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Seasonal growth and reproduction of *Rasbora rubrodorsalis*, a small-sized cyprinid fish from central Laos (Teleostei: Cyprinidae)

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Growth, sexual maturation and feeding habits were investigated in *Rasbora rubrodorsalis*, collected in the inland hilly region of Vientiane Province, Central Laos from November 2011 to October 2012. Gonadal sexual dimorphism was identifiable in all specimens. Throughout the sampling period, a notably female-biased sex ratio (proportions of males : females = 0.43 : 1) was observed. Ages of fish, based on otolith daily increment counts, were 43–116 days during the warmer period (WP, March to October) and 44–121 days during the colder period (CP, November to February) for females (13.1–31.1 mm SL), 35–92 (WP) and 48–84 (CP) days for males (12.0–25.5 mm SL). Growth patterns (regressed by logistic growth equations) in the WP and CP revealed faster growth of both females and males in the WP than in the CP, females growing larger and living longer than males. The size of females at sexual maturation was estimated as greater than ca. 20 mm SL in the WP and ca. 23.0 mm SL in the CP. The age at reproductive size and maximum ages recorded showed *R. rubrodorsalis* to be progenetic with a short lifespan, allowing approximately three successive generations per year. The ratio of mature to immature females was greater during the WP, being clearly correlated with the extension of day length. The ratio of male occurrence also tended to increase with increasing day length during the WP. Feeding incidence rates (%) were high (> 90 % throughout the sampling period), gut contents comprising mainly unidentifiable detritus followed by zooplankton, aquatic/terrestrial insects, algae and insect eggs, indicating that *R. rubrodorsalis* has an omnivorous feeding habit.

Introduction

Rasbora rubrodorsalis is a small-sized cyprinid fish widely distributed on the Indochinese peninsula, and reported as occurring in Laos, Thailand, Vietnam and Cambodia (Kottelat, 2001). Fourteen other species of *Rasbora* are known from Laos, *R. rubrodorsalis* being distinguishable from them owing to its small size (33 mm maximum size; Kottelat, 2001) and clear reddish dorsal and caudal fin bases in life (Vidthayanon, 2008). The species has only been described recently (Donoso-Büchner & Schmidt, 1997), and information on its biology is still limited except for recent phylogenetic studies (Fang et al., 2009; Liao et al., 2010). The species is often abundant in streams,

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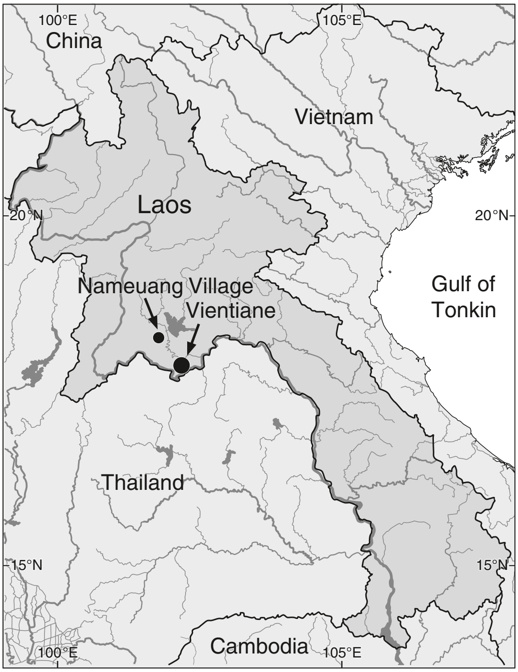

Fig. 1. Laos; arrows indicate collection sites of *Rasbora rubrodorsalis*.

agricultural canals and swamps in plain and semi-mountainous areas, largely year-round. Accordingly, it is an important food fish in rural inland communities (often in a fermented form).

In central Laos, the rainy season extends from June to October and the dry season from November to May, the temperatures generally incerasing during March and May and remaining high until October (relatively warmer period), but declining from November and remaining low until February (relatively colder period). Despite such climatic variations, the population of *R. rubrodorsalis*, characterized by random size composition (< 15 mm SL to > 30 mm SL) persists throughout the year in the same areas (Morioka, unpubl. data), suggesting a short life span and multiple generations within a year, as reported in sympatric small-sized fishes, e. g., *Brachygobius mekongensis* (Gobiidae, see Morioka & Sano, 2009) and *Parambassis siamensis* (Ambasidae, see Okutsu et al., 2011).

The above notwithstanding, the establishment and expanding distributions of introduced fishes (approx. 20 species, including tilapia *Oreochromis* spp. and the Chinese carp *Hypophthalmichthys molitrix*) in the Mekong River basin (Phillips, 2002; Welcome & Vidthayanon, 2003; Hung et al., 2011), as well as environmental changes (e. g. urbanization and land exploitation for agriculture), have become a source of concern due to the decline of native/endemic fish diversity and stock levels. Accordingly, there is increasing necessity for biological research on indigenous fishes, including *R. rubrodorsalis*.

