V Discussion

A. Milkfish

1. Sampling

The milkfish were collected by means of gillnetting on all sampling days, a fishing method normally associated with a certain measure of size selection. In spite of this, it is unlikely that the mean size of the fish caught on a particular sampling day deviated significantly from the true average of the fishpen population. This was because it was observed that the fish were observed to become not only gilled but also entangled in the net so that a very wide size spectrum was caught. This was particularly true on those sampling days which were timed a considerable period after stocking when the size of the faster growing fish would have been expected to have diverged most from that of the slower growing individuals. When the fact that all fish were stocked at the same size on the same day is also taken into account, it is likely that the sampling method extracted fish randomly.

2. Growth, Condition & Body Composition

The growth rates, condition factors and body composition of milkfish reflect the annual cycle of clear and turbid water conditions in Laguna de Bay. During the dry season, intruding saltwater clears the lake, giving rise to algal blooms which improve the feeding conditions for phytoplanktivorous filter-feeders. Milkfish growth rates speed up, condition improves and considerable fat reserves are laid down. At the same time, the differences observed for the same time of year between 1995 and 1997 are probably related to differences in the precise timing of saltwater intrusion and the biomass and digestibility of the dominant algal species at times of clear water (*Anabaena spiroides* in 1995; *Oscillatoria sp*. in 1997). After the return of turbid water conditions, the situation is reversed: growth rates and condition decline and fat reserves are used up. From the data obtained here, it seems that these parameters reach a low point around April, just before the next occurrence of saltwater intrusion. On the basis of the fat content, it appears that in April, just before saltwater intrusion, these fish are approaching the limit of their reserves.

The growth rates calculated for milkfish in Laguna de Bay can evidently match or even exceed those in most other environments when conditions are favourable in the lake. Both Sumagaysay (1993) and Kühlmann (1998) did not record higher SGR and MGR values for this species in pond culture even when given feed while Agbayani *et al*. (1989) obtained comparable values in modular pond culture without feeding. This suggests that, given the proper management, this species can be grown quite adequately without supplemental feed. In the modular pond system, no feed is given but fertiliser is used. This is both impractical in such a large system as Laguna Lake as well as unnecessary, since the lake is well supplied with nutrients from agricultural run-off and domestic and industrial waste. When nitrogen supplies become depleted in the latter half of the season of clear water, nitrogen-fixing blue-green algae such as *A. spiroides* or *Oscillatoria sp.* dominate the phytoplankton to compensate for this. The high growth rates of milkfish at that time of year, which match or exceed those found in most other systems, suggest that throughout this three-month period, fish growth is not affected by nitrogen limitation.

When the body composition of milkfish is analysed on a wet matter basis, it is clear that the deposition of fat takes place mainly at the expense of body water rather than other components. In this respect, milkfish resemble the common carp, *Cyprinus carpio* L. which also has a fairly constant protein and ash content in the wet matter (Focken & Becker 1993). These authors analysed an extensive data set spanning practically the entire range of body composition likely to be encountered in that species. The range of fat contents determined here for milkfish comes close to that calculated for common carp and rather exceeds the values given by other authors for *C. chanos* (Coloso *et al*. 1988, Shiau *et al*. 1988) who tested the effect of a variety of feeding levels and dietary components in this species. Even those fish reared by Kühlmann (1998), which were offered a combination of natural and supplemental feed, only reached 6.9% body fat (wet matter basis) at the end of their rearing period. These comparisons demonstrate that the feeding conditions for milkfish in Laguna de Bay reach both extremes: abundant, high quality food in the period following saltwater intrusion but a prolonged phase in which natural food is either scarce, of bad quality or both when the water is turbid.

3. Daily Ration

The daily rations calculated by Sumagaysay (1993) for milkfish given pelleted feed are rather higher than those determined here, whereas those of her milkfish kept on natural food alone consumed slightly less. These differences reflect the fact that filter-feeders such as milkfish ingest small particles so that their ingestion rates, and therefore also the overall food consumption, are low. Therefore, when this species is given pelleted feed, irrespective of any improvement in dietary quality, this can help to raise the quantity of ingested matter to a considerable degree. Kühlmann's (1998) fish were also given supplemental feed, which made up between about 30% and 75% of total ingested matter. Consequently, the daily rations calculated by Kühlmann (1998) were also rather in excess of those determined here. However, when one takes into account that the highest growth rates recorded here for fish living only on natural food exceed those of Kühlmann (1998), this demonstrates the enormous potential of Laguna de Bay for fish production which is nowadays only realised in the season of clear water.

