sampling was deemed too dangerous because of the presence of large saltwater crocodiles (*Crocodylus porosus*) in the area. On most

sampling days, both nets were set across each tributary some 200 m apart for 3–6 h under varied tidal conditions and inspected every 20 min. All caught nurseryfish were placed on ice and later fixed in 10% formalin.

Ovarian eggs were removed from a 269 mm SL running-ripe female nurseryfish caught at the mouth of Scott’s Creek on 12 July 2001. Late-stage eggs were removed from a partial egg mass found in a gill net set in Marrakai Creek on 20 June 2001, immediately next to a captured male nurseryfish. Water in both locations was fresh, with temperatures of 25–26 C.

Larval nurseryfish described here include museum specimens caught 10 km upstream in the Wildman River (12°21.7’S, 132°08.2’E) on 29 May 1998 by Northern Territory Museum staff using a beam trawl towed at a depth of 10 m (Northern Territory Museum [NTM] S.14644–005) and larvae collected during this study in the Adelaide River, 80 km upstream from its mouth, and in Marrakai Creek, with a 50-cm² mouth 500- μ m mesh plankton net. Collections were made during daytime on 7, 17, and 30 August, 11 and 21 September, 5 and 22 October, and 4 and 13 November 2001. The plankton net was towed at a depth of approximately 1 m behind a power vessel for an average of 20 min. Samples were fixed on board using 10% formalin and later preserved in 70% ethanol.

A total of 55 larval nurseryfish (5.5–23.0 mm BL) were examined to describe morphometrics, meristics, and pigmentation. Of these, two yolk-sac larvae (5.5 and 5.8 mm) were removed from the partial egg mass found in the Adelaide River on 20 June 2001, seven (5.5–8.3 mm) came from net tows in the Adelaide River, and the remaining 46 (6.7–24.1 mm) from the Wildman River. Another 24 larvae from the Wildman River were cleared and stained following the methodology of Potthoff (1984) to obtain fin-ray and vertebral counts. Adelaide River larvae were retained by one of us (TMB) for future study.

Terminology used to describe head spines and morphometrics follows Neira et al. (1998). Measurements were made to the nearest 0.01 mm using an eyepiece micrometer fitted to a stereomicroscope. Larval lengths always refer to body length (BL), that is, notochord length (tip of snout to tip of notochord) in flexion larvae and standard length (tip of snout to posterior hypural margin) in postflexion larvae. Measurements of body depth (BD), head length (HL), eye diameter (ED), and preanal length (PAL) were converted to percentage (%) of BL, and the ranges and means (\pm 95% C.I.) given for each of the flexion and postflexion stages (Ta-

TABLE 1. BODY LENGTH AND BODY PROPORTIONS OF LARVAL NURSERYFISH, *Kurtus gulliveri*, CAUGHT IN THE WILDMAN RIVER IN MAY 1998. BL, body length; N, no. larvae; HL, head length, ED, eye diameter; BD, body depth; PAL, preanal length. Values for HL, ED, BD, and PAL are given as percentage of body length (% BL), and shown as range and mean \pm 95% C.I. (in parentheses) for each stage.

	Flexion	Postflexion
BL (mm)	5.5–6.6	6.7–24.1
N	7	48
HL	18.9–26.2 (23.8 \pm 2.6)	26.5–33.9 (29.7 \pm 0.5)
ED	4.1–5.0 (4.6 \pm 0.3)	3.7–4.8 (4.3 \pm 0.1)
BD	24.5–36.0 (29.3 \pm 4.3)	24.7–36.3 (33.2 \pm 0.8)
PAL	43.7–50.0 (46.1 \pm 2.2)	35.3–43.6 (39.1 \pm 0.6)

ble 1). Values given throughout the text correspond to mean % BL. Pigment described refers solely to melanin. Illustrations were made with the aid of a camera lucida. All nurseryfish larvae removed from plankton samples obtained in the Adelaide River and its tributaries ($n = 1250$) were measured and the data plotted in individual length-frequency histograms for each sampling occasion.

RESULTS

Eggs.—Ovarian eggs squeezed from the running-ripe female nurseryfish were slightly elliptical and measured 2.1–2.5 mm in diameter. The eggs possessed multiple small oil globules at one pole and a relatively thick, single chorionic strand made of many fine filaments at the opposite pole. The filaments arise from a circular base (rosette) on the chorion and twist upon themselves to form the strand that keeps the eggs entangled in the gelatinous matrix.

