

Results

A. Sampling of Milkfish & Tilapia at Commercial Setups

1. Monthly Changes in Phytoplankton Biomass & Composition

The results of the SEAFDEC plankton monitorings is shown in Fig. 5. It is obvious that the lake is, for most times of the year, dominated by diatoms, mainly belonging to the genus *Coscinodiscus*. There are occasional blooms of blue-green algae, mainly *Anabaena spiroides* Klebahn 1895 and members of the genus *Oscillatoria* which comprised the cyanobacterial blooms in May-June 1995 (both species) and June- August 1997 (*Oscillatoria* only). The other blue-green alga likely to occur in great numbers is *Microcystis aeruginosa* Kützing 1833, as was the case in September 1995 at Station C and September 1996 at Stations P & W. The third algal group conspicuous during the 3-year study period were the dinoflagellates, represented here by *Ceratium hirundinella* Dujardin 1841, which caused a short but intense bloom in July 1996. In contrast, the green algae never contributed much to algal biomass.

There were obvious differences between stations for the same sampling months, even between Stations W & P which were geographically close to each other. These differences may to some extent be attributed to the fact that no station could be visited at the same time, and the difference between Stations P & W on the one hand and Stations S & C on the other was always about 24 hours. In this time, the weather could change dramatically and this would have influenced algal biomass. Nevertheless, the discrepancies would also have reflected differences between the different geographical sectors of the lake, showing not only that the algal populations differ between bays but also that the fishpens have an effect on algal biomass and community structure. This could be due to either the grazing effect of the cultured fish or the flow of water being impeded by the netting.

The biggest difference between the years was the occurrence of dinoflagellates rather than blue-greens in 1996. One possible reason for this is that because of high lake levels following the strong typhoon in November 1995 and the subsequent closure of the NHCS, the water level did not fall sufficiently low for saltwater intrusion to take place that year. Nevertheless, this bloom took place to a greater or lesser degree at all stations. This shows that, regardless of these differences between years and bays, the results of the algal monitoring demonstrate some overall similarities for the lake, namely the dominance of the

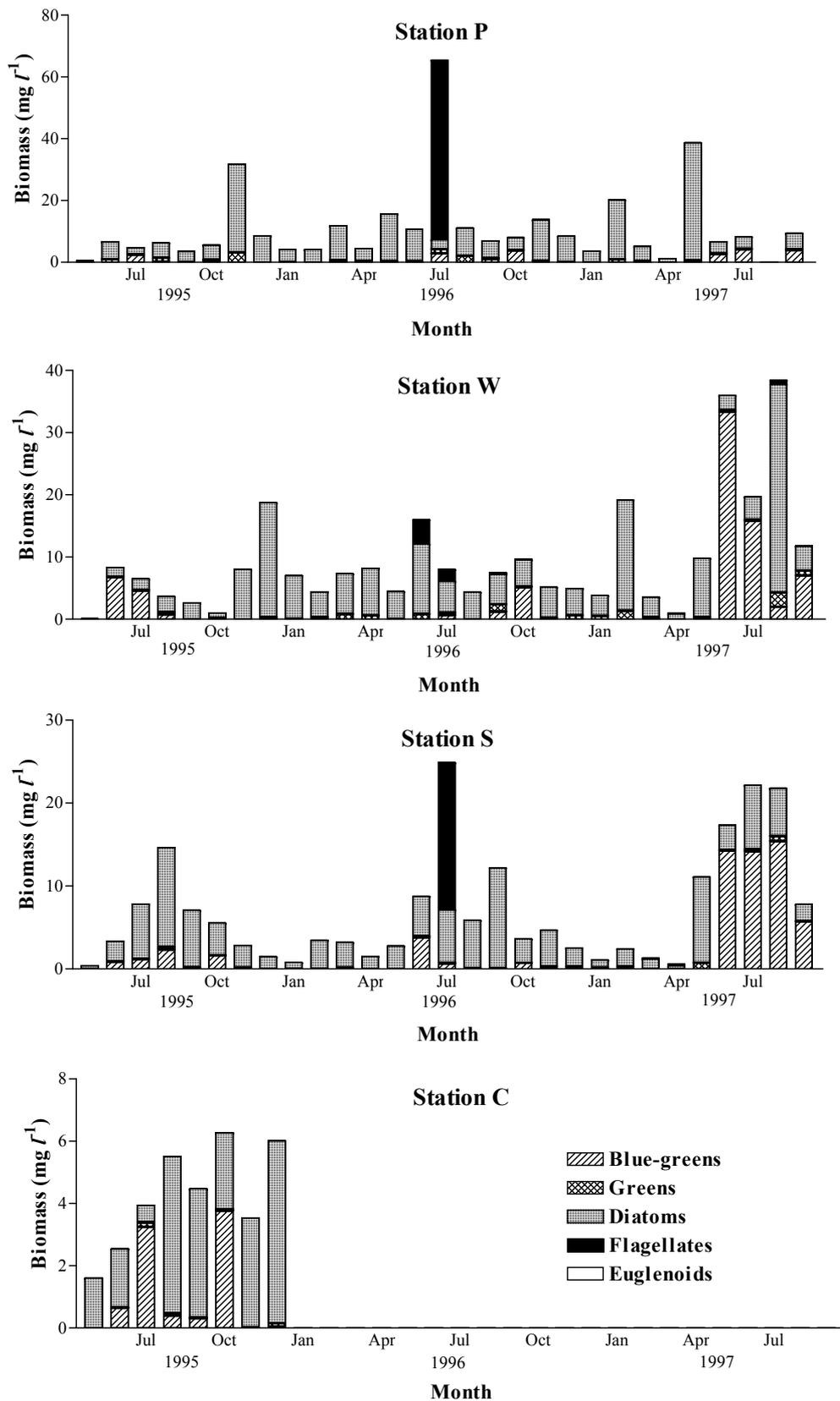


Figure 5. Phytoplankton biomass in a fishpen (Station P), in West Bay (Station W), South Bay (Station S) and Central Bay (Station C) from May 1995 to September 1997 inclusive. No sampling at station C throughout 1996 and 1997 or at Station P in August 1997). Common legend shown at Station C. Note different Y-axis scales. Data taken from SEAFDEC (1996, 1997, 1998)

diatoms for most of the time, which are replaced by blooms of blue-greens or dinoflagellates around the middle of the year.

2. Milkfish

a) Growth Rates

Milkfish were sampled on seven occasions in June and August 1995, October 1996 and February, April, June and August 1997. The strong typhoon in November 1995 destroyed all fishpens in the lake so that sampling was not possible for one year during which the industry slowly recovered. The mean standard lengths, total and gutted weights of the milkfish sampled are summarised in Tab. 2. In spite of their large maximum size, milkfish are harvested in Laguna de Bay when they reach a marketable size of about 250-500g. In fact, our final sampling (21.-22. August 1997) could not have been delayed much longer since these fish were harvested only a few days later. The fish collected here therefore span practically the entire size range found in the lake. The standard and metabolic growth rates calculated from these figures (Tab. 3) contrast markedly between different seasons. Growth is evidently far superior between mid-June and the beginning of August than at other times of the year; at the same time, differences for practically the same time of year were observed between 1995 and 1997.

Table 2. Details of milkfish sampling dates, fishpen code (cf. Fig. 2), number of fish collected and standard lengths (SL), total (TW) and gutted (GW) weights (Mean \pm Standard Deviation) of the fish sampled throughout the project

Sampling Date	Fishpen Code	No. of fish	SL (cm)	TW (g)	GW (g)
16.-17. June 1995	M1	80	13.2 \pm 1.1	45.8 \pm 11.6	37.9 \pm 9.7
7.-8. August 1995	M1	80	21.9 \pm 1.3	200.5 \pm 34.9	182.4 \pm 32.6
3.-4. October 1996	M2	120	11.3 \pm 1.9	26.5 \pm 15.3	22.0 \pm 13.5
6.-7. February 1997	M2	86	14.1 \pm 2.3	44.7 \pm 30.3	40.4 \pm 26.0
29.-30. April 1997	M2	85	14.7 \pm 2.8	48.6 \pm 28.0	44.2 \pm 25.9
19.-20. June 1997	M3	99	22.8 \pm 1.5	220.9 \pm 50.2	194.8 \pm 44.5
21.-22. August 1997	M3	88	30.5 \pm 1.4	528.0 \pm 66.7	495.8 \pm 63.3

Table 3. Specific Growth Rates, SGR, and Metabolic Growth Rates, MGR of milkfish between those sampling occasions when fish were collected from the same fishpen

Time Span	No. of Days	SGR (%)	MGR (g kg ^{-0.8} day ⁻¹)
16.6.1995 - 7.8.1995	52	2.8	16.5
3.10.1996 - 6.2.1997	126	0.4	1.1
6.2.1997 - 29.4.1997	82	0.1	0.6
19.6.1997 - 21.8.1997	63	1.4	10.9

b) Condition

The regression coefficient between the standard lengths and gutted weights was determined to be 3.238 ($SE_b = 0.0131$; $r^2 = 0.990$; $df = 642$, difference from 3.0 very highly significant [p for similarity <0.001] by Student's t-test), suggesting some measure of allometric growth in this species. This factor was used to calculate the individual condition factors K' for the different sampling days, the averages of which are summarised in Tab. 4. Condition is obviously highest in June and August, gradually drops to a low in the early part of the year and then rises again between April and June. This was presumably due to the water clearing as a results of saltwater intrusion and the subsequent algal blooms, improving feeding conditions for filter feeder such as milkfish. Fish condition was found to be significantly different for most times of the year (ANOVA and Duncan's multiple range test; Tab. 4). Again, there are significant differences not only for different times of year but also between matching seasons in different years.

c) Body Composition

The chemical composition of the fish obviously varies dramatically between different months (Tab. 4). The fat content decreases from October to April only to increase sharply before June to a level maintained in August. This fluctuation takes place mainly to the advantage or at the expense of moisture content while protein and ash content remained fairly constant on all sampling occasions. Fat and moisture content once again differed between almost identical times of the year in 1995 and 1997; furthermore, in 1995, there were obvious differences between June and August whereas these values did not differ so greatly in 1997.

Table 4. Mean condition factors and body composition (wet matter basis) of milkfish sampled throughout the project. Condition factors with different superscripts differ at $p < 0.05$

Sampling Date	Condition Factor K'	Crude Protein (%)	Lipid (%)	Ash (%)	Moisture (%)
16.-17. June 1995	0.510 ^a	17.3	6.3	2.7	74.0
7.-8. August 1995	0.479 ^b	17.0	11.1	2.8	68.3
3.-4. October 1996	0.456 ^c	16.0	3.9	2.7	75.8
6.-7. February 1997	0.410 ^e	18.3	2.9	3.3	74.1
29.-30. April 1997	0.378 ^f	17.1	0.6	1.9	77.6
19.-20. June 1997	0.445 ^d	16.8	10.6	2.8	67.6
21.-22. August 1997	0.447 ^{cd}	18.5	10.0	2.6	66.8

d) Food Composition

The most prominent item in the diet of milkfish in Laguna de Bay was amorphous detritus which was not only found in considerable quantities in the stomachs of all fish analysed here but made up well over half the contents at all times of day on several sampling occasions (Fig. 6). The other component that was virtually never absent in the stomachs analysed were diatoms of the genus *Coscinodiscus*, although these were frequently only present at trace level. In February 1997, however, *Coscinodiscus sp.* made up a substantial portion of the stomach contents (Fig. 6b). The October 1996 sampling caught the tail end of the heavy September bloom of the blue-green alga *M. aeruginosa*, which was reflected in the diet of milkfish sampled at that time (Fig. 6a). This was not the case with a similar, protracted bloom of the cyanobacterium *Oscillatoria sp.* in June 1997: although this alga was present in such numbers as to turn the water green, only small amounts were detected in the stomach contents of milkfish sampled at the time (Fig. 6d).

There was very little variability over the 24-hour period in the stomach contents of fish analysed on any particular sampling day. Most were obviously filter-feeding pelagically, ingesting detritus and algae. Differences between fish caught on the same sampling occasions were found mainly in June 1997 (Fig. 6d) when some individuals caught around midnight had been feeding mainly on the bottom. This was demonstrated by the presence of large amounts of sediment and fibrous detritus (probably dead plant material) as well as some

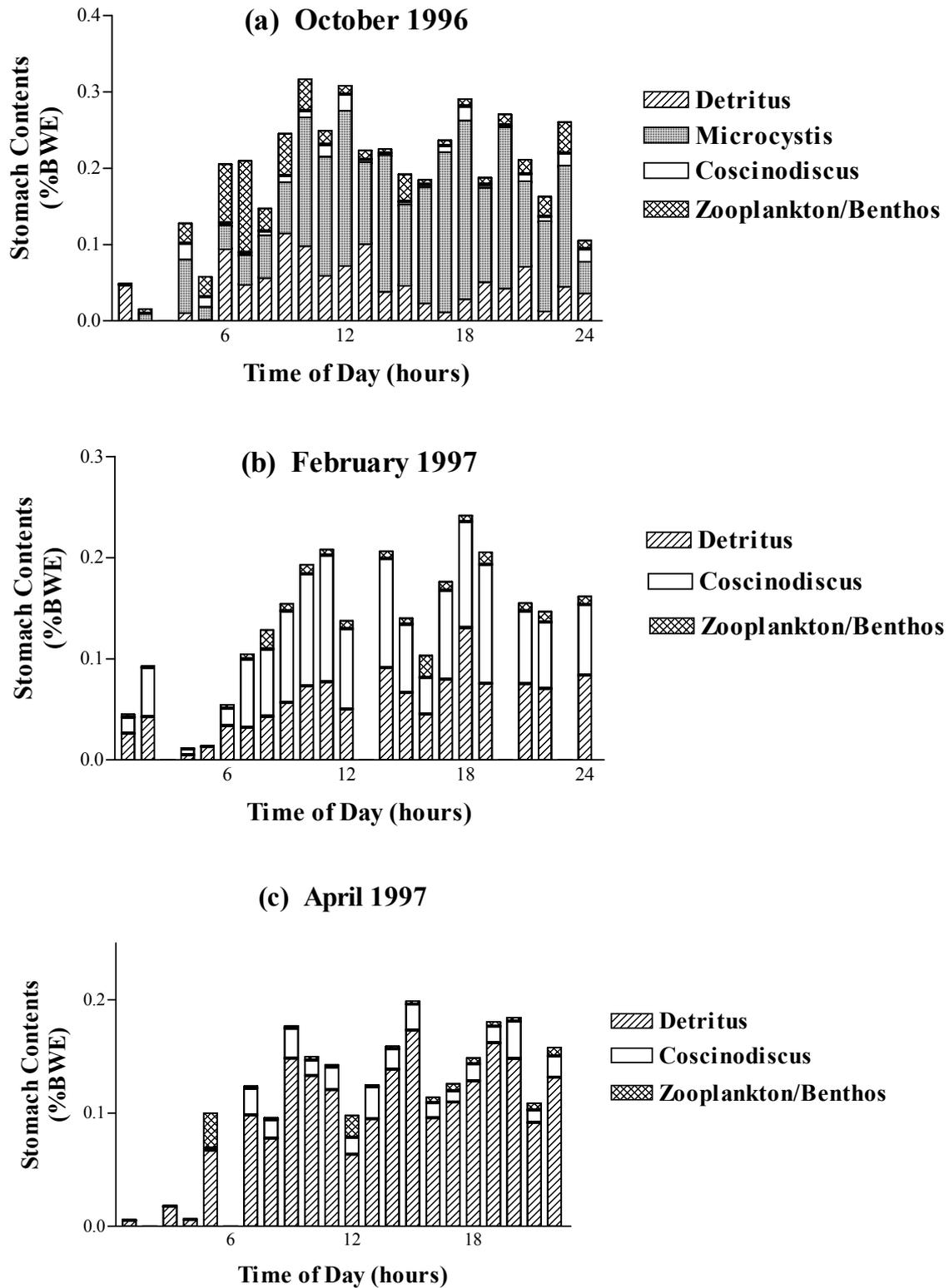


Figure 6. Stomach content composition of milkfish sampled throughout the project. Each bar represents the average of up to five fish. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Note different Y-axis scales. (a) October 1996 (b) February 1997 (c) April 1997

