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Reproductive strategy and recruitment dynamics of amphidromous goby *Sicyopterus japonicus* as revealed by otolith microstructure

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The daily ages of 312 of 879 newly recruited postlarvae of *Sicyopterus japonicus*, collected from the Shuang-Chi Estuary in north-eastern Taiwan during February 1996 to April 1997, were determined from daily growth increments in their otoliths. Pelagic larval duration, growth rate of the marine larval stage and hatching dates were estimated, and recruitment timing was linked to environmental factors. The mean ± S.D. total length (L_T) and daily ages of *S. japonicus* at recruitment to the estuary were estimated to be 33·95 ± 1·31 mm (range 30·7 to 38·1, $n = 317$) and 163·72 ± 12·79 days (range 130 to 198, $n = 312$), respectively. The recruitment of *S. japonicus* larvae is size dependent not age dependent because L_T of the larvae is independent of age at recruitment. Periodic analysis indicated that L_T and growth rate of the larvae were inversely correlated with the age at recruitment, which means that the fast-growing individuals recruited earlier. The growth rate of *S. japonicus* in the marine larval stage was synchronous with marine productivity in this subtropical area, *i.e.* the spring cohort recruited in the autumn had a higher growth rate than the autumn cohort recruited the following spring. The main spawning season of *S. japonicus* as backcalculated from otolith daily increments was in autumn, a relatively low productivity period compared with spring. During this season, there were fewer competitors and predators than in the more productive spring. The recruitment of 95% of postlarva coincided with low salinity (14) and low water temperature (23° C) in the river mouth that provided a buffer area for the adaptation of the larvae for upstream migration. This unique reproduction strategy and prolonged larval duration facilitated the widespread distribution of the fish along the coasts of East Asia.

Key words: daily growth increment; goby; pelagic larval duration.

INTRODUCTION

Sicyopterus japonicus (Tanaka) is an amphidromous goby, mainly distributed in Japan and Taiwan (Shen *et al.*, 1998; Shen & Tzeng, 2002; Watanabe *et al.*, 2006). Amphidromous fishes migrate between marine and fresh water at some stage in their life history, but the migration is not for spawning (Myers, 1949). They spawn in streams, and their newly hatched larvae drift with the downstream

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current to the marine environment in their early life history and return to the stream at the postlarval stage (Shen & Tzeng, 2002). Every year, >5–10 million transparent postlarvae of *S. japonicus* were estimated to recruit from the ocean to streams in eastern Taiwan. An estimated 1 366 752 recruiting individuals of *S. japonicus* were recorded during the main fishing season (30 January to 7 May) in 1997 in Hsuikuluan River in mid-eastern Taiwan (Shiao, 1998). The recruitment of amphidromous gobies is known to be correlated with the lunar phase (Delacroix & Champeau, 1992; Shiao, 1998; Keith, 2003; Hoareau *et al.*, 2007*a*). For example, *S. japonicus* is recruited mainly in the evening between the last quarter and the first quarter of the lunar phase during spring (Shiao, 1998). After developing pigment and metamorphosing to a benthic life in the lower reaches of the river for a few days, they start their upstream migration (Shen & Tzeng, 2002), climbing even the walls of dams. At this stage, however, they are preyed upon by humans, birds (*e.g.* striated heron *Butorides striatus* L. and little egret *Egretta garzetta* L.) and other carnivorous fishes, such as *Eleotris acanthopoma* Bleeker and freshwater eels (*Anguilla japonica* Temminck & Schlegel and *Anguilla marmorata* Quoy & Gaimard) (Shiao, 1998; Liu *et al.*, 2000; K. N. Shen, Y. C. Lee & W. N. Tzeng, unpubl. data; C. S. Tzeng, unpubl. data). *Sicyopterus japonicus* is one of the few amphidromous gobies that can migrate far inland (Liu *et al.*, 2000). Some individuals can be found 80 km upstream from the estuary in the Hsuikuluan River (C. S. Tzeng & J. C. Shiao, unpubl. data).

