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A systematic literature review of the major factors causing yield gap by affecting growth, feed conversion ratio and survival in Nile tilapia (*Oreochromis niloticus*)

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Abstract

Productivity among small- and medium-scale tilapia farms varies considerably. The difference between the best performers and lower ones (yield gap), is affected by differences in growth rate and feed conversion ratio (FCR). FCR at the farm level is strongly influenced by survival of fish. In this study a systematic literature review of two databases (ASFA and CAB-Abstracts) identified 1973 potentially relevant articles. Data from 32 articles that met the inclusion criteria were analysed using linear mixed models for the most important factors with significant contributions to growth [investigated through analysis of the thermal growth coefficient (TGC)], survival and FCR of Nile tilapia. Increasing crude protein (CP), dissolved oxygen (DO) and pH significantly decreased FCR and increased TGC. Increasing stocking weight (SW) significantly improved both FCR and survival. Temperature had the largest effect on FCR followed by DO, pH and CP. DO had the largest effect on TGC followed by CP and pH. This study confirms that the optimal rearing temperature for Nile tilapia is between 27 and 32°C. Improving management to optimize DO (> 5 mg/L), stocking density (3–5 fish/m^2), SW (> 10 g) and CP (25 − 30%) will improve performance and survival in small- and medium-scale tilapia farming. However, it is hard to influence temperature in ponds and cages while DO is largely influenced by aeration. Since many small- and medium-sized farms do not have aeration, these major tilapia farming systems could benefit from genetically improved strains selected for resilience to highly fluctuating diurnal temperature and DO levels.

Key words: feed conversion efficiency, growth, survival, tilapia, yield gap.

Introduction

The supply of fish for human consumption has been increasing at a rate of 3.2% per year since the 1970s until 2013. Aquaculture made a substantial contribution to this increase, with inland finfish farming contributing 65% of the increase in fish production from 2004 to 2014 (FAO 2016). Among the finfish, Nile tilapia *(Oreochromis niloticus)* ranked second in terms of production volume next to carps (grass carp, silver carp and common carp) with a total production volume of 3.7 million tons worth about 6 billion USD (FAO 2016). Nile tilapia is farmed in more than 80 countries and in different production systems ranging from artisanal to intensive systems (Norman-López & Bjørndal 2009). Tilapia is an important fish species for home markets in Asia, South America and Africa; the United States of America is the major export market for tilapia (FAO 2016). Therefore, many selective breeding programs have been established for Nile tilapia (Neira 2010) including an important non-commercial breeding program by WorldFish that developed the genetically improved farmed tilapia (GIFT). The GIFT strain has been disseminated to many countries (Komen & Trinh Quoc 2014). According to Neira (2010), 10 out of 17 Nile tilapia breeding programs had used the GIFT strain as their base population.

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Nile tilapia production systems can be classified in terms of input utilization as extensive, semi-intensive and intensive farming systems. The earthen-pond production systems are the dominant ones practiced by small- and medium-sized tilapia farms. Such farms typically produce fish of 200–500 g weight targeting local markets. Larger fish with harvest weights above 800 g are produced by large farms that mostly use larger ponds with aeration, or cages in lakes and reservoirs (Omasaki *et al.* 2016b, Hoong Yip Yee, pers. comm., 2016). Currently there is a big difference in productivity among many small- and medium-sized tilapia farms. The difference in productivity between the best performing farms and low performing farms is defined as a yield gap, the difference between achieved production and that which is possible with optimal management. Many factors can contribute to differences in productivity but all have their action ultimately in their effects on growth, survival and feed efficiency, and this can be summarized as a difference in feed conversion ratio (FCR). There are large differences in FCR and survival among many small- and medium-sized tilapia farms.

FCR at the level of production units is defined as the ratio of the total feed given divided by total biomass harvested. FCR is determined by individual feed efficiency and survival, because fish that die during the grow-out period eat feed until death, but do not contribute to the total biomass harvested. Reported FCR values for tilapia vary widely, ranging from 1.5 to 2.5 in pond environments and from 1.0 to 1.71 in cage environments (Rana & Hassan 2013). Thoa *et al.* (2016) reported FCR values of 1.08 and 1.89 in freshwater and saline water pond environments, respectively. FCR is considered acceptable when it is not higher than 2 (Craig 2009) but the acceptable level can vary with the feed price. Feed cost is the major cost in fish farming (El-Sayed 1999; Craig 2009) representing over 50% of the variable costs during the grow-out period (El-Sayed 1999). In places where the feed price is high, a small increase in FCR could considerably increase the variable cost. Therefore, underperformance in terms of FCR is a major concern for aquaculture as it strongly and negatively affects the profitability of fish farms.

Both primary determinants of FCR at the production unit level, mortality and individual differences between fish in converting feed to biomass, are strongly influenced by the environment (de Verdal *et al.* 2018). Mortality, especially late mortality, is an important determinant of FCR. Rates of mortality for Nile tilapia vary considerably, with 20–71% mortality being reported for Nile tilapia reared in fertilized ponds with or without supplementary feeding (Abdalla *et al.* 1996; Abdelghany & Ahmad 2002). According to Rana and Hassan (2013), the reported mortality varies between 25 and 60% in pond environments. Trọng *et al.* (2013) reported a mortality rate of 71–72% for the cage culture environment, 48% for the pond nucleus environment and 32% in the polyculture production environment in Vietnam. The economic effect of mortality depends on the stage during which fish mortality happens. Mortalities occurring during the later stages of the grow-out phase have the largest economic impact due to the accumulated cost of production. The amount of feed delivered at any one time is usually based on the estimated standing stock of fish and the FCR is measured based on the amount of feed fed and the biomass harvested. Overestimating the standing stock will increase the feed waste, which has a negative effect on profit and environment, while underestimating leads to underfeeding of the fish and reduced production.

The wide range of FCR and mortality values reported indicate a large difference between the best and worst performing farms and suggest significant room for improvement with respect to more efficient husbandry. The investment in genetic improvement programs designed to improve performance in farming systems is undermined by these inefficiencies. Investigating the factors that contribute to the reduced productivity of tilapia fish farms is critical to providing the information needed to tackle the yield gap problem. First, by determining whether husbandry approaches can be optimized, and second, for those aspects of the environment that cannot be managed, identifying whether farmed strains can be genetically improved to be more efficient in those environments.

Work over the last two decades has established some of the main parameters for optimizing the environment for rearing tilapias (Popma & Masser 1999; El-Sayed 2006; Mjoun *et al.* 2010). However, there has been no comprehensive analysis of the actual performance of Nile tilapia in farm systems that provide the critical information as to how best to address the yield gap for this globally important aquaculture resource – either through improved husbandry or through selective breeding. The objective of this study was to quantify the effects of the most likely environmental and management factors on FCR, mortality and growth of Nile tilapia and to identify the most important of these factors associated with the yield gap.

Material and methods

Literature search

A systematic literature search was conducted for peer-reviewed journal articles that had been published in English in the ASFA (1971–2016) and CAB-Abstracts (1979–2016) databases on the 7th of July 2016. We used the following search terms and Boolean operators ('feed efficiency' OR FCE OR 'feed conversion' OR FCR OR 'growth rate' OR survival OR mortality) AND ('Nile tilapia' OR

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'*Oreochromis niloticus*'). Based on the above search terms, we found 889 and 1739 articles from ASFA and CAB-Abstract databases respectively. The two searches were combined and duplicates were removed using EndNoteX7. This resulted in 1973 articles, which were then checked against the search terms in the title and abstract, which resulted in 140 eligible peer-reviewed articles. From these potentially relevant studies, 108 studies were excluded for one of the following reasons: (i) because articles were not accessible (21 studies), (ii) because they did not report a sufficient proportion of the variables included in the different models (20 studies), or (iii) because studies were outside the scope of this review. Studies on the effect of density on survival during transportation, lethal dose of salinity, compensatory growth with feed restriction and refeeding, sex reversal, or varying crude protein levels during the study period were considered as being outside the scope of the review (Fig. 1). The data were extracted from the remaining studies for analysis.

Data extraction and statistical analysis

We extracted data on the following variables: study (since each study can be regarded as a separate element), 'study length', which is the grow-out period studied, stocking density, feeding rate, feeding frequency, levels of crude protein (CP) in the diet expressed as percentage, stocking weight (SW), which is the weight at the beginning of the experiments, harvest weight (HW), water temperature, pH, dissolved oxygen (DO), salinity, ammonia, nitrate, nitrite, growth and survival. We also extracted FCR or calculated it as the inverse of total biomass harvested/total feed given. Based on the number of treatments within experiments in an article, multiple data records or results of treatments were extracted from each article. In most of the studies, the numbers of fish used in the experiments or the standard errors were not reported and thus we gave equal weight to all the studies.

