

Coexisting invasive gobies reveal no evidence for temporal and trophic niche differentiation in the sublittoral habitat of Lake Erhai, China

Zhiqiang Guo^{1,2,3,4}, Jiashou Liu¹, Sovan Lek^{1,2}, Zhongjie Li¹, Fengyue Zhu¹, Jianfeng Tang¹, Robert Britton⁴, Julien Cucherousset²

¹State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, The Chinese Academy of Sciences, Wuhan, China

²CNRS, ENFA, UMR5174 EDB (Laboratoire Évolution & Diversité Biologique), Université Toulouse III Paul Sabatier, Toulouse, France

³Key Laboratory of Tropical Marine Bio-resources and Ecology, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou, China

⁴Centre for Conservation Ecology and Environmental Change, Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Bournemouth, UK

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Abstract – Niche differentiation facilitates the coexistence of species within a community through avoidance of competition via mechanisms involving spatial, temporal and/or trophic dimensions. Where invasive species coexist in their non-native range, niche differentiation could allow their persistence at higher levels of abundance. Here, we tested whether there was temporal and/or trophic niche differentiation between two congeneric invasive goby species (*Rhinogobius cliffordpopei* and *Rhinogobius giurinus*) in the sublittoral habitat of Lake Erhai (south-west China) through quantifying their diel and seasonal rhythm of locomotion activities, feeding activities and diet composition. Both species displayed two similar diel peaks in activity and two main feeding periods (6:00–10:00 and 18:00–22:00), with rhythms of locomotion and feeding activity not differing significantly between the species in each season. Their diets had a high degree of overlap, being primarily composed of macrozooplankton, aquatic insects and shrimp larvae, with no diel changes across the seasons. Thus, in this habitat, there was no clear temporal or trophic niche differentiation between the invasive congeners, indicating their coexistence with high temporal and trophic overlap. In conjunction with data from the littoral and profundal habitats, the gobies revealed different strategies across the habitats (e.g. spatial segregation, trophic niche differentiation) that minimised their competitive interactions and promoted their coexistence. This suggests that the interactions of invasive fishes during the integration into native communities can be context dependent, varying according to factors including habitat and the availability of food resources.

Key words: gobies; ecological niche; diel activity; feeding rhythm; niche differentiation

Introduction

Understanding the mechanisms that allow ecologically similar species to coexist within ecosystems is a central aspect of community ecology (Chesson 2000; Amarasekare 2003; Kylafis & Loreau 2011). The competitive exclusion theory predicts that species will eventually out-compete and displace each other when they compete for limited resources (Hardin 1960), whereas the niche differentiation theory predicts that other mechanisms, including increased

specialisations in resource use that develop as levels of interspecific competition increase, will facilitate their stable coexistence (Jones et al. 2001; Amarasekare 2003; Kylafis & Loreau 2011). When non-native species are introduced into communities, then these mechanisms are integral to determining their outcomes (Baiser et al. 2010), such as through influencing their ability to establish abundant populations (Lockwood et al. 2005) and then determining their ecological interactions and consequences (Woodford et al. 2005; Tran et al. 2015).

Correspondence: J. Liu, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, The Chinese Academy of Sciences, Wuhan 430072, China. E-mail: jsliu@ihb.ac.cn

Ecological niche differentiation involves a spatial axis (habitat), trophic axis (diet), a temporal axis and/or their combination (Chesson 2000; Kronfeld-Schor & Dayan 2003). In heterogeneous environments, the most frequent mechanisms facilitating the coexistence of ecologically similar species involve specialisation in microhabitat use and feeding (Jones et al. 2001; Amarasekare 2003). The temporal dimension has tended to be overlooked in many studies, despite theory suggesting it should mediate ecological interactions among competitors through diel and/or seasonal partitioning in resource exploitation (Kronfeld-Schor & Dayan 1999, 2003; Kronfeld-Schor et al. 2001; Richards 2002). Thus, even where there is spatial and trophic overlap in niches, diel and seasonal differences in resource exploitation between potential competitors could still result in niche differentiation and so facilitate the coexistence of the species (Richards 2002; Kronfeld-Schor & Dayan 2003; Blanchet et al. 2008). Whilst there is now a growing number of studies providing empirical evidence of temporal partitioning between competing species of ants (Albrecht & Gotelli 2001), bats (Adams & Thibault 2006), mice (Jones et al. 2001) and birds (Veen et al. 2010), there is little supporting evidence from fishes (Blanchet et al. 2008).

Gobies of the genus *Rhinogobius* (Gill 1859) are common benthic fishes in most East Asian countries and some areas of south-eastern Asia (Wu & Zhong 2008). *Rhinogobius giurinus* (Rutter 1897) and *Rhinogobius cliffordpopei* (Nichols 1925), native to Japan, and central and south-east China (Wu & Zhong 2008), were accidentally introduced into several lakes in Yunnan–Guizhou Plateau (south-west China) in the 1950/1960s and have since spread into neighbouring watersheds (Xie et al. 2001; Yuan et al. 2010) where they display relatively similar life histories and diet compositions (Xie et al. 2000, 2005; Zhang 2005). They were introduced into Lake Erhai in 1961, a 250 km² lake in the Yunnan Province of China, and have since become the dominant benthic fish species (Du & Li 2001). In their native range, *R. giurinus* is associated with vegetation-free or sparsely vegetated lentic habitats (Xie et al. 2005; Li et al. 2010) where *R. cliffordpopei* occurs only at very low densities. Thus, there is no information available about their habitat preferences when the two species co-occur naturally. By contrast, in the littoral and profundal habitats of Lake Erhai, work has revealed considerable habitat segregation and trophic niche differentiation between them, with highly contrasting abundances (Guo et al. 2012, 2014). In the sublittoral habitat, however, their populations coexist in comparable and moderate abundances, suggesting that this is a mixing or transition zone for the species (Guo et al. 2012). Consequently, their sublittoral

