



Aquaculture carrying capacity of Nile tilapia Oreochromis niloticus and Nile crocodile Crocodylus niloticus in Lake Kariba, Zambia and Zimbabwe

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ABSTRACT: Increased aquaculture production can improve food and nutrition security and economic growth in developing countries, but comes with environmental risks. In recent years, aquaculture has increased tremendously in Lake Kariba, which is located on the border between Zambia and Zimbabwe. We calculated the carrying capacity of aquaculture production in Lake Kariba using the Beveridge P balance model with data for lake-wide total-P concentrations, river flows and data from aquaculture farms and feed producers in the Lake Kariba area. The maximum permissible P load for aquaculture farms in Lake Kariba is 1.2×10^6 kg P yr⁻¹. Average loss of P to the environment in Lake Kariba through farming is 13.92 kg P t⁻¹ for Nile tilapia *Oreochromis niloticus* and 92.5 kg P t⁻¹ for Nile crocodile Crocodylus niloticus. Consequently, sustainable aquaculture carrying capacity in Lake Kariba is $86\,900$ t yr^{-1} for *O. niloticus* and $13\,000$ t yr^{-1} for *C. niloticus*. We expect aquaculture production in Lake Kariba to account for 71% of the total allowable aquaculture P load by 2028. The total-P concentration is expected to increase to 28.5 mg m⁻³ by 2028 due to growth in aquaculture, and its development should be carefully monitored. In future, we recommend that our predictions should be compared to observed changes in order to validate the model. We also illustrate that companies can greatly improve the carrying capacity of a system by improving the feed conversion ratio, the efficiency of nutrient uptake and the processing of mortalities.

KEY WORDS: Cage culture \cdot African lakes \cdot Oreochromis niloticus \cdot Crocodylus niloticus \cdot Phosphorus

1. INTRODUCTION

Aquaculture is one of the fastest-growing food production sectors, with an average annual growth of 5.8% from 2000 to 2016 (FAO 2018). Fish is one of the most important sources of animal protein in developing countries (FAO 2018). However, African countries currently account for only 2.5% of global aquaculture production, with the majority of production in Egypt (FAO 2018). There is great potential for aquaculture in African countries due to the avail-

ability of land and water, ideal temperatures, and availability of local crops for feed production (Genschick et al 2018). Overexploitation has led to the decline of many species in wild populations; aquaculture can provide commodities such as food and skins, and reduce negative impacts on wild populations. Furthermore, an increase in aquaculture can improve food and nutrition security and stimulate economic growth in developing countries. However, the development of an industry usually comes with environmental risks.

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Like other industries, such as fisheries, tourism and agriculture, aquaculture is heavily reliant on water. Water bodies are often a resource shared among countries, businesses and local inhabitants. As with any common resource, a lack of adequate management may ultimately lead to environmental, economic and social degradation (Ostrom et al. 1999). In order to ensure the sustainability of aquaculture and other water-based industries, it is therefore essential that the carrying capacity of utilised water bodies is considere.

This study aims to calculate an accurate estimate of the carrying capacity of aquaculture production in Lake Kariba, located in southern Africa on the border between Zambia and Zimbabwe. Lake Kariba is one of the largest man-made lakes in the world, covering an area of 5580 km² (Magadza 2006). It was created in 1958 with the construction of the Kariba dam, which was built to harness the Zambezi river for hydroelectric power (Balon & Coche 1974). The Kariba dam produces 1470 MW of energy, making it an important source of energy for the region (World Bank 2010). Apart from its main function as a source of hydroelectric power, the creation of the lake has allowed for the development of other sectors, including wild-catch fisheries, tourism and aquaculture, supporting many local residents (Maulu & Musuka 2018, Hasimuna et al. 2019). The greater part of aquaculture in Lake Kariba consists of Nile tilapia Oreochromis niloticus (Genschick et al. 2018), and to a lesser extent, Nile crocodile Crocodylus niloticus (Jenkins et al. 2004). C. niloticus skin exports make up about 15% of total worldwide crocodile skin exports, where Zambia and Zimbabwe contributed about half of the total worldwide C. niloticus skin exports between 2009 and 2016 (Caldwell 2018). There is scarce data on the size of individual crocodile farms, but in 2004, 5 out of 26 Zimbabwean crocodile farms and 6 out of 9 Zambian crocodile farms were situated along Lake Kariba (Jenkins et al. 2004). These farms generally use water from the lake for their crocodile pens and flush the nutrient-rich effluent back into the lake. Aquaculture fish production in Lake Kariba has increased tremendously in recent years. It has grown from, annually, 3500 t in Zimbabwe and 30 t in Zambia in the 1990s to an estimated annual yield of 10000 t in Zimbabwe and 13600 t in Zambia in 2014 (Genschick et al. 2018). Crocodile skin exports from Zambia and Zimbabwe increased annually, on average, by 11.7% in the period 2010-2016 (Caldwell 2018). Growth in both the tilapia and crocodile production provides job security for local residents and economic growth and

nutrition security for sub-Saharan Africa. However, unlimited growth in aquaculture could have a negative impact on the lake's ecosystem; nutrient outputs from aquaculture waste and faeces could cause eutrophic conditions. A reduction in water quality would impact water-dependent industries and the local population. This emphasises the need for an accurate estimate of the total allowable nutrient input, or carrying capacity, of Lake Kariba.

Lake Kariba is currently characterised as a mesotrophic lake according to Carlson's trophic state index (Carlson 1977), which is considered to be intermediate water quality. High algal population densities are widely assumed to be negatively correlated with water quality (especially dissolved oxygen conditions) and growth and survival of fish (Beveridge 1984). Since phosphorus (P) is the limiting factor for algal growth in most freshwater ecosystems (Beveridge 1984), various phosphate mass-balance models have been developed to estimate the carrying capacity of aquatic ecosystems. The most widely used and tested models are those of Dillon & Rigler (1975), OECD (1982) and Beveridge (2004), which are all modifications of Vollenweider's original model (Vollenweider 1976). The objective of this study was to estimate the carrying capacity of Lake Kariba using Beveridge's model for intensive cage aquaculture and assuming different cage aquaculture intensities in the lake, as the resulting information may be of great importance to the regulating bodies of Lake Kariba and its users.

