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Changes in Pelagic Fish Community Composition, Abundance, and Biomass along a Productivity Gradient in Subtropical Lakes

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Abstract: How fish communities change with eutrophication in temperate lakes is well documented, while only a few studies are available from subtropical lakes. We investigate the fish community structure in 36 lakes located in the Yangtze River basin, covering a wide nutrient gradient. We found that fish species richness and total fish catch per unit effort (CPUE) increased significantly with chlorophyll *a* (Chl*a*). Among the different feeding types, the proportion of zooplanktivores increased significantly with Chl*a*, while the percentage of omnibenthivores showed no obvious changes; the CPUE of piscivorous *Culter* spp. increased with Chl*a*, while their proportion of total catch decreased pronouncedly. Based on the index of relative importance (IRI), the most important and dominant fish species was the zooplanktivorous Sijiao (*Toxabramis swinhonis*), followed by the omniplanktivorous sharpbelly (*Hemiculter leucisculus*) and the omnibenthivorous crucian carp (*Carassius carassius*), a small-sized species belonging to the Cyprinidae family. The CPUE of these three species increased significantly with Chl*a*. The focus has, so far, been directed at large fish, but as emphasized by our results, the abundant small fish species were dominant in our subtropical study lakes even in terms of biomass, and, accordingly, we recommend that more attention be paid to the population dynamics of these species in the future.

Keywords: lake eutrophication; fish community structure; total phosphorus; chlorophyll *a*; shallow lake; Yangtze River basin

1. Introduction

Fish play an important role in structuring aquatic ecosystems through various pathways. Predation by planktivorous fish on zooplankton affects the abundance, size, and species composition of the zooplankton community [1–3] and, thereby, indirectly, the phytoplankton, having cascading effects even down to physicochemical conditions [4]. Benthivorous fish may also affect the water quality by inducing sediment disturbance and resuspension, resulting in reduced water transparency and increased nutrient release from the sediment [5]. Fish abundance and community structure are influenced by the nutrient state and productivity of lakes [6–10]. Anthropogenic eutrophication has become a severe problem in lake ecosystems worldwide, often accompanied by an increase in phytoplankton biomass and loss of water clarity, with implications for the fish community as well. For instance, the feeding efficiency of piscivorous fish in productive lakes is reduced due to decreased water transparency, while planktivorous fish species may be less affected [11]. Consequently, planktivorous and omnivorous fish may benefit from the released predation pressure by piscivores and the enhanced food availability in terms of higher biomasses of zooplankton [12] and macroinvertebrates [13–15] in eutrophic lakes.

The responses of fish community structure to lake eutrophication have been intensively investigated, especially in Europe. Typically, the total biomass of fish increases with eutrophication [10,16]; the fish community changes to a dominance of cyprinids, especially roach (*Rutilus rutilus*) and bream (*Abramis brama*) [7,8], and the percentage of piscivorous fish declines with nutrient enrichment in European lakes [3]. However, in a study of 36 Finnish lakes, the biomass of both cyprinids and percids increased with lake productivity [7]. At lower nutrient levels, eutrophication leads to a shift from dominance by salmonids to percids [17,18]. Fish size is also affected by eutrophication, with a shift from dominance by large-sized to smaller-sized specimens [3,19]; this may, in part, be due to the weaker predator control of planktibenthivorous fish by piscivorous fish in more eutrophic lakes.

The response of fish community structure to lake eutrophication in subtropical lakes has been comparatively less investigated [20–25]. The richness of omnivorous fish species is reported to increase with decreasing latitude [26]; fish, overall, become smaller, and their abundance is higher [27,28]. In China, crucian carp (*Carassius carassius*), common carp (*Cyprinus carpio*), sharpbelly (*Hemiculter leucisculus*), Sijiao (*Toxabramis swinhonis*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Hypophthalmichthys nobilis*), and some smaller-sized zooplanktivorous fish species are common, especially in shallow subtropical lakes [21,29]. A large number of shallow lakes are located in the Yangtze River basin [30] (subtropical zone). These lakes exhibit contrasting nutrient states [31], but little is known about their fish communities and how they respond to changes in productivity. We conducted a survey of 36 Yangtze River basin lakes with contrasting nutrient concentrations. Based on existing relationships for temperate lakes, we hypothesized that (1) fish species richness would be higher in the more productive lakes and that (2) fish total catch per unit effort would increase with increasing productivity, while (3) mean body size would decrease because of the dominance by small-sized species. We also predicted that (4) zooplanktivorous fish would constitute an increasing proportion at the expense of piscivores and that the proportion of omnivores would be high in the more productive lakes.

2. Materials and Methods

2.1. Sample Collection and Analysis

In the summer (June to August) of 2016, fish community structure and lake physicochemical variables were investigated in 36 lakes (Figure 1). Multisized gill nets—eight mesh sizes (5, 10, 15, 20, 25, 30, 35, and 40 mm), 10 m long, and 1.5 m high—were used to sample the fish community. The nets are pieced together, from small to large, the 5–15 mm mesh nets being pelagic and the remaining benthic. New nets were used in each lake as holes may often occur after net retrieval and the removal of fish. During each sampling event, at around 9:00 to 10:00 a.m., one net was set randomly perpendicular to the shoreline in the pelagic area of each lake and left for 2 h, after which total catch per net was recorded as biomass per unit effort (per hour) (BPUE) and number per unit effort (NPUE). We classified fish species by their feeding habits, following Teixeira-de Mello et al. (2009) [20]: planktivores, omnibenthivores, omniplanktivores, omniherbivores, and piscivores. According to Teixeira-de Mello et al. (2009) [20], zooplanktivorous fish feed only on zooplankton, while omnivorous fish feed on at least two trophic levels; piscivores feed mainly on fish but also include shrimps in their diet. Nevertheless, we adapted this classification for the omnivorous species with omniplanktivores (feeding mainly on plankton) and omnibenthivores (collecting food mostly from the sediment).

