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Variations in CO_2 fluxes from grass carp *Ctenopharyngodon idella* aquaculture polyculture ponds

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ABSTRACT: Monthly and diurnal CO_2 fluxes at the water–air interface were measured in 3 grass carp *Ctenopharyngodon idella* polyculture ponds using the closed-chamber method during the farming season from April to September 2013. The results showed that the mean CO_2 emission rate from the 3 ponds was 97.8 mg m^{-2} h^{-1} (range 50.6 to 151.0 mg m^{-2} h^{-1}). Apparent seasonal and diurnal variations in CO_2 fluxes were observed; the lowest (1.73 mg m^{-2} h^{-1}) occurred in April and the highest occurred in July and August (212.9 and 181.9 mg m^{-2} h^{-1}, respectively). The night-time to daytime CO_2 emission ratio was <1 (range 0.44 to 0.83) in May during the early part of the farming season. Night-time CO_2 emissions in early August were higher than those during the daytime (range 1.06 to 1.37). The night-time to daytime CO_2 emission ratios were 0.84 to 1.36 during late September. The CO_2 fluxes from the freshwater aquaculture ponds were higher than those of lakes and reservoirs, whereas they were lower than those of marshes in previous studies. The increases in nutrient load and pelagic respiration from feeding the fish were significantly associated with CO_2 emissions from the freshwater aquaculture ponds. Freshwater aquaculture ponds in temperate monsoon climate regions contribute an estimated 2.98 million t yr^{-1} CO_2 based on the mean investigated CO_2 emission rate, contributing 0.0088% of the current annual global CO_2 emissions, and represent a small but previously unquantified CO_2 emission source.

KEY WORDS: Freshwater aquaculture ponds · Carbon dioxide · Water–air interface · Nutrient load · Diurnal variation

INTRODUCTION

The long-lived greenhouse gases (LLGHGs) carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) have reached new high levels since the industrial revolution. CO_2, which contributes about 64% of radiative forcing by LLGHGs, has increased from 280.0 ppm in 1800 to 389.0 ppm in 2010 (Tarasova et al. 2012). Global warming caused by increasing atmospheric LLGHG concentrations could affect ecosystem structure and function, and many studies on terrestrial and aquatic ecosystem CO_2 cycles have been performed (Butman & Raymond 2011, Keenan et al. 2013, Raymond et al. 2013).

Most studies on carbon cycles of freshwater ecosystems have focused on lakes, reservoirs and rivers. Total carbon sinks in lakes, including both inorganic and organic carbon, amount to 0.077 Gt yr^{-1}, of which the atmosphere accounts for 0.0532 Gt yr^{-1} (Downing et al. 1993). Furthermore, there is a higher retention rate (500 g m^{-2} yr^{-1}) of carbon in reservoirs than in lakes, and the total carbon sinks will reach 0.2 Gt yr^{-1} in 2050 (Walsh 1991, Yan & Liu 2001). Inland freshwater ecosystems have huge carbon sequestration

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potentials. However, the freshwater ecosystem is also considered a source of CO_2 to the atmosphere (Cole et al. 1994, Huttunen et al. 2002, Eugster et al. 2003, Huttunen et al. 2003, Jonsson et al. 2003, Xing et al. 2005, Repo et al. 2007). Both processes play important roles in the carbon cycle of the Earth system.

According to statistical data on aquaculture production maintained by the Food and Agriculture Organization of the United Nations, the combined water surface area of freshwater aquaculture ponds is estimated to be 25 669 km^2 in China and 87 500 km^2 worldwide (Verdegem & Bosma 2009). Freshwater aquaculture ponds sequester an estimated 13.1 Mt yr^{-1} of carbon globally, as organic carbon from uneaten feed, organic fertilizers, dead plankton and excreta from different species settle to pond bottoms (Boyd et al. 2010, Adhikari et al. 2012). However, no detailed studies have considered CO_2 sink/source functions of freshwater aquaculture ponds across the water–air interface.

Freshwater aquaculture pond ecosystems are generated semi-artificially by daily feeding and photosynthesis of phytoplankton. He (1993) reported that phytoplankton primary production accounts for 29.7 to 49.7 % of the total organic carbon in aquaculture ponds and that feeding and organic fertilizer comprise 50.3 to 70.3 %. However, a large quantity of nutrients from residual feed is retained in aquaculture pond water. The feed conversion rate in grass carp polyculture ponds is 1.69 to 2.86 (Zhang et al. 2011). Xia (2013) revealed that only a small portion of nutrient input into grass carp culture ponds is converted into fish production and that most of it (81.7 % C, 65.6 % N, 67.5 % P) remains in pond sediment or is discharged to adjacent bodies of water.

Many studies have indicated that decomposition of allochthonous organic carbon from inland freshwater ecosystems is a significant source of atmospheric CO_2 (Jones et al. 1998, Jonsson et al. 2001, Karlsson et al. 2007). The accumulation of residual feed and feces increases nutrient load and plankton biomass in ponds (Zhao et al. 2002, Burford et al. 2003). Nevertheless, the effects of nutrient load on carbon sink/source functions are controversial. Several studies have shown that carbon sequestration is enhanced with an increase in nutrient load (Downing et al. 1993), or that carbon emissions decrease when primary production is high in freshwater (Xing et al. 2005, 2006). In contrast, other studies have reported that high primary production contributes to atmospheric carbon owing to the intense mineralization of organic matter derived from primary production (Hamilton et al. 1994, Roulet et al. 1997, Huttunen et al. 2003, Rantakari & Kortelainen 2005, Aller & Blair 2006, Zheng et al. 2009).

Grass carp *Ctenopharyngodon idella* is a very popular freshwater aquaculture species, accounting for about 18.8 % of freshwater aquaculture production in China and 12.2 % worldwide (Fisheries Department of Agriculture Ministry of China 2013, FAO 2013). Pond-farmed grass carp are fed a low-protein pellet feed (Bostock et al. 2010). Generally, a number of filter fish species, such as silver carp *Hypophythalmichthys molitrix* and bighead carp *Aristichthys nobilis*, are stocked into aquaculture ponds to limit plankton biomass. In addition, some benthic fish species, such as common carp *Cyprinus carpio* and white leg shrimp *Litopenaeus vannamei*, are stocked to take full advantage of pond space (Dong 2011). As the role of freshwater aquaculture ponds in temperate monsoon regions within the global carbon cycle has not been investigated, we measured the CO_2 fluxes at the water–air interface from 3 representative grass carp polyculture ponds to determine the influence of aquaculture on CO_2 emissions from freshwater.

