



# Habitat segregation between two congeneric and introduced goby species

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With 3 figures and 6 tables

**Abstract:** Spatial segregation is one of the most important mechanisms that facilitates coexistence among competing species. Large populations of two introduced and congeneric goby species (*Rhinogobius giurinus* and *Rhinogobius cliffordpopei*) now co-occur in Lake Erhai, a plateau lake in the Yunnan-Guizhou Plateau (China). Herein we quantified the spatio-temporal distribution of the two species to determine whether spatial segregation occurred within the same ecosystem. A total of 67,819 individuals of *R. giurinus* and 36,043 of *R. cliffordpopei* were sampled across four seasons. The results indicated that *R. giurinus* mostly occupied profundal habitat (PH) while *R. cliffordpopei* mainly used littoral habitat (LH). Correlation analysis revealed the abundance of *R. giurinus* was positively associated with deep water, silt and coarse sand substrata, whereas the distribution of *R. cliffordpopei* was positively associated with high densities of macrozooplanktons and high abundances of other fish species, high concentration of dissolved oxygen and high densities of submerged macrophytes. Except in spring, the body condition of *R. giurinus* was significantly higher in the PH than in the LH. The body condition of *R. cliffordpopei* did not differ significantly between habitats in the four seasons. These findings demonstrate that the two congeneric and introduced goby species occupy distinct habitats, indicating that spatial segregation enables coexistence of the two invasive species at high abundances within an ecosystem.

**Key words:** habitat segregation, biological invasions, body condition, ecological niche.

## Introduction

Phylogenetically-related or ecologically-similar species often show separation along niche axes involving several dimensions such as habitat, food and time (Friberg et al. 2008, Gross et al. 2009, Amundsen et al. 2010). Habitat is arguably the most important dimension that can promote resource partitioning and has often been implicated as a primary mechanism

for coexistence among sympatric species with similar ecological functions (Hernaman & Probert 2008, Hesselschwerdt et al. 2008, Amundsen et al. 2010). Habitat segregation has been widely observed in fishes including closely related species (Sone et al. 2006, Horinouchi 2008, Hernaman & Probert 2008), different age and size classes (Johnson et al. 2011), or polymorphic populations (Kahilainen et al. 2004). As substrata-associated species, most goby species show

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limited capacity for quick and/or long distance swimming after they settle in the benthos and habitat use has substantial effects on access to trophic resources and individual performances (Hayden & Miner 2009). Several sympatric goby species have been found to show spatial segregation in use of microhabitats that differ in water flows (Sone et al. 2006), water depths (Horinouchi 2008), aquatic vegetation (Hernaman & Probert 2008), types of substrata (Hernaman & Probert 2008, Horinouchi 2008), salinities and prey abundances (Gill & Potter 1993). However, most of these studies were conducted within the native ranges and not much is known about the habitat segregation once the species have been introduced into new environments (Keller & Taylor 2008).

*Rhinogobius giurinus* (Rutter, 1897) and *Rhinogobius cliffordpopei* (Nichols, 1925) are small-bodied (maximal total body length < 80 mm) and ecologically similar species with comparable life histories and feeding habits in native lakes along the middle and lower reaches of the Yangtze River in China (Zhang 2005, Wu & Zhong 2008). They usually spawn from April to June with a life span of one-year in native lakes (Xie et al. 2005, Zhang 2005). Their diet is mainly composed of large zooplankton (Cladocera and Copepoda) and aquatic insects (Chironomidae larvae) (Xie et al. 2000b, Xie et al. 2005, Zhang 2005). *Rhinogobius giurinus* is associated with vegetation-free or simple-structured vegetation habitats in native lakes (Xie et al. 2000a, Xie et al. 2005, Li et al. 2010). In those lakes, however, *R. cliffordpopei* has been reported to occur only at very low densities and no information is available about habitat selection when the two species co-occur in their native areas. Both species were introduced inadvertently into Lake Erhai in 1961, populations densities rapidly increased in the 1970s and the two gobies are now the most dominant fish species in the lake (Du & Li 2001). Therefore, they provide an excellent opportunity to study habitat segregation of congeneric species at very high abundances.

The aim of the present study was to determine if spatial segregation occurs when two introduced goby species coexist in high abundances. We also examined how habitat occupancy affects the individual performance of each species. Specifically, the following questions were examined: (1) does the abundances of the two goby species differ across the habitats and seasons; (2) how are the abundances of the two goby species associated with environmental characteristics and (3) does habitat use influence individual performance (i.e., body-condition) differently for the two species?

