Abstract of thesis is entitled

**"Non-governmental Organization Approaches to Cooperative Development:
Two Case Studies of the Philippine Experience"**

submitted by

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Cooperative development in the Philippines has generally been a state initiative but with minimal success. Recently, however, non-governmental organizations (NGOs) have become involved in this endeavor. This study, therefore, looks into the experiences of two NGOs that organize agricultural cooperatives. The first is the People's Livelihood Foundation-Tarlac Integrated Livelihood Cooperative (PLF-TILCO), the Aquino Administration's government model cooperative. The PLF-TILCO was established by New People's Army (NPA) founder, Bernabe "Commander Dante" Buscayno. The other one is the Cooperative Foundation of the Philippines Inc. (CFPI). Its executive director, Horacio "Boy" Morales, was the National Democratic Front's (NDF) erstwhile leader. He now currently heads one of the country's biggest development NGOs.

Both the PLF-TILCO and the CFPI have emphasized the importance of popular participation and self-reliance in their economic ventures. Increments were made possible by utilizing government agencies to train the PLF-TILCO members to run their enterprise and by holding management

seminars and closely supervising the cooperatives in the case of the CFPI. Self-reliance in the PLF-TILCO to a certain extent was attained by accessing capital, infrastructure and technical support from the government. CFPI, on the other hand, assisted its enterprises in initially generating capital from within. Adverse social factors, however, have made it impossible for cooperatives to remain a purely economic venture and these NGOs have also provided the means by which the farmers may take on socio-political concerns. The CFPI, for example, assisted a cooperative in fighting its members' former landlord who wanted to get back her land from them. Moreover, the NGO has shown the need to engage in advocacy work from the national to the local levels in order to bring about a more favorable environment for cooperative development.

Detrimental internal as well as external factors, however, threaten the sustainability of these undertakings. Leadership dependency, centralized decision-making processes and the farmers' "dole-out mentality", for example, have hindered popular participation in some of these cooperatives. Efforts towards self-reliance, on the other hand, have been daunted by the economic elite's control of the rice and sugar industries and by the perpetuation of patronage politics by the country's politicians and cooperative leaders. These shortcomings in NGO advocacy work have been aggravated by a failure to counter-act unfavorable government policies and illegal land use conversions which endanger these economic ventures. Unless such challenges are

effectively addressed, NGO-organized or assisted cooperatives may very well go the way of the failed government attempts in this area.

Acknowledgements

There comes a time in any such thesis when one is permitted, albeit for a brief moment, to adopt the sort of frivolous tone which might arguably be suited to a broader spectrum of the scientific literature, if only to make its consumption more bearable. I would therefore like to extend the official dedication of this work in the appropriate fashion at this point, before the censors start messing around with the subsequent sections, and list in more detail all those people who made this work possible in one way or another. If anyone subsequently mentioned has any doubt as to the sincerity of my acknowledgement, I can only say that they ought to know me better than that!

As is customary in such a work, I would at this point like to thank Prof. Dr. Klaus Becker for placing such a large amount of faith in an overaged drop-out with a track record as colourful as mine and accepting me as his Ph.D. student. Further thanks go to Dr. Ulfert Focken for the direct supervision of this effort and for laying the groundwork for the write-up with his comments to all the publications prepared from it. I am, however, sure that they would have stumbled across a quite different candidate if Prof. Dr. Walter Nellen, in keeping with the common departmental policy, had channelled my application and CV into that familiar round object on the floor instead of passing it on to them. As the list of referees shows, his contribution to this work has been acknowledged by giving him the dubious pleasure of reading it before it is inflicted on the general public.