The present study aimed to answer the following questions. (1) What is the sustainable aquaculture carrying capacity for Nile tilapia and Nile crocodile in Lake Kariba? (2) What is the sustainable aquaculture carrying capacity for Nile tilapia and Nile crocodile in Lake Kariba under expected future production scenarios? (3) How can P waste reduction measures, implemented by aquaculture companies, affect the carrying capacity of Lake Kariba?

2. MATERIALS AND METHODS

Lake Kariba (17° S, 28° E) is located between Zambia and Zimbabwe, with the border situated along the middle of the lake. It is divided into 4 basins, namely the Mlibizi, Binga, Sengwa and Sanyati basins, separated from each other by topographical features (Balon & Coche 1974) (Fig. 1). The main morphometrical parameters of the lake, at the normal operating water level of the Kariba dam, are summarised in Table 1.

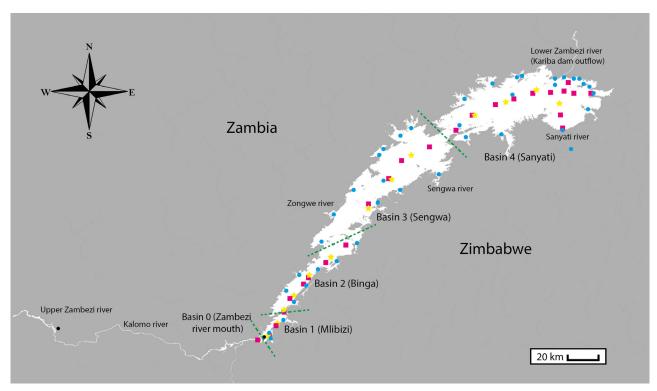


Fig. 1. Lake Kariba, its basins and most important rivers. Symbols indicate [total-P] sampling locations from the different studies. Sampling periods and studies are indicated by coloured symbols; magenta: 1964–1965, Coche (1968); yellow: 1987–1993, Magadza (2010); blue: 2008–2018, Zambezi River Authority (unpubl. data). Map tiles by Stamen Design, under CC BY 3.0.

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Table 1. Morphometry of Lake Kariba and its basins at normal operating water level (485 m), adapted from Balon & Coche (1974)

Basin	Name	Mean depth (m)	Area (km²)	Volume (km³)
0	Zambezi mouth	22.0	18	0.4
1	Mlibizi	12.6	91	1.1
2	Binga	24.0	644	16.3
3	Sengwa	26.5	2033	54.0
4	Sanyati	33.2	2563	85.1
Whole lake	Kariba	29.2	5364	157.0

2.1. Carrying capacity

The total allowable aquaculture production (carrying capacity) of Lake Kariba for Nile tilapia *Oreochromis niloticus* and Nile crocodile *Crocodylus niloticus* were estimated using the Beveridge phosphate balance model for intensive cage aquaculture (Beveridge 2004). A flow chart of the equations required to calculate the carrying capacity for one aquaculture species is depicted in Fig. 2, and all variables used in this study are summarised in

Table 2. To determine the carrying capacity of Lake Kariba, 2 main variables must be estimated: the permissible total-P load from aquaculture ($L_{\rm aq}$, kg P yr⁻¹) and the loss of P into the environment from the aquaculture species under consideration ($P_{\rm env}$, kg P t fish⁻¹) (Eq. 1 in Fig. 2).

2.2. P_{env}

 $P_{\rm env}$ can be calculated from the P content in feed ($P_{\rm feed}$, kg P kg feed⁻¹), the feed conversion ratio (FCR), and the amount of P accumulated in fish (here, tilapia and crocodile, see Table 2) production ($P_{\rm fish}$, kg P kg fish⁻¹) (Fig. 2, Eq. 2). Data on $P_{\rm feed}$ was supplied by the major fish feed producers in the Lake Kariba area. The weighted mean of $P_{\rm feed}$ for tilapia in Lake Kariba was estimated based on the relative proportions of feed types produced (Table 3). The FCR for tilapia was calculated using production data from the major tilapia farms in Lake Kariba (Table 4), using Eq. 2.1; for crocodile, it was taken directly from the literature (Beyeler 2011). $P_{\rm fish}$ is the proportion of P in the total wet weight of the species at harvest and was calculated from Hoffman et al. (2000).

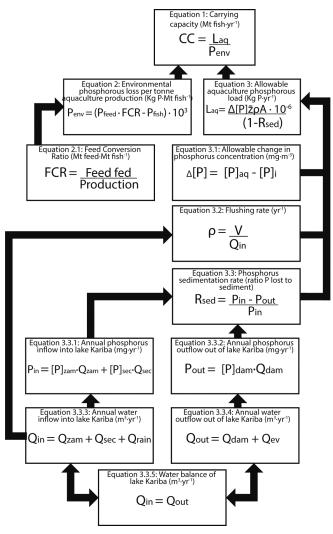


Fig. 2. Flow chart of equations used in this study in order to calculate the carrying capacity of Lake Kariba. See Table 2 for a description of all variables used in these equations

2.3. Allowable P load (L_{aq})

The total allowable P load (L_{aq}) is a measure of the total amount of P that may enter the model system (in mg m⁻² yr⁻¹). It is calculated using the allowable change in total-P concentration in the lake water ($\Delta[P]$, mg m⁻³), the mean lake depth (\overline{z}, m) , the flushing rate of the lake (ρ, yr^{-1}) , the area of the lake (A, m^2) and the P-sedimentation rate $(R_{sed}, unitless)$ (Fig. 2, Eq. 3).

 $\Delta[P]$ depends on the initial total-P concentration in the lake prior to exploitation ([P]_i, mg m⁻³) and maximum allowable total-P concentration in the lake water ([P]_{aq}, mg m⁻³) after aquaculture exploitation (Fig. 2, Eq. 3.1). [P]_{aq} depends on the desired function of the lake and was determined using several allowable total-P concentrations proposed by Beveridge (1984)

for different lake functions (Fig. 3). For the purposes of this study, we chose a $[P]_{aq}$ value of 30 mg m⁻³, which is safely within the optimal range for warmwater fisheries and intensive cage aquaculture.

