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Gastropods on Submersed Macrophytes in Yangtze Lakes: Community Characteristics and Empirical Modelling

key words: epiphytic gastropods, Yangtze shallow lakes, community structure, empirical models, preference analyses.

Abstract

Epiphytic gastropods in Yangtze lakes have suffered from large-scale declines of submersed macrophytes during past decades. To better understand what controls gastropod community, monthly investigations were carried out in four Yangtze lakes during December, 2001–March, 2003. Composed of 23 species belonging to Pulmonata and Prosobranchia, the community is characterized by the constitution of small individuals. The average density and biomass were 417 ± 160 ind/m^2 and 18.05 ± 7.43 g/m^2, with maxima around August. Submersed macrophyte biomass is shown to be the key factor affecting species number, density, and biomass of gastropods. Accordingly, a series of annual and seasonal models yielding high predictive powers were generated. Preference analyses demonstrated that pulmonates and prosobranchs with different respiratory organs prefer different macrophyte functional groups.

1. Introduction

Epiphytic gastropods (gastropods living on macrophytes) are known to play an important role in energy transmission in shallow lake ecosystems. They are herbivores or detritivores, and are prey of molluscivorous fish and other predators (THORP and COVICH, 2001). By grazing, epiphytic gastropods greatly affect the species composition, biomass and productivity of epiphytic communities and stimulate macrophyte growth (BRÖNMARK, 1985; UNDERWOOD *et al.*, 1992; THORP and COVICH, 2001). Reciprocally, submersed macrophytes provide ideal habitats for epiphytic gastropods.

In the Yangtze Basin of China, there are hundreds of shallow lakes with a total area exceeding 20,000 km^2 (LIU, 1984), where the submersed macrophytes as well as the epiphytic gastropods used to be remarkably abundant. However, on account of the increasing human activities in recent decades, the deterioration of submersed macrophytes has occurred widely (NI, 1999). It resulted in habitat fragmentation or even loss of epiphytic gastropods and, correspondingly, the change of gastropod community. For the conservation of gastropods, it is necessary to investigate their community *status quo* in these lakes and create models to predict their status of well-being under different conditions.

Previous researches in relation to status of well-being of epiphytic gastropods has focused on two aspects: the macrophytic and non-macrophytic factors. Among the macrophytic factors, abundance and diversity of macrophytes and their periphyton were often considered the major factors determining the community structure of epiphytic gastropods (LODGE, 1985,

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1986; COLLIER *et al.*, 1999; TESSIER *et al.*, 2004). Plant growth types (submersed, emergent, and floating-leaved) (LODGE and KELLY, 1985; TESSIER *et al.*, 2004) and morphology (degree of leaf dissection, or leaf surface structure) (KRECKER, 1939; CYR and DOWNING, 1988; TANIGUCHI *et al.*, 2003) were also considered as the important factors. Among the non-macrophytic factors, molluscivorous predators such as sunfish and crayfish were believed to play a strong role in governing gastropod abundance (BROWN and DEVRIES, 1985; LODGE *et al.*, 1994; JONES and SAYER, 2003). Some physico-chemical parameters (depth, current, sediments, and calcium) were also suggested to determine the distribution of gastropods (LACOURSIÈRE *et al.*, 1975; LAMARCHE *et al.*, 1982; VINCENT *et al.*, 1991).

However, few modelling works for predicting the dynamic response of epiphytic gastropods to changing environmental conditions have been reported so far.

Works concerning epiphytic gastropods are still preliminary in Chinese Yangtze lakes. CHEN (1965) compared the relative body sizes of snails from submersed and emergent macrophytes. Later, CHEN and HE (1975) gave absolute abundance of epiphytic gastropods at several sites in Lake Donghu, a shallow lake, but no environmental analysis was made. Besides, YU (1996) described the weak relationship between the diversity of macrophytes and their epiphytic gastropods.

The present study was conducted in 20 regions of four Yangtze lakes during December 2001–January 2003. Its purpose is fourfold: 1) to evaluate the ecological role of epiphytic gastropods in Yangtze lakes; 2) to present community characteristics of the epiphytic gastropods; 3) to determine the key factors governing the gastropod community; 4) to generate empirical models based on the key factors to predict diversity and abundance of the epiphytic gastropods. We hope it will benefit the conservation of gastropods in shallow lakes and offer scientific knowledge for ecology and fishery management.

2. Lakes and Methods

The four research lakes (114°08′–48′ E, 30°07′–23′ N), Baoan Lake, Niushan Lake, Lu Lake and Western Liangzi Lake are all located in middle Yangtze basin, Hubei Province, China. Networks or dikes subdivided the waters into 20 regions in total (Fig. 1). Regions range 145–6,667 ha, 2–4 m deep.

Environmental investigations were conducted during December 2001–January 2003. The sampling sites were evenly distributed in each region (105 sites in total, Fig. 1). Submersed macrophyte biomass (B_{Mac}, wet weight), epiphytic gastropod density (D_{Gas}) and biomass (B_{Gas}, wet weight), mean water depth (Z_M), transparency (Z_{SD}) and water temperature (T) were measured once per month, while pH, conductivity (Cond), concentration of total nitrogen (TN), ammonium nitrogen (NH_3–N), total phosphorus (TP), chlorophyll *a* in phytoplankton (Chl *a*) and standing crop of zoobenthos were determined once per season in December 2001–January 2002, April, July, October 2002 and January 2003. It should be noted that periphyton was not included in our modelling study.

Submersed macrophytes were sampled by scythes (1/5 m^2) 2–4 times at each site just above the sediment. After scything, plants were gathered with a 425 μm handnet and put into plastic bags. In the laboratory, the plants were rinsed, rid of superfluous water and weighed for wet weight. Epiphytic gastropods were picked up from the rinsed samples. Zoobenthos were sampled with a modified Peterson sampler (1/16 m^2) one time at each site, cleaned gently with a 425 μm sieve and then sorted. Both epiphytic and benthic animals were preserved in 10% formalin for identification, counting and weighing (wet weight, gastropods with the shell). Z_M and Z_{SD} were measured one time at each site by sounding lead and Secchi Disc respectively. pH and Cond were measured in the field with the YSI Environmental Monitoring Systems 6600. TN, NH_3–N, TP and Chl *a* were determined according to Chinese Water Analysis Methods Standards (HUANG *et al.*, 1999); TN was determined by alkaline potassium persulfate digestion-UV spectrophotometric method, NH_3–N by Nessler's reagent colorimetric method, and TP by the ammonium molybdate-UV spectrophotometric method. Chl *a* was determined by reading absorbances at 665 nm and 750 nm using spectrophotometer after acetone extractions. The stocking and catch data of the crabs and fishes were obtained from the records of local fish farms.

STATISTICA6.0 was used for Pearson correlation, simple regression and stepwise multiple regression analyses to determine the key factors affecting epiphytic gastropod community. A simple and easy