Since the experimental basis of this work was conducted in a faraway country, many miles from Hohenheim, the post of direct supervisor had to be delegated to some unfortunate senior scientist at the host institution and this task was fulfilled more than admirably by Dr. Corazon Santiago. She was assisted in this respect by Angelito Gonzal whose inside information and contacts proved invaluable in organizing the sampling at commercial fish farms. I will never forget the patience with which they both assisted me repeatedly on those many occasions when I got past the defences of their office fortress at times when they had undoubtedly more useful things of their own to get done. Of those people at SEAFDEC who endured my persistent whining and requests for information (even after I had returned to Germany, forcing me to resort to terror by e-mail), a special mention goes to Malou and Emil Aralar and Susan Baldia.

As is often the case in such projects, the amount of work involved was far too great for one person to master so I delegated some of the work, usually of the more tedious type, to the vast army of lab slaves hired out from Cora, Lito and Malou. Two of these characters were of sufficient help during the frequent 24-hour fish murdering sessions that they attained co-author status, namely Wally Afuang and Manny Laron. Others who deserve special mention are Maria Geronilla for preparing fish for body composition analysis, sparing me from a task unworthy of any person with a fully functioning nose (sorry, Maria!), Florence Jarder for the further processing, Rene Arcilia for counting plankton and "Professor" Totoy Reyes *et al.* for cleaning and labelling filmcases as hi-tech vials for the fish stomach contents.

A project doing so much for population control in Laguna de Bay fishpens and -cages would not have been possible without the wholehearted cooperation of those people who normally make a living growing fish for a more conventional form of ultimate consumption. I would therefore like to thank Messrs. Joseng Montevillas, Chris Manlapaz, Tiboy Reyes and Boyet Flores for permitting stock reductions of more or less drastic proportions at their aquaculture operations. I should also mention those members of their staff who were kept awake for most of the night by our sampling antics, sometimes taking an active part in the massacre, but I never got to know them by name so that they have to share a general acknowledgement.

Three years in the Philippines is a long time and would be impossible to survive without new friends or a decent TV programme schedule. In the absence of the latter, I was forced to strain the patience of many of those around me. Particular thanks goes to Lito for introducing me to the more interesting parts of Manila - including some pretty entertaining ones! - Emma Alinas and her family for treating me as one of their own, the same applying to Lito's family, and to my colleagues Myrna Kock and Martina Bocci for inviting me to all that pasta and (in Myrna's case) fighting over who gets to read the weekly German newspaper first. I could also count on the support of all those people in Tigbauan whenever I escaped to the "glorious south" for a dip in the sea and other diversions, most notably Kai Kühlmann, Andreas Groth and Christian Lückstädt.

Back in Germany, the completion of this work extended over a rather longer time span than most professors like to put up with. Irrespective of the defensibility of the reasons for this, I would also like to acknowledge those people who made life more bearable, thereby no doubt contributing towards extending the completion of this work still further! First and foremost are the members of the Landsmannschaft Württembergia, particularly Klaus Matheis, Frank Graf, Aljoscha Grimm and Matthias Höfer. My colleagues in Hohenheim also deserve thanks, especially George Francis for taking more than the average amount of stick. Another name which crops up in this section is that of Lito who followed me to Germany, officially to do his M.Sc. at Hohenheim but more likely to get his own back on me for what I did to him and all the others in the Philippines. He deserves a special mention here for without his efforts, I would never have met my dear wife Nahid (never mind how hard George tried to get me hitched!). Although she arrived only rather recently on the scene, I would like to thank her very much for the special support she gave me in the terminal stages of this thesis. My family, particularly my mother, also supported me throughout the work, helping me sort out other disasters and keeping me informed of what was going on in Germany when I was in the Philippines, as did my father for the first year of my stay in Southeast Asia. Had he not died tragically at that stage, I am sure that his support would also have extended throughout my time there.

No project gets off the ground without at least some funds and, although I didn't have to fight for it personally, I would like to thank the European Union for coughing up the cash for the major part of the overall Laguna de Bay project, thereby enabling Prof. Becker to hire me and set the ball in motion. Finally, an acknowledgement to the countless cups of tea that fuelled the making of this work and without which I would have spent a major part of my time fighting off the *delirium tremens* and dehydrating in the tropics.

