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Reproductive anatomy, gonad development and spawning seasonality of nurseryfish, *Kurtus gulliveri* (Perciformes: Kurtidae)

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Abstract. The nurseryfish, *Kurtus gulliveri*, of northern Australia, is remarkable for the fact that the males carry the egg mass on a supraoccipital hook on their forehead. Plankton samples of larval nurseryfish indicate a prolonged spawning season (June–November) that more or less corresponds with the dry season in the Northern Territory. The paired, elongate testes are located in the posterior portion of the body cavity suspended by the mesorchium. The gonadosomatic index (GSI) of males was small and highly variable (mean 0.14, range 0.01–0.27) from June to November. The histological structure of testicular lobes showed maturing and mature stages that contained spermatocytes, spermatids, and spermatozoa. The paired, bean-shaped ovaries contained about 5500 oocytes (1176–9783) and were located in the rear of the abdominal cavity. GSI averaged 1.58 (range 0.36–4.48). Ovarian histology revealed primary growth, cortical alveolar oocytes, vitellogenic oocytes, coalesced yolk, and atresia. The occurrence of postovulatory follicles and late vitellogenetic oocytes in the ovaries clearly indicate that nurseryfish females are batch spawners. Maturing testes showed signs of previous spawnings indicating that males are capable of spawning several times throughout the spawning season. We speculate that nurseryfish may spawn in a manner similar to their closest relatives, cardinalfishes (Apogonidae), with eggs carried on the male's hook instead of orally.

Introduction

The family Kurtidae consists of two species, *Kurtus gulliveri* from northern Australia and southern New Guinea, and *Kurtus indicus* from India to Borneo (Berra 2001). This family is placed in the Kurtoidei, a monotypic suborder of the Perciformes (Nelson 2006). The nurseryfish, *Kurtus gulliveri* Castelnau, is noted for its unusual mode of parental care. The male carries an egg mass on a supraoccipital hook overhanging the head. This is referred to as 'forehead brooding' (Balon 1975). *Kurtus indicus* is not known to carry eggs (Hardenberg 1936). Weber (1910, 1913) first reported this unusual egg-carrying behaviour from a single male, and Guitel (1913) described the early-stage oocytes from Weber's specimen. De Beaufort (1914) illustrated skeletal anatomy and discussed some aspects of soft anatomy of *K. gulliveri*. Weber (1913), repeated by de Beaufort and Chapman (1951), reported a maximum size of 590 mm total length (TL). Until recently, these 90-year-old accounts were the latest published record of this bizarre species.

Fieldwork, started in 2001 and continued in 2003, 2004 and 2005, has begun to shed some light on the life history of the nurseryfish. Berra and Wedd (2001) reported that its diet consisted of crustaceans, isopods, insect larvae and small fishes. Berra and Humphrey (2002) demonstrated that the skin in the cleft of the hook is folded into crypts that lack secretory and neurosensory cells which are present in the hook's dorsal epidermis. This anatomy is considered an adaptation for adhesion of the egg mass matrix in the hook's cleft. The dermis of the hook is highly vascularised, and engorgement with blood likely helps hold the egg mass in place. Berra and Neira (2003) described the eggs and larval development of nurseryfish and suggested that spawning is a dry-season phenomenon. Berra (2003) confirmed that *Kurtus gulliveri* and *K. indicus* are separate species, provided a colour description of *K. gulliveri*, and mapped its distribution. The unusual lobed swim bladder and expanded ribs of *K. gulliveri* were studied by high-resolution computed tomography and described as an accessory acoustic organ by Carpenter *et al.* (2004). Otolith morphology and age and growth were examined by Berra and Aday (2004), who reported that most fish in a sample were one or two years old and that the oldest fish was four years old. Berra *et al.* (2004) discussed predation on nurseryfish, teratology, associated species and other natural history topics. Humphrey and Berra (2006) reported epizootic ulcerative syndrome for the first time in nurseryfish, and Ezaz *et al.* (2007) determined a diploid chromosome number of $2n = 44$. The purposes of this paper are to describe and illustrate the gonads of both sexes and to use this information to understand aspects of the reproductive life history of nurseryfish.