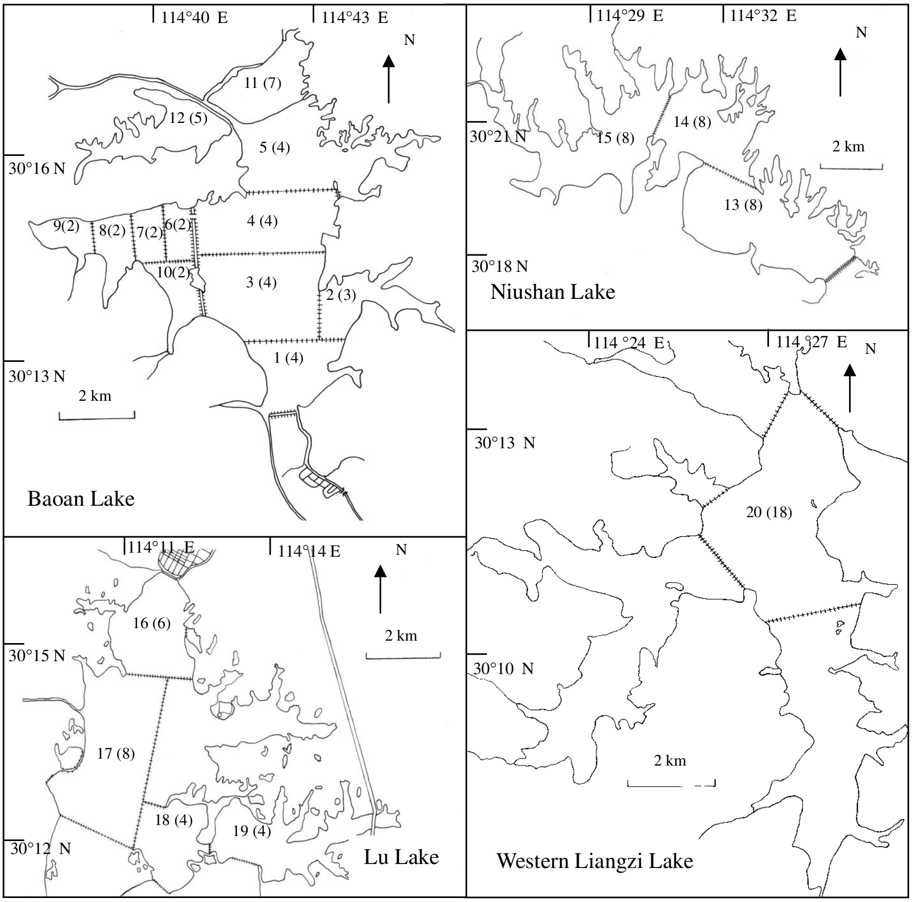

Figure 1. Regions in four lakes. The number in front is region-code and the number in parenthesis denotes the number of sampling sites in each region.

method was applied to test normality of data distribution: the mean/median ratio gives a value of one for normal distribution, a value far from one for skew distribution (HÅKANSON and LINDSTRÖM, 1997). Those skew-distributed data were transformed in common ways (logarithmic, ln (x) and square root, $x^{0.5}$).

3. Results

3.1. Abiotic and Biotic Environments

Table 1 and Table 3 show the area and annual data of the environmental parameters of the research regions. According to these parameters, all investigated waters were meso-eutrophic lakes. They are all macrophyte-dominated lakes representing almost the full range of plant conditions in Yangtze lakes, with B_{Mac} from 30–8500 g/m^2 (biomass of macrophytes). Macrophyte communities in lakes were similar (Table 3), mainly consisting of *Ceratophyllum dermersum* KOM., *Myriophyllum spictum* LINN., *Hydrilla verticillata* (LINN. f.),

Table 1. Annual means of physico-chemical parameters and standing crops of zoobenthos in research regions.

Lake	Region	Area	Z_M	Z_{SD}	T	Cond	pH	NH_3–N	TN	TP	Chl *a*	CY	Benthos Density				Benthos Biomass			
													Gas	Oli	Ins	Tot	Gas	Oli	Ins	Tot
Baoan Lake	Baoankou (1)	363	2.18	1.54	17.6	0.376	7.92	0.171	0.441	0.011	3.91	62	412	44	182	646	94.7	0.46	0.28	95.51
	Huangfengkou (2)	188	1.93	1.87	17.8	0.885	7.94	0.083	0.257	0.015	1.11	88	184	32	344	560	43.7	0.48	1.89	46.10
	Changlingzhou (3)	880	2.50	1.97	17.3	0.457	8.06	0.136	0.257	0.009	1.49	82	292	20	119	436	83.7	0.21	0.42	84.34
	Zhuzhou (4)	645	2.55	1.72	17.3	0.355	8.03	0.141	0.188	0.013	4.28	70	56	4	244	302	10.6	0.06	3.95	14.60
	Longwangtou (5)	625	2.54	1.65	17.3	0.374	7.96	0.158	0.230	0.017	4.27	38	43	21	313	376	18.9	0.38	1.88	21.11
	Lianhuazhou (6)	157	2.64	1.70	18.2	0.252	8.10	0.177	0.241	0.015	2.47	38	12	28	704	744	0.21	0.12	1.97	2.30
	Outang (7)	145	2.53	1.87	18.3	0.236	8.18	0.143	0.180	0.013	3.99	111	800	32	1512	2344	18.1	0.21	2.91	21.22
	Shuimiao (8)	157	2.33	2.08	18.3	0.213	8.38	0.137	0.194	0.011	2.22	105	664	4	1100	1772	28.6	0.01	1.76	30.43
	Changlingtou (9)	149	1.86	1.77	18.8	0.199	8.41	0.154	0.268	0.016	1.98	111	156	16	240	412	9.07	0.60	0.59	10.26
	Tongshawan (10)	191	2.21	1.44	18.6	0.253	8.08	0.219	0.205	0.016	2.04	78	188	52	1220	1460	11.6	0.43	4.15	16.20
	Biandantang (11)	333	2.17	1.36	17.3	0.193	8.07	0.214	0.270	0.018	4.46	57	58	29	266	357	3.52	0.79	0.50	4.82
	Xiaosihai (12)	150	1.80	1.27	16.9	0.321	7.90	0.152	0.190	0.032	2.04	47	21	73	381	476	43.0	0.86	0.29	44.20
Niushan Lake	Dongpian (13)	1750	3.63	2.93	20.5	0.129	8.17	0.110	0.861	0.008	2.75	34	29	29	84	142	32.8	0.63	0.14	33.56
	Zhongpian (14)	1175	3.61	2.79	20.7	0.137	7.85	0.107	0.931	0.005	1.80	38	17	21	59	97	7.58	0.29	0.34	8.21
	Xipian (15)	1333	3.46	2.65	20.9	0.134	8.03	0.115	0.977	0.005	3.30	28	47	15	79	140	65.9	0.13	1.01	67.01
Lu Lake	Wuqianmu (16)	571	2.36	0.80	17.9	0.241	7.69	0.330	0.783	0.037	7.05	18	26	108	222	360	40.9	2.19	1.83	44.95
	Yiwanwu (17)	1210	2.48	0.72	17.6	0.195	7.60	0.263	0.530	0.033	4.24	16	4	75	321	411	2.58	2.69	2.15	7.45
	Hongqicha (18)	451	1.91	0.98	17.6	0.168	7.48	0.096	0.254	0.022	5.87	44	52	40	442	540	10.6	0.38	17.3	28.35
	Caimohu (19)	712	2.07	1.32	18.0	0.142	7.82	0.107	0.286	0.020	1.85	ND	44	60	102	226	21.9	1.34	1.23	24.62
Western Liangzi Lake (20)		6667	3.79	2.48	21.0	0.110	7.82	0.130	0.438	0.013	2.37	26*	60	24	84	168	70.7	0.86	0.06	71.64
	Mean	893	2.53	1.75	18.4	0.269	7.97	0.157	0.399	0.016	3.17	59	158	36	401	598	30.9	0.66	2.23	33.84
	CV	161	24.4	35.5	7.1	64.8	2.9	38.4	67.4	53.5	48.9	45	141	71	103	98	91	106	168	81

Note: Number in the parenthesis, region-code; Area, ha; Z_M, mean water depth in m; Z_{SD}, Secchi depth in m; T, temperature in °C; Cond, conductivity in mS/cm; NH_3–N (Ammonium nitrogen), TN (Total nitrogen), TP (Total phosphorus), mg/L; Chl *a*, chlorophyll *a* of phytoplankton in μg/L; CY, yield of Chinese mitten crab, kg/ha; Density, ind/m^2; Biomass, g/m^2; Gas, gastropods; Oli, oligochaetes; Ins, insects; Tot, total; ND, no data; CV, coefficient of variation in %.

Vallisneria spiralis, *Potamogeton crispus* Linn., *P. maackianus* A. Benn. Benthic animals mainly consisted of gastropods, oligochaetes and insects.