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List of Abbreviations

SI Units

$^{o}/_{o}$	percent
$^{o}/_{oo}$	per thousand
µm	micrometre
°C	degrees Centigrade
C°	Centigrade degrees (difference between two temperatures)
cm	centimetre
g	gramme
h	hour
ha	hectare
km	kilometre
km^2	square kilometre
l	litre
m	metre
m^2	square metre
min	minute
m*l*	millilitre
mm	millimetre
mm Hg	millimetres of mercury (gas pressure)
nm	nanometre
kg	kilogramme
t	tonne
y	year

Mathematical terms

∞	infinity
ANOVA	analysis of variance
b	regression coefficient
CC	correlation coefficient
Cov	covariance
df	degrees of freedom
e	Euler's number, base of the *logarithmus naturalis*
ln	natural logarithm
p	probability level
r	correlation coefficient
r^2	coefficient of determination (regression)
SE_b	standard error of the regression coefficient *b*
SSR	sum of squared residuals
St. Dev.	standard deviation
Var	variance

General

° 'E	degrees and minutes eastern longitude
° 'N	degrees and minutes northern latitude
° 'S	degrees and minutes southern latitude
° 'W	degrees and minutes western longitude
% BME	Percent Body Mass Equivalent
β	power quotient for stomach content S
A	Average Stomach Contents over analytical period (Bajkov model)
AlcWC	Alcohol preserved Weight of the Stomach Contents
AlcWI	Alcohol preserved Weight of the Intestinal Tract
App.	Appendix
B	condition factor after Jones *et al.* (1999)
B'	condition factor after Richter *et al.* (2000)
C_t	food consumption over time t (Elliott-Persson model)
cf.	compare (from latin *confer*)
Chl-a	Chlorophyll-a
cont.	continued
D	Food Consumption over 24 hour period (Bajkov model)
E	Instantaneous Stomach Evacuation Rate
e.g.	for example (from latin *exempli gratia*)
Eqn.	Equation
et al.	and coworkers (from latin *et alii*: and others)
Fig.	Figure
$f_i(t)$	mathematical evacuation function of food type i (Olson-Mullen model)
FrWC	Fresh Weight of the Stomach Contents
FrWI	Fresh Weight of the Intestinal Tract
g	Growth Rate
G_0	Initial Growth Rate
gC	gramme Carbon
GW	Gutted Body Weight
H	Body Height
ICLARM	International Council for Living Aquatic Resource Management
i.e.	that is to say (from latin *id est*)
J_1	Ingestion Rate
J_2	Instantaneous Ingestion Rate
k	rate constant
K	condition factor after Fulton (1911)
K'	condition factor after Ricker (1975)
kJ	kilojoule
L	Body Length
L.	Linnaeus
LLDA	Laguna Lake Development Authority
MGA	Manufacturer's Guaranteed Analysis
MGR	Metabolic Growth Rate
$M(i)_{avg}$	Average Weight of items of food type i when ingested (Olson-Mullen model)
n	number of hours taken to evacuate stomach fully (Bajkov model)
NFE	Nitrogen-free Extract

NHCS	Napindan Hydraulic Control Structure
P_c	critical oxygen partial pressure (for fish)
pers. comm.	personal communication
PIOM	Particulate Inorganic Matter
POM	Particulate Organic Matter
PVC	Polyvinylchloride
R_d	Daily Ration
S	Stomach Contents
S_∞	Actual (asymptotic) Maximum Stomach Contents at which ingestion equals evacuation
S_{avg}	Average Stomach Contents over analytical period
S_f	Stomach Contents at the start of a non-feeding phase
S_m	Theoretical Maximum Stomach Contents at which ingestion is zero
S_r	Residual Stomach Contents at the start of a feeding phase
S_t	Stomach Contents at time t
SEAFDEC AQD	Aquaculture Department, Southeast Asian Fisheries Development Center
SGR	Specific Growth Rate
SL	Standard Body Length
SOGREAH	Société Grenobloise d'Etudes et d'Applications Hydrauliques
SR	Spectrophotometric Reading
t	Time
t_0	Initial Time
$T(i)_{avg}$	Average Time Interval between ingestion of individual items of food type i (Olson-Mullen model)
T_f	Time at start of a non-feeding phase in MAXIMS model
T_r	Time at start of a feeding phase in MAXIMS model
Tab.	Table
TW	Total Body Weight
V	Volume of Water Sample (spectrophotometry)
v	Volume of Extractant (spectrophotometry)
W	Body Weight
W_0	Initial Body Weight
W_t	Body Weight at time t
$W(i)_{avg}$	Average Weight of food type i in the stomach over a sampling period (Olson-Mullen model)