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Materials and methods

Study site

The Adelaide River, 65 km east of Darwin, is a 226-km-long turbid river that empties into an inlet of the Timor Sea at 12°13′S, 131°13′E. It is subject to twice-daily high and low tides, and the tidal difference may exceed 7 m. Marrakai Creek (12°40.950′S, 131°20.030′E) is a major, tidal, freshwater tributary of the Adelaide River ~82 km upstream from the mouth of the river. See Berra (2003) for a map of the river system and a detailed description of the study area. Nurseryfish were collected from Marrakai Creek during daylight between April and November 2001, October–November 2003, July–August 2004, and November–December 2005 by gill netting. Night-time sampling was considered too dangerous due to the presence of large saltwater crocodiles (*Crocodylus porosus*). Most fish were released alive but voucher specimens retained were immediately placed on ice, measured and weighed, and gonads were removed, weighed, and preserved in 10% formalin. Plankton tows to sample for larval nurseryfish were carried out between the Arnhem Highway boat ramp and the mouth of Marrakai Creek. A 500-μm mesh plankton net with a 50-cm^2 mouth was towed just below the surface for 20 min as described by Berra and Neira (2003) in various months and years of the study.

Gross anatomy

Fixed fish were dissected to investigate appearance and location of testes and ovaries in the body cavity. In order to obtain a clear view, the heads of some specimens were removed during dissection. Gonads of 26 males collected from 1 June to 4 November 2001, 3–17 October 2003 and 6 August 2004, and of 31 females collected from 1 June to 11 September 2001, were examined macroscopically. Gonadosomatic Index (GSI) was determined as the ratio of gonad weight to fish weight (×100). Testes of 20 males and the ovaries of all 31 females were also investigated histologically.

Histology

Gonad samples were placed in omnisette tissue cassettes, embedded in paraffin, sectioned at 3–6 μm, and stained with haematoxylin and eosin following standard histological procedures. Histological slides were examined at 100–1000× with a compound microscope. Stages of testes development were determined according to a classification slightly modified from Smith and Walker (2004). Oocyte stages follow Wallace and Selman (1981) and Selman and Wallace (1986). These stages include primary growth (PG), cortical alveoli (CA), and vitellogenic (V). In addition, terminal-stage oocytes with coalesced yolk (CY) were noted. This last stage differs from that of Wallace and Selman (1981) and Selman and Wallace (1986) due to the difference between the final maturation stages of marine (hydration) and freshwater (no hydration) (Thompson 1997) fishes. Relative frequency of oocyte stages for each ovary was determined by starting at a random spot on each histological slide; stages were identified and counted, then a new field of oocytes was examined. Movement along this transect was inward towards the centre of the ovary cross-section. Only oocytes that were at least 50% in the field were counted, and numbers of oocytes of each stage were expressed as percentages of total oocyte number (Fitzhugh *et al.* 1993; Render *et al.* 1995). One hundred oocytes were staged from each female.

In addition to relative frequency of oocyte stages, each histological section was examined for postovulatory follicles and atretic oocytes to provide further information on the reproductive cycle.

Number of oocytes

The same 31 ovaries used for histology were also dissected under a binocular microscope, and all macroscopic oocytes were counted but not measured. The eggs from one of three complete egg masses taken from a gill net were counted to verify the estimates previously presented in Berra and Neira (2003).

Results

Gross anatomy

In total, 1261 adult nurseryfish (65% males, 35% females) were caught and sexed during the study. Most of these were released alive without measurement. Throughout the study hundreds of unsexed nurseryfish under 100 mm standard length (SL) were caught but released. Data on size and GSI of males are presented in Table 1. GSI was highly variable: from 0.01 to 0.27 (mean 0.14) (Table 1). Macroscopic examinations revealed that paired elongated testes of the nurseryfish are located in the posterior portion of the abdominal cavity and suspended by the mesorchium (Fig. 1*A*).

