UPTAKE OF NATURAL FOOD AND SUPPLEMENTAL FEED BY CULTURED NILE TILAPIA, Oreochromis niloticus L. IN LAGUNA DE BAY, PHILIPPINES

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Abstract

Nile tilapia were sampled on five occasions at a commercial cage culture set up in Diablo Pass, Laguna de Bay, Philippines between March 1996 and January 1997 with supplemental feed provided on two sampling days. Sampling took place over the 24-hour cycle and the stomach contents were analysed microscopically to determine their composition. The fish feeding model MAXIMS was used to calculate the daily ration. It was found out that in most sampling days, the fish showed diel feeding periodicity, feeding mostly during the day, and that the natural food consisted mostly of detritus, with phytoplankton found mainly when there was an algal bloom. The culture in small cages evidently restricted the fish from utilizing localized blooms throughout their feeding period when the bloom quickly passed through the cages, thus lowering food intake and diet quality. The daily ration ranged from 0.73-4.46% Body Mass Equivalent (% BME) throughout the year and was highest when the fish were supplemented. Supplemental feed, however, contributed surprisingly little to the daily ration unless given in excess. The results suggested that large portions of this valuable resource were wasted. The daily rations generally fell short of the maximum possible food consumption but were comparable to those calculated by other authors for wild fish in African lakes, relying only on natural food. It is widely reported that tilapia cultured in Laguna de Bay grow slowly unless supplemented and the present results suggest that this may be attributed more to diet quality than quantity. Suggestions for culture technique improvements were also made.

Introduction

Laguna de Bay is the largest lake in the Philippines, located immediately southeast of the national capital Manila. Despite its large size (911km²), it is very shallow (av. depth: 2.8m) that it has been used for aquaculture since the early 1970s. The main species grown is the milkfish, *Chanos chanos* (Forsskål), which is cultured extensively in large netpens. The other species reared are the Nile tilapia, *Oreochromis niloticus* (L.), and the bighead carp,

Aristichthys nobilis (Richardson), with Mossambique tilapia, Oreochromis mossambicus (Peters), and silver carp, Hypophthalmichthys molitrix Valenciennes, being of minor importance. All these other species are grown mainly in small netcages (ca. 2-200 m²).

Due to the shallow nature and large expanse of the lake, the wind stirs the water for most of the year, lowering Secchi depth to <30 cm. This helps suppress primary production but algal blooms still occur at certain times, most notably when the water clears in the latter half of the dry season (May-July) due to the backflow of saline water from the sea (Secchi depth: >100 cm) as well as in some years during a period of calmer weather around September before the start of the typhoon season. These blooms are usually dominated by blue-green algae whereas at times of turbid water, diatoms prevail. However, these algal blooms that tilapia farmers give supplemental feeds for their fish.

Despite the widespread application of supplemental feed in Laguna de Bay, not much is known about the precise impact of this material on the diet of tilapia in the lake. Although fish grow slowly without supplementation, (Basiao & San Antonio 1986), little work has been done on quantifying the food consumption of fed or unfed tilapia throughout the year. The present work therefore attempts to determine whether slow growth of not supplemented tilapia for most of the year is due to lack of food, whether supplemental feed makes a significant contribution to the diet and whether this material is being used efficiently at the supplementation levels normally applied in the lake. To this purpose, commercially cultured fish were sampled on several occasions between March 1996 and January 1997 and their daily food consumption calculated with the help of the feeding model MAXIMS developed by ICLARM (now the World Fish Centre) (Jarre *et al.* 1991).

Materials and methods

Tilapia were sampled on five occasions over a 24-hour cycle at a commercial set up in Diablo Pass, close to the Binangonan Freshwater Station of SEAFDEC. The fish were kept in small netcages about 3 x 6m and deep enough to reach the bottom of the lake (1.5-2.5m at the sampling site, depending on time of year). The sampling dates are summarised in Table 1, which also includes the average length and weight of the fish. Normally, tilapia are given supplemental feed from August-April in Laguna de Bay (i.e. outside the period of clear water). In November 1995, however, a large typhoon destroyed all aquaculture set ups in the lake, after which the operators diverted their finances towards rebuilding their ventures rather than the acquisition of fish feed. Even when the fish sampled here were once again provided with feed (September 1996 & January 1997), this consisted of old stock in the form of powder (Starter Crumble, Robinia Starfeeds, Universal Robinia Corporation), normally given to fry and fingerlings. On the first occasion, the supplementation rate was 8% BME in one dose at 8:30 whereas the second occasion, due to a calculating error of the fish farmer, the fish received 40% BME in two doses at 8:30 and 14:30 which is considered to be excessive.