In eastern Taiwan, *S. japonicus* are only found in some less polluted streams (Shiao, 1998; Liu *et al.*, 2000) and are used as an indicator species for stream pollution because they will only migrate to streams with good water quality (Liu *et al.*, 2000; Wang, 2002). *Sicyopterus japonicus* is one of the most abundant and dominant amphidromous gobies in these streams. In the Hsuikuluan River, for example, it is the second most dominant goby species and constitutes 21% of the fishes. Therefore, the conservation of habitat is important for the sustainable use of these amphidromous gobies (Liu *et al.*, 2000; Wang, 2002). Amphidromous gobies are also found in other subtropical or tropical areas (Manacop, 1953; Radtke *et al.*, 1988; Bell *et al.*, 1995; Radtke & Kinzie III, 1996; Hoareau *et al.*, 2007*a*, *b*). Their life histories are similar, but the length of marine larval duration and size at recruitment varies (Bell *et al.*, 1995; Radtke *et al.*, 2001; Hoareau *et al.*, 2007*a*, *b*). For example, two Hawaiian amphidromous gobies, *Stenogobius hawaiiensis* Watson and *Awaous guamensis* (Valenciennes), have a remarkably long pelagic larval duration (119–151 days and 150–169 days, respectively) (Radtke *et al.*, 1988). *Sicyopterus lagocephalus* (Pallas) is known to have the longest pelagic larval duration (mean ± S.D. 199 ± 33 days) and is distributed over a wide area in the Indo-Pacific (Keith *et al.*, 2005; Hoareau *et al.*, 2007*a*). In two Dominican gobies, *Sicydium punctatum* Perugia and *Sicydium antillarum* Ogilvie-Grant, the pelagic larval stages are long and seasonally inverse cyclic changes in age and total length (L_T) at recruitment occur (Bell *et al.*, 1995), which means the individuals recruited at a large size are younger and *vice versa*. The seasonal difference in growth rate may be influenced by environmental factors, such as water temperature and food availability (Yu & Ueng, 2001).

Otoliths of many fishes provide a daily record of previous events, including the duration of the pelagic larval stage (Brothers *et al.*, 1976, 1983; Victor, 1986*a*; Radtke *et al.*, 1988; Thresher & Brothers, 1989; Wellington & Victor, 1989), settlement timing (Victor, 1982, 1984; Shen & Tzeng, 2002) and relative growth rates during different life-history stages (Victor, 1986*b*; Thorrold & Milicich, 1990; Jones, 1992; Searcy & Sponaugle, 2000). The marine larval stage of *S. japonicus* has been confirmed by otolith Sr:Ca ratio analysis (Shen *et al.*, 1998; Shen & Tzeng, 2002), but little is known about their spawning strategy, early growth history and seasonal recruitment dynamics and how these life-history variables contribute to the abundance of *S. japonicus* in East Asia. The aim of the present study was to understand not only the pelagic larval duration but also the spawning seasons and recruitment regime of *S. japonicus* by counting the daily growth increments in the otolith of the postlarvae collected year round from the surf zones at the river mouth during their upstream migration. The seasonal variation in the age and size at recruitment and the growth rate of the marine life stage in relation to physical and biological factors were also analysed.

MATERIALS AND METHODS

SAMPLING DESIGN

The Shuang-Chi River is a less polluted river than most rivers in Taiwan in north-eastern Taiwan with a length of *c.* 26·8 km and catchment of 132·5 km^2. The width of the river mouth is *c.* 50 m. The water from Shuang-Chi River discharges into the Yen-Liao Bay where the outer part of the bay faces the Kuroshio Current some 100 km away from the shore (Tzeng *et al.*, 1997). A total of 879 newly recruited *S. japonicus* postlarvae were collected with a stationary net set against flood tide in the surf zones at the mouth of the Shuang-Chi River (Fig. 1). Sampling was conducted twice a month (one close to the last quarter and another close to first quarter of the lunar cycle) at night during spring tide from May 1996 to April 1997. Each sampling lasted for 3 h before high tide, collecting the fish entering the river with the tidal current. A sub-sample collected from the by-catch of the glass eel fishery on 22 and 24 February and 11 March 1996 at the same location was also used for otolith analysis. Almost all the samples were used for age determination except those collected on 10 May 1996, where 50 of the 612 individuals collected were randomly selected for L_T measurement and age determination from the major recruitment. The sampling dates, numbers of individuals from 3 h collections and the number of individuals used for L_T measurement and age determination are shown in Table I. Physical factors including salinity and water temperature were measured with a salinometer (WTW Cond 330i, Weilheim, Germany) at a depth of 0·5 m during sampling.

OTOLITH AGEING

The sagittal otoliths of the postlarvae were extracted under a stereomicroscope. After cleaning with distilled water and drying in air, the otoliths were mounted with DPX (Fluka, Steinheim, Germany) on a glass slides with a cover slip. The daily growth increment in otoliths could easily be examined with light microscope under ×200 magnifications without polishing (Fig. 2). The growth increments in the otoliths of *S. japonicus* are assumed to be deposited on a daily basis similar to other gobies (Radtke *et al.*, 1988; Bell *et al.*, 1995). The number of daily growth increments in each of the otoliths was independently counted twice. If the two readings were different by 1%, the otolith was rejected to reduce the ageing error. To understand if recruitment is size dependent or age dependent, the regression of L_T and age at recruitment was calculated. The coefficient of variation (C.V., y) was from $y = 100s\bar{x}^{-1}$, where $\bar{x}$ is the sample mean and s is the S.D.