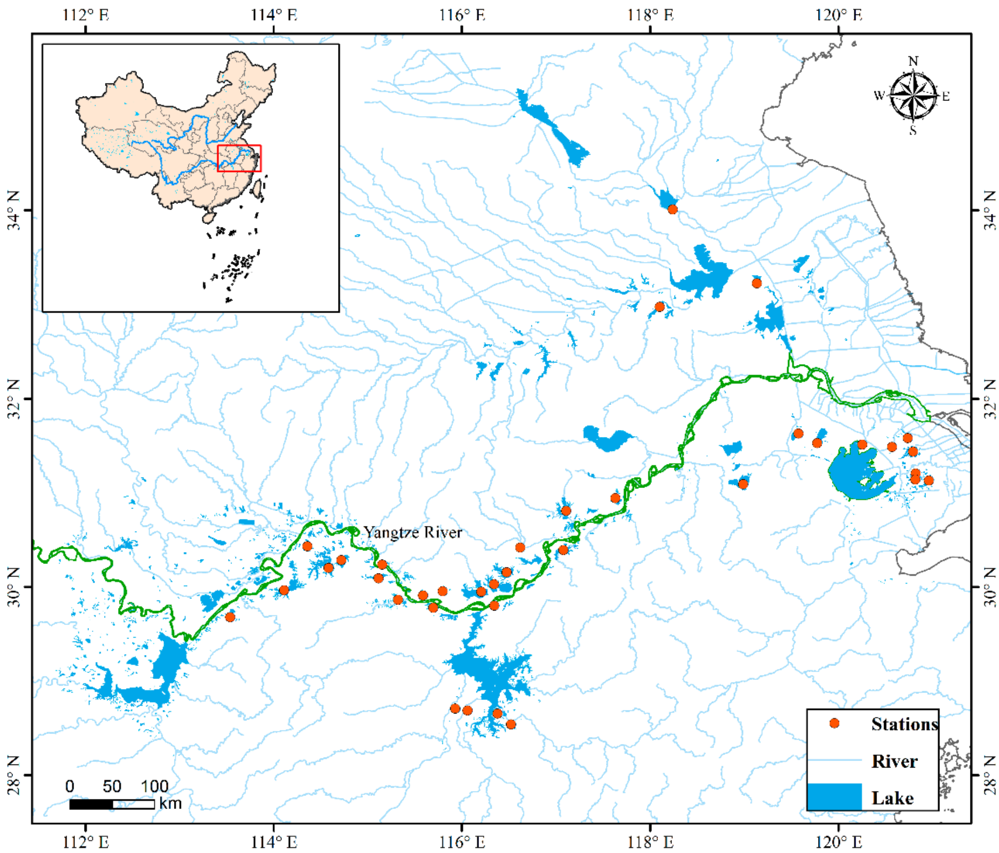

Figure 1. Locations of the study lakes. The red dots indicate the sampling lakes; the blue lines represent rivers or tributaries of the lake.

Physicochemical samples and variables of the study lakes were collected from three stations per lake. A Secchi disc was used to measure the transparency (SD), and water depth was recorded with a sensor (SM-5 Depthmate Portable Sounder, Laylin Associates LTD., Unionville, VA, USA) at each sampling site. The integrated water samples, pooled from three subsamples collected at different depths (0.5, 1.0, and 1.5 m), were taken with a 5-L water sampler (made by plexiglass) at each site; a 5-L subsample was brought back to the laboratory. There, total nitrogen (TN) was determined using an alkaline potassium persulfate digestion-UV spectrophotometric method, and total phosphorus (TP) was determined following the ammonium molybdate spectrophotometric method after digestion with $K_2S_2O_8$ solution according to the Chinese Standard Methods for Monitoring Lake Eutrophication [32]. Chlorophyll *a* was measured using a 90% acetone/water (volume/volume) solution extraction, followed by spectrophotometry, and calculated without correcting for pheophytin interference [33]. Total suspended solid (TSS) samples were prepared by filtering 0.5–2 L lake water through preweighed GF/C filters, which were then dried at 60 °C.

2.2. Data Analysis

An index of relative importance (IRI) [34,35] was used to estimate the contribution of each fish species to the total catch. Potential collinearity among predictors (e.g., Chl*a*, TP, TN, SD, lake size, average depth) was checked using the variance inflation factor (VIF < 5). Thereafter, multiple regressions were performed to identify the significant explanatory variables in fish compositional data (e.g., NPUE, BPUE, richness, average fish size, proportion of each fish trophic group) with a generalized linear model (GLM). Akaike Information Criterion (AIC) was used to select the best model. Finally, the most powerful predictor in explaining fish compositional patterns in our study lakes was chosen for further analysis.

For relationships between different trophic groups of fish and environmental variables, fish were categorized into zooplanktivores, omnivores (omniplanktivores and omnibenthivores), and piscivores. Linear regression was used to analyze the relationships between fish species richness, total catch per unit effort (NPUE and BPUE), mean fish size (BPUE/NPUE), NPUE of small- (TL < 15 cm) and large-sized (TL > 15 cm) fish, NPUE and BPUE of the dominant species, and their own best explanatory variables. The data were $\log_{10}{}^{x}$ transformed to meet the requirements of normal distribution and homogeneity of variance. Data used for the analysis of correlations, such as TP, Chl*a*, and SD, were the average of three sampling sites in each lake. All analyses were performed in the R4.0.3 statistical software [36] using both "raster" [37] and "usdm" [38] packages.

3. Results

3.1. Physicochemical Parameters of the Studied Lakes

The study lakes were, overall, shallow and turbid (Table 1), having a mean depth of 4.2 m (1.5–7.1 m) and an average Secchi depth of 0.8 m (0.1–2 m). Total nitrogen and TP varied markedly, averaging 1.2 mg N L^{-1} and 89 µg P L^{-1} (Table 1). The concentration of Chl*a* ranged between 4.4 and 84 µg L^{-1} (mean: 32 µg L^{-1}; Table 1).

Table 1. Characteristics of the investigated lakes. SD represents the standard deviation of the sampling lakes. Chl*a*, chlorophyll *a* concentration in phytoplankton.

