Assessing the efficiency of herbivorous fish as nutrient sinks in an integrated freshwater cage aquaculture system using a phosphorus mass balance model

by

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Abstract

Integrated aquaculture systems simultaneously culture multiple species to reduce waste outputs by increasing trophic efficiency and nutrient retention. Using a phosphorus (P) mass balance model, this study assessed the efficacy of an integrated aquaculture system that used herbivorous fish to reduce waste loading into a freshwater reservoir in Guizhou Province, China.

Six modified cages featured the addition of a 1 m wide outer cage surrounding a 10 m square inner cage stocked with intensively fed channel catfish (*Ictalarus punctatus).* Outer cages were stocked with filter-feeding herbivorous fish including, bighead carp (*Hypophthalmichthys nobilis*), common carp (*Cyprinus carpio*), and Nile tilapia (*Oreochromis nilocticus*). These species fed on phytoplankton, particulate waste from the inner cage, and periphyton, thereby retaining nutrients and possibly improving water quality around the cages. This experiment compared phosphorus balances of modified cages with three traditional cages also stocked with channel catfish, but which did not include an outer cage. Additional experiments compared growth rates of fish in outer cages to fish in a control cage distant from any impacts of intensively fed inner cages. Water samples were also taken to measure total phosphorus concentrations inside the cages, 1 m outside cages, and at reference sites 500-1000 m away from cages.

Outer cage fish retained 0.08-0.1 kg P ton^{-1} harvested fish or <1% of total P inputs $cage^{-1}$. Catfish in traditional cages grew slower ($p<0.05$) than fish in modified cages. However, there was no difference in retained phosphorus, total waste, soluble waste, or solid waste ton^{-1} of fish cultured between the cages. Total kg P input ton^{-1} fish harvested ranged from 14.1-18.8. According to the

model, catfish retained 24-43% of total P inputs; in addition, catfish particulate waste was 38.5% and soluble waste 18-37% of total P inputs, respectively. During grow-out, bighead carp and tilapia in outer cages increased body mass by 21% and 75%, respectively, while these same species in the control cage exhibited -3% and 0% growth. This supports the hypothesis that fish in outer cages had access to surplus energy drifting out of inner cages and successfully retained nutrients from inner cages. Contrary to expectations, total phosphorus concentrations in water samples showed no difference ($p>0.05$) between modified cages, traditional cages, and reference sites. Even though I concluded that outer cage fish retained nutrients from inner cages, retention was not substantial enough to improve water quality around modified cages. However, since phosphorus loading from cages had no impact on reservoir water quality, this suggests that phosphorus inputs from aquaculture are rapidly diluted and dispersed in the reservoir.

Introduction

In recent decades, aquaculture has become the fastest growing agricultural sector in the world (FAO, 2009). Growth primarily occurred in the developing world establishing aquaculture as a significant driver for economic development (Diana, 2009; FAO, 2009). The last 30 years also experienced increasing reservoir construction in the developing world. This expansion of aquatic surface area creates potential for aquaculture to provide additional economic benefits to reservoirs beyond traditional hydroelectric revenue, drinking water storage, and agricultural irrigation (Costa-Pierce, 1998). Cage aquaculture utilizes floating cages to contain fish and relies on water exchange with the water body to dilute wastes and replenish water. The minimal initial capital investment required makes cage aquaculture a logical system to implement in reservoirs (Beveridge, 2004; Diana, 2009).

Aquaculture presents reservoir managers and fish farmers with a dilemma. How can production be maximized while maintaining water quality for human use and ecological integrity? Like terrestrial agriculture, intensive aquaculture aggregates and concentrates waste into a small area impacting local and regional ecosystems. An aquaculture system only retains about 24% of carbon, 31% of nitrogen, and 31% of phosphorus inputs within the fish biomass, the rest is released into the water column (Troell and Norberg, 1998). In aquaculture, water quality degradation primarily occurs from poorly designed cages, overcapacity of cages, or improper feeding strategies, which highlights the importance of understanding the water body's assimilation capacity (Wu et al., 2000; Guo et al., 2009). When cages produce an excess of uneaten food or feces, nutrient levels around the cages increase and benthic habitats are disturbed, altering ecological relationships in the reservoir (Bureau and Hua, 2010).

Solid waste from cage aquaculture affects the benthic habitat below cages (Kalantzi and Karakassis, 2006). High organic content in aquaculture wastes enriches benthic sediments and can elevate benthic biomass, but sediment accumulation may also reduce benthic biodiversity (Mente et al., 2006; Rooney and Podemski, 2009). Diversity decreases due to deoxygenation as organic material decomposes (Kalantzi and Karakassis, 2006; Giles, 2008; Rooney and Podemski, 2009). Mitigating benthic degradation usually involves ceasing production over an area to allow the benthic community to rehabilitate, mechanical sediment removal, or oxygenation of sediments (Angel et al., 2005; Buryniuk et al., 2006). These methods result in decreased farm production and additional management costs.

Phosphorus generally limits phytoplankton biomass in temperate freshwater lakes (Schindler et al., 1978; Bureau and Hua, 2010). However, tropical systems exhibit a more variable relationship between total phosphorus and chlorophyll-a levels (Huszar et al., 2006). If nutrient levels, especially phosphorus, surpass certain thresholds then phytoplankton blooms can have detrimental affects on the water column leading to hypoxic conditions in the hypolimnion, fish kills, reduced water clarity, and cyanobacteria blooms that degrade the taste of fish (Buyukates et al., 2000) and reduce nutritional quality (Mares et al., 2009). Therefore, nutrients released from cage aquaculture into the environment must be kept below thresholds prone to induce negative biological events. Dilution has long been the human solution to nutrification of waters, but in many areas increased anthropogenic nutrient loading has exceeded the assimilative capacities of freshwater systems (Halwart et al., 2007; Troell et al., 2009). How can aquaculture systems be engineered to profitably culture fish while reducing their ecological footprint?

Polyculture, long practiced in aquaculture, offers a potential solution. Earliest aquaculture systems in China involved culturing organisms at different trophic levels to manage waste

products, for example raising fish in conjunction with rice paddies (Beveridge and Little, 2002). Furthermore, biomanipulation methods in reservoirs use polyculture principles by stocking planktivorous fish to control phytoplankton concentrations, though these programs are met with varying levels of success (Zhang et al., 2008). Most polyculture systems are pond based and relatively little research has been done on freshwater cage polyculture.

Yi et al. (2003) researched polyculture by culturing hybrid catfish and tilapia together in ponds. The pond was partitioned into a catfish and tilapia compartment. Catfish were fed intensively in cages, while tilapia fed upon solid waste and algae whose growth was stimulated by nutrient enrichment from the catfish compartment. The presence of tilapia improved water quality of the effluent released from ponds and their presence did not reduce catfish growth. Tilapia served as an effective and inexpensive method for water quality improvement that also allowed farmers to bring two species of fish to the market. Increasing revenue via waste mitigation is unique to polyculture systems (Troell et al., 2009).

In marine systems, researchers are studying the viability of Integrated Multi-Trophic Aquaculture (IMTA) (Neori et al., 2004; Chopin et al., 2006; Troell et al., 2009). These systems culture organisms of varying trophic levels to maximize the system's energy and nutrient utilization efficiency. Fish are intensively fed in cages, with shellfish beds residing below the cages consuming suspended solids. Seaweed surrounds the cages to remove dissolved nutrients (Neori et al., 2007; Chopin et al., 2007; Troell et al., 2009). Culturing three crops simultaneously increases nutrient retention and reduces the environmental footprint. Though freshwater algae can take up nutrients, no economic market currently exists for these organisms; therefore, algal production must be consumed by a marketable herbivorous fish species. Though system

components and trophic pathways differ, the principles of IMTA can still be applied to freshwater production.

The experiment studied in this thesis assessed the implementation of a polyculture freshwater cage system. A new cage design with two modifications (Fig. 1) was tested for reductions in waste releases compared to traditional cage designs. The first modification involved a sediment collection cone underneath the cage. This captured particulate waste feed and feces descending in the water column. These particles would normally settle on the lake bottom disturbing benthic communities (Kalantzi and Karakassis, 2006; Rooney and Podemski, 2009). The second modification was an outer cage around the main cage. In this space filter-feeding fish were stocked and not fed, but rather consumed plankton and suspended solids that drifted out of the inner cage. Top down control exerted by fish can affect lower trophic levels; Milstein and Hepher (1985) and Xiao et al. (2010) both found that high densities of silver carp (*Hypophthalmichthys molitrix*) suppressed phytoplankton biomass in water bodies. Therefore, this experiment assessed whether fish in the outer cage served as an effective nutrient sink, consuming plankton and wastes from the inner cage and reducing the environmental impacts from the cage.