Likewise, the paired ovaries are located in the posterior portion of the abdominal cavity. Ripe ovaries are bulbous, bean-shaped, highly vascularised and contain several thousand visible

Table 1. Standard length, gonadosomatic index and number of oocytes in ovaries of nurseryfish over different sampling times

Period	No. of fish	Standard length		Gonadosomatic index		No. of oocytes	
		Mean ± s.d.	Range	Mean ± s.d.	Range	Mean ± s.d.	Range
Males							
June–July	12	200 ± 28	175–260	0.10 ± 0.05	0.01–0.19	–	
August–September	6	212 ± 25	180–240	0.16 ± 0.09	0.02–0.25	–	
October–November	8	191 ± 29	147–240	0.18 ± 0.08	0.02–0.27	–	
Females							
June	9	269 ± 16	236–290	1.25 ± 0.57	0.54–1.91	4506 ± 1690	1176–7329
July	4	259 ± 18	255–275	2.29 ± 1.51	1.12–4.48	5617 ± 1719	3831–7777
August	14	252 ± 20	214–273	1.51 ± 0.81	0.36–2.98	5974 ± 1951	3245–9783
September	4	235 ± 46	204–304	1.87 ± 0.48	1.39–2.54	5603 ± 1694	4233–8078

oocytes mostly between 1 and 2 mm diameter (Fig. 2*B*, *C*). Ovaries with a GSI greater than 1.0 were covered with external blood vessels and oocytes were visible through the ovary wall. Table 1 shows the GSI and number of oocytes present in the ovaries of 31 nurseryfish collected in the dry season during a 103-day period in 2001. The average number of oocytes in each female was 5453 (range 1176–9783). These specimens averaged 255 mm SL (204–304 mm), and the average GSI was 1.58 (0.36–4.48). A running-ripe 269-mm SL female was caught on 12 July in fresh water at 25°C. Eggs freely flowing from this female were 2.1–2.5 mm in diameter. A count of all macroscopic oocytes in both ovaries totaled 4745, and the GSI was 4.48 (Fig. 2*C*).