Parameters	Minimum	Maximum	Mean	±SD
Lake area (km^2)	7.3	375	94	102.6
Secchi depth (m)	0.1	2	0.8	0.5
Depth (m)	1.5	7.1	4.2	1.6
Secchi depth: water depth ratio	0.02	0.4	0.2	0.09
Total suspended solids (mg L^{-1})	3.2	59	16.5	10.5
Total nitrogen (mg L^{-1})	0.5	2.7	1.2	0.6
Total phosphorus (µg L^{-1})	17.6	393	89	87.2
Chl*a* (µg L^{-1})	4.4	84	32	21.7

3.2. Relationships between Chla and Lake Nutrients and Transparency and Results of GLM Analysis

The concentration of Chl*a* was quadratically correlated with TN (Figure 2A; R^2 = 0.25) and significantly positively linearly related to TP (Figure 2B; p = 0.0004); Secchi depth declined with Chl*a* (Figure 2C; p < 0.0001). Likewise, the ratio of Secchi depth to water depth (SD:WD) declined significantly with Chl*a* (Figure 2D, p = 0.015), with an average of 0.19, ranging from 0.04 to 0.43.

Parameters (e.g., estimate, t-value, p-value) of GLM analysis of the selected environmental variables are given in Table 2. Overall, Chl*a* was the most powerful explanatory variable for most of the fish community traits tested in our study (e.g., fish species richness, NPUE, BPUE, and N% of both zooplanktivores and piscivores; Table 2). Moreover, TP, TN, Secchi depth, and lake size were also important explanatory variables for some fish community traits, e.g., TN for mean fish size and the biomass proportion of both benthivores and piscivores, TP for the biomass proportion of piscivores, lake size for mean fish size, and both NPUE and BPUE of the piscivorous *Culter* spp. (Table 2 and Table S1).

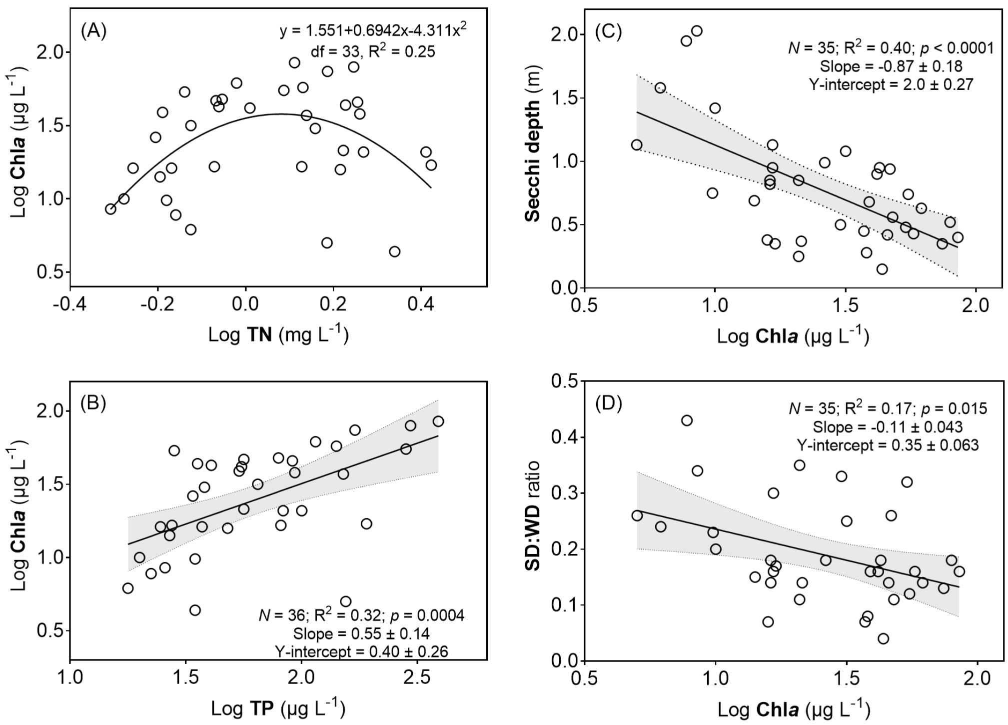

Figure 2. Relationships between (**A**) total nitrogen (TN) and (**B**) total phosphorus (TP) in the water, (**C**) water transparency (Secchi depth, SD), and (**D**) the ratio of Secchi depth to water depth (SD:WD) versus the concentration of Chl*a*. *N*, number of lakes; Chl*a*, chlorophyll-*a* concentration in phytoplankton. The dashed lines represent the 95% confidence band.

3.3. Fish Species Richness along the Chla Gradient

On average, five species were caught per lake, ranging from three to 13 species. Lake primary productivity (Chl*a*) was the most powerful explanatory variable for fish species richness in our study lakes (Table 2). A significant positive linear relationship was found between species richness and Chl*a* (Figure 3).

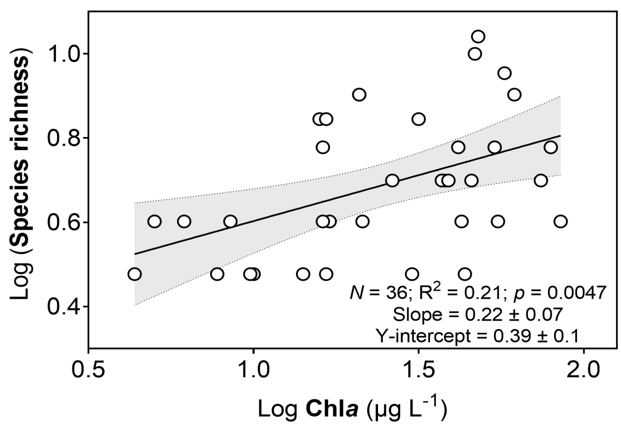

Figure 3. Relationships between richness of the fish species caught and Chl*a*. The dashed line represents the 95% confidence band. *N*, number of lakes; Chl*a*, chlorophyll *a* concentration in phytoplankton.

Table 2. Results of the multiple regressions using a generalized linear model (GLM) to select the significant explanatory environmental variables for fish compositional data. Environmental variables: chlorophyll *a* concentration in phytoplankton (Chl*a*, μg L^{-1}), mean depth (m), total nitrogen in the water (TN, mg L^{-1}), lake surface size (km^2), Secchi depth (SD, m), and total phosphorus in the water (TP, μg L^{-1}). AIC, Akaike Information Criterion. Fish community traits: NPUE, number per unit effort (ind. net^{-1} h^{-1}); BPUE, biomass per unit effort (kg net^{-1} h^{-1}); mean fish size (BPUE/NPUE, g $ind.^{-1}$); TL, total length; N%, percentage in number; B%, percentage in biomass; Sijiao, *Toxabramis swinhonis*; sharpbelly, *Hemiculter leucisculus*; crucian carp, *Carassius carassius.* Note: both significant and insignificant explanatory environmental variables for fish community traits are shown in Table S1.