The partial egg mass found attached to the gill net (Fig. 1B) was immediately adjacent to a 224 mm SL male *K. gulliveri*. The sticky egg mass contained six late-stage eggs attached to a gelatinous matrix by individual chorionic strands (Fig. 2A), a 5.0-mm newly hatched nurseryfish larva still embedded in the matrix and two yolk-sac larvae (5.55 and 5.80 mm) that were apparently dislodged from the matrix during handling. Late-stage embryos had the tail curled toward the head and possessed large yolk sacs with unsegmented yolk and no oil globules. The embryos were at the flexion stage, having forming hypural plates and caudal fin rays. They also

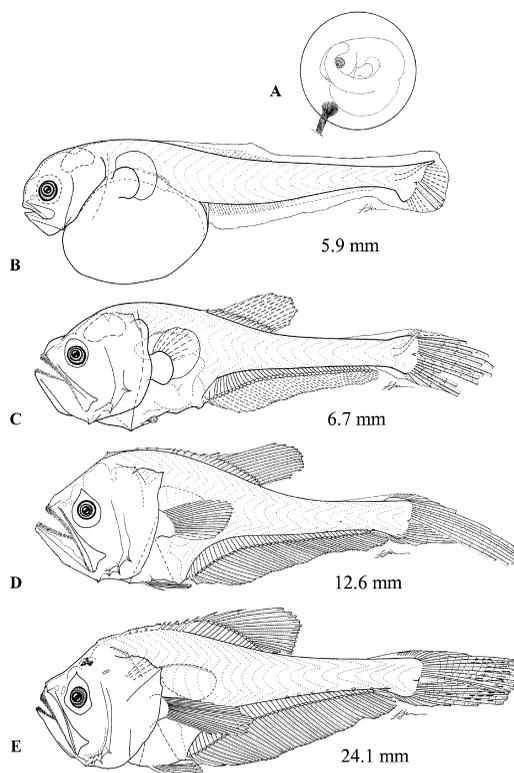


Fig. 2. (A) 2.5-mm diameter late-stage egg and (B–E) larval stages of *Kurtus gulliveri* from rivers of Australia's Northern Territory. Egg in (A) and 5.9 mm flexion larva with large yolk sac in (B) were removed from partial egg mass collected in the Adelaide River on 20 June 2001; note forming dorsal, caudal, and anal fin rays; (C) 6.7 mm; note developing pectoral fin rays and pelvic fin; (D) 12.6 mm; (E) 24.1 mm; (C–E) were collected in the Wildman River in May 1998 (S14644–005). Illustrated by F. J. Neira.

had pigmented eyes, pectoral fin buds, forming dorsal and anal fin rays (Fig. 2A).

Three egg masses were found in a gill net without associated males on 21 September 2001, about 1 km upstream in Marrakai Creek, in 28 C water. Two of the egg masses contained late-stage embryos, whereas the third contained apparently unfertilized eggs. Approximately 900, 1200, and 1300 eggs were estimated in each mass using the gravimetric method, that is, weighing a subsample of loose eggs and extrapolating the weight to that of each whole mass.

Larvae.—Postflexion larvae were identified as *K. gulliveri* Castelnau using a combination of body shape and fin meristics from the literature (Beaufort and Chapman, 1951) and from adult specimens (Dorsal VII [5 pterygiophore-bearing spines embedded in dorsal musculature + II],

11–14; Anal II, 39–49; Pectoral 16–21; Pelvic I, 5; TMB, unpubl. data). Our cleared-and-stained larvae had 11–13 (13) and 40–45 (43) soft rays in the dorsal and anal fins, respectively, and 24 (10+14) vertebrae. A developmental series from the smallest yolk-sac (= flexion) larva to the largest postflexion larva was assembled using body shape, head spines, and pigmentation. Late-stage embryos and the smallest yolk-sac larvae collected in plankton samples (5.50–6.62 mm) were linked together using body shape and the pigment over the gas bladder.

Nurseryfish larvae are pelagic. They hatch at about 5.0 mm at the late flexion stage (Fig. 2B), with a large yolk sac and unsegmented yolk; a formed mouth with no visible teeth; and slightly elliptical, pigmented eyes. Notochord flexion is complete between 6.7 and 6.9 mm; the largest flexion-stage larva was 6.6 mm and the smallest postflexion larva was 6.9 mm (Table 1). The largest yolk-sac larva was 6.6 mm; the yolk sac is no longer visible by 6.8 mm. The body is moderately deep through the postflexion stage (mean BD 29.3–33.2%; Table 1), becoming hatchet-shaped and increasingly laterally compressed with growth. The head is large (mean HL 23.8–29.7%), with a short snout and a concave profile that becomes more prominent with growth. The relatively small, slightly elliptical eyes remain about the same relative diameter through the postflexion stage (Fig. 2B–E; Table 1). The mouth is large, reaching well past the eye, with many small villiform teeth along the premaxilla and dentary. The gill membranes are free from the isthmus. A prominent, inflated gas bladder is present. The gut is triangular-shaped, coiled, and compact from the early postflexion stage and remains moderate in length (mean PAL 39.1–46.1%). There is no gap between the anus and the anal fin origin. There are 24 myomeres (10 + 14 = 24 vertebrae). Scales were absent in the largest larva examined (25.5 mm).