With the marked exception of the August 1997 sample, the consumption estimates calculated here for this species with the aid of the MAXIMS model do not differ greatly between sampling days. The results for the February, April and June 1997 samples are very similar and certainly do not suffice to explain the great discrepancies between the growth rates for February-April on the one hand and April-June on the other. The maintenance requirement for this species has been calculated to be 4.63g $kg^{-0.8}$ day^{-1} at 27.5°C (Schröder 1997), which is typical of the water temperature found in Laguna de Bay for most of the year. Providing that no other limiting factors are at work, the consumption levels of this species should have sufficed for growth at all times other than in August 1997. It therefore seems that the growth of this species in Laguna de Bay is not limited so much by food availability at times of turbid water conditions as by some other factor.

4. Food Composition

The results of the stomach content composition analysis suggest that the principal limitation on milkfish growth in Laguna de Bay is food quality rather than quantity. Several authors have reported that unsupplemented milkfish ingest large quantities of detritus with their food (Trino & Fortes 1989, Sumagaysay 1993, Kühlmann 1998) including those in Laguna Lake (Kumagay & Bagarinao 1981) and this material has repeatedly been shown to be a poor quality food (Persson 1983, Bowen 1987, Bowen *et al.* 1995, Larson & Shanks 1996). Some fish species feeding mainly or wholly on detritus have been found to have high growth rates (Mundahl & Wissing 1987, Yossa & Araujo-Lima 1998) but these are able to select its nutritionally better fractions. Filter-feeding fish such as milkfish have repeatedly been shown to be unable to select their food on any basis other than size (Drenner *et al.* 1984a,b 1987) so that it is unlikely that this species would grow well in Laguna de Bay or other environments when consuming mainly detritus. This contradicts the theory of Trino &

Fortes (1989) that milkfish select detritus for consumption and that other material is ingested incidentally. It also leads to the conclusion that detritus in milkfish stomachs should be regarded more as a useless filler which prevents the animal from ingesting more material of higher nutritional quality.

If the rapid growth of milkfish cannot be attributed to an increase in food intake at the time of clear water, it seems reasonable to assume that this phenomenon is linked to greater food quality at that time of the year. Although differences in stomach content composition were found between sampling days, however, the sampling times during which the fish were found to feed more on algae than detritus were October 1996 and February 1997, i.e. those times during which growth was slow. It also seems highly paradoxial that the cultured fish (including tilapia) on the whole unselectively ingested any particle suspended in the water, the only exception being June 1997 when *Oscillatoria sp*. was in bloom but this alga was almost absent from the stomachs of the milkfish analysed.

Xie investigated the gut contents of silver carp (Xie 1999), generally considered a phytoplanktivore, and bighead carp (Xie 2001), generally considered a zooplanktivore, in relation to their environment with the use of Ivlev's electivity index. Although, for some unspecified reason, two different versions of this index were used for the comparison (indices of -1 to +1 for bighead, negative and positive values respectively indicating avoidance or selection; indices of 0 to ∞ for silver carp, values below or above 1.0 respectively indicating avoidance or selection), his results are of importance to the present investigation. The phytoplankton was usually dominated by the diatom *Cyclotella sp.* and the cryptomonad *Cryptomonas sp.*, nevertheless both carp species were found to ingest a large variety of algal taxa belonging to a wide range of size classes and did so in most cases apparently unselectively. However, the low electivity indices observed for *Cryptomonas* (0.56 in silver carp, 0.14 in bighead) and the closely related *Chroomonas sp.* (0.04 in silver carp, -0.82 in bighead) as well as the chrysophyte *Ochromonas sp.* (0.09 in silver carp, -0.63 in bighead) were attributed to the fragile nature of the cells of these algae which was seen to result in very rapid digestion and their consequent underestimation in the stomach contents. Strangely enough, the even lower electivity indices for *Oscillatoria sp.* (0.03 in silver carp, -0.98 in bighead) were considered indicative of true avoidance since the filaments of this species were only about 1-2μm in thickness. Nevertheless, the filamental colonies of this species were longer (26μm) than the diameter of some algal species with higher indices suggesting neither selection or avoidance (e.g. *Chlorella*: cell diameter 5-10μm, Ivlev's electivity index 0.80 for silver carp; *Melosira varians*: colony length 16µm, Ivlev's electivity index 1.03 in silver and 0.56 in bighead carp) so that it seems unlikely that *Oscillatoria sp.* could have evaded ingestion to such a large extent. Since this species has a high surface are: volume ratio and also lacks the cellulose cell wall of green algae or siliceous shell of diatoms, it is probable that this alga is almost completely digestible. This is supported by the comparison between the stomach and rectal contents of milkfish made here and, in view of the evidence, it appears likely that the contribution of *Oscillatoria sp.* to the diet of filter-feeding fish is generally underestimated.