On all sampling days, five fish were collected randomly per hour by lifting the net. These were killed immediately by immersion in iced water, then brought to the SEAFDEC station. The length and weight were measured; the innards (digestive tract, liver, gall bladder) were dissected out and then preserved in 70% ethyl alcohol (ethanol). At a later

date, the stomach was separated, with the contents flushed into a preweighed vial using fresh 70% ethanol and a small representative sample viewed under the microscope in order to identify the food composition. Planktonic organisms were identified in species where possible. This sample was later recombined with the remainder of the stomach contents, then dried to constant weight at 60°C. The weight was determined indirectly as the difference between the weight of the full and empty vial.

The dried stomach content weights were later standardized by transforming to a percentage body mass equivalent (% BME). This simply involved division by the body mass of the fish and multiplication by 100. The transformed data were then analysed with the fish feeding model MAXIMS (Jarre *et al.* 1991) based on the model of Sainsbury (1986). This model assumes that the fish show diel feeding periodicity, in the version used here feeding only in one clearly defined period over the 24-hour cycle at a constant rate of ingestion (Model 1.1). Other versions are based on two feeding periods (Model 2.1) or ingestion declining with increasing stomach fullness (Models 1.2 & 2.2) but these were not used here. In all versions, stomach evacuation is assumed to take place at all times at an exponential rate. The mathematical equations defining Model 1.1 are:

when feeding

$$dS/dt = J - E \, \widehat{}S$$

$$\bullet S = S_{\rm f} \, \widehat{}e^{-E\widehat{}(t-T_{\rm f})} + \left(\frac{J}{E}\right) \widehat{}e^{(1-e^{-E\widehat{}(t-T_{\rm f})})} \tag{1}$$

when not feeding

$$\blacklozenge S = S_n \, \pounds e^{-E \, \pounds (t-T_n)}$$

 $dS/dt = -E \oplus S$

(*S* = stomach contents, $S_f \& S_n$ = stomach contents at the beginning of the feeding and non-feeding periods respectively, t = time, $T_f \& T_n = \text{time}$ of day at the start of the feeding and non-feeding periods respectively, J = ingestion rate, E = instantaneous evacuation rate, e = Euler's number)

The total food consumption, R_d , is the integral of the feeding rate over the feeding period:

$$R_{\rm d} = \prod_{T_{\rm f}}^{T_{\rm n}} dt = J \, \mathcal{L}(T_{\rm n} - T_{\rm f}) \tag{3}$$

The software used to apply the model was the NLIN procedure of $SAS^{\textcircled{R}}$ 6.12 for Windows, which also permitted the calculation of standard deviations to the daily ration estimates (Richter *et al.* 1999a). Raw data rather than the hourly averages were used for the calculation. On some sampling dates, the feeding habits of the fish did not conform to those assumed by a simple MAXIMS 1.1 model (cf. Results) and the model had to be adapted. This was made possible by reprogramming the equations for SAS rather than using the user-friendly software developed by ICLARM (Jarre *et al.* 1992). Using the standard deviations obtained for the daily ration estimates, these were tested for statistically significant differences by means of a Tukey-Kramer test for unplanned comparisons at a significance level of p 0.05 (Sokal & Rohlf 1995).

This study was part of a project, in which the water quality of the lake was concurrently investigated by SEAFDEC AQD. Relevant data from their investigation (water temperature, phytoplankton composition) will be referred to at appropriate points in order to support our findings.

Results

The precise sampling dates and average lengths and weights of the fish are given in Table 1. Tilapia are usually harvested in Laguna de Bay when they have reached 250-500 g. Clearly, the fish sampled were rather small. Nevertheless, this species switches from its juvenile diet (zooplankton) to its adult diet at around 30-40 mm (Tudorancea *et al.* 1987) so that the fish analysed would have been representative of the majority of tilapia cultured in the lake.

Sampling Date	SL (cm)	TW (g)
19-20. March 1996	10.04 ± 1.28	41.0 ± 11.37
16-17. May 1996	9.07 ± 1.70	30.5 ± 14.30
17-18. July 1996	8.97 ± 1.47	32.5 ± 14.99
26-27. Sept. 1996		
- Supplemented Fish	8.41 ± 1.20	25.1 ± 8.13
- Unsupplemented Fish	8.59 ± 0.92	25.3 ± 8.27
14-15. Jan. 1997		
- Supplemented Fish	7.53 ± 0.78	15.4 ± 5.54
- Unsupplemented Fish	7.52 ± 0.73	14.8 ± 4.95

 Table 1. Details of sampling days, mean standard lengths and total body weights (± standard deviations) of Nile tilapia sampled throughout the project.