Life history information, including growth, sexual development, spawning season and generation time, is a basic requirement for biological investigations of fishes. Daily age determination in teleost fishes using otolith increments has progressed since Pannella (1971), the method having since been broadly applied to age determinations, estimations of growth patterns, spawning season and life span. Among the otolith elements (i. e. sagitta, lapillus and asteriscus), the sagitta and lapillus are useful for daily age determination, although the latter is more suitable than the former in cyprinids due to the structural fragility of the sagitta (Bestgen & Bundy, 1998; Morioka & Matsumoto, 2003). In addition, a combined analysis of daily age and gonadal development can provide further biological insights.

Accordingly, this study analyzed growth, in addition to size and timing at sexual maturity, in *R. rubrodorsalis* based on otolith daily increments and observations of gonads. Examinations of gut contents provided information on feeding habit and food supply at the sample collection sites.

Materials and methods

Characteristics of fish sampling sites. Fish sampling was conducted monthly from November 2011 to October 2012 in the Napathew River, Nameuang Village, Feuang District, Vientiane Province, Laos (Fig. 1), the river flowing from Napathew Reservoir (18°31'18.38" N 102°01' 34.38" E) located in the inland hilly area. Samples were collected at three different sites along the river: site A (18°31'16.38" N 102°01'31.25" E) – the upper zone near the reservoir outlet, characterized by a slow flowing current and < 20 cm depth, the substrates comprising sand, gravel and plant material (mostly decayed); site B (18°31'11.98" N, 102°01'25.90" E) – the mid zone (below a small waterfall), characterized by a slow flowing current and < 20 cm depth except under the water fall (ca. 60 cm depth), with similar substrate to A; site C (18°31'17.39" N 102°01'20.19" E) – the lowest zone near established rice paddies, < 50 cm depth, with characterized by a current slower than at A and B, and the substrate comprising fine sand, sparse gravel and plant material. At all sites, the sides of the river were covered by terrestrial vegetation. From these sites, 30 to 50 specimens were collected each month using a seine net (5 mm mesh, 10 m width, 1 m height). Fish were then preserved in 70 % ethanol soon after capture.

Sex identification and gonad somatic index of females. After standard lengths (SL, mm) and body weight (BW, g) of ethanol-preserved fish were measured (the former with a dial caliper to the nearest 0.1 mm, the latter with a precision balance to the nearest 0.001 g), all specimens (12.0–31.1 mm SL, 0.059–0.462 g, n = 417) were dissected under a stereoscopic microscope (40–80 × magnification) for gonad extraction; the gonads were observed under an optical microscope with transmitted light (100–400 × magnification) for sex determination (identification of ovaries and testes) and the ovary weight were measured for gonadosomatic index (GSI: ovary weight/body weight × 100 %) of females. In addition, oocyte diameters were measured (with a stereoscopic microscope to the nearest 0.01 mm) in variable sized randomly selected females from different periods (50 oocytes per fish, 23 females 14.8–27.0 mm SL, collected in December 2011, January, April and May 2012). Both spherical- and oval- shaped oocytes were present in the ovaries, the maximum axis being measured in the latter. The male : female sex ratios (proportion of males : females) and male occurrence ratios (number of males/number of all specimens × 100 %) were noted monthly.

Gut content and otolith increment observations. After gonad observations, the contents of the anterior portion of the gut were noted, since cyprinids lack a distinctive stomach. Subsequently, the lapilli were removed (n = 392) under a dissecting microscope and mounted in epoxy resin on glass slides. Each lapillus was identified by its fan-shaped form, distinguishable from the sagitta (thin plate-like structure) and the asteriscus (ambiguous core portion occasionally with jagged margin) (Morioka & Matsumoto, 2003, 2007). The lapilli were subsequently ground using sandpaper (#1500) and lapping films (6 and 9 µm mesh), some ground surfaces later being etched by 0.1 N hydrochloric acid to emphasize increment contrast. Maximum lapillus radii (µm) were measured, and increments were counted under an optical microscope with transmitted light (200–400 × magnification) to estimate age and hatch date. Although daily periodicity of increment deposition in otoliths has not yet been validated in *R. rubrodorsalis*, it has been demonstrated in many other cyprinids (Bestgen & Bundy, 1998; Morioka & Matsumoto, 2003; Durham & Wilde, 2008), as well as in a number of other fish species (Campana & Neilson, 1985). Hence, the otolith increments are considered here to have been formed on a daily basis in *R. rubrodorsalis*.