The overall results for the stomach content analysis of milkfish therefore offer some solutions to the question of why growth is so rapid only when the water is clear. The *Microcystis* bloom in October 1996 was not conducive to fish production since this alga was ingested but not digested very well. In addition, the *Microcystis* strain found in Laguna de Bay is capable of producing microcystin toxins (Cuvin-Aralar *et al*. 2002) so that the full digestion of this alga may well not be desirable for the cultured fish in the lake. The *Coscinodiscus* bloom in February 1997 probably sustained fish growth somewhat better but, judging from the results of the weekly water quality sampling done in 1997, such diatom blooms are probably short-lived and the overall effect would have been small. The *Oscillatoria* bloom in June was probably available and highly digestible to the milkfish and, as shown by the results of the SEAFDEC phytoplankton monitoring, lasted for two to three months, so that it would have been the most likely to sustain fish growth. Nevertheless, it should be stressed that these conclusions are somewhat tentative and can only be drawn in the light of an overall picture.

B. Nile Tilapia

1. Growth, Condition & Body Composition

Despite the fact that the growth rates, condition and body composition data for Nile tilapia were obtained from more than one set of fish which were, moreover, analysed at different times of the study period, these results also match the general pattern of fluctuating water quality. The data obtained from the fish collected primarily for stomach content analysis, however, also show clear differences in both condition and body fat content for the same time of year in the 12-month period after May 1995, when saltwater intrusion did take place, and the remainder of the study period after May 1996, when no backflow of saline water was observed. In both of these periods, there is clearly a cycle of maximum fat content and highest condition around July and August, but the values for the first phase are higher than those which were recorded or might be expected for around the respective times of year in the second period. This shows the beneficial effect which the backflow of saline water has at least on Nile tilapia, if not also on milkfish, and lends support to the fears of the fish farmers that the artificial prevention of saltwater intrusion by the closure of the NHCS would have a detrimental effect on the production of cultured fish in Laguna de Bay (Santiago 1988, 1991).

The growth rates recorded for tilapia in 1997 partly confirm the results of Basiao & San Antonio (1986) insofar that the maximum MGRs are around 10.0g $kg^{-0.8}$ day^{-1}. In fact, the MGR at the beginning of the time of clear water was even rather in excess of this figure, suggesting that the diatom *Coscinodiscus sp*. dominating at the time was a better source of food for Nile tilapia than the blue-green alga *Oscillatoria sp*. which followed. It is also clear, however, that the situation in the season of turbid water has if anything deteriorated since the early 1980s. Whereas Basiao & San Antonio (1986) observed MGRs of 7.46g $kg^{-0.8}$ day^{-1} from August-November, the fish kept here in the same period fell well short of this value. Nevertheless, condition declined only slowly, suggesting that the fish were either able to obtain nearly but not quite enough to cover their maintenance requirement or that the food available at the time had a sufficiently high energy content, but practically no protein to support growth. This is supported by the summary of Bowen (1987) who quoted protein content and energy values for detritus from a variety of sources. Of these, the types with the highest share of amorphous detritus were probably epilithic detritus from an English lake (protein content: 0.0-8.6%, energy content: 14.3-19.7 kJ g-1 ash-free dry matter [AFDM]) and periphytic detrital aggregate from lake Valencia, Venezuela (protein content: 0.5-5.8%, energy content not determined). The relatively low condition factors recorded in the first phase may perhaps be partly attributed to the infestation of *Alitrophus typus* and it is possible that those fish which were in worst condition were the ones that died off, so that the recorded average only reflects the relatively better condition of the survivors.