The stomach content composition of the fish on different sampling days is shown in Fig. 1a-g. Visual inspection demonstrated that the major part of the diet of unsupplemented fish was made up of amorphous organic detritus. Diatoms (mostly *Coscinodiscus sp.*) were present in all fish sampled but only in trace amounts. There was also some indication that the fish were feeding on benthos or periphyton since March till May 1996. Some filamentous green algae and amphipods of the genus *Corophium*, inhabiting the netting of the cages, were recorded in the stomachs of the sampled fish. However, their contribution was not great and they were not found again in later samplings. In September 1996, a prolonged bloom of colonies of the blue-green alga *Microcystis aeruginosa* Kützing (SEAFDEC 1997) led to the dominance of this species in the diet of both supplemented and unsupplemented tilapia. Zooplankters were always present in the stomach but were few in number. The smaller

plankters, such as *Bosmina sp.* made up the majority of the zooplankton consumed. This species had difficulty in evading slow filter feeders like tilapia.

Due to the devastating typhoon in November 1995, the lake level remained high that the annual clearing of lake water through saltwater intrusion did not take place. Nevertheless, an algal bloom of dinoflagellate *Ceratium hirundinella* Dujardin, was recorded in July 1996 but with the absence of blue green algae (SEAFDEC 1997). The composition of the stomach over the 24-hour cycle showed that this alga must have occurred in localized patches, one of which drifted through the cages between around 9:00-13:00. This is because it was only available to the fish for that part of their feeding period. It is not certain whether the algae occurred at a higher concentration than the detritus which made up most of the suspended organic matter between patches or whether the fish intensified their feeding activity when the algal bloom passed their cages. In either case, the ingestion rate obviously went up for that part of the feeding period, thereby violating the basic MAXIMS 1.1 assumption of a constant value for J. The model was therefore adapted to allow for a higher feeding rate (J_C) between ca. 9:00-13:00 and a lower feeding rate (J) for the rest of the feeding period. Additional time points was included in the model for the start (T_{Cf}) and cessation (T_{Cn}) of feeding on C. *hirundinella*.

Similar problems occurred when supplemental feed was given (September 1996, January 1997). Tilapia normally filters their food laboriously from the water but when provided with feed, this is available in a much more compact form, whether as pellets or as a floating scum when powdered feed is given, as was the case here. This allows for a much more rapid rate of food intake, again violating the assumption of a constant value for J. In addition, in September 1996, the fish were obviously confronted with a higher concentration of detritus between ca. 13:30-16:30. These two sampling days were therefore modelled with a basic ingestion rate (J_1), a higher ingestion rate (J_2) for supplemental feed and, in the case of September 1996, a further ingestion rate (J_3) for the period of higher detritus concentration. These two days were therefore modelled as follows:

- September 1996 fed fish: feeding starts at $T_{\rm f}$, ingestion rate high $(J_{\rm F})$ while feeding on supplemental feed until this was no longer available $(T_{\rm Fn})$, ingestion rate low (J)while feeding on algae until the fish started ingesting more detritus $(T_{\rm Df})$, ingestion rate moderate $(J_{\rm D})$ until detritus no longer available $(T_{\rm Dn})$, ingestion rate low (J) until the end of the feeding period $(T_{\rm n})$
- January 1997 fed fish: feeding starts at $T_{\rm f}$, ingestion rate low (*J*) when feeding on natural food ($T_{\rm f}$ $T_{\rm F1f}$, $T_{\rm F1n}$ $T_{\rm F2f}$, $T_{\rm F2n}$ $T_{\rm n}$), ingestion rate high ($J_{\rm F}$) when taking in pelleted feed ($T_{\rm F1f}$ $T_{\rm F1n}$, $T_{\rm F2f}$ $T_{\rm F2n}$), feeding ends at $T_{\rm n}$

The MAXIMS curves for all sampling days are shown in Fig. 2a-f with the parameter and daily ration estimates in Table 2. The tilapia in Laguna de Bay are clearly daytime feeders, generally starting close to dawn (ca. 5:30-6:30 in the tropics, depending on time of year) but frequently ceasing food intake well before dusk (ca. 17:30-18:30, depending on time of year). In September 1996, the fish continued to feed until well after dusk, possibly because of the abundance of natural food and the ease with which it could be ingested: *M. aeruginosa* colonies have gas vacuoles so that they form a floating scum at the water surface

which would be more easily taken up than individual algal cells dispersed throughout the water column. Indeed, the fish not receiving supplemental feed that month continued feeding intermittently throughout the night so that the data could not be modelled in a meaningful way. The daily ration estimates are also given in Table 2; in those cases where supplemental feed was given, the estimates have been split into the different contributions from natural and compound feed. Clearly, food consumption ranged from 0.72-4.46% BME per day, of which supplemental feed made up 26-55%. Consumption was significantly higher when fish were given feed at a time of algal bloom (September 1996 - fed fish) than when no bloom was taking place (January 1997 - fed fish) or when feed was not provided (July 1996). The food consumption on such occasions was, in turn, significantly lower when either event - feeding or algal bloom - did not occur (March 1996, May 1996, January 1997).