populations provide the opportunity to test hypotheses on trophic and temporal niche differentiation in two invasive, coexisting and congeneric fishes, and so, the aim here was to (i) quantify their diel and seasonal rhythms of locomotion and foraging activities to determine their temporal niches and the extent of their overlap and (ii) identify their diel and seasonal diet compositions to determine their trophic niches and the extent of their overlap within this specific habitat. Outputs were then applied to testing the hypothesis that the coexistence of these invasive congeners was facilitated by diel and seasonal differences in their rhythms of locomotion and feeding activity, and/or by their trophic (i.e. diel and seasonal differences in diet composition) niche differentiation.

Materials and methods

Study area

Lake Erhai (105°5-17' E, 23°35-58' N) is an alpine lake located in Yunnan province, south-west China. Available habitats for benthic fish species are classified as littoral habitat (water depths <6 m), sublittoral habitat (water depths range 6–12 m) and profundal habitat (water depths ranges 12–20 m). The abundance of *R. cliffordpopei* is highest in the littoral habitat, moderate in sublittoral habitat and lowest in profundal habitat, whereas the abundance of *R. giurinus* generally shows the opposite pattern, being also of moderate abundance in the sublittoral (Guo et al. 2012). Here, the focus is on the sublittoral, characterised by the presence of few submerged macrophytes and a substrate composed of macrophyte detritus and soft mud. In the habitat, the two gobies dominate the fish community and the other fish species are rare, with species present including *Pseudorasbora parva*, *Hypseleotris swinhonis*, *Hemiculter leucisculus* and *Channa argus* (Guo et al. 2012). The only piscivorous fish species recorded, *C. argus*, had their highest abundance in the littoral (1.46 ind. net⁻¹·day⁻¹), very low abundance in the sublittoral (0.34 ind. net⁻¹·day⁻¹) and were absent in the profundal habitat. The estimated total biomass of the macrozooplankton available for the gobies in each habitat was 1.86, 2.35 and 1.17 ind. l⁻¹ per catch per unit effort of weight (CPUE, g·net⁻¹·h⁻¹) in the littoral, sublittoral and profundal habitats, respectively. The available benthos (aquatic insects and Tubificidae) was 1.09, 1.44 and 0.88 ind. m⁻² per CPUE of the fish in the same habitats (Guo et al. 2012, 2014).

Fish sampling and diet composition

Rhinogobius giurinus and *R. cliffordpopei* in the lake were sampled in each season of 2011: spring (April),

summer (July), autumn (October) and winter (January). Five benthic fyke nets (0.4 cm stretched mesh size) were used on each occasion and were fished over the full 24-h cycle. They were first deployed at 7:00, fished for 2 h, rapidly retrieved, sorted (i.e. all fish removed) and then redeployed approximately 500 m from the last sampling point for a further 2 h. This was repeated until the 24-h cycle had been sampled. Gobies collected in each of the five nets per 2 h sampling time were identified to species and counted per net before the samples were pooled for that entire 2 h sample, and a random subsample of approximately 30 individuals preserved in 8% formalin for 2 weeks before being transferred to 75% ethanol for further analyses.

Dietary data were generated using gut content analyses (GCA). The total body length (L_T , nearest mm) and body mass (M_T , to 0.01 g) were recorded for each preserved specimen (Table 1) before the foregut was removed (Xie et al. 2000, 2005). All nonempty guts were then weighed to the nearest 0.01 mg, food contents removed and the emptied guts weighed once more so that food weight could be calculated. The food items were identified to the lowest possible taxonomic level under a dissecting microscope and then were classified into ten categories: macrozooplankton, aquatic insects, shrimp larvae, Tubificidae, Gastropoda, fish larvae, fish eggs, Ostracoda, plant material and unidentified items. For each food category, the following indices were calculated: frequency of occurrence (%O), percentage of number (%N) and percentage of weight (%W). Diet composition was then estimated using the index of relative importance (%IRI) using %O, %N and %W (cf. Guo et al. 2014). Schoener's index (S) indicated the overlap in diet between the two species at each diel period and by season (Schoener 1970) and was calculated from: $S_{xy} = 1 - 0.5 \sum_1^n |P_{xi} - P_{yi}|$, where S_{xy} is the dietary overlap between species x and y , and P_{xi} and P_{yi} are the proportions in number of prey item i in the diet of species x and are the proportions in number of prey item i in the diet of species y , respectively. The values of S range from 0 (indicating no overlap) to 1 (indicating complete overlap), and

values higher than 0.60 indicate high overlap; values between 0.33 and 0.59 indicate moderate overlap, and values lower than 0.33 indicate low overlap.