2. Daily Ration

The results of the MAXIMS modelling for Nile tilapia do not conform to those obtained for milkfish. Although the food composition of unsupplemented tilapia is rather similar to that for milkfish, which suggests that Nile tilapia are also limited by food quality, the daily rations calculated for the tilapia match the changing pattern of water quality in the lake rather more closely than those for milkfish. Food consumption in March and May 1996 as well as that of unsupplemented fish in January 1997, all of them months in which phytoplankton contributed little towards the diet, was significantly lower than in May 1995 (small fish) and July 1996 when the fish also or mainly consumed algae. The only set of fish for which the daily ration determined is unexpectedly low is the large fish collected in May 1995. At the same time, the importance of supplementation to the diet of Nile tilapia is obvious: all those fish given supplemental feed consumed significantly more than fish kept without feed in months without algal bloom. Nevertheless, this was evidently achieved at some expense to the farmer since by far not all the supplemental feed provided was actually ingested. On the three sampling occasions when the fish were given feed, the predicted daily rations never exceeded 60% of the supplementation level. On top of that, it should be remembered that natural food still made up a considerable portion of ingested matter when feed was given so it is clear that far less than 50% of the feed given was actually consumed.

Since it is clear that the supplementation levels maintained by fishfarmers in the lake are horrendously wasteful and it is certain that food must go to waste, it might be worth comparing the quantity of food given with the maximum possible consumption level of this species on pelleted food. Toguyeni *et al*. (1997) kept juvenile Nile tilapia in concrete tanks on a demand feeding regime and observed feeding levels of between 3.6 and 4.1% BME with practically no unconsumed feed recorded. Of the three occasions when feed was given, only once (September 1996, supplemented fish) did the total food consumption reach such a level. If one assumes that supplemental feed is provided to make up the difference between the amount of natural food available to unsupplemented fish and the maximum which they could possibly consume, then the August 1995 and January 1997 samplings demonstrate that the fish are not even achieving this physiological maximum value when supplemented despite being presented with a vast excess of food. The August 1995 and, to a lesser extent, the January 1997 samplings suggest that large doses of feed can be utilised over an extended period of several hours. This is probably because uneaten food drops to the bottom which can be reached by the fish because of the shallow nature of the lake and the depth of the netting. Nevertheless, it is likely that the fact that a large amount of feed is given in few doses throughout the day (normally not more than three and sometimes as little as one according to personal communication with the cooperating fishfarmer) contributes towards this level of wastage. In consequence, it seems advisable to lower the supplementation level and spread the feed provision evenly over the course of the day, possibly with the use of more or less sophisticated automatic feeding systems.

Although previous data on the daily ration of tilapia is available (Moriarty & Moriarty 1973, Harbott 1975, Getachew 1989), it is difficult to make comparisons between them and the present work since the former authors used a different method for their analysis. The original data obtained in the African lakes were re-examined with the aid of the MAXIMS model by Palomares & Pauly (1996); these authors, however, did not explicitly state whether Model 1.1 or 1.2 was used, nor is it clear what units their daily ration estimates were given in. Furthermore, the associated figures suggest that the data used for their analysis does not relate well to that of the original publications. In order to facilitate a comparison, the original data of Moriarty & Moriarty (1973), Harbott (1975) and Getachew (1989) were reanalysed here with the MAXIMS Model 1.1. For the sake of comparison, all data were converted to the same units used for tilapia in Laguna de Bay (% BME) and the results of this analysis are presented in Table 10.

The MAXIMS model evidently gives slightly lower estimates than the method of Moriarty & Moriarty (1973); nevertheless, there is generally a fair match between the two. A comparison with the daily ration estimates obtained here also suggests that tilapia in other lakes are more severely limited by food availability than those in Laguna de Bay at any time of the year. Only the fish in Lake George consumed as much as those sampled here at times of turbid water and the provision of supplemental feed or the occurrence of an algal bloom usually sufficed to raise the daily ration above that recorded in the African lakes.

3. Food Composition

There were greater similarities between the food composition of milkfish and Nile tilapia than in the seasonal pattern of their daily rations. Although the latter were given supplemental feed on some occasions, the main stomach content component was detritus, accompanied by the dominant algal species. The main difference was the nature and origin of benthic items, which highlight the different methods used to culture the two fish species. The fact that tilapia ingested significant quantities of *Aufwuchs* was probably due to their being cultured in small cages with a far greater net area in relation to the volume of the enclosure than the huge netpens which milkfish are kept in. The presence of sediment and Ostracods in the stomachs of milkfish demonstrates that these also ingest their food other

Table 10. MAXIMS Model 1.1 results (± St. Dev.) for wild tilapia in various East African Rift Valley lakes. Data for Lake George from Moriarty & Moriarty (1973), for Lake Rudolf from Harbott (1975) and for Lake Awasa from Getachew (1989).