MATERIALS AND METHODS

Experimental ponds

The study was carried out at a freshwater fish farm in Gaoqing, Shandong Province, in the north of China (37° 04′ N, 117° 33′ E), which represents a typical temperate monsoonal climate with mean annual temperature of ~13.1°C. The mean annual precipitation is 539.4 mm and there is much more precipitation in summer than in other seasons. The study was conducted in 3 representative grass carp polyculture ponds. The GSB pond was stocked with grass carp, silver carp and bighead carp; the GSBL pond was stocked with grass carp, silver carp, bighead carp and shrimp; and the GSBC pond was stocked with grass carp, silver carp, bighead carp and common carp. Pellet feed was provided daily at 07:00, 10:00, 13:00 and 16:00 h. There was no water exchange during the farming season. The basic information of the 3 ponds is shown in Table 1.

Sample collection

Water samples were collected with a horizontal sampler monthly during the farming season from April to September 2013. The samples were stored in clean plastic 1 l bottles and were transported imme-

Table 1. Basic information on the experimental ponds. The GSB was stocked with grass carp fingerlings of 0.07 to 0.08 kg ind.$^{-1}$, and the GBSL and GBSC were stocked with young grass carp of 0.30 to 0.35 kg ind.$^{-1}$. The other species stocked were the same size in all 3 ponds with young silver carp of 0.11 to 0.14 kg ind.$^{-1}$, young bighead carp of 0.32 to 0.37 kg ind.$^{-1}$. Fishes were stocked in mid-April, shrimps at the beginning of June. Fishes and shrimps were yielded at the beginning of October, except for 60% cultured fishes in GSBL, which were yielded in mid-August. Feeds input refers to the total feeds input during the culture period. G: grass carp; S: silver carp; B: bighead carp; L: white leg shrimp; C: common carp. Means are given ± SD

Parameter	GSB	GSBL	GSBC
Stocking (kg m^{-3})	0.14	0.34	0.37
Stocking density (ind. m^{-3})	G: 1.58; S: 0.07; B: 0.01	G: 0.97; S: 0.09; B: 0.02; L: 32.4	G: 0.95; S: 0.09; B: 0.02; C: 0.26
Yield (kg m^{-3})	1.61	1.42	1.58
Feeds input (kg m^{-3})	3.15	2.24	2.54
Transparency (m)	0.20 ± 0.08	0.25 ± 0.15	0.17 ± 0.05
pH	8.30 ± 0.65	8.20 ± 0.58	8.08 ± 0.58
Phosphate (mg l^{-1})	0.35 ± 0.18	0.47 ± 0.35	0.47 ± 0.35
Ammonia (mg l^{-1})	0.92 ± 1.06	0.91 ± 0.98	1.51 ± 1.71

diately to the laboratory. At the same time, CO_2 gas samples were collected at the water–air interface at 09:00 to 11:00 h on sunny days using the floating closed-chamber method (Xing et al. 2005, 2006). Diurnal CO_2 variations were measured during different times of the culture season on 16 to 17 May, 1 to 2 August and 28 to 29 September. The floating chambers (50 cm in height and 30 cm in diameter) were made from Plexiglas and covered by aluminum foil to avoid high temperatures in summer resulting from direct sunlight (Duchemin et al. 1999, Huttunen et al. 2003). A small vertical vent stopped by a silicone septum on the top was used for sampling, and a 4.5 V dry battery-driven fan was used inside the chamber to mix the air but not disturb the water–air interface. Three replicate chambers were placed on each pond. Prior to sampling, the syringe was pumped several times to mix the air inside the chamber. Four samples were drawn from the chamber via 100 ml Tygon syringes 0, 10, 20 and 30 min after deployment. These air samples were driven into dedicated sample bags and transported to laboratory in a cool box. During sampling, the air temperature inside and outside the chamber was measured and noted.

Sample measurements

Water temperature and dissolved oxygen were measured with a YSI dissolved oxygen meter (Model 5000, 230 V), and pH was measured with a PHS-3C acidometer (Shanghai REX Instruments) *in situ* when the water samples were collected. The quantity of feed supplied to the ponds was determined monthly, and the feed conversion rate was calculated as the total quantity of feed provided (kg)/total weight gain of fish (kg) during the farming season. Organic carbon content of the feed was determined using a PE-24 CHN analyzer (Heraeus) after acidifying a feed sample for 4 h with 1 N HCl to remove inorganic carbon (Holmer et al. 2007). Chl *a* was extracted with acetone (90%) in the darkness for 24 h after filtration of water samples through GF/F glass microfiber filters and analyzed according to the method of Wu (2006). The absorbance values of filtrate were measured at 750, 663, 645 and 630 nm with the blank of 90% acetone, and the concentration of chl *a* was determined by the given equation (in Wu 2006). Water samples for dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) concentrations were analyzed by a multi-2100s TOC analyzer (Analytik Jena) after being filtered through pre-combusted (450°C, 2 h) Whatman GF/F filters. Primary production and pelagic respiration were measured using the light–dark bottle method (Eaton et al. 1995). Measurements were made by recording the change in O_2 concentration during 24 h at water depths of 0.05, 0.5 and 1.5 m, but the depths at which the bottle samples were collected were adjusted according to water transparency. After collecting the samples to determine the initial oxygen concentration, 2 light and 2 dark bottles were suspended at each water depth in each pond. Oxygen concentrations were measured using the Winkler method. Primary production and pelagic respiration were determined by cumulative mean values at each depth using the differences between the light and dark bottles, and initial values and dark bottles, respectively.

Gas samples were analyzed as soon as possible using the GC-2010 Plus gas chromatograph (Shimadzu) connected to a MGS-4 gas sampler and a MTN-1 methanizer. The gas samples were driven into the MGS-4 gas sampler, then converted into CH_4 in the MTN-1 methanizer by a nickel catalyst at 375°C after being separated on a 2 m × 2 mm stainless steel column at 40°C packed with poropak Q 60-80 mesh. The CO_2 concentrations in gas samples were determined with a flame ionization detector at 220°C. The carrier gas (N_2) flow rate was 22 ml min^{-1}, and flame gases (H_2 and compressed air) were set at 20 and 30 ml min^{-1}, respectively. Standard gases were measured every 4 gas samples in order to determine the sample concentrations and check the errors. The CO_2 fluxes were calculated from the linear changes in time inside the chamber.

