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BRIEF COMMUNICATIONS

Changes in the life history of *Abbottina rivularis* in Lake Fuxian

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After invading Lake Fuxian, China, *Abbottina rivularis* showed marked changes in its life history traits, including alterations in annuli formation, extension to the length of the breeding season, and an increase in fecundity and growth rate. The results are explained in the context of the enemy release hypothesis.

Key words: enemy release hypothesis; invasive species; life history evolution.

Abbottina rivularis (Basilewsky) is widely distributed throughout China, with the exception of the Qingzang and Yungui Plateaus (Chen, 1998). In the latter half of the 20th Century, however, *A. rivularis* was unintentionally introduced from the River Yangtze into lakes on the Yungui Plateau. The species has naturalized successfully in the region, and its introduction is believed to have led to a severe decrease in the diversity of the native fishes in those lakes in which it now occurs, including Lakes Fuxian, Dianchi and Erhai (Yang & Chen, 1995; Yang, 1996; Chen *et al.*, 1998). Lake Fuxian (24°21′–24°38′ N; 102°49′–102°57′ E), located in the Chengjiang Basin in the upper reaches of Nanpan River, is the second deepest lake in China, with a maximum and mean depth of 155 and 87 m respectively (Wang & Dou, 1998). In this study, life history traits of *A. rivularis* in Lake Fuxian, the area in which it is naturalized, and Lakes Chao (31°25′–31°43′ N; 117°16′–117°51′ E) and Dongting (28°44′–29°35′ N; 111°53′–113°05′ E), within its original distribution, were compared to investigate changes associated with the expansion of its distribution.

Abbottina rivularis were collected by netting from Lakes Fuxian (from February 2003 to January 2004), and Chao and Dongting (both from October

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2003 to September 2004). The total length (L_T) (to the nearest 0·01 mm), total mass (M_T), somatic mass (M_S) (both to the nearest 0·1 g) and gonadal mass (M_G) (to the nearest 0·005 g) were measured for 535 (Fuxian), 374 (Chao) and 405 (Dongting) freshly caught specimens. Sex was determined by macroscopic examination of gonadal tissues, and gonad developmental stage was scored following Bariche *et al.* (2003).

Absolute fecundity (F_A) was estimated in terms of the number of the oocytes with vitellinogenic granules, and relative fecundity (F_R) was estimated from $F_R = F_A M_S^{-1}$. Gonado-somatic index (I_{GS}) was calculated from $I_{GS} = 100 M_G M_S^{-1}$. Age was determined from growth checks on scales taken from the left side of the body between the lateral line and the anterior section of the dorsal fin. Scale radius was measured using the Photo Analysis System software, version 2.01 (Zhu *et al.*, 2002) and the time of annuli formation was estimated following Deng *et al.* (1981). To estimate L_T at age, backcalculation of L_T was conducted using the Fraser-Lee equation: $L_n = a + (L - a) R_n R^{-1}$, where $L_n = L_T$ at the formation of the nth annulus, a = correction factor corresponding to the intercept, R_n = the scale radius between the core and the nth annulus, R = the whole scale radius and $L = L_T$ at capture. A growth index was estimated from $C_{lt} = l_1(\log_{10} l_2 - \log_{10} l_1)[0{\cdot}4343(t_2 - t_1)]^{-1}$, where l_2 or $l_1 = L_T$ at t_2 or t_1.

ANOVA was used to test for differences in body size and fecundity among populations. When significant differences were observed, *post hoc* multiple comparisons were used to determine which groups were different.

Both immature and mature *A. rivularis* within its original range, as well as mature individuals in Lake Fuxian, formed annuli in late spring or early summer. In contrast, immature individuals in Lake Fuxian formed annuli in winter or early spring (Table I). In addition, the life span of *A. rivularis* in Lake Fuxian was higher (3+ years) than those of the original populations (both 2+ years).