Locality	Lake George	Lake Rudolf	Lake Awasa
Ingestion Rate *J1* (%BME $hour^{-1}$)	0.085 ± 0.021	0.414 ± 0.067	0.0457 ± 0.003
Evacuation Rate *E* ($hour^{-1}$)	0.343 ± 0.104	0.755 ± 0.132	0.064 ± 0.006
Begin Feeding, F_b (time of day)	7:53 ± 31mins	8:34 ± 17mins	5:44 ± 19mins
Stop Feeding, F_s (time of day)	19:00 ± 42mins	16:14 ± 7mins	16:21 ± 27mins
Daily Ration, R_d (%BME)	0.945 ± 0.246	0.635 ± 0.092	0.485 ± 0.041
Daily Ration calculated by Original Author (%BME)	1.04	0.94	0.59

All figures in %BME given as dry weight food/wet weight fish. Original data for Moriarty & Moriarty (1973) was given as dry weights and were transformed to %BMEs. Original data in Harbott (1975) was given as dry weight/dry weight %BMEs; in transforming the data points, a proportion of 20% dry matter in wet fish weight was used. Original data in Getachew (1989) was given as wet/wet weight %BMEs; data points were transformed on the basis of the regression equation in the original publication (Dry weight food = 0.05 + 0.05 x Wet weight food). Original daily ration estimates given by all authors have been transformed from g $fish^{-1}$ basis to %BMEs (dry/wet) basis.

than by filter-feeding and it is possible that, given a greater relative area of netting, they would also consume *Aufwuchs*.

Apart from this additional source of food available to tilapia, the relatively confined space which they are cultured in also seems to affect the quality and quantity of their diet. The consumption pattern of the dinoflagellate *Ceratium hirundinella* in July 1996 can only be explained by the assumption that a localised bloom of this alga must have drifted through the culture area for a short time between mid-morning and just after midday. This bloom certainly helped boost the food consumption of these fish on that particular sampling day, as shown by the higher ingestion rate for the period of *Ceratium* consumption, and it seems likely that the daily ration would have been even higher if the tilapia had been able to feed on it for a longer period. If such a bloom had drifted through a large fishpen, the milkfish could have followed it to a greater extent than was possible for the tilapia in their comparatively small fishcage and this may be a reason why no great differences in stomach composition at different times of day were found for milkfish on any particular sampling day.

C. Comparison between Fish Growth in the 1970s & the Present

Although the growth rates of cultured fish were not recorded for the entire annual cycle, using the results obtained here, we can make some comparison with the situation in the early seventies. At that time it was reportedly possible to obtain two harvests per year which it will be assumed here to have been spread over four months (May-August inclusive) and eight months (September-April inclusive) respectively. For fish to grow from fingerling (ca. 10g) to harvestable size (at least 200g), mean standard and metabolic growth rates of 2.5% and 10.4 g kg^{-1} day^{-1} respectively would be necessary. These rates were attained by both species in 1997 and even exceeded by milkfish in 1995, so we can conclude that fishfarmers would have no problem producing the first crop in the period of clear water conditions. On the other hand, in order to achieve a second harvest per year, the system would under the present conditions be stretched beyond its limits. On the basis of the growth rates recorded for milkfish for October 1996 to April 1997, the standard and metabolic growth rates for September would have to be 6.7% and 32.2 g kg^{-1} day^{-1} respectively for a second harvest to be achieved. It appears highly unlikely that this should be possible, even considering that during this month, the fish would be small and therefore at the developmental stage when at least the SGR is usually at its highest. The belief that a second harvest would not be feasible even assuming favourable conditions in September is supported by the results obtained for tilapia in 1997, which ceased growing by the middle of August, as well as the findings of other workers (Basiao & San Antonio 1986).

Although Delmendo (1974) did not give precise details of stocking size and culture period, we can make some comparisons using her data. Assuming that fish are stocked at 10g, that one month is equal to 30 days and basing the data of Delmendo (1974) on full months (e.g. "five months" is exactly equal to 150 days), her data reveal SGRs of 1.64-2.60% or MGRs of 6.97-10.93g $kg^{-0.8}$ day^{-1}. Since the study period extended over a part of the year in which the water was cooler than from June-August, the period on which the high growth rates in the present study are based, it is reasonable to conclude that the growth rates in 1974 were even higher in the favourable part of the growing season and probably closer to those obtained here for milkfish in 1995.