[P], was determined from historical data of the mean total-P concentration of surface waters in Lake Kariba from 3 lake surveys in 1964, 1990, and 2018 (Coche 1968, Magadza 2010; Zambezi River Authority unpubl. data). Sample locations are depicted in Fig. 1. The model works with the mean total-P concentration of the whole lake in order to cover the state of the lake as a whole. The mean total-P concentration was calculated separately for each basin in each sampled year. In order to test the assumption of spatial homogeneity, a repeated-measures ANOVA was carried out; this reveals any significant differences between the total-P concentrations of the basins (Text S1 in the Supplement at www.int-res.com/ articles/suppl/q014p113_supp.pdf). Furthermore, in order to test the assumption that the total-P concentration of Lake Kariba is temporally stable, the weighted mean total-P concentration was calculated for the whole lake (Table S1, Text S1). This calculation was based on basin volume for the years in which sampling was carried out. An ANOVA was carried out to test whether there were significant differences in the total-P concentration of Lake Kariba between the years (see Texts S2 & S3 for more information on temporal variation). [P], was calculated as the average total-P concentration of the weighted mean total-P concentrations in all years.

 ρ was calculated from the total inflow ($Q_{\rm in},\,m^3$ yr $^{-1}$) and lake volume (V, m^3) (Fig. 2, Eq. 3.2). $Q_{\rm in}$ was determined using a water flow balance model of Lake Kariba (see Text S4 for more information on the water balance model).

 $R_{\rm sed}$ is a measure of the ratio of the P load to the system that is lost to the sediment. The model assumes that the sedimentation rate is the only significant form of P loss in the system. The sedimentation rate is therefore the same as the retention rate of the system, which is the fraction of inflowing P load that is retained in the system. We calculated $R_{\rm sed}$ using the annual average total-P load into Lake Kariba ($P_{\rm in}$, mg yr⁻¹) and the annual average P load leaving the lake ($P_{\rm out}$, mg yr⁻¹) (Fig. 2, Eq. 3.3) (see Text S5 for more information).

Since P mainly enters and exits the lake system through river flows, P_{in} and P_{out} could be estimated using flow rates and total-P concentrations of in- and outflowing rivers. The Zambezi River is Lake Kariba's main water supply, accounting for at least 75% of the total inflow into the lake (Balon & Coche 1974, Du Toit 1982, World Bank 2010), the rest of the inflow is

Table 2. List of all variables used in the main carrying capacity estimate, their values, the equations they are used in and their sources.

Variables with empty cells were calculated using other variables

Variable	Symbol	Value	Unit	Calculated from	Used in	Sources
Carrying capacity with no aquaculture	CC _{Tilapia} CC _{croc}	86 868 13 054	t fish yr ⁻¹	Eq. (1)		
Environmental P loss	P _{env, Tilapia} P _{env, Croc}	13.9 92.5	kg P t fish ⁻¹	Eq. (2)	Eq. (1)	Table 5
Allowable aquaculture P loading	L_{aq}	1.21×10^{6}	$kg P yr^{-1}$	Eq. (3)	Eq. (1)	Table 7
Feed conversion ratio of aquaculture species	$FCR_{Tilapia}$ FCR_{Croc}	1.66 4.50	t feed t fish ⁻¹	Eq. (2.1)	Eq. (2)	Tables 4 & 5
Ratio P in feed	$ m P_{feed} \ P_{feed}$	0.012 0.021	kg P kg feed ⁻¹		Eq. (2)	Tables 3 & 5
Ratio P in aquaculture species	${ m P_{fish,\ Tilapia}} \ { m P_{fish,\ Croc}}$	0.006 0.002	kg P kg fish ⁻¹		Eq. (2)	Table 5
Total annual feed fed tilapia	Feed fed	29 500	t		Eq. (2.1)	Table 4
Total annual tilapia production	Production	17 800	t		Eq. (2.1)	Table 4
Allowable change in total-P concentration	$\Delta[\mathrm{P}]$	5.3	${ m mg~m^{-3}}$	Eq. (3.1)	Eq. (3)	
Mean lake depth	\overline{Z}	29.2	m	1 , ,	Eq. (3)	Balon & Coche (1974)
Flushing rate	ρ	0.32	yr^{-1}	Eq. (3.2)	Eq. (3)	
Lake area	Å	5.36×10^9	m^2	1 \ /	Eqs. (3) & (3.2)	Balon & Coche (1974)
P sedimentation rate	R_{sed}	0.78	unitless	Eq. (3.3)	Eq. (3)	Table 6
Initial total-P conc. before aquaculture	$[P]_{i}$	24.7	$mg m^{-3}$	1 (/	Eq. (3.1)	Table S1
Allowable total-P conc. with aquaculture	[P] _{aq}	30	$mg m^{-3}$		Eq. (3.1)	Beveridge (1984)
Total lake volume	V	0.157×10^{12}	m^3		Eq. (3.2)	Balon & Coche (1974)
Total annual water inflow	Q_{in}	49.7×10^9	$\mathrm{m^3~yr^{-1}}$	Eqs. (3.3.3) & (3.3.5)	Eq. (3.2)	Table S4
Total annual P inflow	P_{in}	4.65×10^{12}	$mg yr^{-1}$	Eq. (3.3.1)	Eq. (3.3)	
Total annual P outflow	P _{out}	1.03×10^{12}	$mq vr^{-1}$	Eq. (3.3.2)	Eq. (3.3)	
Mean total-P conc. of upper Zambezi river	[P] _{zam}	106	$mg m^{-3}$	1 ()	Eq. (3.3.1)	Table S2
Mean total-P conc. of secondary rivers	[P] _{sec}	79	$mg m^{-3}$		Eq. (3.3.1)	Table S2
Total annual water flow upper Zambezi river	Q_{zam}	38.4×10^9	$m^{3} yr^{-1}$		Eqs. (3.3.1) & (3.3.3)	Table S2
Total annual water flow of secondary rivers	Q_{sec}	7.30×10^{9}	$\mathrm{m^3~yr^{-1}}$		Eqs. (3.3.1) & (3.3.3)	Table S2
Mean total-P conc. of Kariba dam outflow (lower Zambezi)	$[P]_{dam}$	24	${\rm mg~m^{-3}}$		Eq. (3.3.2)	Table S2
Total annual water outflow of Kariba dam (lower Zambezi)	$\mathrm{Q}_{\mathrm{dam}}$	42.8×10^9	$m^3 yr^{-1}$		Eqs. (3.3.2) & (3.3.4)	Table S4
Total annual rainfall at Lake Kariba	Q_{rain}	4.00×10^{9}	$\mathrm{m^3~yr^{-1}}$		Eq. (3.3.3)	Table S4
Total annual water outflow	Q _{out}	49.7×10^9	$m^3 \text{ yr}^{-1}$	Eq. (3.3.4)	Eq. (3.3.5)	Table S4
Total annual evaporation out of Lake Kariba	$\overline{Q}_{\mathrm{ev}}$	6.90×10^9	$m^3 \text{ yr}^{-1}$	1. ()	Eq. (3.3.4)	Table S4