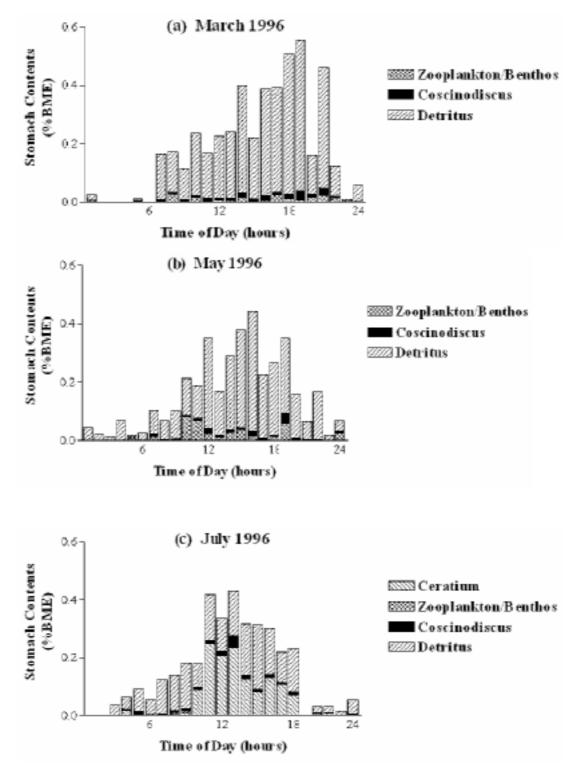


Figure 1. Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of five fish. Note different Y-axis scales. (a) March 1996 (b) May 1996 (c) July 1996.

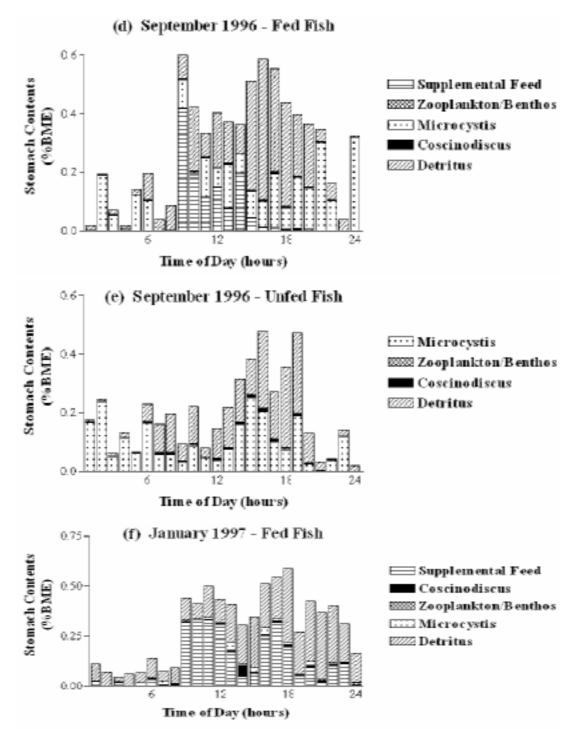


Figure 1 (con't.). Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of five fish. Note different Y-axis scales: (d) September 1996 - supplemented fish (e) September 1996 - unsupplemented fish (f) January 1997 - supplemented fish.

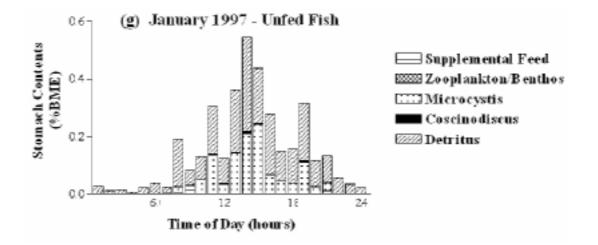


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Discussion

The fish analyzed here generally satisfied the basic MAXIMS assumptions so that this model could be applied for daily ration determination. Nevertheless, individual variability was high and it is possible that the analysis of more fish per hourly sub sample would have reduced this. However, for most sampling days, the model could be fitted relatively easily and the low number of replicate fish simply resulted in higher standard deviations to the parameter estimates. Whenever serious problems in fitting the model were encountered, this was associated with systematic deviations from the basic model assumptions, usually due to changes in the ingestion rate during the feeding period. The data for supplemented fish in September 1996 represent the limit of what may be modelled using MAXIMS and that for the unsupplemented fish in the same month could probably not have been analyzed in a meaningful way even if distinctly more fish had been collected per sub sample. The results show that under the present conditions (feed type, feeding frequency), the supplemental feed provided could make a substantial contribution to the diet of this species in culture. Even when given only once a day and during an algal bloom (September 1996), it was made up of about 25% of the total food consumed and at times of low availability of natural feed (January 1997), it provided more than half (55%) of the daily ration. At the same time, a large portion of the feed given was obviously not consumed. However, in view of the excessive amounts provided, it would be unreasonable to expect the fish to be able to eat all the food given. It is therefore worth comparing the daily ration estimates with the maximum amount of food that tilapia can possibly consume over a 24hour period. Toguyeni et al. (1997) observed consumption of 3.6-4.1% BME for juvenile tilapia kept in concrete tanks on a demand feeding regime (automatic feeders) with practically no uneaten food recorded. Clearly, the fish analysed here did not even come close