Data and statistical analyses

The diel and seasonal rhythms of locomotion activity were determined using CPUE (ind. net⁻¹·h⁻¹) of the benthic fyke nets for each 2-h sampling period. Differences in CPUE [$\log(x + 1)$ transformed] between species, seasons and sampling periods were tested using three-way ANOVAS. A t -test was then used to test for differences in locomotion activity between the two species in each of the four seasons (i.e. spring, summer, autumn or winter).

Diel and seasonal rhythms of feeding activity were determined using the vacuity index (VI) and weight of gut content (WGC). For each sampling period, VI was expressed calculated as the proportion (%) of empty guts in the total sample. WGC was calculated as (food weight of nonempty gut/eviscerated weight of the body) \times 100. Differences in VI between the two species within the same season were tested using Mann–Whitney U -tests as there was only one measurement of VI for each fish in the same sampling period in each season. Note that diel differences in VI between the two species in the same sampling period were not tested. Differences in WGC [$\log(x + 1)$ transformed] between species, seasons and sampling periods (i.e. each of the 2 h) were tested using three-way ANOVAS.

Diet composition was quantified using %IRI of each of the ten food categories. As sample size on each sampling occasion was occasionally small due to high proportions of empty guts, especially in winter, and when the number of guts with food was below 6, then the samples were pooled for further analyses into four time periods: morning (6:00–11:59 h), afternoon (12:00–17:59 h), early night (18:00–23:59 h) and late night (00:00–5:59 h). Thus, the %IRI was calculated for each of the four diel time periods and for each season. Chi-square tested differences in %IRI between species in the same time period and in the same season.

Table 1. Mean (\pm SD) total length (TL in mm) and body mass (BM in g) of *Rhinogobius giurinus* and *Rhinogobius cliffordpopei* used for gut content analyses in the four seasons of 2011 in Lake Erhai (China).

	<i>R. giurinus</i>		<i>R. cliffordpopei</i>	
	TL (mm)	BM (g)	TL (mm)	BM (g)
Spring	37.7 \pm 7.9 ($n = 125$)	0.45 \pm 0.23	36.1 \pm 4.9 ($n = 112$)	0.44 \pm 0.19
Summer	40.3 \pm 6.6 ($n = 118$)	0.52 \pm 0.27	27.4 \pm 3.2 ($n = 132$)	0.18 \pm 0.08
Autumn	33.6 \pm 4.4 ($n = 134$)	0.36 \pm 0.15	30.7 \pm 5.4 ($n = 127$)	0.27 \pm 0.11
Winter	35.4 \pm 4.5 ($n = 103$)	0.40 \pm 0.21	32.5 \pm 2.7 ($n = 98$)	0.32 \pm 0.15

Normality and homogeneity of data were tested using one-sample Kolmogorov–Smirnov test and Levene’s test. All statistical analyses were performed using R version 2.15.3 (R Development Core Team 2014).

Results

Diel and seasonal differences in locomotion activity

In the 24-h sampling periods of each season, both species displayed two clear peaks in locomotion activity when their CPUE increased, occurring from 6:00 to 10:00, and then 18:00 to 22:00 (Fig. 1). The interaction term between species, seasons and sampling periods was significant (three-way ANOVAS, Table 2). Although this diel pattern was similar between the species, their actual CPUE was

Table 2. Three-way ANOVAS used to test the differences in catch per unit effort [log (x + 1) transformed] of *Rhinogobius giurinus* and *Rhinogobius cliffordpopei* between species, seasons and sampling periods in 2011 in Lake Erhai (China).

Sources	d.f.	F	P
Species	1	267.99	<0.001
Seasons	3	2475.05	<0.001
Sampling periods	11	6087.62	<0.001
Species × Seasons	3	325.91	<0.001
Species × Sampling periods	11	228.85	<0.001
Seasons × Sampling periods	33	254.18	<0.001
Species × Seasons × Sampling periods	33	1119.55	<0.001
Error	384		

significantly different (three-way ANOVAS, $F_{1,384} = 26799$, $P < 0.01$, Table 2), with differences dependent on seasons and sampling time (three-way ANOVAS, $F_{33,384} = 1119$, $P < 0.01$, Table 2).