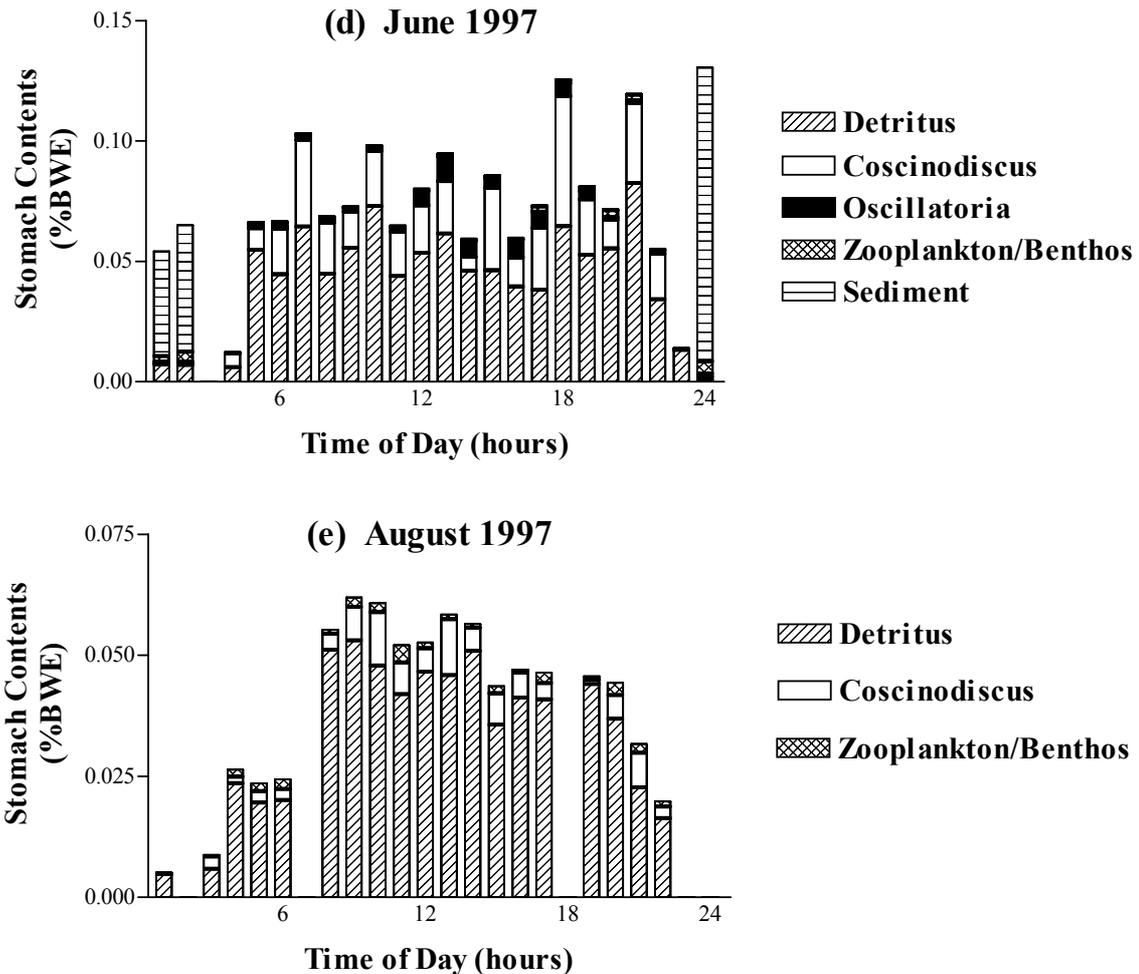


Figure 6 (cont.). Stomach content composition of milkfish sampled throughout the project. Each bar represents the average of up to five fish. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Note different Y-axis scales. (d) June 1997 (e) August 1997

ostracods in their stomachs. These fish had a distinctly higher level of stomach fullness than others which were filter-feeding so that they were deleted from the MAXIMS analysis in order to avoid distortions in the regression curve.

The visual comparison between the stomach and rectal contents suggested that *Coscinodiscus sp.* and *Oscillatoria sp.* were digested with great efficiency. There was no trace of the latter in the rectal content of any fish analysed. In the case of diatoms, the siliceous shells were perfectly preserved after passage through the gut but lacked any content so that the organic material may again be presumed to have been completely digested. When *M. aeruginosa* was ingested, on the other hand, large lumps consisting of numerous cells of this species were discovered intact in the rectum. It is possible that these were protected by

their gelatinous coating. It was not clear whether milkfish were able to remove this protective layer, e.g. by abrasion, from at least some of the colonies and digest them, in which case *M. aeruginosa* would have been at least of some use to this species. It is difficult to estimate the digestibility of detritus since this material was practically without structure to start with but it was noticed that the rectal contents consisted of appreciable quantities of material of similar appearance. The same considerations therefore apply for detritus as for *M. aeruginosa*: while it is possible that some of this was digested and assimilated, the digestibility must have fallen well short of 100%.

e) Feeding Periodicity & Daily Ration

A comparison of the level of stomach fullness at different times of the day demonstrates that milkfish in Laguna de Bay have a very prolonged feeding period, starting before dawn and lasting well into the night. Indeed, the stomachs were generally found to be wholly or nearly empty only for a short time after midnight (Fig. 7). The MAXIMS analysis generally supports this (Tab. 5); the model predicted that feeding started between 3:00 and 5:00 hours and usually finished between 22:00 and 23:30. The feeding period observed in October 1996 was particularly long (19h 38mins), while the shortest feeding period was found in August 1997 (16h 9mins), mainly because on this occasion, the fish ceased feeding only a little after sunset.

After deleting the data points pertaining to fish with sediment in their stomachs, the daily rations calculated with the aid of the MAXIMS model for the 1996 and 1997 samplings were fairly similar for most months (Tab. 5). A considerably lower value was only observed in August 1997, partly attributable to the shorter feeding period for this sampling occasion.

Although bigger fish consume more than smaller ones under the same conditions, it is known that bigger fish generally consume less relative to their body size (Jobling 1994). Since the fish sampled here differed considerably in size between the sampling months, this was compensated by converting the daily rations to $\text{g}[\text{food}] \text{kg}[\text{body-mass}]^{-0.8} \text{day}^{-1}$ (Tab. 5), a conversion previously employed by Dabrowski *et al.* (1986). When examined on this basis, there were almost no differences in the daily rations recorded for the first few samplings in 1997, despite the strongly contrasting growth rates for these periods. The difference between the relatively low daily ration calculated for August 1997 and the other months of that year was reduced a little by allowing for metabolic fish size; nevertheless, even on a metabolic

Table 5. MAXIMS parameters (F_b , F_s , J_1 , E), the daily ration calculated from them (R_d) and the ingestion rate and daily ration converted to metabolic basis ($\text{g kg}^{-0.8} \text{ day}^{-1}$) for milkfish sampled between October 1996 and August 1997. Standard errors are given in brackets. Parameter estimates and daily rations with different superscripts differ at $p < 0.05$

Parameter (units)	Oct. 1996	Feb. 1997	April 1997	June 1997	Aug. 1997
No. of fish	118	84	83	87	88
Feed begin, F_b (time of day)	3:22 ^c (34.3 mins)	4:55 ^a (30.8 mins)	4:59 ^b (27.7 mins)	3:52 ^b (13.5 mins)	3:17 ^c (22.2 mins)
Feed stop, F_s (time of day)	23:00 ^a (58.3 mins)	23:19 ^a (27.4 mins)	22:00 ^b (210.0 mins)	22:00 ^b (20.2 mins)	19:26 ^c (18.8 mins)
Ingestion rate, J_1 (%BWE h^{-1})	0.15 ^a (0.070)	0.12 ^b (0.048)	0.13 ^b (0.068)	0.08 ^c (0.035)	0.03 ^d (0.005)
Evacuation Rate, E (h^{-1})	0.66 ^c (0.306)	0.66 ^c (0.275)	0.85 ^b (0.483)	1.01 ^a (0.442)	0.51 ^d (0.107)
Daily Ration, R_d (%BWE day^{-1})	3.02 ^a (1.467)	2.19 ^b (0.878)	2.14 ^b (1.405)	1.46 ^c (0.627)	0.43 ^d (0.087)
Ingestion Rate ($\text{g kg}^{-0.8} \text{ h}^{-1}$)	0.74	0.64	0.69	0.61	0.23
Daily Ration ($\text{g kg}^{-0.8} \text{ day}^{-1}$)	14.60	11.77	11.68	10.77	3.78

basis the daily ration was rather lower than those determined for the remainder of the study period.

3. Nile tilapia

a) Condition

The standard lengths and total weights of the tilapia collected on different sampling occasions are summarised in Tab. 6. The smallest fish caught were little more than fingerling sized but the largest were well short of what would be required to consider them marketable. Unlike in the case of the milkfish, the data set collected here therefore only covers the lower section of the size range encountered among cultured Nile tilapia in Laguna de Bay.

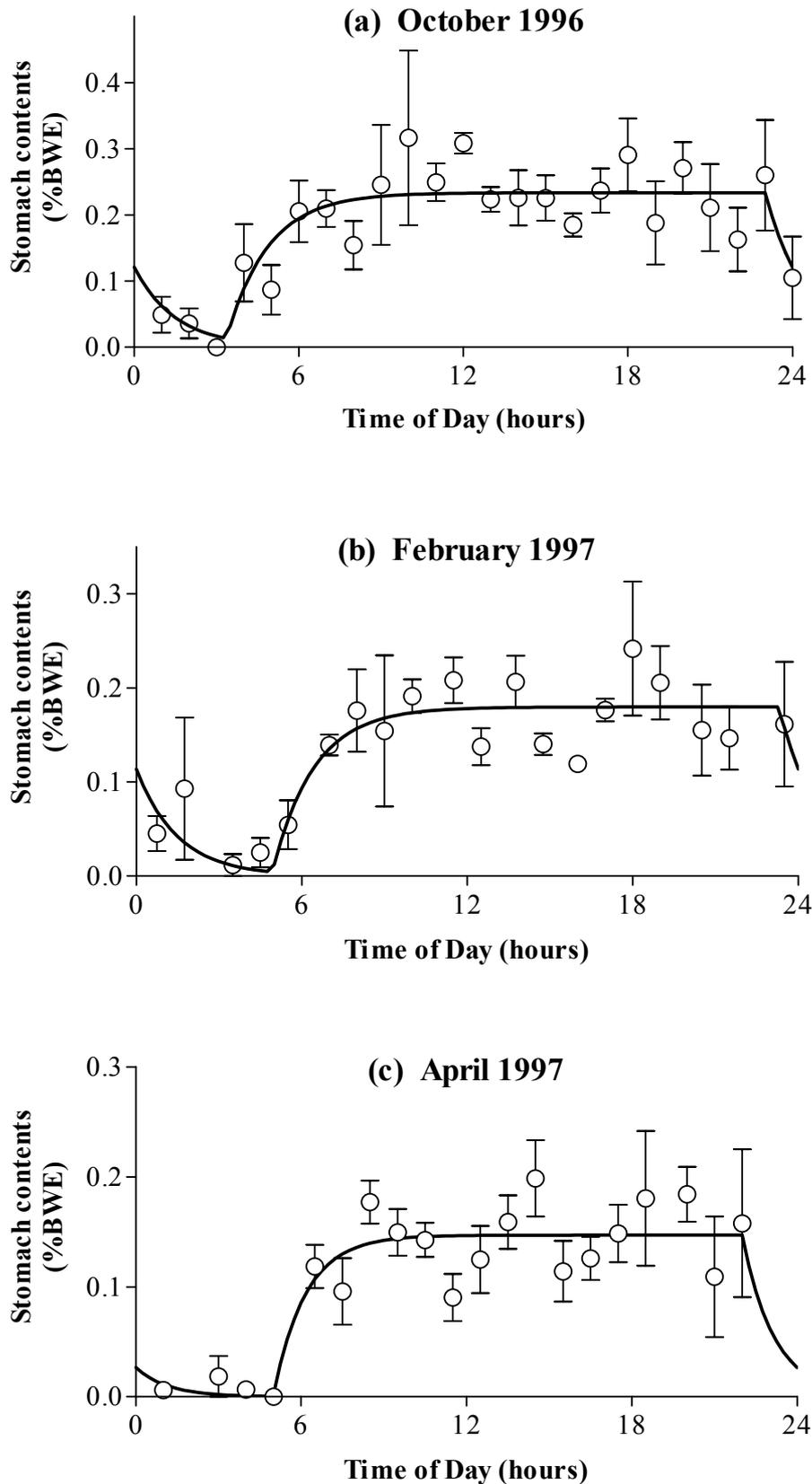


Figure 7. Mean observed stomach contents \pm standard deviations (\odot) and MAXIMS curves (—) for milkfish sampled throughout the project. Each data point represents the average of up to five fish. Note different Y-axis scales. (a) October 1996 (b) February 1997 (c) April 1997