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I Introduction

Laguna de Bay, also known as Laguna Lake, is the largest inland water body in the Philippines, and the third largest in Southeast Asia after Tônlé Sap (Cambodia) and Lake Toba (Sumatra, Indonesia). It covers an annual mean area of 911km^2 at an annual mean depth of 2.8m, is located just southeast of the national capital Manila (14°2'-14°5'N, 121°0'-121°5'E) and its surface is close to sea level (10.43m above chart datum). The lake has twenty-one tributaries but only one outlet, the Pasig River, which flows to the sea through Manila. Laguna de Bay's watershed stretches over 2,900km^2 so that the area of the entire catchment (watershed plus lake) encompasses 3,800km^2. The western part of the watershed is heavily industrialized, apart from which it is also home to the majority of the population in the area (ca. 8.5 million). The eastern section is more rural and predominantly hilly, with rice, coconuts and bananas grown where possible (Francisco 1993).

The lake has been used extensively, probably ever since man first settled on its shores, for a number of purposes, including fishing, navigation, water abstraction and waste disposal. The fishery has been based mainly on native species such as the Manila catfish, *Arius manillensis* Valenciennes 1840, the silver perch, *Leiopotherapon plumbeus* (Kner 1864), and the white goby, *Glossogobius giuris* (Hamilton 1822), as well as macrobrachiid shrimps. However, in terms of landed catch, the finfish and crustacean fishery has traditionally been overshadowed by the snail fishery with most of the catch used as animal feed. Overfishing and subsequently declining catches in the sixties of this century led first to the introduction of exotic species, such as the Mossambique tilapia *Oreochromis mossambicus* (Peters 1852) and the common carp *Cyprinus carpio* L. 1758 in order to boost capture fisheries, and later to the development of aquaculture.

The introduction of aquaculture was proposed for a number of reasons. Firstly, it was hoped that the quantity and quality of fish production could be improved: not only were catches declining but also the quality of the wild fish, though acceptable, was considered inferior to that of species already being farmed elsewhere. Secondly, none of the native fish species was a primary consumer and the aim was to utilise the primary production of the lake more efficiently by farming herbivorous species, such as the milkfish, *Chanos chanos* Forsskål 1775 and the Nile tilapia, *Oreochromis niloticus* (L. 1758). Thirdly, declining catches meant declining incomes for small-scale fishermen and it was hoped that they might benefit from this new source of income. Fourthly, the long-term inputs of domestic and

industrial waste, as well as agricultural run-offs, had caused Laguna de Bay to eutrophy and there were expectations that an increase in fish production would lead to an increased removal of nutrients from the lake in the form of high quality protein.

