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COMPOSITION AND DIVERSITY OF COMMUNITIES OF *DACTYLOGYRUS* SPP. IN WILD AND FARMED GOLDFISH *CARASSIUS AURATUS*

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ABSTRACT: Species composition and diversity of dactylogyrids were compared on gills of wild and cultured goldfish (silver crucian carp) *Carassius auratus* from 3 naturally populated lakes and 3 stocked aquaculture ponds in the Hubei province of China to examine the differences in the gill parasite community between these natural and farmed waters. Of the 7 *Dactylogyrus* spp. detected, all were found in lakes and 5 in ponds, with *Dactylogyrus inexpectatus* and *Dactylogyrus anchoratus* being absent from ponds. No significant correlation was found between the species richness and habitat area or host size, nor was there a significant difference in mean species richness between lakes (0.41–0.65) and ponds (0.30–0.76). Brillouin's diversity in lakes (0.049–0.067) was higher than that in ponds (0.024–0.046), but not significantly so. Although the diversity of parasite communities was higher in wild goldfish, higher mean abundance of some *Dactylogyrus* spp. was found in cultured goldfish. Based on Bray–Curtis similarity, it was difficult to differentiate parasite communities in lakes from those in ponds at the infracommunity level, whereas the 3 lakes and Guanqiao pond differed markedly from the remaining 2 ponds at the component community level. Although infracommunities differed among waterbodies, no effects of fish length or waterbody type were found on infracommunity or component community structure. Together, these results suggest that abundance and species richness of *Dactylogyrus* spp. on goldfish in lakes and farm ponds are influenced by habitat-specific environmental factors.

Parasites that cause little apparent damage in fish populations under natural conditions may become causative agents of diseases in farmed fish (Scholz, 1999). Even in natural parasite communities, mean abundance and prevalence are usually dependent on host density (Arneberg et al., 1998). In intensive fish farming, high fish density and environmental stress, including low dissolved oxygen, increased pollutant levels, and accumulation of metabolic waste products, can reduce the immunological capabilities of farmed fish, rendering them more susceptible to some parasites (Thoney and Hargis, 1991). In several studies of monogeneans, prevalence and abundance were higher on farmed fish than on wild fish, including in 6 *Cichlidogyrus* spp. on cultured *Oreochromis niloticus*, *Pseudorhabdosynochus epinepheli* on cultured grouper *Epinephelus malabaricus*, *Diplectanum grouperi* on cultured groupers *Epinephelus* spp., 3 of 4 species on cultured brown-marbles grouper *Epinephelus fuscoguttatus*, and 1 of 3 *Gyrodactylus* spp. on farmed Atlantic cod *Gadus morhua* (Leong and Wong, 1988; Luo et al., 2010; Rückert et al., 2010; Heuch et al., 2011; Ibrahim and Soliman, 2011).

Metazoan ectoparasite abundance and community structure in fish are affected by host traits such as body length, age, and immunocompetence (Koskivaara et al., 1991; Rohde et al., 1995; Lo et al., 1998). Environmental factors such as latitude, depth, season, temperature, habitat, eutrophication, and pollution also affect helminth ectoparasite community structure and abundance (Koskivaara, 1992; Koskivaara and Valtonen, 1992; Rohde et al., 1995; Rohde and Heap, 1998; Šimková et al., 2001; Knipes and Janovy, 2009). Parasite community structure may also be affected by habitat area and geographic distance (Locke et al., 2012; Zelmer, 2014). These studies suggest there may be differences in the diversity of monogenean communities between wild and farmed fish, possibly due to differences in environmental parameters.

The goldfish (silver crucian carp) *Carassius auratus* is one of the most common fish in lakes in the lower and middle reaches of the Yangtze River in China. The goldfish has also been widely farmed in ponds in the past 30 yr. Dactylogyriasis (caused by dactylogyrid monogeneans) is one of the most serious parasitic diseases in intensive carp aquaculture (Molnár, 1971). However, under natural conditions, infections of *Dactylogyrus* spp. cause little apparent damage or mass mortality of carp. To date, 8 species of *Dactylogyrus* in total have been reported from goldfish in China (Chen, 1973). Herein, we compared the species composition, richness, and diversity of dactylogyrid communities in wild and farmed goldfish, while testing for effects of certain extrinsic (habitat area, geographic proximity) and intrinsic (host size) factors that often affect species richness and community structure.