Head spination appears in early postflexion larvae at about 6.7 mm and consists initially of two spines each along the lower anterior and posterior margins of the preoperculum, and of a supracleithral spine (Fig. 2C). Preopercular spines soon increase to three to four along the anterior and posterior margins, the posterior spines remaining prominent. The supracleithral spine remains throughout larval development. A low supraoccipital crest bearing two tiny cusps develops by about 7 mm and remains in the largest postflexion larvae examined with up to 6–8 cusps, including an elevated median cusp (Figs. 1C, 2E).

Late-stage embryos and newly hatched larval

nurseryfish possess pectoral fin buds and developing dorsal, caudal, and anal fin rays but no traces of pelvic fins. The full complement of principal caudal fin rays (9 + 8) is present by 12 mm; a total of 12–13 upper and 9–11 lower procurrent rays are visible in cleared-and-stained larvae > 17 mm. Cleared-and-stained larvae > 7 mm reveal three supraneurals each with serrations dorsally, followed by seven spine-bearing pterygiophores. The first pterygiophore is clearly Y-shaped, the anterior arm bearing serrations similar to those in the supraneurals, and the posterior bearing a small spine, similar to those present in the next six pterygiophores (Fig. 1C); the last two pterygiophores bear distinctly longer spines (VI and VII), which remain exposed in late postflexion larvae and adults (Fig. 2E). These spines and the 11–13 soft rays of the short-based second dorsal fin are completely formed by about 12 mm; the two spines and 40–45 soft rays of the long-based anal fin are also formed by 12 mm (Fig. 2). In the adults, both the three serrated supraneurals and the first five short spines are difficult to see but easy to feel along the dorsal surface of the body. Pectoral fin rays start developing at 6.5 mm, and all 19–20 rays are formed by 20 mm. Pelvic fin buds appear by 6.5 mm, and all I, 5 elements are formed by 12 mm. The sequence of fin formation and completion can be expressed as: C → D, A → P₂ → P₁.

Freshly caught larvae are nearly unpigmented and almost entirely transparent (Fig. 2). In general, pigment is present on the head, brain, over the gas bladder, along the ventral surface of the tail, and on the caudal fin. Head pigment first appears at the junction of the mid- and hind brain by about 7 mm. External head pigment usually forms in larvae > 18 mm and consists of a patch of small melanophores above each eye. Tail pigment includes a single series of up to 18 (usually 5–10) small, widely spaced melanophores along the ventral surface, with a distinct melanophore above the last anal fin pterygiophore. Melanophores along the principal caudal fin rays form in postflexion larvae > 15 mm. Internal pigment always is present dorsally over the gas bladder.

Larval occurrence and size frequency.—Nurseryfish larvae were caught in the Wildman River in May 1998 and in the Adelaide River on every sampling occasion between 7 August and 13 November 2001 (Fig. 3). Larvae from the Wildman River ($n = 265$) ranged from 5.0 to 23.0 mm. Larvae from the Adelaide River ranged from 5.6 to 25.5 mm with a distinct mode at 7–9 mm from mid-August to early November. Percentage