Milkfish had always been part of the lake fauna, being a catadromous species which entered the lake through the Pasig River. However, following the increasing pollution of this link to the sea, this species was becoming scarcer in Laguna Lake. The stocking of milkfish fingerlings in the lake to improve capture fisheries dates back as far as 1959 (Delmendo & Bustrillo 1968) and in 1965, the Bureau of Fisheries and Aquatic Resources (BFAR) made first, unsuccessful attempts to culture this species in enclosures in the lake. A second pilot study was carried out by the Laguna Lake Development Authority (LLDA) in 1970 in Central Bay, close to the municipality of Cardona, and this was so successful that it triggered the rapid spread of aquaculture structures. The LLDA, although instructed in principle to manage aquaculture in the lake, was in practice powerless to control this so that a large number of fishpens quickly exceeding the legal limit of 50ha. At this stage, it was possible to grow milkfish from fingerling to marketable size in only three to four months (Davies 1988, Sly 1993). At the same time, the production of wild fish also increased just after the introduction of aquaculture, partly due to the escape of milkfish from damaged fishpens which were then available to the capture fishery and partly because the newly formed fishpens served as a sanctuary area for wild species. The Manila catfish, which had been fished almost to extinction by the early seventies, suddenly increased in number and is today once again one of the dominant wild species in the lake (Delmendo 1987). Nevertheless, despite the beneficial effect of aquaculture on overall fish production, most small-scale fishermen did not have the necessary starting capital to venture into the business, so that at least one of the initial aims had not been realised. Indeed, the more of the lake area was devoted to aquaculture, the less space did the fishermen have to carry out their operations, leading to serious social conflicts (Delos Reyes 1993).

In the late seventies, a second type of fish culture was introduced on a commercial scale, namely that of fish in small cages. Since the start of the fishpen industry, it had been common practice to stock milkfish nursery areas with Mossambique tilapia after the release of the fingerlings into the main part of the pen. However, the growth of this species was slow and fish were liable to escape in large numbers by slipping under the side netting. This led to the introduction of the Nile tilapia and the use of nets with a bottom, suspended from bamboo poles, to prevent their escape. Since these structures required less capital input than the

larger fishpens, tilapia culture was accessible to a broader spectrum of society than milkfish culture. Nonetheless, most people were still excluded from farming fish due to their lack of starting funds, and remained dependent on the capture fishery.

The maximum expansion of the fishpen industry was reached in 1985 at which point the total coverage was 29,011ha or nearly one third of the lake (Delmendo 1987). However, while the total fishpen area was growing steadily throughout the seventies and early eighties, productivity was not keeping pace. Indeed, when viewed on a yield per hectare basis, the maximum was reached as early as 1976 (6.7 t ha^{-1} y^{-1}), after which it declined, fluctuating between about 1.5 and 4.0 t ha^{-1} y^{-1} in the eighties (Delmendo 1987). This phenomenon was attributed to the excessively high aquaculture coverage in the lake and milkfish stocking rates (up to 100,000 ha^{-1}) which were seen to lead to the overexploitation of the natural production and consequently a shortage of food for both the wild and cultured species. The owners of fishcages circumvented the problem by giving supplemental feed to tilapia at times when growth would otherwise be slow. While this improved the growth rates of this species, it also constituted a net input of nutrients into the lake in the form of wasted feed, thus sabotaging another intended benefit from aquaculture.

Following the decline in fish production and the reduction of the area devoted to aquaculture after 1985, catches of wild fish increased again on a per hectare basis, while the overall cultured fish production remained steady. Since then, the area covered by fishpens and -cages has fluctuated, sometimes reaching a similar coverage to that in the early eighties. Nevertheless, the production per unit area has never reached those levels recorded in the seventies and this was still generally attributed to overstocking and overexploitation of the lake's natural resources. Several authors have attempted to calculate the carrying capacity of the lake (SOGREAH 1974, Nielsen 1983, Centeno *et al.* 1987) and, although their approaches vary somewhat, the general recommendation is that 9,000 ha, equivalent to one tenth of the lake, should be the optimum coverage to maximise the production of cultured fish. In practice, however, the efficacy of this level of coverage has never been adequately tested because it has been too difficult to implement this figure for a sustained period.