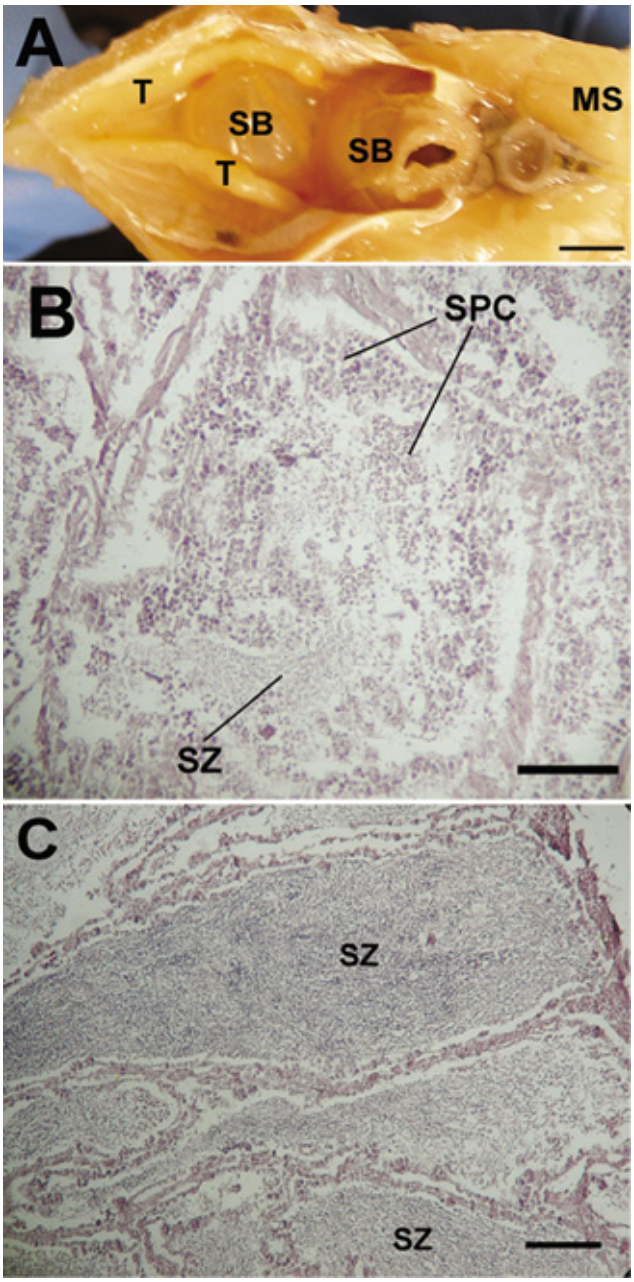

Fig. 1. Gross and histological anatomy of nurseryfish testes. (*A*) Ventral view of testes in body cavity in nurseryfish male. Male TMB03-6#2 (17 October), SL =198 mm, GSI = 0.18. TS – testes, SB – swim bladder, MS – muscle. Scale bar = 5 mm. (*B*) Section of testis at maturing development stage. Lobule with spermatocysts (SPC) and spermatozoa (SZ). (*C*) Section of testis at mature development stage. Lobules filled with spermatozoa (SZ). Scale bar = 100 μm for *B* and *C*.

Histology

Histological examination showed that nurseryfish testes have a lobular structure, which is typical for fish of the order Perciformes (Nagahama 1983; Parenti and Grier 2004). The investigated testes were at either maturing or mature development stage. In maturing testes (Fig. 1*B*) the lobules contained spermatocysts with male sex cells at different stages (primary and secondary spermatocytes, and spermatids); lobule lumens contained some amount of spermatozoa. In mature testes (Fig. 1*C*) the lumens of lobules were filled with spermatozoa. Testes at obviously spent (post-spawning) developmental stage have not been identified. However, from August some maturing testes had signs (semi-empty lobular lumens and some amount of cellular debris in lumens) of probable previous spawning.

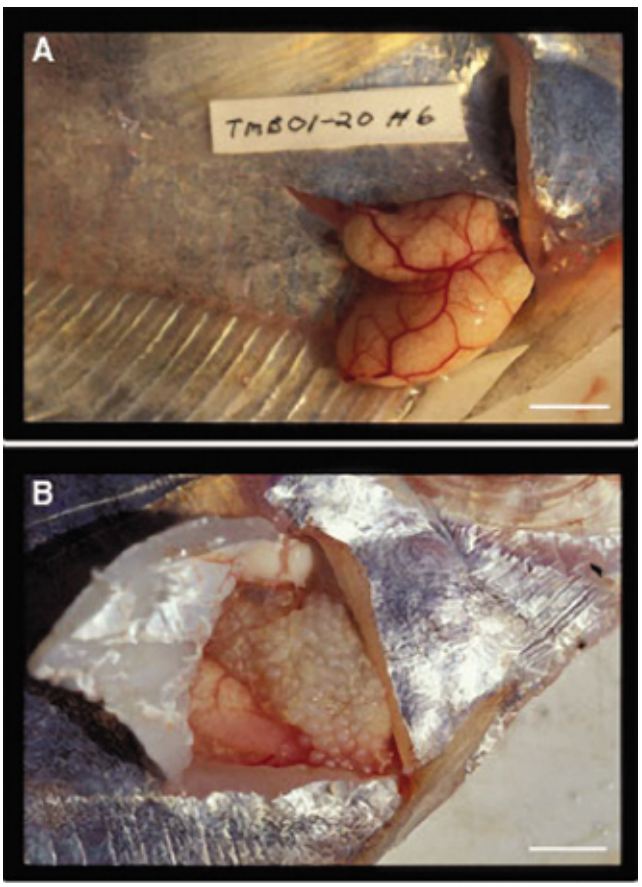

Fig. 2. (*A*) Left and right ovaries freshly removed from a 271-mm SL, 279-gm female with a GSI of 1.53 collected on 3 August 2001 from Marrakai Creek. (*B*) Right ovary of a running-ripe 269-mm SL, 294-gm female with a GSI of 4.48 collected on 12 July 2001 from the Adelaide River. Histology of this ovary is shown in Fig. 3*C*. Scale bar = 15 mm.