Chinese mitten crab (*Eriocheir japonica sinensis* (H. Milne Edwards, 1854)) and filter-feeding fishes (mainly silver carp (*Hypophthalmichthys molitric* (Cuvier et Valenciennes) and bighead carp (*Aristichthys nobilis* (Richardson)) constitute the main commercial fisheries in these lakes. Molluscivorous fishes are rare in these lakes, especially the black carps (*Mylopharyngodon piceus* (Richardson)), which were found only 2–3 times (1–2 individuals per time) throughout the year.

3.2. Community Structure of epiphytic gastropods

Altogether 23 gastropod species belonging to 12 genera and 7 families were identified from the submersed macrophytes in the regions (Table 2).

The community mainly consisted of small body-sized animals (Fig. 2). The mean body weight was 0.05 g/ind and the dominant (99%) size was less than 0.2 g/ind. The smaller-sized classes were mainly represented by *Radix* spp., Planorbidae spp., *Alocinma longicornis* and *P. striatulus*.

The taxa constituting >1% in relative abundance of any region are given in Table 3. The density of total gastropods was 417 ± 160 ind/m^2 (mean ± SE) and the biomass was 18.05 ± 7.43 g/m^2. In density, the most predominant taxa were those of Planorbidae (46%), followed by *Parafossarulus* (32%). In biomass, *Parafossarulus* ranked first (64%) and *Bellamya* second (20%). At subclass level, prosobranchs comprised 46.8% in density and 90% in biomass; pulmonates comprised 53.2% in density and 10% in biomass.

The seasonal changes of the standing crops of five common gastropod families, their juveniles and the total were given in Figure 3. The abundances of planorbids, bithyniids, pleuroserids and the total increased from spring and reached maximum in summer and then decreased to minimum in winter (Fig. 3B, D, E and G); while the maximum abundances of

Table 2. Taxonomic composition of epiphytic gastropods in research regions (Dec., 2001–Jan., 2003).

- Subclass Pulmonata
  - Lymnaeidae
    - *Acella haldemani* (Binney)
    - *Lymnaea stagnalis* (Linnaeus)
    - *Radix auricularia* (Linnaeus)
    - *R. lagotis* (Schrank)
    - *R. plicatula* (Benson)
    - *R. swinhoei* (H. Adams)
    - *R.* sp.
  - Planorbidae
    - *Gyraulus convexiusculus* (Hütton)
    - *G. compressus* (Hütton)
    - *Hippeutis umbilicalis* (Benson)
    - *Polypylis hemisphaerula* (Benson)
    - Gen. sp. 1
    - Gen. sp. 2
  - Ancylidae
    - *Ferrissia* sp.
- Subclass Prosobranchia
  - Viviparidae
    - *Bellamya* spp.
    - *cf. Bellamya*
  - Stenothyridae
    - *Stenothyra glabra* (A. Adams)
  - Bithyniidae
    - *Alocinma longicornis* (Benson)
    - *Parafossarulus eximius* (Frauenfeld)
    - *P. striatulus* (Benson)
  - Pleuroseridae
    - *Semisulcospira cancellata* (Benson)
    - *S.* sp. 1
    - *S.* sp. 2

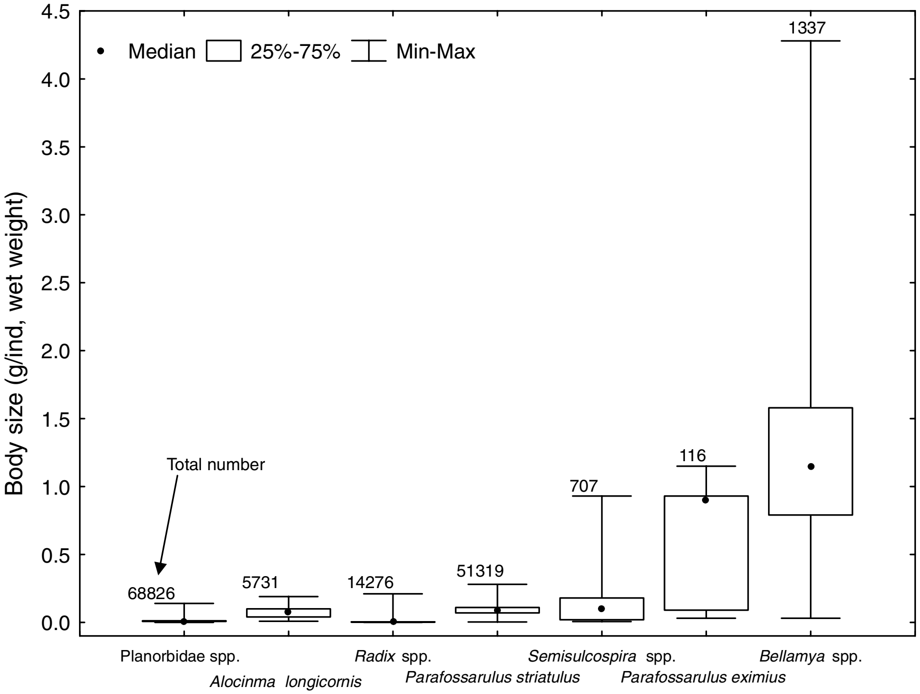

Figure 2. Body sizes of the common epiphytic gastropods.

lymnaeids, viviparids and juvenile snails were observed in spring and then the abundances tended to decrease (Fig. 3A, C and F).

3.3. Key Factors Affecting the Community Structure of Epiphytic Gastropods

Pearson correlations based on absolute (non-transformed) data (Table 4) show that species number (SN_{Gas}), density (D_{Gas}) and biomass (B_{Gas}) of epiphytic gastropods were all significantly correlated positively with biomass of submersed macrophytes (B_{Mac}). There were also significantly positive correlations between Z_{SD}-SN_{Gas}, pH-SN_{Gas}, CY-SN_{Gas}, pH-D_{Gas}, CY-D_{Gas} and negative correlation between TP-SN_{Gas}. However, there were no significant relationships between SN_{Gas} and lake area (Area) or species number of submersed macrophytes (SN_{Mac}). According to the *r*-values, B_{Mac} is the most important factor affecting the variations of SN_{Gas}, D_{Gas} and B_{Gas} in these waters. The positive correlations between CY-SN_{Gas} and CY-D_{Gas} indicate that molluscivorous predators in these lakes did not bring great feeding pressures on the community of epiphytic gastropods. Simple regressions between normal-distributed data (Non-normal data were transformed) of gastropod parameters (SN_{Gas}, D_{Gas}, B_{Gas}) and the above major environmental factors (Z_{SD}, pH, TP, B_{Mac}) also indicates that B_{Mac} is the most important affecting factor (Fig. 4). Stepwise multiple regression analyses made with both absolute and normal-distributed data further indicate that B_{Mac} makes the greatest contribution to explain the variations of SN_{Gas}, D_{Gas} and B_{Gas} (Table 5). Therefore, among our studied environmental factors, B_{Mac} can be statistically considered as the key factor affecting the community structure of epiphytic gastropods. The large number

Table 3. Density (ind/m^2), biomass (wet weight, g/m^2) of common epiphytic gastropods and macrophyte biomass (wet weight, g/m^2) in research regions. – no occurrence.