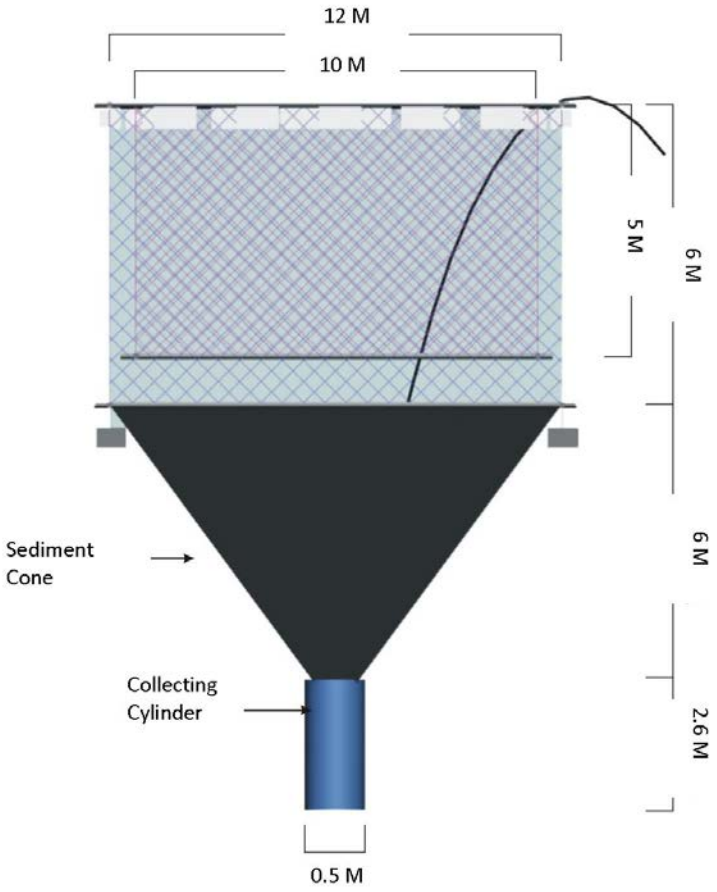

Figure 1. Design of modified cage showing sediment retention trap underneath and outer cage housing filter-feeding fish.

The objectives of this study were to determine the effectiveness of the new cage design by quantifying nutrient releases from modified and traditional cages. This was done by: 1) evaluating growth rates of fish in the inner and outer cages, 2) using a mass balance model to quantify phosphorus dynamics of both types of cages, and 3) collecting water samples to assess any changes in water chemistry between the modified and traditional cages and the reservoir. Due to sampling complications, no data could be collected on the sediment trap and no performance analysis of the trap is included in this experiment. I hypothesized that, due to the accumulation of nutrients in the filter-feeding fish and the extraction of sediments from the water column, modified cages would reduce nutrient loads into the reservoir. I also expected that additional nutrient inputs from the inner cage would elevate growth rates of the extensively fed fish in the outer cage. If the new modifications prove effective, it would produce significant improvements for the freshwater cage industry.

Materials and Methods

Cages were situated in Longtan Reservoir (25.33 N, 106.87 E) on the Hongshui River in southwestern China (Fig. 2). The reservoir straddles southern Guizhou province and northern Guangxi province. With a surface area of 360-540 km^2 and a depth at the facility of approximately 100 m, Longtan is characterized as a narrow and deep reservoir surrounded by a karst landscape. The experiment was located in a small embayment formed by a minor tributary and shared with 4-5 other commercial aquaculture facilities and artisanal cages owned by local villagers. These facilities were >300 m away from the experiment and were not expected to directly influence conditions around experimental cages. Landscape upstream and surrounding this embayment was undeveloped with limited agricultural land use or urban development.

The facility used for my experiment had approximately 50 cages of which 10 were dedicated to the experiment (Fig. 3): six modified cages divided into two sets of three, three traditional cages, and one control cage stocked with planktivorous/omnivorous fish. Modified-a cages contained an outer cage and no sediment trap, while modified-b cages contained both an outer cage and sediment trap. Modified cages (Fig. 1) were 12x12 m in surface area and 6 m deep, not including the sediment collector below. Traditional cages were 5x5 m in surface area and 5 m deep, and the control cage was 3x3 m in surface area and 3 m deep.

On 24 May 2010, channel catfish (*Ictalurus punctatus*) were stocked in inner modified cages and traditional cages at a density of 160 fish m^{-2}, equaling 16,000 fish in modified cages and 4,000 catfish in traditional cages.

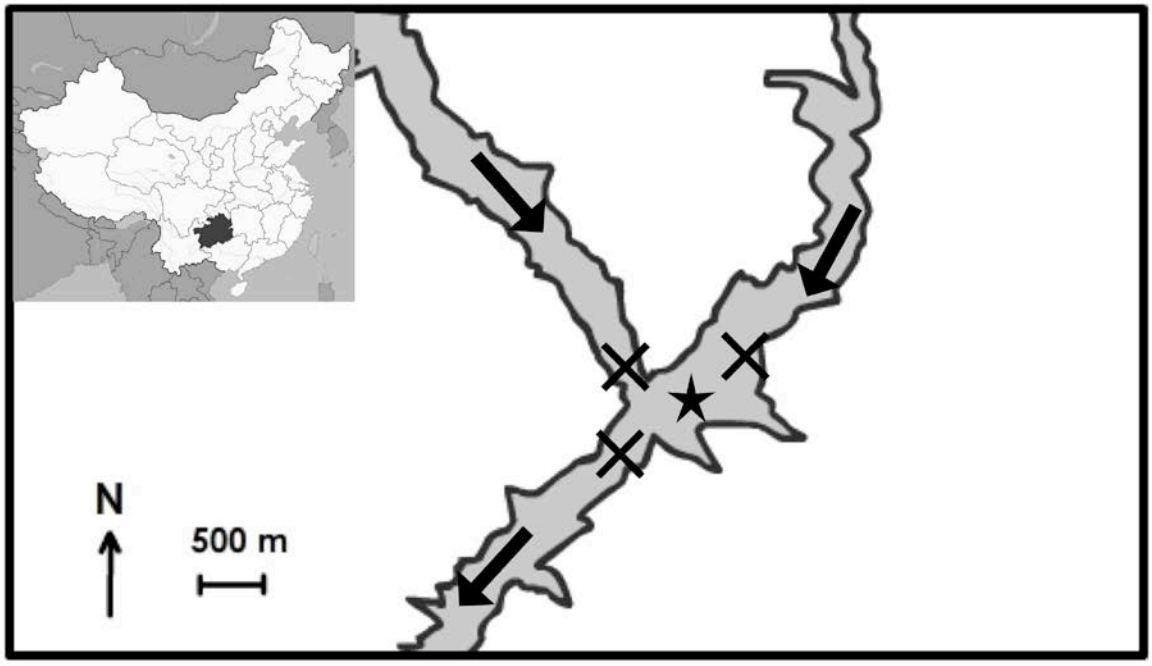

Figure 2. Location of cages (star) and reference water quality sampling sites (X's) within Longtan Reservoir, China. Arrows show flow direction. Inset shows Guizhou province (black); Longtan is on the southern border of Guizhou Province.

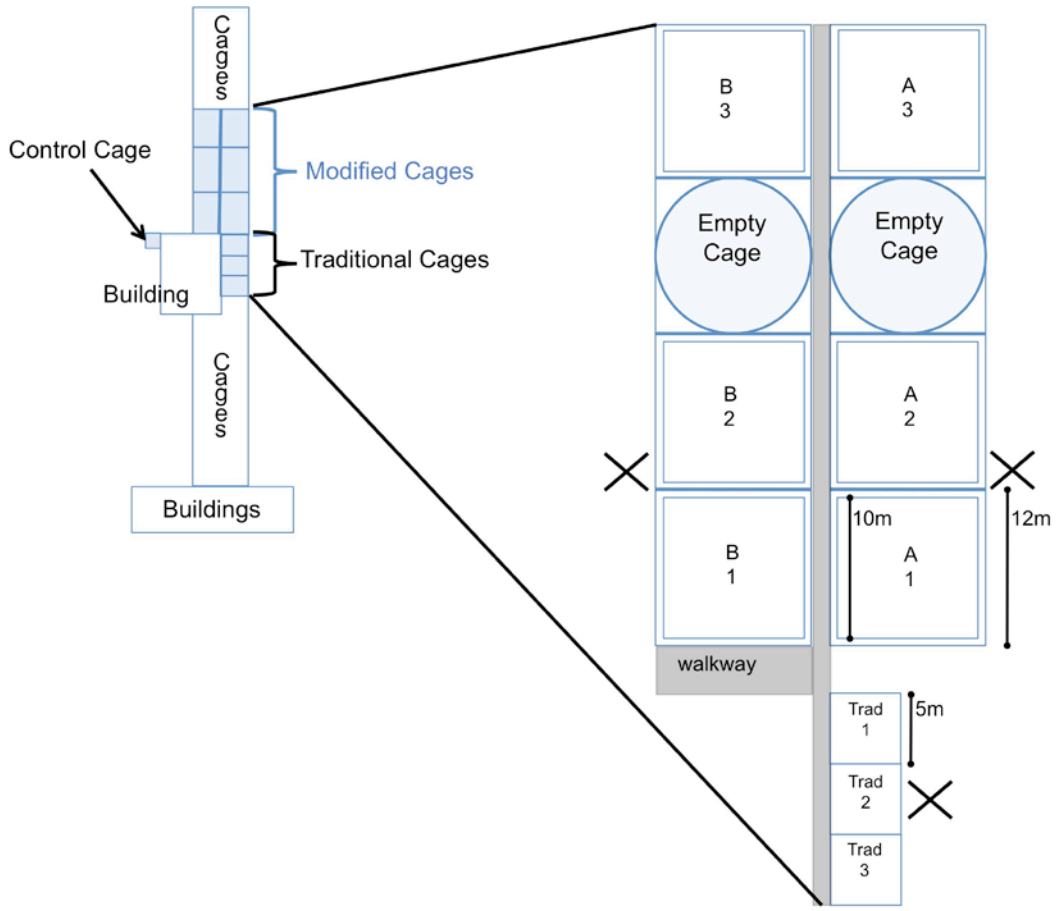

Figure 3. Map of commercial aquaculture facility with three traditional and six modified cages enlarged. Additional facility cages were not related to the experiment. X indicates location of a water quality sampling site 1m outside of the respective cages. Figure not to scale.