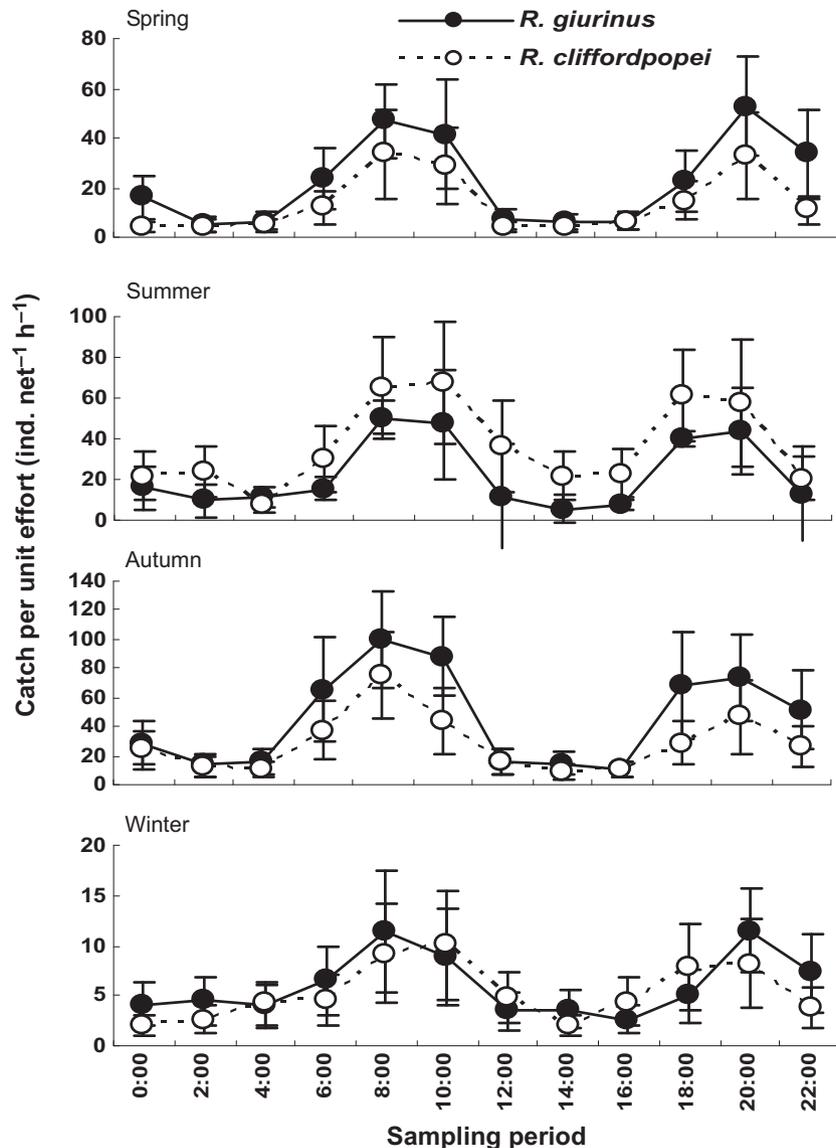


Fig. 1. Diel changes in catch per unit effort (CPUE, ind. net⁻¹·h⁻¹) of *Rhinogobius giurinus* and *Rhinogobius cliffordpopei* in the four seasons of 2011 in Lake Erhai (China). Bars are standard deviations (n = 5). Note the differences in values of the Y-axes.