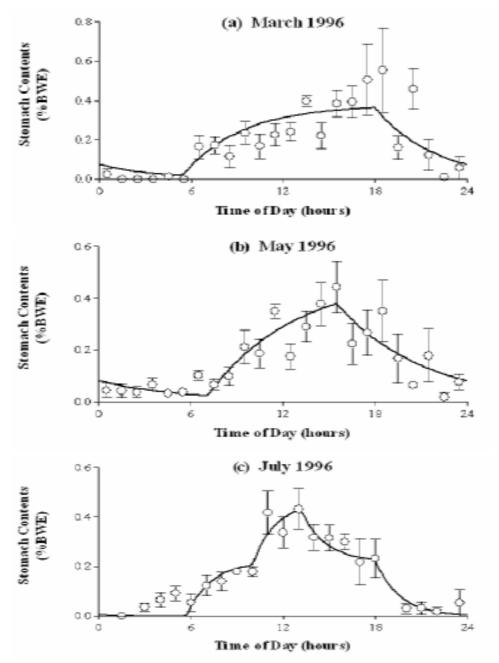


Figure 2. Mean observed stomach contents ± standard deviations (;) and MAXIMS curves (—) for Nile tilapia sampled throughout the project. Each data point represents the average of five fish. Note different Y-axis scales. (a) March 1996 (b) May 1996 (c) July 1996.

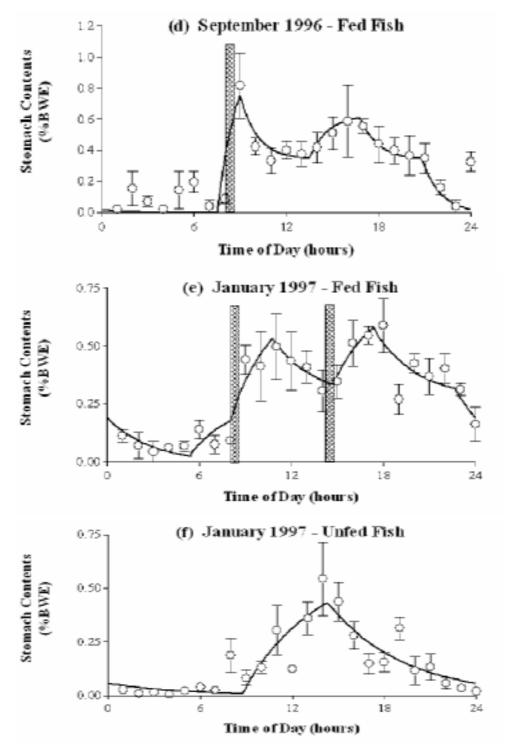


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Table 2. MAXIMS parameters (J, E, $T_{\rm f}$, $T_{\rm n}$ and derivatives) and the daily rations calculated from them ($R_{\rm d}$) for Nile tilapia sampled throughout the project. Standard deviations of the parameter estimates are given in brackets. Daily rations with different superscripts differ at p 0.05. SF denotes that supplemental feed was given.

Parameter	March 96	May 96	July 96	Sept. 96 SF	January 97 SF	January 97
Feed begin (time of day)						
$T_{\rm f}$ (General start of feeding)	5:25	7:05	5:54	-	5:30	8:44
	(40mins)	(33mins)	(29mins)		(37mins)	(26mins)
$T_{\rm F1f}$ (First period of pelleted feed	-	-	-	7:55	8:00	-
ingestion)				(7mins)	(55mins)	
$T_{\rm F2f}$ (Second period of pelleted feed	-	-	-	-	14:43	-
ingestion)					(33mins)	
$T_{\rm Cf}$ (Ingestion of <i>Ceratium</i>)	-	-	9:59	-	-	-
			(21mins)			
$T_{\rm Df}$ (Ingestion of more detritus)	-	-	-	13:34	-	-
· · · · ·				(48mins)		
Feed cessation (time of day)						
$T_{\rm n}$ (General cessation of feeding)	18:00	15:30	17:58	21:16	22:36	14:18
	(1h 20mins)	(53mins)	(26mins)	(45mins)	(39mins)	(38mins)
$T_{\rm F1n}$ (First period of supplemental	-	-	-	8:54	10:44	-
feed ingestion)				(45mins)	(33mins)	
$T_{\rm F2n}$ (Second period of supplemental	-	-	-	-	17:19	-
feed ingestion					(41mins)	
$T_{\rm Cn}$ (Ingestion of <i>Ceratium</i>)	-	-	13:07	-	-	-
			(44mins)			
$T_{\rm Dn}$ (Ingestion of more detritus)	-	-	-	16:51	-	-
				(42mins)		

Table 2 (con't.). MAXIMS parameters (J, E, T_f, T_n and derivatives) and the daily rations calculated from them (R_d) for Nile tilapia sampled throughout the project. Standard deviations of the parameter estimates are given in brackets. Daily rations with different superscripts differ at p 0.05. SF denotes that supplemental feed was given.