Temporal changes in I_{GS} were closely synchronized from April to July in Lakes Chao and Dongting. In contrast, in Lake Fuxian the *A. rivularis* population spawned from April to August (Fig. 1). Further, although age at maturity was 1+ years for all three study populations, size at maturity varied (Table II). For L_T, no significant difference existed between the two original populations (ANOVA, d.f. = 1, 125, $P > 0{\cdot}05$), while that of the population introduced into Lake Fuxian was significantly larger than the other two populations (ANOVA, d.f. = 2, 216, $P < 0{\cdot}05$). In addition, *A. rivularis* also appears to have experienced a change in fecundity after invading Lake Fuxian; there was a

TABLE I. Times of annuli formation of *Abbottina rivularis* in Lakes Fuxian (introduced), Chao and Dongting (natural range)

Maturity	Lake Fuxian	Lake Chao	Lake Dongting
Immature individuals	March, April and May	November, December and January	November and December
Mature individuals	March, April and May	March and April	February and March

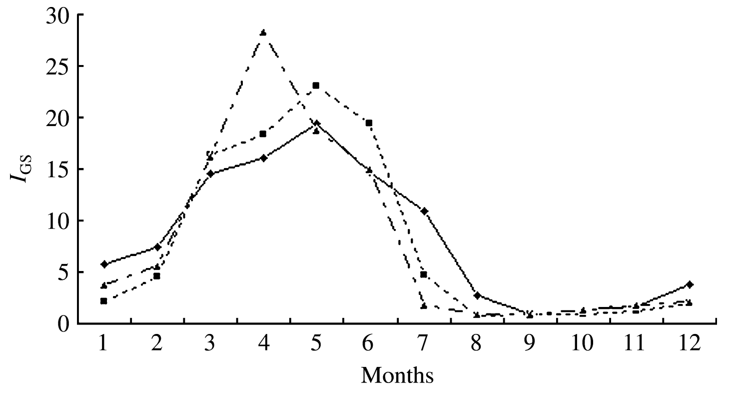

FIG. 1. Monthly changes in gonado-somatic index of female *Abbottina rivularis* in Lakes Fuxian (—♦—), Chao (---■---) and Dongting (— - ▲ - —).

significant difference in the relationship between absolute fecundity and body size between the Fuxian population and the two original populations (ANOVA, d.f. = 2, 143, $P < 0{\cdot}05$; Table III).

A linear relationship was detected between L_T and scale radius in *A. rivularis*. There were no differences, however, among populations consistent with invasion history (Table IV).

Annuli formation in fishes is typically a result of either a periodic environmental event, such as a change in water temperature or food supply, or biological event, such as reproduction, migration or behaviour changes. In temperate regions annuli often form during winter, when water temperatures are low and growth is constrained (Junk, 1985; Lowe-McConnell, 1987; Junk *et al.*, 1989; Welcomme, 1992; Fabré & Saint-Paul, 1998). Lake Fuxian is a deep plateau lake characterized by relatively moderate changes in water temperature throughout the year, the lowest water temperature in winter is 12·7° C, considerably higher than that of Lake Chao which falls to 4·0° C or lower (Fig. 2) (Yang & Chen, 1995; Wang & Dou, 1998). Both Lake Chao and Dongting are shallow lakes in the middle and lower reaches of the Yangtze River, and both experience similar changes in water temperature (Wang & Dou, 1998). In these lakes immature *A. rivularis* appear to form annuli in late winter or early spring in response to low water temperatures. In contrast, in Lake

TABLE II. Ages and body sizes (total length, L_T, and total mass, M_T) at sexual maturity of *Abbottina rivularis* in Lakes Fuxian (introduced), Chao and Dongting (natural range)

		L_T (mm)		M_T (g)	
Lakes	Age (years)	Mean ± S.D.	Range	Mean ± S.D.	Range
Fuxian Lake	1+	$82{\cdot}7 \pm 11{\cdot}6^{a}$	99·7–65·0	4·3 ± 1·0	6·8–2·2
Chao Lake	1+	$67{\cdot}6 \pm 8{\cdot}7^{b}$	87·5–61·5	3·9 ± 0·9	6·6–1·9
Dongting Lake	1+	$63{\cdot}5 \pm 71{\cdot}4^{b}$	71·4–59·9	3·9 ± 0·9	5·6–1·9

Different superscript lower case letters in the same row indicate significant differences ($P < 0{\cdot}05$).