MATERIALS AND METHODS

Sampling localities

Wild goldfish were collected from 3 lakes in November 2013: Chenhu Lake and Wuhu Lake in Wuhan City and Liangzi Lake in Ezhou City. In the same month, cultured goldfish were obtained from 3 ponds in 3 fish farms in Shishou (Jingzhou City), Guanqiao (Wuhan City), and Yingshan (Huanggang City). All goldfish were caught by gill net, and all the sampling localities are

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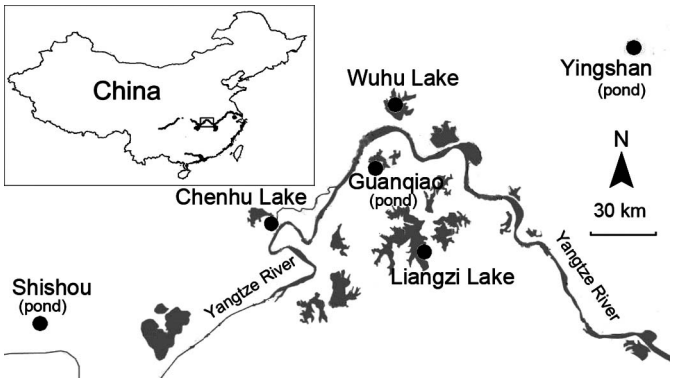

FIGURE 1. Sampling localities of the goldfish (*Carassius auratus*) in 3 lakes and 3 ponds in the floodplain of the Yangtze River in Hubei province of China.

located in the floodplain of the Yangtze River in Hubei province (Fig. 1). The 3 lakes are typically shallow (less than 3 m) and macrophytic, and they range in area from 22 to 482 km^2 (Table I). All ponds had a surface area of 0.01 km^2 (Table I). Only goldfish were stocked in Guanqiao pond, whereas the remaining 2 ponds were inhabited by mixed cultures with grass carp (*Ctenopharyngodon idella*) and silver carp (*Hypophthalmichthys molitrix*), which are incompetent hosts to *Dactylogyrus* spp. from goldfish. The goldfish fry stocked in ponds were obtained by artificial reproduction from the local fish hatchery. Farmed fish with the same density of about 2 to 3 fish/m^3 were fed with large amounts of formula feed in the 3 ponds. Blooms of blue-green algae were observed in these ponds, indicating eutrophication. Based on the visible blooms and water color, the trophic state in the 3 ponds was markedly higher than in the 3 lakes. There was no connection among the 6 waterbodies by water source. No anthelmintic was used in any of the systems during the study.

Parasitological examination

At least 50 goldfish (50–152) in each sampling locality were transported alive to a nearby field laboratory within 1 hr and then euthanized. Fork length was measured to the nearest millimeter, and the gills were examined for monogeneans within 24 hr of collection. *Dactylogyrus* spp. were identified and the number of each species was recorded. Identification was based on sclerotized parts of the haptor (anchors, connective bars, marginal hooks) and reproductive organs (male copulatory organs) (Gusev, 1985) by using a stereomicroscope and a compound microscope.

Data analysis

Prevalence is defined as the number of goldfish infected with *Dactylogyrus* spp. divided by the total number of goldfish sampled, expressed as a percentage. Mean abundance is the average number of parasites of a given species found in a host population in a sampling locality (Bush et al., 1997). The dactylogyrid communities were analyzed at the infracommunity level (all individuals of all parasite species in a single host) and component community level

Table I. Prevalence and mean abundance ± SD of *Dactylogyrus* spp. on gills of *Carassius auratus* in 3 lakes and 3 ponds in the flood plain of the Yangtze River in Hubei province of China. The bold text indicates the highest value of the dactylogyrid among the 6 sampling sites. — means the parasite was absent.