Parameter	March 96	May 96	July 96	Sept. 96 SF	January 97 SF	January 97
Ingestion rate, (%BME h ⁻¹)						
J (General ingestion rate)	0.100	0.086	0.140	0.230	0.099	0.131
	(0.031)	(0.013)	(0.047)	(0.204)	(0.057)	(0.020)
$J_{\rm F}$ (Ingestion rate supplemental feed)	-	-	-	1.130	0.268	-
				(0.822)	(0.082)	
$J_{\rm C}$ (Ingestion rate <i>Ceratium</i>)	-	-	0.299	-	-	-
			(0.077)			
$J_{\rm D}$ (Ingestion rate detritus)	-	-	-	0.448	-	-
				(0.263)		
Evacuation Rate (h ⁻¹)						
E	0.264	0.179	0.639	0.716	0.363	0.208
	(0.115)	(0.032)	(0.201)	(0.508)	(0.131)	(0.042)
Daily Ration (%BME d ⁻¹)						
•	1.255	0.723	2.220	3.359	1.167	0.728
$R_{\rm d}$ - Natural Food						
	-	-	-	1.101	1.428	-
$R_{\rm d}$ - Supplemental Feed	c	C	h	я	Ь	C
	1.255 ^c	0.723 ^c	2.220 ^b	4.460 ^a	2.595 ^b	0.728 ^c
<i>R</i> _d - TOTAL	(0.475)	(0.137)	(0.668)	(2.967)	(0.937)	(0.127)

to this figure when kept without food but also failed to reach it on one of the two occasions that they were supplemented. It is possible that a different feeding regime involving more frequent feed applications or even the installation of demand feeders could help increase food intake and thereby also food uptake efficiency in Laguna de Bay.

The data for July 1996 demonstrate the effect of localized algal blooms on the feeding habits of fish kept in small cages. Since the presence of *C. hirundinella* allowed the fish to increase their rate of food intake, it is probable that given the chance, they would have followed the bloom as it drifted past in order to utilize it to the maximum possible extent. The amount of food taken up during the time of *C. hirundinella* availability was 42% of the total daily ration (Rd: 2.22% BME, *Ceratium* consumption: $J_2 \times (T_{Cf} - T_{Cn}) = 0.94\%$ BME) while it was only available for 26% (3h 8mins) of the total feeding period (12h 4mins) which shows the importance that the bloom had for the diet of these fish that day. If the tilapia had been kept in large netpens, like those used for milkfish, it is likely that the increased mobility of the fish would have helped them increase their daily ration.

The July 1996 data also demonstrate that even when supplemental feed is not given, the uncritical use of a standard MAXIMS model may lead to questionable results since even natural food may not be available in the same quantities throughout the feeding period. These feeding scenarios require situation-specific models based on the general MAXIMS equations but with greater flexibility with regard to feeding times and the rate of food uptake. However, such models must always be backed up by information on the stomach content composition. It should be noted that in the data for unfed fish sampled in January 1997, there is considerable scatter around the curve and that on the basis of the three peaks around 8:00, 11:00 and 14:00, the feeding period could theoretically be divided into three phases of more intense feeding activity separated by periods of lower food intake or even a cessation of feeding. In practice, there is no significant change in stomach content composition so that these peaks probably represent individual variability more than any true change in feeding behaviour. In such cases, a standard MAXIMS model should still be applied.

The daily rations determined here compare favourably with those calculated for tilapia in other habitats. Moriarty & Moriarty (1973), using a different approach to the MAXIMS model, obtained daily ration estimates from 1.04-1.80% BME for various size groups of this species in Lake George, Uganda. Harbott (1975) and Getachew (1989), both using the same method as Moriarty & Moriarty (1973), calculated daily food consumption to be 0.94 and 0.59% BME respectively for tilapia in Lake Rudolf (Kenia) and Lake Awasa (Ethiopia), respectively. The lower estimates obtained here were of the same order and the maximum ones well in excess of those tilapia in African Rift Valley lakes. Richter et al. (2002) calculated the maintenance ration for this species at 24.3 °C in formulated, high protein (44%) or medium protein (25%) diets to be 2.52 and 2.81g kg^{-0.8} day⁻¹, respectively, which are equivalent to 0.53 and 0.59% BME, respectively for a 25g tilapia. No water temperature was quoted by Harbott (1975) and Getachew (1989) but Moriarty & Moriarty (1973) gave an average temperature of 25°C. In spite of the fact that the water temperatures in Laguna de Bay throughout the year are a little higher (range: 25-31°C, SEAFDEC 1997, 1998), it seems that the quantity of food consumed even by unsupplemented tilapia in the lake in most months exceeds that required for maintenance so that there should be scope for growth. If these fish are not growing, it is probable that this may be attributed more to the quality of the food than to the quantity consumed.