## Material and methods

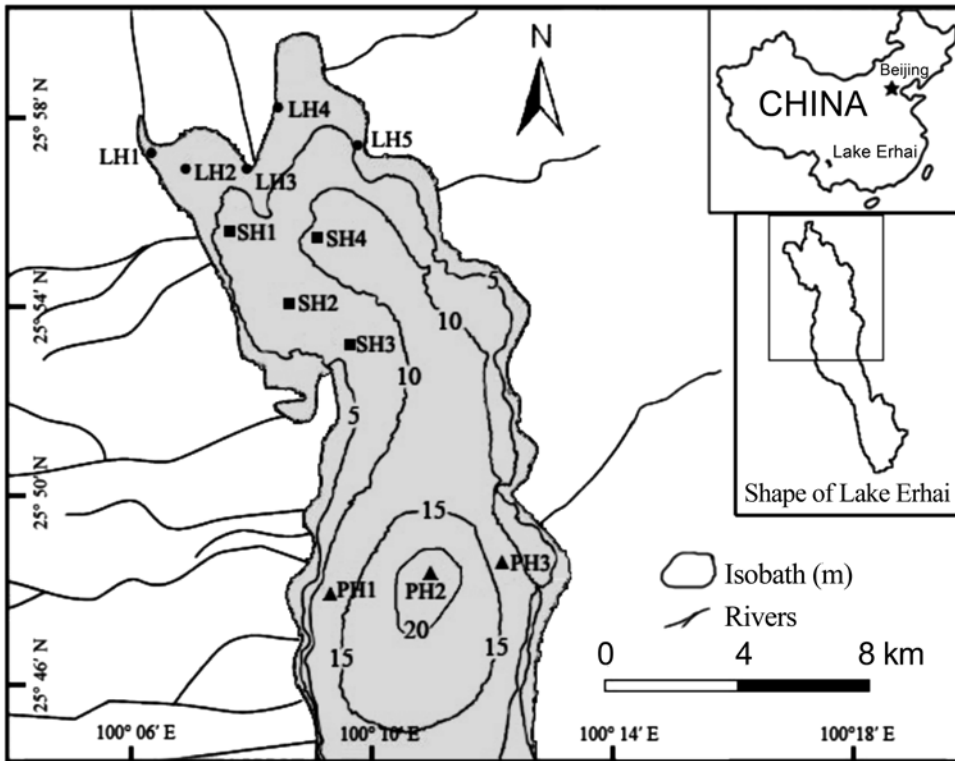
### Study sites and habitat characteristics

Lake Erhai (105° 5–17' E, 23° 35–58' N) is a freshwater plateau lake with a surface area of 250 km<sup>2</sup> and a catchment area of 2,600 km<sup>2</sup> in Yunnan-Guizhou Plateau of China (Fig. 1). The maximum water depth is approximately 21 m without thermal or dissolved oxygen stratification. Twenty-eight fish species have been found in the lake in recent years and most of them are planktivorous. The dominant species are small-bodied fishes, especially non-native species, including freshwater gobies *R. giurinus* and *R. cliffordpopei*, *Neosalanx taihuensis* (Chen, 1956), *Pseudorasbora parva* (Temminck & Schlegel, 1846), *Hypseleotris swinhonis* (Günther, 1873) and *Hemiculter leucisculus* (Basilewsky, 1855). *Channa argus* (Cantor, 1842) is the only recorded piscivorous fish species. *R. giurinus* and *R. cliffordpopei* are the most abundant benthic fish species with annual yields representing about 48 % of total fish yields (kg) in the lake.

Habitat characteristics of the lake were investigated prior to fish sampling (Table 1). For each sampling site, water temperature, dissolved oxygen and conductivity were measured *in situ* using a handheld meter (YSI Model Pro20, Ohio, USA). A handheld pH meter was used to measure pH *in situ* (YSI Model EcoSense pH10A, Ohio, USA). Total nitrogen, total phosphorus and Chlorophyll-*a* were determined using a standard colorimetric method (APHA et al. 1995). Macrozooplanktons were collected by hand-nets (mesh size 64 µm) and counted under a dissecting microscope. Substrata structures were sampled by Peterson dredge (0.0625m<sup>2</sup>) and determined by macroscopic appearance. Biomass (wet weight) of submerged macrophytes was determined using a 30 cm × 50 cm clamp at three random measurements within each sampling site. Habitats for benthic fishes in Lake Erhai were classified into three types: 1) littoral habitat (LH, water depth less than 6 m, high abundance of submerged macrophytes, submersed-macrophyte detritus substrata); 2) sub-littoral habitat (SH, water depths range 6 to 12 m, few submerged macrophytes, submersed-macrophyte detritus and silt substrata); and 3) profundal habitat (PH, water depths ranges 12 to 20 m, no submerged macrophytes, silt and coarse sand substrata).

### Fish sampling and data collection

Five (LH1-LH5), four (SH1-SH4) and three (PH1-PH3) sites were sampled for each habitat in the middle and northern section of the lake (Fig. 1, Table 1). Fish sampling was carried out in the first week of February (winter), May (spring), August (summer) and November (autumn) of 2010 using benthic fyke nets. The net comprised a trunk stem with twenty traps, two end traps and two end pockets. Total length of the net was 15 m, including 12 m of trap (0.6 m for each trap), 2 m of end trap (1 m for each trap) and 1 m of end pocket (0.5 m for each one). The framework of each trap was made of iron wire with the width of 0.35 m and the height of 0.62 m. The end trap was round and the diameter gradually decreased from 0.3 m to 0.1 m. The mesh size of all nets was 4 mm. At each sampling site, eight nets were deployed separately with a stone in each end of the nets. After 24 hours, the catches in the end pockets were collected and rapidly transferred to -20 °C in the laboratory. In each season, the nets were deployed at 8:00 to 10:00 am and we sampled three sites per day (twenty four nets were used each day). The order



**Fig. 1.** Sample sites in the three habitats located in the central and northern section of Lake Erhai (China). Five (LH1-LH5), four (SH1-SH4) and three (PH1-PH3) sites were sampled in littoral (●), sub-littoral (■) and profundal (▲) habitats, respectively.

of site sampling was identical in the four seasons. Hence, fish sampling lasted four days in each season. All the procedures complied with Chinese legislation.