Data analysis

The data were analyzed using the statistical software package SPSS (Ver. 18.0). Linear regressions were used to identify the relationships between seasonal CO_2 fluxes and other environmental factors (the concentrations of chl *a* and DOC, quantity of organic carbon supplied by feed, pelagic respiration and water temperature). The relationships between diurnal variations of CO_2 and environment factors were determined by bivariate correlation, and r-values were reported.

RESULTS

Characteristics of the experimental ponds

The variations in air and water temperature during the farming season are shown in Fig. 1a. The maximum air temperature of 40.0°C occurred in July, and the minimum of 17.5°C occurred in April. The water temperature (range 22.2 to 32.8°C) varied similarly to the air temperature.

The yield and quantity of feed supplied to the ponds are shown in Table 1. The total quantities of feed added to the GSB and GSBC were 3.15 and 2.54 kg m^{-3}, respectively. The inputs of fish and shrimp feed into the GSBL were 1.94 and 0.30 kg m^{-3}, respectively. The feed conversion rate was 2.13 in the GSB, 2.07 in the GSBL and 2.08 in the GSBC. The mean ± SD organic carbon contents of the fish and shrimp feed were 42.7 ± 1.09 and 41.7 ± 2.02%, respectively. The monthly quantities of organic carbon supplied by feed, which reached a maximum in July or August (0.33 kg m^{-3} in the GSB, 0.24 kg m^{-3} in the GSBL and 0.28 kg m^{-3} in the GSBC), are shown in Fig. 1b.

The chl *a* concentrations in the ponds are shown in Fig. 1c. Maximum chl *a* concentrations occurred in July or August (mean ± SD: 0.49 ± 0.03 mg l^{-1} in the GSB, 0.26 ± 0.02 mg l^{-1} in the GSBL and 0.48 ± 0.01 mg l^{-1} in the GSBC), and mean (±SD) chl *a* concentrations were 0.34 ± 0.13 (GSB), 0.16 ± 0.06 (GSBL) and 0.30 ± 0.11 mg l^{-1} (GSBC).

DOC concentrations accumulated in the water column with farming time (Fig. 1d), and the mean (±SD)

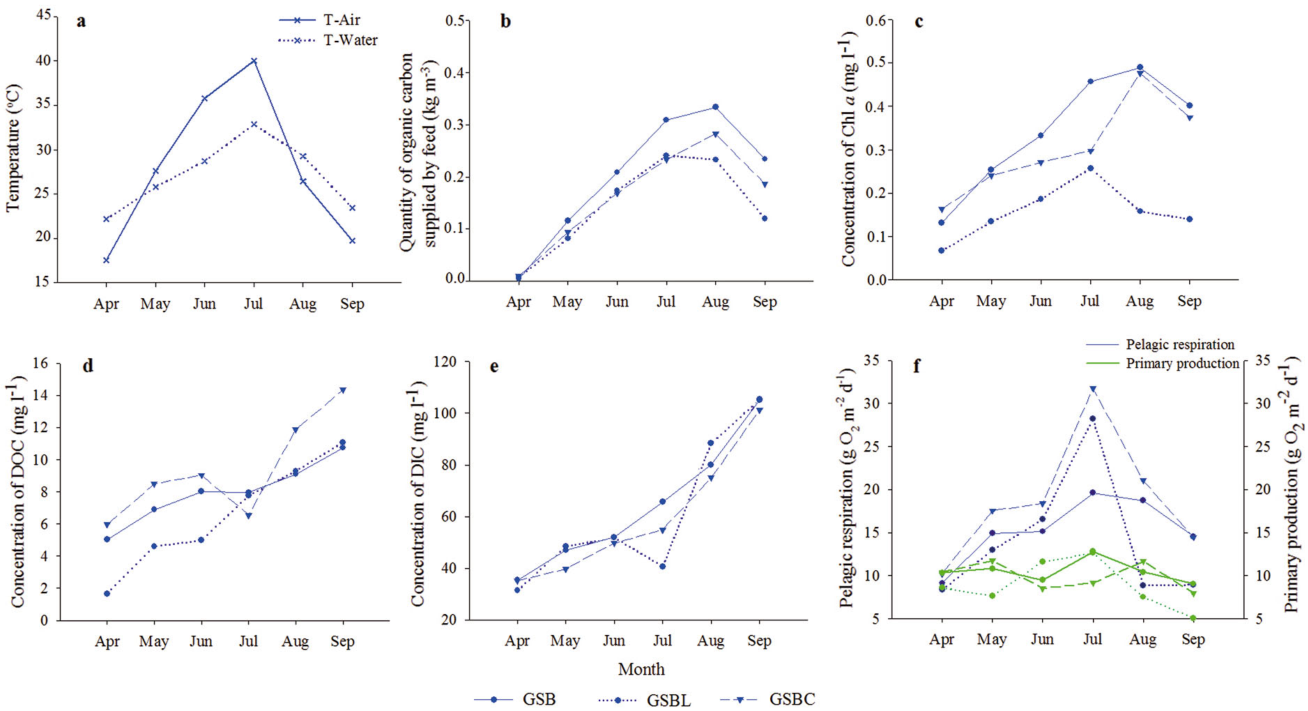

Fig. 1. Monthly variation in (a) temperature, (b) quantity of organic carbon supplied by feed, (c) chl *a*, (d) DOC, (e) DIC and (f) pelagic respiration and primary production in the GSB, GSBL and GSBC ponds (see Table 1 for abbreviations). DOC: dissolved organic carbon; DIC: dissolved inorganic carbon

DOC concentrations in the GSB, GSBL and GSBC were 7.95 ± 1.94, 6.55 ± 3.45 and 9.37 ± 3.21 mg l^{-1}, respectively.

DIC concentrations also increased gradually along with farming time (Fig. 1e). Mean DIC concentrations were 64.2 ± 25.3 mg l^{-1} in the GSB, 61.0 ± 29.1 mg l^{-1} in the GSBL and 59.3 ± 24.8 mg l^{-1} in the GSBC. DIC was positively correlated with DOC ($p < 0.01$).

The pelagic respiration results are shown in Fig. 1f and ranged from 9.13 to 19.6 g O_2 m^{-2} d^{-1} in the GSB, from 8.33 to 28.2 g O_2 m^{-2} d^{-1} in the GSBL, and from 10.3 to 31.7 g O_2 m^{-2} d^{-1} in the GSBC. The ranges of primary production were 9.06 to 12.8, 5.06 to 12.6 and 7.95 to 11.7 g O_2 m^{-2} d^{-1} in the GSB, GSBL and GSBC, respectively (Fig. 1f). The primary production/pelagic respiration (P/R) values of the 3 ponds were <1 during most of the farming season (Fig. 1f).