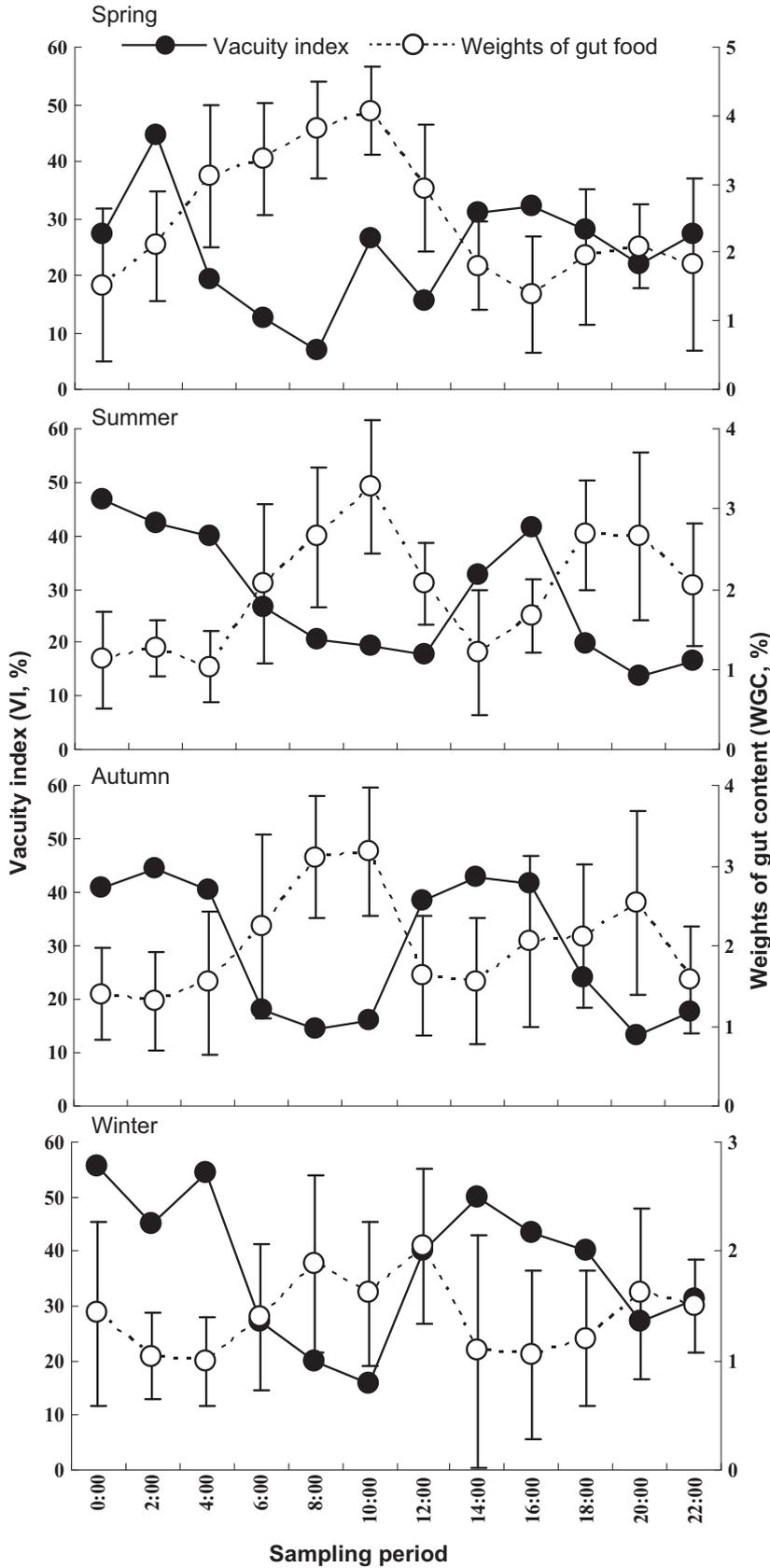


Fig. 2. Diel changes in vacuity index (VI, %) and weights of gut content (WGC, %) of *Rhinogobius giurinus* in the four seasons of 2011 in Lake Erhai (China). Bars are standard deviations ($n = 18-30$).

Although the CPUE was significantly different between the two species, the temporal patterns in the diel changes of CPUE were very similar between the

two species, suggesting a similar diel rhythm of locomotion activities between the two gobies (Fig. 1). In each of the seasons, *R. giurinus* displayed

Niche differentiation of two invasive gobies

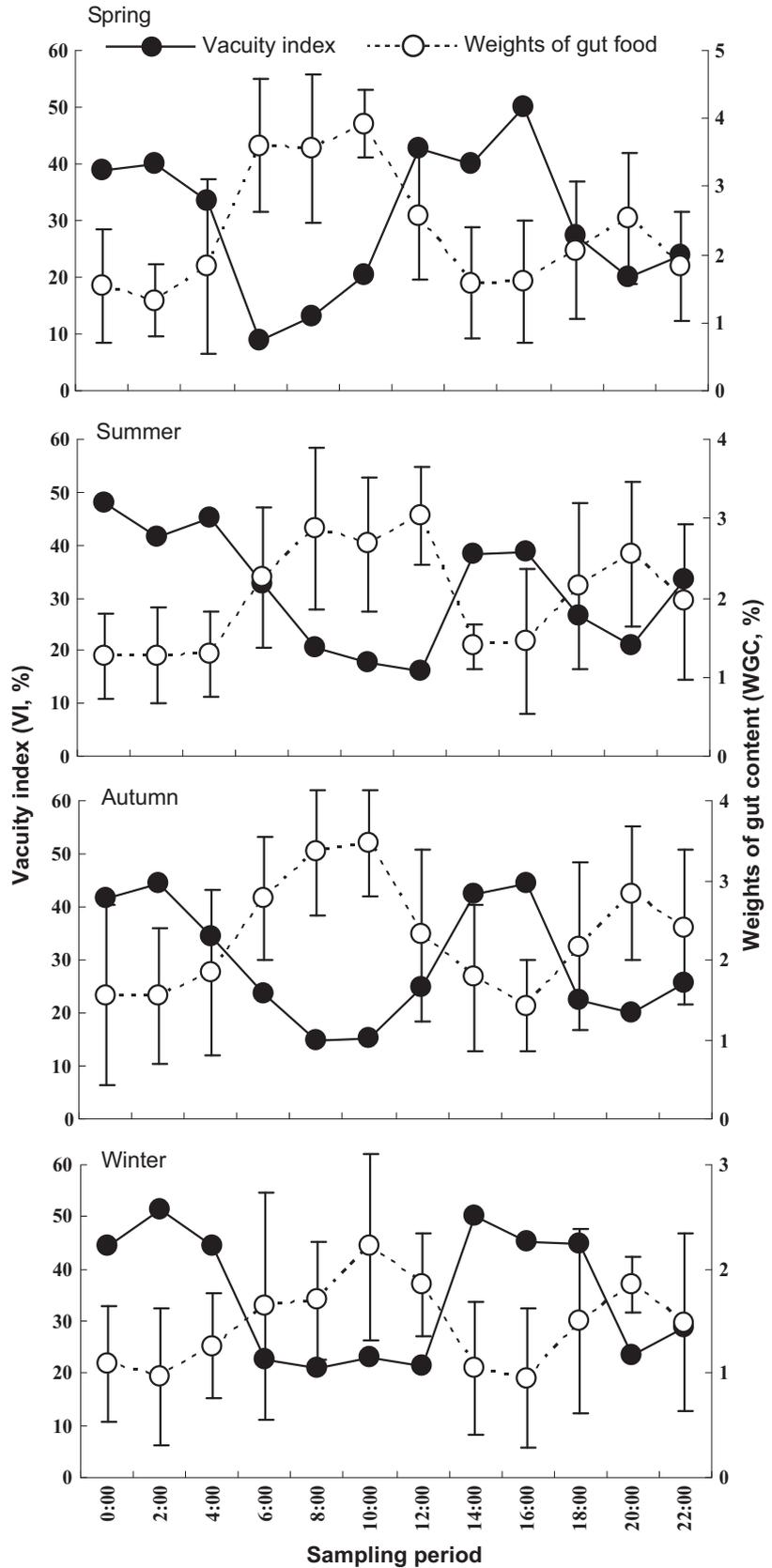


Fig. 3. Diel changes in vacuity index (VI, %) and weights of gut content (WGC, %) of *Rhinogobius cliffordpoei* in the four seasons of 2011 in Lake Erhai (China). Bars are standard deviations ($n = 18-30$).