The relationship between sexual maturation (females, based on GSI) and growth patterns of *R. rubrodorsalis* relative to seasonal environmental changes, was examined from the following two perspectives: one being the rainy and dry seasons in Laos, the former generally occurring from June to October (RS) and the latter from November to May (DS), and the other being the warmer and colder periods, based on the trends in water temperature fluctuations throughout the year, the former from March to October (WP) during which the water temperature becomes relatively high (occasionally exceeding 30 °C), and the latter from November to February (CP) during which the water temperature is relatively low (occasionally less than 20 °C). Monthly average day-length information was accessed from "timeanddate.com (http://www.timeanddate.com/)", i. e., 677.43 min. in November and 646.65 min. in December 2011, 655.29 min. in January, 684.24 min. in February, 721.90 min. in March, 760.77 min. in April, 793.03 min. in May, 808.90 min. in June, 800.74 min. in July, 772.55 min. in August, 735.43 min. in September and 716.10 min. in October 2012, for comparisons between female sexual maturation and day-length.

Results

Fish size and age. From the overall samples (n = 417), 291 females and 126 males were observed, the male : female sex ratio being strongly female-biased (0.43 : 1). The size range of females and males were 13.1–31.1 (mean ± SD: 22.56 ± 4.64) mm SL and 12.0–25.5 (18.80 ± 2.88) mm SL, respectively, indicating that females grow larger than males (size sexual dimorphism) (Fig. 2). Otoliths of 392 specimens (270 females and 122 males) were observable with daily increments

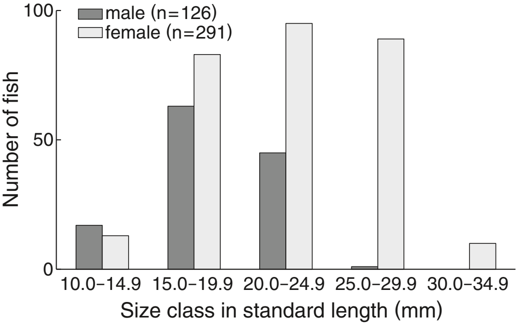

Fig. 2. Frequency distributions of standard lengths of *Rasbora rubrodorsalis* by sex.

being clearly visible in the lapilli (Fig. 3). Increment numbers varied from 43 to 121 and 35 to 92 in females and males, respectively. Hatch dates, estimated from the number of lapillus increments, were observed throughout the year, indicating year-round breeding of the species.

Seasonal growth comparisons based on otolith increment analyses and otolith size. Growths of females and males hatched/grown in the rainy (RS) and dry seasons (DS) were regressed by the following logistic formulae, where t and Lt denoted the age in days and size at age t-days, respectively;

Females:
$Lt = 28.93/(1 + \exp(-0.047(t - 38.98))$
($R^2 = 0.88$, $n = 139$) (RS),
$Lt = 29.15/(1 + \exp(-0.048(t - 43.23))$
($R^2 = 0.79$, $n = 131$) (DS),

Males:
$Lt = 22.39/(1 + \exp(-0.057(t - 27.63))$
($R^2 = 0.96$, $n = 48$) (RS),
$Lt = 24.17/(1 + \exp(-0.050(t - 32.97))$
($R^2 = 0.88$, $n = 74$) (DS).

These formulae indicated that the growth of both females and males did not differ significantly between RS and DS (ANOVA, $p > 0.05$). For contrast, growth of females and males hatched/grown in the WP and CP were regressed by the following logistic formulae (Figs. 4a,b);

Females:
$Lt = 29.38/(1 + \exp(-0.050(t - 38.40))$
($R^2 = 0.82$, $n = 185$) (WP),
$Lt = 29.22/(1 + \exp(-0.043(t - 48.37))$
($R^2 = 0.87$, $n = 85$) (CP),

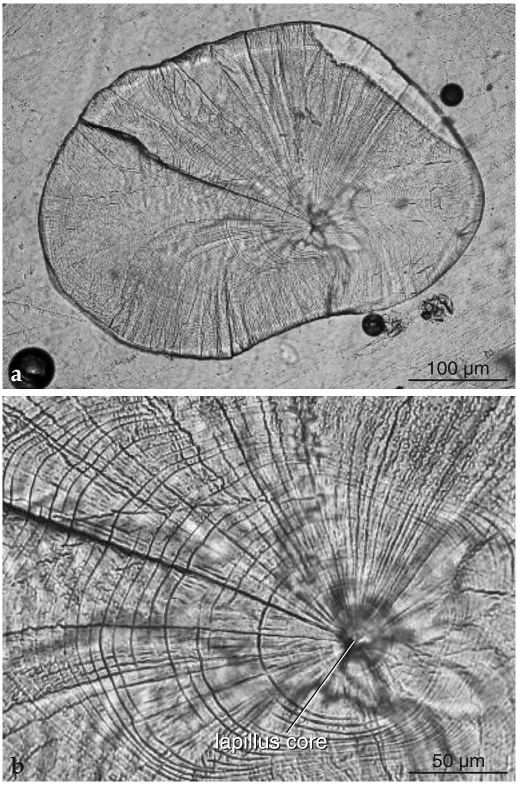

Fig. 3. Otolith (lapillus) of *Rasbora rubrodorsalis* (25.5 mm SL). **a,** entire lapillus; **b,** core portion of lapillus.