Lake	Region	Gastropod Density							Gastropod Biomass							Macrophyte Biomass						
		Rad	Pla	Bel	Alo	Par	Sem	Tot	Rad	Pla	Bel	Alo	Par	Sem	Tot	Cd	Ms	Hv	Vs	Pc	Pm	Tot
Baoan Lake	Baoankou (1)	28	639	17	68	856	5	1755	0.44	7.69	24.29	5.69	92.52	0.54	131.35	4219	734	0	2166	169	0	6415
	Huangfengkou (2)	8	246	4	12	72	1	345	0.10	2.56	3.43	1.36	11.16	0.07	18.68	936	599	0	2341	618	67	3763
	Changlingzhou (3)	6	215	9	65	215	12	541	0.13	2.07	10.19	4.32	23.13	1.13	41.11	1365	582	0	25	122	179	2211
	Zhuzhou (4)	5	9	0	4	20	–	42	0.02	0.10	0.00	0.62	4.25	–	4.99	12	467	0	0	24	34	661
	Longwangtou (5)	1	6	0	5	9	–	41	0.00	0.06	0.34	0.68	1.55	–	2.66	22	43	0	0	134	11	239
	Lianhuazhou (6)	1	15	0	1	5	0	23	0.02	0.20	0.66	0.14	0.88	0.07	1.96	0	2	0	0	0	0	26
	Outang (7)	633	803	–	–	68	–	1699	2.59	7.62	–	–	8.97	–	19.49	0	7	0	0	842	2077	3426
	Shuimiao (8)	23	358	–	–	70	–	450	1.83	8.54	–	–	8.46	–	18.83	0	0	0	0	263	8138	8508
	Changlingtou (9)	82	1312	2	1	738	0	2302	0.79	8.56	3.54	0.10	55.99	0.01	69.19	0	289	0	0	500	5790	6747
	Tongshawan (10)	71	77	5	6	6	1	208	0.49	0.80	6.28	0.94	1.06	1.03	10.66	0	0	0	0	66	891	1703
	Biandantang (11)	4	13	0	1	9	0	36	0.01	0.04	0.00	0.12	1.51	0.00	1.69	138	91	0	2	0	0	307
	Xiaosihai (12)	0	0	1	–	2	0	4	0.00	0.00	1.94	–	0.26	0.00	2.20	0	45	0	827	0	0	914
Niushan Lake	Dongpian (13)	13	1	1	1	7	0	24	0.11	0.00	0.34	0.05	0.40	0.01	0.91	0	568	196	198	0	77	1052
	Zhongpian (14)	2	35	1	0	46	2	88	0.03	0.62	1.52	0.04	4.49	0.97	7.74	0	17	87	0	0	22	138
	Xipian (15)	42	62	0	47	79	1	334	0.22	0.61	0.13	1.90	2.93	0.01	6.17	0	19	583	16	2	241	972
Lu Lake	Wuqianmu (16)	–	–	0	–	0	–	1	–	–	0.71	–	0.11	–	0.81	0	0	0	10	42	0	49
	Yiwanwu (17)	0	0	–	–	–	–	1	0.00	0.00	–	–	–	–	0.00	34	24	0	0	1	0	63
	Hongqicha (18)	0	1	–	3	8	–	16	0.00	0.01	–	0.47	1.83	–	2.33	3	16	1	1	13	0	30
	Caimohu (19)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	1	62	230	8	0	300
Western Liangzi	Lake (20)	0	1	2	0	0	0	4	0.01	0.01	1.97	0.01	0.05	0.09	2.15	0	58	0	573	0	0	663
	%	8.0	46.0	0.8	3.6	32.4	0.5	100	1.2	8.8	19.5	5.2	63.7	1.2	100	17.6	9.3	2.4	16.7	7.3	45.9	100
	Mean	51	211	3	15	123	2	417	0.38	2.19	3.69	1.17	12.20	0.33	18.05	336	178	46	319	140	876	1909
	CV	289	172	167	162	205	192	167	189	152	172	148	198	140	179	292	144	291	218	170	248	134

Note: Rad, *Radix* spp.; Pla, planorbid genera, mainly *Gyraulus*; Bel, *Bellamya*; Alo, *Alocinma longicornis*; Par, *Parafossarulus* spp.; Sem, *Semisulcospira* spp.; Tot, total; Cd, *Ceratophyllum demersum*; Ms, *Myriophyllum spicatum*; Hv, *Hydrilla verticillata*; Vs, *Vallisneria spiralis*; Pc, *Potamogeton crispus*; Pm, *Potamogeton macckianus*; CV, coefficient of variation in %.

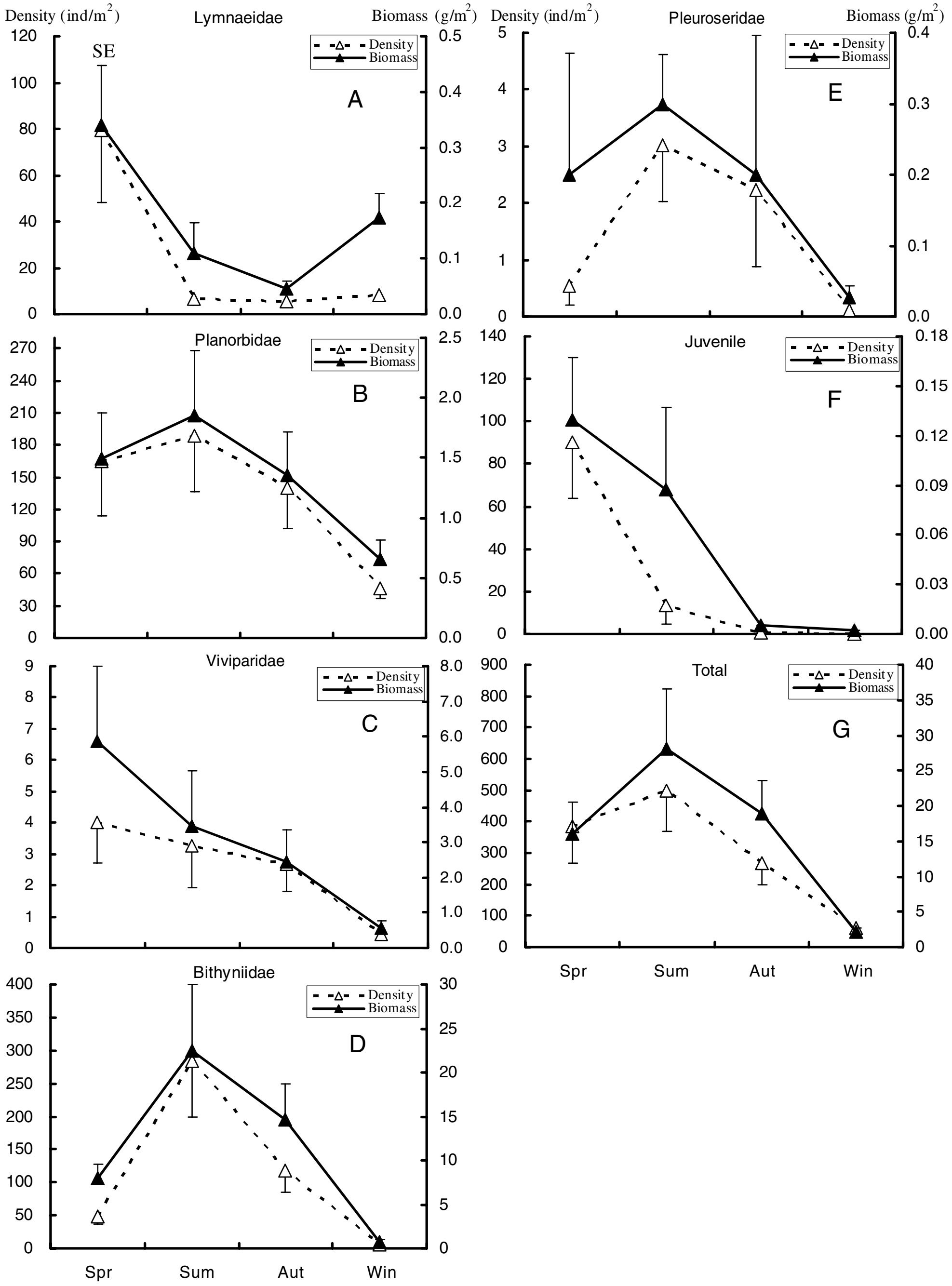

Figure 3. Seasonal changes of the standing crops of the epiphytic gastropods.