Fish Compositional Parameters	Environmental Variables	AIC	Estimate	*t*-Value	Pr (>|t|)
Log Fish species richness	Log Chl*a*	160.5	2.7	2.6	0.012
Log NPUE	Log Chla	43.2	0.8	4.2	0.00017
Log BPUE	Log Chl*a*	40.7	0.9	4.5	<0.0001
Log Mean fish size	Log TN	39.6	1.0	2.6	0.014
	Log Lake size	42.5	−0.3	−2.5	0.019
Log NPUE of fish TL < 15 cm	Log Chl*a*	60.0	0.9	3.6	0.0012
Log NPUE of fish TL > 15 cm	Log Chl*a*	48.0	0.7	3.2	0.0028
Log N% of zooplanktivores	Log Chl*a*	−64.9	0.1	3.0	0.006
	Log SD	−64.0	−0.1	−2.2	0.04
Log B% of zooplanktivores	Log SD	25.0	−0.6	−2.5	0.02
	Log Chl*a*	27.5	0.4	2.3	0.033
Log B% of benthivores	Log TN	33.2	−0.9	−2.3	0.028
Log N% of piscivores	Log Chl*a*	14.2	−0.5	−2.6	0.019
Log B% of piscivores	Log Chl*a*	24.1	−1.4	−6.5	<0.0001
	Log TN	29.7	−2.8	−5.4	<0.0001
	Log TP	30.5	1.2	4.3	0.00063
	Log SD	31.9	−1.0	−3.8	0.0019
Log NPUE of Sijiao	Log Chl*a*	53.4	0.8	2.7	0.012
Log BPUE of Sijiao	Log Chl*a*	53.5	0.8	2.6	0.014
Log NPUE of sharpbelly	Log Chl*a*	45.6	1.3	3.5	0.0022
Log BPUE of sharpbelly	Log Chl*a*	38.6	1.1	3.2	0.0041
Log NPUE of crucian carp	Log Chl*a*	25.4	1.3	4.2	0.00048
	Log SD	32.9	0.9	2.7	0.016
Log BPUE of crucian carp	Log Chl*a*	29.3	0.9	2.8	0.011
Log NPUE of *Culter*	Log Chl*a*	2.5	0.5	3.7	0.002
	Log Lake size	12.0	−0.2	−2.2	0.042
Log BPUE of *Culter*	Log Lake size	18.8	−0.5	−3.0	0.008
	Log Chl*a*	22.1	0.5	2.2	0.04
Log Mean size of Sijiao	Log TN	−16.5	0.6	3.8	0.00059
Log Mean size of sharpbelly	Log SD	−2.9	−0.8	−4.4	0.00016
Log Mean size of crucian carp	Log Lake size	5.9	−0.2	−2.2	0.042
Log mean size of *Culter*	Log Chl*a*	13.2	−0.4	−2.1	0.05

3.4. Relationships of Fish Catch with Lake Productivity

Fish NPUE increased significantly with Chl*a* (Figure 4A; $p < 0.0001$), varying from 4 to 309 ind. net^{-1} h^{-1} (mean = 60 ind. net^{-1} h^{-1}). BPUE was also higher in lakes with high Chl*a* (Figure 4B; $p < 0.0001$) and varied from 0.1 to 6.8 kg net^{-1} h^{-1} (mean = 1.5 kg net^{-1} h^{-1}).

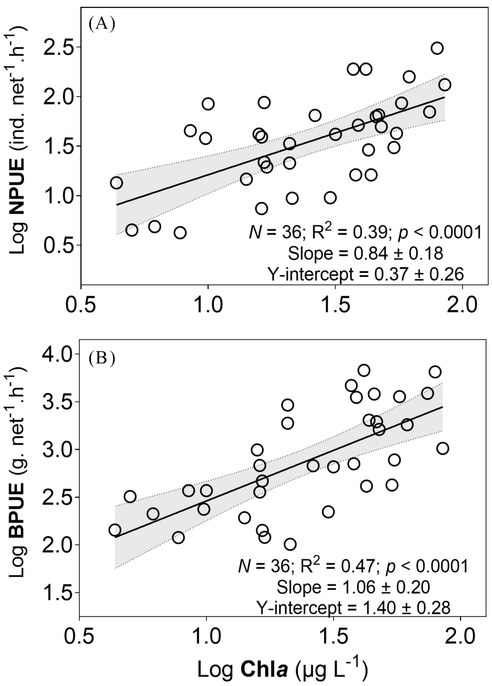

Figure 4. Relationships between fish catch per unit effort (NPUE, number per unit effort (**A**); BPUE, biomass per unit effort (**B**) and Chl*a*. *N*, number of lakes; Chl*a*, chlorophyll-*a* concentration in phytoplankton. The dashed lines represent the 95% confidence band.

3.5. Fish Size and NPUE of Different Size Classes of Fish

The average body weight of fish (calculated as BPUE/NPUE) was negatively related to lake surface size (Figure 5A; $p = 0.034$) and positively related to TN (Figure 5B; $p = 0.034$).