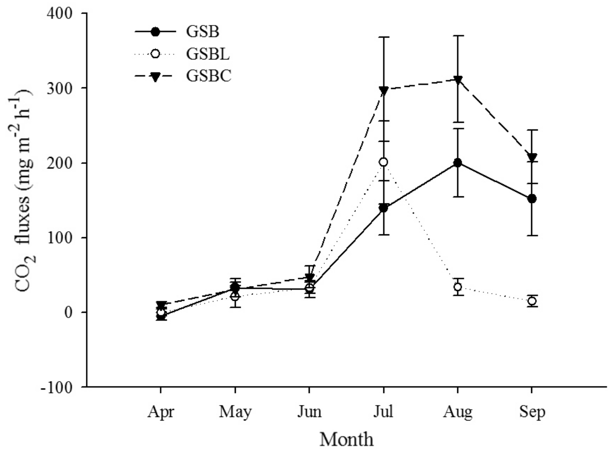

Fig. 2. Monthly variation in CO_2 flux in 3 grass carp polyculture ponds of Gaoqing, China

CO_2 flux values at the water–air interface

Monthly CO_2 flux variations

The mean CO_2 fluxes at the water–air interface of the 3 ponds were 91.9 mg m^{-2} h^{-1} (range, –4.95 to 200.3 mg m^{-2} h^{-1}) in the GSB, 50.6 mg m^{-2} h^{-1} (range, –0.13 to 200.8 mg m^{-2} h^{-1}) in the GSBL and 151.0 mg m^{-2} h^{-1} (range, 10.3 to 311.8 mg m^{-2} h^{-1}) in the GSBC (Fig. 2). These data demonstrate that the investigated aquaculture ponds were a source of atmospheric CO_2 for most of the farming time, except for the GSB and GSBL during April. The CO_2 fluxes for the GSB and GSBL in April were –4.95 and –0.13 mg m^{-2} h^{-1}, respectively. Maximum CO_2 fluxes in the GSB (200.3 mg m^{-2} h^{-1}), GSBL (200.8 mg m^{-2} h^{-1}) and GSBC (311.8 mg m^{-2} h^{-1}) occurred in July or August.

The correlation analysis showed that CO_2 emissions were positively correlated with chl *a* concentrations (Fig. 3), quantity of organic carbon supplied by feed, pelagic respiration, water temperature and DOC concentrations ($p < 0.05$) of the ponds (Table 2). There were no significant correlations between DIC and CO_2 fluxes ($p > 0.05$).

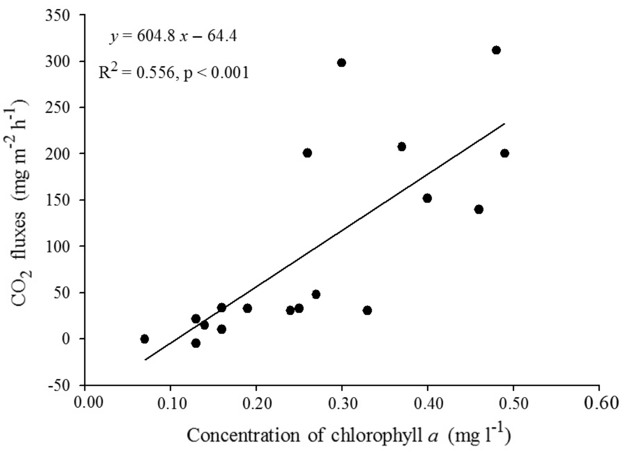

Fig. 3. Correlations between CO_2 fluxes and chl *a* concentration of the ponds

Diurnal CO_2 flux variations

Mean diurnal CO_2 fluxes in May were 19.9 ± 15.1 (GSB), 26.4 ± 10.7 (GSBL) and 31.3 ± 21.6 mg m^{-2} h^{-1} (GSBC). The night-time to daytime CO_2 flux ratios were 0.72, 0.83 and 0.44 in the GSB, GSBL and GSBC, respectively. Similar CO_2 flux trends were observed; CO_2 fluxes were relatively low at 16:00 to 20:00 h, reached a peak at 24:00 h, decreased to lower values at 04:00 h with the decrease in temperature in the early morning, and thereafter increased gradually (Fig. 4a). The night-time to daytime CO_2 flux ratios in

Table 2. Regression equations showing the relationships between CO_2 fluxes (mg m^{-2} h^{-1}; *y*) and some environmental factors (*x*)

Environmental factors	Regression equations	
Chl *a* (mg l^{-1})	$y = 604.8x - 64.4$	($R^2 = 0.556$, $p < 0.01$)
Feed organic carbon input (kg m^{-3})	$y = 746.8x - 28.05$	($R^2 = 0.532$, $p < 0.01$)
Pelagic respiration (g O_2 m^{-2} d^{-1})	$y = 12.1x - 98.9$	($R^2 = 0.573$, $p < 0.01$)
Water temperature (°C)	$y = 15.7x - 326.9$	($R^2 = 0.313$, $p < 0.05$)
DOC (mg l^{-1})	$y = 17.4x - 41.0$	($R^2 = 0.249$, $p < 0.05$)