All fishes collected in each fyke net were identified to species level, counted and batch-weighed. A random sub-sample from homogeneous catches of the total catches at each habitat in each season was preserved in 8% formalin for two weeks and then transferred to 75% ethanol for storage. About 1000 individuals of *R. giurinus* and 400 individuals of *R. cliffordpopei* (only around 400 individuals of *R. cliffordpopei* were sampled in PH in winter and autumn) were measured for each habitat and each season. Total length (TL, nearest mm) and body mass (BM, nearest 0.01 g) of individuals from the sub-samples were measured after preservation. Since preservation can affect the length/mass ratio, all subsequent analyses were performed based on preservation-corrected TL and BM. Specifically, TL and BM were measured individually before and after preservation for 100 specimens and the relationships between fresh and preserved TL and BM were established ( $TL_{\text{Fresh}} = 1.007 TL_{\text{Preserved}} + 0.417$ ,  $R^2 = 0.956$  and  $BM_{\text{Fresh}} = 0.877 BM_{\text{Preserved}} + 0.011$ ,  $R^2 = 0.967$ ,  $n = 100$ ). These equations were then used to calculate preservation-corrected TL and BM.

### Statistical analysis

Goby abundances in the three habitats were estimated using catch per unit effort (CPUE), defined as the number of individuals caught in one net per day ( $\text{ind. net}^{-1} \text{ day}^{-1}$ ). Differences

in goby abundances (i.e., CPUE) between habitats and seasons were tested using repeated-measures ANOVA (RM-ANOVA) with habitats as a fixed factor and seasons as a random factor. Sphericity assumption was tested using Mauchly's test and the degrees of freedom were adjusted by Greenhouse-Geisser Epsilon when data violated the assumption of sphericity. Because the interactions between habitats and seasons were significant (Table 2), one-way ANOVAs with Tukey's multiple comparisons were subsequently used to test the differences in goby abundances between habitats in each season separately. Data of goby abundances were log-transformed to achieve normality and homoscedasticity.

Correlation analyses with Pearson correlation coefficients were used to explore how goby abundances were associated with environmental variables. Correlation analyses were conducted separately for the two goby species. Environmental variables and goby abundances were averaged in each season in correlation analysis.

Residuals from a linear regression of TL (log-transformed) and BM (log-transformed) were used as an index of body condition (Schulte-Hostedde et al. 2005). A positive body condition value indicated that the individual had a heavier body mass related to body length compared to the rest of the population. Differences in body condition of the two goby species between habitats and seasons were tested using General Linear Model (GLM) procedures with habitats as a fixed factor and seasons as a random factor. GLM were run initially with the interaction term (full model) between habitats and seasons and again with-

**Table 1.** Environmental variables measured in the three habitats in Lake Erhai (China). Reported values are mean  $\pm$  standard deviation.