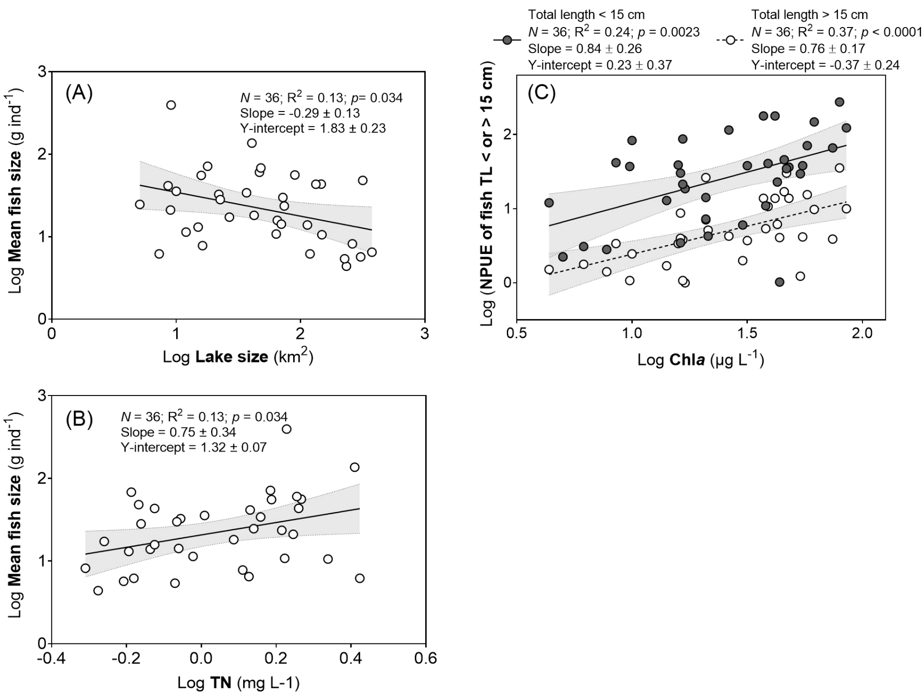

Figure 5. Relationships between mean body weight (total biomass/total numbers) of all fish caught (**A**,**B**) and when divided into two size classes based on fish total length (TL, (**C**)) and environmental variables. NPUE, catch per unit effort in numbers; Chl*a*, chlorophyll-*a* concentration in phytoplankton; TN, total nitrogen concentration in the water. The dashed lines represent the 95% confidence band.

For both size classes of fish (total length <15 and >15 cm), the catch was significantly positively related to Chl*a* (Figure 5C). The average NPUE of smaller-sized fish (TL < 15 cm, 52 ind. net^{-1} h^{-1}) was almost 7-fold higher than that of fish with TL > 15 cm (7.6 ind. net^{-1} h^{-1}), the mean percentage of smaller-sized fish being 79% (ranging between 20% and 99.5%).

3.6. Composition of Fish Community Structure and Trophic Groups

In total, 3384 fish were caught, belonging to 20 species, of which 16 came from the Cyprinidae family. The zooplanktivorous *T. swinhonis* had the highest frequency of occurrence (FO%, 89%), followed by the omniplanktivorous *H. leucisculus* (78%) and the omnibenthivorous *C. carassius* (69%) (Table 3). The piscivorous *Culter* spp. had a relatively high FO% (56%), but its number percentage (N%, 1.2%) and biomass percentage (B%, 3%) were low (Table 3). Zooplanktivorous fish dominated the fish community structure in terms of numbers (65%), and omniplanktivores and omnibenthivores contributed 25% and 8%, respectively, while the piscivores and omniherbivores constituted <2%. In terms of biomass, omniplanktivores (48%) and omnibenthivores (30%) were the most important, while zooplanktivores and omniherbivores constituted 15% and 4%, respectively. The contribution of piscivores was low (3%).

Table 3. Frequency occurrence (FO%), relative contribution by number (N%) and biomass (B%), and index of relative importance (IRI) of the fish sampled. Note: The highest value for each trophic group is given in bold when there are more than one species in the trophic group.

Trophic Group	Species	FO%	N%	B%	IRI	IRI%
Zooplanktivores	*Toxabramis swinhonis* [a]	**89**	**62**	**14**	**6719**	**52**
	Coilia nasus [b]	42	3	1	187	1.5
	Hyporhamphus intermedius [c]	28	0.5	0.1	17	0.1
	Neosalanx taihuensis [d]	6	0.05	0.01	0.3	0.0
Omniplanktivores	*Hemiculter leucisculus* [a]	**78**	**21**	6	**2164**	**17**
	Hypophthalmichthys nobilis [a]	28	1	**36**	1027	8
	Hypophthalmichthys molitrix [a]	11	0.6	5	57	0.4
	Pseudobrama simoni [a]	11	0.8	1	21	0.2
	Acheilognathus macropterus [a]	17	0.3	0.2	9	0.07
	Pseudorasbora parva [a]	6	0.3	0.05	2	0.01
Omnibenthivores	*Carassius carassius* [a]	**69**	**7**	**26**	**2253**	**18**
	Tachysurus fulvidraco [e]	28	0.7	2	75	0.6
	Cyprinus carpio [a]	6	0.05	1	7	0.06
	Xenocypris microlepis [a]	8	0.1	0.6	6	0.05
	Xenocypris hupeinensis [a]	6	0.04	0.06	0.5	0.0
	Xenocypris davidi [a]	3	0.02	0.05	0.2	0.0
	Hemibarbus labeo [a]	3	0.02	0.08	0.3	0.0
	Sarcocheilichthys sinensis [a]	3	0.04	0.1	0.4	0.0
Omniherbivore	*Megalobrama amblycephala* [a]	11	0.9	4	54	0.4
Piscivores	*Culter* spp. [a]	56	1.2	3	234	2

Note: label of different fish families, [a] = Cyprinidae, [b] = Engraulidae, [c] = Hemiramphidae, [d] = Salangidae, [e] = Bagridae.

The smaller-sized *T. swinhonis* was the dominant zooplanktivorous species, constituting 62% of the total fish catch by numbers, while the omniplanktivorous *H. leucisculus* and omnibenthivorous *C. carassius* made up 21% and 7%, respectively (Table 3). In terms of biomass, the large-sized *H. nobilis* and medium-sized *C. carassius* contributed 36% and 26%, respectively, to the total catch and *T. swinhonis* 14% (Table 3).

According to the IRI score, the planktivorous *T. swinhonis* was the most important or abundant fish in the study lakes, followed by the omnibenthivorous *C. carassius* and the omniplanktivorous *H. leucisculus* (Table 3). Less abundant fish were the omniplanktivorous *H. nobilis*, the zooplanktivorous *C. nasus*, and the piscivorous *Culter* spp.

3.7. Correlations of Different Trophic Groups of Fish with Chla and TN

Lake primary productivity (expressed as Chl*a*) was the most powerful predictor for the number (N%) and biomass (B%) proportions of both zooplanktivorous and piscivorous fish, while TN was the best explanatory variable for the B% of omnibenthivorous fish (Table 2).