The data of LLDA (1978) provide an even better comparison between the mid-1970s and the present study since sampling was conducted at regular intervals and more precise information on dates and sizes is given. The SGRs and MGRs for various parts of the year are summarised in Table 11, together with the values derived from Delmendo (1974). It is clear that in 1976, growth was rapid and relatively constant from mid-April to mid-August. When one compares the results of LLDA (1978) with those of Delmendo (1974), there seems to be a decline in fish growth in as little as two years between the respective study periods. This difference is even more marked when one remembers that the values derived from Delmendo's (1974) study refer to a more extended part of the year which includes part of the season of cold water. It is difficult to determine if these differences are attributable to sampling error, annual variation (such as those found between 1995 and 1997 in the present work) or reflect a real deterioration over such a short period.

Irrespective of whether the differences between the studies of Delmendo (1974) and LLDA (1978) reflect such a real deterioration or simply fluctuations between years or sampling uncertainties, the most notable differences in milkfish growth are between October-April in the mid-seventies and the same period in the present study. They confirm that even in 1976, it was still possible to grow two crops per annum but that this is certainly no longer possible.

Tab. 11. Growth rates of milkfish calculated for fish from twelve fishpens in 1974 and three pens in 1976 (respective sources: Delmendo 1974, LLDA 1978). Data for LLDA Fishpen II also split into two time periods for comparison

Source	Fishpen No.	Time of year	Length of Study Period	SGR (%)	MGR (g $kg^{-0.8}$ day^{-1})
Delmendo (1974)	All fishpens	Not given	120-180 days (range)	1.64 - 2.60 (range)	6.97 - 10.93 (range)
LLDA (1978)	I	June-Aug.	57 days	0.93	7.62
	II	Oct.-Aug. Oct.-April April-Aug.	266 days 176 days 90 days	0.97 0.90 1.11	4.89 4.56 7.70
	III	April-June	56 days	1.08	7.13

D. Water Quality Sampling

1. General

The relationship between Chl-a and algal dry biomass is in good agreement with that found generally. Prescott (1969) quotes a maximum of around 6% Chl-a content in the dry biomass but states that values of 0.5-1.5% are more usually observed. A rearrangement of Eqn. 34 suggests a figure of 0.73% for phytoplankton in Laguna de Bay. Some workers have criticised the estimation of algal biomass from Chl-a levels on account of species differences in Chl-a content as well as differences between algae cultured at different light intensities (Schwoerbel 1980). This is inconsistent with the relatively close relationship found for algae in Laguna de Bay. It is possible that the fact that the phytoplankton was dominated by so few taxa throughout the study period, presumably with similar Chl-a content, would have eliminated species differences. There is some indication that algae in Phases 1 & 3 have a slightly higher Chl-a content than in Phase 2 (Fig. 18; lower mass of POM per mg Chl-a) but the difference is not great. It is possible that due to the turbulent water conditions in the lake, the algae are mixed so much throughout the water column that the average light intensity which any given algal cell is exposed to does not vary much over extended periods of time. This would have minimised differences in Chl-a level due to different light conditions.

The water quality samples collected in 1997 show that almost all PIOM is found in the small size fraction. This confirms that most clay particles are of a minute size and helps to explain why these rarely settle from the water column unless flocculated by cations in the water. It also demonstrates why these particles were not found to any extent in the stomachs of the cultured fish: it is unlikely that they were large enough to be filtered from the water. The dominant item in the suspended matter of the lake at most times of the year was detritus, probably in amorphous form. It might be thought that this material would also be settled from the water column by the intrusion of saline water but the 1997 water sampling confirmed this not to be the case. As pointed out by Santiago (1991), the clearing of Laguna de Bay is caused by the negatively charged clay particles making up PIOM being bound together by the positively charged cations in the seawater, causing them to flocculate and settle more rapidly. It is unlikely that organic detritus also carries an ionic charge which would help in its removal from the water in a similar manner. The level of detritus in the water did decrease towards the end of Phase 1 but this was before the arrival of saltwater intrusion. It is likely that the reduction of detritus in the water column was associated more with the seasonal reduction in wind speed and helps to explain why some of the phenomena associated with saltwater intrusion (better condition, higher body lipid levels) were observed in tilapia in 1996 despite the fact that no backflow of seawater took place that year.