	Liangzi Lake	Chenhu Lake	Wuhu Lake	Shishou pond	Yingshan pond	Guanqiao pond
Habitat area (km^2)	482	116	22	0.01	0.01	0.01
Mean fish length ± SD	13.64 ± 1.82	13.43 ± 6.33	18.83 ± 2.56	17.57 ± 3.69	13.31 ± 1.92	12.75 ± 1.58
D. vastator						
Prevalence (%)	16.45	3.39	—	**29.29**	3.70	16.67
Mean abundance ± SD	0.34 ± 1.24	0.03 ± 0.18		**0.55 ± 1.26**	0.04 ± 0.19	0.18 ± 0.43
D. arcuatus						
Prevalence (%)	**11.18**	—	—	9.09	7.41	3.33
Mean abundance ± SD	**0.30 ± 1.33**			0.12 ± 0.41	0.11 ± 0.42	0.05 ± 0.29
D. intermedius						
Prevalence (%)	22.37	10.17	**36.54**	5.05	3.70	3.33
Mean abundance ± SD	0.93 ± 3.02	0.32 ± 1.25	**1.44 ± 3.52**	0.06 ± 0.28	0.04 ± 0.19	0.03 ± 0.18
D. baueri						
Prevalence (%)	1.97	—	—	—	**12.96**	—
Mean abundance ± SD	0.03 ± 0.20				**0.20 ± 0.59**	
D. formosus						
Prevalence (%)	8.55	16.95	15.38	2.02	1.85	**53.33**
Mean abundance ± SD	0.16 ± 0.66	0.64 ± 2.12	0.31 ± 1.06	0.02 ± 0.14	0.02 ± 0.14	**1.43 ± 2.29**
D. inexpectatus						
Prevalence (%)	2.63	8.47	3.85	—	—	—
Mean abundance ± SD	0.03 ± 0.16	0.12 ± 0.46	0.04 ± 0.19			
D. anchoratus						
Prevalence (%)	—	1.72	9.62	—	—	—
Mean abundance ± SD		0.02 ± 0.13	0.25 ± 0.81			

Table II. Community characteristics of *Dactylogyrus* spp. on gills of *Carassius auratus* in 3 lakes and 3 ponds in the floodplain of the Yangtze River in Hubei province of China.

	Liangzi Lake	Chenhu Lake	Wuhu Lake	Shishou pond	Yingshan pond	Guanqiao pond
Sample size	152	59	52	50	54	60
Infracommunity level						
Mean species richness/fish ± SD	0.63 ± 0.84	0.41 ± 0.79	0.65 ± 0.71	0.45 ± 0.66	0.30 ± 0.43	0.76 ± 0.69
Brillouin index ± SD	0.067 ± 0.164	0.049 ± 0.145	0.056 ± 0.143	0.029 ± 0.111	0.024 ± 0.103	0.046 ± 0.133
Evenness ± SD	0.083 ± 0.197	0.063 ± 0.180	0.080 ± 0.207	0.039 ± 0.141	0.028 ± 0.119	0.062 ± 0.174
Component community level						
Number of species	6	5	4	4	5	4
Berger–Parker index	0.52	0.57	0.70	0.73	0.50	0.84
Dominant species	*D. intermedius*	*D. formosus*	*D. intermedius*	*D. vastator*	*D. baueri*	*D. formosus*

(all individuals of all parasite species in a host species in a sampling locality) (Bush et al., 1997). Mean species richness was calculated as the mean number of parasite species per fish in each locality. Diversity at the infracommunity level was measured as Brillouin's index and evenness (H/H_{max}, where H is the Brillouin's index and H_{max} is the maximum possible diversity for a given number of parasite species and individuals) (Washington, 1984). Similarities of dactylogyrid communities between individual fish (only infected hosts) were compared within and between locality and waterbody types (for infracommunities) and between localities and component community types (for component communities). Dominance was measured by the Berger–Parker index at the component community level.

Correlations between mean species richness and waterbody surface area, as well as between infracommunity species richness and host body size, were analyzed by Spearman's rank correlation analysis. Differences in mean species richness, evenness and Brillouin's diversity between lakes and ponds were tested using analysis of covariance, with fish length as a covariate. Statistical analyses were carried out using STATISTICA 10.0 (StatSoft Inc., Tulsa, Oklahoma). Non-metric multidimensional scaling was performed with Primer-E 7 to visualize Bray–Curtis similarity of *Dactylogyrus* communities. Infracommunity differences among waterbody types (lake vs. pond) were tested in permutational multivariate analysis of variance (PERMANOVA) with 9,999 permutations, with locality nested within lake and fish length as a covariate. Statistical significance was as $\alpha \leq 0.05$.