In view of the decline in fish production since the introduction of aquaculture and the uncertainty regarding the underlying causes of this phenomenon, the present study was carried out to quantify the growth of the two main cultured fish species, the milkfish and the Nile tilapia, at different times of the year and relate it to their food composition and daily ration. This work was part of a larger project aimed at constructing a management plan for

Laguna de Bay so that supporting data on water quality gathered by the Southeast Asian Fisheries Development Center (SEAFDEC) was sometimes relied on. The role of this part of the project was to answer the question of what factors limit the production of cultured fish in the lake and what changes have most likely taken place since the introduction of aquaculture in the early seventies when, judging by the information available from reports from that time, this limitation was not yet in place.

II Literature Review

A. Study Site Description

1. Origins and Hydrology

Laguna de Bay has been in existence since prehistoric times and, on the basis of marine shells found in its sediments, it is believed that the lake was once part of Manila Bay. Despite this, it derives its name not from that water body but rather from the town of Bay (pron.: Ba-i) in the southern part of the catchment, close to Los Baños. The lake was probably cut off through a rise in the land mass and the deposition of material from volcanic eruptions, forming a land bridge between it and the sea. It is possible that the lake was once much larger, extending perhaps as far as the province of Batangas, but that the southern portion was filled in by further volcanic material (SOGREAH 1974). Presently, it is broadly divided into four regions, commonly known as West Bay, Central Bay, South Bay and East Bay (Fig. 1). Since its separation from the sea, the lake has silted up and shallowed to a considerable extent, with the deposits around the mouth of the Pasig River being at least 70-80m deep (SOGREAH 1974).

The hydrology of Laguna de Bay is determined principally by its large size, shallow nature, silty bottom and horizontal and vertical proximity to the sea. Due to its location in the tropics, the lake water is warm throughout the year with temperatures ranging from 25°C to 35°C annually. Laguna Lake is shallow and well mixed, preventing the establishment of a pronounced thermocline, so that the difference between surface and bottom temperature rarely exceeds 2C° (SEAFDEC 1996). Due to the almost constant stirring by the wind, dissolved oxygen also remains comparatively high at most times, rarely dropping below 5mg l^{-1}. However, during hot, calm weather, usually in July and August, the algal blooms often formed around this time of the year are prone to collapse, depleting oxygen levels and causing problems for wild and cultured fish. Readings of pH and total hardness are almost constant throughout the year and fall well within limits acceptable for fish life.

The levels of several other physical and chemical parameters, most importantly salinity, turbidity and nutrient concentrations, are influenced by the seasonal flow of water from and to the lake. During the rainy season (August to February), precipitation keeps the lake level high enough for excess water to flow out through the Pasig River while the monsoon winds stir the sediment to keep turbidity at a high level. During the dry season