TABLE III. Fecundity and relative fecundity of *Abbottina rivularis* in Lakes Fuxian (introduced), Chao and Dongting (natural range)

Lakes	Fecundity (eggs) Mean ± S.D.	Fecundity (eggs) Range	Relative fecundity (eggs g^{-1}) Mean ± S.D.	Relative fecundity (eggs g^{-1}) Range	Ovaries (n)
Fuxian	3796 ± 1440	6221–1162	990·5 ± 296·7[a]	1574·4–499·3	50
Chao	2409 ± 996	4683–1071	708·7 ± 303·3[b]	1385·6–320·3	50
Dongting	3386 ± 1058	5637–1092	753·6 ± 305·4[b]	1389·5–389·3	50

Different superscript lower case letters in the same row indicate significant differences ($P < 0·05$).

Fuxian, where water temperatures are relatively more stable, immature *A. rivularis* appear not to form annuli during winter. Instead they form annuli in late spring and early summer, which corresponds with the spawning season.

The timing of reproduction in fishes is a product of the interaction of extrinsic and intrinsic factors (Roff, 1992; Yin, 1993). Variation in environmental conditions can explain differences in the timing of breeding among different geographic populations (Munro, 1990; Huber & Bengtson, 1999). In Lake Fuxian maximum water temperatures (22·4° C) are seen in August, later than those of Lake Chao and Dongting, which reach a maximum in July. The asynchronous maximum water temperature between lakes may be responsible for the difference in the timing of breeding among these populations. Additionally, Lake Fuxian is a deep plateau lake and relatively oligotrophic; while Lakes Chao and Dongting are relatively eutrophic (Wang & Dou, 1998). According to a study by Yang & Chen (1995), the native fishes in Lake Fuxian all show long breeding seasons, which may result from low productivity in the lake constraining reproduction. The same explanation could explain the more extended breeding season observed for *A. rivularis* in Lake Fuxian.

Food supply plays an important role in determining the reproduction and growth investments of fishes. Fishes often experience the decrease in fecundity

TABLE IV. Backcalculation of mean ± S.D. total length (L_T) for age and growth index (C_{lt}) of *A. rivularis* in Lakes Fuxian (introduced), Chao and Dongting (natural range)

Lake	Age (years) 1		2		3
Fuxian					
L_T	65·9 ± 9·4[a]		79·7 ± 3·9[a]		87·3 ± 1·8
C_{lt}		12·6		7·25	
Chao					
L_T	54·0 ± 14·1[b]		66·5 ± 9·8[b]		
C_{lt}		11·2			
Dongting					
L_T	61·0 ± 15·7[a]		74·4 ± 10·3[a,b]		
C_{lt}		127			

Different superscript lower case letters in the same row indicate significant differences ($P < 0·05$).

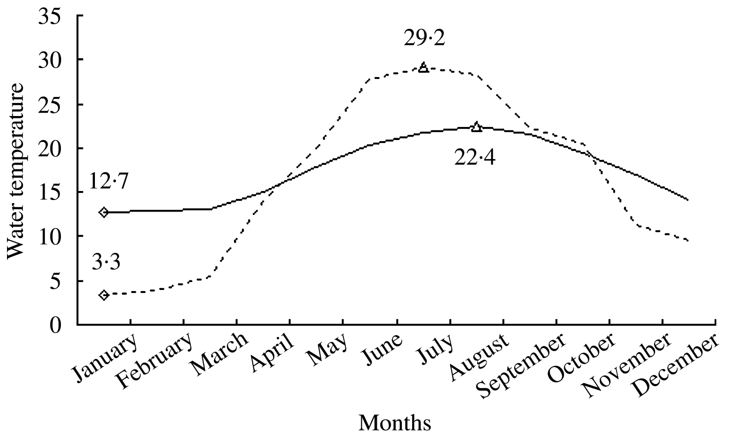

FIG. 2. Monthly changes in water temperature in Lakes Fuxian (———) and Chao (-----), (◇, maxima; Δ, minima).

and growth rate when food supply is constrained (Wootton, 1990; Yin, 1993; Heath & Roff, 1996). Alternatively, in the absence of natural enemies, invasive species are often able to achieve a larger body size, higher fecundity and faster growth outside their natural range (Blossey & Notzold, 1995; Blair & Wolf, 2004). In the present study, despite the relatively oligotrophic status of Lake Fuxian, *A. rivularis* showed higher fecundity and faster growth than populations in Lake Chao and Dongting, and this observation may be explained by the enemy release hypothesis, whereby the abundance or success of a species outside its native range is determined by the scarcity of natural enemies in the introduced range compared with its native range (Torchin *et al.*, 2003).

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