Facility records indicated that modified outer cages were stocked with 1000 (350 kg) bighead carp (*Hypophthalmichthys nobilis*), 250 (100 kg) Nile tilapia (*Oreochromis nilocticus*), and 150 (50 kg) of common carp (*Cyprinus carpio*); this equates to a total loading of 11.36 kg m^{-2}. Initial body weight of outer cage fish was calculated from these facility records (Table 1). Fish in the inner cages were fed by hand twice a day (07:30 & 19:30) with sinking Tongwei Company Feed (Tongli #1 sinking catfish feed, 3-4.5 mm). Outer cage fish were not fed at all, but left to consume waste drifting out of inner cages as well as any natural food in the water column.

A mass balance model was used to quantify phosphorus dynamics, from stocking to harvest, of traditional and modified cages and to estimate the amount of phosphorus retained in outer cages. The model used the following equations from Reid and Moccia (2007) to determine the phosphorus balance (see Table 1 for parameter definitions). Excrement P (P_{ex}) is digestible phosphorus excreted through urine and gills as soluble P and is shown in equation *i*.

$$P_{ex} = (((FA \times (1-F_{UF})) \times F_{feed} \times F_{di}) - RP)\ (g) \qquad (i)$$

Where FA is food available, F_{UF} is fraction uneaten food, F_{feed} is fraction of phosphorus in feed, F_{di} is fraction of phosphorus that is digestible in feed, and RP is phosphorus retained in the fish body (eq. *ii*). To derive F_{di} I obtained the ingredient list for feed used at the facility (Table 2). Using published values in the literature, I determined percent digestible phosphorus for each ingredient in the feed. Then, the fraction of each ingredient in the feed was multiplied by the fraction of available phosphorus and all values were summed to create a weighted average of digestible phosphorus in the feed. Digestibility values were not available for soybean oil, which was assumed to have equal digestibility as soybean meal, and for multivitamin premix feed which contained no phosphorus and was excluded from the calculation.

Table 1. Parameter definitions and constants for the mass balance model**.**

Model Nomenclature

FA = feed applied (g)	$F_{carcass}$ = fraction of P in the fish carcass
F_{UF} = fraction uneaten food	P_{fecal} = fecal phosphorus P (g)
P_{ex}= soluble excrement P (g)	$P_{ns,fecal}$ = non-settleable feces P (g)
F_{feed} = fraction of P in feed	P_{UF} = waste P from uneaten feed (g)
F_{di} = fraction of F_{feed} that is digestible	P_{sol} = sum of soluble P waste components (g)
RP = retained P in fish at harvest (g)	F_{NS} = fraction suspended/soluble feces
FBW = final body weight (g)	$P_{tot\text{-}waste}$ = total P loading from cage (g)
IBW = initial body weight (g)	

Parameter Constants	**Source**
IBW =	facility records
Catfish = 100 g	
Bighead Carp= 350 g	
Tilapia = 400 g	
Common Carp = 333 g	
F_{UF} = 0.02	Cho and Bureau, 1998
F_{feed} = 0.0079	this study
F_{di} = 0.5283	see Table 2
$F_{carcass}$	this study
Catfish initial= 0.00545	
Catfish final= 0.00418	
Tilapia = 0.0055	
Bighead carp= no samples, tilapia value used	
Common carp = 0.00675	
F_{NS} = 0.177	Brown et al., 1989

Table 2. Digestible phosphorus (F_{di}) calculation involving feed ingredients and their digestible phosphorus fractions.

Ingredient	Fraction Ingredient Amount	Fraction Digestible Phosphorus	Ingredient Amount * Digestible Phosphorus	Source
Soybean Meal	0.250	0.35	0.088	Buyukates et al., 2000
Fish powder	0.300	0.75	0.225	Li and Robinson, 1996
Secondary meatmeal	0.050	0.84	0.042	Li and Robinson, 1996
Cotton Seed cake	0.090	0.43	0.039	Li and Robinson, 1996
Rapeseed Cake	0.050	0.06	0.010	Higgs et al., 1995
Distiller Dried Grains	0.050	0.25	0.013	Webster et al., 1992
Fishmeal	0.120	0.84	0.101	Li and Robinson, 1996
Ricebran	0.030	0.51	0.015	Buyukates et al., 2000
Soybean Oil	0.010	0.35	0.004	Same as soybean meal
Multivitamin Premix	0.050	N/A	N/A	----
Sum	1.000		**F_{di} = 0.5283**	

Table 3. Feeding regiment data as documented in facility records and adjusted for survival. (see text for derivation of values).

	Trad 1	Trad 2	Trad 3	Mod-a1	Mod-a2	Mod-a3	Mod-b1	Mod-b2	Mod-b3
Feed Available (kg fish^{-1})									
May, 25 – Aug. 25	No Record	No Record	No Record	0.431	0.431	No Record	0.431	0.431	No Record
Aug, 25 – Nov. 6	0.687	0.687	0.687	No Record	No Record	0.763	No Record	No Record	0.763
Nov, 7 – Dec, 26	0.133	0.133	0.133	0.18	0.835	0.593	0.18	0.835	0.593
Overall	1.251	1.251	1.251	1.375	2.030	1.789	1.375	2.030	1.789
Survival Rate									
Overall	94.1%	94.7%	92.3%	89.3%	96.2%	95.2%	89.7%	96.5%	97.1%
Feed Available Corrected for Survival (kg fish^{-1})									
Overall	1.329	1.321	1.355	1.540	2.110	1.879	1.533	2.104	1.842

FA was calculated from facility records (Table 3). Records indicated total kg of feed applied per day to each cage. To estimate the amount of feed available per fish, total feed applied in kg per cage was divided by the number of fish stocked in traditional and modified cages (initially 4,000 and 16,000). Records were incomplete, so when no record was kept it was assumed that cages were fed the same amount as other cages for which records did exist. To adjust for survival rates, overall feed applied per individual fish was divided by the percent fish survival for each cage and that value used for the mass balance model as total feed available per fish.

Retained phosphorus, was modeled by equation *ii*.

$$RP = ((FBW \times F_{carcass}) - (IBW \times F_{carcass})) \qquad (ii)$$

FBW and IBW are final and initial body weight, respectively, and $F_{carcass}$ is fraction of P in fish body tissue. According to stocking records initial body weight was 100 g wet weight. Final body weight was determined from 27 December 2010 weight sampling data, the final sampling date.

Fecal P is indigestible P and was determined by establishing the total phosphorus ingested and then multiplying by indigestible P fraction in feed shown in equation *iii*.

$$P_{fecal} = ((FA \times (1-F_{UF})) \times F_{feed} \times (1-F_{di})) \qquad (iii)$$

Most feces settled into sediments but non-settleable feces ($P_{ns,fecal}$) remain suspended in the water column and contributed to P loading (equation *iv*).

$$P_{ns,fecal} = P_{fecal} \times F_{NS} \qquad (iv)$$

where F_{NS} is the fraction of fecal material that remains suspended in the water column. Reid and Moccia (2007) used a constant $P_{ns,fecal}$ value in their study on trout. The present study required a relevant constant, F_{NS}, for catfish; Brown et al. (1989) found that 14% of nitrogen-free extract and 22% of crude ash leeched out of catfish feces after 80 minutes. These numbers were

averaged together to estimate F_{NS} as 0.177 of original fecal mass. Waste loaded from uneaten feed (F_{UF}) equals the product of uneaten feed and phosphorus content of feed shown in equation *v*.

$$P_{UF} = (FA \times F_{UF} \times F_{feed}) \qquad (v)$$

Total soluble waste is the sum of excrement and non-settleable fecal waste and shown in equation *vi*.

$$P_{sol} = P_{ex} + P_{ns,fecal} \qquad (vi)$$

Total phosphorus waste from traditional cages (Tot-P_{wasteT}) is total P content of particulate waste, non-settleable feces, and excrement phosphorus described by equation *vii*.

$$\text{Tot-}P_{wasteT} = P_{par} + P_{ns,fecal} + P_{ex} \qquad (vii)$$

$P_{ns,fecal}$ and P_{ex} represent the soluble portion of phosphorus waste, and P_{par} the particulate phosphorus waste.