via smaller rivers. In- and outflow of Lake Kariba $(Q_{in} \& Q_{out}, m^3 \ yr^{-1})$ is therefore subdivided into 3 main flows: Zambezi River inflow $(Q_{Zam}, m^3 \ yr^{-1})$, secondary river inflows $(Q_{sec}, m^3 \ yr^{-1})$, and the outflow regulated by the Kariba dam $(Q_{dam}, m^3 \ yr^{-1})$. P loads from the main flows were thus calculated using mean annual flow rates $(Q_{zam}, Q_{sec}, Q_{dam})$ and mean total-P concentrations ($[P]_{zam}, [P]_{sec}, [P]_{dam}, mg \ m^{-3}$) (Fig. 2, Eqs. 3.3.1 & 3.3.2) (see Text S5 for more information on the sedimentation rate).

The total-P concentration of the Zambezi River inflow ($[P]_{zam}$, mg m⁻³) was taken from historical data of the mean total-P concentration as the river enters

Lake Kariba reported in 3 lake surveys from 1964, 1990, and 2018 (Coche 1968, Magadza 2010, Zambezi River Authority unpubl. data). [P]_{dam}was determined from monthly sampling data from the Sanyati basin, close to the Kariba dam, between 2006 and 2017 (Zambezi River Authority unpubl. data). [P]_{sec} was determined using data from the Sanyati river, as well as the mean total-P concentration of 8 other rivers with unknown flow rates (Balon & Coche 1974, Zambezi River Authority unpubl. data). If a river was sampled more than once, a mean total-P concentration was calculated for each year. Since the Sanyati river accounts for about 80% of secondary river

Table 3. P content of tilapia feeds supplied to Yalelo and Lake Harvest Group farms at Lake Kariba

Feed type	Proportion of to	
	feed used	content (P _{feed})
Aller Aqua feeds		
3–5 mm cage & pond feed	d 0.865 ^a	$0.012^{\rm b}$
Other feed	0.135^{a}	$0.014^{\rm b}$
Lake Harvest Pro feeds		
Tilapia grower pellets		0.0099^{c}
Tilapia grower pellets		0.0096^{c}
Tilapia starter mixed MC	R	0.015^{c}
Skretting feed		
Standard feed		$0.009^{\rm d}$
Combined		
Yalelo weighted mean	0.48^{a}	0.012
Lake Harvest mean	0.52	0.011
Lake Kariba weighted me	ean	0.012

Harvest Group (unpubl. data); dSkretting (unpubl. data)

Table 4. Tilapia feed use, production, and the resulting feed conversion ratio (FCR) of farms in Lake Kariba belonging to Yalelo and the Lake Harvest Group in 2018

Variable	Lake Harvest Group	Yalelo	Total
Feed fed (t) Tilapia production (t) FCR	16 000	13 500	19 500
	8800	9000	17 800
	1.82	1.50	1.66

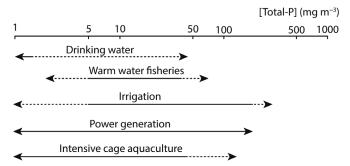


Fig. 3. Optimal (solid line) and allowable (dashed line) total-P concentration ranges for several lake functions, adapted from Beveridge (1984)

inflow, [P]sec was calculated as the weighted mean total-P concentration of the Sanyati river (weight 0.8) and other rivers (weight 0.2) (World Bank 2010).

The river flow rates were determined by taking the mean of all sources used. Missing flow rates could be calculated using a water balance model of Lake Kariba, where $Q_{in} = Q_{out}$ (Fig. 2, Eqs. 3.3.5, 3.3.3 & 3.3.4).

2.4. Aquaculture production scenarios

We estimated the carrying capacity under 3 aquaculture production scenarios: carrying capacity with no aquaculture (CC, t fish yr⁻¹) and the remaining allowable aquaculture production (CC_{rem}, t fish yr⁻¹) under current (2018) and future (2028) aquaculture production scenarios. Furthermore, we used the model to estimate how the total-P concentration of Lake Kariba has changed since aquaculture began and to predict how it will change in the future. We also calculated the carrying capacity for a wide range of allowable total-P concentrations in order to show how this affects the aquaculture carrying capacity of Lake Kariba.

CC_{rem} in 2018 for both aquaculture species in Lake Kariba was calculated from the current total aquaculture P load (Ltot, kg P yr-1), the total allowable aquaculture P load (Lag.), and the environmental P loss for each species (P_{env}) using Eq. (4) (Eqs. 1–3 are shown in Fig. 2):

$$CC_{rem} = \frac{L_{aq} - L_{tot}}{P_{env}}$$
 (4)

 L_{tot} into Lake Kariba was calculated using P_{env} and the total annual aquaculture production (Y, t yr⁻¹) of tilapia and crocodile:

$$L_{tot} = Y_{Tilapia} \times P_{(env,Tilapia)} + Y_{Croc} \times P_{(env,Croc)}$$
 (5)

These calculations were made using estimated and predicted aquaculture production in Lake Kariba in the period 1990-2028.

Total tilapia production in Lake Kariba (Ytilapia, t yr⁻¹) in 2018 was estimated using production data from the 3 largest tilapia farms: Lake Harvest Zambia, Lake Harvest Zimbabwe and Yalelo (Lake Harvest Group unpubl. data, Yalelo unpubl. data). An estimate of the total aquaculture production of smallscale tilapia farms was made by multiplying the total feed sold by the feed companies in the region, Skretting and Aller Aqua, to smaller Lake Kariba farms (Aller Aqua Zambia unpubl. data, Skretting Zambia unpubl. data), with an assumed FCR of 1.7.

Total (Zambian and Zimbabwean) crocodile production between 2003 and 2016 in farms in Lake Kariba (Y_{crocodile}, t yr⁻¹) was estimated from historical data on crocodile skin exports (Jenkins et al. 2004, Tosun 2013, Caldwell 2018); the average annual skin production (skins farm⁻¹ yr⁻¹) was multiplied by the total number of farms and the average body weight of animals skinned $(3.5 \times 10^{-3} \text{ t})$ (Davis 2001, Jenkins et al. 2004, Tosun 2013, Caldwell 2018). Production in 2018 and 2028 was extrapolated using the annual average growth rate in skin production for the period 2003 to 2016.