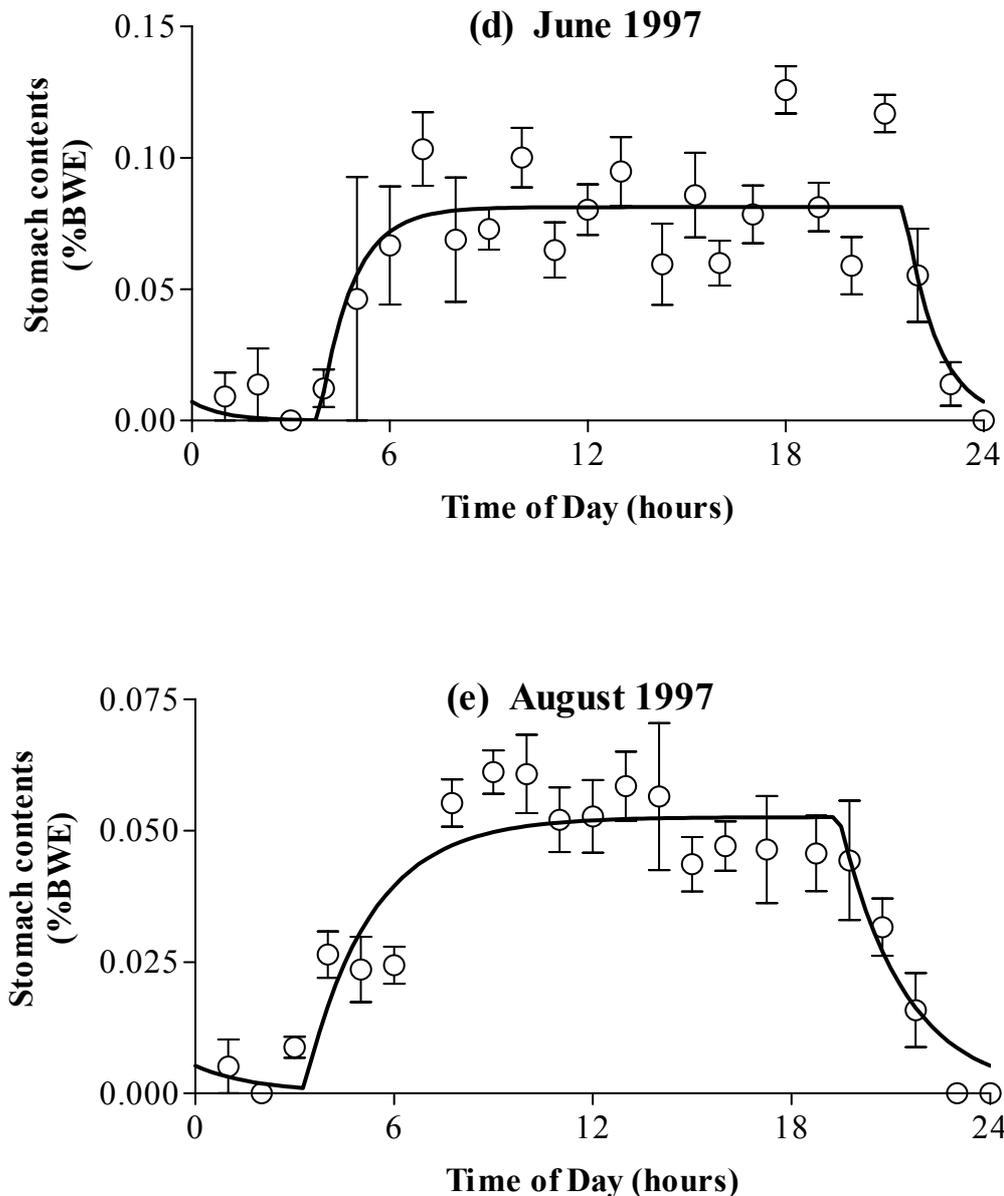


Figure 7 (cont.). Mean observed stomach contents \pm standard deviations (\bigcirc) and MAXIMS curves (—) for milkfish sampled throughout the project. Each data point represents the average of up to five fish. Note different Y-axis scales. (d) June 1997 (e) August 1997

The condition of this species follows a similar pattern to that of milkfish (Tab. 7): the condition factors reach a peak around the middle of the year towards the end of the season of clear water but, in contrast to milkfish, the lowest values were not recorded just before saltwater intrusion but in January 1997. Differences were again observed for the same seasons in different years with the results obtained in May 1995 significantly higher than those for May 1996 and comparable to those collected in July 1996. It should be noted that practically no differences were recorded for fish kept with and without supplemental feed in

Table 6. Details of Nile tilapia sampling dates, number of fish collected and standard lengths (SL), total (TW) and gutted (GW) weights (Mean \pm Standard Deviation) of the fish sampled throughout the project

Sampling Date	No. of Fish	SL (cm)	TW (g)	GW (g)
28-29. May 1995				
- Large Fish	40	8.97 \pm 0.53	31.5 \pm 6.01	27.7 \pm 5.37
- Small Fish	40	6.14 \pm 0.62	9.8 \pm 3.58	8.4 \pm 2.89
4-5. August 1995	80	12.21 \pm 1.20	81.7 \pm 23.83	71.6 \pm 21.31
19-20. March 1996	120	10.04 \pm 1.28	41.0 \pm 11.37	35.3 \pm 9.77
16-17. May 1996	120	9.07 \pm 1.70	30.5 \pm 14.30	26.8 \pm 12.67
17-18. July 1996	110	8.97 \pm 1.47	32.5 \pm 14.99	27.8 \pm 12.9
26-27. Sept. 1996				
- Supplemented Fish	120	8.41 \pm 1.20	25.1 \pm 8.13	21.0 \pm 7.00
- Unsupplemented Fish	120	8.59 \pm 0.92	25.3 \pm 8.27	21.6 \pm 7.18
14-15. Jan. 1997				
- Supplemented Fish	120	7.53 \pm 0.78	15.4 \pm 5.54	13.2 \pm 4.84
- Unsupplemented Fish	120	7.52 \pm 0.73	14.8 \pm 4.95	13.0 \pm 4.53

September 1996 and January 1997, despite the fact that these had been on their respective feeding regime for about a month prior to the experiment.

b) Body Composition

The body composition of tilapia reflects the time of year at which the samples were taken in a manner similar to that of the condition factors (Tab. 7). Maximum water content was found at the beginning of the year, which was also the time of minimum protein and lipid content. This continues up to about the time of seawater intrusion, after which protein and particularly lipid increase to displace body water. After the water becomes turbid again, the trend is reversed once more. At the same time, differences were found between 1995 and 1996 for similar times of the year with higher lipid values found in the former of the two. Lipid content in tilapia was never as high as that recorded for milkfish at times of algal bloom following saltwater intrusion.

Table 7. Mean condition factors and body composition (wet matter basis) of Nile tilapia sampled throughout the project. Condition factors with different superscripts differ at $p < 0.05$

Sampling Date	Condition Factor <i>K</i>	Crude Protein (%)	Lipid (%)	Ash (%)	Moisture (%)
28-29. May 1995	3.647 ^b	15.5	2.6	3.4	76.3
4-5. August 1995	3.828 ^a	15.5	4.1	4.5	75.1
19-20. March 1996	3.353 ^c	13.5	0.8	4.3	80.4
16-17. May 1996	3.318 ^c	13.0	0.7	4.4	80.2
17-18. July 1996	3.598 ^b	15.3	1.5	4.1	77.6
26-27. Sept. 1996					
- Supplemented Fish	3.356 ^c	14.4	1.1	4.9	78.2
- Unsupplemented Fish	3.308 ^c	13.9	1.1	5.3	78.6
14-15. Jan. 1997					
- Supplemented Fish	2.981 ^d	12.5	0.8	5.0	80.5
- Unsupplemented Fish	2.976 ^d	13.2	0.8	4.6	79.8

The proximate composition of the supplemental feed given to the tilapia (pellets in 1995, powder in 1996 & 1997) is summarised in Tab. 8. The composition varied a little between the two types of feed, particularly with respect to protein content which, surprisingly, fell somewhat short of the manufacturer's guaranteed analysis (Cruz 1997) in both pellets and powder. The moisture content is also somewhat high and it is likely that the feed had been stockpiled for some time and may have taken on moisture in the humid, tropical climate. The increased moisture content could also explain the reduction in protein content relative to the MGA. The high level of nitrogen-free extract reflected the fact that in the Philippines, fish feeds include large proportions of carbohydrates from plant products, such as copra meal, rice bran, yellow corn and soybean.

c) Food Composition

As in the case of milkfish, the food of Nile tilapia was composed mainly of amorphous detritus on most sampling days (Fig. 8), the remainder usually consisting of plankton and, when provided, supplemental feed. Algae again made up the major share of the ingested plankton but only constituted a significant part of the stomach contents when

Table 8. Proximate composition of the supplemental feed (Robina Starfeeds, Universal Robina Corporation) given to Nile tilapia in August 1995, September 1996 and January 1997. Manufacturer's guaranteed analysis (MGA; minimum values for protein and lipid, maximum values for all other components) is included for the sake of comparison

Feed Type	Month(s)	Crude Protein (%)	Lipid (%)	Ash (%)	Fibre (%)	NFE (%)	Moisture (%)
Grower (Pellets)	8/95	25.6	6.1	6.2	4.8	40.5	16.8
MGA	-	30.0	4.0	14.0	6.0	-	13.0
Starter (Crumble)	9/96, 1/97	28.6	5.3	8.9	4.6	38.1	14.4
MGA	-	35.0	4.0	12.0	9.0	-	13.0

they were blooming, as was the case for *Anabaena spiroides* in May 1995, *Ceratium hirundinella* in July 1996 and *M. aeruginosa* in September 1996. *Coscinodiscus sp.* was present in practically all stomachs on all sampling occasions but once more contributed little to the total contents. Zooplankton in the stomachs was mainly made up of the smaller plankters, such as rotifers and the cladoceran *Bosmina longirostris* Müller 1785. While unsupplemented tilapia evidently had a similar food spectrum to milkfish, the main difference observed was in those items of benthic origin. Unlike milkfish, which consumed ostracods, sediment and fibrous detritus, tilapia occasionally ingested filamentous green algae and amphipods of the genus *Corophium*, particularly in March and May 1996. Both of these were found growing on the netting which the fishcages were made of.

In contrast to milkfish, there were occasions when the stomach content composition of tilapia fluctuated markedly over the daily cycle. This was most obvious in those cases where supplemental feed was given (Fig. 8c,g,i) since this food type was provided in only one or two doses per day. Just after feeding, supplemental feed usually made up the major share of the stomach contents but its contribution to ingested matter rapidly declined as it was evacuated and replaced by natural food. In consequence, it had usually disappeared almost entirely from the stomach contents within 6 hours after supplementation (August 1995 and September 1996; Fig. 8c,g) unless a second dose was given later (January 1997; Fig. 8i).

Marked differences in the stomach content composition over the day were, however, observed even on some occasions when the fish were not provided with supplemental feed. The most obvious case was the data for July 1996 (Fig. 8f). When the fish started feeding

around dawn, they ingested mostly detritus but later, at about 10:00 hours, algae in the form of the dinoflagellate *C. hirundinella* made up relatively more of the material consumed. Around 14:00 hours, the contribution of this species to the stomach contents started to decline again and never reached its former high that sampling day. In accordance with these changes, the level of stomach fullness, which had started to level off a little around mid-morning, increased markedly around 10:00 hours and decreased slowly around 13:00 hours. The most obvious explanation is the arrival of a localised bloom of this alga which drifted through the sampling area in the period between 10:00 and 14:00 hours and which had to be taken into account when modelling the stomach contents with MAXIMS for daily ration estimation. A second example of changing stomach content composition in unsupplemented fish was seen in September 1996 when the proportion of detritus in the stomach contents started to increase around mid-afternoon in both fed and unfed fish (Fig. 8g,h) at the same time as the overall level of stomach fullness increased above that which would have been expected if the ingestion rate had remained constant. As a result, the MAXIMS model again had to be adapted to allow for this.

The estimated digestibility of the stomach content components of Nile tilapia was similar to that of milkfish. Diatoms and *Oscillatoria sp.* were almost fully digestible, as was *C. hirundinella*, whose thin cell wall was already broken down into fragments in the stomach. *M. aeruginosa*, on the other hand, was again present in large lumps in the rectum so that it is unlikely that it was digested any more than in milkfish. The spiral colonies of *A. spiroides* were broken up into smaller fragments through the intestinal passage and the cells appeared leached. It is therefore probable that this species was digested to a greater degree than *M. aeruginosa* but not as well as *Oscillatoria sp.* The filamentous green algae ingested in the first half of 1996 were digested to some extent since the cell contents looked shrunk inside their cellulose cell wall by the time they reached the rectum, but digestion was again rather low. The utilization of detritus was again not clear but, since material of similar appearance was present in large quantities in the rectum, the same considerations apply as for milkfish.

d) Feeding Periodicity & Daily Ration

In contrast to milkfish, the feeding periodicity of Nile tilapia in Laguna de Bay was more strongly linked to the hours of daylight which in Laguna de Bay, as elsewhere in the tropics, were confined to between around 5:30 and 18:30 for most of the year. This was demonstrated by the fact that the stomachs of tilapia were wholly or nearly empty for longer

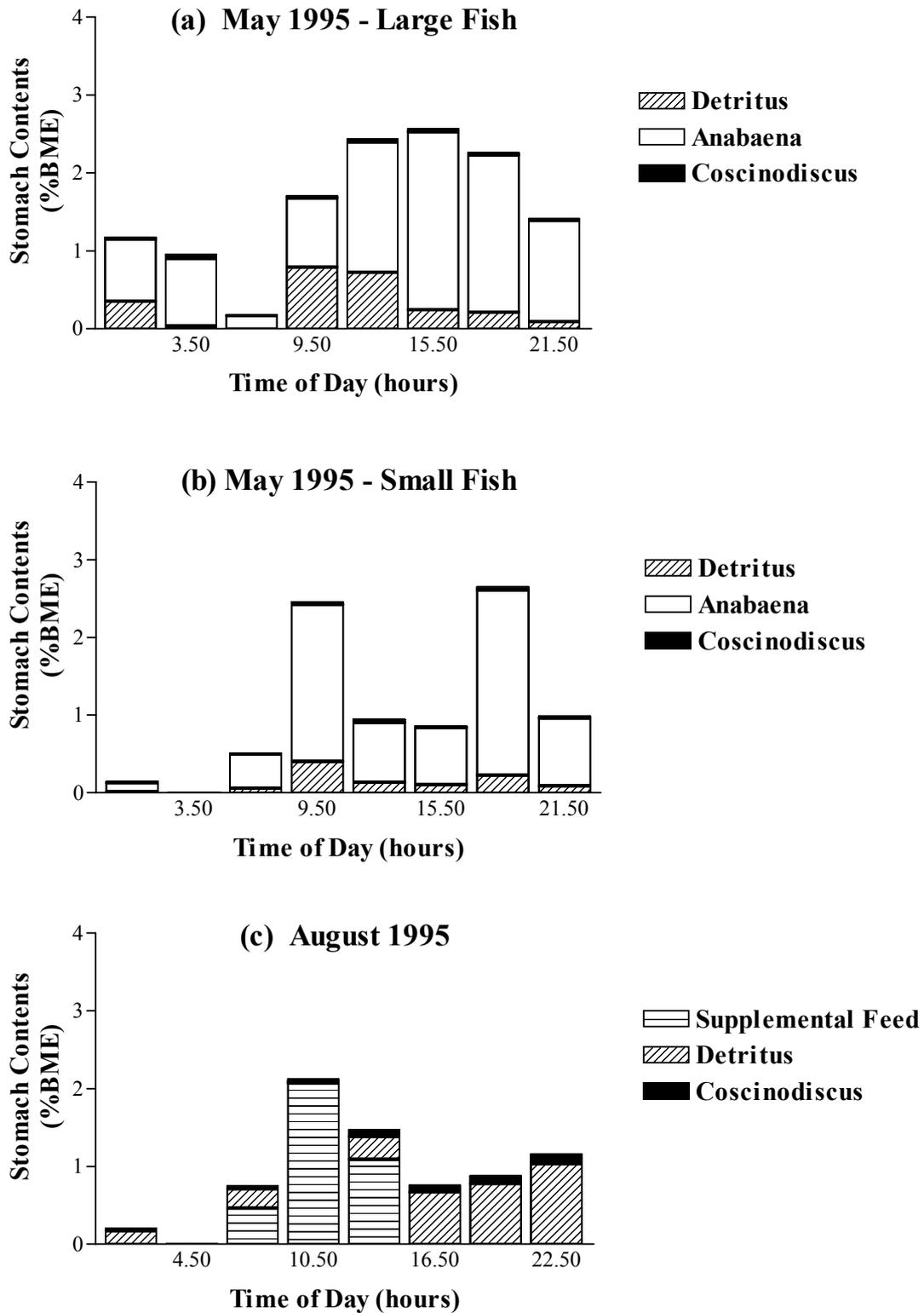


Figure 8. Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (a) May 1995 - large fish (b) May 1995 - small fish (c) August 1995