To derive total phosphorus released from modified cages equation *vi* was modified to account for retention by filter-feeding fish, and since the sediment trap could not be sampled I ignored its effect from calculations. To account for retained phosphorus from fish in the outer cage, equation *ii* was applied to each species, j, in outer cages and reformulated as equation *viii*.

$$\sum RP_{filterSpecies} = (FBW_j \times F_{carcass} - IBW_j \times F_{carcass}) \times N_j \qquad (viii)$$

N_j is number of fish of species j in the outer cage; equation *vii* estimated total amount of phosphorus retained for the entire cage. According to stocking records and assuming 0% mortality, 1000 bighead carp, 250 tilapia, and 150 common carp lived in each outer cage. FBW is average body weight from the 27 December sampling. Due to small sample sizes, fish from individual cages were pooled together into modified-a and modified-b groups, and an average

wet weight estimated. I used this one value for all three cages in each group.

No common carp were sampled for FBW but I obtained mass data for them on 1 August when extracting fish from outer cages to stock the control cage. On 1 August, the average common carp weight was 466±80 g. Since they were stocked at 333 g $fish^{-1}$, this is a growth rate of 2.02 g day^{-1}. I assumed this constant growth rate over the whole experiment and estimated that by 26 December final body weight would be 762 g.

A major assumption is that filter-feeding fish only ate material derived from inner cages and thereby reduced total phosphorus released from cages. Based on this assumption, the $RP_{filterSpecies}$ value could be subtracted from equation *vii*. Therefore, equation *ix* estimates phosphorus discharged from modified cages.

$$\text{Tot-}P_{wasteM} = P_{par} + P_{ns,fecal} + P_{ex} - \sum RP_{filterSpecies} \qquad (ix)$$

To compare model outputs, the total phosphorus input and feed conversion ratios (FCR) were calculated for each cage. Phosphorus input was measured by multiplying total feed applied to the cage by the fraction of phosphorus in the feed. FCR was calculated as

$$\text{total feed applied / ((FBW-IBW) x number of fish harvested)} \qquad (x)$$

Catfish weight and length were measured five times to assess growth rates. Fish were removed from the cage and anesthetized with MS-222 at 100 mg L^{-1} water, measured for wet weight and total length, and returned to the cage.

Since fish were harvested on different days, I back-calculated estimated weight on 27 December 2011 to assess if sample sizes were accurate at estimating fish weight. To obtain the average weight per fish, I took the total cage weight at harvest and divided it by the number of fish

extracted. Then I divided this by the number of grow-out days to find the average daily growth rate. Then to estimate weight on 27 December I took the weight at harvest and subtracted any additional growth since 27 December.

To test the efficacy of the outer cages in removing effluent waste, an additional control cage was used to determine growth rates of fish supplied with only natural food. This control cage was stocked with 42 kg bighead carp, 24 kg tilapia, and 6 kg common carp for a total loading of 8 kg m^{-2}, slightly less than the loading of the modified outer cages. The cage was situated adjacent to a facility building approximately 10 m away from all cages. To estimate growth rates, each fish was weighed at stocking and a sample of 44 fish from this cage weighed on 27 December. Average wet weight per fish at stocking for bighead carp was 312±96 g (mean±SD), tilapia 339±98 g, and common carp 466±80 g.

To determine the amount of phosphorus in fish carcasses ($F_{carcass}$), 171 catfish were sampled in July and September 2010. Fish were frozen at -4˚C until analysis. Individual fish were homogenized in a blender, and 3 g removed as a sample. Total phosphorus in fish and feed was determined using wet $HClO_4$ and HNO_3 digestion, after which concentration was measured spectrophotometrically according to Chinese standard methods (CSBS, 2009). To measure phosphorus in the feed (F_{feed}), a sample of feed was homogenized in a blender, then one 3 g subsample was removed to test for total phosphorus according to the same wet digestion method.

Allometric growth in fish reduces the phosphorus composition of fish carcasses as mass increases, because the body mass increases more rapidly than the skeletal mass, and most phosphorus is bound in skeletal tissue of fishes (Lall, 1991; Hendrixson et. al., 2007). To account for differences in $F_{carcass}$ values as fish grew, I compared $F_{carcass}$ measurement from July 30 and

September 30 with the average fish weights from those same days (Fig. 4). The natural log of fish weight was used to decrease the positive skew of the distribution of fish weight on each sampling date. Increased fish mass was correlated with lower $F_{carcass}$ values ($p<0.05$). To account for this trend in the model, I used the average $F_{carcass}$ value from July 30 (0.00545) as the initial value and the average value from September 30 (0.00418) as the final value (Table 3). These values are within the range of carcass phosphorus content in Lall (1991) but not as ideal as having actual $F_{carcass}$ values throughout the experiment, although they still serve to capture the trend of allometric growth in catfish. Not enough $F_{carcass}$ estimates were collected from outer cage fish to input multiple values into the model. Since the magnitude of outer cage fish growth was substantially lower than catfish, I did not suspect a substantial change in $F_{carcass}$ of outer cage fish over the course of the experiment. Therefore, the use of a single $F_{carcass}$ estimate for outer cage fish should not significantly affect model outputs due to their allometric growth.

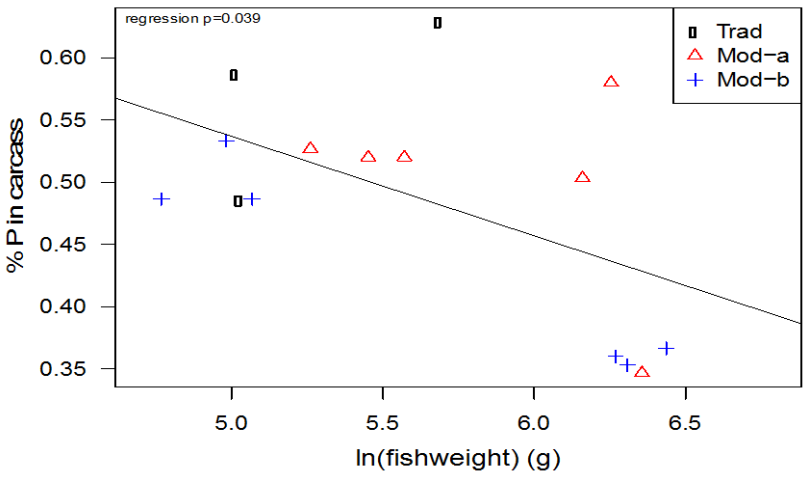

Figure 4. % Phosphorus in catfish carcasses compared to the natural log of average catfish weight in each treatment from July 30 and September 30, 2010.

Water samples were taken from July - December approximately every two weeks to assess if there was a reduction in phosphorus around modified cages. Water samples were taken 1 m outside each modified and traditional cage at depths of 0.5, 5, and 15 m. Samples were also taken inside each traditional cage at 0.5 m deep, and inside each modified cage at 0.5 and 5m deep (Fig. 3). Three additional samples were collected approximately 0.5-1 km away from cages to establish the background reservoir water characteristics independent of any experimental influences. These samples were taken at locations shown in Figure 2 at 0.5, 5, and 15 m depths.

Water samples were processed at Guizhou Normal University for total phosphorus (TP), chlorophyll *a* (chla), and total nitrogen (TN). TN and TP were determined with persulfate digestion in an autoclave, and concentrations measured colorimetrically (EPAC, 2002). Chla samples were filtered through a 0.45 µm glass fiber paper, and then the filter was steeped in 90% acetone for 24 hours and chla concentration determined by spectrophotometer (Lin et al., 2005).

Due to seasonal changes in water chemistry, variables violated the assumption that all data came from an identical distribution, so statistical tests for water quality data were done using a sign test to assess difference in means. Nutrient concentrations inside and outside cages were subtracted from one another, and then sign test used to determine if the difference was significantly greater or lesser than zero. One-way analysis of variance (ANOVA) tests were conducted on final estimates from the mass balance model. When significant differences were detected, Tukey HSD test was used to establish which groups were significantly different from each other. All statistics were computed on *R: A Language and Environment for Statistical Computing* (R Development Core Team, 2010). For statistical tests alpha was set at 0.05.

Results

Fish in the traditional cages grew slower (Table 6) and were smaller at harvest (Table 4; Fig. 4) than fish in the modified cages. Slower growth rates resulted in lower catfish production from traditional cages. Final body weight samples varied between -29.1% to +56.3% of back-calculated final harvest data estimates (Table 5). FCR values ranged from 1.52-2.77 and were not statistically different between cage types. Taken across all cages, FBW samples averaged 107 g (±263 g) less than back-calculated harvest data; therefore, fish samples underestimated the total fish production averaged across all cages by approximately 5%.

As expected tilapia and bighead carp in the control cage grew slower than fish in the modified outer cages (Fig. 5). Outer cage tilapia and bighead carp increased their weight 75% and 21% respectively, while control cage tilapia had no weight change and bighead carp decreased in mass by 3%. The average weight of tilapia and bighead carp on December 27 in the outer cages was 702 and 424 g, while in the control cage the weight was 339 and 304 g, respectively. Common carp could not be collected in the outer or control cages on 27 December and without FBW estimates were not included in growth analysis.

Based on mass balance model outputs, outer cage fish retained 0.08-0.11 kg P ton^{-1} fish produced (Table 7). Retention values did not differ between modified-a and modified-b cages. This retention was smaller than expected, equaling 0.51-0.75% (Table 8) of the total phosphorus input (9.82-18.09 kg P ton^{-1}) into the system (Table 8). Catfish retained 18-34% of total phosphorus

inputs. ANOVA analysis of model outputs only found a difference in retained P of catfish between traditional and modified cages.