RESULTS

Seven species of were found in the goldfish from the 6 localities, i.e., *Dactylogyrus vastator*, *Dactylogyrus intermedius*, *Dactylogyrus arcuatus*, *Dactylogyrus baueri*, *Dactylogyrus formosus*, *Dactylogyrus inexpectatus*, and *Dactylogyrus anchoratus*. Prevalence and mean abundance of all the *Dactylogyrus* spp. were not high in any of the localities. The highest prevalence (53.33%) and mean abundance (1.43) in ponds was for *D. formosus* in Guanqiao pond, whereas the highest prevalence (36.54%) and mean abundance (1.44) in lakes were for *D. intermedius* in Wuhu Lake. Four species were found in at least 4 localities, but 2 species (*D. inexpectatus* and *D. anchoratus*) only occurred in lakes (Table I).

Although 4–6 species of *Dactylogyrus* were found in each locality, the maximum infracommunity species richness was 3, in 5 of 6 localities (Table II). No significant correlation was found between species richness and habitat area or host size ($R = 0.03$, df $= 476$, $P = 0.95$ and $R = 0.22$, df $= 476$, $P = 0.55$, respectively). Mean species richness was highest in Guanqiao pond (0.76) and lowest in Yingshan pond (0.30) (Table II). There was also no significant difference in mean species richness between lakes (0.41–0.65) and ponds (0.30–0.76) ($F = 0.10$, df $= 5$, $P = 0.77$). The Brillouin's index in lakes (0.049–0.067) was higher than in ponds (0.024–0.046), but not significantly ($F = 6.79$, df $= 5$, $P = 0.07$), with the highest in Liangzi Lake (0.067) and the lowest in Yingshan pond (0.024) (Table II). The evenness in lakes (0.063–0.083) was also higher than in ponds (0.028–0.062), but not significantly ($F = 5.50$, df $= 5$, $P = 0.10$).

Berger–Parker dominance ranged from 0.52 to 0.70 in lakes and from 0.50 to 0.84 in ponds; dominance was highest in Guanqiao pond and lowest in Yingshan pond (Table II). *Dactylogyrus intermedius* was the dominant species in Liangzi Lake and Wuhu Lake, *D. formosus* in Chenhu Lake and Guanqiao pond, *D. vastator* in Shishou pond, and *D. baueri* in Yingshan pond (Table II). Based on the Bray–Curtis similarity at the infracommunity level, it was difficult to differentiate parasite communities in lakes from those in ponds (Fig. 2A). A PERMANOVA revealed infracommunities differed across waterbodies, but no main effect was observed for fish length or waterbody type (Table III). At the component community level, the 3 lakes and Guanqiao pond differed markedly from the remaining 2 ponds (Fig. 2B). There was no relationship between the resemblance of parasite component communities and their physical proximity (Rho $= 0.354$, $P = 0.149$). For example, component communities were not particularly similar between Guanqiao pond and Wuhu Lake, although they were the closest localities (32 km apart, see dendrogram in Fig. 2B).

DISCUSSION

Overall, our results showed no effect of habitat area, geographic distance or host size on species richness of dactylogyrids on goldfish, with only limited differences in community structure between lakes and farm ponds. Prevalence and abundance of dactylogyrids varied among lakes and ponds, being highest in ponds for 3 of the 5 species. Mean infracommunity richness was similar between lakes and ponds, and there was also no significant correlation between mean species richness and habitat area. At the component community level, 7 species were