Table 4. Pearson correlation coefficients (*r*, upper triangle) and probability levels (*p*, lower triangle) between non-transformed parameters.

	SN_{Gas}	D_{Gas}	B_{Gas}	Area	Z_M	Z_{SD}	T	Cond	pH	NH_3–N	TN	TP	Chl *a*	SN_{Mac}	B_{Mac}	CY
SN_{Gas}		0.36	0.42	–0.02	0.08	**0.46**	0.10	0.30	**0.50**	−0.24	−0.11	**−0.49**	−0.34	0.41	**0.50**	**0.61**
D_{Gas}	0.12		**0.80**	−0.24	−0.26	0.17	−0.03	0.09	**0.50**	−0.08	−0.18	−0.25	−0.11	−0.01	**0.74**	**0.66**
B_{Gas}	0.06	**<0.001**		−0.18	−0.26	0.08	−0.14	0.24	0.26	−0.04	−0.10	−0.26	−0.11	0.08	**0.70**	0.40
Area	0.95	0.31	0.44		**0.68**	0.35	**0.61**	−0.31	−0.22	−0.14	0.29	−0.16	−0.10	−0.13	−0.25	**−0.59**
Z_M	0.74	0.26	0.27	**0.001**		**0.70**	**0.84**	−0.42	0.02	−0.20	**0.69**	**−0.52**	−0.11	0.07	−0.30	−0.41
Z_{SD}	**0.04**	0.48	0.75	0.13	**<0.001**		**0.77**	−0.09	**0.55**	**−0.61**	0.41	**−0.84**	**−0.56**	0.21	0.25	0.24
T	0.66	0.89	0.56	**0.004**	**<0.001**	**<0.001**		**−0.48**	0.14	−0.31	**0.69**	**−0.54**	−0.28	0.07	−0.06	−0.16
Cond	0.19	0.71	0.32	0.18	0.07	0.71	**0.04**		0.04	−0.15	−0.36	0.00	−0.24	0.26	0.24	0.31
pH	**0.02**	**0.03**	0.26	0.34	0.94	**0.01**	0.56	0.88		−0.19	−0.22	**−0.53**	**−0.47**	−0.13	**0.62**	**0.68**
NH_3–N	0.30	0.75	0.88	0.57	0.39	**0.004**	0.18	0.52	0.42		0.08	**0.66**	**0.55**	**−0.45**	−0.17	−0.34
TN	0.63	0.45	0.67	0.22	**<0.001**	0.07	**0.001**	0.12	0.35	0.74		−0.17	0.15	0.27	−0.27	**−0.61**
TP	**0.03**	0.29	0.27	0.49	**0.02**	**<0.001**	**0.01**	1.00	**0.02**	**0.001**	0.49		**0.48**	−0.29	−0.30	−0.36
Chl *a*	0.14	0.63	0.64	0.67	0.65	**0.01**	0.24	0.30	**0.04**	**0.01**	0.52	**0.03**		0.05	−0.30	−0.45
SN_{Mac}	0.08	0.97	0.75	0.60	0.76	0.36	0.78	0.27	0.60	**0.046**	0.31	0.21	0.85		−0.09	−0.16
B_{Mac}	**0.02**	**<0.001**	**0.001**	0.30	0.19	0.28	0.80	0.31	**0.003**	0.48	0.24	0.20	0.19	0.71		**0.76**
CY	**0.007**	**0.003**	0.10	**0.009**	0.09	0.33	0.52	0.20	**0.002**	0.17	**0.007**	0.15	0.06	0.52	**<0.001**	

Note: Significant correlation ($p < 0.05$) in bold letters. SN_{Gas}, D_{Gas}, B_{Gas}, species number, density and biomass of epiphytic gastropods; Z_M, mean water depth Z_{SD}, Secchi depth; T, temperature; Cond, conductivity; Chl *a*, chlorophyll *a* of phytoplankton; SN_{Mac}, B_{Mac}, species number and biomass of submersed macrophytes; CY, yield of Chinese mitten crab, kg/ha.

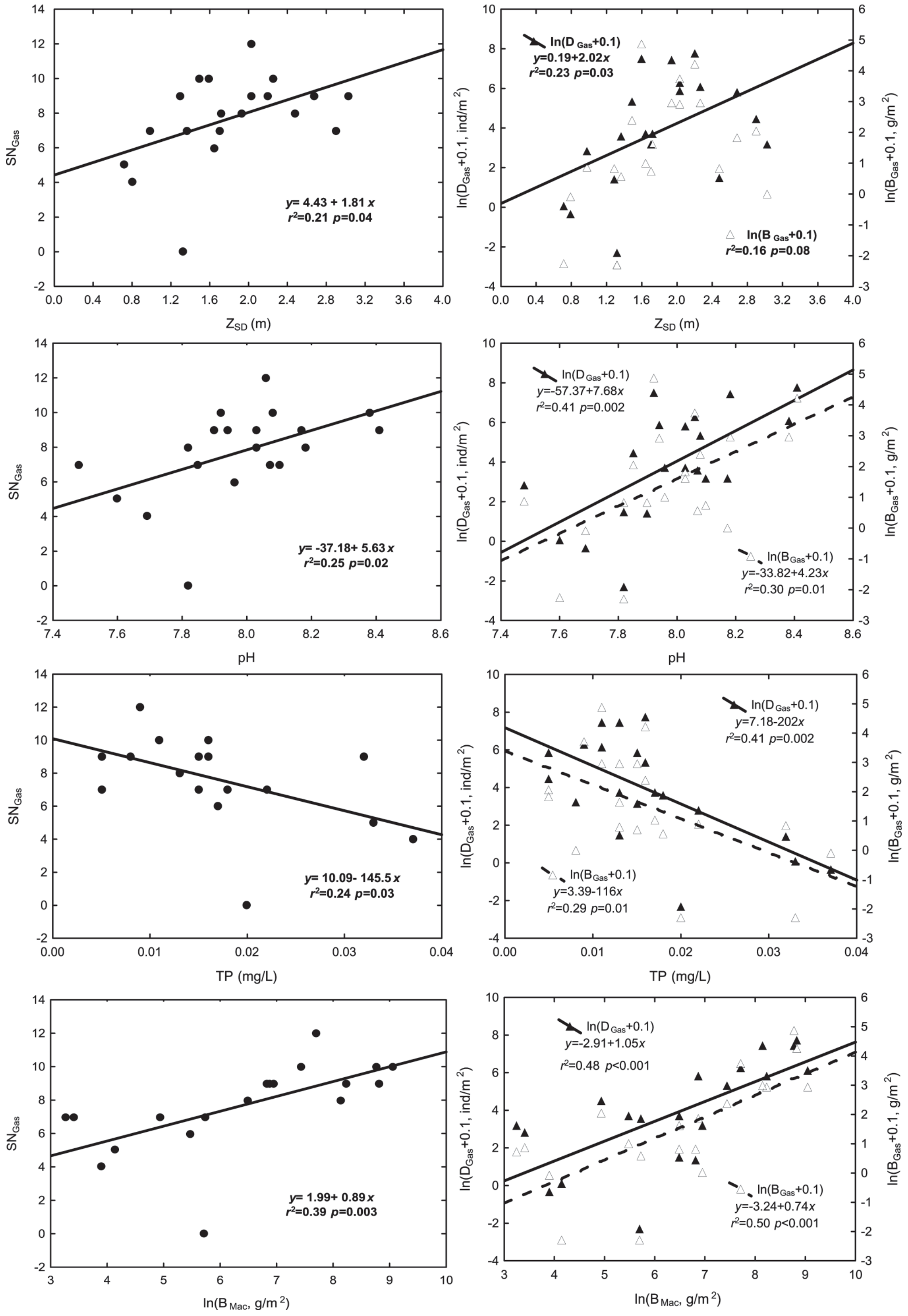
SN$_{Gas}$
Z$_{SD}$ (m)
y= 4.43 + 1.81 x
r^2=0.21 p=0.04
ln(D$_{Gas}$+0.1, ind/m^2)
ln(B$_{Gas}$+0.1, g/m^2)
ln(D $_{Gas}$+0.1)
y=0.19+2.02x
r^2=0.23 p=0.03
ln(B $_{Gas}$+0.1)
r^2=0.16 p=0.08
pH
y= -37.18+ 5.63 x
r^2=0.25 p=0.02
ln(D$_{Gas}$+0.1)
y=-57.37+7.68x
r^2=0.41 p=0.002
ln(B$_{Gas}$+0.1)
y=-33.82+4.23x
r^2=0.30 p=0.01
TP (mg/L)
y= 10.09- 145.5 x
r^2=0.24 p=0.03
ln(D$_{Gas}$+0.1)
y=7.18-202x
r^2=0.41 p=0.002
ln(B$_{Gas}$+0.1)
y=3.39-116x
r^2=0.29 p=0.01
ln(B $_{Mac}$, g/m^2)
y= 1.99+ 0.89 x
r^2=0.39 p=0.003
ln(D $_{Gas}$+0.1)
y=-2.91+1.05x
r^2=0.48 p<0.001
ln(B$_{Gas}$+0.1)
y=-3.24+0.74x
r^2=0.50 p<0.001