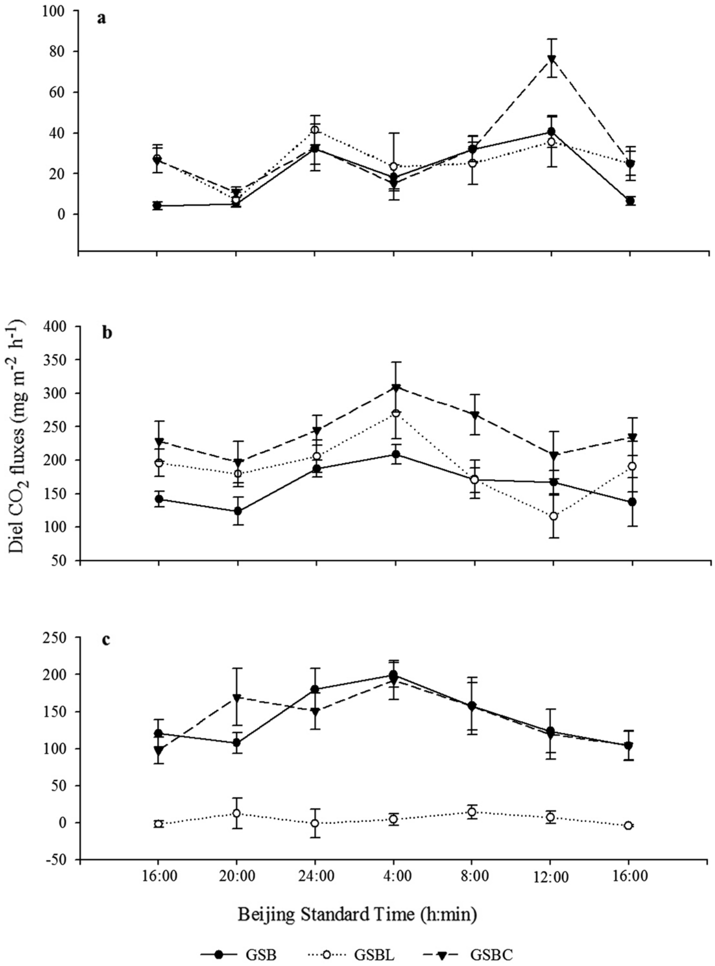

Fig. 4. Diel variation in CO_2 emission from GSB, GSBL and GSBC ponds in (a) May, (b) August and (c) September. Note different *y*-axis scales. For abbreviations see Table 1

early August were 1.09, 1.37 and 1.06 in the GSB, GSBL and GSBC, respectively. Flux maxima were observed at 04:00 h, and minima in the GSB and GSBC occurred at 20:00 h, whereas the minima occurred at 12:00 h in the GSBL. The mean diurnal CO_2 fluxes in the GSB, GSBL and GSBC were 162.4 ± 30.0, 189.6 ± 45.9 and 241.4 ± 38.0 mg m^{-2} h^{-1}, respectively (Fig. 4b). Similar CO_2 diurnal flux variations were found in the GSB and GSBC during late September, and the night-time to daytime CO_2 flux ratios were 1.24 and 1.36. Daytime CO_2 flux was higher than that at night-time in the GSBL, and the night-time to daytime CO_2 flux ratio was 0.84. The mean diurnal CO_2 fluxes were 141.9 ± 37.5, 4.34 ± 7.21 and 141.6 ± 35.3 mg m^{-2} h^{-1} in the GSB, GSBL and GSBC, respectively (Fig. 4c). The correlations between the diurnal fluxes and the environment factors are shown in Table 3.

DISCUSSION

Characteristics of CO_2 flux at the water–air interface

Only CO_2 fluxes measured using the closed-chamber method were compared between different inland freshwater systems, as CO_2 flux at the water–air interface can be affected by the measuring method. The mean monthly CO_2 fluxes (range, 1.73 to 212.9 mg m^{-2} h^{-1}) in the 3 grass carp polyculture ponds are listed in Table 4. The CO_2 fluxes we measured in freshwater aquaculture ponds were higher than

Table 3. Pearson correlation coefficients (r) between diel CO_2 fluxes and air temperature (AT), water temperature (WT), dissolved oxygen (DO), pH and chl *a* of surface water. Total: general correlation coefficients between all the diurnal CO_2 fluxes (n = 63) in these 3 ponds and environmental factors (AT, WT, chl *a*, DO and pH) in May, August and September. *p < 0.05; **p < 0.01

	AT (°C)		WT (°C)		pH		DO (mg l^{-1})		Chl *a* (mg l^{-1})	
	Range	r	Range	r	Range	r	Range	r	Range	r
May										
GSB	16.6–30.5	0.023	20.9–25.9	0.241	8.51–8.75	0.172	8.19–17.18	–0.024	0.10–0.35	–0.076
GSBL	16.6–30.5	0.13	20.9–25.9	0.221	8.11–8.50	–0.108	8.02–14.69	–0.116	0.08–0.15	0.011
GSBC	16.6–30.5	0.658	20.9–25.9	0.760*	8.09–8.52	0.026	8.58–13.98	0.506	0.19–0.28	0.443
August										
GSB	31.2–41.0	–0.621	31.2–33.1	–0.757*	7.14–8.37	–0.781*	3.42–12.94	–0.738	0.27–0.40	–0.702
GSBL	31.2–41.0	–0.799*	31.2–33.1	–0.722	7.12–8.39	–0.344	3.54–11.29	–0.575	0.21–0.35	–0.513
GSBC	31.2–41.0	–0.742	31.2–33.1	–0.766*	7.02–8.38	–0.820*	3.28–10.10	–0.626	0.29–0.51	–0.178
September										
GSB	24.6–34.1	–0.778**	19.5–24.1	–0.697	8.17–8.54	–0.817*	5.53–13.75	–0.895*	0.25–0.34	–0.217
GSBL	24.6–34.1	–0.13	19.5–24.1	–0.179	8.34–8.71	–0.423	10.36–18.81	–0.257	0.14–0.16	–0.494
GSBC	24.6–34.1	–0.826*	19.5–24.1	–0.873*	8.10–8.61	–0.586	5.78–13.66	–0.658	0.22–0.54	–0.311
Total	16.6–41.0	0.611**	19.5–33.1	0.633**	7.14–8.75	–0.654**	3.28–18.81	–0.718**	0.08–0.54	0.565**

Table 4. Comparisons of CO_2 fluxes (mg m^{-2} h^{-1}) in different inland freshwater systems. Time given as yyyy.mm

Site	Time	Mean	Range	Reference
Freshwater aquaculture ponds, China	2013.04	1.7	–5.0–10.3	Present study
	2013.05	28.3	21.4–33.1	
	2013.06	37.2	31.3–47.6	
	2013.07	212.9	139.7–298.1	
	2013.08	181.9	33.7–311.8	
	2013.09	124.9	15.0–207.7	
Lokka Reservoir, Finland	1994.06–1994.09	44.6	–32.0–155.0	Huttunen et al. (2002)
Porttipahta Reservoir, Finland	1995.06–1995.08	64.0	36.0–144.0	Huttunen et al. (2002)
Dworshak Reservoir, USA	2001.09	–49.8	–94.9–-30.0	Soumis et al. (2004)
Lake Wallula, USA	2001.09	–14.5	–67.9–44.2	Soumis et al. (2004)
Lake Oroville, USA	2001.09	42.8	11.8–101.3	Soumis et al. (2004)
West Siberian lakes	2005.08	29.2	–2.9–54.2	Repo et al. (2007)
Lake Donghu, China	2003.03–2003.05	–2.5	-	Xing et al. (2005)
	2003.06–2003.08	–5.7	-	
	2003.09–2003.11	5.8	-	
	2003.12–2004.02	58.8	-	
	Average	14.1	–58.6–159.4	
Lake Biandiantang, China	2003.03–2003.05	28.8		Xing et al. (2006)
	2003.06–2003.08	–31.7		
	2003.09–2003.11	–30.0		
	2003.12–2004.02	212.1		
	Average	44.8	–152.3–464.5	
Freshwater marshes, China	2002.06–2002.12	428.8	18.7–965.4	Song et al. (2006)
	2003.01–2003.12	328.5	11.1–779.3	
	2004.01–2004.12	281.1	2.36–873.7	

those reported previously for lakes and reservoirs but lower than those in marshes generally. In addition, mean CO_2 emission rate from the grass carp polyculture ponds was 97.8 mg m^{-2} h^{-1} during the farming season, which was also higher than those of lakes and reservoirs, which range from –49.8 to 64.0 mg m^{-2} h^{-1}, but lower than those of freshwater marshes, which range from 281.1 to 428.8 mg m^{-2} h^{-1}.