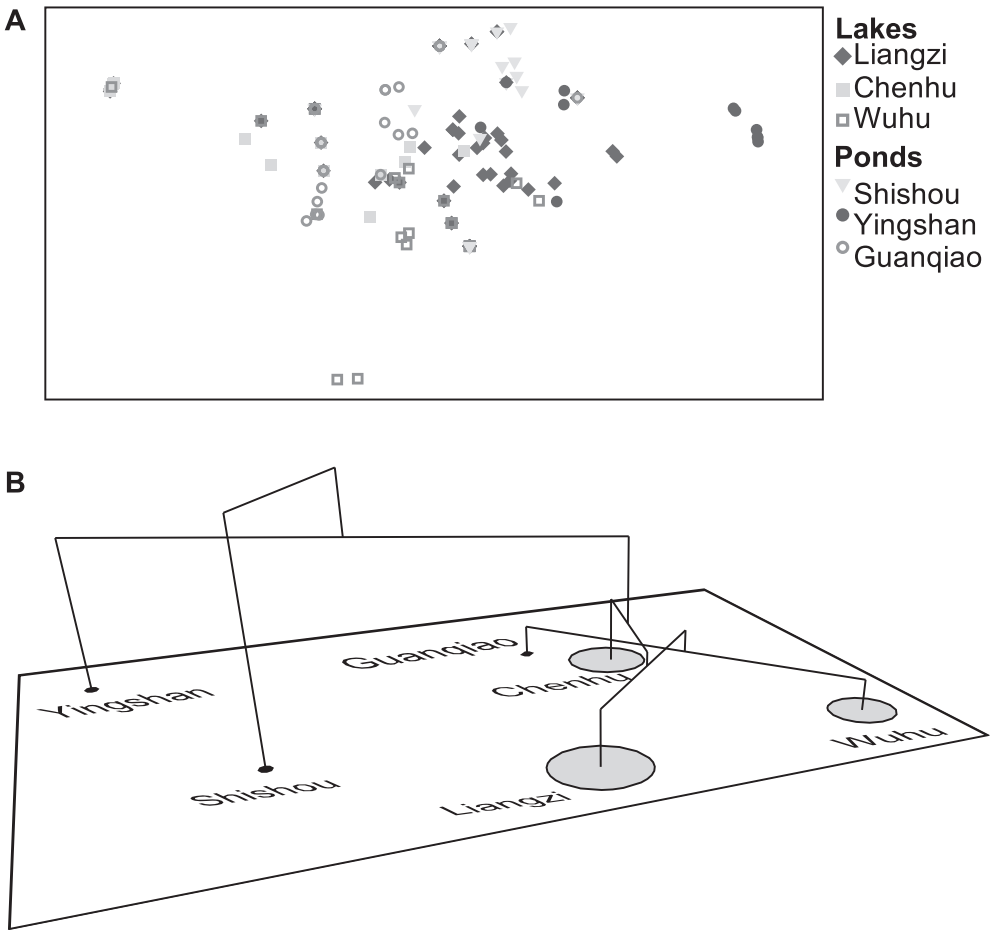

FIGURE 2. Non-metric multidimensional scaling of ranked resemblance among *Dactylogyrus* communities in goldfish (*Carassius auratus*) collected from in the floodplain of the Yangtze River in Hubei province of China, based on (**A**) Bray–Curtis similarities among 195 infracommunities (stress = 0.07) and (**B**) 6 component communities (stress = 0.01). Legend beside (A) shows origin of infracommunities. Black points in (B) are ponds and gray points are lakes. Dendrogram in (B) is computed from geographic distances among localities, and point sizes are scaled to the log of the surface area of the waterbody. Point size of the aquaculture ponds was arbitrarily increased for ease of visualization.

found in lakes but 5 species in ponds, with *D. inexpectatus* and *D. anchoratus* being absent from ponds.

Usually, species richness is positively correlated to habitat area due to larger host population size in larger habitat areas (Zelmer, 2014). Larger habitat areas support more host species, and host species richness is often positively correlated with parasite species richness (Wood and Johnson, 2016). More diverse parasite species composition found in crucian carp (*Carassius carassius*) in lakes than in ponds was attributed to increased opportunities for parasite exchange with other fish species (Karvonen et al., 2005). The 3 lakes in the present study were much larger in area and contained much greater fish diversity than the 3 ponds. However, there was no significant difference in mean species richness, or any form of parasite community resemblance, between lakes and ponds, nor any correlation between habitat area and species richness. First, the lack of a species–area relationship may be due to the strong host specificity of the dactylogyrids. Although more than 50 fish species have been recorded in these lakes (Zhang et al., 2008), which may increase opportunities for parasite exchange with other fish (Karvonen et al., 2005), the goldfish dactylogyrids are highly host specific and do not infect other fishes in the lakes (Chen, 1973). Second, the higher host density in ponds may also be responsible for the absence of a species–area relationship, as host population density is strongly positively correlated to species richness of directly transmitted parasites (Arneberg, 2002). The component species richness in ponds (5 dactylogyrid species) was lower than in lakes (7 species) because the goldfish stocked in ponds were obtained by artificial reproduction from a local fish hatchery and there was no connection among the 6 waterbodies by water source. However, the higher density of goldfish in ponds

Table III. Permanova analysis of Bray–Curtis resemblance among 195 infracommunities of *Gyrodactylus* on *Carassius auratus* from 3 aquaculture ponds and 3 natural lakes in Hubei province, China.