Table 5. Stepwise multiple regression analyses using both the absolute and normal-distributed data. (F to enter is 4, $n = 20$, equation: $y = b_0 + b_1x_1 + b_2x_2 + b_3x_3$).

Step	F	r^2	p	x-variable	b_0 (±SE)	b_1 (±SE)	b_2 (±SE)	b_3 (±SE)
A: y-variable = SN_{Gas}								
1	11.31	0.39	0.003	ln (B_{Mac})	1.99 (±1.76)	0.11 (±0.26)		
B: y-variable = ln (D_{Gas}+0.1)								
1	16.3	0.48	<0.001	ln (B_{Mac})	−2.91 (±1.74)	1.05 (±0.26)		
2	5.82	0.61	0.03	TP	1.09 (±2.26)	0.76 (±0.26)	−129.77 (±53.80)	
3	5.28	0.71	0.04	Area	2.62 (±2.13)	0.68 (±0.24)	−154.69 (±49.30)	−0.001 (±0.0003)
C: y-variable = ln (B_{Gas}+0.1)								
1	18.09	0.50	<0.001	ln (B_{Mac})	−3.24 (±1.15)	0.74 (±0.17)		

Note: Only the results based on the normal-distributed data were given because of the highest $r^2 \cdot SN_{Gas}$, species number of epiphytic gastropods; D_{Gas}, density of epiphytic gastropods in ind/m^2; B_{Gas}, biomass of epiphytic gastropods in g/m^2; TP, total phosphorus in mg/L; Area, ha.

of statistical tests reported here, each with $\alpha = 0.05$, suggests that several type-I errors will probably be committed. However, macrophyte biomass is significantly related to each snail variable in every case examined – a result very unlikely due to change alone.

3.4. Empirical Models and Their Predictive Powers

Using the absolute data and data transformed in common ways (logarithmic, ln (x) and square root, $x^{0.5}$), we generated a series of linear regression models. The models based on annual and seasonal data are given in Table 6 and Table 7, respectively.

Predictive powers of the models based on absolute dependent variables can be judged directly according to the r^2 between $x - y$ (Table 6 and Table 7). As for the models based on transformed dependent variables, we further analyzed the r^2 between absolute predicted and observed dependent variables to indicate their predictive capacities because of the fact that what we want to predict are absolute variables (the last two columns in Table 6). According to their predictive powers, model 2 is thought as the best one for SN_{Gas}. Models 7 and 11 are the best ones for annual D_{Gas} and B_{Gas}, respectively. From Table 6, we may find that models for SN_{Gas} ($r^2 = 0.25–0.39$) have the lowest predictive powers when compared to those for D_{Gas} and B_{Gas}. We may also find that all the models for D_{Gas} ($r^2 = 0.54–0.57$ for annual D_{Gas} and 0.65–0.94 for seasonal D_{Gas}) have higher predictive powers than those for B_{Gas} ($r^2 = 0.46–0.50$ for annual D_{Gas} and 0.49–0.93 for seasonal D_{Gas}) (Tables 6 and 7).

◀ Figure 4. Simple regressions ($n = 20$) between Secchi depth (Z_{SD}), pH, total phosphorus (TP), submersed macrophyte biomass (B_{Mac}) and species number (SN_{Gas}), density (D_{Gas}), biomass (B_{Gas}) of epiphytic gastropods.

Table 6. Linear regression models ($y = b_0 + b_1 x$, $n = 20$) of the annual species number (SN_{Gas}), density (D_{Gas}, ind/m^2) and biomass (B_{Gas}, g/m^2) of epiphytic gastropods based on annual submersed macrophyte biomass (B_{Mac}, g/m^2).

No.	y	x	b_0 (±SE)	b_1 (±SE)	$y - x$		P–O	
					r^2	p	r^2	p
(1)	SN_{Gas}	B_{Mac}	6.73 (±0.65)	0.0005 (±0.0002)	0.25	0.02		
(2)	SN_{Gas}	$\ln(B_{Mac})$	1.99 (±1.76)	0.89 (±0.26)	0.39	0.003		
(3)	SN_{Gas}	$(B_{Mac})^{0.5}$	5.71 (±0.79)	0.06 (±0.02)	0.36	0.005		
(4)	D_{Gas}	B_{Mac}	16.69 (±133)	0.20 (±0.04)	0.55	<0.001		
(5)	D_{Gas}	$(B_{Mac})^{0.5}$	−264 (±171)	19 (±3.92)	0.56	<0.001		
(6)	$\ln(D_{Gas} + 0.1)$	$\ln(B_{Mac})$	−2.91 (±1.74)	1.05 (±0.26)	0.48	<0.001	0.54	<0.001
(7)	$(D_{Gas})^{0.5}$	$\ln(B_{Mac})$	−24.8 (±8.61)	6.01 (±1.29)	0.54	<0.001	0.57	<0.001
(8)	$(D_{Gas})^{0.5}$	$(B_{Mac})^{0.5}$	−1.97 (±3.12)	0.45 (±0.07)	0.69	<0.001	0.54	<0.001
(9)	B_{Gas}	B_{Mac}	0.54 (±6.59)	0.009 (±0.002)	0.49	<0.001		
(10)	B_{Gas}	$(B_{Mac})^{0.5}$	11 (±8.71)	0.81 (±0.2)	0.48	<0.001		
(11)	$\ln(B_{Gas} + 0.1)$	$\ln(B_{Mac})$	−3.24 (±1.15)	0.74 (±0.17)	0.50	<0.001	0.50	<0.001
(12)	$(B_{Gas})^{0.5}$	$\ln(B_{Mac})$	−4.14 (±1.78)	1.12 (±0.27)	0.49	<0.001	0.46	0.001
(13)	$(B_{Gas})^{0.5}$	$(B_{Mac})^{0.5}$	0.06 (±0.65)	0.09 (±0.01)	0.65	<0.001	0.49	<0.001

Note: For SN_{Gas}, only the models reaching significant level ($p < 0.05$) are given; for D_{Gas} and B_{Gas}, only the models yielding higher predictive power ($p \leq 0.001$) are given; P and O, absolute (non-transformed) predicted and observed values of D_{Gas} and B_{Gas}.

3.5. Preference of Gastropod Taxa for Submersed Macrophytic Species

Table 8 gives the Pearson correlations between the absolute standing crops of common gastropod taxa and some species of submersed macrophytes. The abundance of each snail was significantly correlated positively with biomass of 2–3 macrophytic species. At subclass level, pulmonates (*Radix* and Planorbidae) and prosobranchs (*Bellamya*, *Alocinma*, *Parafossarulus* and *Semisulcospira*) showed different preference for macrophytic species.