From the extracted variables CP, water temperature, pH and DO are environmental variables while the rest are management variables. FCR, survival and growth rate are the key determinants of productivity. To allow for comparisons across studies on growth rate, we calculated the thermal growth coefficient (TGC) as $[(\sqrt[3]{W_t} - \sqrt[3]{W_0})/(T \times t)] \times 1000$ where W_t and W_o are final and initial weights, respectively, T is the average temperature during the growth period and t is the length of the growth period (Jobling, 2003). Therefore, the key traits analysed in this study were FCR, survival and TGC.

We first did a principal component analysis (PCA) using prcomp package in R software (R Core Team, 2015) to explore the explanatory variables. If variables were missing for some studies, we used the mean values for those variables and used all the 32 studies in the PCA. Next, we performed linear mixed models to estimate the effects of the explanatory variables on FCR, survival and TGC. The explanatory variables were study, study length, stocking density, SW, CP levels, DO, temperature, pH, feeding rate, feeding frequency, the quadratic terms of CP levels, DO, temperature and pH. Only a few studies reported salinity, ammonia, nitrate and nitrite and therefore the effects of these variables were not investigated. Linear mixed models were used to account for the variation in studies and study was fitted as a random variable, whereas the rest were fitted as fixed effects. All models were analysed using the lme4 package (Bates *et al.* 2015) for R software (R Core Team, 2015). The significance of fixed effects was based on the approximate Student's t-test (Bates *et al.* 2015). The

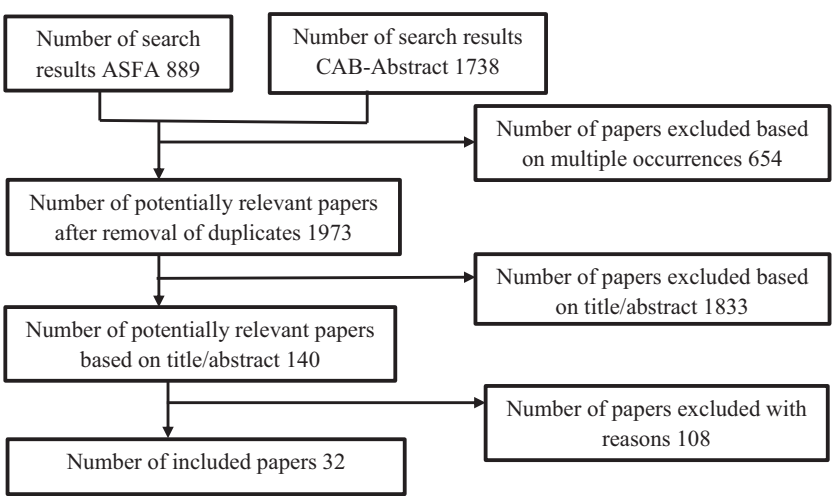


Figure 1 Flow diagram of article selection process.

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non-significant effects were removed stepwise, leaving out the factor with the highest *P*-value.

FCR

The majority of papers reported DO, but pH, feeding rate and feeding frequency were not reported in all the studies. Hence three separate analyses were undertaken, each with a different model.

Model 1 was used for studies that reported study length (L), stocking density (D), SW, CP, DO and temperature (T). The final analysis was based on 179 data records from 28 studies that report FCR:

$$FCR = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times SW + \beta_4 \times CP + \beta_5 \times DO + \beta_6 \times T + \beta_7 \times CP^2 + \beta_8 \times DO^2 + \beta_9 \times T^2 + \text{Study} + \varepsilon \quad (1)$$

After removing the non-significant effects, the reduced model was:

$$FCR = \beta_0 + \beta_1 \times SW + \beta_2 \times CP + \beta_3 \times DO + \beta_4 \times T + \beta_5 \times T^2 + \text{Study} + \varepsilon \quad (1.1)$$

Model 2 used a subset of 23 studies out of the 27 used in model 1 that also reported pH which resulted in 141 data records:

$$FCR = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times SW + \beta_4 \times CP + \beta_5 \times DO + \beta_6 \times T + \beta_7 \times pH + \beta_8 \times CP^2 + \beta_9 \times DO^2 + \beta_{10} \times T^2 + \beta_{11} \times pH^2 + \text{Study} + \varepsilon \quad (2)$$

After removing the non-significant effects, the reduced model was:

$$FCR = \beta_0 + \beta_1 \times CP + \beta_2 \times DO + \beta_3 \times T + \beta_4 \times pH + \beta_5 \times T^2 + \text{Study} + \varepsilon \quad (2.1)$$

Model 3 used a second subset of 11 studies out of the 27 used in model 1 that also reported feeding rate and feeding frequency which resulted in 67 data records:

$$FCR = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times SW + \beta_4 \times CP + \beta_5 \times DO + \beta_6 \times T + \beta_7 \times \text{Feeding rate} + \beta_8 \times \text{feeding freq.} + \beta_9 \times CP^2 + \beta_{10} \times DO^2 + \beta_{11} \times T^2 + \text{Study} + \varepsilon \quad (3)$$

After removing the non-significant effects, the reduced model was:

$$FCR = \beta_0 + \beta_1 \times D + \beta_2 \times \text{SW} + \beta_3 \times CP + \beta_4 \times DO + \beta_5 \times T + \beta_6 \times \text{Feeding rate} + \text{Study} + \varepsilon \quad (3.1)$$

In all of three models, FCR equals feed conversion ratio, β_0 is the overall intercept, β_1 to β_{10} are the regression coefficients of the different explanatory variables on FCR, *Study* is a random study effect assumed to be normally distributed ($N(0, \sigma^2_{study})$, ε is a residual random error assumed to be normally distributed ($N(0, \sigma^2_{\varepsilon})$, σ^2_{study} is the variance due to study and σ^2_{ε} is the residual variance.

Survival

Model 4 was used to investigate the effect of study length, stocking density, SW, CP, DO and temperature on survival, based on 187 data records from 29 studies:

$$\text{Survival} = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times SW + \beta_4 \times CP + \beta_5 \times DO + \beta_6 \times T + \beta_7 \times CP^2 + \beta_8 \times DO^2 + \beta_9 \times T^2 + \text{Study} + \varepsilon \quad (4)$$

The effects of CP, DO and temperature were not significant which led to the following reduced model:

$$\text{Survival} = \beta_0 + \beta_1 \times \text{SW} + \text{Study} + \varepsilon \quad (4.1)$$

β_0 is the overall intercept, β_1 is the regression coefficient of SW on survival, *Study* is a random study effect assumed to be normally distributed ($N(0, \sigma^2_{study})$, ε is a residual random error assumed to be normally distributed ($N(0, \sigma^2_{\varepsilon})$, σ^2_{study} is the variance due to study and σ^2_{ε} is the residual variance.

A few studies on survival reported pH, feeding rate and feeding frequency, hence a separate set of analyses was done to investigate the effect of these explanatory variables, but none of them were significant and details of these models are not presented here.

TGC

Model 5 was used to investigate the effect of study length, stocking density, SW, CP and DO on TGC. This model was fitted on 192 data records from 29 studies that reported TGC:

$$TGC = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times SW + \beta_4 \times CP + \beta_5 \times DO + \beta_6 \times CP^2 + \beta_7 \times DO^2 + \text{Study} + \varepsilon \quad (5)$$

After removing the non-significant effects, the reduced model was:

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$$TGC = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times CP + \beta_4 \times DO + \text{Study} + \varepsilon \quad (5.1)$$

Model 6 was applied to a subset of 23 studies out of the 29 studies used in model 5 that also reported pH resulted in 155 data records:

$$TGC = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times SW + \beta_4 \times CP + \beta_5 \times DO + \beta_6 \times pH + \beta_7 \times CP^2 + \beta_8 \times DO^2 + \beta_9 \times pH^2 + Study + \varepsilon \quad (6)$$

After removing the non-significant effects, the reduced model was:

$$TGC = \beta_0 + \beta_1 \times D + \beta_2 \times CP + \beta_3 \times DO + \beta_4 \times pH + Study + \varepsilon \quad (6.1)$$

Few studies reported feeding rate and feeding frequency together with TGC, hence we did a separate set of analyses, each with a different model, to investigate the effect of these variables on TGC.