2. Limitation of Suspended Matter Composition on Fish Growth

The explanation generally put forward for the reduction in fish growth and per-hectare production is that the lake is overstocked so that the cultured fish are competing with each other as well as the wild fish for the available primary production (Nielsen 1983). From the results of the water quality sampling, however, it seems as if the comparative abundance of detritus represents the root of this problem rather more than competition for food. Milkfish and tilapia are forced to ingest this material if they are to ingest anything at all because their filter-feeding method of food intake does not permit them to select against it. The truly limiting factor is therefore not the absolute quantities of either algae or detritus but their relative contributions to the POM. A large biomass of phytoplankton is of little use to milkfish and tilapia if the accompanying levels of detritus far exceed this.

In the light of this, it seems surprising that the cultured fish are able to grow rapidly at any time of the year, namely after saltwater intrusion, since the ratio of detritus:phytoplankton does not decrease markedly at that time. In the water quality experiments conducted in 1997, however, the most obvious difference between Phase 2 and the other two phases was not in the total algal biomass but in the fact that at times of clear water, the algae were bigger. In conjunction with precise knowledge on the feeding mechanism of filter-feeding fish, specifically Nile tilapia, this fact gives us an explanation for the discrepancy in the growth rates of these fish at different times of the year. As mentioned previously, tilapia have small, stubby gillrakers which are only useful for filtering the larger suspended particles from the water. Small items are trapped by the secretion of mucus, allowing the retention of particles as small as suspended bacteria (Beveridge *et al*. 1989). It has even been shown that this aerosol mechanism can be turned on or off at will by controlling mucus secretion, thus giving the fish a certain degree of control over the size of particles it consumes (Sanderson 1996). Nevertheless, inside a certain size class, no such choice can be exercised. In view of this information, it appears that when the phytoplankton is dominated by large algae, such as the colonial blue-greens prevailing after saltwater intrusion, the fish are able to select these in favour of smaller organic particles such as detritus.

Rather less is known about the filtration mechanism of the milkfish than that of the Nile tilapia. The gillrakers of milkfish are rather longer than those of tilapia so that it is possible that they are capable of straining finer particles from the water than tilapia using this mechanism and might not be able to avoid doing so. Nevertheless, the crucial question here is not so much the size of the gillrakers but whether or not milkfish also use mucus to trap the finest particles so that a certain degree of control over the size of the particles ingested may be exercised. This question has not been satisfactorily answered up to date; however, T. Bagarinao (pers. comm.) considers it probable that mucus is also involved in this species. Xie (2001) noted that the gillrakers of bighead carp were too widely spaced to entrap some of the algal species found in the guts of these fish and mentioned the possibility of such an aerosol mechanism in this species too. It is possible that many more filter-feeding fish rely on this method of particle retention and that its importance in the feeding ecology of these fish has been generally underestimated.

VI Conclusions

The overall conclusion to be drawn from these results is that the growth rates of Nile tilapia and milkfish in Laguna de Bay is not limited by the biomass of the phytoplankton which represents their preferred food category. Since none of the native wild fish species is a filter-feeder, the general assumption that the cultured fish are competing with each other as well as with the wild fish as a result of gross overstocking is clearly wrong, at least when the water is turbid. This also implies that the primary production at times of turbid water, however large or small this figure may be, is either going to waste or being utilised indirectly (via zooplankton and possibly secondary consumers) by the wild fish. In view of this, it is hardly surprising that the production of cultured fish per unit area has never again reached that recorded in the early days of fishpen culture, despite the fact that the total area of the lake devoted to aquaculture in the eighties and nineties has at times been reduced to the levels recommended to be the optimum for exploiting the primary production of the lake (9,000ha or 10% of the lake area). For as long as the concentrations of phytoplankton in the lake remains overshadowed by vast quantities of detritus and the algal cell or colony size remains small, even a reduction of the overall lake aquaculture to only one small fishpen would not raise the per hectare production of cultured fish in the lake.

In the light of the present results, there are two possible explanations, working either singly or in combination, for the deterioration in the feeding conditions for the cultured fish. The first is that the production of phytoplankton in the lake, at least that of the large algal species, has gone down, probably as a result of the increased turbidity. This is supported by the fact that large-scale phytoplankton blooms resulting in lake-wide fishkills no longer occur (Sly 1993). It is also known that the lake has been shallowing at a considerable rate for at least half a century as a result of erosion in the watershed (Sly 1993, University of Hamburg 1998) and the loss of rooted aquatic vegetation (Pancho 1972, Aguilar *et al*. 1990) further eases the resuspension of sediment by wind action. The water quality experiments carried out in 1997 demonstrate that, although algal biomass can be high under turbid water conditions, large blue-green algal species promoting fish growth require clearer water in order to proliferate.