Contrary to expectations, water quality measurements showed no change in TP, TN, and chla concentrations outside the modified or traditional cages. When measured at 0.5 m and 5 m, water quality measurements showed no statistical difference and so these data were pooled. Once pooled, TP, TN, and chla concentrations were the same inside and outside the cages for traditional, modified-a, and modified-b cages (Fig. 6). Additionally, TP, TN, and chla were not elevated near the aquaculture facility compared to reference sites.

Table 4. Average fish wet weight (grams), one standard deviation, and sample size at each sampling event. Different capital superscripts denote significant difference across rows (p>0.05).

Date	Modified-a Cages			Modified-b Cages			Traditional Cages		
	Weight	± SD	#	Weight	± SD	#	Weight	± SD	#
Catfish									
16-Jul-10	154.7	61.6	94	151.6	83.9	75	154.5	103.9	70
30-Jul-10	238.4	78.0	74	154.2	61.7	63	189.5	80.8	102
30-Sep-10	542.1	142.8	60	588.2	164.7	60	487.0	149.9	60
7-Nov-10	718.6	171.1	60	743.5	216.5	60	583.5	147.2	60
27-Dec-10	886.7^{A}	258.9	104	1000.6^{A}	653.8	60	630.8^{B}	216.2	63
Bighead Carp									
27-Dec-10	424.9	151.2	32	522.5	211.7	22			
Tilapia									
27-Dec-10	734.5	370.4	17	679.9	149.3	27			

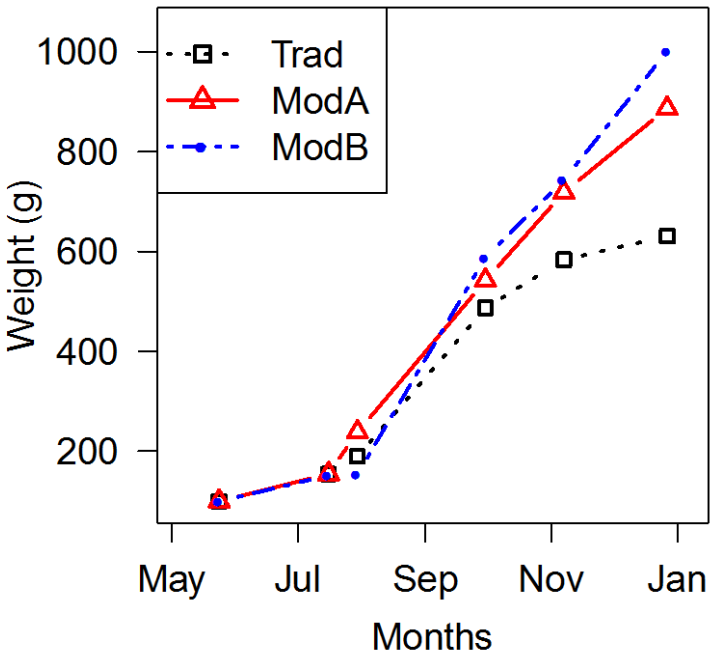

Figure 5. Average catfish weight in traditional, modified-a, and modified-b cages.

Table 5. Comparison of growth performance results between experimental sampling and facility harvest records.

Cages	Harvest Date	Grow-out days	Harvested FBW (kg fish^{-1})	Harvested Growth rates (g / day)	Back-calculated weight for 27-Dec-11 (kg fish^{-1})	Sampled weight on 27-Dec-11 (kg fish^{-1})	Sampled weight – harvested weight (kg fish^{-1})	% difference
Trad 1	4-Jan-11	221	0.831	3.31	0.805	0.579	-0.226	-28.0%
Trad 2	4-Jan-11	221	0.848	3.38	0.821	0.582	-0.239	-29.1%
Trad 3	4-Jan-11	221	0.834	3.32	0.807	0.761	-0.046	-5.8%
Mod-a1	20-Dec-11	210	0.782	3.25	0.805	0.81	0.005	0.7%
Mod-a2	2-Feb-11	270	0.801	2.60	0.705	0.886	0.181	25.7%
Mod-a3	21-Mar-11	301	0.816	2.38	0.616	0.963	0.347	56.3%
Mod-b1	25-Dec-11	210	1.597	7.13	1.611	1.106	-0.505	-31.3%
Mod-b2	12-Mar-11	292	1.549	4.96	1.177	1.042	-0.135	-11.5%
Mod-b3	17-Mar-11	297	1.618	5.11	1.209	0.861	-0.348	-28.8%

Table 6. Growth performance and production results. Capital letter superscripts indicate a significant difference between averaged cage values in each column (p>0.05).

Cages	Survival (%)	Feed Applied (g/fish)	FBW (g)	Growth Rate (g/day)	Tonnes Produced	FCR
Avg. Trad	**93.7%**	**1335**	**640.70^{A}**	**2.49^{A}**	**2.4^{A}**	**2.52**
Trad1	94.1%	1329	579.5	2.2	2.18	2.77
Trad2	94.7%	1321	582.0	2.2	2.2	2.74
Trad3	92.3%	1355	760.6	3.0	2.81	2.05
Avg. Mod-a	**93.6%**	**1843**	**886.7^{B}**	**3.6^{B}**	**13.3^{B}**	**2.34**
Mod-a1	89.3%	1540	810.4	3.3	11.58	2.17
Mod-a2	96.2%	2110	886.6	3.6	13.65	2.68
Mod-a3	95.2%	1879	963.1	4.0	15.67	2.18
Avg. Mod-b	**94.4%**	**1826**	**1003.5^{B}**	**4.2^{B}**	**15.12^{B}**	**2.06**
Mod-b1	89.7%	1533	1106.3	4.6	15.88	1.52
Mod-b2	96.5%	2104	1042.3	4.3	16.09	2.23
Mod-b3	97.1%	1842	861.7	3.5	13.39	2.42

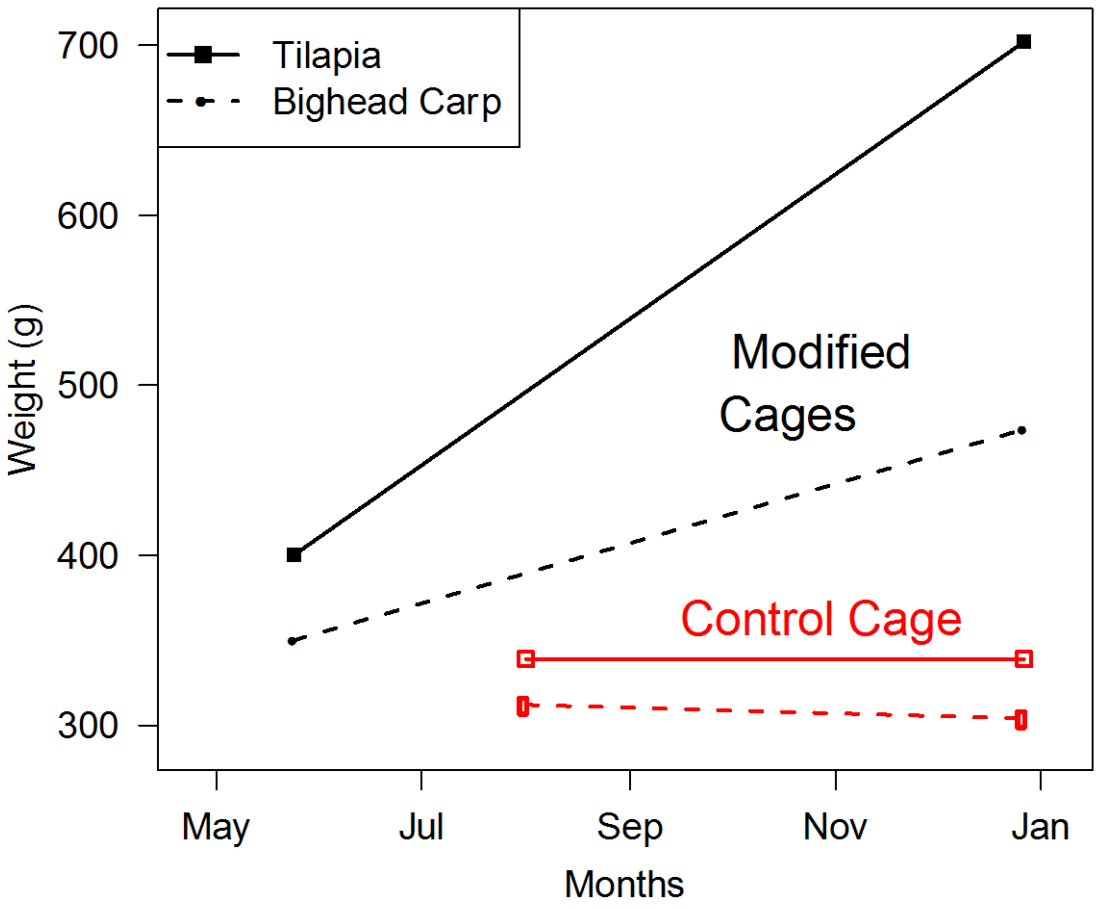

Figure 6. Average weight of bighead carp and tilapia in modified and control cages at stocking and at harvest. Open circles and squares represent the control cage while squares solid circles and squares represent modified cages.