From the microscopic examination of the stomach contents, it is evident that unless the lake is experiencing an algal bloom, the major component of the diet of tilapia is amorphous detritus. This material, which is also abundantly consumed by the other cultured filter feeder in the lake, the milkfish (Kumagay & Bagarinao 1981), has consistently been found to be of low dietary quality (Persson 1983, Bowen 1987, Bowen *et al.* 1995, Larson & Shanks 1996). In general, fish species growing well on a diet consisting mainly of detritus are able to select the nutritionally better fractions (Mundahl & Wissing 1987, Yossa & Araujo-Lima 1998). Filter-feeders such as tilapia have been shown to be unable to select their food on any basis other than size (Drenner *et al.* 1984a,b, 1987) so that unless the algae in the lake are significantly larger than the detrital particles, the tilapia will be forced to ingest the latter when filtering out the former from the water column. The dominant algal species at times of turbid water is the diatom *Coscinodiscus sp.* which is rather smaller than most of the blue-green algal colonies prevailing at times of clear water. It therefore seems unsurprising that this algae is permanently accompanied by large amounts of detritus in the stomachs of tilapia in Laguna de Bay.

Conclusions

The most likely reason for poor tilapia growth at times of turbid water is diet quality rather than the amount of food consumed. The contribution of supplemental feed, when given, can be substantial but this material is invariably used inefficiently, leading to considerable waste. The study period unfortunately coincided with a time period during which the fish were supplemented less frequently than they would normally be and with a different type of feed to that usually used. Nevertheless, the results of Richter *et al.* (1999b) suggest that these results are valid also when pelleted feed is used.

In view of this, the use of supplemental feed for tilapia in Laguna de Bay should be reviewed critically, partly from the environmental aspect but also from a cost-benefit point of view. If, as it seems, a large part of the feed provided is simply eutrophying the lake, measures should be taken to avoid this. These need not be based on a ban on the use of pelleted feed but could also rely on distinct improvements in the culture methods, e.g. cage structure. Regardless of the supplementation levels used in the present study, interviews with fish farmers revealed that feeding levels of 6% BME are common in the lake, which in view of the maximum possible food uptake calculated by Toguyeni *et al.* (1997) must lead to waste. If feed is invariably lost through the bottom of the cage, it should be investigated whether solid-bottomed cages retain the feed long enough for the fish to consume this efficiently. This would allow a reduction in supplementation levels, making culture cheaper, as well as minimising eutrophication from wasted feed.

Further measure that could be taken is to improve conditions for primary production in order to make supplementation unnecessary or at least unprofitable. If the algal production in the lake is diluted too much by amorphous detritus, the sources of this material need to be identified in order to reduce or eliminate the input, giving cultured phytoplanktivores a better chance to filter algae. On the other hand, if aquaculture in the lake is to continue to depend on compound feed, other fish species which may utilize feed better and command a higher market value should be grown. Whatever steps are ultimately taken, it is clear that the current situation of aquaculture in Laguna de Bay is unsatisfactory and that changes to improve it should be taken.