Environmental variables	Littoral habitat (LH)	Sub-littoral habitat (SH)	Profundal habitat (PH)
Water depth (m)	3.11 $\pm$ 1.17 (n=40)	8.13 $\pm$ 1.35 (n=32)	15.92 $\pm$ 3.14 (n=24)
Water temperature ( $^{\circ}$ C)	16.92 $\pm$ 4.74 (n=40)	17.14 $\pm$ 4.48 (n=32)	16.91 $\pm$ 4.64 (n=24)
Submerged macrophytes (g m <sup>-2</sup> )	3307.35 $\pm$ 881.32 (n=40)	102.66 $\pm$ 49.49 (n=32)	0 (n=24)
pH	9.33 $\pm$ 0.30 (n=40)	9.20 $\pm$ 0.33 (n=32)	9.08 $\pm$ 0.26 (n=24)
Secchi depth (cm)	214.17 $\pm$ 35.91 (n=40)	235.43 $\pm$ 22.47 (n=32)	254.66 $\pm$ 25.43 (n=24)
Conductivity ( $\mu$ S cm <sup>-1</sup> )	237.33 $\pm$ 167.50 (n=40)	232.62 $\pm$ 11.89 (n=32)	233.87 $\pm$ 12.76 (n=24)
Dissolved oxygen (mg L <sup>-1</sup> )	9.23 $\pm$ 1.05 (n=40)	7.56 $\pm$ 1.08 (n=32)	7.51 $\pm$ 0.88 (n=24)
Total nitrogen (mg L <sup>-1</sup> )	0.46 $\pm$ 0.12 (n=20)	0.42 $\pm$ 0.08 (n=16)	0.43 $\pm$ 0.05 (n=12)
Total phosphorus (mg L <sup>-1</sup> )	1.38 E-2 $\pm$ 0.81 E-2 (n=20)	1.26 E-2 $\pm$ 0.77 E-2 (n=16)	1.42 E-2 $\pm$ 0.69 E-2 (n=12)
Chlorophyll-a (mg L <sup>-1</sup> )	8.27 $\pm$ 2.88 (n=20)	12.12 $\pm$ 3.82 (n=16)	12.44 $\pm$ 3.09 (n=12)
Macrozooplankton (ind. L <sup>-1</sup> )	296.43 $\pm$ 60.56 (n=20)	198.62 $\pm$ 35.48 (n=16)	92.65 $\pm$ 27.43 (n=12)
Substrata structures <sup>1</sup>	-1	0	1
CF <sup>2</sup>	32.91 $\pm$ 8.16 (n=160)	7.67 $\pm$ 2.74 (n=128)	0.16 $\pm$ 0.09 (n=96)
<i>Pseudorasbora parva</i> <sup>3</sup>	8.83 $\pm$ 4.55 (n=160)	1.52 $\pm$ 0.65 (n=128)	0 (n=96)
<i>Hypseleotris swinhonis</i> <sup>3</sup>	12.51 $\pm$ 5.58 (n=160)	2.08 $\pm$ 1.41 (n=128)	0 (n=96)
<i>Hemiculter leucisculus</i> <sup>3</sup>	5.41 $\pm$ 2.10 (n=160)	1.87 $\pm$ 0.94 (n=128)	0.16 $\pm$ 0.09 (n=96)
<i>Channa argus</i> <sup>4</sup>	1.46 $\pm$ 1.12 (n=160)	0.34 $\pm$ 0.22 (128)	0 (96)

<sup>1</sup> Type of submersed macrophyte detritus, mixture of submersed macrophyte detritus and silt, mixture of silt and coarse sand were assigned value of -1, 0 and 1, respectively.

<sup>2</sup> Total abundances (ind. net<sup>-1</sup> day<sup>-1</sup>) of all fish species except *R. giurinus* and *R. cliffordpopei* caught in fyke nets.

<sup>3</sup> Abundances (ind. net<sup>-1</sup> day<sup>-1</sup>) of the other dominant species (species with relative abundance  $\geq$  10% of total catch) caught in fyke nets

<sup>4</sup> Abundances (ind. net<sup>-1</sup> day<sup>-1</sup>) of piscivorous fish species (i.e., *Channa argus*) in fyke nets.

out the interaction (simplified model) if it was not significant. Because the interactions between habitats and seasons was significant for *R. giurinus*, one-way ANOVAs with Tukey's multiple comparisons were subsequently used to test the differences in body condition between habitats in each season separately. Statistical analyses were performed using SPSS 16.0 software (SPSS Inc., Chicago, USA) and the significance was determined at  $p < 0.05$  in all cases.

## Results

### Goby abundances across habitats and seasons

A total of 67,819 individuals of *R. giurinus* and 36,043 individuals of *R. cliffordpopei* were sampled across four seasons. The abundances of the two goby species were significantly influenced by habitat, season,

**Table 2.** Repeated-measures ANOVAs (RM-ANOVA) used to test differences in the abundances of *R. giurinus* and *R. cliffordpopei* between habitats (fixed factor) and seasons (random factor) in Lake Erhai (China).

Species	Sources	d. f.	F	<i>p</i>
<i>R. giurinus</i>	Habitats	2	288.436	<0.001
	Error	93		
	Seasons	2	46.508	<0.001
	Error	172		
	Habitats × Seasons	4	19.984	<0.001
<i>R. cliffordpopei</i>	Habitats	2	221.213	<0.001
	Error	93		
	Seasons	2	122.403	<0.001
	Error	213		
	Habitats × Seasons	5	36.529	<0.001

and the interaction between habitat and season (RM-ANOVA, Table 2). The abundance of *R. giurinus* significantly differed between habitats across the four seasons (one-way ANOVAs, Table 3). Specifically, the abundance of *R. giurinus* was significantly higher in PH than in LH and SH for all seasons (Tukey HDS,  $p < 0.001$ ) and in SH than in LH (Tukey HDS,  $p < 0.001$ ) except in winter (Tukey HDS,  $p = 0.079$ ) (Fig. 2). The abundance of *R. cliffordpopei* also significantly differed between habitats across the four seasons (one-way ANOVAs, Table 3). In spring, autumn and winter, the abundance of *R. cliffordpopei* was significantly higher in PH than in SH and in LH (Tukey HDS,  $p < 0.001$ ), whereas there were no significant differences between LH and SH (Tukey HDS,  $p = 0.132, 0.095$  and  $0.422$ , respectively). In summer,

the abundance of *R. cliffordpopei* was significantly different between the three habitats (Tukey HDS, LH vs SH,  $p = 0.016$ , LH vs PH,  $p < 0.001$ , SH vs PH,  $p < 0.001$ ) (Fig. 2).