Table 7. Mass balance model outputs. Capital letter superscripts indicate a significant difference between averaged cage values in each column (p>0.05).

Cages	Total P Input (kg / ton)	P Retained in Catfish (kg / ton)	Total P Waste (kg / ton)	Fecal P Waste (kg / ton)	Soluble P Waste (kg / ton)	P Retained in Outer Cage (kg / ton)	Uneaten Feed P Waste (kg / ton)
Avg. Trad	**16.71**	**3.32**	**13.06**	**6.36**	**6.70**	**N/A**	**0.33**
Trad1	18.12	3.24	14.52	6.89	7.63	N/A	0.36
Trad2	17.93	3.24	14.33	6.82	7.51	N/A	0.36
Trad3	14.08	3.46	10.33	5.36	4.98	N/A	0.28
Avg. Mod-a	**16.41**	**3.56**	**12.52**	**6.24**	**6.28**	**0.10**	**0.33**
Mod-a1	15.01	3.57	14.86	5.71	5.49	0.11	0.30
Mod-a2	18.80	3.61	11.49	7.15	7.71	0.10	0.38
Mod-a3	15.41	3.56	12.52	5.86	5.63	0.09	0.31
Avg. Mod-b	**14.59**	**3.63**	**10.67**	**5.55**	**5.12**	**0.09**	**0.29**
Mod-b1	10.95	3.66	11.97	4.16	2.87	0.08	0.22
Mod-b2	15.94	3.55	13.01	6.07	5.90	0.08	0.32
Mod-b3	16.89	3.63	10.67	6.43	6.58	0.1	0.34

Table 8. Fate of phosphorus expressed as a percent of total P introduced into the system from feed. See Table 1 for definition of categories.

Cages	P Retained in Catfish	Total Waste P	Fecal Waste P	Soluble Waste P	P Retained in Outer Cage	Uneaten Feed Waste P
Avg. Trad	**20.19%**	**77.81%**	**38.04%**	**39.77%**	N/A	**2.00%**
Trad1	17.87%	80.13%	38.04%	42.08%	N/A	2.00%
Trad2	18.09%	79.91%	38.04%	41.87%	N/A	2.00%
Trad3	24.60%	73.40%	38.04%	35.35%	N/A	2.00%
Avg. Mod-a	**21.93%**	**76.07%**	**38.04%**	**38.03%**	**0.59%**	**2.00%**
Mod-a1	23.37%	74.63%	38.04%	36.59%	0.75%	2.00%
Mod-a2	18.96%	79.04%	38.04%	40.99%	0.51%	2.00%
Mod-a3	23.45%	74.55%	38.04%	36.51%	0.58%	2.00%
Avg. Mod-b	**25.88%**	**72.12%**	**38.04%**	**34.08%**	**0.61%**	**2.00%**
Mod-b1	33.69%	64.31%	38.04%	26.27%	0.75%	2.00%
Mod-b2	22.94%	75.06%	38.04%	37.02%	0.51%	2.00%
Mod-b3	21.00%	77.00%	38.04%	38.95%	0.58%	2.00%

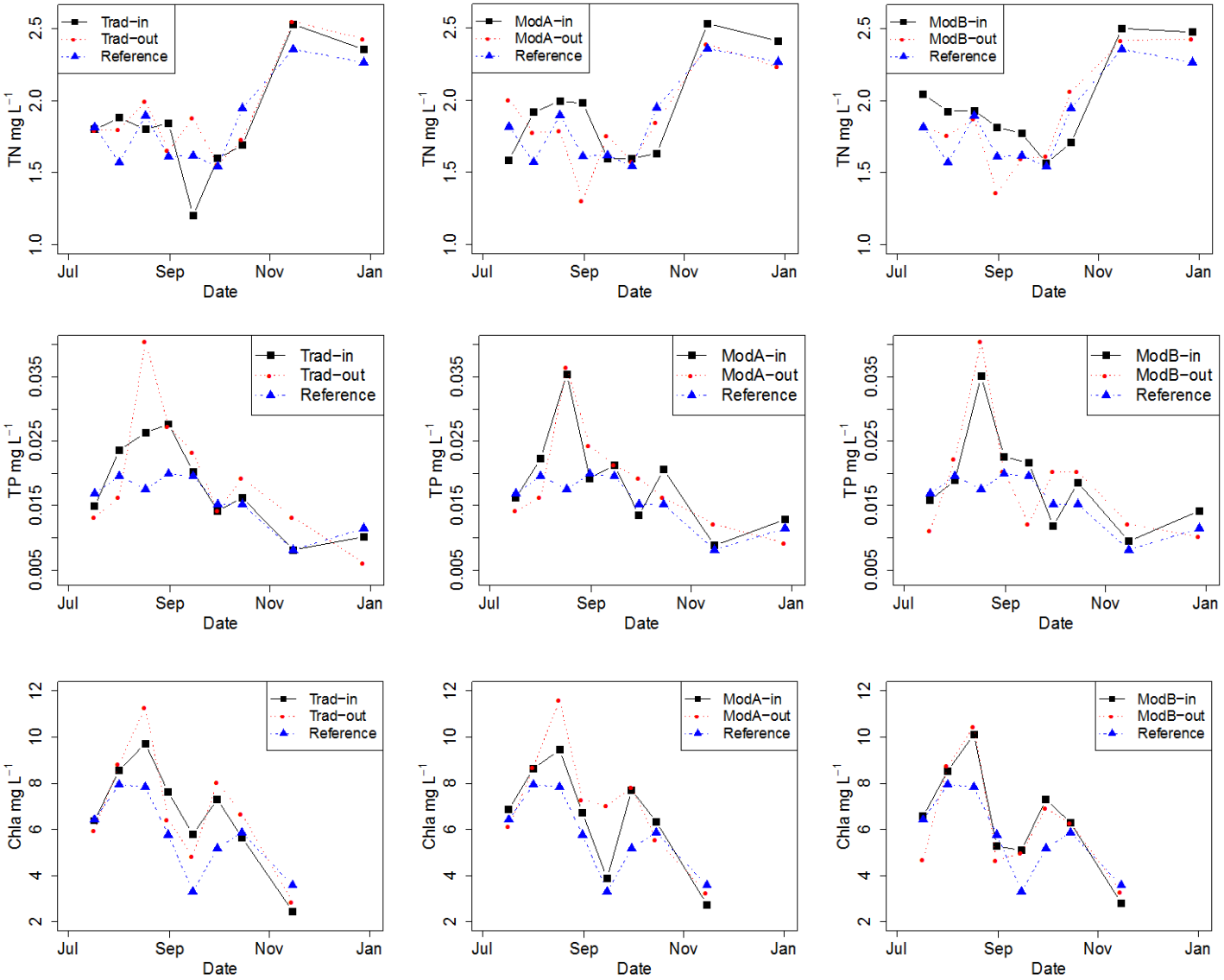

Figure 7. Nutrient concentrations during fish culture from water samples inside cages, 1m outside cages, and at reference sites.

Discussion

This experiment assessed nutrient retention capabilities of an integrated freshwater cage system. Fish in outer cages were expected to experience elevated growth and sequester waste nutrients exiting inner cages. Outer cage fish did grow faster than control fish, but they retained only <1% of total phosphorus input from cages. There was no significant difference in water quality measurements between modified cages, traditional cages, and reference sites; therefore, phosphorus loading from cages had no measurable impact on reservoir water quality. Since fish in outer cages grew faster than fish in the control cage, it seems that they had access to energy drifting out of the inner cage, most likely in the form of particulate waste. This finding supports other studies that discovered elevated production near aquaculture facilities (Angel et al., 2002; Spanier et al., 2003; Mente et al., 2006; MacDonald et al., 2011). However, some publications found no increase in productivity around cages (Taylor et al., 1992; Cheshuk et al., 2003; Navarette-Mier et al., 2010; Aguado-Gimenez et al., 2011). Surplus production dynamics are complex as illustrated in Paterson et al. (2010) where cages elevated phytoplankton and total phosphorus concentrations in nearby waters, but no resulting change in zooplankton biomass occurred there.

FCR values from my study were reasonable though slightly elevated, averaging 2.31 between the nine catfish cages. Comparing FCR across culture systems is difficult (Robinson and Li, 2010), especially since most channel catfish production occurs in ponds and my study was in cages. Additionally, FCR at commercial facilities are usually higher than research sites (Brown et al., 2011), and my study occurred at a commercial facility. Elevated FCR values (2.52) in traditional

cages were most anomalous in my study. Usually FCR is lowest for smaller fish (Robinson and Li, 2010), while my experiment found highest FCR in traditional cages with the lowest final body weight. FCR values from modified cages (1.52-2.68) were also elevated compared to other published results. For example, De Silva et al. (2010) found a median FCR of 1.69 for commercial catfish farmers in the Mekong delta. Cage studies at research sites obtained FCR of 0.92-1.27 for Asian catfish (*Pangasius hypophthalmus*) (Liu et al., 2011) and 1.8-1.9 for channel catfish (Williams et al., 1987). Though affected by many factors, FCR is particularly sensitive to feeding rates (Robinson and Li, 2010). Large FCR values from this study likely indicate that fish were being overfed in all cages. This likely means that my estimate of 2% waste feed was too small and model outputs should reflect a higher phosphorus loading from uneaten feed. However, since feeding regimes were similar between modified and traditional cages, feeding regime alone cannot explain elevated FCR in traditional cages. Cage modifications were not expected to affect catfish growth rates between modified and traditional cages, and so mechanisms depressing catfish growth and elevating FCR in traditional cages remain unknown.