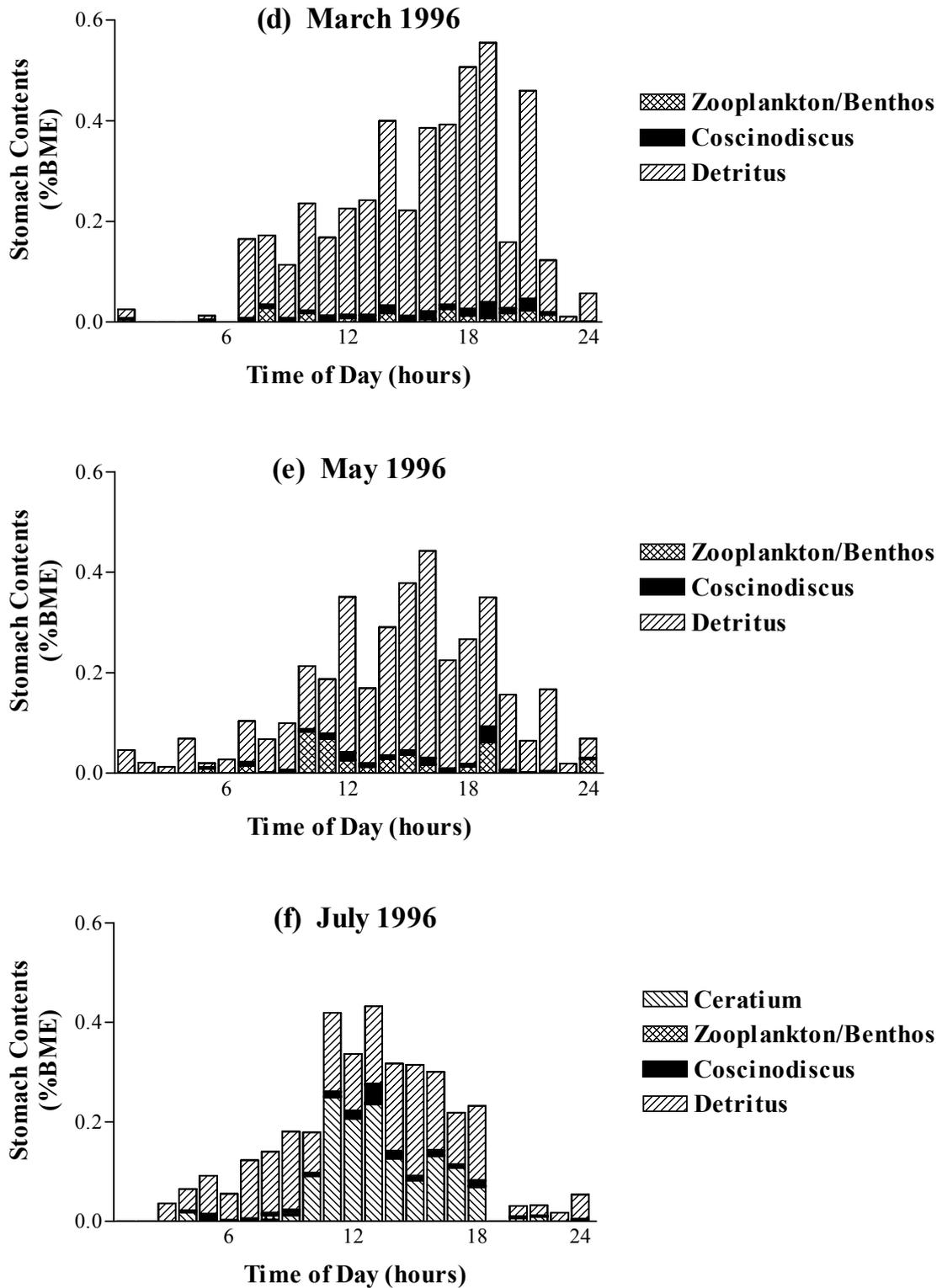
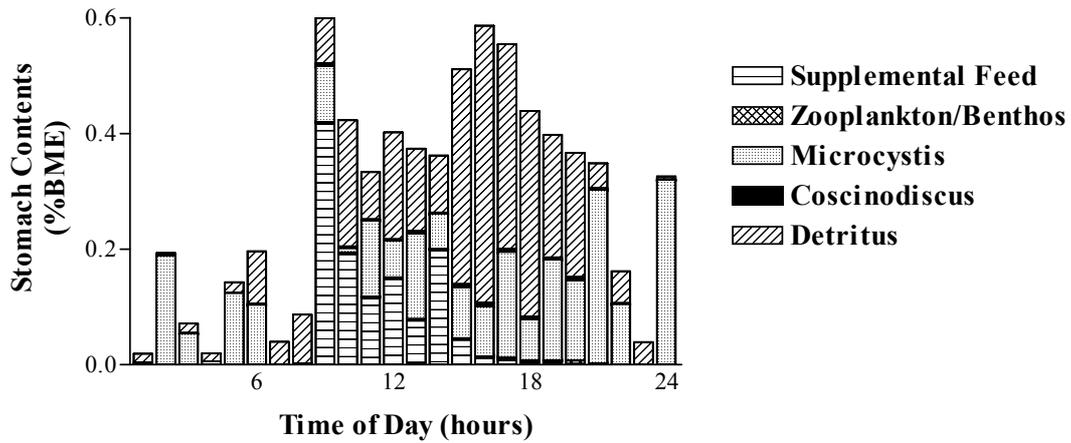
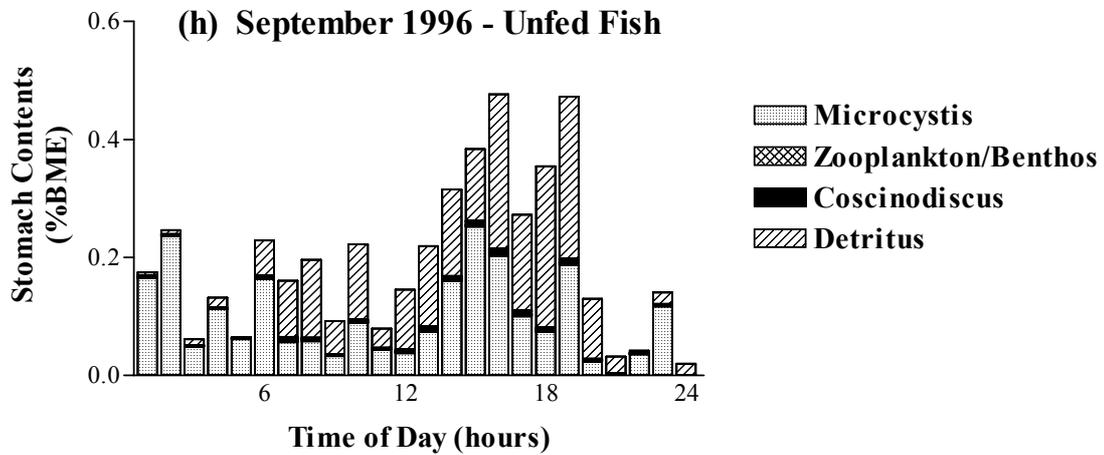


Figure 8 (cont.). Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (d) March 1996 (e) May 1996 (f) July 1996

(g) September 1996 - Fed Fish



(h) September 1996 - Unfed Fish



(i) January 1997 - Fed Fish

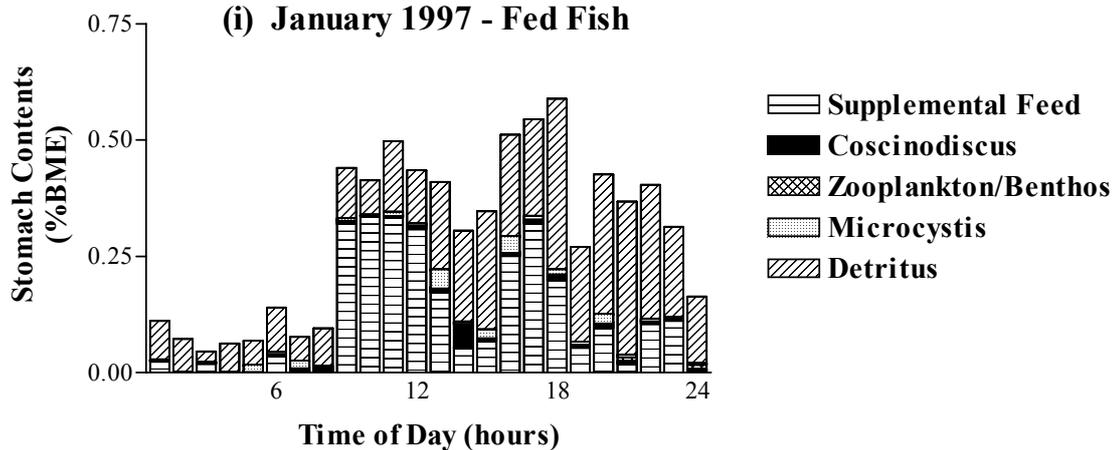


Figure 8 (cont.). Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. g) September 1996 - supplemented fish (h) September 1996 - unsupplemented fish (i) January 1997 - supplemented fish

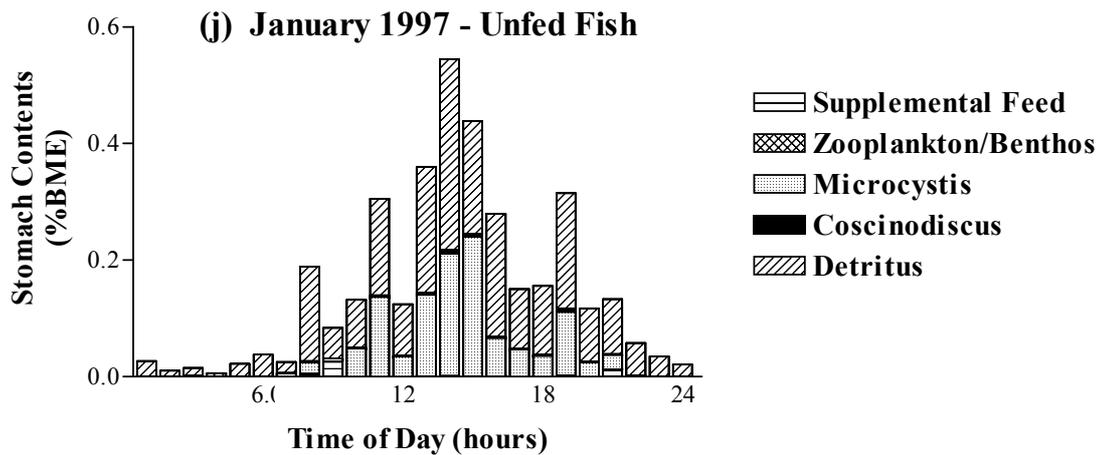


Figure 8 (cont.). Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (j) January 1997 - unsupplemented fish

periods at night (Fig. 9). However, in some cases, feeding activity could also be observed during the hours of darkness whereas in others, the fish ceased feeding before the sun had set. In one case (September 1996, unfed fish), sporadic feeding was recorded throughout the entire night, making it impossible to fit a MAXIMS curve since the precise values for the evacuation rate as well as the end of the feeding period could not be determined. Generally, unsupplemented fish had only one feeding period per sampling day but the smaller fish collected on the first sampling occasion (May 1995) ceased feeding around midday until mid-afternoon so that two ingestion phases were observed.

For each sampling day, daily ration estimates were again obtained by modelling the change in stomach content over the 24-hour cycle and integrating the ingestion rate over the feeding period. As mentioned previously, it was possible to achieve this by using the conventional MAXIMS model only in those cases in which the rate of ingestion remained more or less constant over the feeding period. This was the case for the fish sampled in May 1995 (large size group), March 1996, May 1996 and January 1997 (unsupplemented fish), which were all analysed with Model 1.1, as well as the May 1995 (small size group) fish which were investigated with Model 2.1 since these had two feeding periods. The results of these analyses are summarised in Figure 9a,b,d,e,i and Table 9. There is obviously only one ingestion rate (J_1 -general) in these models which applies to the period defined by F_b -general and F_s -general (two such periods in the case of the small fish in