### Goby abundances in relation to environmental variables

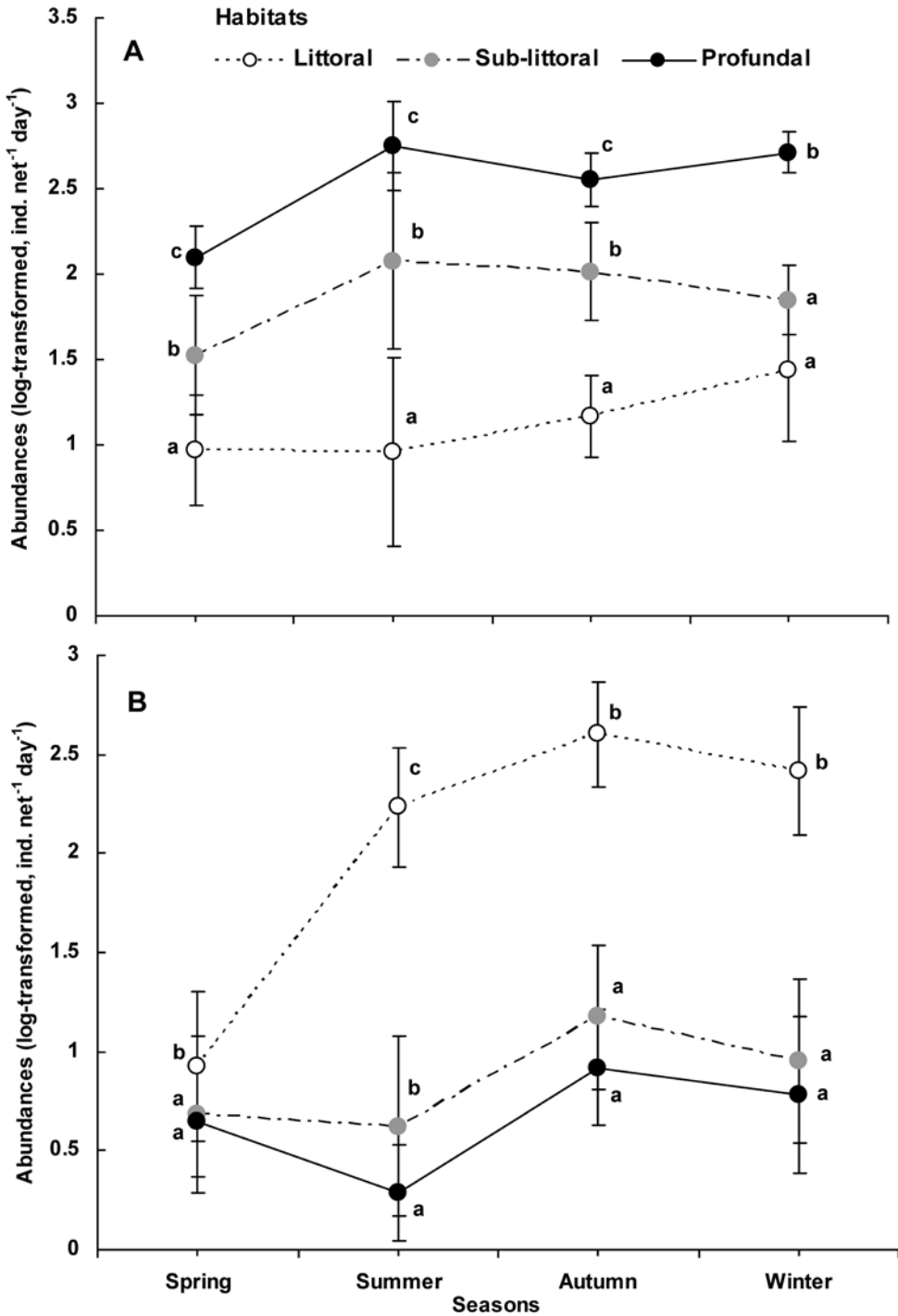
A strong association between environmental variables and goby abundances was observed for the two species. Specifically, Pearson correlation coefficients ( $r$ ) demonstrated that the abundances of *R. giurinus* were positively associated with water depth ( $r = 0.667$ ,  $p < 0.001$ ), silt and coarse sand substrata ( $r = 0.640$ ,  $p < 0.001$ ). In contrast, the abundances of *R. cliffordpopei* were positively correlated with submerged macrophytes ( $r = 0.662$ ,  $p < 0.001$ ), abundances of other fish ( $r = 0.606$ ,  $p < 0.001$ ), densities of macrozooplankton ( $r = 0.363$ ,  $p < 0.001$ ), concentrations of dissolved oxygen ( $r = 0.323$ ,  $p < 0.001$ ), submersed macrophyte detritus substrata ( $r = -0.608$ ,  $p < 0.001$ ) (Table 4).