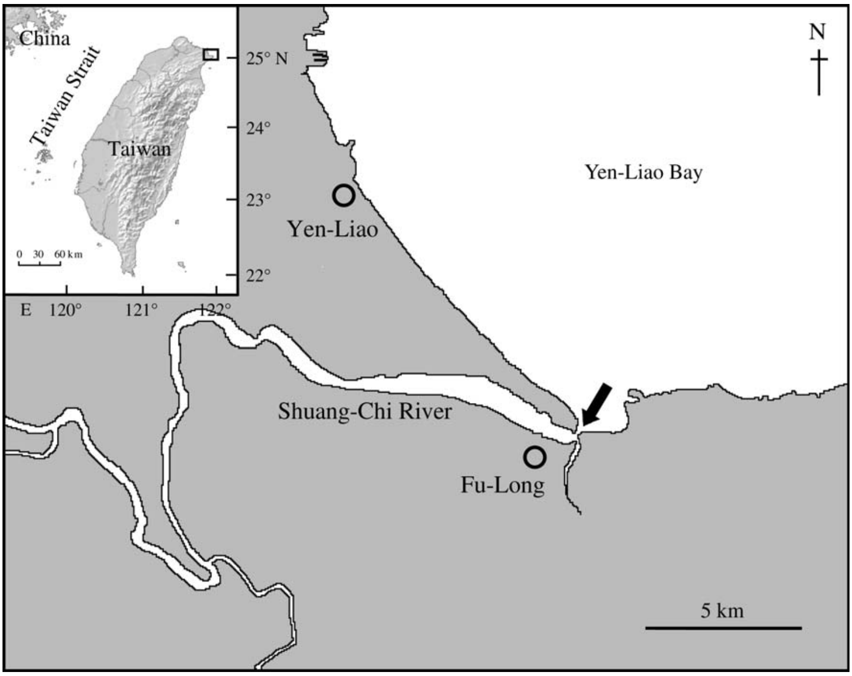

FIG. 1. The sampling site (➡) of *Sicyopterus japonicus* in Shuang-Chi River estuary, north-eastern Taiwan.

BACKCALCULATION OF HATCHING DATES AND PERIODIC REGRESSION ANALYSES

It is not known when the first increment was deposited in the otolith of *S. japonicus*, but it was assumed that it was deposited at hatching as in other amphidromous goby species (Bell *et al.*, 1995). No obvious check marks were found in the otoliths of the newly recruited postlarvae because when they arrive in the estuary metamorphosis is not complete (Shen & Tzeng, 2002). The hatching dates of the larvae were backcalculated from the sampling dates and the daily age at recruitment. Meanwhile, a periodic regression curve (Batschelet, 1981) was fitted for the L_T and daily age at recruitment and from these, the growth rate was estimated to understand the seasonal changes in age, L_T and the growth rate of the larvae at recruitment. In addition, periodic regressions between L_T at recruitment and hatching dates were also calculated (Bell *et al.*, 1995). The calculation for periodic regression was based on the formula $y = M + A \cos (\omega t - \omega t_0)$, where M is the mean level, A is amplitude ($A \geq 0$), ω is angular frequency and t and t_0 are the time and time of peak phase, respectively. The significance of periodic regression was tested after periodic regression transfer to the linear regression (Batschelet, 1981).

THE RELATIONSHIP BETWEEN SEASONAL ABUNDANCE AND ENVIRONMENTAL FACTORS

The seasonal abundances of *S. japonicus* at recruitment during the different sampling dates were $\log_{10}$ transformed due to the large variances in the abundance of recruiting individuals and were plotted against water salinities and temperatures separately. The optimal environmental condition for postlarvae at recruitment was defined as the 95% of the total catch.

TABLE I. The sampling date, lunar phases, number of fish collected, numbers of fish used for total length (L_T), daily age measurement and the salinity and water temperature during sampling

Sampling date	Lunar phase	Number of fish collected	The number of fish used for L_T (mm)	The number of fish used for Age (days)	Salinity	Temperature (° C)
22 February 1996	First quarter	32	32	30	—	—
24 February 1996	First quarter	7	7	7	—	—
11 March 1996	Last quarter	34	34	34	—	—
10 May 1996	Last quarter	612	50	48	14·0	20·0
24 May 1996	First quarter	0	0	0	0·2	21·0
8 June 1996	Last quarter	7	7	7	4·5	29·0
20 June 1996	First quarter	0	0	0	18·5	26·5
4 July 1996	Last quarter	0	0	0	32·5	28·8
18 July 1996	First quarter	0	0	0	32·0	28·8
5 August 1996	Last quarter	0	0	0	12·0	27·5
19 August 1996	First quarter	0	0	0	29·5	26·5
5 September 1996	Last quarter	3	3	3	9·0	26·0
19 September 1996	First quarter	0	0	0	28·0	25·0
4 October 1996	Last quarter	3	3	3	8·0	23·8
17 October 1996	First quarter	37	37	37	9·8	23·0
4 November 1996	Last quarter	0	0	0	0·9	23·7
18 November 1996	First quarter	11	11	11	0·8	19·0
3 December 1996	Last quarter	0	0	0	24·0	18·0
18 December 1996	First quarter	9	9	9	15·0	16·3
4 January 1997	Last quarter	29	29	28	2·0	17·9
15 January 1997	First quarter	14	14	14	0·5	16·3
1 February 1997	Last quarter	0	0	0	10·5	16·1
17 February 1997	First quarter	4	4	4	1·1	16·2
4 March 1997	Last quarter	15	15	15	1·0	18·1
19 March 1997	First quarter	40	40	40	0·2	18·5
1 April 1997	Last quarter	22	22	22	31·9	21·2
Total		879	317	312		

—, no data.