We predicted CC_{rem} of tilapia and crocodile farms in 2028 according to the same method used for 2018, where L_{tot} is the predicted aquaculture P load in 2028. L_{tot} was calculated from predicted $Y_{tilapia}$ and $Y_{crocodile}$ in 2028, estimated by reviewing expansion plans for the main tilapia farms in Lake Kariba (Zamgreen Aquaculture 2019, Lake Harvest Group unpubl. data, Yalelo unpubl. data).

Based on the estimated P load, we estimated how the total-P concentration of Lake Kariba has changed since the commencement of aquaculture in Lake Kariba and predicted how it will change in the future. These calculations were made based on the observed and predicted values for total-P load from aquaculture. To calculate the expected change in total-P concentration, $L_{\rm aq}$ was replaced by $L_{\rm tot}$ in Eq. 3:

$$CC_{rem} = \frac{L_{aq} - L_{tot}}{P_{env}}$$
 (6)

The resulting expected total-P concentration in Lake Kariba was calculated by adding $\Delta[P]$ to $[P]_i$. This was done for all estimated and predicted values of aquaculture P load during the period 1990–2028.

For this study, we proposed a maximum allowable total-P concentration of 30 mg m⁻³, based on values proposed by Beveridge (Fig. 3). But we also illustrate the carrying capacity for different scenarios of the allowable total-P concentration. We therefore calculated the carrying capacity of Lake Kariba for different values of [P]_{aq}, ranging from the current total-P concentration of the lake ([P]_i) to 80 mg m⁻³, which is the maximum allowable (but suboptimal) total-P concentration for freshwater fisheries (Fig. 3).

2.5. Waste-reduction scenarios

In order to investigate the effects of P waste-reduction measures by aquaculture companies, we calculated the crocodile carrying capacity in Lake Kariba under several waste-reduction scenarios based on improved FCR, uptake efficiency, and mortality processing.

Improving FCR is desirable because less food is required for the same amount of harvest. This may also reduce $P_{\rm env}$, thereby increasing carrying capacity. We predicted carrying capacity based on FCR scenarios ranging between 2 and 1. These scenarios were determined using information from global trends in FCR values and the potential FCR values provided by Lake Kariba aquaculture companies.

P has the lowest average digestibility of all major nutrients in tilapia feed (only 54 %) (Montanhini Neto

& Ostrensky 2015). Plant-based fish diets contain phytase-bound P, which fish cannot take up. It has been shown that adding phytase supplements to plant-based feed can increase dietary P uptake efficiency in fish, reducing P excretion of tilapia by 30 % (Nwanna & Olusola 2014). We therefore estimated how a reduction in P excretion by 30 %, due to phytase supplementation, could affect the carrying capacity of tilapia production in Lake Kariba. This was done by multiplying tilapia $P_{\rm env}$ by a factor of 0.7, before estimating the carrying capacity.

A certain percentage of mortalities is normal in aquaculture. If disposed of correctly, the P content in the mortalities does not end up in the lake. However, the calculation of $P_{\rm env}$ does not take into account mortalities that are removed from the cages and processed on land, whilst these mortalities are included in the calculation of the FCR. If we assume all mortalities are disposed of correctly, we could alter Eq. (4.1) to include the P content of mortalities per tonne of fish production:

$$P_{\text{env}} = P_{\text{food}} \times FCR - \left(\frac{P_{\text{fish}}}{1 - R_{\text{mortalities}}}\right)$$
 (7)

The mortality rate ($R_{mortalities}$, unitless) is calculated as follows:

$$R_{\text{mortalities}} = \frac{M + H}{M} \tag{8}$$

where M is the total annual processed mortalities (kg yr⁻¹) and H is total harvest (kg yr⁻¹). M and H were estimated from production data made available by the major tilapia farms in Lake Kariba.

2.6. Model calculation

All model parameter values and their descriptions can be found in Table 2. The sources, values and steps used in the model calculations for P_{env} for tilapia and crocodile are summarised in Tables 3–5. The sources and values used in the model calculations for L_{aq} are summarised in Table 6 and Tables S1–S4. Consult Texts S1–S9 for more in-depth information on model assumption testing and implications of uncertainty in the model estimation.

3. RESULTS

If the total-P concentration of Lake Kariba is allowed to increase to $30~\text{mg m}^{-3}$, the maximum per-

Table 5. Estimation of the environmental P loss ($P_{\rm env}$) in Lake Kariba for tilapia and crocodile culture

Variable	Tilapia	Crocodile
Feed P content, P _{feed} (kg P kg feed ⁻¹) Body P content, P _{fish} (kg P kg fish ⁻¹) Feed conversion ratio, FCR (kg feed kg fish ⁻¹) P lost to environment, P _{env} (kg P t fish ⁻¹)	0.012 0.006 ^b 1.66 13.92	0.021^{a} 0.002^{c} 4.5^{d} 92.5

^aSkretting (unpubl. data); ^bMean calculated from Beveridge (2004), Dantas & Attayde (2007), and Montanhini Neto & Ostrensky (2015); ^cCalculated from Hoffman et al. (2000); ^dCalculated from Beyeler (2011)

Table 6. Calculation of the sedimentation rate (R_{sed}) from annual total-P fluxes in Lake Kariba (P_{zam} , P_{sec} , P_{out})

Flow	Mean flow rates, Q (m ³ yr ⁻¹)	Mean [total-P] (mg m ⁻³)	Annual total-P flux (mg yr ⁻¹)
Zambezi River	38.4×10^{9}	106	4.07×10^{12}
Secondary rivers	7.30×10^9	79	0.577×10^{12}
Kariba dam outflow	42.8×10^9	24	1.03×10^{12}
R_{sed}			0.78

Table 7. Estimation of the total allowable aquaculture P load $(L_{\rm aq})$ into Lake Kariba

Variable	Value
Allowable change in [total-P], ΔP (mg m ⁻³)	5.3
Mean lake depth, \overline{z} (m)	29.2
Flushing rate, ρ (yr ⁻¹)	0.32
Lake area, A (m ²)	$5.36 \ 10^9$
P sedimentation rate, R _{sed}	0.78
L _{aq} (kg P yr ⁻¹)	1.21×10^{6}

missible P load from aquaculture farms in Lake Kariba (L_{aq}) would be 1.2×10^6 kg P yr $^{-1}$ (Table 7). The average environmental P loss (P_{env}) from aquaculture farms in Lake Kariba is 13.92 kg P t $^{-1}$ Nile tilapia *Oreochromis niloticus* production, and 92.5 kg P t $^{-1}$ Nile crocodile *Crocodylus niloticus* production. The total sustainable aquaculture carrying capacity of Lake Kariba could therefore be estimated as 86 900 t yr $^{-1}$ for tilapia and 13 000 t yr $^{-1}$ for crocodile.