Model 7 used another subset of 14 studies from model 5 that reported feeding rate and feeding frequency in addition to the other variables fitted in model 5, which resulted in 86 data records:

$$TGC = \beta_0 + \beta_1 \times L + \beta_2 \times D + \beta_3 \times SW + \beta_4 \times CP + \beta_5 \times DO + \beta_6 \times \text{feeding rate} + \beta_7 \times \text{Feeding freq.} + \beta_8 \times CP^2 + \beta_9 \times DO^2 + Study + \varepsilon \quad (7)$$

After removing the non-significant effects, the reduced model was:

$$TGC = \beta_0 + \beta_1 \times \text{feedingrate} + \text{Study} + \varepsilon \quad (7.1)$$

With TGC being thermal growth coefficient, β_0 is the overall intercept, β_1 to β_9 are the regression coefficients of the different variables on TGC, *Study* is a random effect assumed to be normally distributed ($N(0, \sigma^2_{study})$, ε is a residual random error assumed to be normally distributed ($N(0, \sigma^2_{\varepsilon})$, σ^2_{study} is the variance due to study and σ^2_{ε} is the residual variance.

The studies used in each model are given in Appendix 1.

Results

Principal component analysis

The first two principal components explained 42% of the variation in the whole data set. The correlations among DO, pH and feeding rate were positive. Stocking density and temperature were negatively correlated with DO, pH and feeding rate, whereas SW was negatively correlated with CP, DO, pH and feeding rate. Study length was negatively correlated with CP, feeding rate and DO (Fig. 2).

Feed conversion ratio

The linear effects of CP, DO and temperature on FCR were significant in all three models (1, 2 and 3, $P < 0.05$, Fig. 3a), whereas the quadratic term of temperature was significant in model 1 and 2 but not in model 3 when corrected for feeding rate (Table 1). The positive quadratic term of temperature in models 1 and 2 indicated that the relationship between FCR and temperature was not linear as demonstrated clearly in Figure 3b. The FCR was above 2.0 when the temperature was below 26°C and above 33°C. Optimum FCR was between 27°C and 32°C. FCR increased dramatically when the temperature drops below 25°C and reaching 4.4 at 20°C.

Increasing levels of CP (15−50.7%) and DO (1−11.1 mg/L) decreased FCR in all three models ($P < 0.05$, Table 1, Fig. 3a), as did increasing pH (6.42−8.3) in model 2 ($P < 0.001$, Table 1, Fig. 3c). Other variables tested in more than one model did not show a consistency of response or were not significant. FCR increased significantly with increasing stocking density when corrected for feeding rate in model 3 ($P = 0.017$), but was not significant ($P > 0.05$) in model 1 and 2. The effect of SW on FCR was significant and positive (0.003, $P < 0.001$) in model 1, not significant in model 2 ($P = 0.084$) but significant and negative (−0.016, $P = 0.017$, Table 1) when corrected for feeding rate in model 3. In model 1 and 2 the SW range is similar while in model 3 it is much smaller. The difference in the sign of coefficients of SW in model 1 and 2 is most likely due to the difference in SW ranges in the two models (0.003–311 g and 0.012–110 g, Table 1). The effect of feeding frequency, the quadratic terms of CP levels, DO and pH on FCR were not significant ($P > 0.05$) in any of the three models.

In summary, FCR decreased with increasing CP, DO and pH, and was optimal in a temperature range from 27.0–32.0°C. Results were inconsistent for stocking density and SW. Among the environmental variables, temperature had the largest effect on FCR followed by DO and pH.

Survival

The analysis of model 4 showed a significant effect of only SW ($P = 0.025$, the linear equation is: $\text{Survival} = 89.767 + 0.03 \times SW$) on survival and no significant effect of any of the other variables ($P > 0.05$). Survival increased by 0.03% per gram increase in SW. Increasing stocking weight from 5 to 50 g would improve survival by 1.4%

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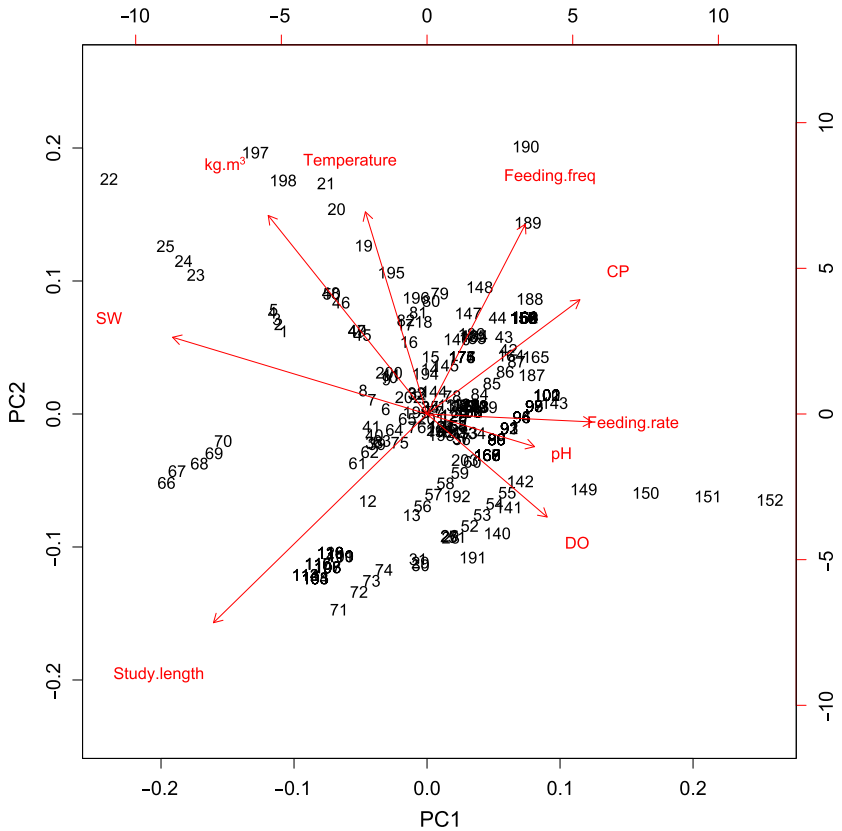


Figure 2 Loading plot from principal component analysis of all the data points from 32 studies.

(Fig. 4). The effects of feeding frequency, feeding rate and pH on survival were not significant for the range of values investigated (results not shown).

Thermal growth coefficient (TGC)

TGC increased with increasing levels of CP (15−50.7%) and DO (1−11.1 mg/L) tested in models 5 and 6 ($P < 0.05$, Tables 2, Fig. 5a) but when corrected for feeding rate in model 7 these effects became not significant. TGC increased with increasing pH (6.42 − 8.2) in model 6 ($P = 0.001$, Table 2, Fig. 5b) and feeding rate (2−60%) in model 7 ($P = 0.030$, the linear equation is: $TGC = 0.611 + 0.01 \times$ feeding rate).

Increased stocking density decreased TGC significantly in models 5 and 6 ($P < 0.05$) but not in model 7 ($P > 0.05$) which included feeding rate. The effect of study length on TGC was significant in model 5 ($P < 0.001$), but not in models 6 and 7 ($P > 0.05$). The effect of feeding frequency and the quadratic term of CP levels on TGC were not significant ($P > 0.05$). In summary, TGC increased with increasing CP, DO and pH and decreased with increasing stocking density and study length, although not in every analysis. Among the environmental variables DO had the largest effect on TGC while, as expected, feeding rate had the largest effect on TGC from the management variables investigated.