RESULTS

AGE AND SIZE AT RECRUITMENT

The mean ± S.D. L_T of *S. japonicus* at recruitment to the Shuang-Chi River estuary was 33·95 ± 1·31 mm (range 30·8 to 38·1 mm, $n = 317$) with a mean ± S.D. age of 163·72 ± 12·79 days (range 130 to 198 days, $n = 312$). The L_T at recruitment was significantly and positively correlated with the daily age ($r^2 = 0{\cdot}1608$, $P < 0{\cdot}001$, $n = 312$), but the coefficient of determination was low (Fig. 3). The C.V. of the L_T (3%) was less than age (8%).

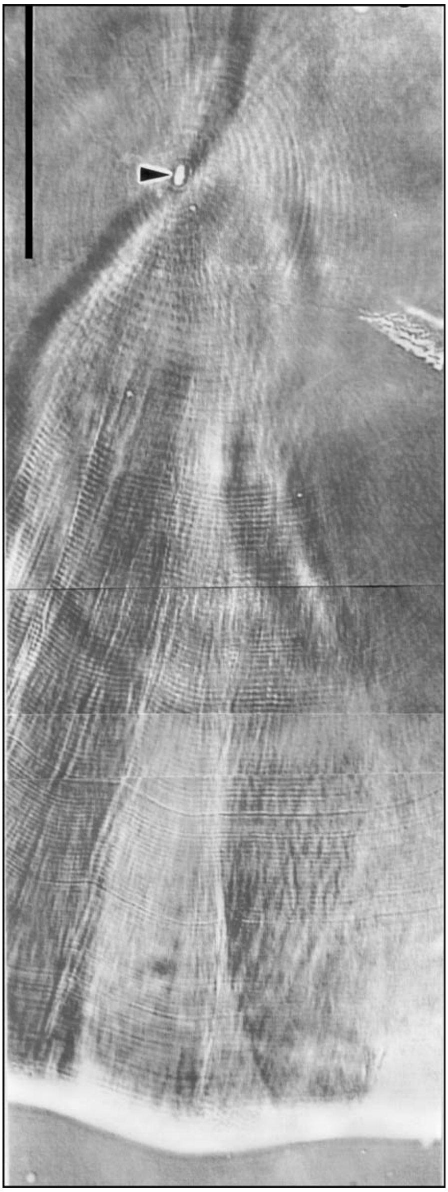

FIG. 2. Daily growth increments in the otolith of the juvenile *Sicyopterus japonicus*, 33 mm total length. ►, primordium. Scale bar = 100 μm.

SEASONAL CHANGES IN TOTAL LENGTH AND DAILY AGE AT RECRUITMENT AND SOMATIC-GROWTH RATE

The mean L_T at recruitment changed cyclically with sampling date [Fig. 4(a)]. A periodic regression equation of the L_T at recruitment on the sampling date was calculated ($r^2 = 0{\cdot}280$, $n = 16$, $P < 0{\cdot}05$). The slope of the regression was significant, indicating that L_T at recruitment displayed a yearly cyclic

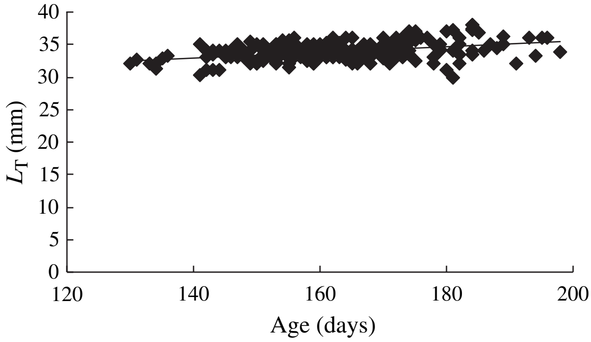

FIG. 3. The relationship between total length (L_T) and daily age at recruitment of *Sicyopterus japonicus*. The curve was fitted by: $y = 0{\cdot}0041x + 2{\cdot}7256$.

change with the largest size at recruitment appearing on 15 November 1996 and the smallest size at recruitment appearing on 16 May 1996. In other words, the gobies recruited to the estuary were larger in autumn and smaller in spring.

The mean daily age at recruitment of the fish also changed cyclically with sampling date [Fig. 4(b)]. A periodic regression equation of the daily age at recruitment on the sampling date was calculated ($r^2 = 0{\cdot}315$, $n = 16$, $P < 0{\cdot}05$). The regression was significant, indicating that the age of the fish at recruitment also displayed a yearly cyclic change with the older fish at recruitment appearing on 29 June 1996 and the younger fish at recruitment appearing on 18 December 1996. The peak phase of L_T and age at recruitment was inversely related, the larger fish were younger at recruitment and *vice versa*.