Males:
$Lt = 24.91/(1 + \exp(-0.054(t - 31.61))$
($R^2 = 0.92$, $n = 80$) (WP),
$Lt = 31.28/(1 + \exp(-0.036(t - 54.85))$
($R^2 = 0.95$, $n = 42$) (CP).

These formulae indicated that both females and males grew significantly faster during the WP than during the CP (ANOVA, $p < 0.01$). The two growth comparisons between the RS and DS, and between the WP and CP, suggested that the growth of *R. rubrodorsalis* was more dependent on seasonal temperature changes than seasonal changes in precipitation. In addition, relative growth ($RG = L_{T+1} - L_T$, mm) obtained from the logistic formulae for each sex in the WP and CP, illustrated that growth was accelerated over ca. 40 days in the WP and 50 days in the CP for females, and over 30 and 50 days for males respectively, subsequently slowing down for both the sexes and periods (Figs. 4a',b').

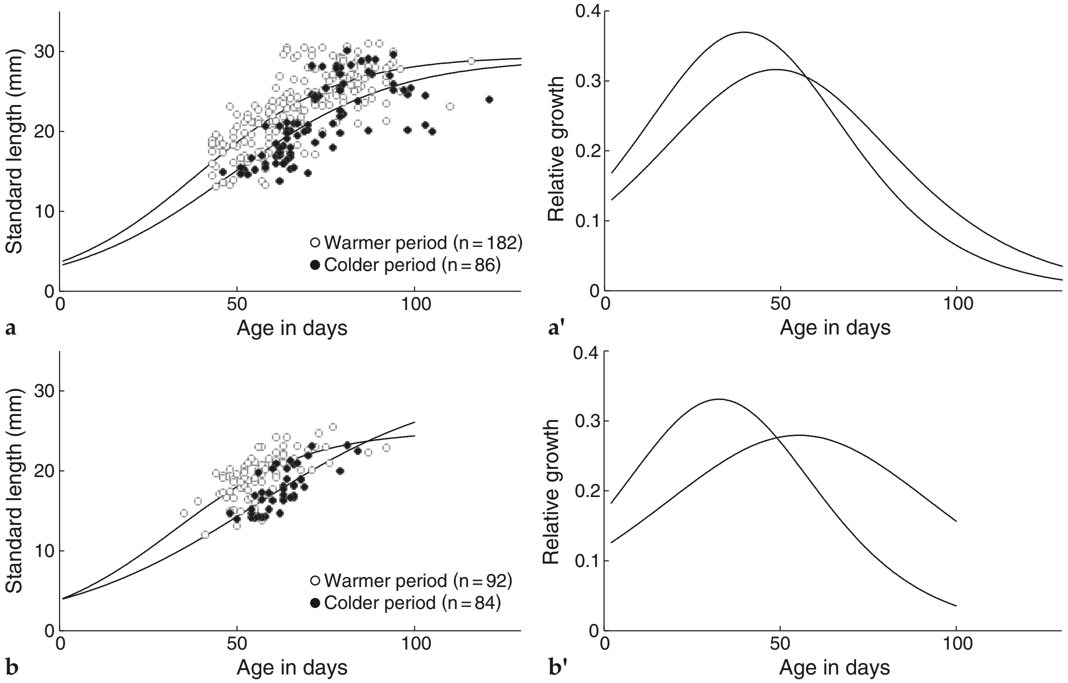

Fig. 4. Comparisons of growth patterns and relative growths of *Rasbora rubrodorsalis*. **a, a'**, females; **b, b'**, males. **Open** and **closed circles** in **a** and **b**, fish hatched in warmer and colder periods, respectively. **Solid** and **dotted lines** in **a'** and **b'**, fish hatched in warmer and colder periods, respectively.

Gonadosomatic index of females, mature female occurrence and male occurrence ratios. The gonadosomatic index (GSI) of all females varied from 0.28 to 16.9 % (13.1–31.1 mm SL, n = 291). The relationship between the GSI and SL of females during the WP increased from <1 % to approx. 10 % in females of approx. 15.0 to 20 mm SL and became more or less constant between 11–16 % in females larger than approx. 20 mm SL, although females larger than 20 mm SL with <11 % of GSI were noted (48.9 %; Fig. 5). In the CP, the GSI increased from <1 % to 10 % in fe-