Histological sections of nurseryfish ovaries collected from June to September showed several females from early June with only primary growth and cortical alveolar-stage oocytes (70% PG, 30% CA) (Fig. 3*A*), signaling the onset of reproductive activity. These females had GSI values below 0.5. Most females collected between June and September showed mid- to late-stage vitellogenic oocytes (50% V, 40% PG, 10% CA) (Fig. 3*B*), indicating their ability to be reproductively active. These females with high proportions of vitellogenic oocytes had GSI values from ~1.1 to 3.0. We captured only one female nurseryfish (12 July 2001, GSI = 4.48) that showed gross and histological evidence of maturity and ovulation (Figs 2*B*, 3*C*). These large oocytes contained coalesced yolk and had been ovulated (Fig. 3*C*). Berra and Neira (2003) reported the study area as fresh water so hydration was not part of this species' oocyte development. This ovary had a large number of fresh postovulatory follicles (Fig. 3*C*) indicative of very recent ovulation. For a short time following ovulation these follicles remain in the ovary before being reabsorbed.

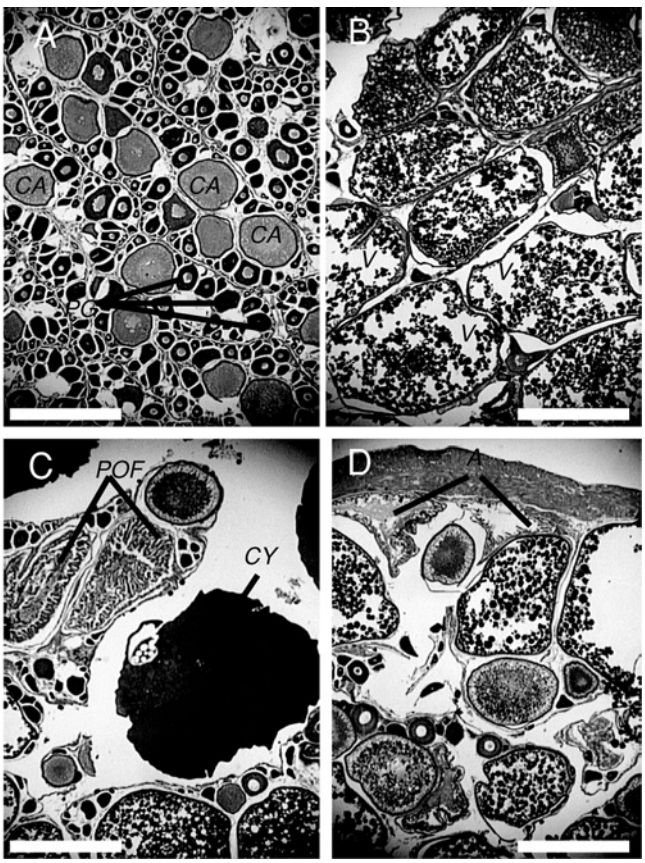

Fig. 3. Photomicrographs of *Kurtus gulliveri* ovary sections. (*A*) TMB01-10#9 (1 June), 236-mm SL female, GSI = 0.19, ovary showing primary growth (PG) and cortical alveoli (CA) stage oocytes (bar = 200 μm). (*B*) TMB01-12#1 (15 June), 290-mm SL female, GSI = 1.07, ovary having mostly vitellogenic (V) stage oocytes (bar = 600 μm). (*C*) TMB01-17 (12 July), 269-mm SL female, GSI = 4.48, showing terminal-stage oocyte with coalesced yolk (CY) and postovulatory follicles (POF) (bar = 600 μm). The gross morphology of this ovary is shown in Fig. 3. (*D*) TMB01-26#4 (11 September), 215-mm SL female, GSI = 1.78, ovary showing all oocyte stages, some undergoing atresia (A) (bar = 600 μm).

Several histological sections from September showed late-stage vitellogenic oocytes undergoing atresia (the breakdown of cellular structure) (Fig. 3*D*), indicating that in 2001 the reproductive season extended at least until the end of September; however, ovarian samples were not collected during October or November.

Spawning season and larval nurseryfish.

Fig. 4 shows the number and size of larval nurseryfish collected in plankton tows from 26 May through 15 December over the years 2001–06.