3.1. Aquaculture production developments in Lake Kariba

Since the initiation of tilapia culture in Lake Kariba in 1996, total tilapia production at the 3 largest farms $(Y_{tilapia})$ has grown to $16\,300\,t\,yr^{-1}$ in 2018 (Lake Harvest Zimbabwe, Lake Harvest Zambia and Yalelo).

The total estimated production of smallscale farms in the lake constitutes only 69 t yr⁻¹. The annual percentage growth rate (APR) of tilapia culture in Lake Kariba, between 2010 and 2018, was as high as 27%. We expect tilapia production to increase to 53 000 t yr⁻¹ by 2028 based on the growth plans of the largest farms (Fig. 4) as well as plans for a new 10000 t yr⁻¹ tilapia farm (Zamgreen Aquaculture 2019). These growth plans correspond with an APR of 12.4% between 2018 and 2028. The estimated total production of crocodile farms $(Y_{crocodile})$ in Lake Kariba has grown from 13 t yr⁻¹ in 1990 to a 343 t yr⁻¹ in 2016. By extrapolating crocodile production using the average APRs between 2010 and 2016 (11.7%), we would expect a total crocodile production of about 1300 t yr⁻¹ by 2028 (Fig. 4).

3.2. Remaining carrying capacity under current and future production scenarios

The current total aquaculture P load (L_{tot}) in Lake Kariba is estimated at around 268 000 kg P yr⁻¹ (Fig. 5). Tilapia production is the main source of P, accounting for 85.2% of the total load. This allows for an increase in P load from aquaculture to up to 932 000 kg P yr⁻¹ before the total allowable production in Lake Kariba is reached. The difference between current and potential sustainable aquaculture production (remaining carrying capacity of the lake, CC_{rem}) can therefore be calculated as 67 000 t yr⁻¹ for tilapia and 10 000 t yr⁻¹ for crocodile. Furthermore, under current growth expectations, Ltot would be 857 000 kg P yr⁻¹ by 2028, which would account for 71% of the total allowable P load (L_{ag}) (Fig. 5). The remaining allowable growth in P load would then be around 343 000 kg P yr⁻¹. Therefore, in 2028, the difference between the actual and future potential aquaculture production (CC_{rem}) would be approx. $25\,000\ t\ yr^{-1}$ for tilapia and $3700\ t\ yr^{-1}$ for crocodile.

3.3. Predicted change in total-P concentration in Lake Kariba

Since aquaculture first started in Lake Kariba in 1997, the total-P concentration has increased from

24.7 mg m⁻³ ($[P]_i$) to 25.9 mg m⁻³ in 2018, due to the aquaculture P load. We predict a further increase to a total-P concentration of 28.5 mg m⁻³ in 2028 as a result of further growth in aquaculture (Fig. 6).

3.4. Allowable total-P concentration scenarios

The carrying capacity of tilapia and crocodile greatly depends on the value chosen for the allowable total-P concentration ($[P]_{aq}$). We chose a $[P]_{aq}$ value that is situated safely within the optimum total-P concentrations for power generation, irrigation, warmwater fisheries, and cage aquaculture, as well as within the allowable range for drinking water (Fig. 7). The current total-P concentration in Lake Kariba, 24.7 mg m⁻³, is already above the optimum for drinking water, but still below the allowable upper limit of 45 mg m^{-3} . The optimal range for warm-water fisheries has an upper limit of 40 mg m⁻³, which corresponds to a carrying capacity of 250 000 t yr⁻¹ for tilapia and 380 00 t yr⁻¹ for crocodile. The optimal range for cage aquaculture and drinking water (allowable range) have an upper limit of 50 mg m^{-3} , which corresponds to a carrying capacity of 414 000 t yr⁻¹ for tilapia and 62 000 t yr⁻¹ for crocodile.

3.5. Aquaculture waste-reduction scenarios

If aquaculture feed suppliers for Lake Kariba were to include phytase supplements in their feeds, P excretion could be reduced by up to 30 %. This is based on the assumption that feed suppliers use proportionally less P in these supplemented diets. As a consequence, tilapia culture $P_{\rm env}$ in Lake Kariba could decline to 10.08 kg P t⁻¹ tilapia production. In turn, the carrying capacity of tilapia would increase from 86 900 to 119 800 t yr⁻¹.

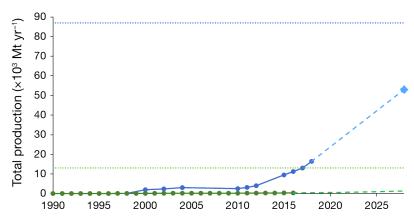


Fig. 4. Developments of tilapia (blue) and crocodile (green) aquaculture production in Lake Kariba. Solid lines indicate estimated total production as calculated from historical data, dashed lines indicate predicted total production based on growth expectations, dotted horizontal lines: total sustainable carrying capacity

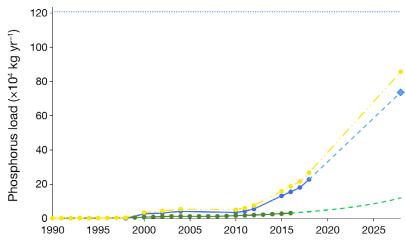


Fig. 5. Developments of total aquaculture P load (L_{tot}) (yellow) and P load from tilapia (blue) and crocodile (green) farms in Lake Kariba. For tilapia and crocodile, solid lines indicate estimated P load as calculated from historical production data, and dashed lines indicate predicted P load based on growth expectations. The total allowable P load in lake Kariba is indicated with the dotted horizontal blue line