Both in terms of number and biomass, the percentage of all zooplanktivorous fish increased significantly with Chl*a* (Figure 6A,B). However, the contribution of piscivores decreased pronouncedly with Chl*a* (Figure 6C,D). The B% of omnibenthivores was significantly negatively related to TN (Figure 6E); in contrast, the relationships between N% of omnibenthivores and environmental variables were insignificant.

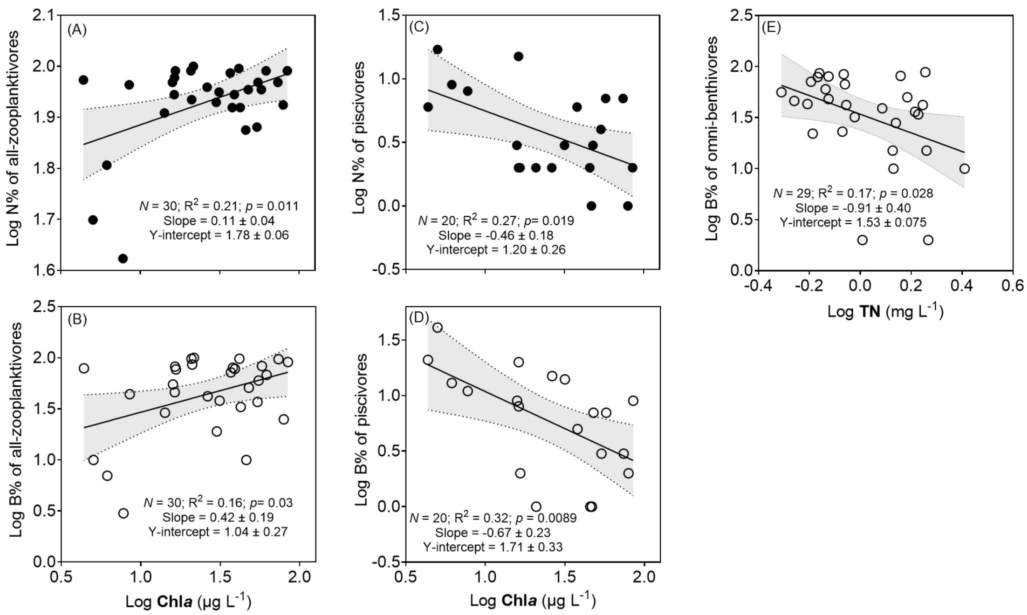

Figure 6. Percent abundance (N%) and biomass (B%) of all zooplanktivores (zooplanktivores + omniplanktivores (**A**,**B**)) and piscivores (**C**,**D**) along the Chl*a* gradient and of omnibenthivores (**E**) along the TN gradient. *N*, number of lakes; Chl*a*, chlorophyll-*a* concentration in phytoplankton. The dashed lines represent the 95% confidence band.-

3.8. Relationships between the Catch of Three Dominant Species and Piscivorous Fish and Chla

Chl*a* of phytoplankton was the best explanatory variable for both NPUE and BPUE of three dominant fish species from different trophic groups and the piscivorous *Culter* spp. (Table 2). Both NPUE and BPUE of *T. swinhonis* increased markedly with Chl*a* (Figure 7). Similarly, NPUE and BPUE of *H. leucisculus* demonstrated a significant positive linear correlation with Chl*a* (Figure 7). In addition, both NPUE and BPUE of the omnibenthivorous *C. carassius* increased markedly with Chl*a* (Figure 7). Contrary to the proportional decline of piscivores with Chl*a*, NPUE and BPUE of *Culter* spp. increased markedly with Chl*a* (Figure 7).

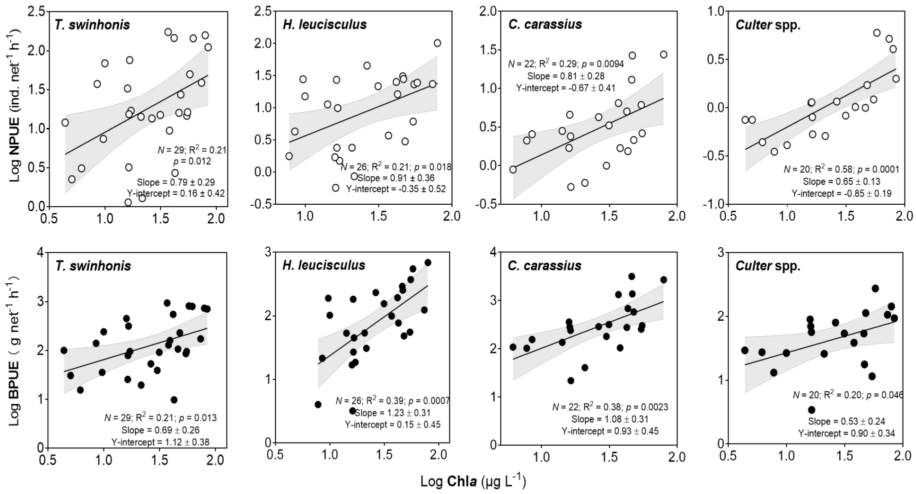

Figure 7. Relationships between catch per unit effort (NPUE and BPUE) of the three dominant fish species and piscivores and Chl*a*. *N*, number of lakes; Chl*a*, chlorophyll-*a* concentration in phytoplankton; NPUE, catch per unit effort in numbers; BPUE, catch per unit effort in biomass. Notes: *Toxabramis swinhonis* (zooplanktivore), *Hemiculter leucisculus* (omnizooplanktivore), *Carassius carassius* (omnibenthivore) and *Culter* spp. (piscivore). The dashed lines represent the 95% confidence band.

3.9. Relationships between Mean Body Weight of Three Dominant Species and Piscivorous Fish and Environmental Variables

The mean body weight (averaging 7 g ind.$^{-1}$) of the zooplanktivorous *T. swinhonis* increased significantly and linearly with TN (Figure 8). By contrast, the average body weight of the omniplanktivorous *H. leucisculus* showed a markedly negative linear relationship with Secchi depth (Figure 8). However, lake size was the most powerful determinant for crucian carp; thus, the mean size of the omnibenthivorous *C. carassius*, having a mean body weight of 120 g ind.$^{-1}$, decreased linearly with lake size (Figure 8). The average body weight of the piscivorous *Culter* spp., having a mean body weight of 48 g ind.$^{-1}$, decreased significantly with Chl*a* (Figure 8).