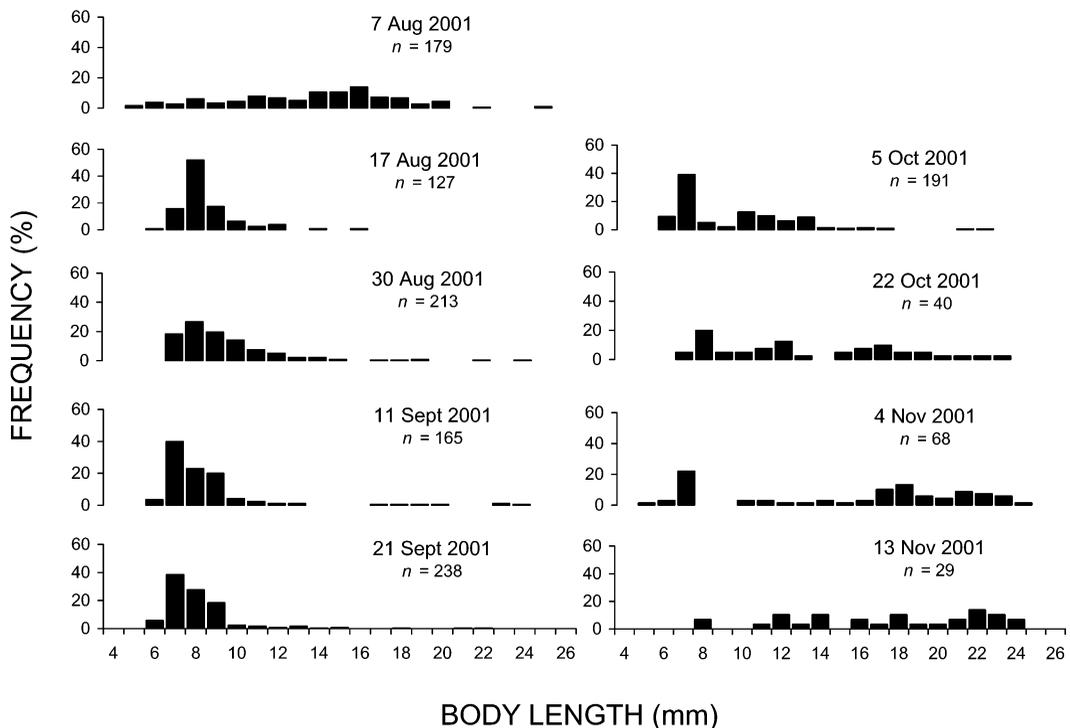


Fig. 3. Length-frequency distributions (body length, mm) of larval *Kurtus gulliveri* caught in surface waters (~1 m) of the Adelaide River fortnightly between 7 August and 13 November 2001.

frequency of 7–9 mm nurseryfish larvae decreased gradually toward mid-November, whereas the proportion of larvae > 10 mm increased substantially from early October, particularly the 17–22 mm larvae caught between late October and mid November. No clear modes were observed in the lengths of nurseryfish larvae caught in the Adelaide River on 7 August, except for perhaps a slight dominance of 15–18 mm larvae. Newly hatched nurseryfish larvae (5.0–6.0 mm) were caught only on 7 August and 4 November (Fig. 3).

DISCUSSION

Our observations on egg masses and late-stage embryos parallel those of Weber (1910, 1913) and Guitel (1913), including egg diameters (2.1–2.5 mm) and the presence of a chorionic strand that connects each egg in a cluster. The single chorionic strand closely resembles that found in the eggs of the mouthbrooding apogonid *Apogon semilineatus* (Ebina, 1932) and the chaenopsid *Neoclinus blanchardi* (Watson, 1996). We estimated the number of brooded eggs to be around 0900–1300 in three apparently complete egg masses found attached to gill nets in the Adelaide River. However, the ac-

tual number of eggs in each mass may be less than our estimates because of the unknown weight of the gelatinous matrix holding the eggs together.

There are no data on fecundity, so we cannot comment on whether most or all eggs released by a female during spawning end up on the male's hook. Furthermore, despite the intense sampling carried out during this study, we were unable to capture a male carrying eggs or observe an egg mass being deposited and/or collected on the male's hook. In fact, no one has yet been able to describe how eggs are attached to the male's hook, despite repeated sightings of males carrying eggs by both commercial barramundi fishers and staff from the Department of Primary Industry and Fisheries working in Australia's Northern Territory rivers. Moreover, captures of forehead brooding males are extremely rare and only include the 420-mm TL male caught in the Lorentz River (New Guinea) in March 1910 (Weber, 1910) and a 190-mm SL male with eggs captured in the Ajkwa Estuary near Timika (Papua Province, Irian Jaya) in 2000 (Fig. 1B, inset). As far as we can determine, neither egg-carrying specimen was preserved.

A substantial fraction of the development of

K. gulliveri takes place within the eggs, as evident in the facts that both late-stage embryos and our smallest field-collected yolk-sac larvae (5.5–6.6 mm) were undergoing notochord flexion and had forming caudal, dorsal, and anal fins. We have no information on the incubation time or on whether newly hatched larvae remain near the male parent. The presence of yolk residuals in field-collected yolk-sac larvae suggests that they still depend on it posthatching, even though the presence of many tiny villiform teeth along the premaxilla and dentary would indicate that they are able to capture prey and thus feed exogenously.