Discussion

A χ^2 test indicated that the skewed sex ratio is highly significant ($P < 0.01$). The deviation from a 50/50 sex ratio in favour of males may result from increased vulnerability of males to gill netting due to the presence of the supraoccipital hook by which they were often caught. Unknown sexual differences related to behaviour of spawning females, habitat preference, social interactions, seasonal movements, etc. could affect the sex ratio.

Hickling and Rutenberg (1936), Hunter and Goldberg (1980), Hunter *et al.* (1985), Hunter and Macewicz (1985) and others have discussed the details of multiple or batch spawning strategies in fishes in which the GSI is small and the spawning season prolonged. This is in contrast to an alternative strategy of isochronal spawning (Render *et al.* 1995) where GSI can be very large and spawning season very short. The Australian grayling, *Prototroctes maraena*, is a classic example of an isochronal species with a mature GSI of 28 (female) and 14 (male) during a two-week spawning period (Berra 1984, 1987). Burt *et al.* (1988) discussed hypothetical advantages of batch spawning as a way of increasing total fecundity in cases where body size might limit the number of mature oocytes that a female could hold at any one time. Batch spawning may also provide a strategy to ensure at least some reproductive success under variable environmental conditions.

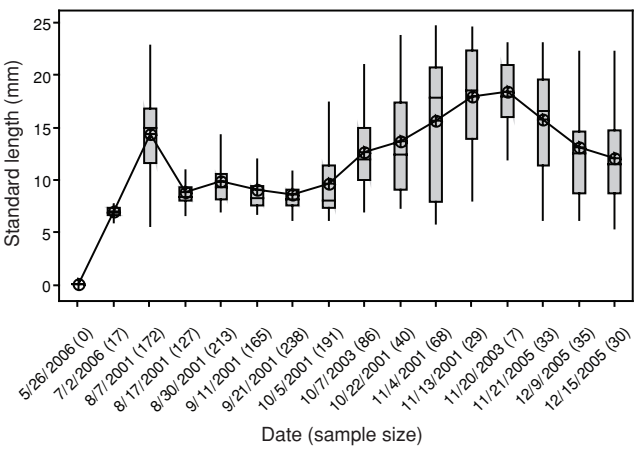

Fig. 4. Standard length (mm) of larval nurseryfish and sample size collected on various dates (month/day/year) over a five-year period. Means are indicated by circles. Medians are shown by horizontal lines and ranges are indicated by vertical lines. The box plots represent the middle 50% of lengths with 25% above and 25% below it.

On the basis of our examination of histological ovarian sections, the reproductive strategy of the nurseryfish may be interpreted as batch spawners. This is supported by the fact that ovaries that recently ovulated contained late-stage vitellogenetic oocytes along with postovulatory follicles. These vitellogenic oocytes are the possible resource for the next batches of the same spawning season. The long reproductive season (June–November) is similar to that of many batch-spawning species. The presence of vitellogenic oocytes between June and September suggests that oocytes are continually recruited into vitellogenesis. Yolk coalesence would be followed shortly by ovulation of a portion of the vitellogenic oocytes carried by the female. Only a single female was found with ovulated oocytes with coalesced yolk. Thompson (1997) also commented on how few females with ovulated oocytes were present in his study, suggesting that this may be a short-timed phenomenon. This situation in nurseryfish might be analogous to observations by Washio *et al.* (1993), where no mudskippers were found with terminal stage oocytes; they suggested that this final maturation took place as reproductively active adults moved to their actual spawning location.