### Individual performances and habitat use

Habitats, seasons and their interaction term had significant effects on the body condition of *R. giurinus* (RM-ANOVA, Table 5). Body condition of *R. giurinus* differed significantly in summer, autumn and winter but not in spring (one-way ANOVAs, Table 6). In summer and autumn, *R. giurinus* had significantly higher body condition in PH compared with LH (Tukey HDS,  $p = 0.001$  and  $0.001$ , respectively) and SH (Tukey HDS,  $p < 0.001$  and  $p = 0.005$ , respectively) (Fig. 3, Table 6). In winter, body condition of *R. giurinus* was significantly lower in LH

**Table 3.** One-way ANOVAs used to test the differences in the abundances of *R. giurinus* and *R. cliffordpopei* between habitats for each season in Lake Erhai (China).

Seasons	Sources	<i>R. giurinus</i>			<i>R. cliffordpopei</i>		
		d.f.	F	<i>p</i>	d.f.	F	<i>p</i>
Spring	Between Habitats	2	82.014	<0.001	2	139.383	<0.001
	Within Habitats	93			93		
	Total	95			95		
Summer	Between Habitats	2	239.734	<0.001	2	179.449	<0.001
	Within Habitats	93			93		
	Total	95			95		
Autumn	Between Habitats	2	216.930	<0.001	2	131.972	<0.001
	Within Habitats	93			93		
	Total	95			95		
Winter	Between Habitats	2	65.013	<0.001	2	5.286	0.007
	Within Habitats	93			93		
	Total	95			95		

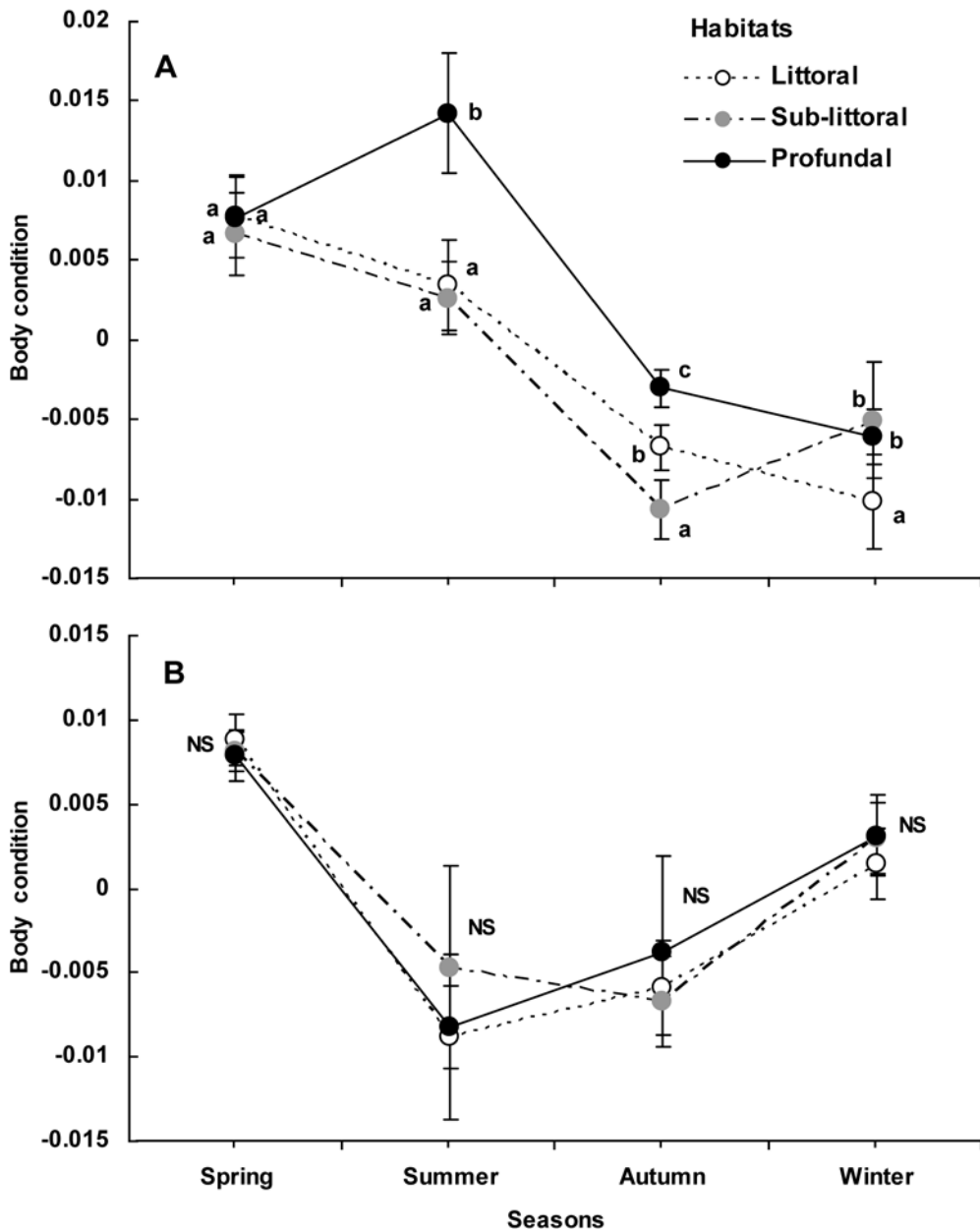


**Fig. 2.** Mean abundances (log-transformed) of *R. giurinus* (A) and *R. cliffordpopei* (B) across habitats and seasons (sampling sizes were 40, 32 and 24 for littoral, sub-littoral and profundal habitat in each season, respectively) in Lake Erhai (China). The abundances in the same season with different letters were significantly different. Error-bars represent the standard deviations.