The development of larval *K. gulliveri* is similar to that found in most generalised percoids (Johnson, 1984). This includes formation of the caudal, dorsal, and anal fin anlagen during notochord flexion, completion of flexion at < 7 mm, which coincides with the attainment of the full complement of principal caudal fin rays, and the presence of preopercular spines, which are retained in the adults (Beaufort, 1914; Johnson, 1984). There are no apparent morphological specializations of *K. gulliveri* to pelagic larval life, except perhaps the serrated supraoccipital crest and the almost transparent body of live larvae.

Although frequently placed in a separate perciform suborder, Johnson (1993) noted that there is nothing in the osteology of *Kurtus* to exclude it from the Percoidei and proposed that Kurtidae may be closely related to Apogonidae based on shared similarities of the sensory papillae of the head and body and the specialized configuration of the dorsal gill arches. This hypothesis needs to be addressed further, but there is little we can offer at present based on larval characters to either support or dispute a relationship. In fact, apart from both families having two anal fin spines and 10+14 vertebrae, their larvae are indeed quite different (e.g., Neira, 1991; Neira and Bruce, 1998).

Larval *K. gulliveri* are easily distinguished by their distinct hatchet-shaped, compressed body; narrow caudal peduncle; large head and large, oblique mouth with distinct, early-forming villiform teeth; preopercular spines; compact, triangular-shaped gut; considerably longer anal than dorsal fin base; and 24 myomeres. The unique shape and largely unpigmented body are sufficient to separate larval *K. gulliveri* from other fish larvae such as sciaenids that also occur in the upper Adelaide River (FJN, pers. obs.; Leis and Carson-Ewart, 2000). Indeed, from the early postflexion stage, larval nurseryfish are miniature copies of the adults. Our length-frequency data, the finding of egg masses in June

and September, and the presence of newly hatched larvae in early August and November suggest that nurseryfish in the Adelaide River are capable of breeding for an extended period.

Although we did not attempt to age the larvae, our length-frequency histograms suggest the presence of at least two or three cohorts. Larvae in the 7–9 mm range observed on 17 August were still present on 22 October, albeit in small numbers. A clear shift from 7–9 mm to 17–19 mm is evident between 17 August and 4 November, which translates into a growth rate of about 0.8 mm/week. Assuming that this estimate is accurate, we could argue that the 15–17 mm larvae caught in early August were produced around early May, which implies that the breeding period is even longer than that suggested from the egg and larval data. The conclusion of a spawning in May is supported by the capture of nurseryfish larvae in late May 1998 in the Wildman River, a system geographically close to the Adelaide River. Moreover, the breeding season may be even longer, if we consider the male carrying eggs caught in the Lorentz River in March 1910 (Weber, 1910). We have no information on whether nurseryfish are serial or total spawners, a question that may only be answered after detailed ovarian histology.

It is possible that the spawning period of nurseryfish is timed to coincide with the dry season typical of Australia's northern region as suggested by gradual decrease in numbers of larval nurseryfish toward November, that is, just before the start of the wet (= monsoon) season. If this is the case, we could argue that an extended breeding period during the dry season may be more advantageous to the larvae than if they were produced during the climatically severe wet season, which brings about highly turbid and flushing conditions while washing terrestrial nutrients into the river enriching the food supply for small nurseryfish. The adaptive significance of forehead brooding in nurseryfish remains a matter of conjecture. In this context, it is possible that it may serve several functions, such as to protect the eggs from being swept away by the twice-daily tides or floods, as well as from sedimentation and low oxygen habitats that are typical of northern Australian rivers.

ACKNOWLEDGMENTS

Our special thanks to D. Wedd and Q. Allsop for their field assistance. Many thanks also to the fish section staff of the Museum and Art Gallery of the Northern Territory (Darwin) and

the Australian Maritime College (Tasmania) for the in-kind contribution to this project. Our sincere gratitude to G. D. Johnson, J. M. Leis, and R. Mooi for their advice and comments on the manuscript. Our thanks also to K. Hortle for allowing us to use the photo of the male with eggs in Plate 1B and to G. Allen for providing it. This research was supported by small grants from the National Geographic Society (6895-00), the Columbus (Ohio) Zoo, and Bioscience Productions, Inc., to TMB. This research was carried out under Special Permit 2000-2001/S17/1521 from the Director of Fisheries of the Northern Territory to TMB while the permit holder was a research associate at the Northern Territory Museum. All institutional animal care and use guidelines were followed during the execution of this project.

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