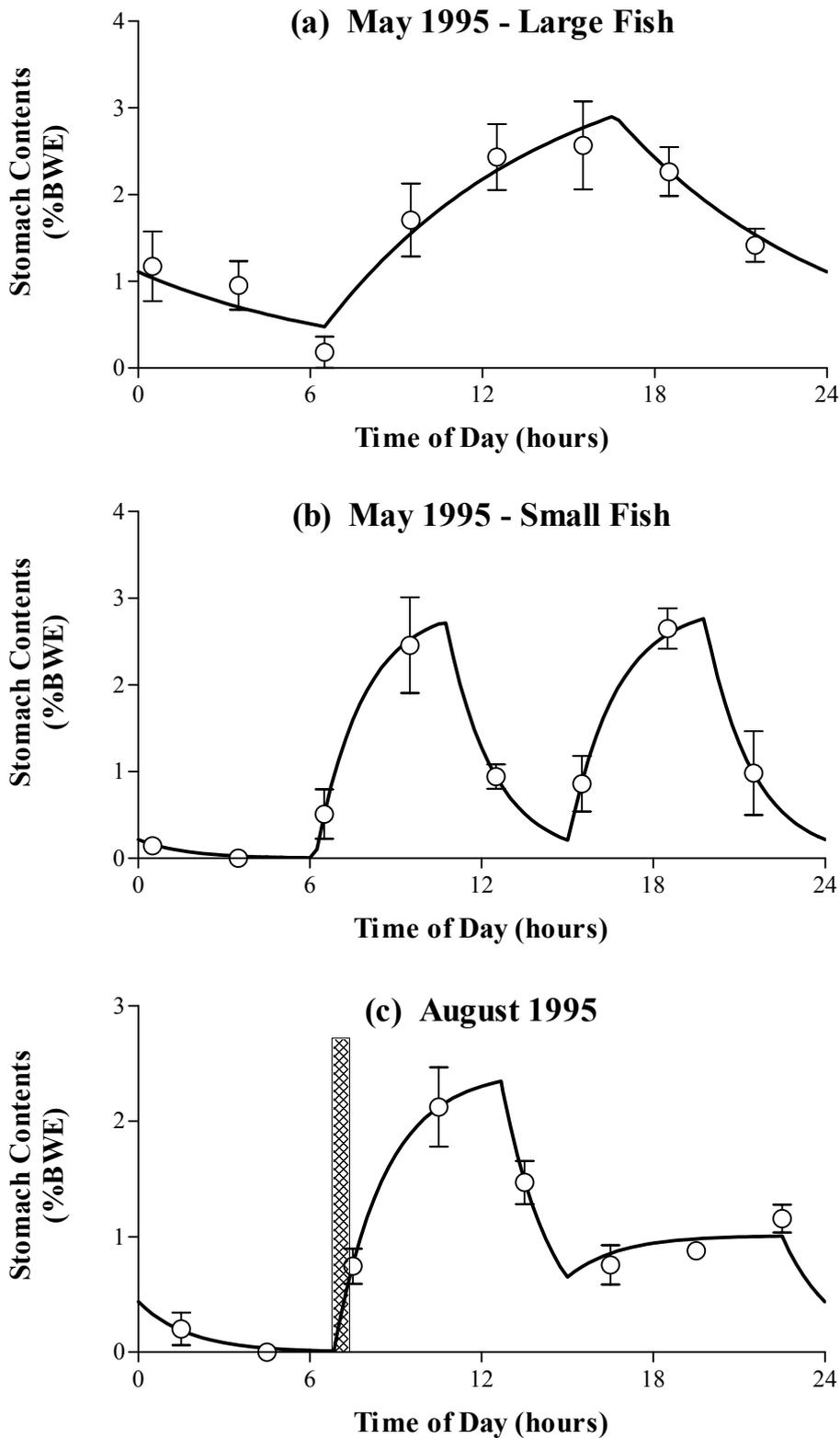


Figure 9. Mean observed stomach contents \pm standard deviations (\bigcirc) and MAXIMS curves (—) for Nile tilapia sampled throughout the project. Each data point represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (a) May 1995 - large fish (b) May 1995 - small fish (c) August 1995 ▨ denotes supplemental feed given at that time of day

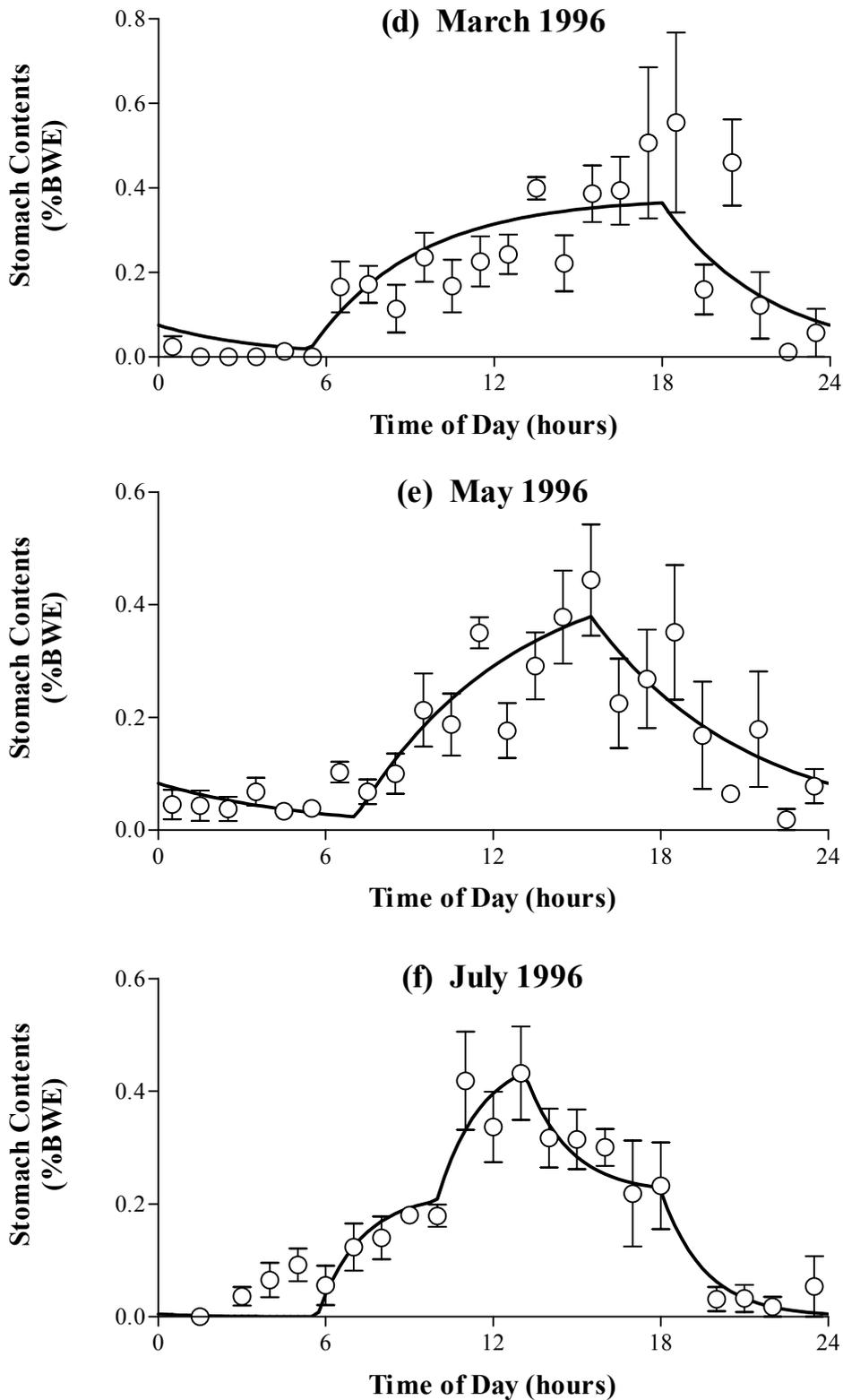


Figure 9 (cont.). Mean observed stomach contents \pm standard deviations (\bigcirc) and MAXIMS curves (—) for Nile tilapia sampled throughout the project. Each data point represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (d) March 1996 (e) May 1996 (f) July 1996

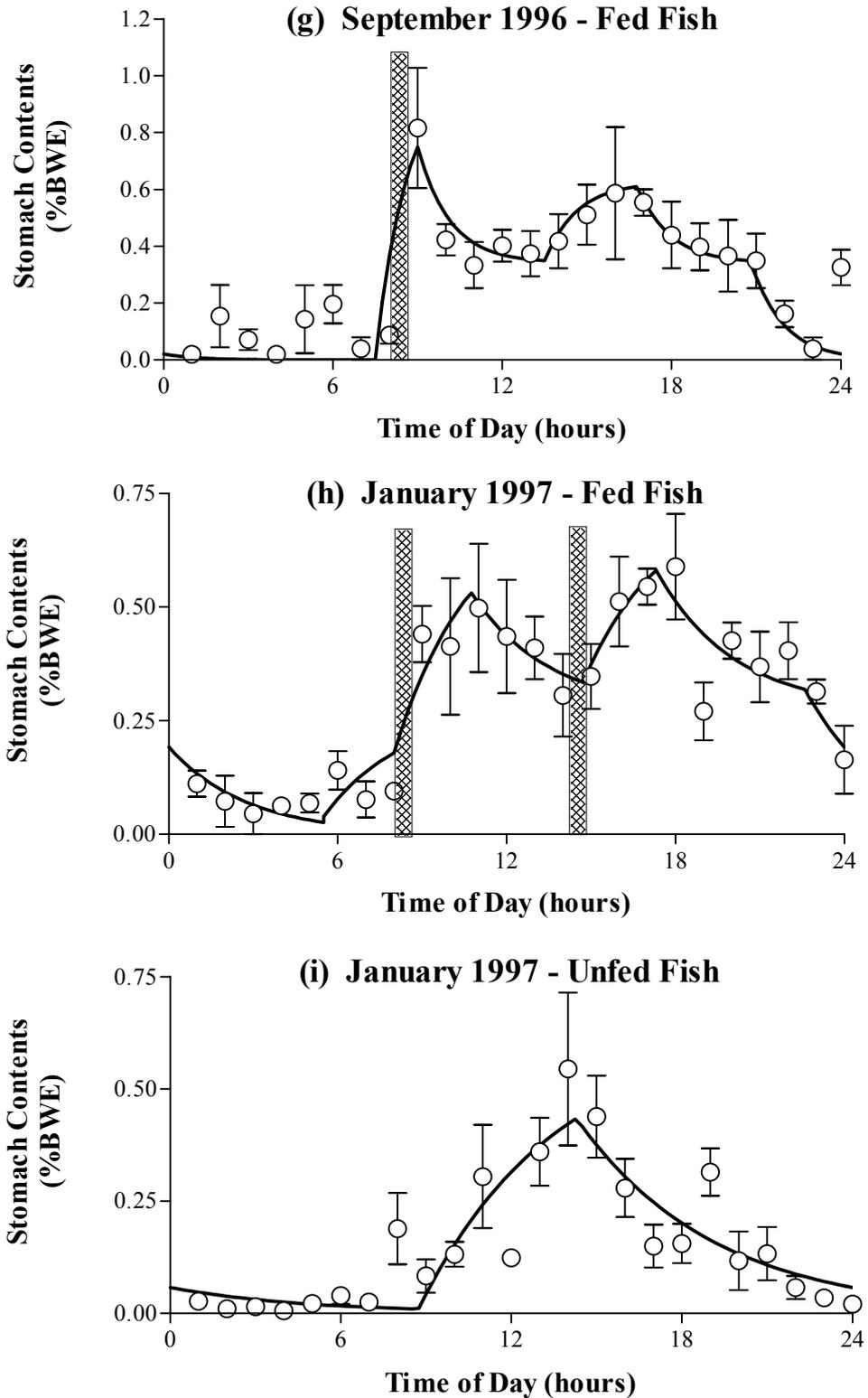


Figure 9 (cont.). Mean observed stomach contents \pm standard deviations (\bigcirc) and MAXIMS curves (—) for Nile tilapia sampled throughout the project. Each data point represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (g) September 1996 - supplemented fish (h) January 1997 - supplemented fish (i) January 1997 - unsupplemented fish. ▨ denotes supplemental feed given at that time of day

May 1995). The daily rations and their confidence limits have been determined in the same way as for milkfish (App. 3).

The remaining samplings had to be treated with models specially designed for the dataset in question in order to arrive at a daily ration estimate. For this purpose, the feeding phase was split into several subphases (with or without non-feeding phases to separate them), each with its own ingestion rate which was nevertheless kept constant for the subphase to which it applied. These special models incorporated the following specific assumptions with regard to the feeding rate:

- August 1995 (Fig. 9c) - two distinct feeding periods, ingestion rate high (J_1 -feed) for the first period (F_b -feed 1 - F_s -feed 1), low (J_1 -general) for the second period (F_b -general - F_s -general)
- July 1996 (Fig. 9f) - one feeding period, ingestion rate high (J_1 -*Ceratium*) when *Ceratium* was ingested (F_b -*Ceratium* - F_s -*Ceratium*), low (J_1 -general) at other times (F_b -general - F_b -*Ceratium* and F_s -*Ceratium* - F_s -general)
- September 1996, supplemented fish (Fig. 9g) - one feeding period, ingestion rate high (J_1 -feed) when supplemental feed was eaten (F_b -feed 1 - F_s -feed 1), moderate (J_1 -detritus) when excessively large quantities of detritus were consumed (F_b -detritus - F_s -detritus), low (J_1 -general) at other times (F_s -feed 1 - F_b -detritus and F_s -detritus - F_s -general)
- January 1997, supplemented fish (Fig. 9h) - one feeding period, ingestion rate high (J_1 -feed) during the two phases when feeding on supplemental feed (F_b -feed 1 - F_s -feed 1 and F_b -feed 2 - F_s -feed 2), low (J_1 - general) at other times (F_b -general - F_b -feed 1, F_s -feed 1 - F_b -feed 2 and F_s -feed 2 - F_s -general)

The parameter estimates and daily rations calculated with the conventional and special models for the various sampling days are also summarised in Table 9. On those occasions when supplemental feed was given, the separate contributions of this component and natural food to the total ration were determined by integrating the feeding rate only over

that part of the feeding period during which the respective food type was consumed. As mentioned previously, only the wet stomach weights were available for the May and August 1995 samplings. It was impossible to construct any type of model for the data set obtained in September 1995 (unsupplemented fish) since there was no way of obtaining a reliable evacuation rate estimate.

The average regression coefficients between back-calculated wet and observed dry weights for the 1996 and 1997 samplings was 0.167 (range: 0.109-0.232). Despite the fact that the dry matter content of supplemental feed is much higher than this, a comparison between those fish with only this component in their stomachs (sampled immediately after supplementation) and fish feeding only on natural food (sampled immediately before supplementation) did not reveal great differences. This demonstrates that, once ingested, supplemental feed is quickly moistened with the aid of gastric juices or water swallowed specifically for this purpose before it can be processed. The ingestion rate and daily ration estimates for the 1995 samplings were converted by multiplication with the factor 0.167. None of the other parameters would have been affected and have been left unchanged. A statistical comparison between the various sampling occasions was only possible for the evacuation rate and the daily ration since these were the only factors common to all sampling days. This was again done with the aid of a Tukey-Kramer test for unplanned comparisons at a $p \leq 0.05$ significance level; the results of this analysis are included in Table 9.

There was evidently more variation in the daily ration estimates between different sampling days for Nile tilapia than for milkfish. In particular, the occurrence of algal blooms (*Anabaena* in May 1995, *Ceratium* in July 1996, *Microcystis* in September 1997) was reflected in the diet to a better degree: the three highest food consumption values for natural food were recorded on these occasions and only the large fish sampled in May 1995 fell well short of these. Supplemental feed, on the other hand, was consumed inefficiently, making up only 65%, 25% and 55% of the total food in August 1995, September 1996 and January 1997 respectively, and even in August 1995 when comparatively least was given (5.4% BME when converted to a [dry weight food] : [wet weight fish] basis), the fish consumed only 1.26% BME, i.e. less than a quarter of the food provided.