Phosphorus loading from cages at Longtan was less than the 25-35 kg P ton^{-1} fish harvested that were reported in two previous studies on cage aquaculture (Guo and Li, 2003; Guo et al., 2009). Larger waste output from both these studies can be explained by an imprecise feeding regime for cultured fish consisting of forage fish, grass, and formulated feed. Using nutritionally imprecise feed increases phosphorus loading from aquaculture (Cho et al., 1994; Cho and Bureau, 2001; Bureau and Hua, 2010). Results from De Silva et al. (2010) support this conclusion by finding that waste from artisanal feeds loaded more phosphorus than waste from commercial feeds. Longtan's facility used commercial feed and so lower phosphorus loadings were expected. Loading values from my study seem realistic, as they are within the range encompassed by De

Silva et al.'s (2010) results, which showed loadings of 9-20 kg phosphorus ton^{-1} fish cultured. Furthermore, compared to back-calculated harvest data, FBW samples may have underestimated fish weight and as a result phosphorus loading ton^{-1} of fish cultured could be overestimated by about 5%. Even with elevated FCR, phosphorus loading from my study was not outside the range of other published values (Hakanson et al., 1998; Islam, 2005; Tucker et al., 2005). The commercial low phosphorus feed (0.79% TP) used at Longtan may mean that even with overfeeding, phosphorus loading would remain low. This reflects the importance of low phosphorus, high digestibility feeds as a method to reduce nutrient loading from aquaculture (Cho et al., 1994; Bureau and Hua, 2010).

Since I could find no previous research using filter-feeding fish in outer cages to reduce nutrient loading, nutrient retention results from this study must be compared to other integrated aquaculture designs. From outer cage fish growth, my experiment on Longtan showed retention of 0.5-0.7% of total phosphorus inputs. Lupatsch et al. (2003) cultured benthivorous grey mullet (*Mugil cephalus*) below intensively fed gilthead seabream (*Sparus aurata*) in a cage mariculture system, to assess if mullets could remediate waste material falling to the sediments. The mullet were estimated to have retained 5.6-10.6% of particulate phosphorus falling from seabream cages. To convert their values into percent of total phosphorus input, I multiplied them by 44%, which Lupatsch and Kissil (1998) estimated for the percentage of particulate fecal phosphorus from total phosphorus input. Therefore, grey mullet retained 2.5-4.7% of total P input into the system. A study in ponds conducted by Yi et al. (2003) found that Nile tilapia cultured in ponds with hybrid catfish (*Clarias macrocephalus x C. gariepinus*) fed in cages retained 0.84-1.29% of total phosphorus from catfish feed. My experiment had less phosphorus retention than both Lupatsch et al., (2003) and Yi et al. (2003). However, not all integrated experiments have

demonstrated elevated nutrient retention near cages. Using elevated growth rate as a metric for retention, other studies have found minor to no waste retention when culturing mussels in close proximity to cages (Taylor et al., 1992; Stirling and Okumus, 1995; Navarette-Mier et al., 2010).

The high ratio of intensively fed fish to filter-feeding fish (11.4:1) in this study may have resulted in low phosphorus retention rates. Yi et al. (2003) cited phosphorus retention values ranging from 0.86-17% by filter-feeding fish in integrated pond systems. The respective stocking ratios of intensively fed to filter-feeding fish ranged from 2.5-9:1, and lower ratios achieved higher retention. In partitioned aquaculture systems, the optimal catfish to tilapia stocking ratio to control algal growth was found to be 4:1 (Brune et al., 2003). However, increasing stocking rates of filter-feeding fish would eventually decrease growth rates due to density dependent mechanisms. Beyond stocking ratios the species stocked in outer cages should affect nutrient retention. There are diverse feeding mechanisms in different fish species, resulting in varying phytoplankton extraction and digestion efficiencies (Dong and Li, 1994; Turker et al., 2003; Jancula et al., 2008). Optimizing outer cage retention rates will require understanding specific feeding niches of stocked fish and an accurate assessment of stocking density to maximize nutrient retention.

Many factors influence aquatic phosphorus dynamics, which could explain why no difference in nutrients was found between cages or reference sites. Watersheds have multiple phosphorus inputs, ranging from sediment resuspension to urban and agricultural run-off. Kelly (1995) concluded that total phosphorus models based on Dillon and Rigler (1974) could only accurately model aquaculture impacts in basins with relatively few nutrient inputs apart from aquaculture. Longtan Reservoir is 55 km long and encircled by a complex watershed. Therefore, the magnitude of phosphorus retained with outer cage fish may is small in relation to the phosphorus

emitted from cages. Alternatively, the total phosphorus loading from experimental cages may be inconsequential in relation to the loading from other sources in the watershed. My study did not find a significant difference between nutrient concentrations inside cages and reference sites. This is inconsistent with other studies that found elevated nutrient concentrations near cages (Hakanson et al., 1998; Guo and Li, 2003; Stirling and Dey, 1990). These studies were performed on smaller and substantially shallower (2-4 m) lakes than the 100 m deep Longtan Reservoir, which may explain differences in nutrient concentrations around aquaculture facilities. To dispose of waste without deleterious consequences, cage aquaculture relies on the water column to dilute and flush waste away from the facility; therefore, shallower water bodies are able to absorb less waste than deep reservoirs before harmful nutrient concentrations are reached. Even though the cages in Longtan exhibited no impact on reservoir water quality, a loading threshold probably exists that if exceeded would reduce water quality in the reservoir. The depth and watershed complexity of Longtan suggest that large, deep reservoirs may be more resilient to nutrient loadings from aquaculture facilities than shallower systems.

I hypothesize that particulate waste and periphyton consumption substantially contributed to fish growth rates in outer cages. Chlorophyll *a* tests from Longtan showed no difference in chlorophyll *a* concentrations between cages or reference sites. Therefore, fish in the control cage had access to the same chlorophyll *a* concentrations in phytoplankton as fish in outer cages, yet exhibited no growth over the course of the experiment. This suggests that phytoplankton could supply maintenance metabolic requirements, but may not be sufficient for fish growth in this system. Particulate waste from inner cages is the most probable cause for outer cage fish growth. Uneaten feed was estimated as 2% of total feed applied. This equates to total uneaten feed P loadings from the modified cages of 3.5-5.1 kg cage^{-1}. Outer cage fish retained about 1.25 kg P

cage^{-1} or 24-36% of the equivalent amount of uneaten feed P loading. Due to weak currents in Longtan, most uneaten feed would sink to the bottom of the cage or disintegrate from fish swimming turbulence and remain suspended. Therefore, it is unknown what fraction of the uneaten feed was actually consumed by outer cage fish. If uneaten feed was >2%, which is likely given high FCR values, then there would be more energy available than modeled for outer cage fish to consume.

Over the course the experiment, solid waste from catfish feces in modified cages loaded 63-93 kg P cage^{-1} into the reservoir, and the phosphorus retained by the outer cage fish was equivalent to only 1-2% of loading from this source. The bioenergetics linkage between catfish feces and outer cage fish appears to be weak. Either feces were not reaching the fish or the fecal digestibility was very low. Turbulence, sloppy feeding, or unconsolidated fecal discharge could disintegrate fecal pellets leaving them suspended and too small to be filtered by outer cage fish (Troell and Norburg, 1998). Additionally phytoplankton and periphyton should sequester nutrients leached from the fecal mass. Even if feces are filtered or consumed by outer cage fish, the digestible fraction of fecal wastes is probably low and few nutrients should be assimilated. Since so little fecal energy was likely assimilated into outer cage fish, I conclude that energetically dense uneaten feed is most probably energetic linkage between inner cages and outer cage fish.

Additional energetic inputs could also come from periphyton consumption. This could help explain why fish in outer cage fish grew, while fish in control cage exhibited no growth. Tilapia are known to feed on periphyton (Williams et al., 1987; Milstein et al., 2008), while bighead carp prefer zooplankton but can diversify their diets (Zhang et al., 2008). Inner and outer modified cage structures contain more surface area for periphyton to colonize than the control cage.

Control cage surface area to volume ratio was 1.3 while in outer cages it was 39% larger at 1.84. Assuming periphyton biomass densities on outer cages were equal to or greater than periphyton biomass densities on the control cage, then more surface area means more available energy for outer cage fish, facilitating increased growth. Periphyton sequestration of waste nutrients from catfish may also help explain why suspended nutrient levels were not elevated in and around cages. It is possible that periphyton, not phytoplankton, were sequestering most of the nutrients discharged from catfish cages, but periphyton was not sampled in this experiment. In light of these data, I surmise that outer cage fish growth was not sustained by phytoplankton consumption, but rather periphyton grazing and consumption of uneaten waste feed drifting from cages.