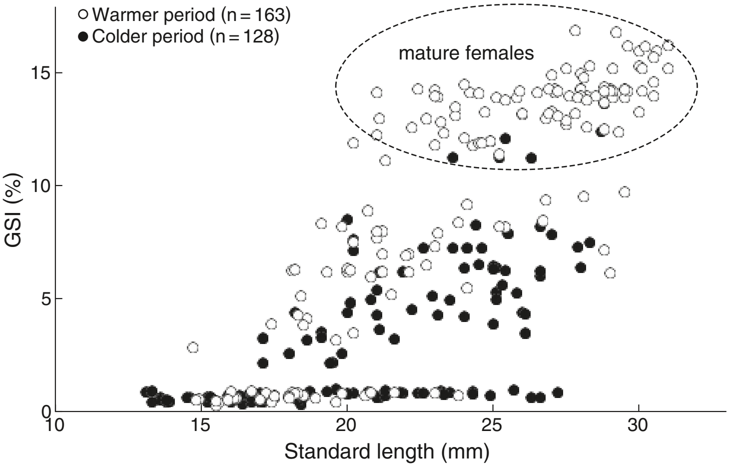

Fig. 5. Relationship between standard length (mm) and gonadosomatic index in female *Rasbora rubrodorsalis*.

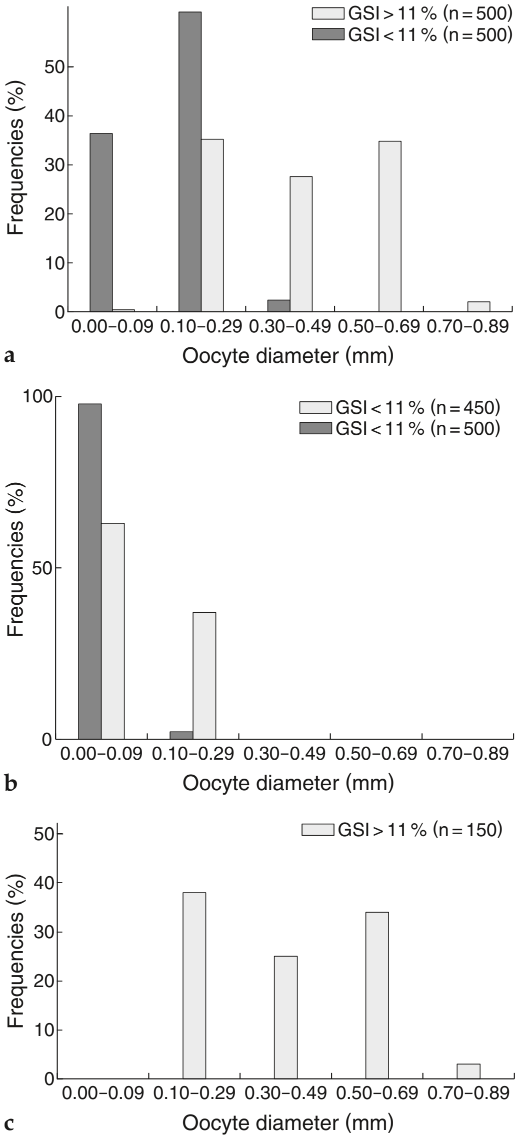

Fig. 6. Frequency distributions of oocyte diameter (mm) in female *Rasbora rubrodorsalis*. **a,** fish collected in warmer period [■, 5 smaller specimens (14.8–19.8 mm SL) with GSI < 11%; □, 5 larger specimens (21.0–26.5 mm SL) with GSI > 11%]; **b,** fish collected in colder period [■, 5 small specimens (15.0–20.8 mm SL) with GSI < 11%; □, 5 larger specimens (23.7–27.0 mm SL) with GSI < 11%]; **c,** fish collected in colder period (3 females of 23.5–26.8 mm SL with GSI > 11%).

males of approx. 17.0 to 20 mm SL, reaching greater than 11 % in several females larger than approx. 23 mm SL, although a large proportion of immature females larger than 23 mm SL (87.2 %; Fig. 5) were encountered. Accordingly, we considered that the females with GSI > 11 % were in sexual maturation phase, the size at sexual maturation being approx. 20 mm SL in the WP and approx. 23 mm SL in the CP. Based on this categorization, sexually mature females were observed throughout most of the 12-month sampling period (except January 2012) (Fig. 7a), indicating that *R. rubrodorsalis* breeds year round. During the WP, oocyte diameters were mostly smaller than 0.3 mm in females < 20 mm SL with GSI < 11 %, but approx. 40 % of oocytes were larger than 0.5 mm in females > 20.0 mm SL with GSI > 11 % (Fig. 6a). In contrast, during the CP, oocyte diameters were smaller than 0.3 mm in most females regardless of size (Fig. 6b), although a similar size distribution of oocytes to that in the WP was observed in a few females (three females in November, two in December 2011 and one in February 2012) (Fig. 6c).

In addition to growth patterns, the mature female occurrence ratios (number of mature females / total number of females × 100 %, MFO) between the WP and CP, and the RS and DS were also compared. The MFO fluctuated monthly (0–88.9 %), and comparisons of the MFO averages between the WP and CP indicating that the ratio was significantly higher in the WP (Table 1; Fig. 7a). By contrast, a comparison of MFOs between the RS and DS showed no significant difference, suggesting that sexual maturation of females was more dependent on temperature than on seasonal precipitation. In addition, the relationship between the average monthly day-length (ADL) and the MFO was regressed by the following linear regression; $\mathrm{MFO} = 0.53\,\mathrm{ADL} - 348.60$ ($R^2 = 0.90$, $n = 12$) (Fig. 7b), which indicated that the sexual maturation of females progressed with seasonal extension of day length.