Source of variation	Degrees of freedom	Sum of squares	Mean sum of squares	Pseudo-*F*	*P*
Fish length	1	27640	27640	1.4294	0.23
Waterbody type	1	51698	51698	1.2614	0.3197
Waterbody (nested in waterbody type)	4	98895	24724	8.5648	0.0001
Residual	188	5.369×10^5	28856.7		
Total	194	7.152×10^5			

(2 to 3 fish/m^3), which is obviously greater than in lakes, undoubtedly contributes to transfer of parasites among goldfish and increases species richness in ponds at the infracommunity scale. Thus, the higher infracommunity species richness maintained by the higher host density may weaken the influence of small area in fish ponds. In addition, the lack of a species–area relationship may be attributed to the limited colonization potential of autogenic parasite species (Fellis and Esch, 2005), such as the monoxenous dactylogyrids.

Host size, as habitat for the parasite, is the most common correlate of infracommunity species richness of parasites, as increasing age and vagility increases the probability of colonization by new parasite species (Zelmer, 2014). In this case, diet breadth does not apply as dactylogyrids are directly transmitted. A positive relationship between host size and species richness is also found in monogenean communities (Guégan et al., 1992), which is explained by the hypothesis that larger host body size increases host vagility, which in turn enhances exposure to more and more infective oncomiracidia (Sasal et al., 1997). Lo et al. (1998) also found a positive relationship between host size and adult ectoparasite diversity on the gills of 2 species of reef fish. In the present study, however, no significant correlation was detected between host body size and infracommunity species richness, which may be due to the limited range of goldfish with schooling behavior. Increasing age and time for colonization would not apply either, as dactylogyrids have limited lifespan and species do not necessarily accumulate over time. Similarly, in fathead minnows (*Pimephales promelas*) there was no relationship between infections of *Dactylogyrus* spp. and host size (Knipes and Janovy, 2009).

The Brillouin diversity is determined by both the number of parasite species and individuals (Pontasch and Brusven, 1988). Evenness correlates negatively with parasite abundance in fish hosts (Poulin, 1996; Norton et al., 2003). Thus, although some *Dactylogyrus* spp. have a higher prevalence and mean abundance in the 3 ponds, the evenness of parasite community was comparatively lower, which may result in lower diversity in ponds. Nevertheless, it should be reiterated that the difference was not significant.

Although higher host density contributes to higher prevalence and abundance of monogeneans (Johnson et al., 2011), higher infection levels of some dactylogyrids may be due to the extreme environmental conditions in the ponds. Furthermore, in this study, infracommunity and component community structure (species composition and abundance) differed among all habitats, but these differences were not affected by fish size, waterbody type, or geographic distance. Thus, habitat-specific effects unmeasured in this study may contribute to differences in parasite community structure. Similar results were obtained for dactylogrids in fathead minnows (Knipes and Janovy, 2009). Usually, transmission of fish monogeneans is affected by environmental factors (Koskivaara, 1992; Dušek et al., 1998). In cultured fish ponds, physiochemical parameters are often abnormal, including extremely high eutrophic levels, high ammonia nitrogen concentration, and low water transparency (Pechar, 2000). For example, mean abundance of *Dactylogyrus* spp. is higher on gills of crucian carp in some ponds with hypoxia and low pH (Karvonen et al., 2005). In addition, diversity of dactyogyrids on roach (*Rutilus rutilus*) was the highest in a polluted, eutrophic lake compared with that of other lakes (Koskivaara and Valtonen, 1992). These environmental extremes may contribute to the differences in diversity and evenness between ponds and lakes. The implication of unmeasured factors here is strengthened by the lack of effects of geographic proximity, which often affects parasite community structure (Locke et al., 2012), including endoparasites in *Cyprinus carpio* in the same region as in our study area (Nie et al., 1999; Poulin and Morand, 1999). Together, these results suggest that abundance and species richness of *Dactylogyrus* spp. on goldfish in lakes and farm ponds are influenced by habitat-specific environmental factors.