B. Tilapia Growth & Water Quality Study

2. Water Quality

a) Secchi Depth

The Secchi depth fluctuated markedly over the study period as a whole, reaching maximum values of 90cm and minimum values of 15cm (Fig. 10). Nevertheless, three distinct phases can be identified in the pattern. The first phase (hereafter Phase 1) was characterised by consistently low Secchi visibility (15cm) and lasted from the beginning of the experiment up to the end of April when saltwater intrusion was first recorded in the lake (SEAFDEC 1998). The spread of saline water to the study area in early May was aided by light westerly winds around mid-May, initiating the second phase (hereafter Phase 2) in which Secchi depth remained consistently high (90cm). This phase lasted until the end of July when the onset of the monsoon winds stirred up the water, causing the Secchi depth to drop to 20cm between 23. July and 12. August. Thereafter, the Secchi depth increased again and for the remainder of the study period (hereafter Phase 3) fluctuated between 40-60cm but never again reached its former high. In summary, the study period was divided into three phases defined principally by environmental conditions, being separated by saltwater intrusion in early May and the arrival of the monsoon season in early August.

b) Chlorophyll-a

There was no clear pattern in the overall Chl-a concentrations throughout the study period; several peaks and troughs were recorded but these did not follow the three phase pattern observed for Secchi depth. Nevertheless, once the three size fractions are analysed separately, the three phases are once again evident (Fig. 11). In Phase 1, all Chl-a was found in the small fraction where, despite the extremely turbid water conditions, it was sometimes found at high levels. The results of the SEAFDEC phytoplankton samples suggest that the most likely source of Chl-a in this fraction were small cycloid diatoms, particularly *Coscinodiscus sp.* Phase 2 was characterised by the prevalence of Chl-a in the middle fraction, probably due to *Oscillatoria sp.*, although at the beginning of this phase, some diatoms persisted in the small fraction. The return of turbid water conditions due to the stirring of the lake at the beginning of Phase 3 again did not depress the overall Chl-a levels, but this pigment was once again found mainly in the small fraction. Nevertheless, in contrast

Table 9. MAXIMS parameters (F_b , F_s , J , E) and the daily ration calculated from them (R_d) for Nile tilapia sampled throughout the project. Standard errors are given in brackets. Instantaneous evacuation rates and daily rations with different superscripts differ at $p < 0.05$. No MAXIMS analysis possible for September 1996 unfed fish. SF denotes that supplemental feed was given.

Parameter	May 95 Large fish	May 95 Small fish	August 95 SF	March 96	May 96	July 96	Sept. 96 SF	January 97 SF	January 97
No. of fish	40	40	80	110	112	85	114	119	120
Feed begin (time of day)									
F_b -general (1. Period)	6:30 (1h 22mins)	6:12 (18mins)	-	5:25 (40mins)	7:05 (33mins)	5:54 (29mins)	-	5:30 (37mins)	8:44 (26mins)
F_b -general (2. Period)	-	15:02 (16mins)	14:59 (1h 23mins)	-	-	-	-	-	-
F_b -feed 1	-	-	6:50 (15mins)	-	-	-	7:55 (7mins)	8:00 (55mins)	-
F_b -feed 2	-	-	-	-	-	-	-	14:43 (33mins)	-
F_b - <i>Ceratium</i>	-	-	-	-	-	9:59 (21mins)	-	-	-
F_b -detritus	-	-	-	-	-	-	13:34 (48mins)	-	-
Feed stop (time of day)									
F_s -general (1. Period)	16:37 (1h 22mins)	10:44 (1h 51mins)	-	18:00 (1h 20mins)	15:30 (53mins)	17:58 (26mins)	21:16 (45mins)	22:36 (39mins)	14:18 (38mins)
F_s -general (2. Period)	-	19:47 (1h 57mins)	22:30 (1h 3mins)	-	-	-	-	-	-
F_s -feed 1	-	-	-	-	-	-	8:54 (45mins)	10:44 (33mins)	-
F_s -feed 2	-	-	-	-	-	-	-	17:19 (41mins)	-
F_s - <i>Ceratium</i>	-	-	-	-	-	13:07 (44mins)	-	-	-
F_s -detritus	-	-	-	-	-	-	16:51 (42mins)	-	-

Parameter	May 95 Large fish	May 95 Small fish	August 95 SF	March 96	May 96	July 96	Sept. 96 SF	January 97 SF	January 97
No. of fish	40	40	80	110	112	85	114	119	120
Ingestion rate, (%BWE h ⁻¹)									
<i>J₁</i> -general	0.083 (0.021)	0.836 (0.241)	0.095 (0.027)	0.100 (0.031)	0.086 (0.013)	0.140 (0.047)	0.230 (0.204)	0.099 (0.057)	0.131 (0.020)
<i>J₁</i> -feed	-	-	0.227 (0.058)	-	-	-	1.130 (0.822)	0.268 (0.082)	-
<i>J₁</i> - <i>Ceratium</i>	-	-	-	-	-	0.299 (0.077)	-	-	-
<i>J₁</i> -detritus	-	-	-	-	-	-	0.448 (0.263)	-	-
Evacuation Rate (h ⁻¹)									
<i>E</i>	0.130 ^d (0.042)	0.604 ^{ab} (0.599)	0.557 ^b (0.161)	0.264 ^{cd} (0.115)	0.179 ^d (0.032)	0.639 ^{ab} (0.201)	0.716 ^a (0.508)	0.363 ^c (0.131)	0.208 ^d (0.042)
Daily Ration (%BWE d ⁻¹)									
<i>R_d</i> - Natural Food	0.836	2.738	0.715	1.255	0.723	2.220	3.359	1.167	0.728
<i>R_d</i> - Supplemental Feed	-	-	1.325	-	-	-	1.101	1.428	-
<i>R_d</i> - TOTAL	0.836^d (0.241)	2.738^{bc} (2.981)	2.401^c (0.561)	1.255^d (0.475)	0.723^d (0.137)	2.220^{bc} (0.668)	4.460^a (2.967)	2.595^b (0.937)	0.728^d (0.127)

The ingestion rates and daily ration estimates and their standard errors for May 1995 (both sizes) and August 1995 have been converted to dry weight of stomach contents equivalent on the basis of the average dry weight:fresh weight ratios of stomach contents for the 1996 and 1997 samples, which was calculated to be 0.167:1. The evacuation rates and feeding/non-feeding period times for these samplings would not have been affected by the conversion and were therefore left unchanged.

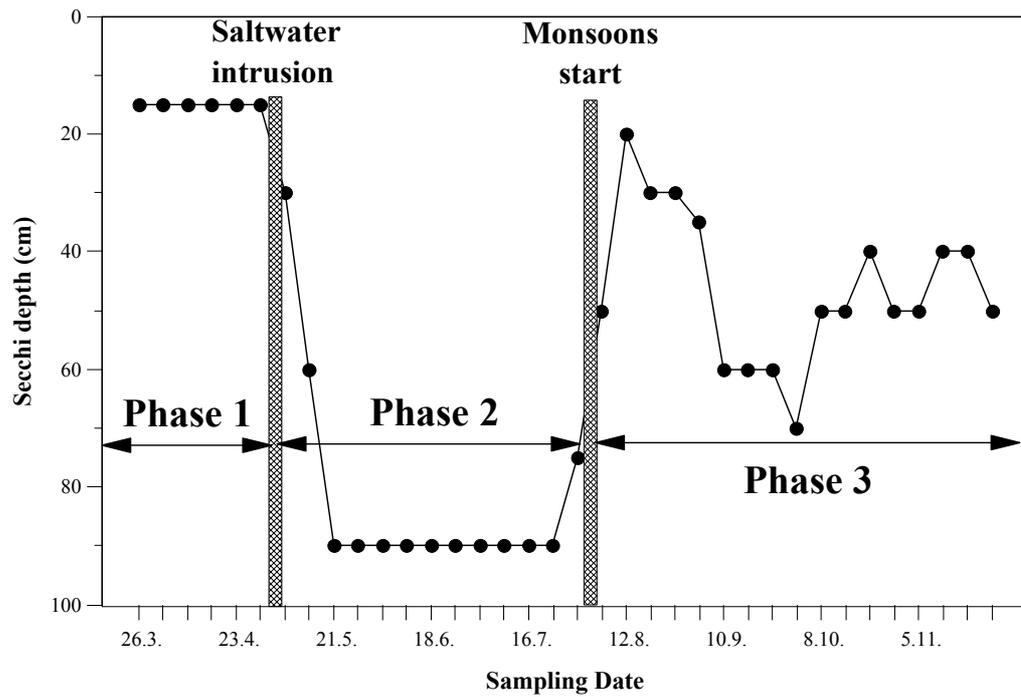


Figure 10. Secchi depth between March and November 1997, showing the three-phase pattern demarcated by the arrival of saltwater intrusion and the start of the monsoon winds

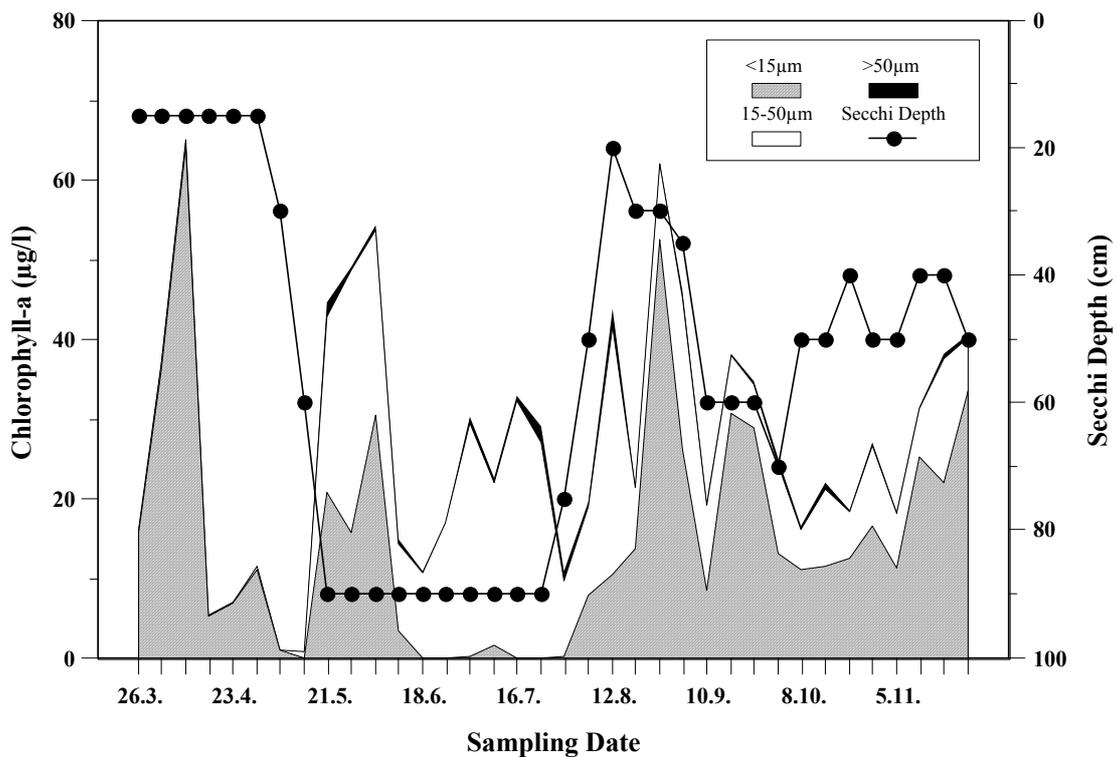


Figure 11. Chlorophyll-a concentrations in three size fractions between March and November 1997. Secchi depth is included to demarcate the three study phases (see text)

to Phase 1, the larger algae were able to survive better under the prevailing light conditions since Chl-a levels in the middle fraction did not drop to zero. Practically no Chl-a was found in the large fraction throughout the entire study period.

c) Particulate Organic & Inorganic Matter

A comparison between the levels of total suspended solids between the three size fractions shows that throughout the study period, the majority of this material was found in the small fraction (Fig. 12a). Here, particulate inorganic matter (PIOM) always exceeded particulate organic matter (POM), even in Phase 2 when the Secchi disk visibility was at its highest (Fig 12b). There is, however, generally good agreement between Secchi depth and levels of PIOM with the former peaking at times of low PIOM. This material will have been made up not only of silt and clay particles but also of diatom shells at those times when these were abundant.

In the middle fraction, there was very little of either POM or PIOM in Phase 1, which indicates that practically all clay particles were $<15\mu\text{m}$ and therefore found in the small fraction (Fig. 12c). In Phases 2 and 3, PIOM rose as a result of increasing levels of diatoms. These were the first algae to bloom immediately following saltwater intrusion (SEAFDEC 1998). POM in the middle fraction was somewhat higher in the second phase than in the third, reflecting the higher concentrations of algae between saltwater intrusion and the return of the monsoon season.

Levels of both POM and PIOM in the large fraction were well below those in the other two fractions (Fig. 12d). Almost no discernible pattern can be identified; the only characteristic peak was observed at the beginning of Phase 2, demonstrating that the diatom bloom also had an effect on the concentration of suspended matter in the large size fraction. The level of zooplankton was marginally higher between saltwater intrusion and the return of turbid water but fluctuations within the three phases of the experiment were rather greater than those between.

d) Zooplankton

The changing numbers and biomass of the three zooplankton groups are shown in Fig. 13. The copepods were evidently the dominant group, both in terms of numbers and biomass. Although the rotifers were also well represented on a numerical basis, their small size prevented them from ever contributing much to the biomass, the only exception