The second possible cause for the decline in fish productivity is that the levels of detritus in the lake may have risen over the years to a point where this material overshadows the phytoplankton biomass. While nothing is known about the concentrations of detritus in the early seventies, it is certainly true that the numbers of all of the potential contributors have gone up. Domestic waste, especially faeces, is very likely one of the biggest sources, particularly as even today, up to 30% of households in some of the most densely populated areas close to the lake lack a septic tank in their toilet (University of Hamburg 1998). A comparison between the study of SOGREAH (1974) and the latest population statistics (NSO 1995) shows that the population of those municipalities whose waste enters the lake rather than being flushed directly to the sea via the Pasig and lower Marikina Rivers more than trebled between 1970 and 1995. The number of industrial establishments has increased by nearly an order of magnitude from 115 in 1974 (SOGREAH 1974) to 1,075 in 1990, 444 of these generating wastewater for which only half (51%) had any sort of treatment facility (Santos-Borja 1993).

Apart from these long-standing sources of solid organic waste, there is, of course, a more recent contributor whose precise input has never been quantified but must be quite considerable: the aquaculture industry itself. The netpens used to culture milkfish are constructed from bamboo (*Bambusa spinosa* Roxb. 1814) and *anahaw* palm (*Livistonia rotundifolia* (Lam.) Mart. 1838) stems which have a useful life of only 1-2 years (Beveridge 1984), after which most are left to rot in the lake. Cariaso (1983, cited in Beveridge 1984) estimated that a one-hectare fishpen can consume as much as 2,000 bamboo and 100 *anahaw* poles and, although larger fishpens require less wood because of their reduced perimeter:surface ratio, this gives an idea of the vast quantities of structural material needed to produce 10,000ha of fishpens which, in addition, have to be replaced at least every other year. Another significant input is the pelleted feed used to supplement tilapia, most of which, as the present results have shown, are not consumed by the fish but contribute towards detrital matter. Although lake-wide fishkills are a phenomenon of the past, local kills still occur towards the end of the dry season and in such cases, the dead fish are not removed from the lake but in most cases simply transferred from inside the fishpen to the open water where they are left to rot (pers. observ.)

In view of the above, there is a serious need to reduce the input of sediment from erosion on the one hand and trace and quantify the sources of detrital matter in the lake on the other if the fishpen industry based on milkfish and tilapia is to be revived. The fact that the retention period of the lake water is only about one year (Santos-Borja 1993) suggests that if these inputs were to be cut significantly, the removal of material by flushing may lower the equilibrium concentrations. This would have two beneficial effects. Firstly, the relative biomass of phytoplankton would rise, thus allowing the cultured fish to filter more of this material rather than detritus. Secondly, the lower suspended sediment and detritus levels would reduce the turbidity to at least some extent, thereby increasing primary production and resulting in a higher absolute algal biomass. Conversely, in view of the large self-flushing capacity of the lake, it also seems as if the situation must have deteriorated very rapidly in the mid-seventies for the growth rates of the cultured fish to have been reduced so drastically over such a short space of time. This seems to implicate the aquaculture industry more than the other sources since it represents the biggest and most sudden change at that time.

Regardless of whether the fishpen industry is the main culprit in raising detritus levels over the years, thereby, in a sense, cutting its own throat, or whether it is merely the victim of the expanding population and industry, putting ever more pressure on the lake and its water quality, there is a lesson for aquaculture to be learnt from the example given by Laguna de Bay. Filter-feeding fish that operate at the lower trophic levels of the food web are some of the most important fish used in extensive aquaculture worldwide where they are mainly represented by the milkfish, Nile tilapia, bighead and silver carp. Evidently, such fish not only require a high concentration of particles of their preferred food in the water in order to be cultured successfully but also that these preferred food particles are not contaminated by other particulate matter of the same size. If such water quality demands cannot be met, these fish cannot be cultured on an extensive basis and if semi-intensive or even intensive culture has to be resorted to, it may be more favourable to grow other, more valuable species anyway. Either way, semi-intensive culture is obviously not the way to exploit the natural resources of a large water body such as Laguna de Bay and this case clearly demonstrates the necessity for good management before aquaculture is introduced or, at least before things get so badly out of hand.