Among the 3 ponds with the same high fish density, mean species richness and Brillouin diversity index were both the highest in Guanqiao pond. Given that it is a monoculture in Guanqiao pond but multi-species in the other 2 ponds, a dilution effect resulting from the presence of high densities of incompetent hosts may have played a role in reducing infection levels in mixed-species ponds (Johnson and Thieltges, 2010; Johnson et al., 2013). Whether the dilution effect can reduce transmission of dactylogyrids with high host specificity in fish polyculture, a common and traditional aquaculture model in China, needs to be confirmed by further experiments as a potential means to control dactylogyriasis.

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LITERATURE CITED

Arneberg, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: Comparative analyses of directly transmitted nematodes of mammals. Ecography **25:** 88–94.

Arneberg, P., A. Skorping, B. Grenfell, and A. F. Read. 1998. Host densities as determinants of abundance in parasite communities. Proceedings of the Royal Society of London **265:** 1283–1289.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology **83:** 575–583.

Chen, C. L. 1973. An illustrated guide to the fish disease and causative pathogenic fauna and flora in the Hupei Province Beijing. Science Press, Beijing, China, 456 p.

Dušek, L., M. Gelnar, and S. Šebelová. 1998. Biodiversity of parasites in a freshwater environment with respect to pollution: Metazoan parasites of chub (*Leuciscus cephalus* L.) as a model for statistical evaluation. International Journal for Parasitology **28:** 1555–1571.

Fellis, K. J., and G. W. Esch. 2005. Autogenic-allogenic status affects interpond community similarity and species area relationship of macroparasites in the bluegill sunfish, *Lepomis macrochirus*, from a series of freshwater ponds in the Piedmont area of North Carolina. Journal of Parasitology **91:** 764–767.

Guégan, J. F., A. Lambert, C. Lévêque, C. Combes, and L. Euzet. 1992. Can host body size explain the parasite species richness in tropical freshwater fishes? Oecologia **90:** 197–204.

Gusev, A. V. 1985. Keys to parasites of freshwater fish of the USSR, Vol. 2, Parasitic Metazoa. Nauk, Leningrad, Russia, 425 p.

Heuch, P. A., P. A. Jansen, H. Hansen, E. Sterud, K. MacKenzie, P. Haugen, and W. Hemmingsen. 2011. Parasite faunas of farmed cod and adjacent wild cod populations in Norway: A comparison. Aquaculture Environment Interactions **2:** 1–13.

Ibrahim, M. M., and M. F. Soliman. 2011. Parasite community of wild and cultured *Oreochromis niloticus* from Lake Manzalah, Egypt. Journal of the Egyptian Society of Parasitology **41:** 685–697.

Johnson, M. B., K. D. Lafferty, C. van Oosterhout, and J. Cable. 2011. Parasite transmission in social interacting hosts: Monogenean epidemics in guppies. PLOS ONE **6:** e22634. doi:10.1371/journal.pone.0022634.

Johnson, P. T. J., D. L. Preston, J. T. Hoverman, and B. E. LaFonte. 2013. Host and parasite diversity jointly control disease risk in complex communities. Proceedings of the National Academy of Sciences of the United States of America **110:** 16916–16921.

Johnson, P. T. J., and D. W. Thieltges. 2010. Diversity, decoys and the dilution effect: How ecological communities affect disease risk. Journal of Experimental Biology **213:** 961–970.

Karvonen, A., A. M. Bagge, and E. T. Valtonen. 2005. Parasite assemblages of crucian carp (*Carassius carassius*) – Is depauperate composition explained by lack of parasite exchange, extreme environmental conditions or host unsuitability? Parasitology **131:** 273–278.

Knipes, A. K., and J. Janovy Jr. 2009. Community structure and seasonal dynamics of *Dactylogyrus* spp. (Monogenea) on the fathead minnow (*Pimephales promelas*) from the Salt Valley watershed, Lancaster County, Nebraska. Journal of Parasitology **95:** 1295–1305.

Koskivaara, M. 1992. Environmental factors affecting monogeneans parasitic on freshwater fishes. Parasitology Today **8:** 339–342.

Koskivaara, M., and E. T. Valtonen. 1992. *Dactylogyrus* (Monogenea) communities on the gills of roach in three lakes in central Finland. Parasitology **104:** 263–272.

Koskivaara, M., E. T. Valtonen, and M. Prost. 1991. Dactylogrids on the gills of roach in central Finland: Features of infection and species composition. International Journal for Parasitology **21:** 562–572.

Leong, T. S., and S. Y. Wong. 1988. A comparative study of the parasite fauna of wild and cultured grouper (*Epinephelus malabaricus* Bloch et Schneider) in Malaysia. Aquaculture **68:** 203–207.