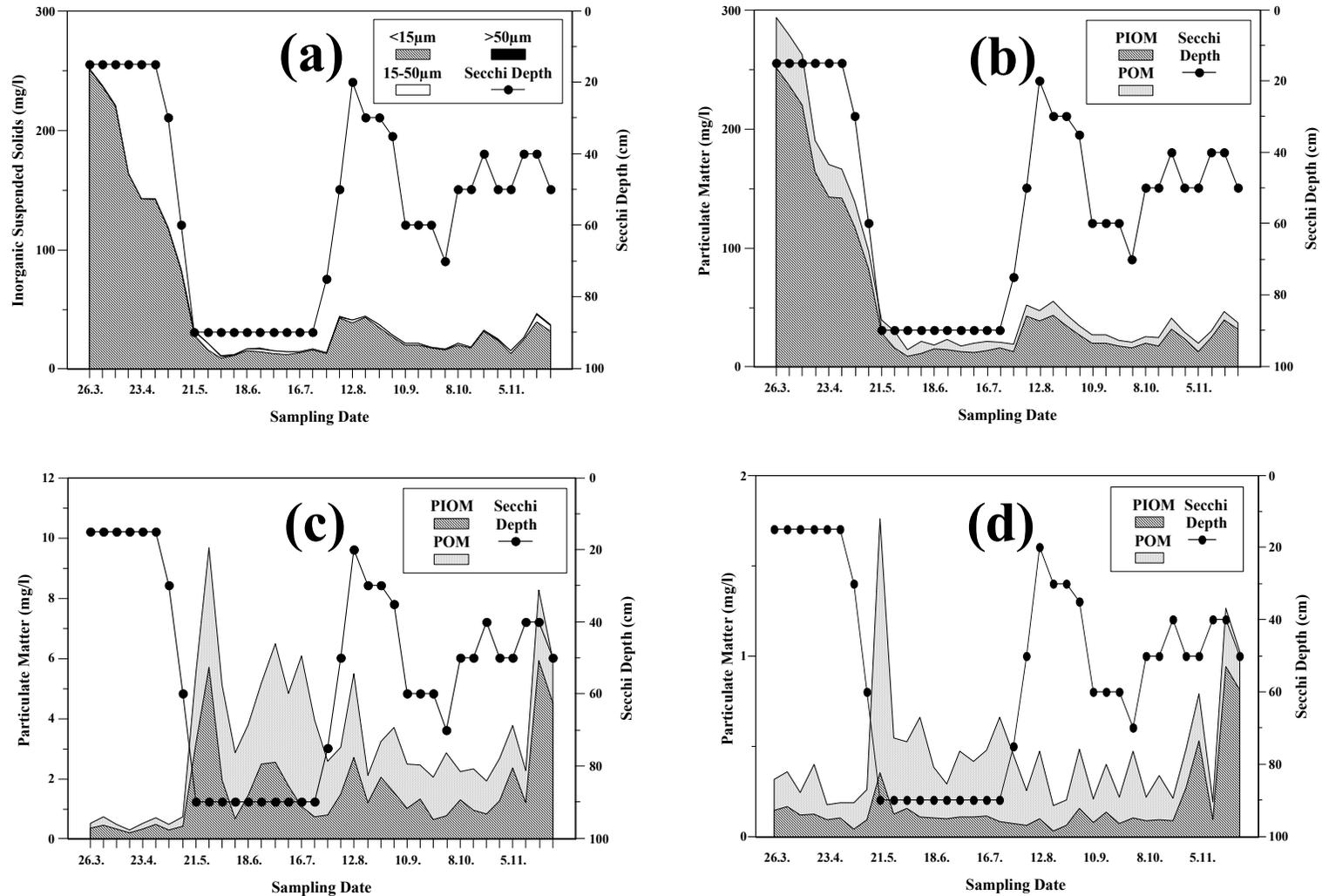


Figure 12. Concentration of total suspended solids in the three size fractions (a) and of particulate organic and inorganic matter in the small (b), middle (c) and large (d) size fractions between March and November 1997. Secchi depth is included in each case to demarcate the three study phases

being at the beginning of Phase 2, presumably due to the dominance of *Conochiloides dessuarius* (Hudson 1885), one of the larger rotifer species. The Cladocera, mainly represented by *B. longirostris*, were particularly prominent in the early part of the study but rarely dominated in terms of biomass or numbers.

The three-phase pattern appears once again in the numbers of zooplankton individuals and taxonomic composition but less so in the biomass. Zooplankters were distinctly more numerous in Phase 2 than in Phase 1 and their numbers fell to intermediate levels in Phase 3. At the same time, the rotifers were practically absent in Phase 1 but dominated the zooplankton in terms of numbers in the subsequent phases. It is well known that blooms of phytoplankton usually give rise to a corresponding zooplankton bloom (Wetzel 2001) and this seems to be the case here. In particular, the algal blooms at the beginning of each phase (Fig. 11; Phase 1: 2.-9. April; Phase 2: 21. May - 4. June; Phase 3: 26. August) were reflected in the zooplankton biomass.

2. Tilapia

a) Growth Rates

The mean weights of Nile tilapia analysed in 1997 reflect the clear three-phase pattern observed for the water quality parameters (Fig. 14). In Phase 1, fish weight remained fairly constant, thereafter rising rapidly throughout Phase 2, after which it levelled off again in Phase 3. Some differences in mean fish weight were observed between the cages with Cage 1 maintaining a faster growth rate after the beginning of June, thus having the largest fish at the end of the experiment, and Cage 4 falling behind after the beginning of July so that it ended up with the smallest fish. The aforementioned pattern was also reflected in the average MGRs (Fig. 15): growth was slow in Phases 1 and 3 and high in Phase 2. A comparison of the MGRs also demonstrates that the fish grew particularly rapidly at the beginning of Phase 2, just after saltwater intrusion had reached the study site. In Phase 3, on the other hand, weight losses were even recorded for some time spans between successive samplings.

b) Condition

The condition factors of the fish were low at the beginning of the experiment and only started to rise substantially in Phase 2 of the experiment (Fig. 16). After July, condition

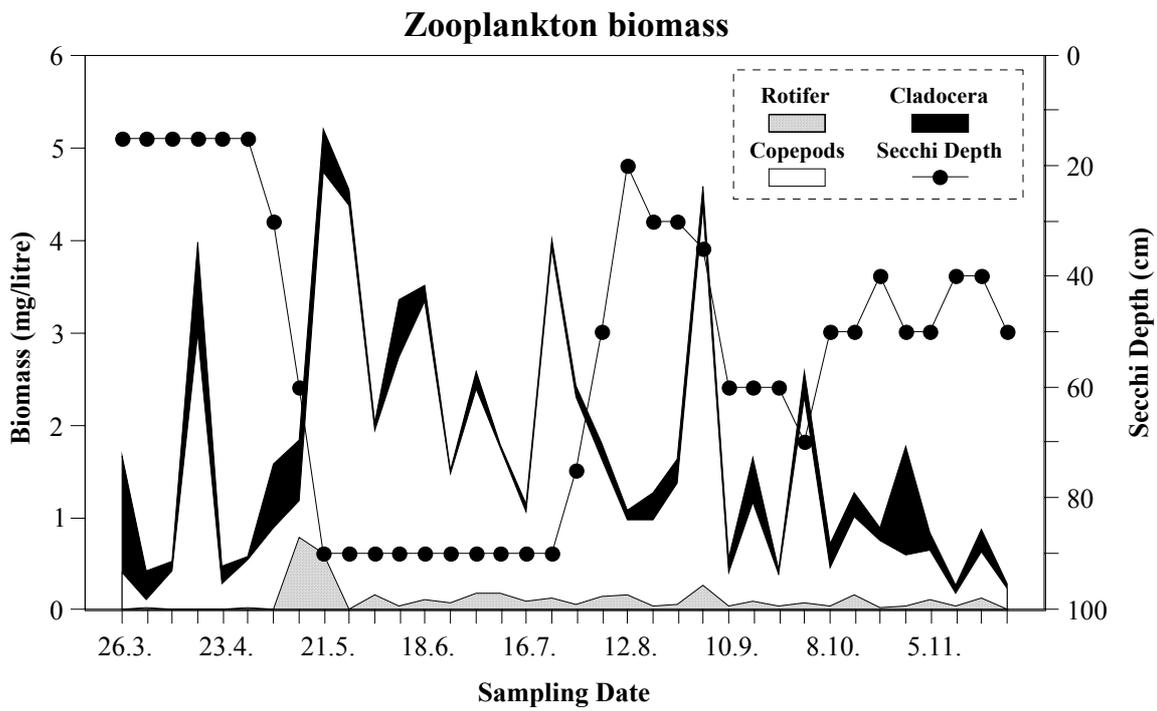
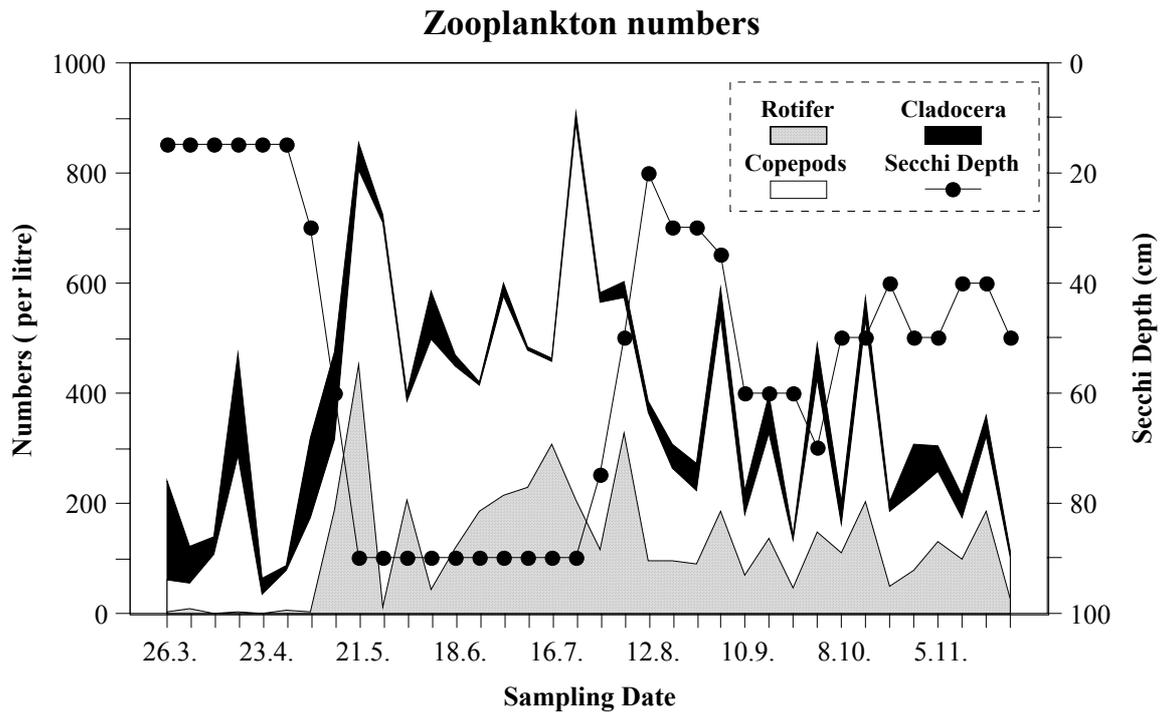


Figure 13. Zooplankton numbers and biomass between March and November 1997. Secchi depth is included for comparison

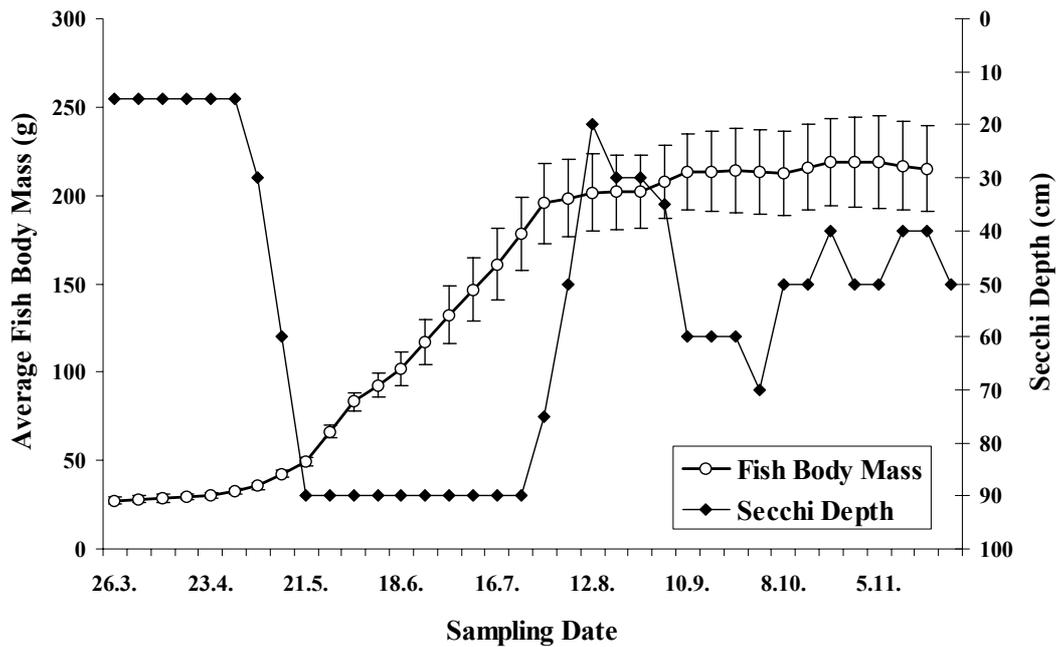


Figure 14. Secchi depth and body mass of Nile tilapia (Mean \pm St. Dev. of four cages) between March and November 1997. Secchi Depth is included to demarcate the three study phases (see text)

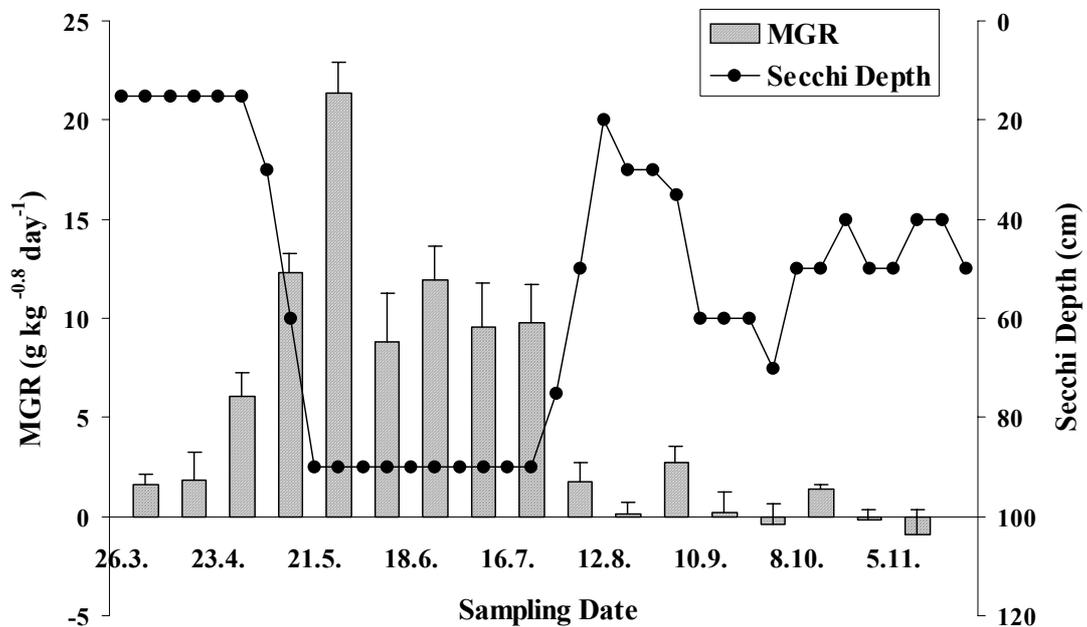


Figure 15. Metabolic Growth Rates (MGR; Mean \pm St. Dev. of four cages) of Nile tilapia between March and November 1997. Secchi Depth is included to demarcate the three study phases (see text)