Discussion

The main environmental and management factors influencing survival, FCR and growth of Nile tilapia in the 32 papers identified in a systematic literature survey were DO, temperature, pH, CP, SW, feeding rate and stocking density. Ammonia, nitrite, nitrate and salinity are important water quality parameters worth of inclusion in the analysis but data on these parameters were only available in few studies and therefore these parameters were not investigated. We discussed the main environmental and management factors influencing yield gap focusing mainly on pond production which is the predominant production system. The PCA analysis showed a correlation between explanatory variables. Pearson correlations between the explanatory variables were non-significant to weak or moderate correlations. The highest correlation between stocking density and stocking weight was 0.57 ($P < 0.01$). Using median values of the significant variables and coefficients from Table 1, model 1 and varying

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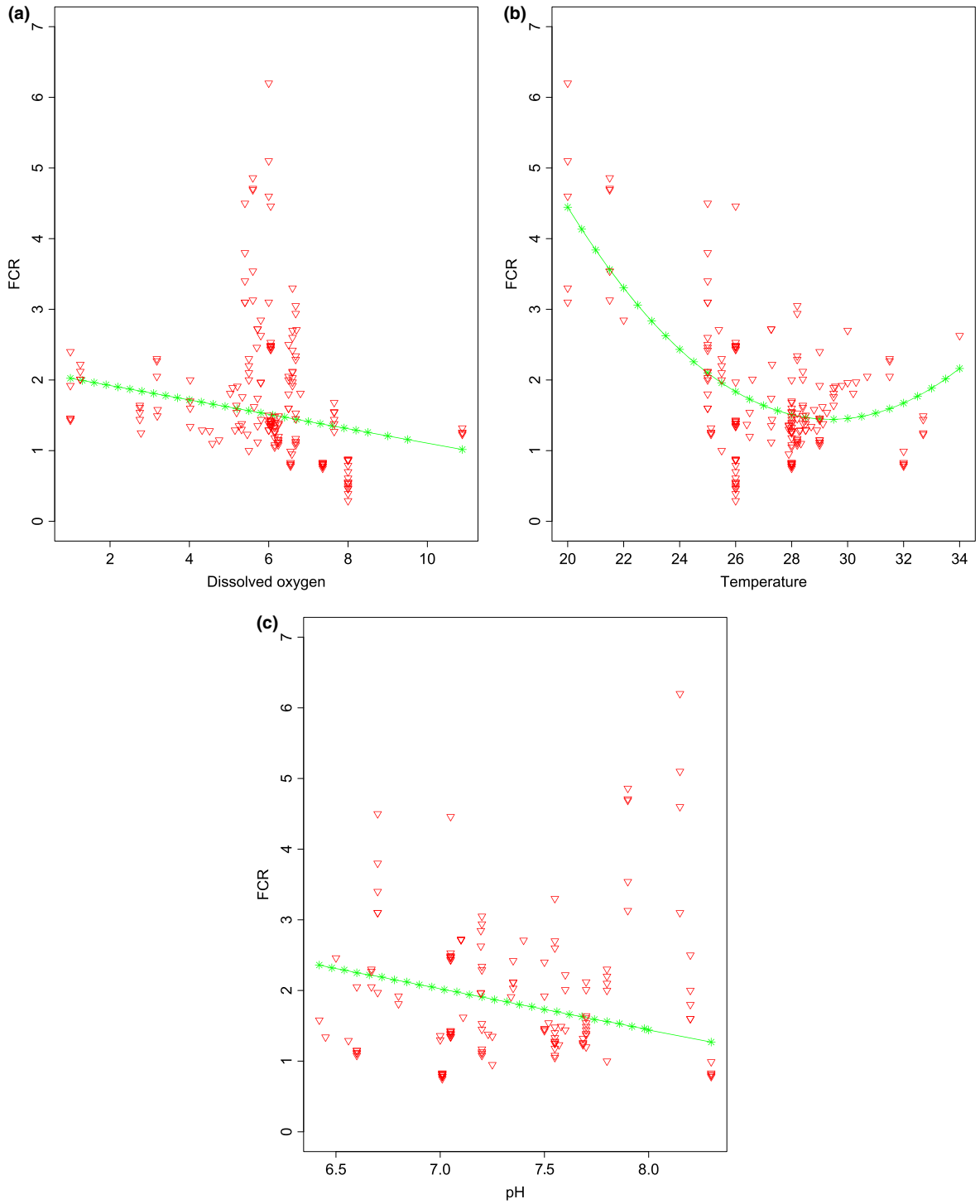


Figure 3 (a) The effect of dissolved oxygen on FCR calculated based on the coefficient estimates from Table 1, model 1 and median values (SW=9.3, CP=34% and Temp. = 28°C) for other variables. The linear equation is: $FCR = 32.4 + 0.003 \times 9.3 - 0.029 \times 34 - 0.102 \times DO - 1.99 \times 28 + 0.034 \times 28^2$, ✳ Modelled, ▽ Raw data. (b) The effect of temperature on FCR calculated based on the coefficient estimates from Table 1, model 1 and median values (SW=9.3, CP=34%, and DO=6.05) for other variables. The linear equation is: $FCR = 32.4 + 0.003 \times 9.3 - 0.029 \times 34 - 0.102 \times 6.05 - 1.99 \times Temp. + 0.034 \times Temp.^2$, ✳ Modelled ▽ Raw data. (c) The effect of pH on FCR calculated based on the coefficient estimates from Table 1, model 2 and median values (CP=31%, DO=6.05 and Temp. = 28°C) for other variables. The linear equation is: $FCR = 38.615 - 0.034 \times 31 - 0.101 \times 6.05 - 2.107 \times 28 - 0.579 \times pH + 0.036 \times 28^2$, ✳ Modelled ▽ Raw data.

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Table 1 Regression coefficient estimates ± standard errors given to one decimal place for factors that affect FCR for reduced Models 1, 2 and 3.

Parameters	Model 1 28 (179)†		Model 2 23 (141)†		Model 3 11 (67)†	
	Parameter range	Coefficient ± SE	Parameter Range	Coefficient ± SE	Parameter range	Coefficient ± SE
Intercept		32.4 ± 3.5***		39.0 ± 4.3***		8.7 ± 1.5***
Stocking density (kg m^{-3})					0.003–22.0	0.1 ± 0.0*
SW (g)	0.012–311.1	0.0 ± 0.0***			0.012–110.2	−0.0 ± 0.0*
CP (%)	15–50.7	−0.0 ± 0.0**	15–50.7	−0.0 ± 0.0***	17.2–50.7	−0.0 ± 0.0***
DO (mg/L)	1–11.1	−0.1 ± 0.0**	1–10.9	−0.1 ± 0.0**	3.2–10.9	−0.2 ± 0.1*
Temperature (°C)	20–34	−2.0 ± 0.3***	20–34	−2.2 ± 0.3***	20–31.5	−0.2 ± 0.1***
pH	NA	NA	6.42–8.3	−0.6 ± 0.2***	NA	NA
Feeding rate (% of body weight)	NA	NA	NA	NA	2–60	0.1 ± 0.0***
Temperature^2		0.0 ± 0.0***		0.0 ± 0.0***		
Study variance		0.112		0.118		0.050
Residual variance		0.248		0.289		0.337

†The number of studies and data records (in parentheses) utilized in each model are given below the model number and the studies are listed in detail in Appendix 1. Significance levels are indicated as *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

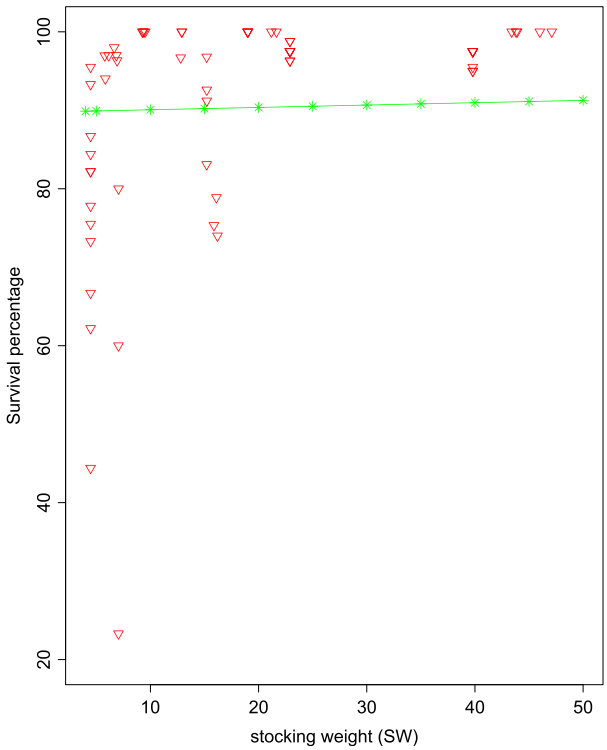


Figure 4 The effect of stocking weight on survival. The fitted line was based on the estimated coefficients from model 5 and varying stocking weight from 4 to 50 g. The resulting equation is: **Survival** = **89.767**+ **0.03** × **stocking weight**, Modelled ▲ Raw data.

DO from the lowest values to the highest value improved FCR by 50%. Using median values of the significant variables and coefficients from Table 1, model 1 and varying temperature from 20 to 29.5°C improved FCR by 68%. Using median values of the significant variables and coefficients from Table 1, model 2 and varying pH from the lowest values to the highest value improved FCR by 46%. Using the median values of the significant variables from Table 2, model 5 for DO and from Table 2, model 6 for pH and varying DO and pH levels from minimum to maximum improved TGC by 88 and 52% respectively (Fig. 5a,b). These results are now discussed with a view to determine whether changes to husbandry practices can reduce the yield gap or whether it is possible to provide solutions through selective breeding for those variables that are difficult or impossible to control in given farming systems.