Table 7. Linear regression models ($y = b_0 + b_1 x$) of density (D_{Gas}, ind/m^2) and biomass (B_{Gas}, g/m^2) of epiphytic gastropods based on submersed macrophyte biomass (B_{Mac}, g · m^{-2}) in spring (_Spr), summer (_Sum), autumn (_Aut) and winter (_Win).

No.	y	x	b_0 (±SE)	b_1 (±SE)	r^2	n	p
(14)	D_{Gas}_Spr	B_{Mac}_Spr	−619.9 (±572.2)	1.07 (±0.14)	0.80	17	<0.001
(15)	D_{Gas}_Sum	$(B_{Mac}\_Sum)^{0.5}$	−589.4 (±650.5)	73.88 (±13.03)	0.65	19	<0.001
(16)	D_{Gas}_Aut	B_{Mac}_Aut	49.33 (±177.9)	0.28 (±0.04)	0.86	12	<0.001
(17)	D_{Gas}_Win	B_{Mac}_Aut	−16.1 (±22.31)	0.1 (±0.01)	0.94	20	<0.001
(18)	D_{Gas}_Win	B_{Mac}_Win	0.06 (±23.38)	0.15 (±0.01)	0.94	20	<0.001
(19)	B_{Gas}_Spr	$(B_{Mac}\_Spr)^{0.5}$	−9.36 (±20.59)	1.55 (±0.41)	0.49	17	0.002
(20)	B_{Gas}_Sum	$(B_{Mac}\_Sum)^{0.5}$	−45.76 (±48.99)	4.53 (±0.98)	0.56	19	<0.001
(21)	B_{Gas}_Aut	$(B_{Mac}\_Aut)^{0.5}$	−11.49 (±16.43)	1.82 (±0.31)	0.78	12	<0.001
(22)	B_{Gas}_Win	B_{Mac}_Aut	−0.59 (±0.90)	0.004 (±0.0002)	0.93	20	<0.001
(23)	B_{Gas}_Win	B_{Mac}_Win	−0.05 (±0.87)	0.005 (±0.0004)	0.93	20	<0.001

Note: Only the models yielding the highest predictive power are given.

Table 8. Pearson correlation coefficients (r) and probability levels (p) between the standing crops of the common taxa of epiphytic gastropods and submersed macrophytes.

$n = 20$		D_{Rad}	B_{Rad}	D_{Pla}	B_{Pla}	D_{Bel}	B_{Bel}	D_{Alo}	B_{Alo}	D_{Par}	B_{Par}	D_{Sem}	B_{Sem}
B_{Cd}	r	−0.07	−0.01	0.30	0.41	**0.94**	**0.95**	**0.78**	**0.90**	**0.72**	**0.83**	**0.59**	0.36
	p	0.77	0.93	0.22	0.09	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**<0.001**	**0.008**	0.14
B_{Ms}	r	−0.14	−0.13	0.27	0.25	**0.66**	**0.63**	**0.58**	**0.67**	**0.54**	**0.60**	**0.55**	0.23
	p	0.53	0.54	0.29	0.33	**0.001**	**0.004**	**0.01**	**0.002**	**0.02**	**0.007**	**0.02**	0.38
B_{Hv}	r	−0.04	−0.09	−0.15	−0.17	−0.16	−0.16	0.31	0.09	−0.08	−0.14	−0.06	−0.09
	p	0.84	0.67	0.50	0.69	0.50	0.49	0.20	0.72	0.71	0.56	0.80	0.69
B_{Vs}	r	−0.11	−0.10	0.16	0.24	**0.62**	**0.61**	0.38	**0.51**	0.42	**0.51**	0.16	0.03
	p	0.62	0.63	0.53	0.36	**0.004**	**0.006**	0.12	**0.03**	0.08	**0.03**	0.54	0.95
B_{Pc}	r	**0.73**	**0.74**	**0.75**	**0.72**	0.09	0.08	−0.01	0.04	0.32	0.31	−0.03	−0.12
	p	**<0.001**	**<0.001**	**<0.001**	**0.001**	0.73	0.80	0.91	0.94	0.19	0.21	0.88	0.57
B_{Pm}	r	0.21	**0.69**	**0.63**	**0.76**	−0.12	−0.09	−0.17	−0.18	0.31	0.24	−0.13	−0.14
	p	0.39	**0.001**	**0.004**	**<0.001**	0.62	0.69	0.46	0.42	0.20	0.35	0.57	0.53

Note: Significant correlation ($p < 0.05$) in bold letters. D, density in ind/m^2; B, biomass in g/m^2; Rad, *Radix*; Pla, Planorbidae; Bel, *Bellamya*; Alo, *Alocinma*; Par, *Parafossarulus*; Sem, *Semisulcospira*; Cd, *Ceratophyllum dermersum*; Ms, *Myriophyllum spicatum*; Hv, *Hydrilla verticillata*; Vs, *Vallisneria spiralis*; Pc, *Potamogeton crispus*; Pm, *P. maackianus.*

In Yangtze lakes, *P. crispus* and *P. maackianus* often grow luxuriantly enough to be emergent to water surface, while the other macrophytes are entirely submersed. Accordingly, we divided these macrophytes into two functional groups, group I comprising *C. dermersum*, *M. spictum, H. verticillata* and *V. spiralis* and group II comprising *P. crispus* and *P. maackianus*. Regression analyses showed that pulmonate abundances had significant relationships with biomass of group II macrophytes (Fig. 5B); while prosobranch abundances had significant relationships with biomass of group I macrophytes (Fig. 5C).

4. Discussion

4.1. Ecological Role of Epiphytic Gastropods

In comparison with the data taken merely by Peterson sampler from the same research regions, epiphytic gastropod density was about 3.6 times greater than benthic gastropod density (mainly *Bellamya*) and 1.6 times greater than total benthos density; epiphytic gastropod biomass was about 34% of benthic gastropod biomass and 33% of total benthos biomass. Although using data from different methods for comparison may not be reasonable, at least it indicates that epiphytic gastropods contribute a great deal to the secondary production in these macrophyte-dominated lakes. A study in several backwaters and lakes of New Zealand (Biggs and Malthus, 1982) also showed the great contributions of epiphytic gastropods to secondary production, amounting to 42–66% of total epiphytic invertebrate biomass.

4.2. Characteristics of the Community Structure

The epiphytic gastropod communities in Yangtze lakes are characterized by the constitution of small individuals. Their mean body weight (0.05 g/ind) was much lesser than that of benthic gastropods (0.2 g/ind). As compared to that of the benthic gastropods in algae-dom-