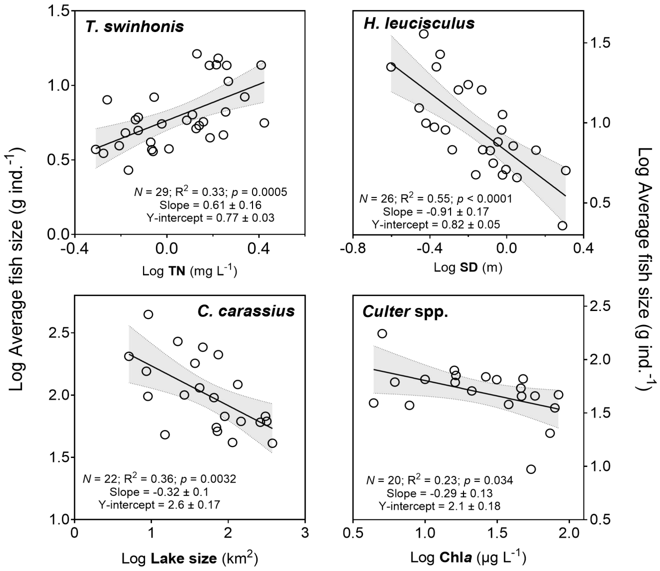

Figure 8. Relationship between average fish weight of the dominant fish species and the selected environmental variables. *N*, number of lakes; TN, total nitrogen concentration in the water; SD, Secchi depth; Chl*a*, chlorophyll-*a* concentration in phytoplankton. *Toxabramis swinhonis* (zooplanktivore), *Hemiculter leucisculus* (omni-zooplanktivore), *Carassius carassius* (omni-benthivore), and *Culter* spp. (piscivores). The dashed lines represent the 95% confidence band.

4. Discussion

We found that species richness was significantly linearly related to lake productivity (expressed as Chl*a*), which is in accordance with several studies from the temperate climate zone [7,39,40]. The relationship between species richness and environmental factors has been well studied in Europe [3,7,10,16,41,42]. Our results differ from those of Jeppesen et al. (2000) [3], which showed a unimodal relationship with TP, and those of Helminen et al. (2000) [43], which revealed a reduction in species number in eutrophic Finnish lakes that was attributed to oxygen deficiency. The difference in fish species between the European studies and the present studies may reflect the somewhat smaller Chl*a* gradient of our study lakes. We found that 16 out of 20 species came from the Cyprinidae family, and the increase in species richness along a Chl*a* gradient was mainly attributed to an increasing number of cyprinids, especially omnivorous species. A similar trend has been found in temperate European lakes [7].

Fish species richness is reported to increase markedly with lake area [10,16,39,40,44,45], but we found no such relationship, confirming an earlier study of 109 Chinese lakes [46]. Most of our study lakes were shallow and eutrophic, which may have resulted in reduced habitat availability [47], weakening the effect of lake area on fish species richness. Moreover, our data were collected offshore only, and most fish species are typically found in the littoral zone of lakes, even in very large lakes [48]. Accordingly, in a study of 56 Danish lakes, Menezes et al. (2013) [42] found that lake area was a poor predictor of fish species richness in offshore samples, while it emerged as the best predictor for littoral samples.

As expected, both NPUE and BPUE increased markedly with lake productivity, as also recorded for European lakes [7,10,16,43,49], Florida lakes [22,44], Argentinian lakes and reservoirs [50], and Canadian lakes [51]. When divided into species, both NPUE and BPUE of the three most dominant species increased markedly with productivity; for instance, the average NPUE of the most abundant species, *T. swinhonis*, was 61 ind. net^{-1} h^{-1} in high productive lakes (Chl*a* > 40 μg L^{-1}), which was 2.5-fold higher than at lower Chl*a*. A similar trend was found for *H. leucisculus* and *C. carassius*, for which average BPUE was 3.1- and 3.5-fold higher, respectively, than in lakes with Chl*a* < 40 μg L^{-1}. The contribution of the three most dominant species, all from the Cyprinidae family, to the total fish catch of the 36 lakes averaged 90% in abundance and 47% in biomass, respectively. Our results from shallow subtropical lakes show that lake eutrophication results in cyprinid species dominance, as previously seen in temperate lakes [7,27,52].

The mean body weight (BPUE/NPUE) of fish has been reported to decline with lake eutrophication [10]. However, we found that the mean fish size of the total catch increased significantly with TN despite the overall dominance of small-sized species in our study lakes, as previously observed in other subtropical lakes [20,28]. In our study lakes, the NPUE increase of large-sized fish (TL > 15 cm) with Chl*a* resulted in a larger mean fish size in the high-TN lakes.

We found a dominance of zooplanktivorous and omnivorous species in high productive lakes, which is in accordance with former studies [8,27,52]. In our study, the zooplanktivorous Sijiao was the most dominant species, followed by the omnibenthivorous crucian carp and the omniplanktivorous sharpbelly, all being highly linearly related to Chl*a*. The dominance of these species may, in part, reflect an increase in the biomass of zooplankton with the increasing Chl*a*/eutrophication, as seen in both shallow subtropical lakes [12,53] and mesocosm experiments in this climate region [54]. Sijiao feed mainly on zooplankton, especially cyclopoid copepods [55], and although sharpbelly is a typical omniplanktivorous fish, they feed substantially on zooplankton in eutrophic lakes [56]. Thus, a higher biomass of zooplankton in eutrophic lakes [4] may facilitate the population growth of both Sijiao and sharpbelly. A notable difference from the studies of north temperate lakes was that the proportion of omnibenthivorous fish was overall high and did not differ along the lake productivity gradient, as otherwise seen in lakes in both northern Europe [27] and the USA [57]. High dominance of omnivores is, however, to be expected in warm lakes [26,57]. In our study, crucian carp was the dominant omnivorous species and constituted about 90% of the total omnivore CPUE in the 36 lakes, both in terms of abundance and biomass. They can use macrophytes as a food resource [55,58,59] in clear water lakes and detritus in turbid lakes [59], in addition to feeding on benthic animals such as oligochaetes and chironomids [60,61]. In a study of a restored subtropical lake, sharpbelly and crucian carp utilized plant material rather effectively [55], and they were also the most abundant (IRI) fish species in Poyang Lake [25], which receives a large seasonal input of plant detritus. Higher abundance and biomass of benthic macroinvertebrates in more productive (high TP and Chl*a* contents) lakes [13–15] may have further favored omnibenthivorous fishes such as crucian carp.