Tilapia farmers practice and the effects of husbandry management

Stocking weight and study length

In this study, we found significant effects of stocking weight (SW) on FCR, when corrected for feeding rate, and on

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Table 2 Regression coefficient estimates ± standard errors given to one decimal place for factors that affect TGC for Models 5 and 6.

Parameters	Model 5 29 (192)† Parameter range	Coefficient ± SE	Model 6 24 (155)† Parameter range	Coefficient ± SE
Intercept		0.4 ± 0.2*		−1.1 ± 0.4*
Study length (days)	25–196	−0.0 ± 0.0*		
Stocking density (kg m^{-3})	0.003–41.4	−0.0 ± 0.0**	0.003–39.0	−0.0 ± 0.0*
CP (%)	15–50.7	0.0 ± 0.0**	15–50.7	0.0 ± 0.0*
DO (mg/L)	1–11.1	0.1 ± 0.0**	1–11.1	0.1 ± 0.0**
pH	NA	NA	6.42–8.2	0.2 ± 0.1***
Study variance		0.158		0.200
Residual variance		0.027		0.024

†The number of studies and data records (in parentheses) utilized in each model are given below the model number and the studies are listed in detail in Appendix 1. Significance levels are indicated as *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

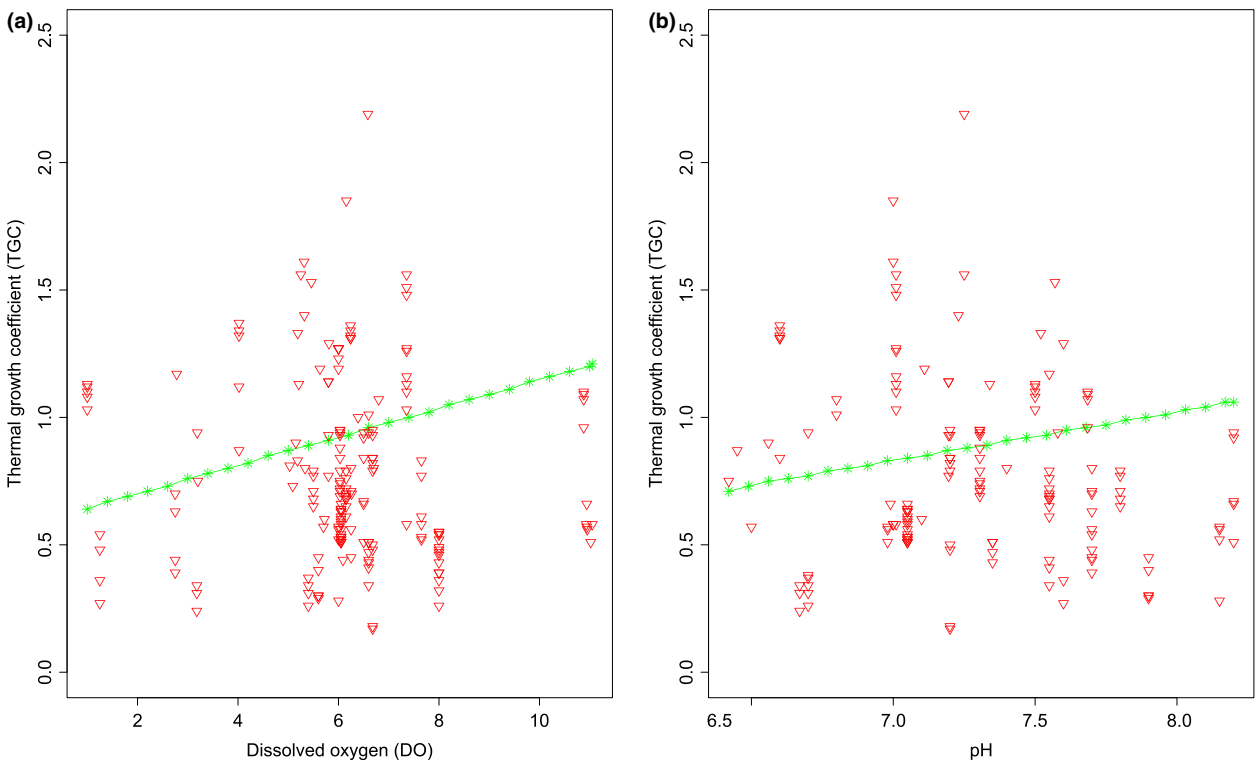


Figure 5 (a) The effect of dissolved oxygen on TGC. The modelled data were calculated based on the coefficient estimates from Table 2, model 5 and median values (study length = 70 days, stocking density = 0.894 and CP = 34%) for other variables. The resulting linear equation is: $TGC = 0.436 - 0.003 \times 70 - 0.014 \times 0.894 + 0.010 \times 34 + 0.047 \times DO$, ✳ Modelled ▽ Raw data. (b) The effect of pH on TGC. The modelled data were calculated based on the coefficient estimates from Table 2, model 6 and median values (stocking density = 0.894 and CP=34%) for other variables, resulting in the following equation: $TGC = -1.128 - 0.011 \times 0.894 + 0.01 \times 34 + 0.047 \times DO + 0.191 \times pH$

survival, with survival (Fig. 4) and FCR (Fig. 6) increasing with increasing SW. It is clearly seen from Figure 4 that increasing SW increased survival in the range of SW 4 to 10 g, whereas the relationship looks like a sigmoid curve when considering the whole range from 4 to 50 g. Fessehaye *et al.* (2006) found significant mortality due to size dependent cannibalism for Nile tilapia weighing 0.03 to 15.08 g. They found a sigmoid relationship between predator to prey weight ratio and the probability of prey being killed. This would explain the sigmoid relationship between SW and survival. Stocking fish larger than 10 g and graded for size uniformity could help to avoid size dependent

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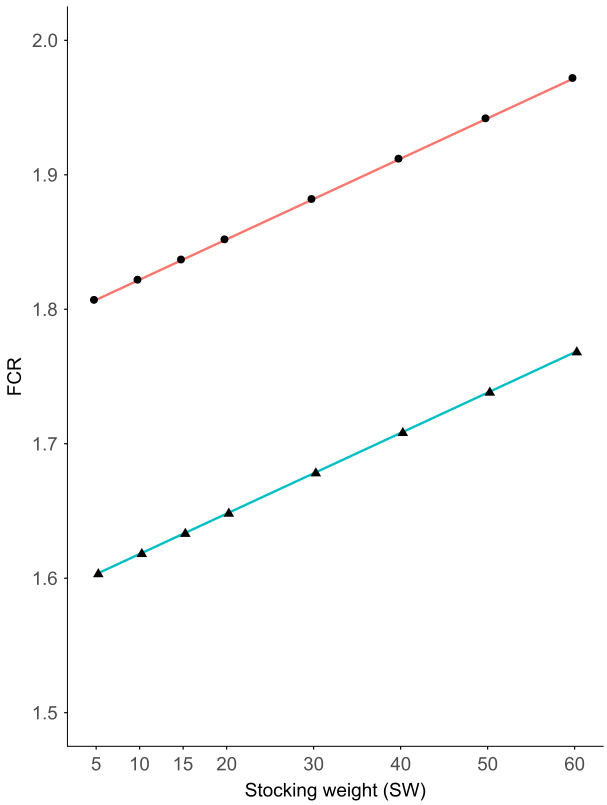


Figure 6 The effect of SW and dissolved oxygen on FCR using coefficients from Table 1, model 1 and the median values (CP=34%, T = 28°C) for the variables while varying SW from 5 to 60 g and fixing dissolved oxygen (DO) at $3mgl^{-1}$(hypoxia) or $5mgl^{-1}$ (normoxia) ($FCR = 32.4 + 0.003 \times SW - 0.029 \times 34 - 0.102 \times DO - 1.999 \times T + 0.034 \times T^2$), DO 3 mg/l 5 mg/l.