significantly higher CPUE than *R. cliffordpoei* in spring and autumn (t -test, $t = -3.02$ and $P < 0.01$ in spring and $t = -2.43$ and $P = 0.02$ in autumn,

respectively), whereas the CPUE of *R. cliffordpoei* was higher than *R. giurinus* in summer (t -test, $t = -4.02$, $P < 0.01$). No significant differences

were observed in winter (t -test, $t = 1.26$, $P = 0.21$). Given the seasonal changes in day length, the relatively stable time-dependency of CPUE over seasons suggested that locomotion activity of the two species shifted accordingly, that is they were synchronous with seasonal light:dark patterns.

Diel and seasonal differences in feeding activity

Diel VI data indicated that both species had two main periods of feeding activity, with reduced proportions of empty guts from 6:00 to 10:00 and from 18:00 to 22:00 (Figs 2 and 3). Concomitantly, the WGC was higher during both of these periods (Figs 2 and 3). Differences in WGC between the two species were not significant (three-way ANOVAS, $F_{1,1432} = 1.59$, $P = 0.21$, Table 3), but differences were dependent on seasons and sampling time (three-way ANOVAS, $F_{33,384} = 1.45$, $P = 0.048$, Table 3). In each season, the rhythm of feeding activity was similar between the two species, with no significant differences in VI (Mann–Whitney U -test, $P = 0.23$, 0.41, 0.72 and 0.96 in spring, summer, autumn and winter, respectively). In addition, the feeding activities of the two gobies showed a similar seasonal shift with the locomotion activity.

Differences in diel and seasonal changes of diet composition

The diet of the two gobies primarily consisted of macrozooplankton, aquatic insects and shrimp larvae (Fig. 4). Diet composition (%IRI) did not differ significantly between the two species at the same time period of a day (χ^2 test, $P > 0.05$, Table 4), and there was a common pattern of high dietary overlap between the species (Schoener's index >0.60 for a given time period, Table 5). In each season, the species displayed high Schoener's index values (Table 5) and similar %IRI in each season (χ^2 test; d.f. = 9; $\chi^2 = 13.09$, 10.56, 2.01, 6.13; and $P = 0.16$, 0.31, 0.99, 0.73 in spring, summer, autumn and winter, respectively).

Table 3. Three-way ANOVAS used to test the differences in weights of gut food (log $(x + 1)$ transformed) between species, seasons and sampling periods in 2011 in Lake Erhai (China).

Sources	d.f.	F	P
Species	1	1.590	0.208
Seasons	3	52.522	<0.001
Sampling periods	11	28.582	<0.001
Species \times Seasons	3	10.182	0.001
Species \times Sampling periods	11	2.802	0.001
Seasons \times Sampling periods	33	4.054	<0.001
Species \times Seasons \times Sampling periods	33	1.450	0.048
Error	1425		

Discussion

The diel activity of the two goby species in this sublittoral habitat of Lake Erhai was crepuscular, with the two main activity peaks in the early morning and evening. Their feeding rhythm was closely associated with their activity rhythm, with little evidence for seasonal variation. In combination, this suggests there was no differentiation in the spatial, trophic and temporal (diel and seasonal) niches of the two species in the sublittoral habitat, contrary to the hypothesis.

In complex and dynamic environments, diel locomotion activity and feeding rhythm of fishes are highly diverse, varying among species but also among individuals within species (Reebs 2002; Blanchet et al. 2008). Most gobies have been described as primarily nocturnal (Thetmeyer 1997; Erös et al. 2005; Ehrenberg & Ejdung 2008), although variable feeding rhythms between goby species have been detected (e.g. crepuscular, Grabowska & Grabowski 2005; nocturnal and crepuscular, Kanou et al. 2005; no clear variation in feeding activity within a 24-h periodicity, Grabowska et al. 2009). Whilst habitat niche differentiation is generally more frequent than trophic and temporal niche differentiations (Schoener 1974), a review of 37 studies examining habitat, trophic and temporal niche differentiation in fish assemblages concluded that 57% of studies found niche differentiation via food partitioning, 32% via habitat segregation and 11% via time separation (Ross 1986). Many gobies have been observed to display habitat segregation (e.g. Malavasi et al. 2005; Sone et al. 2006; Hernaman & Probert 2008; Horinouchi 2008) and/or trophic differentiation (e.g. Kakareko et al. 2005; Borza et al. 2009; Borcharding et al. 2013), whereas we know of no study reporting temporal differentiation among gobies, supporting our findings. Nevertheless, studies of other fishes have demonstrated that competitive interactions between fish species can influence their temporal niche (e.g. Harwood et al. 2001; Blanchet et al. 2008) with, for example, the daytime activity of Atlantic salmon *Salmo salar* significantly increasing when competing with exotic rainbow trout *Oncorhynchus mykiss* (Blanchet et al. 2008).