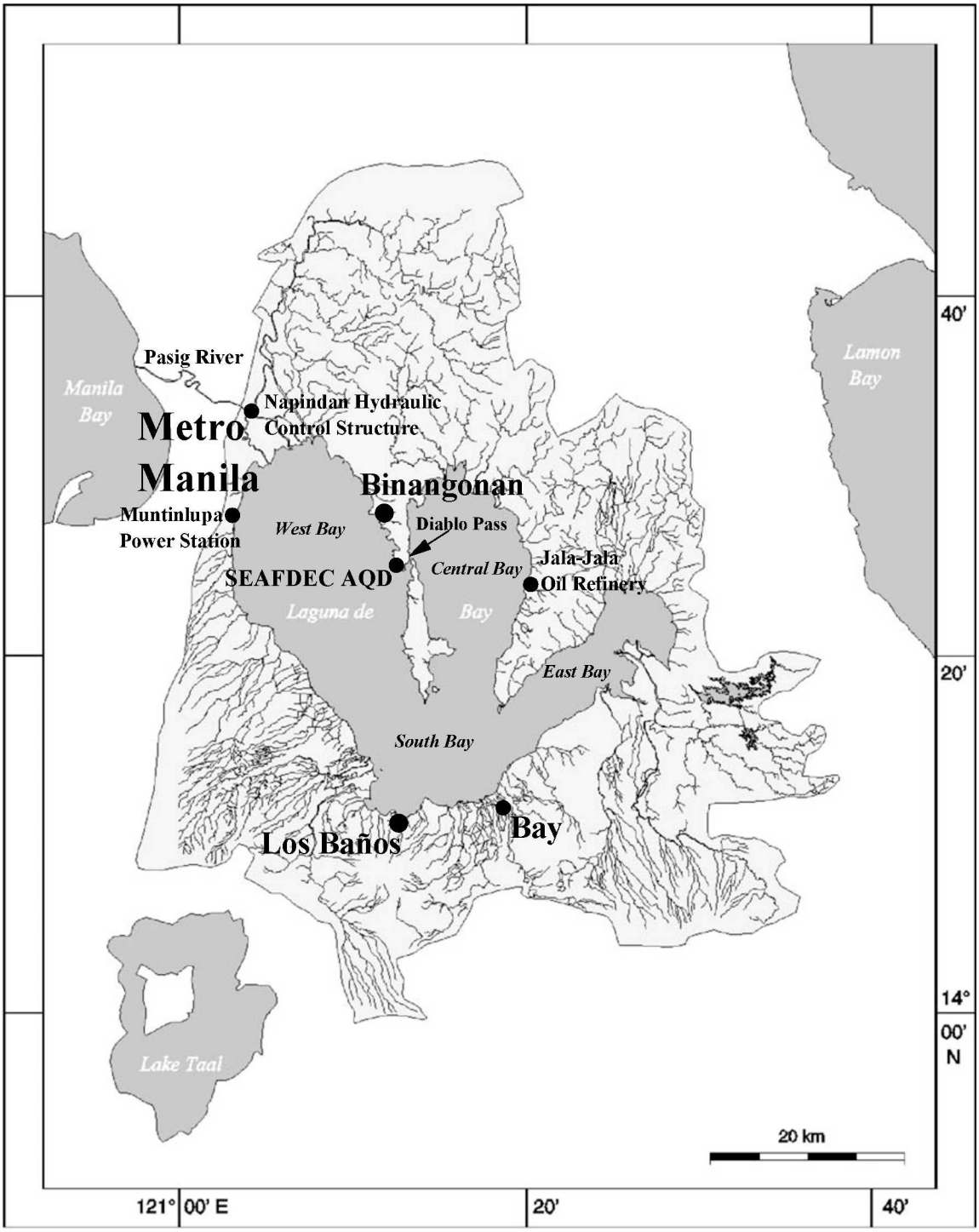


Figure 1. Map of Laguna de Bay and its watershed, showing the landmarks most important to this project (diagram by courtesy of the University of Hamburg)

(March to July), the lake generally dries to the point where the water level falls slightly below sea level at high tide in Manila Bay so that in most years there are periodic intrusions of saline water via the Pasig River. The negatively charged ions bind the fine suspended particles, flocculating them and, with the assistance of the calm weather at this time, speed their settling from the water column (Santiago 1991). The resulting drop in turbidity leads to a sudden rise in algal biomass and primary production. Consequently, when the water is turbid, light is the factor limiting primary production so that nitrogen and phosphorous accumulate to create eutrophic conditions. When the water clears, the plankton blooms quickly exhaust the nutrient supply, particularly that of nitrogen, so that nitrogen-fixing blue-green algae tend to dominate. These blooms are prone to collapse and cause fish kills towards the end of the dry season. With the onset of the monsoon season in late July, the water is stirred up and becomes turbid again.