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References

- Basiao, Z. & San Antonio, A. 1986. "Growth and Survival of Nile Tilapia Fingerlings in Net Cages without Supplemental Feed in Laguna Lake, Philippines." *In*: J.L. Maclean, L. B. Dizon &. L. V. Hosillos. (eds.). First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines; pp. 533-538.
- Bowen, S.H. 1987. "Composition and nutritional value of detritus." pp. 192-216. *In:* D.W.J. Moriarty & R.S.V. Pullin (eds.). "Detritus and microbial ecology in aquaculture", ICLARM Conference Proceedings, ICLARM, Manila, 420 pp.
- Bowen, S.H., Lutz, E.V. &. Ahlgren, M.O. 1995. "Dietary protein and energy as determinants of food quality: trophic strategies compared." Ecology 76(3): 899-907.
- Drenner, R.W., Mummert, J.R., de Noyelles, F. & Kettle, D. 1984a. "Selective Particle Ingestion by a Filter-feeding Fish and its Impact on Phytoplankton Community Structure." Limnol. Oceanogr. 29 (5): 941-948.
- Drenner, R.W., Taylor, S.B., Lazzaro, X. & Kettle, D. 1984b. "Particle grazing and plankton community impact of an omnivorous cichlid." Trans. Am. Fish. Soc., 113: 397-402.
- Drenner, R.W., Hambright, D., Vinyard, G.L., Gophen, M. &. Pollingher, U. 1987. "Experimental study of size-selective phytoplankton grazing by a filter-feeding cichlid and the cichlid's effect on plankton community structure." Limnol. Oceanogr., 32 (5): 1138-1144.
- Getachew T. 1989. "Stomach pH, feeding rhythm and ingestion rate in *Oreochromis niloticus* L. (Pisces, Cichlidae) in Lake Awasa Ethiopia." Hydrobiologia 174(1): 43-48.
- Harbott, B.J. 1975. "Preliminary observations on the feeding of *Tilapia nilotica* L. in Lake Rudolf." African J. Trop. Hydrobiol. Fish., 4: 27-37.
- Jarre-Teichmann, A. Palomares, M.L., Soriano, M.L., Sambilay Jr., V.C. & Pauly, D. 1991. "Some new analytical and comparative methods for estimating the food consumption of fish." ICES mar. Sci. Symp., 193: 99-108.
- Jarre-Teichmann, A., Palomares, M.L., Gayanilo Jr., F.C., Soriano, M.L. & Pauly, D. 1992.
 "A user's manual for MAXIMS (Version 1.0): A computer program for estimating food consumption of fishes from diel stomach contents data and population parameters." ICLARM Software 4, ICLARM, Manila, Philippines, 27 pp.
- Kumagai, S. &. Bagarinao, T.U. 1981. "Studies on the habitat and food of juvenile milkfish in the wild." Fish. Res. J. Philipp. 1 (1): 44-51.
- Larson, E.T. & Shanks, A.L. 1996. "Consumption of marine snow by two species of juvenile mullet and its contribution to their growth." Mar. Ecol. Prog. Ser.; 130: 19-28.
- Moriarty, C.M. & Moriarty, D.J.W. 1973. "Quantitative estimation of the daily ingestion of phytoplankton by *Tilapia nilotica* and *Haplochromis nigripinnis* in Lake George, Uganda." J. Zool. Lond., 171: 15-23.
- Mundahl, N.D. & Wissing, T.E. 1987. "Nutritional importance of detritivory in the growth and condition of gizzard shad in an Ohio reservoir." Env. Biol. Fish. 20(2): 129-142.

- Persson, L. 1983. "Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake." Oikos, 41: 118-125.
- Richter, H., Focken, U. & Becker, K. 1999a. "A review of the fish feeding model MAXIMS." Ecol. Modell., 120: 47-63.
- Richter, H., Focken, U., Becker, K., Santiago, C.B. & Afuang, W.B. 1999b. "Analysing the diel feeding patterns and daily ration of Nile tilapia, *Oreochromis niloticus* (L.), in Laguna de Bay, Philippines." J. Appl. Ichthyol., 15(6): 165-170.
- Richter, H., Francis, G. & Becker, K. 2002. "A reassessment of the maintenance ration of red tilapia." Aquacult. Int., 10: 1-9.
- Sainsbury, K. 1986. "Estimation of food consumption from field observations of fish feeding cycles." J. Fish Biol., 29: 23-36
- SEAFDEC. 1997. "Scientific Progress Report for 1996." *In*: Focken U. (Ed.). "Laguna de Bay, Philippines: An ecosystem approach for sustainable management. Scientific Progress Report to the European Union for the period January 1st December 31st 1996." Hohenheim University, Stuttgart, Germany, 153 p.
- SEAFDEC. 1998. "Scientific Progress Report for 1997." *In*: Focken U. (Ed.). "Laguna de Bay, Philippines: An ecosystem approach for sustainable management. Scientific Progress Report to the European Union for the period January 1st - December 31st 1997." Hohenheim University, Stuttgart, Germany, 118 pp.
- Sokal, R.R. & Rohlf, F.J. 1995. "Biometry (3rd edition.)." W.H. Freeman & Co., New York. 887 pp.
- Toguyeni, A., Fauconneau, B., Boujard, T., Fostier, A., Kuhn, E.R., Mol. K.A. & Baroiller, J.-F. 1997. "Feeding behaviour and food utilization in tilapia, *Oreochromis niloticus*: Effects of sex ratio and relationships with the endocrine status." Physiol. Behav., 62 (2): 273-279.
- Tudorancea, C., Fernando, C.H. & Paggi, J.C. 1987. "Food and feeding ecology of O. niloticus (Linnaeus 1758) juveniles in Lake Awassa, Ethiopia." Arch. Hydrobiol. Suppl., 79: 267-289.
- Yossa, M.I. & Araujo-Lima, C.A.R.M. 1998. "Detritivory in two Amazonian fish species." J. Fish Biol. 52: 1141-1153.