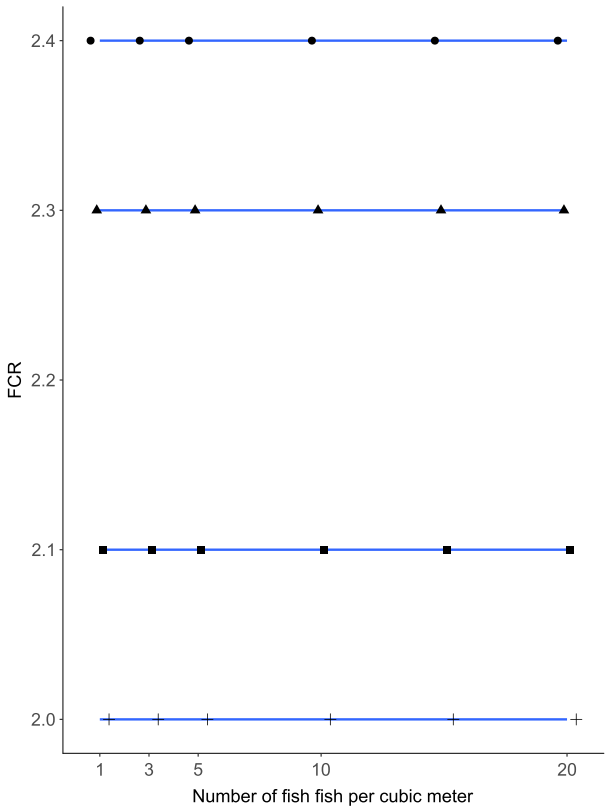


Figure 7 The effect of stocking density on FCR in low oxygen (3 mg/l) and high oxygen (5 mg/l) levels. FCR was calculated based on the coefficient estimates from Table 1, model 3 and varying the density level for 5 g and 10 g fish, fixing dissolved oxygen level to 3 or 5 mg/l and median values (stocking density = 0.06, CP=34%, Temp. = 26°C and feeding rate = 4% of body weight) for the other variables ($FCR = 8.728 + 0.097 \times 0.06 - 0.016 \times SW - 0.048 \times 34 - 0.165 \times DO - 0.163 \times 26 + 0.047 \times 4$), DO.SW ● DO 3 mg/l, SW 10 g ▲ DO 3 mg/l, SW 5 g ■ DO 5 ml/l, SW 10 g + DO 5 mg/l, SW 5 g.

cannibalism at smaller SW. The ranges of stocking density tested in our models were from 0.003 to ~22–41 kgm^{-3}. When keeping DO constant at 3 mg/L or 5 mg/L and varying stocking density from 1 − 20 fish per cubic meter, FCR and TGC hardly changed indicated by the almost flat lines (Figs 7 and 8). However, when keeping stocking density constant and increasing DO from 3 to 5 mg/L, FCR reduced from 2.3 and 2.4 to 2.0 and 2.1 and TGC increased from 0.77 to 0.88 (Figs 7 and 8).

Under small-holder tilapia farm conditions diurnal DO fluctuation is very high. Therefore, stocking densities of 3–5 fish of size larger than 10 g per square meter would give a better result than stocking smaller and/or more fish (Figs 6, 7 and 8).

The effect of study length on FCR was not significant while it was significant on TGC in model 5 while not significant in models 6 and 7. This is due to the fact that the analysis with model 5 has more data points with short study length. When two studies with short study length (El-Sayed & Teshima 1992; Tran-Duy *et al.* 2008) were removed, the effect of study length on TGC turned from statistically significant to non-significant. These studies are highly influential because the study length is relatively short at 25–30 days (average study length was 87.44 days) and the studies contributed 19 data points to the analysis.

Stocking density, corrected for feeding rate, had a significant effect on FCR (model 3), but it was not significant in model 1 and 2. It also had a significant effect on TGC (model 5 and 6). Increasing stocking density negatively affected both FCR and TGC. This agrees with what is generally observed in aquaculture (Ellis *et al.* 2002; Papoutsoglou *et al.* 2006; Li *et al.* 2012). Our estimates of the regression of stocking density on FCR (0.097) and stocking density on TGC (−0.014) suggest that increasing stocking density by one unit would lead to an increase in FCR by about 0.01 kg feed per kg biomass harvest and a reduction in TGC by 0.014.

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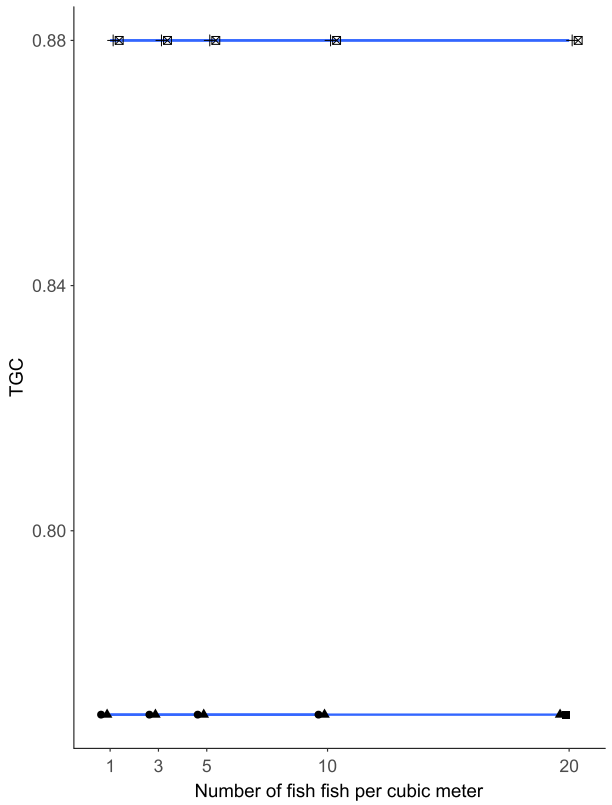


Figure 8 The effect of stocking density on TGC in low oxygen (3 mg/l) and high oxygen (5 mg/l) levels. TGC was calculated based on the coefficient estimates from Table 2, model 5 and varying the density level for 5 g and 10 g fish, fixing dissolved oxygen level to 3 or 5 mg/l and median values (study length = 70, CP=34%) for the other variables ($TGC = 0.436 - 0.003 \times 70 - 0.014 \times D + 0.011 \times 34 + 0.56 \times DO$), DO. SW ● DO 3 mg/l, SW 10 g ▲ DO 3 mg/l, SW 5 g ■ DO 3 mg/l, SW 10 g + DO 5 mg/l, SW 10 g ⊠ DO 5 mg/l, SW 5 g.

Under small-scale tilapia production systems, stocking density, number of fish per square meter and stocking size differ from country to country. In Malaysia, five fish of 5 g per square meter are stocked (Azlan Bin Azizan, pers. comm., 2017); in China, 4–6 fish of 4 g on average are stocked per square meter in summertime, while in the winter time they stock bigger fish, on average 18 g (Liu *et al.* 2013). In the Philippines, stocking density in extensive production systems is less than one fish of 10–20 g per square meter, in semi-intensive systems it is 1–5 and in intensive systems it is 5–10 fish of the same size, but in intensive systems using aeration, the preferred stocking size by farmers is five to twenty grams (Romana-Eguiaa *et al.* 2013). The growth period varies from two to nine months depending on the targeted market niche (Rana & Hassan 2013, Hoong Yip Yee, pers. comm., 2016) and therefore the length of the growth period, that is study length in this study, is not so much determined by its effect on FCR and TGC. The stocking density in Thailand is two to five fish (Bhujel 2013). The effect of stocking density is dependent on DO levels. Figs 7 and 8 suggest that 3–5 fish would give better FCR and TGC in a low oxygen environment. The above stocking densities used in different countries are in agreement with this study and will result in good FCR and TGC.

Feeds and feeding

FCR (models 1, 2 and 3) and TGC (models 5 and 6) improved with increasing CP. Model 3 and model 7 showed that both FCR and TGC increased with increasing feeding rate. The effect of feeding rate on FCR and TGC is well described in the literature (e.g. review by de Verdal *et al.* 2018). As in terrestrial animals, protein plays a vital role in fish. It constitutes about 65–75% of fish body weight on dry matter basis (Halver & Hardy 2002). Fish require protein for growth, development and reproduction. Protein deficient feeds can negatively affect growth or lead to interruption of growth and loss of weight (Halver & Hardy 2002). Feed cost constitutes the major portion of the variable cost in fish farming (El-Sayed 1999) and protein is the most expensive feed ingredient. Profitability is a key factor in any commercial fish farming system. Therefore cost effective feed composition that can satisfy nutritional requirements and feed management that can optimize FCR and TGC is crucial.