With the sublittoral habitat of the lake appearing to provide a mixing or transition zone for the gobies then their potential diel movements from the neighbouring habitats might have influenced their abundances here and thus influenced their temporal niches. However, given they are benthic species with pelvic fins that form a small sucking plate for attachment to the benthos, they tend to have limited capacity for quick and long distance swimming (Xie et al. 2000; Hayden & Miner 2009). Correspondingly, diel movement across the habitats for feeding would be

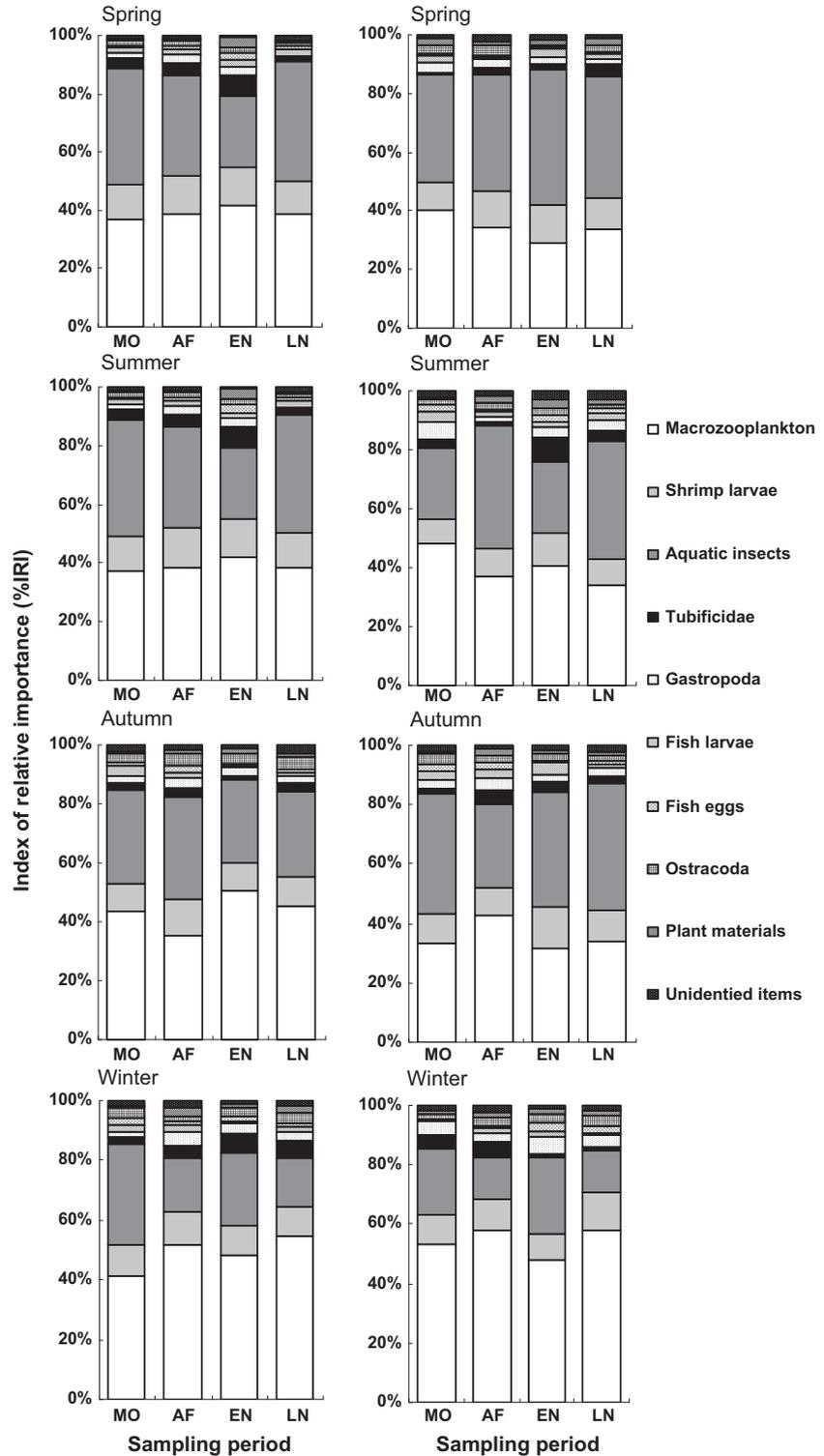


Fig. 4. Diel changes in diet compositions [%index of relative importance (IRI)] of (left) *Rhinogobius giurinus* and (right) *Rhinogobius cliffordpopei* in morning (MO), afternoon (AF), early night (EN) and late night (LN) in the four seasons of 2011 in Lake Erhai (China).

time- and energy-costly and thus movements between habitats would appear unlikely. Testing this interhabitat diel movement would require further study, such as through telemetry approaches. Moreover, the density of predator (i.e. *C. argus*) varies greatly across the different habitats in the lake. The predator pressure is a potential drive for the habitat segregation and the inferior fish growth performance in the

littoral habitat with a high abundance of *C. argus* (Guo et al. 2012). Within the sublittoral habitat, however, the density of predator is very low, and the predator pressure shows no negative effect on goby growth in relation to those in the profundal habitat where the predator is absent (Guo et al. 2012). Therefore, there seems to be no convincing evidences suggesting the predator as a determining factor shaping

Table 4. Chi-square test (χ^2 test) used to test the differences in diet compositions (%index of relative importance) between *Rhinogobius cliffordpopei* and *Rhinogobius giurinus* in the same sampling period (i.e. morning, afternoon, early night and late night) in the four seasons of 2011 in Lake Erhai (China).