A comparison of monthly male occurrence ratios (number of males / number of females × 100%, MOR) in the WP and CP showed no significant differences similarly between RS and DS (Fig. 8a), although the average MOR was higher during the WP than the CP (32.1 % and 27.0 %, respectively. However, the MOR was also tended to increase as an extension of ADL during the WP, as indicated by the following linear regression $\mathrm{MOR} = 0.43\,\mathrm{DL} - 277.79$ ($R^2 = 0.41$, $n = 8$), although no correlation was observed during the CP (Fig. 8b).

Gut contents and feeding habit. High feeding incidence rates (93.3–100.0 % throughout the sampling period) were observed. Gut contents most often included unidentifiable detritus (70.9 %, 296 specimens of 417) followed by zooplankton (copepods, rotifers and daphniids) (70.5 %, 294 of 417), aquatic/terrestrial insects (47.2 %, 197 of 417), algae (diatoms and blue-green algae) (25.9 %, 108 of 417) and insect eggs (21.1 %, 88 of 417; Fig. 9). Remarkable high occurrence frequencies of detritus and zooplankton suggested these two are the most important food items in the collection sites; the presence of algae and material likely of plant origin in the unidentifiable detritus indicated that *R. rubrodorsalis* is omnivorous.

Discussion

In tropical and subtropical regions with distinct dry and rainy seasons, such as in Laos, rapid water level fluctuations associated with the onset of the rainy season are known to trigger fish breeding (Baily et al., 2008), as has been observed in *Pangasianodon hypophthalmus* (Pangasiidae, see Legendre et al., 1998), *Clarias gariepinus* (Clariidae, see Van Del Waar, 1998), *Thynnichthys thynnoides* and *Labeo cylindricus* (Cyprinidae, see Ali & Kadir, 1996 and Weyl & Booth, 1999). Breeding in fishes that is stimulated by an increase in temperature rather than rainfall has also been reported by Munro (1990; *Alestes baremoze*, *Systomus tetrazona*). At the collection sites for the present study, water temperatures were generally warmest during March to May, and the rainy season predominated from June to October with limited rainfall at other times (H. Ikeura, unpubl. data). Based on the monthly changes in the MFO (Fig. 7a), the breeding of *R. rubrodorsalis* is considered to be more likely during the WP. Because the greatest proportion of mature females was observed in April 2012, with this proportion subsequently decreasing even during the rainy season (Fig. 7a), the breeding of *R. rubrodorsalis* is likely to be more dependent upon the seasonal increase in temperature. In addition, a clear correlation between the MFO and the day length (Fig. 7b) during the WP indicated that the sexual maturation of females is also strongly associated with an extension of day length as has been reported in other fish species (Sundararaj & Sehgal, 1970, *Heteropneustes fossilis*; Burns, 1985, *Poeciliopsis gracilis*, *Poecilia sphenops*).

Pannella (1971) and Brothers et al. (1976) reported that otolith increments from small-bodied fishes were nearly always deposited daily. In addition, subsequent studies (Bestgen & Bundy, 1998; Morioka & Matsumoto, 2003; Durham & Wilde, 2008) have illustrated daily periodicity of lapillus increments in cyprinids, suggesting that our assumption of the daily deposition of increments in the lapilli of *R. rubrodorsalis* is reasonable.

The fish hatched/grown in the WP showed significantly faster growth and earlier sexual maturation (of females) than those from the CP (Fig. 4). This difference is probably attributable to seasonal water temperatures, since higher temperatures lead to both faster growth within a population (Morioka, 2002; Morioka & Kaunda, 2005) and earlier sexual maturation (Dotsu, 1982; Kon & Yoshino, 2003). Figure 4a', b' indicates that the relative growths of both sexes peaked at higher levels in the WP, with growth subsequently decreasing on approaching maximum size. Mature females (min. 20.2 mm SL in the WP, 23.6 mm SL in the CP) were observed soon after the onset of the slowdown in relative growth, probably due to the vitellogenesis of oocytes before sexual maturation. In addition, the maximum size of *R. rubrodorsalis* has been previously reported as 33 mm SL (Kottelat, 2001); this is consistent with our observations for the females in the present study (31.1 mm SL, Figs. 2, 4). However, the smaller maximum size of males observed here (25.5 mm SL) indicated that sexu-

Table 1. Statistical comparisons of mature female occurrence ratios (MFO) between warmer and colder periods (WP and CP), and the rainy and dry seasons (RS and DS). SD, significantly different; NS, not significantly different.