The CP requirement for starter, grower and finisher fish is 30–35%, 30–32% and 28–30% respectively (FAO, 2018). Least-cost feed contains 20, 25 and 30 CP levels for finisher, grower and starter, respectively, at a feeding rate of 1.5–5% body weight and 3–4 feeds per day (Ng & Romano 2013). El-Saidy and Gaber (2005) found that the economic optimum is at 25% CP and feeding rate of 2% compared with 30% CP and 2% feeding rate for adult Nile tilapia reared in concrete tanks. According to a review by El-Sayed (2013), most smallholder farmers in sub-Saharan Africa fertilize their ponds to boost natural feed. In addition, some farmers use farm-made feed, cotton seed cake, wheat bran, rice bran or maize bran for supplementary feeding. In Thailand and the Philippines, small-holder tilapia farmers fertilize their ponds and use commercial feed, cereal brans, restaurant wastes or bakery wastes as supplementary feeding (Bhujel 2013; Romana-Eguiaa *et al.* 2013). According to a review by Rana and Hassan (2013), the CP content of tilapia feed used ranges between 16 and 32%. CP and feeding rate can be easily managed to optimize production and should be kept at the optimum level to maximize profit and minimize yield gap. The optimum feeding rate is the rate that gives the lowest FCR, this feeding rate is lower than the feeding rate required for maximum growth (for instance in salmon and trout Lovell 1989). With respect to CP, in olive flounder, Kim *et al.* (2002) found that growth increased with increasing CP levels up to 55% and then decreased with further increase in CP. This would suggest a

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non-linear relationship between growth and CP. Therefore, we would expect also a non-linear relationship between FCR and CP. However, we found a linear relationship between CP and FCR within the range of values tested. Most of the studies used in this systematic review may have used CP levels close to the optimal or lower than the optimal levels with respect to FCR. If feed cost is increasing with CP, the economic optimum CP would be even lower than the CP that results in minimum FCR. Feed cost is the major cost in fish farming (El-Sayed 1999; Craig 2009) and among the feed ingredients CP is the most expensive. Therefore, feeding should be optimized to the level where marginal feed cost is equal to marginal revenues and where yield gap is minimal.

The effects of farm-made feeds, supplementary feeds and pond fertilization on yield gap were not investigated in our analysis. Farm-made feeds may vary in their nutrient content depending on the ingredients used. The CP content, CP source (NRC, 2011) and CP to energy ratio can affect feed efficiency (Kabir *et al.* 2019). Algae is a natural feed source for tilapia and the contribution of algae to tilapia growth is estimated to be between 40 and 68% in smallholder tilapia farms (Kabir *et al.* 2019). The amount of pond fertilization affects algae production in the pond. To reduce yield gap feeds should contain the optimum amount of nutrients and Bhujel (2014) recommends to maintain Secchi disc visibility at 30–40 cm depth for appropriate amounts of algae. If future studies include information on the type of farm made feeds, CP contents, CP source, CP to energy ratio and Secchi disc visibility, future meta-analyses could include these parameters to quantify the contribution of these factors to the yield gap, which would help in further minimizing the yield gap.

Environmental factors

Dissolved oxygen

In this study, we found significant effects of DO on FCR (models 1, 2 and 3) and on TGC (models 5 and 6) with FCR and TGC improving with increasing DO. The effect of the quadratic term of DO on FCR was not significant. Here we found only a significant linear association between DO and FCR, whereas the relationship might actually be curvilinear since there will be a DO level beyond which FCR will no longer improve. The reason that we did not find a curvilinear relation might be due to a lack of data points in the lower concentration range. Interestingly, DO had no significant effect on survival, at least not in the studies that were analysed in this paper. Our estimate of the regression of DO on FCR (-0.111) and DO on TGC (0.056) suggests that decreasing DO from the highest level investigated 11 mg/L to 3 mgL, which is the minimum level required for tilapia production, would lead to an increase in 0.9 unit FCR (e.g. From 1 to 1.9) and to a reduction in 0.4 unit TGC. Using median values of the significant variables and coefficients from Table 1, model 2 and varying DO from 1 to 10.88 mg/L improved FCR by 50% (Figs 3a). Using coefficients and the median values of the significant variables from Table 2, model 5 and varying DO from 1 to 11.05 mg/L improved TGC by 88% (Figs 5a). The effect of DO on FCR is larger than the effect of pH, but lower than the effect of temperature, whereas the effect of DO on TGC is larger than the effect of pH.

DO is one of the main limiting environmental variables that affect fish performance. Low DO affects feed intake negatively (Wang *et al.* 2009) and reduces digestibility (Tran-Duyn *et al.* 2012). At high DO, feed assimilation is improved, which may be due to improved blood flow to the gastrointestinal tract (Axelsson *et al.* 2002) and lower energy cost of feed digestion and absorption of nutrients (Duan *et al.* 2011). Therefore, more energy is available for growth. Tran *et al.* (2016) found Nile tilapia performed significantly less in terms of final body weight, specific growth rate and FCR under hypoxia ($3 mgL^{-1}$) compared with under normoxia 5 mg/L which is 50% of saturation. They also found that hypoxia affected intestinal morphology negatively. Therefore, optimum DO is a very important environmental factor for improving FCR and TGC.

In non-aerated ponds, DO levels fluctuate during the day and will be somewhere $0 - 15$ mg/L with the highest values in the afternoon and the lowest values just before sunrise (Bhujel 2014). However, DO level should be kept at least 5 mg/L and when it drops to ≤ 3 mg/L, feeding should be stopped and remedial action should be taken to improve the DO levels (Stickney 2017). Pond aeration keeps DO at an acceptable level with minimal fluctuations. However, DO is often beyond control in many small-scale farms where aeration for fishponds is not available or too expensive.

In areas where aeration is available, ponds should be aerated during critical times of the day especially early in the morning and on cloudy days. Managing the algae load in the water to optimal levels also helps in minimizing the DO demand during the night and prevents a large drop of DO. Usually DO is not a problem in flowing rivers due to ample water movement, in lakes it can become a problem when it is highly eutrophic which results in algae bloom and hypoxia during nights. If aeration of ponds is not possible, it is clear that there is a need for fish that are resilient to low DO levels during parts of the day with low FCR and high TGC despite the extreme DO variation.

Temperature

Temperature had a significant effect on FCR (models 1, 2 and 3), while it had no significant effect on survival (model 4). The significant positive quadratic term clearly showed that the relationship between FCR and temperature is non-

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linear. FCR was optimum between 27 and 32.0°C and increased significantly when the temperature dropped below 25°C reaching 4.4 at 20°C (Fig. 3b). Nile tilapia performs best in the upper end of the optimal temperature range of 27–32°C, which is in agreement with older reports quoting 29–31°C being the optimal temperature range for Nile tilapia (Popma & Lovshin 1996; Popma & Masser 1999). Note that the quadratic term of temperature was not significant in model 3 when accounting for feeding rate, which is most likely due to the fact that feeding rate was adjusted for temperature in the studies concerned. Using median values of the variables and coefficients from Table 1, model 1 and increasing temperature from 20 to 29.5°C improved FCR by 68%, which was the highest effect compared with DO and pH (Fig. 3b). Increasing temperature within the tolerable range increases appetite, food consumption rate and accelerates digestion of feed (Brett & Groves 1979; Jobling 1993). Management of water temperature in ponds and cages is not practical; thus, optimizing temperature is not possible. Therefore, it can be concluded that it is important to select fish under conditions that are similar to the prevailing temperatures in commercial environments to optimize FCR.

pH

Our estimates of the regression of pH on FCR (−0.548) and pH on TGC (0.191) suggest that increasing pH by one unit from 6.42 to 7.42 would improve FCR by about 0.5 unit and TGC by 0.2 unit, respectively. Using median values of the significant variables and coefficients from Table 1, model 2 and varying pH from 6.42 to 8.3 improved FCR by 46%. Using values from Table 2, model 6 and the same approach as above, increasing pH from 6.42 to 8.2 improved TGC by 52%. The factors pH and DO had a comparable effect on FCR, whereas the effect of pH on TGC is half of the effect of DO on TGC. In line with our analysis, Popma and Masser (1999) found the best FCR and growth in a pH range from 7 to 9. However, unionized ammonia, which is toxic to fish, increases with increasing pH and water temperature (Randall & Tsui 2002). Therefore, in order to achieve best results pH should be maintained between 7 and 8. This can be practically achieved in ponds using lime (Calcium carbonate ($CaCO_3$)) (Lekang 2013).

Among the environmental factors pH can be easily managed to optimize growth, FCR and survival. Small-scale farmers manage water pH using lime, particularly under intensive pond production systems, while usually pH is not a problem for river cage production systems, where water exchange is sufficient to maintain pH at optimum levels. Aeration can also help to reduce the amount of carbon dioxide that would otherwise interact with water and produce carbonic acid.