compared to SH (Tukey HDS,  $p < 0.001$ ) and PH (Tukey HDS,  $p = 0.027$ , Table 6). The body condition of *R. cliffordpopei* differed significantly between seasons ( $p < 0.001$ ) but not between habitats ( $p = 0.095$ , RM-ANOVA, Table 5) (Fig. 3).

## Discussion

The present study demonstrated that two congeneric and introduced freshwater goby species display a strong level of habitat segregation in Lake Erhai.



**Fig. 3.** Body condition of *R. giurinus* (A,  $n = 1000$  individuals in each habitat and season) and *R. cliffordpopei* (B,  $n = 400$  in each habitat and season) across habitats and seasons in Lake Erhai (China). Body conditions in the same season with different letters were significantly different (NS: not significantly different). Error-bars represent the standard deviations.

*R. giurinus* mostly occupied PH that was characterized by an absence of submerged macrophytes, no predator (*C. argus*) and lower interspecific competition (i.e., the presence of other small-bodied species including *P. parva*, *H. swinhonis* and *H. leucisculus*). These results are in accordance with the reports from native range lakes along the Yangtze River (Xie et al. 2000a, Xie et al. 2005, Li et al. 2010) where *R. giurinus* mainly occupies habitats without vegetation or with simple-structured vegetation (e.g., *Nelumbo*

*nucifera* and *Trapa bispinosa*) located in the central parts of the lakes. Habitat complexity from aquatic plants may be unimportant for benthic small-bodied goby species because they have two pelvic fins that form a small sucking plate enabling attachment to the lake bottom, and thus are probably less vulnerable to predators compared with those staying off the bottom (Aboul Hosn & Downing 1994, Xie et al. 2000a, Xie et al. 2005, Horinouchi 2007). In Lake Erhai, however, *C. argus* was the only potential predator of the two

**Table 4.** Correlation analyses (Pearson correlation coefficients ( $r$ ) and  $P$ -values) between the abundances of *R. giurinus*, *R. cliffordpopei* and environmental variables in Lake Erhai (China).

Environmental variables	<i>R. giurinus</i>		<i>R. cliffordpopei</i>	
	$r$	$p$	$r$	$p$
Water depth (m)	0.677	<0.001	-0.572	<0.001
Water temperature (°C)	0.169	0.001	0.174	0.001
Submerged macrophytes (g m <sup>-2</sup> )	-0.448	<0.001	0.662	<0.001
pH	-0.053	0.300	0.093	0.068
Secchi depth (cm)	0.209	<0.001	-0.224	<0.001
Conductivity (μS cm <sup>-1</sup> )	-0.015	0.743	0.051	0.318
Dissolved oxygen (mg L <sup>-1</sup> )	-0.226	<0.001	0.323	<0.001
Total nitrogen (mg L <sup>-1</sup> )	-0.089	0.064	0.083	0.104
Total phosphorus (mg L <sup>-1</sup> )	0.013	0.794	0.097	0.084
Chlorophyll-a (mg L <sup>-1</sup> )	0.188	<0.001	-0.010	0.894
Macrozooplankton (ind L <sup>-1</sup> )	-0.524	<0.001	0.363	0.011
CF <sup>1</sup>	-0.452	<0.001	0.606	<0.001
Substrata structures <sup>2</sup>	0.640	<0.001	-0.608	<0.001

**Table 5.** General Linear Model used to test differences in body condition of *R. giurinus* and *R. cliffordpopei* between habitats (fixed factor) and seasons (random factor) in Lake Erhai (China).

Species	Sources	d.f.	F	$p$
<i>R. giurinus</i> Full model	Habitats	2	6.266	0.002
	Error	7		
	Seasons	3	13.644	0.004
	Error	6		
	Habitats × Seasons	6	8.269	<0.001
	Error	11855		
<i>R. cliffordpopei</i> Full model	Habitats	2	0.008	0.992
	Error	31		
	Seasons	3	23.333	<0.001
	Error	10		
	Habitats × Seasons	6	1.345	0.234
	Error	4613		
Simplified model	Habitats	2	2.359	0.095
	Error	4169		
	Seasons	3	11.653	<0.001
	Error	4169		

goby species (Ma & Xie 1999, Table 1) and its distribution was limited exclusively to LH. Moreover, the other small fish species (e.g., *H. swinhonis*, *P. parva* and *H. leucisculus*, Table 1) also used LH in Lake Erhai, which is similar to what has been found in native shallow lakes (Xie et al. 2000a, Xie et al. 2005, Li et al. 2010). Therefore, *R. giurinus* may have lower predation risk and interspecific competition when using PH in Lake Erhai. In contrast, *R. cliffordpopei* mainly used LH that was characterized as a substantially heterogeneous habitat with abundant prey but stronger predation risks (i.e., *C. argus*) and interspecific com-

petition with similar fishes (Xie et al. 2000a, Li et al. 2010, Neaher et al. 2010).