Berra and Neira (2003) reported on three egg masses taken from a gill net in Marrakai Creek on 21 September 2001. They estimated the number of eggs in each mass by gravimetric methods at 900, 1200 and 1300 respectively. The actual count of the eggs in the largest mass was 1239, or 95.3% of the estimated 1300 eggs. Egg masses are illustrated in Berra (2003) and Berra *et al.* (2004). Egg diameter was ~2.5 mm (Berra and Neira 2003). The size of an ovulated egg mass (900–1300 eggs) versus the average number of oocytes in a female (5453: Table 1) is consistent with a batch-spawning strategy. Ovaries with over 5000 oocytes and a GSI greater than 1.0 were found in specimens collected from 1 June through 11 September 2001 in fresh water that ranged from 23 to 29°C. On the basis of their size, these females were most likely at least two years old (Berra and Aday 2004). This reflects the dry season (June–November) spawning period deduced from the frequency of occurrence and size of planktonic larvae (see Fig. 4; Berra and Neira 2003). Although there will be slight differences from year to year in the timing of the wet/dry seasons, Fig. 4 clearly indicates that some spawning occurred in June because a few larvae were present in early July. No larval nurseryfish were caught in late May, indicating that spawning had not yet occurred. The size of the larvae peaked in early August and again in mid-November (Fig. 4). The data of Fig. 4 clearly demonstrate continuous spawning from June to November since small larvae (5–7 mm) were detected in each sample from the beginning of July to mid-December. The number of larvae caught was greatest in August and September. Temperature and other environmental variables may account for variation in samples from different years.

The data on dynamics of GSI in males and histological analysis of testes do not show a seasonal cycle. This may reflect a situation in which each male spawns several times during the spawning season (June–November).

Berra *et al.* (2004) hypothesised that eggs were deposited on the male's hook before fertilisation, and then the male released a cloud of sperm and swam though it to fertilise eggs. The data of the present study do not support that hypothesis. Testes of mature nurseryfish are relatively small. The maximum observed value of GSI was 0.27. Testes with very small relative sizes (GSI 0.02–0.07) were maturing and contained some agglomeration of spermatozoa in the lumens of lobules. Relatively small testes presume small amounts of released sperm. Fishes with low intensity of sperm competition during spawning tend to be pair spawners (Stockley *et al.* 1997). It was also noted by Billard and Cosson (1990) that fishes that spawn in open water release large amounts of sperm and have large testes relative to their body size. On the basis of these considerations we suggest that nurseryfish spawn in pairs and males do not widely broadcast sperm into the environment but fertilise eggs by close contact and that the eggs somehow become attached to the male's hook after fertilisation.

It is highly improbable that eggs are attached to the hook before fertilisation because of the characteristics of teleost eggs immediately after release. The contact of eggs with water induces the process of activation that results in cortical reaction, formation of perivitelline space and hardening of eggshell (Ginsburg 1968; Kunz 2004). In most freshwater teleosts the process of activation lasts only several minutes and eggs then lose the ability to be fertilised (Ginsburg 1968). In order to be attached to the male's hook the mass of unfertilised eggs should require some degree of toughness and time. During this period the eggs may lose the ability to be fertilised. Therefore we suggest that the eggs are fertilised very quickly after their release by the female and then attach to the male's hook.

Smith and Wheeler (2006) indicated that *K. gulliveri* is the sister group to a clade consisting of oral-incubating cardinalfish (Apogonidae) and gobioids. Vagelli (1999) observed spawning Banggaii cardinalfishes (*Pterapogon kauderni*) and videotaped the male pulling an egg mass from the female's vent with his mouth after a period of fertilisation that occurred immediately after egg release. This may shed some light on how nurseryfish males acquire the egg mass on the supraoccipital hook. We can speculate that after egg release and rapid fertilisation, instead of grasping and pulling the eggs from the female's vent with his mouth, as in *P. kauderni*, the male may push the egg mass with his hook, to which the egg mass adheres. This may be assisted by the presence of neurosensory cells reported from the epidermis on the dorsal surface of the male's hook (Berra and Humphrey 2002). How the eggs are fertilised and how the egg mass becomes attached to the male's hook will be revealed only when courtship and spawning can be witnessed in captivity. So far, this has not been possible. DNA paternity analysis is currently underway and will eventually demonstrate whether the male is the father of the embryos he is carrying and if multiple paternity is involved.

We realise that some details of the reproduction of nurseryfish will require additional study. For example, is there a correlation between spawning and tidal movement? Because of the extreme tidal fluctuation we were forced to sample on the rising tide during neap tide weeks. This is the time of relatively less turbidity and water movement. We have few collections during outgoing or spring tides because of the physical difficulty of using gill nets under these extreme conditions. What is the effect of salinity on spawning? We could work in only one locality, and we chose the fresh waters of Marrakai Creek. We do not know what, if any, spawning was occurring downstream in brackish waters.

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