Lo, C. M., S. Morand, and R. Galzin. 1998. Parasite diversity/host age and size relationship in three coral-reef fishes from French Polynesia. International Journal for Parasitology **28:** 1695–1708.

Locke, S. A., M. S. Levy, D. J. Marcogliese, S. Ackerman, and J. D. McLaughlin. 2012. The decay of parasite community similarity in ring-billed gulls *Larus delawarensis* and other hosts. Ecography **35:** 530–538.

Luo, Y., C. L. Brown, and T. Yang. 2010. Seasonal dynamics of *Diplectanum grouperi* parasitism on wild versus cultured groupers, *Epinephelus* spp., and the linkage between infestation and host species phylogeny. Journal of Parasitology **96:** 541–546.

Molnár, K. 1971. Studies on gill parasitosis of the grass carp (*Ctenopharyngodon idella*) caused by *Dactylogyrus lamellatus* Achmerov, 1952. III. Therapy and control. Acta Veterinaria Academiae Scientiarum Hungaricae, Tomus **21:** 361–375.

Nie, P., W. J. Yao, Q. Gao, G. T. Wang, and Y. A. Zhang. 1999. Diversity of intestinal helminth communities of carp from six lakes in the flood plain of the Yangtze River, China. Journal of Fish Biology **54:** 171–180.

Norton, J., J. W. Lewis, and D. Rollinson. 2003. Parasite infracommunity diversity in eels: A reflection of local component community diversity. Parasitology **127:** 475–482.

Pechar, L. 2000. Impacts of long-term changes in fishery management on the trophic level water quality in Czech fish ponds. Fisheries Management and Ecology **7:** 23–31.

Pontasch, K. W., and M. A. Brusven. 1988. Diversity and community comparison indices: Assessing macroinvertebrate recovery following a gasoline spill. Water Research **22:** 619–626.

Poulin, R. 1996. Patterns in the evenness of gastrointestinal helminth communities. International Journal for Parasitology **26:** 181–186.

Poulin, R., and S. Morand. 1999. Geographical distances and the similarity among parasite communities of conspecific host populations. Parasitology **119:** 369–374.

Rohde, K., C. Hayward, and M. Heap. 1995. Aspects of the ecology of metazoan ectoparasites of marine fishes. International Journal for Parasitology **25:** 945–970.

Rohde, K., and M. Heap. 1998. Latitudinal differences in species and community richness and in community stucture of metazoan endo- and ectoparasites of marine teleost fish. International Journal for Parasitology **28:** 461–474.

Rückert, S., S. Klimpel, and H. W. Palm. 2010. Parasites of cultured and wild brown-marbled grouper *Epinephelus fuscoguttatus* (Forsskal, 1775) in Lampung Bay, Indonesia. Aquaculture Research **41:** 1158–1169.

Sasal, P., S. Morand, and J. F. Guégan. 1997. Determinants of parasite species richness in Mediterranean marine fishes. Marine Ecology Progress Series **149:** 61–71.

Scholz, T. 1999. Parasites in cultured and feral fish. Veterinary Parasitology **84:** 317–335.

Šimková, A., Pé Sasal, D. Kadlec, and M. Gelnar. 2001. Water temperature influencing dactylogyrid species communities in roach, *Rutilus rutilus*, in the Czech Republic. Journal of Helminthology **75:** 373–383.

Thoney, D. A., and W. J. Hargis Jr. 1991. Monogenea (Platyhelminthes) as hazards for fish in confinement. Annual Reviews of Fish Diseases **1:** 133–153.

Washington, H. G. 1984. Diversity, biotic and similarity indices: A review with special relevance to aquatic ecosystems. Water Research **18:** 653–694.

Wood, C. L., and P. T. J. Johnson. 2016. How does space influence the relationship between host and parasite diversity? Journal of Parasitology **102:** 485–494.

Zelmer, D. A. 2014. Size, time, and asynchrony matter: The species–area relationship for parasites of freshwater fishes. Journal of Parasitology **100:** 561–568.

Zhang, T. L., Z. J. Li, and Q. S. Guo. 2008. Investigations on fishes and fishery of four lakes along the middle and lower basins of the Changjiang River. Acta Hydrobiologica Sinica **32:** 167–177.