The low proportions of piscivorous fish may have contributed to the dominance of smaller-sized fishes in our study lakes. It is widely accepted that predation pressure by piscivorous fish is weak in warm lakes [28]. In a study of a shallow restored subtropical lake, the piscivorous mandarin and snakehead fed mainly on shrimps rather than fish [55], even though the abundance of fish was relatively high. Furthermore, piscivorous fish were reported to have only weak control of the abundance of their prey fish in a subtropical enclosure experiment [62]. *Culter* spp. was the only piscivorous fish caught in our study lakes, and although both NPUE and BPUE of the fish correlated positively with productivity, their proportion of the catch showed a significant negative relationship with Chl*a*. The mean body weight of *Culter* was less than 50 g ind.$^{-1}$ (mean TL = 18.7 cm), indicating that they were not efficient fish predators. Supporting this view, Li et al. (2011) [63] only found fish in the diet of *Culter* when the standard length exceeded 20 cm. Smaller-sized *Culter* fed mainly on zooplankton [63,64]; thus, the higher zooplankton availability in more productive lakes [12,53] may also support the development of small sizes of the piscivorous *Culter*. Accordingly, in our study lakes, both the enhanced food availability and the absence of or weak predation pressure by piscivorous fish at high Chl*a* likely contributed importantly to the dominance of small fish such as Sijiao, sharpbelly, and crucian carp.

A number of studies have documented that the proportions of zooplanktivores and omnivores were positively related to nutrients, whereas the percentage of piscivores decreased markedly with lake productivity [24,27,65]. For our subtropical lakes, we also found that the proportion of all zooplanktivores (zooplanktivores + omniplanktivores) increased significantly with lake productivity, while the proportion of piscivorous fish decreased. The strong correlations of the smaller-sized zooplanktivorous Sijiao and the omniplanktivorous sharpbelly with lake productivity contributed mainly to these general zooplanktivore relationships. The lower proportion of piscivores in more productive lakes may, in part, be due to low water transparency as most piscivores are a visual foraging species, for example, perch [66], pike [67], and mandarin fish [68]. However, prey consumption of planktivorous fish is typically less affected by turbidity [11], making elevated turbidity advantageous for planktivorous fish at reduced predation by piscivores. Moreover, strong food competition for zooplankton between juvenile piscivores and zooplanktivores, which dominated the catches in our study, may contribute to the decline in piscivores [49,69].

Multimesh gillnets have been widely used to investigate lake fish community structure, and the European standard (CEN, 2005) has been applied in many studies [10,70–72]. In China, there is no similar standard. In our study, we used fewer mesh sizes (8 vs. 14) and a smaller mesh size range (5–40 vs. 6.5–75 mm (Lundgreen net type) and 5.5–55 mm (CEN standard)), so the smallest and largest fish were not efficiently captured. However, our gillnets caught fish within a large individual size range of 6–63.5 cm in total length and 1.2–2657 g in wet weight; NPUE and BPUE ranges were 4–309 ind. net^{-1} h^{-1} and 0.1–6.8 kg net^{-1} h^{-1}, respectively. Thus, we believe that our gillnets gave a representative picture of the pelagic fish species community. Another limitation in our study is the limited number of nets used, which gives rise to some uncertainty but still allowed us to identify strong relationships with eutrophication, likely reflecting the large nutrient gradient selected.

A potential caveat in our study is fish stocking, for which there is a long tradition in Chinese freshwaters. Unfortunately, we do not have stocking data for our study lakes. Usually, in China, silver carp, bighead carp, common carp, and grass carp are the dominant cultured species because of their fast growth rate and bigger sizes [73]. However, both the occurrence and proportion of these four species were relatively low in our catches (Table 2). Thus, the FO% of bighead carp, silver carp, and common carp were 28%, 11%, and 6% and their percent abundance (N%) 1.3%, 0.6%, and 0.05%, respectively. We, therefore, assumed a low effect of stocking on our results.

5. Conclusions

We found that fish catches increased significantly with lake productivity and that a high abundance, biomass, and proportion of zooplanktivorous fish, as judged from other studies, e.g., [1–4], lead to high predation pressure on zooplankton, with consequent negative impacts on lake ecosystems through cascading effects. The small-sized zooplanktivorous Sijiao and the omniplanktivorous sharpbelly were the most dominant species in our study lakes, and this may be so in other subtropical lakes along the Yangtze River. In the management and restoration of shallow subtropical lakes, the focus has mainly on larger fish species, but our results also show that small fish, occurring in high abundance, should be considered for the purpose of restoration. Therefore, more attention should be paid to the population dynamics of these species in future investigations.

Supplementary Materials: The following are available online at https://www.mdpi.com/2073-4441/13/6/858/s1, Table S1: Results of the multiple regressions using generalized linear model (GLM) to select the significant explanatory environmental variables for fish compositional data. Environmental variables: chlorophyll *a* concentration in phytoplankton (Chl*a*, μg L^{-1}), mean depth (m), total nitrogen in the water (TN, mg L^{-1}), lake surface size (km^2), Secchi depth (SD, m) and total phosphorus in the water (TP (μg L^{-1}). Fish community traits: NPUE, number per unit effort (ind. net^{-1} h^{-1}); BPUE, biomass per unit effort (kg net^{-1} h^{-1}); mean fish size (BPUE/NPUE, g $ind.^{-1}$); TL, total length; N%, percentage in number; B%, percentage in biomass; Sijiao, *Toxabramis swinhonis*; sharpbelly, *Hemiculter leucisculus*; crucian carp, *Carassius carassius*..

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