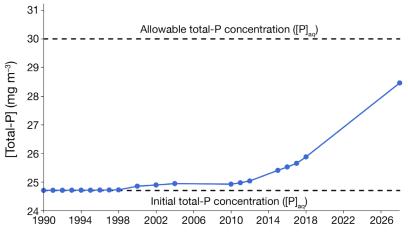


Fig. 6. Predicted changes in total-P concentrations in Lake Kariba, based on historical and predicted P loads from aquaculture. Dashed lines indicate the initial ($[P]_i$) and allowable ($[P]_{aq}$) total-P concentration

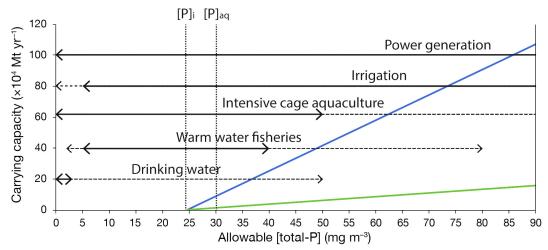


Fig. 7. The carrying capacity of tilapia (blue solid line) and crocodile (green solid line) for different values of the allowable total-P concentration ($[P]_{aq}$). Dotted lines indicate the initial total-P concentration of the lake ($[P]_i$) and our proposed value for the allowable total-P concentration ($[P]_{aq}$). Arrows indicate the optimal (solid lines), and allowable (dashed lines) total-P concentration ranges for several lake functions

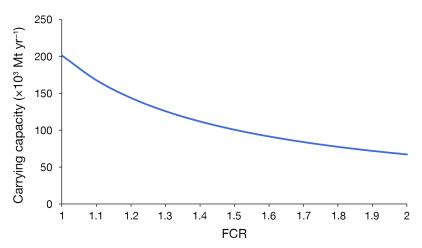


Fig. 8. Carrying capacity of tilapia in Lake Kariba for a range of feed conversion ratios (FCRs)

Currently, the FCR of tilapia in farms at Lake Kariba is 1.66 kg feed kg fish⁻¹ (weighted mean) (Table 3). The carrying capacity is greatly dependent on the FCR of a farm. An FCR of 1.5 (Yalelo) corresponds to a carrying capacity of 100 600 t yr⁻¹, while an FCR of 1.82 (Lake Harvest Zimbabwe) corresponds to a carrying capacity of 76 200 t yr⁻¹ (Fig. 8). Furthermore, if farms in Lake Kariba were able to improve the lake-wide mean FCR down to 1.3, the carrying capacity would increase to 125 800 t yr⁻¹. If the FCR further decreased to 1.0, this would more than double the carrying capacity to 201 200 t yr⁻¹.

In 2018, the mortality rate at Yalelo was 0.075 and in the years 2016–2018, the mortality rate at Lake Harvest Zimbabwe was, on average, 0.065 (Lake Harvest Group unpubl. data, Yalelo unpubl.

data). Therefore, if the mortalities are disposed of correctly, $P_{\rm env}$ for tilapia farming in Lake Kariba could be reduced from 13.9 to 13.4 kg P t⁻¹ fish. This would allow for a 3000 t yr⁻¹ increase in the total carrying capacity for tilapia aquaculture in Lake Kariba.

4. DISCUSSION

We estimated a total aquaculture carrying capacity for Nile tilapia *Oreochromis niloticus* of 87 000 t yr⁻¹, which is more than double that found by Mhlanga et al. (2013) (33 000 t yr⁻¹).

However, Mhlanga et al. (2013) make several incorrect assumptions and calculations in their model (see Text S10 and Table S5). Our estimation, therefore, provides the best current estimate of the carrying capacity of Lake Kariba. Furthermore, to our knowledge, this study is the first to calculate the carrying capacity of Nile crocodile Crocodylus niloticus in a lake system. Crocodile production accounted for a significant proportion (14.8%) of the total aquaculture P load in 2018, whilst only accounting for 2.5% of the total aquaculture production in Lake Kariba. This underscores the importance of evaluating multiple species when estimating aquaculture carrying capacity. This is especially true for species that have a high environmental P loss such as crocodile (Peny = 92.5 kg P t^{-1}).

Our predictions indicate that aquaculture production in Lake Kariba will not have exceeded its carrying capacity by 2028. In 2028 it is forecast that 71% of total allowable aquaculture P load will be reached. The growth plans for tilapia farms in Lake Kariba are in line with annual growth rates seen in the rest of sub-Saharan Africa over the past decades (FAO 2018). However, if aquaculture growth were to continue at the current rate, the carrying capacity would rapidly be surpassed after 2028. Therefore, growth plans for aquaculture farms in Lake Kariba in the short term seem acceptable, but long-term growth needs to be considered with caution.

Model predictions can provide a strong basis for management decisions on aquaculture growth in Lake Kariba; however, there is always some uncertainty, and scientific models have their limitations. See Texts S1-S9 and Figs. S2-S4, S6, & S8 for a more in-depth discussion of model assumptions and uncertainty of the parameters. Due to the large growth in aguaculture production in Lake Kariba, developments in total-P concentration should be carefully monitored. Validation and timely adjustment of the model estimate can only be achieved through longterm monitoring. Due to its relative simplicity, the Beveridge model provides an excellent tool for determining the carrying capacity of a system such as Lake Kariba, but monitoring is key to its effectiveness. The model estimations can be validated by checking whether total-P concentration develops as predicted in Fig. 6. It should be noted that there would be a response time of approximately 3 yr (OECD 1982) for a lake with the depth and water residence time of Lake Kariba before changes in P load are reflected in the total-P concentration. If the total-P concentration of Lake Kariba does not develop as in Fig. 6 (with the 3 yr response time taken into account), management decisions should be altered accordingly.

Currently, no rules or regulations on the allowable total-P concentration limits have been established by the governments of Zambia or Zimbabwe. In our current best estimate of the tilapia carrying capacity of Lake Kariba, the total allowable P-concentration was set at 30 mg m⁻³, which lies safely within the optimal and allowable range for several lake functions (Beveridge 1984). In Brazil, which has tropical environmental conditions similar to Zambia and Zimbabwe, government limits of allowable total-P concentration in lakes are also set at 30 mg m⁻³ (Asmah et al. 2016). Higher values for allowable total-P concentration in Lake Kariba would drastically increase the potential production capacity in the lake (Fig. 3), but would increase the impact of aquaculture on the lake ecosys-

tem. Furthermore, higher values for total-P concentration could make the system less resilient to changes from other sources of P load. The maximum allowable total-P concentration ($[P]_{aq}$) in Lake Kariba should be decided upon by weighing the importance of different lake functions and the effect it could have on them.