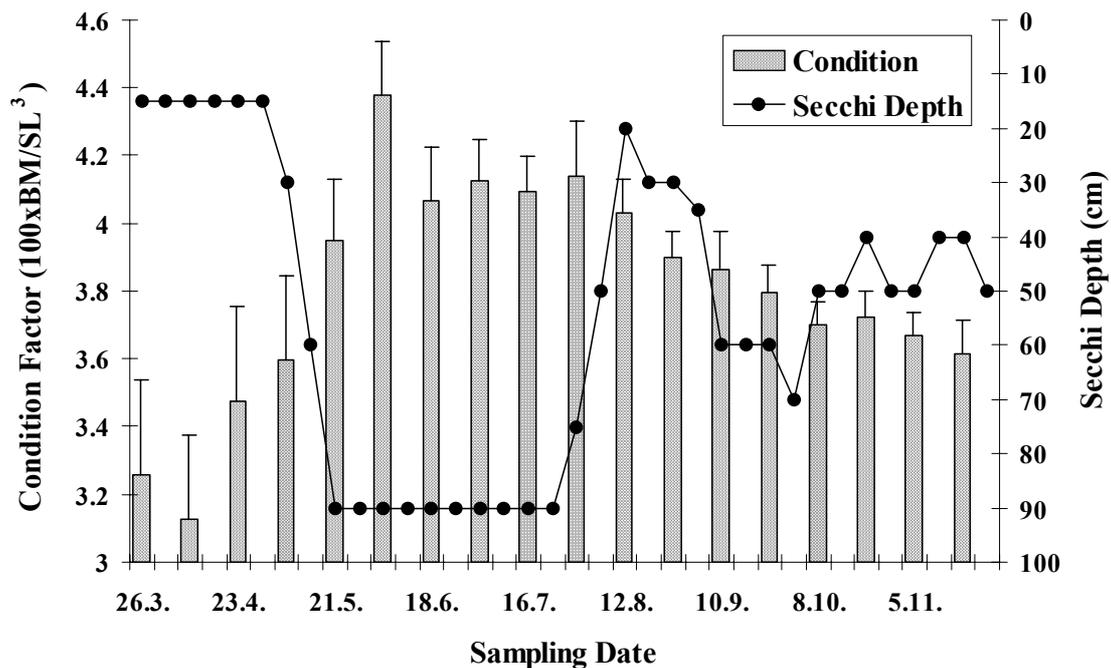


Figure 16. Condition factors *K* of Nile tilapia between March and November 1997. Secchi Depth is included to demarcate the three study phases (see text)

dropped gradually throughout Phase 3, which in conjunction with the fact that growth had to all intents ceased during this time, suggests that it is likely that the fish were living off their reserves. Although the experiment was terminated in November, it is quite possible that condition would have dropped more or less steadily until just before saltwater intrusion the next year, as suggested by the results obtained for milkfish.

c) Mortality

Mortality in all cages was quite high, ranging from 20% to 52% (Fig. 17), but almost all the mortality was observed in the first month of the experiment. This could be attributed to an outbreak of the parasitic isopod *Alitrophus typus* Milne-Edwards 1840 which was in evidence throughout large parts of the lake at the time. Indeed, the experiment had originally been planned to start in early February but stocking was delayed because of this crustacean. When stocking was finally carried out before the end of the infestation, it was because of fears that the period before the expected arrival of saltwater intrusion would not be adequately covered. Since each fish had such a large volume of water available even at the lowest water:fish ratio ($1.5 \text{ m}^3 \text{ fish}^{-1}$ when the water depth was at a minimum of 1.5m), it is

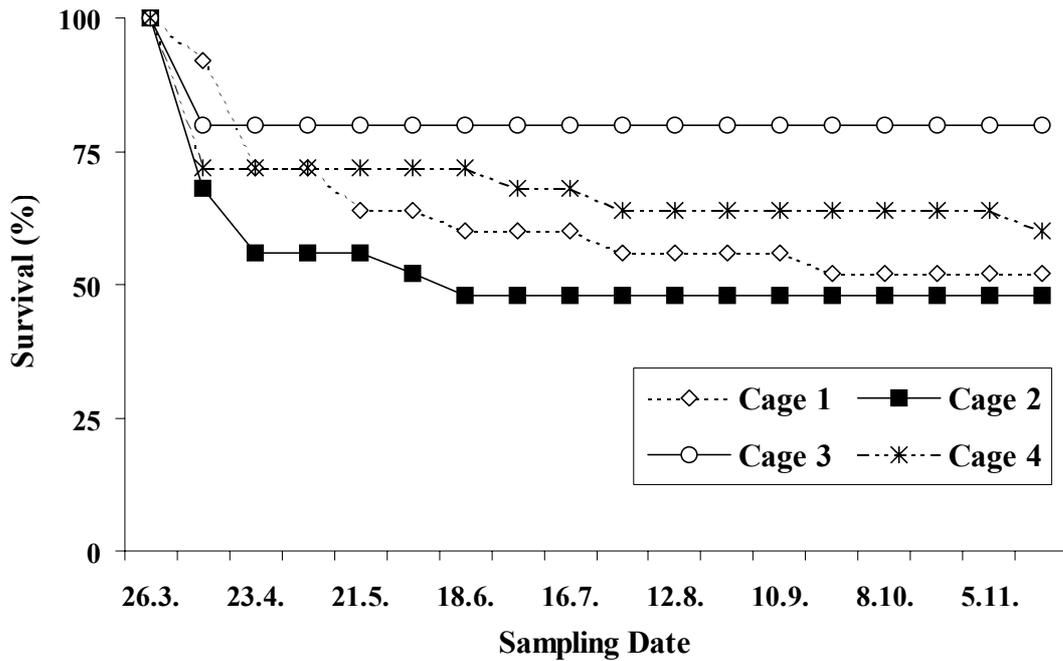


Figure 17. Survival of Nile tilapia in four different experimental cages between March and November 1997

highly unlikely that the fish were competing for food. Restocking fish at any stage of the experiment would have made the calculation of growth rates from one sampling to the next problematic and, since the exact fish number per cage was not expected to have any effect on fish growth at these low stocking densities, it was decided not to replace lost fish.

3. Calculation of Relative Proportions of Detritus & Phytoplankton from Chlorophyll-a & Particulate Matter

POM is made up principally of zooplankton, phytoplankton and detritus, the former being confined mainly to the large size fraction. As demonstrated by the zooplankton sampling, this component did not contribute much to overall POM. Having quantified the level of zooplankton as detailed above, there now remained the problem of distinguishing between phytoplankton and detritus, particularly in the small fraction where most of the overall POM was found. In order to achieve this, a comparison was made between POM and Chl-a in the middle fraction in Phase 2. The underlying assumption was that during this phase, any detritus present in this fraction should settle due to the calmer weather and

possibly also due to the saltwater effect while at the same time, algal biomass would be sufficiently high to overshadow any traces of detritus remaining in the water column.

When the POM and Chl-a data are compared for Phase 2, an excellent relationship between the two was observed (Fig. 18), implying that this could be used to estimate phytoplankton biomass from Chl-a. What is somewhat surprising is that this relationship extends over the entire study period; the ratio between POM and Chl-a in the middle fraction was only slightly lower at times of turbid water (Fig. 18). This suggests that the middle size fraction was made up almost entirely of algae at all times and not only when the water was relatively clear, so that all detritus was fine enough to pass into the small fraction. The water sample data collected throughout the entire study period was therefore analysed with the aid of a Model II (geometric mean) regression (Sokal & Rohlf 1995) and the following relationship obtained with both parameters considered in mg l^{-1} :

$$\text{POM} = 136.9 \times \text{Chl-a} + 0.11 \quad (34)$$

($r = 0.941$, $df = 106$)

On the basis of the above regression, the POM in all three size fractions was split into the three basic components (zoo-, phytoplankton and detritus) on the following assumptions:

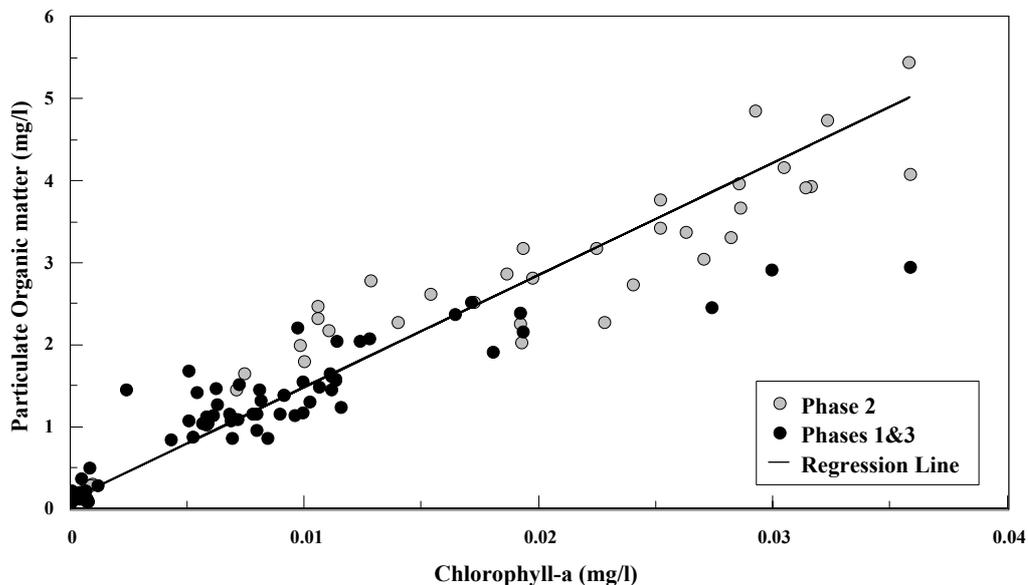


Figure 18. Relationship between Chlorophyll-a and Particulate Organic Matter (POM) in the middle size fraction (15-50 μm) in Phase 2 (11.5.-2.8.1997) and Phases 1 (26.3.-10.5.1997) and 3 (3.8.-26.11.1997) of the water quality study period (March-November 1997). Geometric mean regression line is included for comparison

1. POM in the large fraction made up of zooplankton and larger phytoplankton
2. POM in the middle size fraction is made up entirely of algae
3. POM in the small fraction made up of phytoplankton and detritus
4. Eqn. 32 is valid also for the small fraction throughout the study period

The algal biomass in the small fraction was therefore calculated with the aid of the above regression; the residue was attributed to detritus. All organic suspended matter in the middle fraction was assumed to be made up of algae. Organic matter retained by the 50 μ m plankton net was considered to consist of zooplankton and larger algae; the zooplankton biomass was estimated from the microscopic counts after conversion to dry weights on the basis of a 10:1 wet weight/dry weight ratio (Schwoerbel 1980). The phytoplankton estimates for the middle and large size fractions were then combined for presentation purposes on the assumption that they were equally available to tilapia.

The resulting breakdown of the organic suspended solids shows that total POM was dominated by detritus, particularly the first phase of the experimental period (Fig. 19). Nevertheless, in view of the results from the stomach content analysis, it is perhaps a little surprising that no substantial differences in the level of detritus could be found between Phases 2 and 3; if anything, there was a slight reduction in this material in the latter phase. As indicated by the levels of Chl-a over the study period, there was no consistent pattern in the total phytoplankton biomass enabling a distinction between the three experimental phases; the principal difference was on the basis of size. Zooplankton contributed comparatively little to POM at any time whereas the levels of phytoplankton fluctuated somewhat.

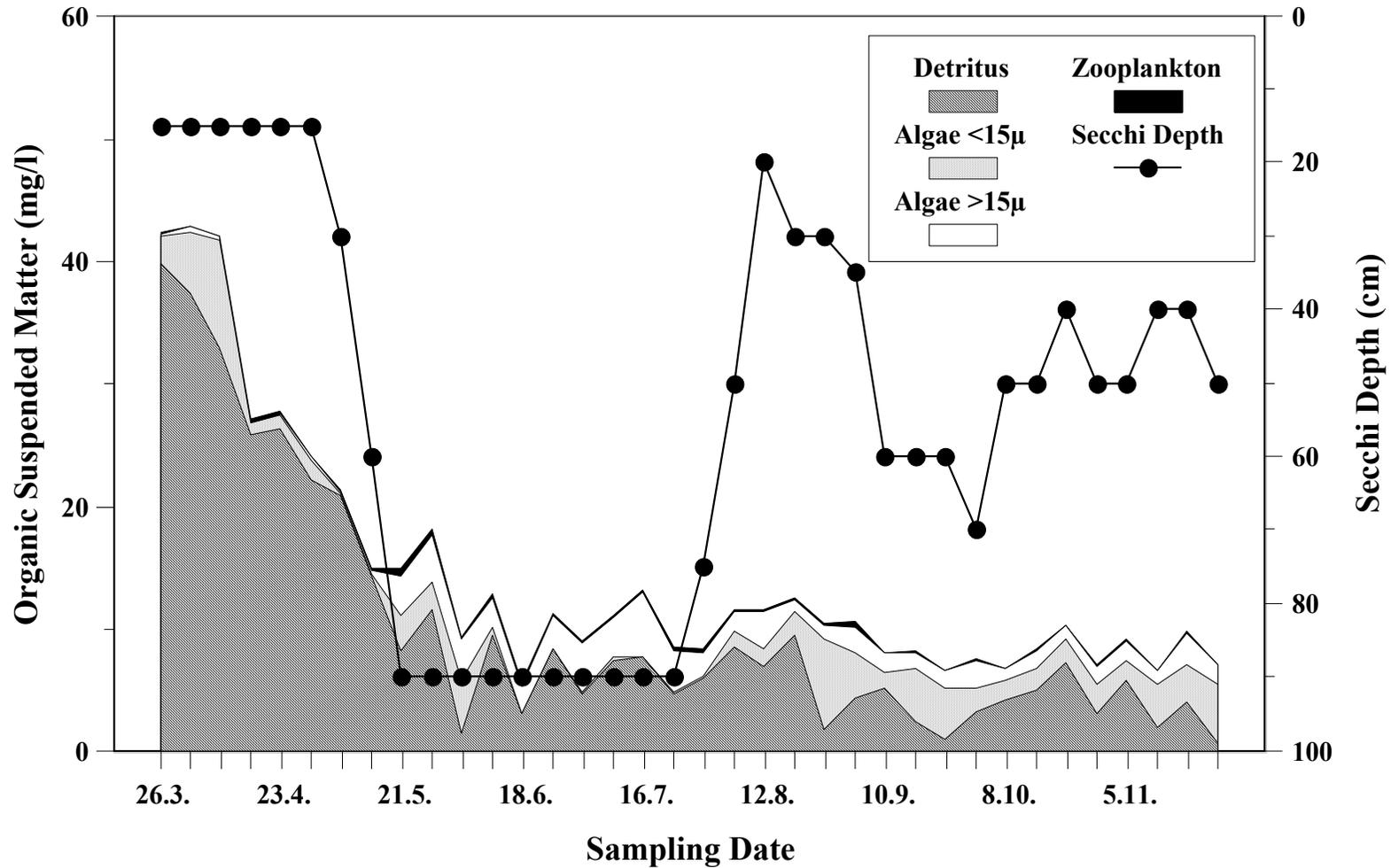


Figure 19. Estimated composition of Particulate Organic Matter (POM) in the three size fractions on the basis of the geometric mean regression between Chlorophyll-a and POM in the middle size fraction over the water quality study period (March-November 1997). Secchi depth is included to demarcate the three study phases (see text)