Cummins (1977) used the river continuum concept to describe the continuous ecological changes of a river from its headwaters, upstream to downstream. Furthermore, the nutrient levels of aquatic ecosystems increase along with the decrease in depth and water body size (Odum & Barrett 2005). Several studies have shown that carbon sequestration is enhanced with an increase in nutrient load (Downing et al. 1993), or that carbon emission decreases when primary production is high in freshwater (Xing et al. 2005, 2006). Moreover, other studies have reported that high primary production contributes to atmospheric carbon owing to the intense mineralization of organic matter derived from primary production (Hamilton et al. 1994, Roulet et al. 1997, Huttunen et al. 2003, Rantakari & Kortelainen 2005, Aller & Blair 2006, Zheng et al. 2009). The lakes or reservoirs, aquaculture ponds and marshes can also be regarded as the continuously integrated series with the gradual increases in nutrient levels. The results in Table 4 indicate that CO_2 fluxes from the freshwater aquaculture ponds were higher than those of lakes and reservoirs, whereas they were lower than those of marshes, which supports the deduction that carbon source functions of freshwaters were enhanced with the increase in nutrient levels.

Factors affecting CO_2 emissions

The P/R values of the 3 ponds in the present study were usually <1 (Fig. 1f), indicating that primary production by phytoplankton was exceeded by pelagic respiration in the water column. Therefore, heterotrophic organisms in ponds must receive an external supply of organic carbon to maintain the ecosystem, and feed was the main organic matter source in the pond ecosystems. Continuous input of feed resulted in an increased nutrient load and plankton biomass (with maximum chl *a* of 0.49 mg l^{-1}), leading to the increased pelagic respiration. A regression analysis showed that CO_2 flux was positively correlated with pelagic respiration (Table 2), indicating that intensive pelagic respiration may have significantly affected CO_2 emissions from the aquaculture ponds. CO_2 emissions from the present ponds were positively correlated with water temperatures and chl *a* concentrations (Table 2), whereas CO_2 flux is negatively correlated with chl *a* and water temperature in highly autotrophic lakes (Xing et al. 2005, 2006), further indicating that pelagic respiration rather than algal activity is a significant factor regulating CO_2 fluxes. Furthermore, CO_2 flux was positively correlated with the quantity of organic carbon supplied by feed (Table 2), and the decomposition of the allochthonous carbon has been revealed to be the main reason for the CO_2 emissions from the inland waters (Jones et al. 1998, Jonsson et al. 2001, Karlsson et al. 2007). A recent study on the shrimp nutrient budget in farming ponds showed that 40.9% of the carbon input into ponds is released to the air as CO_2 (Su et al. 2009).

DOC concentrations accumulated only slightly in the water column during the farming season (Fig. 1d), and mean DOC concentrations in the ponds were similar to those of shrimp farming ponds supplied with artificial feed (Liu et al. 2002). DIC is the largest aquatic carbon pool in ponds and increased continually during the farming season (Fig. 1e). DIC concentrations in our ponds reached 105.0 mg l^{-1} in the GSB, 105.3 mg l^{-1} in the GSBL and 101.3 mg l^{-1} in the GSBC at the end of the farming season, which were higher levels than those reported for natural bodies of water (range, 6.6 to 49 mg l^{-1}) (James et al. 2000). The DOC and DIC concentrations were significantly correlated ($p < 0.01$). We speculated that the organic carbon from residual feed allowed bacteria to flourish (Eugster et al. 2003), leading to intensive mineralization of DOC and the accumulation DIC in the water (Casper et al. 2000, Nakano et al. 2000). The CO_2 flux was significantly and positively correlated with water temperature and DOC concentrations (Table 2). Similar correlations were reported in 75 to 95% of the lakes in northern and temperate regions where the gas emissions are supported by inputs of organic matter (Del Giorgio et al. 1999). Therefore, the decomposition of DOC caused by daily feed supply is also supposed to accelerate CO_2 emissions of the ponds. The CO_2 flux of the GSBL was significantly lower than the GSB and the GSBC in the last 2 mo, which could be explained by the significant decrease in chl *a* concentrations (Fig. 1c) and the lower feed supply after the yield (Fig. 1b) of 60% of fishes in GSBL.

Diurnal and seasonal variations in CO_2 flux

Significant diurnal CO_2 flux variations were detected in the farm ponds. The night-time to daytime CO_2 emission ratios were <1 (range, 0.44 to 0.83) in May, which was early in the farming season. CO_2 water solubility decreases with the increase in water temperature during the day (Parkin & Kaspar 2003). Roulet et al. (1997) also reported that CO_2 flux in beaver ponds is always higher during the day because of higher water temperature. Diurnal CO_2 fluxes are affected by biotic and abiotic factors, such as plankton biomass, instantaneous wind speed and underwater photosynthetically active radiation (Roulet et al. 1997), which may have led to the abnormally high CO_2 flux in the GSBC at 12:00 h. We found negative correlations between CO_2 flux at different air and water temperatures, chl *a* concentrations, pH and dissolved oxygen in early August, and maximum flux occurred in the early morning, indicating high gas exchange. Photosynthesis probably played an important role in removing dissolved CO_2 and releasing O_2 during the higher daytime temperatures, which resulted in a decrease in CO_2 flux and an increase in pH. Respiration at night presumably increased CO_2 emissions and the oxygen deficit with a lower water temperature (Guasch et al. 1998, Dornblaser & Striegl 2013). Higher night-time CO_2 fluxes occurred in the GSB and GSBC during September, and the correlations between diurnal CO_2 flux and the environmental factors were similar to those in August. However, the night-time to daytime CO_2 emission ratios were <1 in the GSBL and higher fluxes occurred at 08:00 and 12:00 h. It is possible that the decrease in chl *a* concentration was the result of a lower photosynthetic rate after part of fish yield. Variations in diurnal CO_2 flux values in aquaculture ponds deserve further study, as they are affected by artificial and natural factors.