Season	Sampling period											
	Morning			Afternoon			Early night			Late night		
	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P
Spring	10.339	9	0.324	2.55	9	0.979	5.85	9	0.755	4.591	9	0.868
Summer	5.709	9	0.768	3.298	9	0.951	15.290	9	0.083	4.137	9	0.902
Autumn	7.185	9	0.618	8.984	9	0.439	5.581	9	0.781	7.756	9	0.559
Winter	3.732	9	0.928	3.180	9	0.957	10.336	9	0.324	5.830	9	0.756

Table 5. Dietary overlap (Schoener's index *S*) between *Rhinogobius cliffordpopei* and *Rhinogobius giurinus* in the same time period (morning, afternoon, early night and later night) in each season and in the same season (spring, summer, autumn and winter) of 2011 in Lake Erhai (China).

Schoener's index (<i>S</i>)	Season			
	Spring	Summer	Autumn	Winter
Morning	0.78	0.71	0.74	0.77
Afternoon	0.76	0.84	0.68	0.86
Early night	0.67	0.82	0.64	0.90
Later night	0.80	0.73	0.79	0.85
Entire season	0.83	0.72	0.78	0.88

the diel feeding activity and niche differentiation between the two gobies within the sublittoral habitat.

When resources are limited, temporal niche differentiation could be a viable mechanism for reducing competition, notably when the shared resources also show activity rhythm or are renewed within the time involved in the differentiation (Kronfeld-Schor & Dayan 2003). Food supply is often the most important factor driving foraging behaviours and levels of inter-specific competition (Alänära et al. 2001; Hansen & Closs 2005). For instance, Letourneur (2000) revealed that the foraging areas and territory sizes of large dominant damselfish (*Stegastes nigricans*) were small when food supplies were high in summer but increased when food supplies were low in winter months. In sublittoral habitat of Lake Erhai, the biomass of the two gobies and other ecologically similar fish species (e.g. *P. parva*, *H. swinhonis*, *H. leucisculus*) were much lower than in the littoral and profundal habitats, despite the higher availability of food resources in this habitat (Guo et al. 2012). Thus, we argue that a potential factor in the lack of niche differentiation between the fishes in the sublittoral was through the food resources not being limiting, and thus, competition between all of the fish species was likely to be low. Moreover, observations suggested that the macrozooplankton and aquatic insect resources, that comprised the main food resources of the two gobies, also did not display clear diel changes

in abundance or renewal patterns, suggesting no requirement for any temporal niche differentiation between the fishes (Z. Guo, personal observations).

The present study indicated that the two species did not show any diel changes in diet composition and no trophic niche differentiation within the sublittoral. Both species mainly consumed Cladocera and Copepod species of zooplankton and Chironomid larvae, as also observed in the littoral and profundal habitats (Guo et al. 2014), as well as in lentic populations in their native range (Xie et al. 2000, 2005; Zhang 2005). Specialisation in food resource is often crucial to enhance coexistence by reducing interspecific competition among closed-related competing fish species, and several invasive gobies have been found to display trophic niche differentiation within a community when they become abundant outside of their native ranges (e.g. Kakareko et al. 2005; Borza et al. 2009; Borcharding et al. 2013). Invader success depends, in part, on the availability of 'niche opportunities' and 'resource opportunities' (Shea & Chesson 2002). In Lake Erhai, we demonstrated that the two invasive and highly abundant gobies displayed a multistrategy across different habitats to maximise the 'opportunities' and to minimise competition between them. Firstly, they occupied distinct macrohabitats with spatial segregation, which was the primary mechanism that promoted their resource partitioning and their coexistence at high abundances within the littoral and profundal habitats of the lake (Guo et al. 2012). In the sublittoral, however, their shared niches indicated no trophic or temporal differentiation, potentially due to abundant food resources, and the two species were able to coexist at similar abundances, albeit reduced from those recorded in the other habitats (Guo et al. 2014). In its entirety, the coexistence of the two species in this habitat may just represent a by-product of their successful segregation along the depth gradient of the lake. These findings suggest that the integration into native fish communities of invasive gobies specifically, and invasive fish generally, represents relatively complex processes involving the interactions of ecological

mechanisms and the physical environment, with some context dependency in their outcomes (Shea & Chesson 2002; Baiser et al. 2010).

In conclusion, this study demonstrated that these two invasive gobies species were primarily nocturnal with crepuscular peaks in activity and feeding. As their diel rhythms of activity and feeding were also similar across the four seasons, this suggested there was no differentiation in their temporal niche. Moreover, their high dietary overlap revealed no evidence of trophic niche differentiation within the sublittoral habitat. Thus, these findings, that were contrary to the hypothesis (i.e. the coexistence of these invasive congeners was facilitated by the differences in their rhythms of locomotion and feeding activity, and/ or by their trophic niche), suggest that other ecological mechanisms were facilitating their coexistence at similar abundances in this habitat, with evidence suggesting this related to their access to sufficiently high food resources that prevented the development of competitive interactions.

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