The average somatic-growth rate changed cyclically with sampling date [Fig. 4(c)]. A periodic regression equation of the somatic-growth rate on sampling date was calculated ($r^2 = 0{\cdot}372$, $n = 16$, $P < 0{\cdot}05$). The regression was significant, indicating that the mean growth rate of the fish at recruitment also displayed a yearly cyclic change with a maximum-somatic growth rate on 8 December 1996 and a minimum-somatic growth rate on 8 June 1996. The seasonal change in somatic-growth rate was similar to that of L_T but opposite to that of age.

THE RELATIONSHIP BETWEEN TOTAL LENGTH AT RECRUITMENT AND HATCHING DATE

The duration of the estimated hatching dates of *S. japonicus* was quite long, almost year around except for the winter (Fig. 5). According to the abundance of the larvae during recruitment in spring, the main spawning season was in autumn. A cyclic regression of L_T at recruitment on hatching date was calculated ($r^2 = 0{\cdot}070$, $n = 312$). The regression was significant ($P < 0{\cdot}001$), indicating that the size of the larvae at recruitment changed with the date at hatching, the larger larvae which recruited to the estuary in the autumn [Fig. 4(a)] were spawned on 22 April 1996 (spring), and the smaller ones at recruitment in spring were expected to have been spawned on 22 October 1995 (autumn). *Sicyopterus japonicus* spawned in spring were larger at recruitment on the

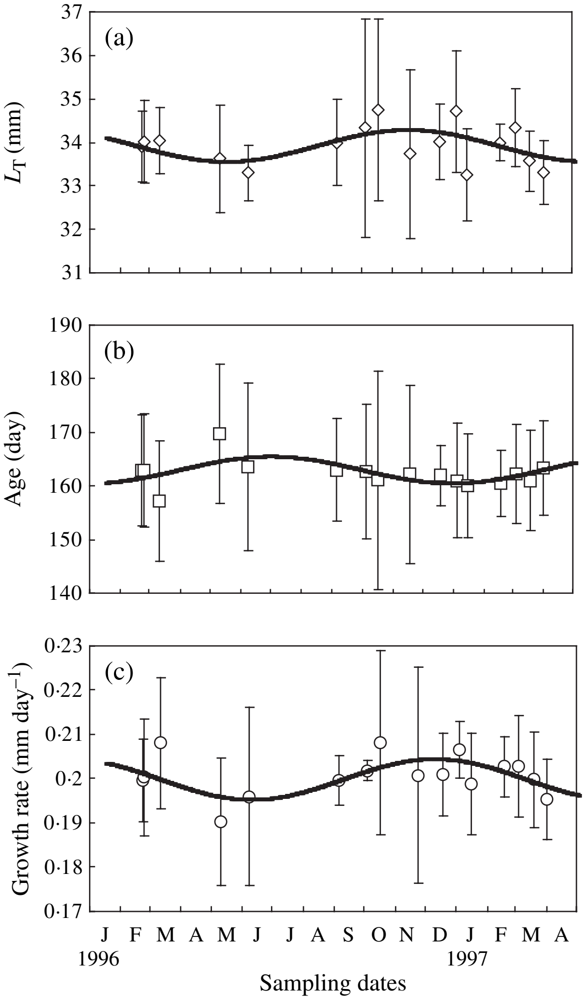

FIG. 4. Seasonally cyclic changes of mean ± S.D. (a) total length (L_T), (b) age and (c) growth rate at recruitment from February 1996 to April 1997. The cyclic changes were fitted with periodic regression equations: (a) $y = 33{\cdot}92 + 0{\cdot}37 \cos(\omega x - 2{\cdot}385)$ (b) $y = 162{\cdot}953 + 2{\cdot}500 \cos(\omega x + 0{\cdot}012)$ and (c) $y = 0{\cdot}200 + 0{\cdot}005 \cos(\omega x - 2{\cdot}7833)$ where $\omega = 2\pi T^{-1}$ ($T = 365$ days). The sample size on each sampling date is the same as shown in Table I.

average than those spawned in autumn. The L_T was more divergent, however, in the spring than the autumn cohort (Fig. 5).

FACTORS AFFECTING THE ABUNDANCE OF RECRUITMENT

Sicyopterus japonicus postlarval recruitment to the estuary was almost year round except during summer (July and August) (Fig. 6). Approximately 95% of the larvae were recruited when the water temperature was ≤23° C [Fig. 6(a)], which coincided with the annual temperature cycle except during summer and