CO_2 fluxes across the water–air interface varied significantly between seasons; lower CO_2 emissions were observed at the beginning of the farming season (mean 1.73 mg m^{-2} h^{-1}), higher values were measured in July and August (means 212.9 and 181.9 mg m^{-2} h^{-1}, respectively), and lower values were observed again in September (mean 124.9 mg m^{-2} h^{-1}). The seasonal variations of CO_2 fluxes were significantly and positively correlated with chl *a* concentrations and water temperature (Table 2). Based on the mean CO_2 emission rate (97.8 mg m^{-2} h^{-1}), the investigated freshwater aquaculture ponds emit 0.43 kg m^{-2} yr^{-1} CO_2 at the water–air interface during farming season. The sampling site represents a typical temperate monsoonal climate, which covers the northeast part of China, the Russian Far East, the Korean Peninsula and north Japan (Wei 2005). Given that northeast China (including Beijing, Heilongjiang, Jilin, Liaoning, Hebei, Shanxi, Tianjin, Shandong, Shanxi, Henan and part of Jiangsu Province) contains the dominant freshwater aquaculture regions (6941.9 km^2) (FAO 2013), freshwater aquaculture ponds emit an estimated 2.98 Mt CO_2 yr^{-1} during farming season in temperate monsoonal climate regions. The estimated annual CO_2 emission rate is much lower than that of inland waters, which have been estimated to contribute 2100 Mt yr^{-1} (Raymond et al. 2013). Nevertheless, freshwater aquaculture ponds in temperate monsoonal climate regions, occupying 7.9% of the global freshwater aquaculture pond area, contribute 0.0088% of current annual global CO_2 emissions of about 34 000 Mt yr^{-1} (Olivier et al. 2012), and represent a small but previously unquantified source of CO_2 emissions, which will be useful in considerations of global carbon balance. Detailed analyses of carbon emissions by freshwater aquaculture ponds in other areas worldwide will be needed to ascertain whether freshwater aquaculture contributes to CO_2 emissions.

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LITERATURE CITED

Adhikari S, Lal R, Sahu BC (2012) Carbon sequestration in the bottom sediments of aquaculture ponds of Orissa, India. Ecol Eng 47:198–202

Aller RC, Blair NE (2006) Carbon remineralization in the Amazon-Guianas tropical mobile mudbelt: a sedimentary incinerator. Cont Shelf Res 26:2241–2259

Bostock J, McAndrew B, Richards R, Jauncey K and others (2010) Aquaculture: global status and trends. Philos Trans R Soc Lond B 365:2897–2912

Boyd CE, Wood C, Chaney PL, Queiroz JF (2010) Role of aquaculture pond sediments in sequestration of annual global carbon emissions. Environ Pollut 158:2537–2540

Burford MA, Thompson PJ, McIntosh RP, Bauman RH, Pearson DC (2003) Nutrient and microbial dynamics in high-intensity, zero-exchange shrimp ponds in Belize. Aquaculture 219:393–411

Butman D, Raymond PA (2011) Significant efflux of carbon dioxide from streams and rivers in the United States. Nat Geosci 4:839–842

Casper P, Maberly SC, Hall GH, Finlay BJ (2000) Fluxes of methane and carbon dioxide from a small productive lake to the atmosphere. Biogeochemistry 49:1–19

Cole JJ, Caraco NF, Kling GW, Kratz TK (1994) Carbon dioxide supersaturation in the surface waters of lakes. Science 265:1568–1570

Cummins KW (1977) From headwater stream to river. Am Biol Teach 39:305–312

Del Giorgio PA, Cole JJ, Caraco NF, Peters RH (1999) Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. Ecology 80:1422–1431

Dong SL (2011) The development, principle and classification of China's integrated aquaculture. J Fish China 18: 1202–1209 (in Chinese)

Dornblaser M, Striegl R (2013) Seasonal variation in diel carbon dynamics, Beaver Creek, Alaska. In: Dornblaser M, Striegl RG (eds) Proc AGU Fall Meeting Abstracts, American Geophysical Union Boulder, CO, p 15–27

Downing JP, Meybeck M, Orr JC, Twilley R, Scharpenseel H (1993) Land and water interface zones. In: Terrestrial biospheric carbon fluxes quantification of sinks and sources of CO_2. Springer, Dordrecht, p 123–137

Duchemin E, Lucotte M, Canuel R (1999) Comparison of static chamber and thin boundary layer equation methods for measuring greenhouse gas emissions from large water bodies. Environ Sci Technol 33:350–357

Eaton AD, Clesceri LS, Greenberg AE, Franson MAH (1995) Standard methods for the examination of water and wastewater. United Book Press, Baltimore, MD

Eugster W, Kling G, Jonas T, McFadden JP, Wüest A, MacIntyre S, Chapin III FS (2003) CO_2 exchange between air and water in an Arctic Alaskan and midlatitude Swiss lake: importance of convective mixing. J Geophys Res D 108:4362

Fisheries Department of Agriculture Ministry of China (2013) China Fisheries Statistical Yearbook. China Agriculture Press, Beijing (in Chinese)

Food and Agriculture Organization of the United Nations (FAO) (2013) FAO statistics. Global statistical collections/global aquaculture production. Available at www.fao.org/fishery/statistics/en

Guasch H, Armengol J, Sabater S (1998) Diurnal variation in dissolved oxygen and carbon dioxide in two low-order streams. Water Res 32:1067–1074

Hamilton JD, Kelly CA, Rudd JW, Hesslein RH, Roulet NT (1994) Flux to the atmosphere of CH_4 and CO_2 from wetland ponds on the Hudson Bay lowlands (HBLs). J Geophys Res D 99:1495–1510

He ZH (1993) A study of aquaria ecosystem in Zhenlai, Jilin Province. J Fish China 17:24–35 (in Chinese with English Abstract)

Holmer M, Marba N, Diaz-Almela E, Duarte CM, Tsapakis M, Danovaro R (2007) Sedimentation of organic matter from fish farms in oligotrophic Mediterranean assessed through bulk and stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analyses. Aquaculture 262:268–280