Model results from this study are highly dependent on growth estimates. To assess the sensitivity of model outputs to changes in FBW, I analyzed model results by inputting mass estimates that were back-calculated to 27 December from catfish size at harvest (Table 5). Most model outputs were a function of constants or available feed, and so as expected, changing FBW resulted in a similar magnitude of change in outputs. Soluble waste was the most sensitive output to changes in FBW. For example, back-calculated values of FBW from modified-b cages were 58% higher than measured values, while soluble waste outputs decreased an average of 85%, a change that was larger than expected. This effect is a consequence of calculating soluble waste phosphorus by subtraction, and the challenges of estimating soluble waste from fish will be discussed in subsequent paragraphs. Overall, with the exception of soluble phosphorus, I believe any potential error in body weight estimates used for the model was unimportant in modifying results.

The model also does not account for size dependent metabolic rates in catfish. Nutrient assimilation rates vary with fish age and size. Robinson and Li (2010) found FCR values doubled

as fish grew from 0.9-1.1 kg as compared to 0.2-0.4 kg. This trend was also seen by Reid and Moccia (2007). Even though FCR represents several processes (i.e., nutrient assimilation and feed uptake), it can be used as a proxy for nutrient assimilation efficiency in fish. If FCR changed with fish mass, then model constants could be erroneous for different size classes of fish. FCR calculated from November 7-December 26 ranged from 2.69-3.18, but from July 15-30, 5 of the traditional and modified-a cages had FCR<1.1. Modified-b cages were excluded from July calculations because they showed only 3g of growth, probably due to small sample sizes. These size related differences in FCR support the conclusion that FCR increased with fish mass.

To assess the impact of changing FCR with mass during catfish grow-out, model outputs from 15-30 July, and from 7 November-26 December were compared to outputs from the entire grow-out period. Two cages from each time period were excluded from this FCR analysis due to negative fish growth over the respective time periods. The 7 November-26 December model outputs were similar to the overall results (Table 8), and similar to known fish digestion models (i.e., Behmer et al., 1993; Hakanson et al., 1998; Troell and Norburg, 1998; Chen et al., 1999; Islam, 2005). For example, results from this time period estimated that catfish retained 24% of total phosphorus inputs averaged across all seven cages. Therefore, I concluded that model parameters accurately represented fish growth dynamics even at the elevated FCR values that occurred during November and December. However, four cages from the July samples produced outputs that demonstrated negative values for excrement waste, which is not possible. These negative values indicate that model outputs did not correctly estimate the metabolic processes of fish in cages. From these results, I concluded that the model was not able to accurately estimate fish digestion processes during low FCR periods such as 15-30 July.

This model applies to a range of phosphorus digestion dynamics; if fish metabolism substantially deviates from fixed input parameters to the model, then model outputs will be less robust. For example, in this model when FCR<1, model outputs of soluble phosphorus waste from excrement become negative revealing a threshold at which model outputs no longer are biologically relevant. FCR<1 occurred in July 15-30 growth estimates from modified-a cages. Negative values of excrement phosphorus result from the values of model constants. Since measuring phosphorus in soluble waste is difficult, models often estimate outputs of excrement waste by subtraction to close the nutrient balance (Bureau et al., 2003; Schneider et al., 2004). However, this makes model outputs of soluble waste impossible to confirm. By modeling soluble phosphorus from excrement in this manner, then the output contains any error in model parameter estimates. If particular experimental replicates differ from model predictions it could produce inaccurate model outputs. For example, phosphorus assimilation is usually elevated when fish are small and growth rapid, as demonstrated in the July 15-30 data with FCR<1. This static model is parameterized for long-term averages and so should not be applied to situations when metabolic processes deviate substantially from average values of the model parameters (i.e. when FCR<1). The combination of a static model and the challenges of estimating fish digestion make it difficult to accurately represent the dynamics of soluble phosphorus excretion. The same modeling challenge revealed itself in Schneider et al. (2004) who also obtained negative soluble waste values as FCR approached 1. However, FCR<1 occurred infrequently during grow-out in my experiment, and overall model outputs are within the range of other published values. Furthermore, uncertainty in soluble phosphorus waste calculations only affects partitioning of model outputs for particulate and soluble waste, leaving other model outputs unaffected. Lastly, the goals of the experiment were to assess nutrient retention in outer cages. Therefore, I am

confident that the model accurately estimated the long-term phosphorus dynamics of the cages during the grow-out period and provided data to confidently assess experimental objectives.

Laboratory analysis for this experiment determined that total phosphorus in feed was 0.79%, a value lower than public documents from Tongwei Company that listed total phosphorus in this feed at 1.2-1.3%. The measured 0.79% value produced an available phosphorus (F_{feed} x F_{di}) estimate of 0.42% as compared to 0.63-0.69% that would result if I used the Tongwei estimates. Available phosphorus content in feed is recommended to be 0.3-0.4% (National Research Council, 1993; Robinson et al., 1996; Eya and Lovell, 1997; Robinson and Li, 2005), and this range is very close to the estimate of 0.42% from my measured total phosphorus value. Ultimately, it is unknown why laboratory measurements resulted in lower total phosphorus values than Tongwei's public documents; however, the measured value was used for the model since it produced the more realistic available phosphorus estimate.

Retention efficiency for phosphorus could increase if periphyton growth and sediment trap retention rates were investigated. By placing structures in ponds to increase surface area for periphyton to colonize, other experiments have elevated fish growth rates (van Dam et al., 2002; Milstein et al., 2008). If objects with extensive surface area (e.g., bamboo rods) were placed in outer cages, it could increase periphyton biomass, which would likely increase nutrient retention and growth rates of fish in outer cages. However, a major experimental assumption was that outer cage fish fed exclusively on material derived from the inner cages. Outer cage fish diets need to be understood to determine if and how they are assimilating nutrients originating from inner cages. For example, if periphyton rather than phytoplankton primarily sequester nutrients in outer cages, then periphyton consuming fish should be stocked to maximize nutrient retention rather than stocking phytoplankton consuming fish. Increasing periphyton biomass on cages and

stocking fish that consume periphyton could further improve nutrient retention in modified cages.

Even though sediment traps were in place in the experimental cages, no data were collected to determine their efficacy. However, the physical properties of solid waste should make its removal easier than the retention of soluble waste from cages, and collection of solids could lead to substantial reductions in nutrient loading. Phosphorus leaching from feces makes 100% removal of particulate phosphorus from sediment traps impossible. Behmer et al. (1993) removed 16.3% of total phosphorus inputs with daily pumping of sediment waste from a sediment trap similar to the design used in this experiment. The magnitude of this reduction was substantially greater than the <1% of total phosphorus inputs retained in outer cage fish. Assuming the same collection rate (16.3%) for this experiment, pumping the sediment trap on a daily basis could reduce the particulate phosphorus loading by 41%. Further insight into the factors affecting retention capacity of sediment traps could increase the retention efficiency of modified cages.

A major constraint to integrated aquaculture in freshwater is the reality that herbivores are less efficient nutrient sinks compared to autotrophs (Schneider et al., 2005). Unlike marine IMTA systems, which are able to use macro algae for inorganic nutrient retention, freshwater systems are constrained to retain nutrients in marketable herbivores that are at least one step up in the food web. Low algal nutrient quality, combined with metabolic conversion losses resulting from increasing a trophic level, reduce nutrient retention when herbivores feed upon autotrophs. For example, if tilapia from this experiment consumed periphyton (which they most likely did), the majority of biomass ingested would be lost as feces or urine and only a fraction of the ingested biomass would be assimilated. Therefore some of the nutrients that were once sequestered in

periphyton were later released to the environment, diminishing nutrient retention efficiency, whereas if periphyton could be directly harvested, more nutrients would be retained. Unfortunately, no market exists for freshwater periphyton. Several studies (this paper; Lupatsch et al., 2003; Yi et al., 2003) have demonstrated that retention values for integrated herbivores ranged 0.59-17% of total phosphorus inputs. These are lower than values where autotrophs were used as nutrient sinks and nutrient retention ranged 10-30% (Krom et al., 1995; Schneider et al., 2005; Li and Li, 2009). Freshwater systems using herbivores will likely experience depressed maximum nutrient retention efficiency unless an economically valuable autotroph can be incorporated into the system.

Integrated cages could be a method to increase the sustainability of freshwater cage aquaculture. In this study outer cage fish experienced elevated growth rates compared to control fish, and even though the specific energetic linkages enabling growth remain unknown, this suggests that integrated cage aquaculture in freshwater is biologically and ecologically feasible. With increasing global aquaculture production and increasing utilization of freshwater resources, it will be necessary to create systems that reduce the ecological footprint of fish farming. The need for innovative aquaculture development is particularly acute in China, where the advent of culture methods for more fish species and increasing commercial feed availability since 1990 have resulted in rapid expansion of freshwater cage culture. In 2004, Chinese inland reservoirs yielded over two million tons of cultured fish (Halwart et al., 2007). A particular advantage of reservoir aquaculture is its minimal competition with existing wild caught fisheries, increasing the business prospects of the enterprise (Costa-Pierce, 2010). Sustained aquaculture growth will require methods that promote ecological and social integrity within aquaculture regions (Costa-Pierce, 2010). Unfortunately, very few other examples exist that researched integrated cage

systems in freshwater. Additional cage improvements to maximize trophic efficiency could increase carrying capacity for aquaculture cage in inland lakes and reservoirs, providing both economic and nutritional benefits to communities.

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