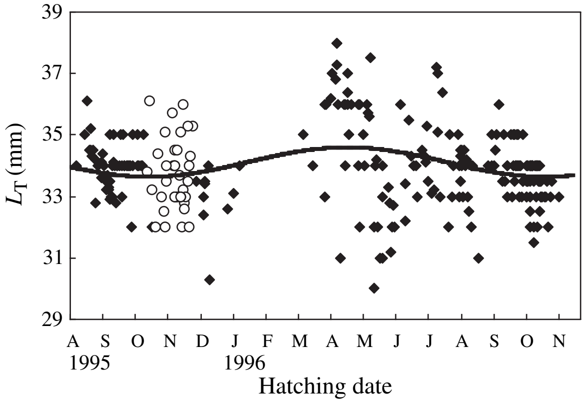

FIG. 5. Total length (L_T) at recruitment and hatching date of *Sicyopterus japonicus* during the period from August 1995 to October 1996. ○, the samples from the main recruitment on 10 May 1996; ◆, samples from year-round recruitment. The curve was fitted by: $y = 34{\cdot}119 + 0{\cdot}48 \cos(\omega x + 1{\cdot}245$, where $w = 2\pi T^{-1}$ ($T = 365$ days).

also 95% of the newly recruited larvae were captured when the salinity was $\leq$14 [Fig. 6(b)]. When the salinity was too high, no fish were caught even during the recruitment period (19 September and 3 December 1996), but there were three sampling dates (24 May and 4 November 1996 and 1 February 1997) when no fish were collected even though the salinity was low. This may have been due to the high water flow from the river after heavy rains (the accumulated precipitation of these 3 months were 384·5, 935·5 and 331·0 mm, respectively).

DISCUSSION

THE SPAWNING STRATEGY OF *S. JAPONICUS*

Backcalculated spawning periods from the otolith daily increments suggest that the spawning of *S. japonicus* is almost year-round except during winter, with a major event in autumn. Reproductive biology research on *S. japonicus* in the Jinlun Stream, in south-eastern Taiwan (Ju, 2001) also found that the gonado-somatic index (I_G) of *S. japonicus* was at a low level from November to April but with a peak during September and October. It increased from 0·59 in May to 6·68 in October and suddenly decreased to 0·43 in November. The fecundity of *S. japonicus* is *c.* 11 000–18 000 and egg size is *c.* 72–103 μm diameter ($n = 3$, 64–78 mm L_T) (Ju, 2001). This shows that the main spawning season is in autumn and that the deposition of the growth increments in the otolith of *S. japonicus* is on a daily basis.

Shuang-Chi River estuary is in a subtropical area where there is a major spring algal bloom and a minor bloom caused by the recycling of the nutrients in the autumn, as in temperate areas (Huang *et al.*, 1985). The spawning season of many fishes coincides with the spring phytoplankton bloom in temperate areas to match the timing of the production cycle (match and mismatch hypothesis; Cushing, 1975). The planktonic foods are critical to the survival, growth and year class strength of many fish species (van der Veer & Witte,

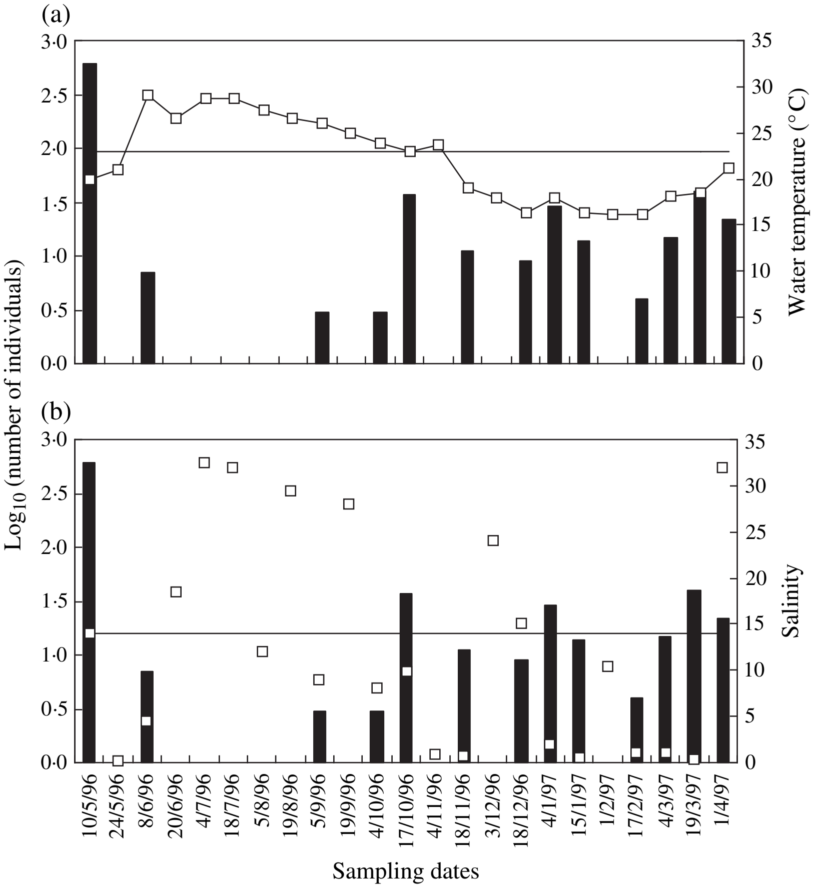

FIG. 6. The log$_{10}$ number of individuals (■) in relation to (a) water temperature (□) and (b) salinity (□). The number of individuals located in salinity <14 and water temperature <23° C is 95%.