	warmer period	colder period	difference
average MFO (±SD) (%)	57.52 (±22.96)	4.57 (±3.37)	SD ($p < 0.01$)
	rainy season	dry season	
average MFO (±SD) (%)	56.94 (±21.79)	27.68 (±33.67)	NS

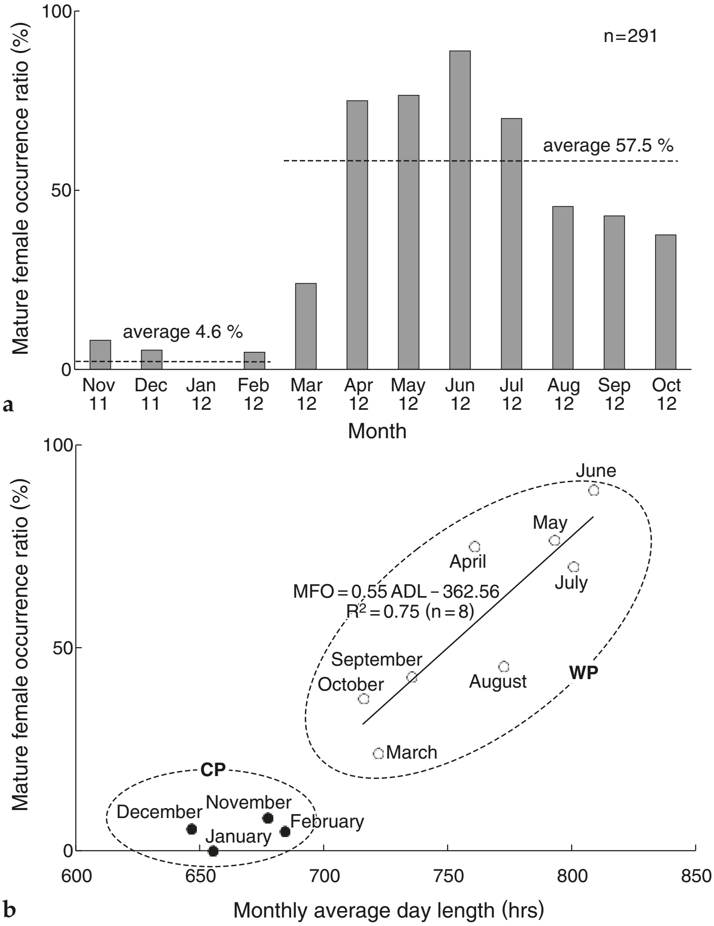

Fig. 7. Monthly changes in mature female occurrence ratio in *Rasbora rubrodorsalis* (**a**), and relationship between monthly average day-length and mature female occurrence ratio (**b**). **DS** and **RS**, dry and rainy seasons, respectively. **WP** and **CP**, warmer and colder periods, respectively.

al dimorphism in size occurs in this species. Pyron et al. (2013) discussed the mating systems in cyprinids on the basis of sexual size dimorphism and mating behavior of each species, and suggested that mating systems in cyprinids have evolved from ancestral taxa that were group spawners (with females the same size or larger than males) to pair spawning systems (in which males tended to be larger than females). Hence, *R. rubrodorsalis* is here postulated to be a group spawner (therefore belonging to a comparatively ancestral group within the Cyprinidae), although further investigations on breeding behavior in the species are necessary.

The maximum ages observed here were 121 days for females and 92 days for males (Figs. 4a,b), suggesting that *R. rubrodorsalis* is a short-lived species. In addition, the youngest age at sexual maturation in females was estimated as ca. 50 days and ca. 80 days in the WP and CP respectively, based on the sizes of the smallest mature females (20.2 mm SL, and 23.6 mm SL in the WP and CP respectively) and the growth models for females in each period (Figs. 4a,b). Furthermore, the occurrence of mature females throughout the year (except in January 2012; Fig. 7a), the year-round hatch dates estimated from otolith increment analysis, and variable sizes of fish sampled regardless of season are also strongly indicative of year-round breeding in *R. rubrodorsalis*. Multiple generation alternations (approximately three successive generations) may thus take place