Huttunen JT, Väisänen TS, Hellsten SK, Heikkinen M and others (2002) Fluxes of CH_4, CO_2 and N_2O in hydroelectric reservoirs Lokka and Porttipahta in the northern boreal zone in Finland. Global Biogeochem Cycles 16: 1003–1029

Huttunen JT, Alm J, Liikanen A, Juutinen S and others (2003) Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. Chemosphere 52:609–621

James MR, Hawes I, Weatherhead M, Stanger C, Gibbs M (2000) Carbon flow in the littoral food web of an oligotrophic lake. Hydrobiologia 441:93–106

Jones RI, Grey J, Sleep D, Quarmby C (1998) An assessment, using stable isotopes, of the importance of allochthonous organic carbon sources to the pelagic food web in Loch Ness. Proc R Soc Lond B 265:105–110

Jonsson A, Meili M, Bergström AK, Jansson M (2001) Whole-lake mineralization of allochthonous and autochthonous organic carbon in a large humic lake (Öerträes-

ket, N. Sweden). Limnol Oceanogr 46:1691–1700
Jonsson A, Karlsson J, Jansson M (2003) Sources of carbon dioxide supersaturation in clearwater and humic lakes in northern Sweden. Ecosystems 6:224–235
Karlsson J, Jansson M, Jonsson A (2007) Respiration of allochthonous organic carbon in unproductive forest lakes determined by the Keeling plot method. Limnol Oceanogr 52:603–608
Keenan TF, Hollinger DY, Bohrer G, Dragoni D, Munger JW, Schmid HP, Richardson AD (2013) Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499:324–327
Liu GC, Li DS, Dong SL (2002) Organic carbon balance in prawn cultivating ponds. Acta Oceanol Sin 24:84–91 (in Chinese with English Abstract)
Nakano T, Kuniyoshi S, Fukuda M (2000) Temporal variation in methane emission from tundra wetlands in a permafrost area, northeastern Siberia. Atmos Environ 34: 1205–1213
Odum EP, Barrett GW (2005) Fundamentals of ecology, 5th edn. Thomson Learning TM, Belmont, MA
Olivier JG, Janssens-Maenhout G, Peters JA (2012) Trends in global CO_2 emissions: 2012 report. PBL Netherlands Environmental Assessment Agency, The Hague
Parkin TB, Kaspar TC (2003) Temperature controls on diurnal carbon dioxide flux. Soil Sci Soc Am J 67:1763–1772
Rantakari M, Kortelainen P (2005) Interannual variation and climatic regulation of the CO_2 emission from large boreal lakes. Glob Change Biol 11:1368–1380
Raymond PA, Hartmann J, Lauerwald R, Sobek S and others (2013) Global carbon dioxide emissions from inland waters. Nature 503:355–359
Repo M, Huttunen J, Naumov A, Chichulin A, Lapshina E, Bleuten W, Martikainen P (2007) Release of CO_2 and CH_4 from small wetland lakes in western Siberia. Tellus B 59: 788–796
Roulet NT, Crill P, Comer N, Dove A, Boubonniere R (1997) CO_2 and CH_4 flux between a boreal beaver pond and the atmosphere. J Geophys Res D 102:29313–29319
Song CC, Zhang LH, Wang YY, Zhao ZC (2006) Annual dynamics of CO_2, CH_4, N_2O emissions from freshwater marshes and affected by nitrogen fertilization. Huan Jing Ke Xue 27:2369–2375 (in Chinese with English Abstract)
Soumis N, Duchemin É, Canuel R, Lucotte M (2004) Greenhouse gas emissions from reservoirs of the western United States. Glob Change Biol 18:GB3022, doi:10.1029/2003GB002197
Su YP, Ma S, Tian XL, Dong SL (2009) An experimental study on nitrogen, phosphorus and carbon budgets in intensive pond of shrimp (*Fenneropenaeus chinensis*). South China Fish Sci (in Chinese with English Abstract)
Tarasova O, Koide H, Dlugokencky E, Hall B and others (2012) The state of greenhouse gases in the atmosphere using global observations through 2010. WMO Greenhouse Gas Bull 8:11012. https://www.researchgate.net/publication/258623194_The_state_of_greenhouse_gases_in_the_atmosphere_using_global_observations_through_2010
Verdegem MCJ, Bosma RH (2009) Water withdrawal for brackish and inland aquaculture, and options to produce more fish in ponds with present water use. Water Policy 11 (Suppl 1):52–68
Walsh JJ (1991) Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen. Nature 350:53–55
Wei ZQ (2005) The cause of the three kinds of monsoon climate and identification. Political history: HS Geog 2005 (5):62–64 (in Chinese)
Wu Y (2006) Determination of chlorophyll *a* method improvement. Fujian Anal Test 15:38–39 (in Chinese with English Abstract)
Xia B (2013) Study on the biological recycling of nutrients in polyculture ponds of grass carp (*Ctenopharyngodon idella*) and silver carp (*Hypophthalmichthys molitrix*). PhD dissertation, Ocean University of China, Qingdao (in Chinese with English Abstract)
Xing YP, Xie P, Yang H, Ni L, Wang Y, Rong K (2005) Methane and carbon dioxide fluxes from a shallow hypereutrophic subtropical lake in China. Atmos Environ 39:5532–5540
Xing YP, Xie P, Yang H, Wu A, Ni L (2006) The change of gaseous carbon fluxes following the switch of dominant producers from macrophytes to algae in a shallow subtropical lake of China. Atmos Environ 40:8034–8043
Yan GA, Liu YD (2001) Aquatic ecosystems: carbon cycle and the sink capacity of atmospheric CO_2 in aquatic ecosystems. Acta Ecol Sin 21:827–833 (in Chinese with English Abstract)
Zhang ZD, Wang F, Dong SL, Gao QF, Zhang MZ, Song S, Zhang JD (2011) Reaserch in structure optimization of grass carp (*Hypophthalmichthys molitrix*), silver carp (*Aristichthys nobilis*) and shrimp (*Litopenaeus vannamei*) integrated aquaculture system. J Ocean Univ China 41:60–66 (in Chinese with English Abstract)
Zhao W, Dong S, Li D, Zhang Z, Shentu Q (2002) The primary productivity of phytoplankton in saline-alkaline ponds. Acta Hydrobiol Sin 27:47–54 (in Chinese with English Abstract)
Zheng ZM, Dong SL, Tian XL, Wang F, Gao QF, Bai PF (2009) Sediment-water fluxes of nutrients and dissolved organic carbon in extensive sea cucumber culture ponds. Clean-Soil Air Water 37:218–224

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