The P contents of tilapia feeds used in Lake Kariba are in line with tilapia feeds used in other tropical lakes worldwide (Montanhini Neto & Ostrensky 2015, Asmah et al. 2016). Similarly, the FCR of Lake Kariba farms is close to the global average for tilapia aquaculture (Tacon & Metian 2008). As a result, the average P waste per tonne tilapia production (Peny) in Lake Kariba is similar to that found in other tropical lakes (Montanhini Neto & Ostrensky 2015). However, our calculations of the carrying capacity of Lake Kariba, based on several waste reduction scenarios, show that there is still room for improvement. Based on global trends (Tacon & Metian 2008) and the FCR currently achieved by Yalelo (Yalelo unpubl. data), it should be possible for fish farms in Lake Kariba to achieve a mean FCR of 1.4, or even 1.3, in the near future. This would greatly increase the carrying capacity of the lake as well as the profitability of the farms themselves (Fig. 8). P_{env} can also be improved if mortalities in aquaculture are disposed of correctly. Furthermore, addition of phytase to fish feeds could increase P uptake efficiency, resulting in a lower Penv, allowing a 30% reduction in dietary P content.

Although improvements in feed quality and farm efficiency can reduce nutrient load and thus increase the carrying capacity, there will be a limit beyond which further improvements are impossible. This is why floating closed containment aquaculture systems may come to play an important role in the aquaculture industry in the future. The closed systems collect and process metabolic waste from the fish, significantly reducing nutrient load. These systems are still under development and it may take some time before they become economically feasible for tilapia farming, but they could eventually be the answer to the limited aquaculture production capacity of freshwater lakes.

Due to a limited availability of data, the total production of crocodile in Lake Kariba and values of FCR, P content of the feed, and carcass P content are largely uncertain. Furthermore, most crocodiles in Lake Kariba are farmed in pens and use Lake Kariba as a water supply, while expelling their effluent wastewater back into the lake. Due to the private nature of crocodile farmers, we were unable to make on-site measurements for effluent P load, and we therefore had to estimate this based on a cage aqua-

culture P balance model (Beveridge 1984). The cage aquaculture model assumes that P waste goes directly into the environment, but effluent treatment can be applied in pen culture. Any P that is removed through effluent treatment reduces the P load to the lake, thus increasing the carrying capacity. Therefore, our estimate of the P load from crocodile farms in Lake Kariba is likely an overestimation. The estimate for crocodile farm P load could be greatly improved if farmers shared their production data (including total feed fed and feed types used) and if total-P concentrations and flow rates could be measured directly from the effluent flows.

We estimated that there is no difference in the carrying capacity when considering separate lake basins, because this is compensated for by an increased flushing rate in smaller-sized basins (Text S2). Nevertheless, due to spatial heterogeneity of flow rates, very densely packed farm sites may exceed the local carrying capacity. The carrying capacity could also be determined separately for farm sites using flow rate measurements to determine the flushing rate and sedimentation rates (David et al. 2015). Furthermore, monitoring the development of total-P concentrations locally at farm sites can provide aquaculture companies and public authorities with forewarnings for local harmful algal blooms.

Sedimentation rate is one of the most important parameters of the model, due to its sensitivity, and the hardest to estimate correctly (Beveridge 2004). When we vary the sedimentation rate, this greatly affects the model outcome (Text S3, Fig. S4). We were able to calculate the sedimentation rate (0.78) using total-P fluxes from in- and outflows. However, a similar sedimentation rate of 0.74 can be calculated based on lake flushing rate (ρ) as follows (from Beveridge 2004):

$$R_{\text{sed}} = \frac{1}{1 + 0.614 \,\rho^{0.491}} \tag{9}$$

In an earlier study, Kunz et al. (2011) estimated a total-P sedimentation rate in Lake Kariba of 0.87 using sediment traps (range: 0.86 – 0.97). This value is significantly higher than what we found from our calculations and would almost double the allowable P load to the lake. Furthermore, there is some uncertainty in the total-P concentrations of in- and outflows of Lake Kariba (Text S3). In order to gain more certainty of the sedimentation rate, total-P concentrations should be monitored at in- and outflows of the lake (e.g. at the Zambezi River inflow and as close to the dam wall as possible, or directly from the water stream that flows through the dam wall).

5. CONCLUSIONS

Based on our calculations, we advise setting the aquaculture production limit in Lake Kariba to a combined maximum P load of 1.2×10^6 kg P yr $^{-1}$. It is in the best interests of both governmental organisations and aquaculture businesses in Zambia and Zimbabwe to collaborate in order to prevent the eutrophication of Lake Kariba. The P load and total-P concentration in Lake Kariba should be monitored on a long-term basis. This is particularly important in the Sanyati basin, where total-P concentration should be measured regularly. We should determine the effects of rapid aquaculture growth and validate our model estimates. Management decisions can then be altered accordingly.

Currently, P load in Zambia is only monitored according to the maximum permissible limit of reactive P in effluent streams, which is currently set at 1 mg l⁻¹ (ZEMA 2013); however, the concentration of reactive P says little about the total-P load in the effluent stream, as this is dependent on the flow rate. A maximum concentration limit allows companies to dilute the effluent with 'clean' lake water in order to comply with regulations if this is more cost-effective than effluent treatment. Diluting the water does nothing to change the P load to the lake, it can only reduce the risk of localised eutrophication. Therefore, it would be better if not only the P concentrations of effluent streams were monitored regularly, but also the flow rates. This would provide greater insight into the total-P load to lakes and rivers, allowing better prediction of the carrying capacity. Furthermore, no regulations seem to be in place for P output for cage aquaculture farms (ZEMA 2013). This could be monitored through estimates of P_{env} (as done in this study), which is a measure of the amount of P lost to the environment per tonne production. Moreover, licencing of farms could be regulated based on the total P waste the farm produces. Even though lowering Peny can benefit farms by reducing costs spent on feed and improving local water quality, the research and effort required to make these changes can be costly. Companies could be encouraged to reduce P waste if production licences were based on the maximum P load of a farm, as opposed to total production limit.

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