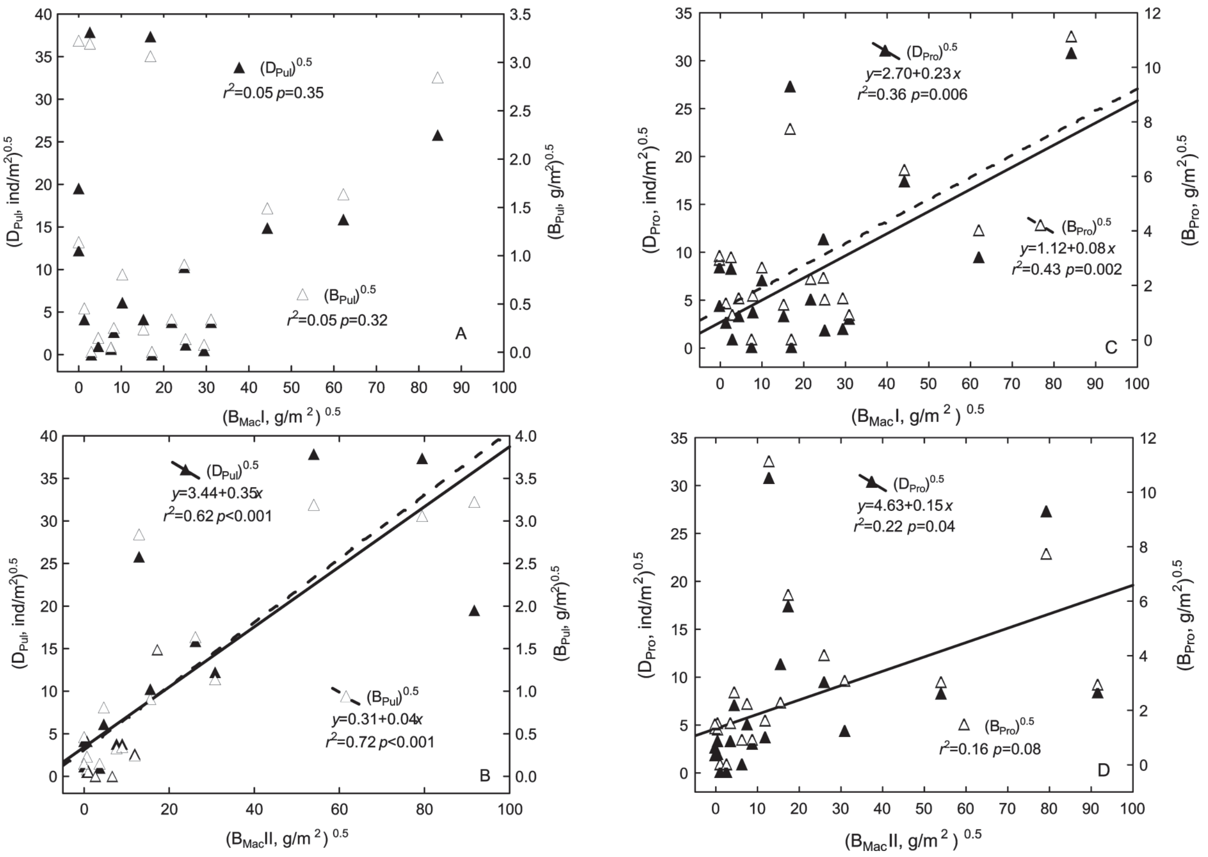

Figure 5. Regressions ($n = 20$) between biomass of the two functional groups of submersed macrophytes (group I, B_{Mac}I; group II, B_{Mac}II) and density, biomass of the two epiphytic gastropod subclasses of (pulmonates, D_{Pul}, B_{Pul}; prosobranchs, D_{Pro}, B_{Pro}).

inated lakes (about 5 g/ind), the difference is even greater (LIANG and LIU, 1995). Generally, in comparison with other habitat types, submersed macrophytes are believed to give more efficient refuge from predators for large animals (TESSIER *et al.*, 2004). Lacking large invertebrates is usually regarded as an indicator of fish predation (BLUMENSHINE *et al.*, 2000). This explanation, however, is less applicable to our research regions because few molluscivorous fish were present there. Different mechanisms such as gravitational effect and resource limitation of larger snails may result in the smaller size structure of the epiphytic gastropod community. This is evident from the seasonal change of the standing crops of *Bellamya* (Viviparidae) (Fig. 3C), a group with largest body size in the community. They live mainly on macrophytes as juveniles and settle to the bottom when they grow larger (CHEN, 1979).

The seasonal changes of the epiphytic gastropod abundances were similar to those of submersed macrophytes (WANG *et al.*, 2005) and benthic gastropods in these research regions. Most of them showed one significant peak around August. Those of Lymnaeidae and Viviparidae showed different patterns, both reached highest around May and decreased in the following months (Fig. 3A and C). The different pattern of Lymnaeidae is mainly due to its close relationship with *Potamogeton crispus* (Table 8), the biomass of which also reached maximum around May and withered abruptly since then. The reasons for the different pattern of Viviparidae may be the settlement of larger animals to bottom due to gravitational effect and resource limitation. The standing crops of benthic gastropods from algae-dominated lakes, however, changed irregularly depending on the occurrence of larger snails such as *Bellamya* (LIANG and LIU, 1995). Probably, such difference is mainly due to the regulating effects of submersed macrophytes on epiphytic gastropods and also benthic gastropods under vegetation.

The seasonal pattern of the abundance of juvenile gastropods (Fig. 3F) indicates that reproductive period of the epiphytic gastropods lasted from spring to autumn (Apr.–Oct.) and spring was the main reproductive season. The moderate number of total snail abundance in spring was mainly because, in spring, the juveniles were just deposited and too small to be effectively sampled. CALOW (1978) has classified life histories of freshwater gastropods into seven patterns (A–G). Among them, Patterns D–F having three reproductive intervals (in spring, summer and autumn) were believed to be the predominant populations in subtropical or tropical environments (THORP and COVICH, 2001). However, no significant reproductive interval was found in our present study. To explain the difference, detailed research dealing with factors affecting life-histories of epiphytic gastropods are needed in mid-lower Yangtze lakes.

4.3. Key Factors Governing the Community Structure

As the key factor, submersed macrophytes may influence the community structure of epiphytic gastropods in the following ways: 1) Submersed macrophytes provide important direct food source for snails (NEWMAN, 1991), and indirect food sources through periphyton they support (JEPPESEN *et al.*, 1998). 2) Submersed macrophytes provide heterogeneous substrates for snails to oviposit on (abundant eggs cemented to plants can be easily seen during reproductive seasons), to crawl on and gain access to the air-water interface (particularly for pulmonates) (BRÖNMARK, 1989). 3) Submersed macrophytes also improve physicochemical environments of snails (SCHEFFER, 1998). They regulate pH through metabolism and reduce phytoplankton densities (Chl *a*) to enhance water clarity (Z_{SD}) through a variety of mechanisms, such as shading, reduction of nutrient availability (e.g., TN and TP) and reduction of resuspension (SCHEFFER, 1998; also evident from the positive correlations of B_{Mac}-Z_{SD}, B_{Mac}-pH and negative correlations of B_{Mac}-TN, B_{Mac}- TP, B_{Mac}-Chl *a* in Table 4).

The relatively lower predictive powers of the models for species number of snails (Table 6) suggest that there must be some other factors colimiting the snail colonization.

Periphyton, as the main food source, may be the factor of primary importance. It has been frequently found that snails prefer specific types of periphyton (MCMAHON *et al.*, 1974; LODGE, 1985, 1986). Therefore, in future research, it is necessary to find out some simple approach to quantify the periphyton community.

4.4. Preference of Gastropod Subclasses over Macrophytic Functional Groups

The preferences of pulmonates and prosobranchs for different macrophytic functional groups are mainly due to the different respiratory organs between two snail subclasses and the different spatial structures between macrophyte groups. Pulmonates breathe with lung alveola and they have to come to water surface for air (THORP and COVICH, 2001) and hence, they tend to live on macrophytes belonging to group II, which can spread their terminal parts on the water surface. Prosobranchs, on the other hand, possess gills, with which they can breathe freely under water (THORP and COVICH, 2001), so that they can normally inhabit the macrophytes of functional group I, the entirely submersed vegetation.

4.5. Applications of the Empirical Models

According to the r^2 in Table 6 and Table 7, most of the models yield high predictive powers; especially, those of winter gastropod abundances have r^2 close very much to ideal 1 (0.93–0.94). In ten Canadian lakes, a regression model based on 12 x-variables was also built for the density of epiphytic gastropods (CYR and DOWNING, 1988). Though its apparent predictive power (adjusted r^2 between model-predicted values and empirical values is 0.63, $n = 199$) is high enough, the uncertainties in so many x-variables may be accumulated or multiplied in the model predictions and hence greatly depress the model accuracy (HÅKANSON, 1995).

Our models can be widely used in lentic macrophyte-dominated lakes in mid-lower Yangtze Basin, where their morphogenesis, depths, bottoms, climate and even landscapes are similar. If these models are to be used in lotic waters, or in other region, or for other plant types such as emergent and floating-leaved macrophytes, it is strongly recommended to calibrate the models according to the characters of local water or reanalyze the key factor.

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