Implications for management and breeding

We conclude that CP, DO, water temperature, pH, stocking density and feeding rate are the most important variables to take into account to reduce the yield gap in tilapia farming. Ammonia, nitrite, nitrate, salinity and Secchi disc visibility are important water quality parameters but they were not investigated due to very few studies reporting these parameters. However, optimizing DO, pH, stocking density and feeding rate positively affects ammonia, nitrite, nitrate, except for salinity. Low DO and high ammonia are not problematic in flowing rivers due to ample water movement. Salinity is a problem in areas with brackish water because Nile tilapia is a fresh water fish and less tolerant to salinity compared with other *Oreochromis spp*. (Watanabe *et al.* 1985). Temperature is practically beyond control in most farms. Tilapia farms should give emphasis to managing optimal stocking density and feeding rate. DO and pH are largely influenced by aeration and liming could improve pH when tilapia are grown in ponds. At present large numbers of small-scale farmers have no means to aerate their ponds, either because it is too expensive, or because they have no access to cheap electricity. Breeding programs should consider this. Selection for higher growth rate will increase feed intake and consequently oxygen consumption (Omasaki *et al.* 2017). As the selection environment is usually well managed, with optimal conditions in terms of DO, pH and CP, there is a risk for genotype by environment interaction (GxE) when improved strains are used in low-input ponds and a yield gap is expected because of lower production than what is genetically possible in an optimum environment.

In the GIFT breeding program, Ponzoni *et al.* (2011) reported a genetic gain of 10–15% per generation for growth. In the presence of GxE interaction, the same gain might not be attained in the production environment when DO and temperature are far from the optimum levels and create a large difference with the selection environment. Estimates of the degree of GxE for growth in Nile tilapia between different rearing environments are inconclusive (Sae-Lim *et al.* 2016). Charo-Karisa *et al.* (2006) found a low genetic correlation (-0.27 ± 0.69) for body weight of fry between ponds. Trọng *et al.* (2013) compared the growth of GIFT Nile tilapia reared in river cages, aerated nucleus ponds and non-aerated low-input ponds, and found a high genetic correlation (0.83) for daily growth coefficient (DGC). Eknath *et al.* (2007) found high genetic correlations (0.76−0.99) among different pond environments and medium to high genetic correlation (0.36−0.82) between pond and cage environments. Bentsen *et al.* (2012) found high genetic correlations (0.53−0.99, mean = 0.89) for body weight between different environments. Robertson (1959) suggested that GxE interactions

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are biologically meaningful when the genetic correlation between environments is less than 0.8. GxE interactions with genetic correlations between environments of 0.8 or higher are considered not strong. However, if indeed the true genetic correlation is 0.8, it means that only 80% of the maximum possible genetic gain can be achieved in the production environment when selection is in the nucleus environment and information of only the selection environment is used in genetic evaluations (Mulder & Bijma 2005). Use of half-sib information from the production environment would reduce the loss in selection response (Brascamp *et al.* 1985; Mulder & Bijma 2005). Omasaki *et al.* (2016a) compared growth of Nile tilapia in a commercial monosex environment and a mixed sex nucleus environment and found significant GxE (genetic correlation = 0.59) which was probably caused by the methyl-testosterone treatment to produce monosex fry. They recommend to use sib information from the monosex production environment, similar to the general recommendation by Mulder and Bijma (2005). Lower prices for genotyping may make it easier to include information of commercial animals in genetic evaluations and reduce the yield gap when using genomic selection (for instance see Mulder 2016).

Conclusion

We found that temperature had the largest effect on FCR followed by DO, pH and CP, whereas DO had the largest effect on TGC followed by CP and pH. Attempting tilapia farming in regions outside the optimal temperature range would have a negative effect on production efficiency unless the strains used are selected for such temperature range. Among the management variables, feeding rate had the largest effect on FCR and TGC followed by stocking density, study length and SW. Management could control these variables. Based on this review analysis we recommend optimizing management in terms of stocking density ($3-5 \text{fish} m^{-2}$), SW (>10 g), CP ($25-30\%$), DO (>5 mg/L) and pH ($7-8$). This will improve FCR, survival and growth rate and reduce the yield gap in tilapia farming. Temperature has a very large effect on FCR, but it is hard to influence water temperature. DO is largely influenced by aeration when tilapia are grown in ponds. Since many small and medium sized farms do not have aeration, these major tilapia farming systems could benefit from genetically improved strains selected for resilience to highly fluctuating diurnal temperature and DO levels.

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APPENDIX 1: List of studies that were the source of data included for each analysis

Model 1.
Investigated factor: FE; number of studies/number of data records: 28/179

Abdel-Tawwab *et al.* (2014)[1], Abdel-Tawwab *et al.* (2015)[1], Abou *et al.* (2007)[1], Al-Hafedh (1999)[1], Alhassan *et al.* (2012)[1, 2], Ali *et al.* (2008)[1], Azaza *et al.* (2008)[1], Azaza *et al.* (2013)[1], Azaza *et al.* (2015)[1], Azevedo *et al.* (2015), Bahnasawy (2009)[, 2], Biswas and Takeuchi (2003)[1, 2], El-Sayed and Teshima (1992), El-Sherif and El-Feky (2009)[1,2], Garcia *et al.* (2013)[1], Huang *et al.* (2015) [1, 2], Kamal and Mair (2005)[1], Kapinga *et al.* (2014)[1, 2], Kaya and Bilgüven (2015)[1, 2], Kpundeh *et al.* (2015)[2], Lanna *et al.* (2016)[1], Mohammad *et al.* (2015)[1], Mohammadi *et al.* (2014)[1], Ridha (2006)[2], Santiago *et al.* (1987)[1, 2], Sweilum *et al.* (2005)[1, 2], Tran-Duy *et al.* (2008)[1], Yi *et al.* (1996)[1]

Model 2.
Investigated factor: FE; number of studies/number of data records: 23/141
Studies mentioned for model 1 above that are marked with superscript 1

Model 3
Investigated factor: FE; number of studies/number of data records: 11/67
Studies mentioned for model 1 above that are marked with superscript 2

Model 4
Investigated factor: Survival; number of studies/number of data records: 29/187
Abdel-Tawwab *et al.* (2014, 2015), Abou *et al.* (2007), Al-Hafedh (1999), Alhassan *et al.* (2012), Azaza *et al.* (2008, 2015), Azevedo *et al.* (2015), Bahnasawy (2009), Biswas and Takeuchi (2003) El-Sayed and Teshima (1992), El-Sherif and El-Feky (2009), Garcia *et al.* (2013), García-Trejo *et al.* (2016), Huang *et al.* (2015), Kamal and Mair (2005), Kapinga *et al.* (2014), Kaya and Bilgüven (2015), Kpundeh *et al.* (2015), Lanna *et al.* (2016), Likongwe *et al.* (1996), Mohammad *et al.* (2015), Mustapha *et al.* (2014), Ridha (2006), Santiago *et al.* (1987), Sweilum *et al.* (2005), Tran-Duy *et al.* (2008), Yakubu *et al.* (2013), Yi *et al.* (1996)

Model 5
Investigated factor: TGC; number of studies/number of data records: 29/192
Abdel-Tawwab *et al.* (2014)[3], Abdel-Tawwab *et al.* (2015)[3], Abou *et al.* (2007)[3], Al-Hafedh (1999)[3], Alhassan *et al.* (2012)[3, 4], Ali *et al.* (2008)[3], Azaza *et al.* (2008)[3], Azaza *et al.* (2013)[3], Azaza *et al.* (2015), Bahnasawy (2009)[3, 4] Biswas and Takeuchi (2003)[3, 4] El-Sayed and Teshima (1992), El-Sherif and El-Feky (2009)[3, 4], Garcia *et al.* (2013)[3,4] García-Trejo *et al.* (2016), Huang *et al.* (2015)[3, 4], Kapinga *et al.* (2014)[3, 4], Kaya and Bilgüven (2015)[3, 4], Kpundeh *et al.* (2015)[4], Lanna *et al.* (2016)[3], Likongwe *et al.* (1996)[3, 4], Mohammad *et al.* (2015)[3], Mohammadi *et al.* (2014)[3] Ridha (2006)[4], Santiago *et al.* (1987)[3,4], Sweilum *et al.* (2005)[3,4], Tran-Duy *et al.* (2008)[3], Yakubu *et al.* (2013)[3,4], Yi *et al.* (1996)[3]

Model 6
Investigated factor: TGC; number of studies/number of data records: 24/155
Studies mentioned for model 6 above that are marked with superscript 3

Model 7
Investigated factor: TGC; number of studies/number of data records: 14/86
Studies mentioned for model 6 above that are marked with superscript 4

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