Habitat segregation is an important strategy that promotes coexistence among sympatric species with niche overlap and it usually leads to multi-dimension resource partitioning involving food, space, shelter or nursery site (Cooper et al. 2008, Friberg et al. 2008, Gross et al. 2009). For example, in Biggjavri lake of Norway, grayling *Thymallus thymallus* (Linnaeus, 1758) were exclusively caught in shallow near-shore areas, feeding chiefly on surface insects and Trichoptera larvae, whereas arctic charr *Salvelinus alpinus*



**Table 6.** One-way ANOVAs used to test differences in body condition of *R. giurinus* between habitats for each season in Lake Erhai (China).

Seasons	Sources	d.f.	F	<i>p</i>
Spring	Between Habitats	2	0.352	0.704
	Within Habitats	3075		
	Total	3077		
Summer	Between Habitats	2	22.656	<0.001
	Within Habitats	2847		
	Total	2849		
Autumn	Between Habitats	2	4.044	0.018
	Within Habitats	2703		
	Total	2705		
Winter	Between Habitats	2	7.987	<0.001
	Within Habitats	3226		
	Total	3228		

(Linnaeus, 1758) were mainly found along the benthic profile, feeding predominantly on insects and snails (Amundsen et al. 2010). Several goby species have been shown to display habitat and food partitioning when they become abundant in non-native ranges (Erös et al. 2005, Borza et al. 2009, Borcharding et al. 2012). The observed habitat segregation of the two goby species may alleviate their food overlap and enhance their coexistence at high abundance in Lake Erhai (Xie et al. 2000b, Xie et al. 2005, Zhang 2005). Therefore, it would be very insightful to determine whether this habitat segregation is potentially associated with trophic niche differentiation. In addition, species of the genus *Rhinogobius* were male-guard nest spawning and nest site availability is crucial for reproduction (Takahashi & Yanagisawa 1999, Tamada 2005). The different habitat preference is also likely to mitigate the competition for nest sites between the two species.

Body condition is known to be an integrative assessment of individual performances and often considered to be important for evaluating habitat quality in fishes (Lloret et al. 2005, Johnson 2007). Occupying high quality habitat usually results in high body condition, which can subsequently affect survivorship, competitive ability and reproductive success (Green 2001, Koops et al. 2004, Lloret et al. 2005). We found that the body condition of *R. giurinus* was significantly higher in PH compared to LH in summer, winter and autumn. So PH might represent a more profitable habitat for this species. Xie et al. (2005) observed a similar pattern where *R. giurinus* showed greater body length and condition factor in the pelagic habitat (less covered by macrophytes) compared to the littoral habitat (heavily covered by macrophytes) in Liangzi Lake. Predation

pressure in LH may affect the body condition of *R. giurinus* since individuals exposed to a high predation risk usually spend more time avoiding predators and forage less frequently with food of lower quality (Madin et al. 2010), leading to lower energy intakes and lipid reserves (Walsh et al. 2012). Additionally, the observed lower body condition of *R. giurinus* in LH might be caused by the lower feeding efficiency resulting from the visual and swimming barriers created by the stems and foliage of macrophytes, as well as stronger competition with ecologically similar species (Tugend & Allen 2004, Xie et al. 2005). In contrast, the body condition of *R. cliffordpopei* did not vary significantly between habitats, suggesting that the quality of the three habitats was similar for this species in Lake Erhai.

Two possible mechanisms might have led to the observed habitat segregation. First, competition between the two goby species might have driven the exclusion of *R. cliffordpopei* from PH. Strong interspecific competition is likely to occur since the species were found to display a high level of diet overlap in native range lakes along the middle and lower reaches of the Yangtze River (Xie et al. 2000b, Xie et al. 2005, Zhang 2005). Indeed, sympatric goby species of the genus *Rhinogobius* have often been observed to show interference competition for resources (Sone et al. 2001, Ito & Yanagisawa 2003, Sone et al. 2006). For instance, in tributaries of the Shimanto River of Japan, habitat partitioning between *Rhinogobius* sp. LD (large-dark type) and *Rinogobius* sp. CB (cross-band type) is a result of interspecific competition (Sone et al. 2001, Sone et al. 2006). Alternatively, the two goby species might display differences in habitat use that could lead to selective habitat segregation (Gill & Potter 1993, Hernaman & Probert 2008, Horinouchi 2008), as observed for *Acentrogobius* sp. 1 and *A.* sp. 2 in Lake Hamana, Japan (Horinouchi 2008). In conclusion, our study represents an empirical case study demonstrating that two congeneric and highly abundant fish species exhibit a strong level of habitat segregation outside of their native range. However, determining the mechanisms triggering the observed segregation will require further investigations.

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