1999). Large numbers of fish eggs and larvae appear in spring because of the plentiful food supply (Su *et al.*, 1981; Huang *et al.*, 1985). Copepods, the main food of *S. japonicus* larvae in the marine larval stage (Dotu & Mito, 1955), are also more abundant in warm than cold seasons in Yen-Liao Bay (Tzeng *et al.*, 1997). Why do the *S. japonicus* choose the low production season (autumn) as their main spawning season?

The climate in subtropical areas is characterized by a dramatically seasonal change with an intermittent precipitation and riverflow (Chapman & Kramer, 1991) similar to Taiwan. Winter and early spring (December to March) is the dry season in Taiwan, and the water level and temperature are low in the river during this period. The following spring rain may initiate the spawning of some individuals, but not the majority. The seasonal heavy rains brought on by typhoons during summer and autumn increases the water volume of small streams in eastern Taiwan. Amphidromous gobies may take this opportunity to spread their larvae downstream and to complete their downstream migration towards the sea, and thus, the spawning season of the fishes may be synchronized with the intermittent precipitation (Ryan, 1991). K. Ego (unpubl. data) found that *A. guamensis* in Hawaii spawns from August to December with a peak spawning during high water following the rainstorms of late summer or autumn. Radtke *et al.* (1988) also suggested that Hawaiian gobies spawn during the rainy season because the larvae may easily be swept downstream to the ocean upon hatching. The positive relationship between spawning period and precipitation was also demonstrated by the I_G of *S. japonicus* in south-eastern Taiwan (Ju, 2001).

Amphidromous gobies are abundant in tropical and subtropical small streams and rivers of the Indo-Pacific, which have a short length, such as in Japan (Watanabe *et al.*, 2006; Yamasaki *et al.*, 2007), in Taiwan (Shen *et al.*, 1998), in Hawaii (Radtke *et al.*, 1988) and in the Caribbean (Bell *et al.*, 1995). The newly hatched larvae in the short streams spent less time without food prior to reaching the plankton-rich, brackish and marine zone (Iguchi, 2007). Therefore, precipitation plays an important role in speeding the larval dispersal of amphidromous gobies (Erdman, 1961; Delacroix & Champeau, 1992; Fitzsimons *et al.*, 1997; Keith *et al.*, 2006). In addition to precipitation, the seasonal decrease in temperature and day length may also be cues that induce fish spawning. For example, in most fish species native to North America, changing day length and water temperature are strong proximate factors that influence the reproductive cycle (Sumpter, 1990).

Bell & Brown (1995) found that a salinity of <10 in an estuary is essential for the survival of 0–5 day-old Sicydiine larvae. The seasonal heavy rain makes the estuary act as a salinity buffer and keeps the larvae away from the deadly high salinity sea water. The adult fishes can detect the cues of these environmental changes and take this chance to disperse their offspring and decrease the risk of mass mortality.

THE GROWTH HISTORY OF *S. JAPONICUS* IN THE MARINE LARVAL STAGE

Information about the early growth history of *S. japonicus* in the marine larval stage is limited, but growth records from otoliths may give some hints. The recruitment period of the *S. japonicus* from ocean to stream is from September to June. The peak phase of cyclic change in age and L_T of the fish at recruitment is inversely related, and the L_T of fish at recruitment is larger in autumn than in spring. The age of fish at recruitment, however, is younger in autumn than in spring, and fish recruited in autumn and winter were hatched in spring as indicated from the backcalculation of the otolith daily growth increments, while the spring recruited fish were hatched in the autumn of the previous year. The significant cyclic regression between L_T at recruitment and hatching date also shows a similar pattern, the fish hatched in autumn were smaller at recruitment and the fish hatched in spring were larger. The significant difference, however, might be due to the large sample size (Kubinger *et al.*, 2007). On the other hand, the size variation among individuals of the same cohort is a common phenomenon in fishes (DeAngelis *et al.*, 1993; van Densen *et al.*, 1996; Huss *et al.*, 2007), which may also contribute to the low coefficient of determination (Fig. 5). The pelagic larval environment (*e.g.* temperature, food availability and oceanographic features) has been shown to alter the rates of larval growth (Hovenkamp & Witte, 1991; Benoît & Pepin, 1999; Otterlei *et al.*, 1999; Keller & Klein-MacPhee, 2000), development time (Benoît & Pepin, 1999; Otterlei *et al.*, 1999; Searcy & Sponaugle, 2000) and survival to settlement (Meekan & Fortier, 1996; van der Veer & Witte, 1999; Keller & Klein-MacPhee, 2000) in a variety of marine fishes.