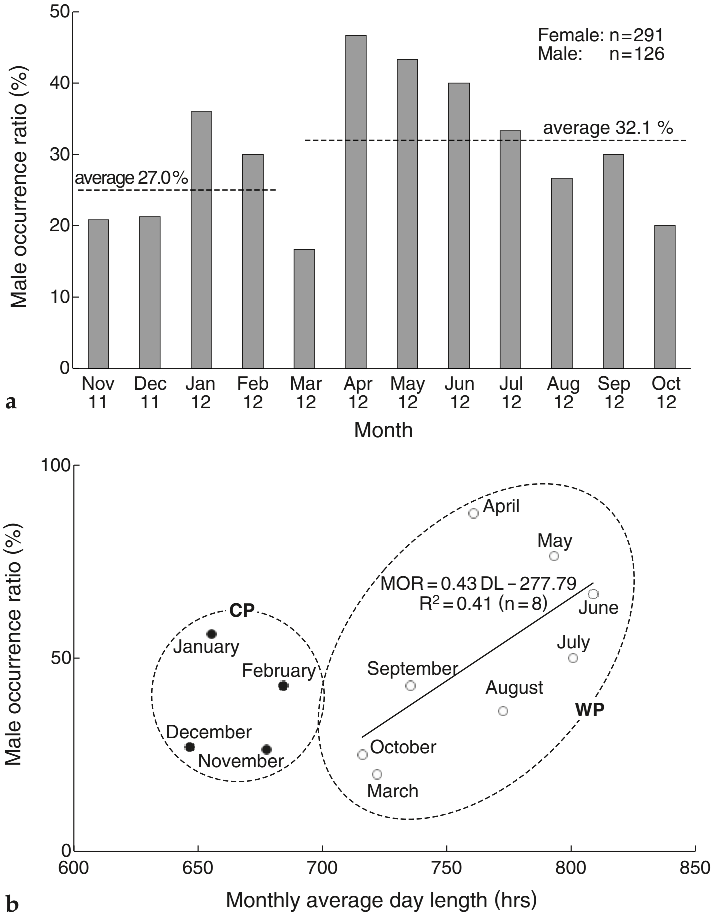

Fig. 8. Monthly changes in male occurrence ratio in *Rasbora rubrodorsalis* (**a**), and relationship between monthly average day-length and male occurrence ratio (**b**). **DS** and **RS**, dry and rainy seasons respectively. **WP** and **CP**, warmer and colder periods respectively.

within a 12-month period. Sizes and ages at sexual maturation estimated here (i. e. 20.2 mm SL and ca. 50 days in the WP, 23.6 mm SL and ca. 80 days in the CP) indicated that higher temperatures induced earlier sexual maturation at a smaller size. A similar phenomenon has been reported for other fishes (Dotsu, 1982, *Dasson trossulus* [now *Petroscites breviceps*, Blenniidae]; Kon & Yoshino, 2003, *Paedogobius kimurai* [Gobiidae]), and other animals (Berrigan & Charnov, 1994). In addition, small-sized oocytes observed in large females with high GSI over the year (Fig. 6) suggested that *R. rubrodorsalis* breeds repeatedly in the course of a lifetime, although further investigation is needed to verify this.

Our study also revealed an elevated MOR during the WP, with increasing day-length (Fig. 8b); this is consistent with previous studies indicating that high temperatures increased the proportions of males (Conover & Kynard, 1981, *Menidia menidia*; Hostache et al., 1995, *Hoplosternum littorale*; Baras et al., 2001, Cichlidae). It is well known that the temperature variation influences the sex ratios in different fish species (Ospina-Álvarez & Piferrer, 2007). In view of this information, seasonal temperature changes at the collection site and the year-round breeding of *R. rubrodorsalis* inferred here may lead to seasonal changes in MOR (= sex ratio), but this hypothesis awaits further confirmation.

Other short-lived fish species, including *Schindleria* spp. (Schindleriidae) (see Johnson &

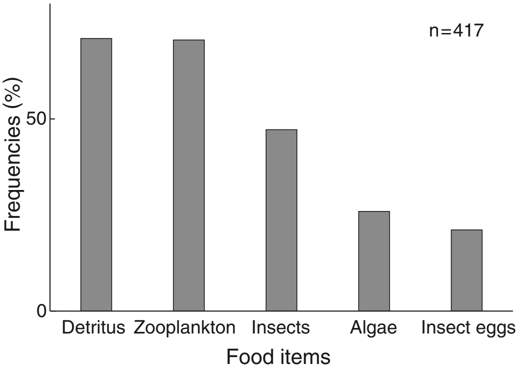

Fig. 9. Frequency distribution (%) of gut content items in *Rasbora rubrodorsalis*.

Brothers, 1993; Kon & Yoshino, 2002), *Crystallogobius linearis* (Gobiidae) (see Caputo et al., 2003), *Brachygobius mekongensis* (Gobiidae) (see Morioka & Sano, 2009), and *Parambassis siamensis* (Ambassidae) (see Okutsu et al., 2011) are all distributed in tropical and subtropical areas in which a stable warm temperature is generally assured. In addition, food availability (particularly the presence of zooplankton, generally comprising the main food organisms for small fishes) is also stable in the tropical and subtropical environments (Cushing, 1990). This is confirmed in the present study, in which individuals with considerable amounts of gut contents (often including zooplankton; Fig. 9) were very frequently encountered, indicating high feeding incidence rates year round. Such stable conditions, being positive for fast growth and early maturation, may have contributed to the evolution of the short-lived and progenetic characteristics of *R. rubrodorsalis*, as suggested for *Schindleria* and *Paedogobius* by Kon & Yoshino (2002).

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