In Yen-Liao Bay, surface water temperatures were high in August (mean ± S.D. 29·3 ± 0·2) and low in winter (18·7 ± 0·2). The abundance of zooplankton, fish larvae and eggs and the number of fish species were all higher in spring and fewer in autumn, reaching a low in winter (Tzeng *et al.*, 1997). Therefore, spring-hatched larvae live in a highly productive and high water temperature environment, while autumn-hatched larvae live in a relatively poor productive and low water temperature environment (Su *et al.*, 1981; Huang *et al.*, 1985; Tzeng *et al.*, 1997). In other words, the environment and nutritional condition were different for spring and autumn-hatched larvae. They may even use different nursery areas as shown in spring and autumn-hatched herring *Clupea harengus* L. (Rinne, 1988). During the high productivity and high water temperature environment in spring, the larvae can grow faster and recruit to the estuary in autumn of the same year, although they may have to face more predation risk and competition with the other species (Warlen & Burke, 1990). This may be the reason why the average size and age of the larvae at recruitment were larger and younger in autumn, but with a higher size variation. Conversely, fish that recruited to the estuary in the late spring and hatched in autumn face a relatively poor productivity and low temperature environment (Su *et al.*, 1981; Huang *et al.*, 1985; Tzeng *et al.*, 1997) but also less competitors and predators, which may cause them to grow relatively slowly and thus lead them to be smaller and older at recruitment.

The low coefficient of determination between daily age and L_T of *S. japonicus* were also found in other amphidromous gobies (Hoareau *et al.*, 2007*b*). The low C.V. of the L_T relative to age indicated that the recruitment of the *S. japonicus* was size dependent rather than age dependent. Fernandez-Diaz *et al.* (2001) showed that metamorphosis and recruitment of the Senegal sole *Solea senegalensis* Kaup is size dependent rather than age dependent. Food quality was probably a principal factor influencing the timing of metamorphosis from larvae to juvenile. In addition, it was also shown that the larval duration was inversely related to growth rate: faster growing larvae spend less time at the planktonic larval stage (Wellington & Victor, 1989).

Where the *S. japonicus* larvae stayed during the marine larvae stage is not clear. Smaller marine larvae were seldom collected in the estuary, suggesting that the estuary is not the place for marine larvae. Research in the Yen-Liao Bay area by Tzeng *et al.* (1997) found the larvae of the amphidromous goby *Rhinogobius* sp. 6 km from the river mouth in March 1993. This may be evidence for coastal retention of these amphidromous gobies during the marine larval stage.

RECRUITMENT DYNAMICS OF *S. JAPONICUS*

Due to the mountainous features of East Taiwan, the rivers are all small and with a steep gradient. Therefore, the streams in eastern Taiwan are usually less polluted than those of western Taiwan, and a better environment for size-dependent rather than age-dependent amphidromous recruitment. The planktonic larval duration of *S. japonicus* is longer than for most other species (Radtke *et al.*, 1988; Bell *et al.*, 1995; Shen *et al.*, 1998; Yamasaki *et al.*, 2007). Longer larval duration makes them more likely to disperse, but it does not guarantee recruitment success (Maeda *et al.*, 2007). This lengthy larval duration has also been observed in the widely distributed amphidromous *S. lagocephalus* in Indo-Pacific area (Hoareau *et al.*, 2007*a*). The L_T size of *S. japonicus* at recruitment is larger than in other amphidromous goby species in Taiwan such as *Rhinogobius gigas* Aonuma & Chen, which is only 17·6 mm at recruitment (Shiao, 1998) and hence liable to be less affected by predators or environmental factors in the estuary (Miller *et al.*, 1988; Bailey & Houde, 1989).

Precipitation and temperature not only play an important role in determining the timing of spawning in amphidromous fishes but also the timing of recruitment of their postlarvae. In this study, *c.* 95% of the specimens were collected at a salinity <14, and seldom collected at a salinity >14, even during the recruitment season. This suggests that low salinity water may provide a suitable environment for the postlarvae to recruit to streams. The timing of the upstream migration of diadromous freshwater eels, for example, is also strongly correlated with rainfall (Jellyman & Ryan, 1983; Chen-Lee *et al.*, 1994). In addition, salinity is the most important factor guiding the choice of water by glass eels of *Anguilla anguilla* (L.) (Tosi *et al.*, 1990). In addition, 95% of the specimens in this study were collected at a temperature of <23° C. The absence of recruitment in a high temperature environment during summer in north-eastern Taiwan coincides with the spawning gap of *S. japonicus* in winter, and lunar phases are also a major factor affecting the recruitment of amphidromous gobies (Delacroix & Champeau, 1992; Shiao, 1998; Keith, 2003; Hoareau *et al.*, 2007*b*).

In summary, the abundance of *S. japonicus* in eastern Taiwan and their wide distribution in East Asia indicates that their spawning strategies are successful. These life-history strategies and their relationship to environmental cues are the result of a long-term evolutionary adaptation that coincides with environmental cues that facilitate the dispersal and survival of the larvae by a matching of abiotic and biotic factors. The conservation and management of this species will depend on both this basic life-history information together with habitat conservation.

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