2. Macrofauna of Laguna de Bay

Since Laguna de Bay was once connected to the sea, several animal species are freshwater representatives of marine families and some are endemic to the lake. As late as last century, Laguna de Bay was also inhabited by saltwater crocodiles, *Crocodylus porosus* (Cuvier 1807), and largetooth sawfish, *Pristis microdon* Latham 1794, but these died out or were hunted to extinction as the watershed became more populated. The Chacunda gizzard shad, *Anodontostoma chacunda* (Hamilton 1822), and penaeid shrimps were found in the lake as recently as the middle of this century but have also become extinct since then, probably due to pollution (Delos Reyes 1993). Vallejo (1985) listed 25 species of fish as occurring in the lake of which the *ayungin* or silver perch, *Leiopotherapon plumbeus*, the *biyang puti* or white goby, *Glossogobius giuris*, and the endemic *kanduli* or Manila catfish, *Arius manillensis*, are the most common. Apart from the fish fauna permanently confined to the lake, Laguna de Bay has always been visited by migratory species such as the milkfish, *Chanos chanos,* and mullets, Mugilidae, which entered via the Pasig River, but due to increasing pollution levels in this waterway since the Second World War, their passage has become progressively more difficult.

The precise status of the lake's fish population today is uncertain; however, the number of introduced species is slowly growing. The Nile tilapia, *Oreochromis niloticus*, brought in in the early seventies has become one of the major fish species in Laguna de Bay and most recently, there have been increasing number of Loricariid catfish caught by local

fishermen which are rumoured to have escaped from cages in the southern part of the lake. Other than the fish, the most notable representative of the vertebrate macrofauna is the banded elephant trunk snake, *Chersydrus granulatus* (Schneider 1799), a fish-eating colubrid known locally as *dohol* which is frequently taken by fisherman in their gears. Little is known about the invertebrate macrofauna since interest has mainly concentrated on the commercially fished species, notably shrimps of the genus *Macrobrachium*, the Manila clam, *Corbicula manilensis* Philippi 1844 and snails of the genera *Pomacea*, *Thiara* and *Melanifera.*

3. Macroflora of Laguna de Bay

In view of the extremely turbid state of the lake water, it is hardly surprising that submerged macrophytes are practically non-existent. This was not always the case. Pancho (1972) recorded 24 species of aquatic angiosperms of which only 14 were found again in the southern part of the lake by Aguilar *et al.* (1990), five of them submersed. Today, the macrophytic flora is dominated by free-floating plants, particularly the introduced water hyacinth, *Eichhornia crassipes* (Martius) Solms-Laubach 1883, with duckweed, *Lemna perpusilla* Torrey 1843, ferns of the genus *Azolla* and the water lettuce, *Pistia stratiotes* (L. 1758), also found. The reasons for the decline in numbers between the studies of Pancho (1972) and Aguilar *et al.* (1990) are not known for certain. The most likely reasons for the lack of rooted plants offshore in the lake, however, are the soft sediments which do not offer any means of attachment, as well as the continuous dredging activity of fishermen, particularly snailfishers, which would disturb anything that did manage to get a hold. The extremely turbid state of the water at most times of the year also prevents the necessary light from reaching all but the upper layers of the water column and the sometimes extensive cover of water hyacinth further reduces this to a minimum.

4. Growth Rates of Cultured Fish in Laguna de Bay

It has often been claimed that the growth rates of cultured fish have declined since the early 1970s (Santiago 1988, Delos Reyes & Martens 1994) or even that in the early days of culture, it was possible to grow fish from fingerling (5-10g) to marketable size (200-300g) in only three to four months whereas by the early 1980s, eight to fifteen months were required to achieve this (Davies 1988, Sly 1993). These figures are probably based on the studies of Delmendo (1974) and the Laguna Lake Development Authority (LLDA 1978) who seem to

represent the only sources of information quantifying the growth of milkfish to any extent. Delmendo (1974) visited twelve fishpens in the 1973-74 growing period and quoted final weights ranging from 117-448g after growing periods of four to six months. No details were given about the time of the year the fish were stocked, nor the stocking size. It was stated, however, that "the initial part of the rearing period was in the cool season of the year", suggesting that at least part of the study period took part before saltwater intrusion. It was also mentioned that "the LLDA experience is that a higher growth prevails during the warm season of the year and the time to raise a crop to a saleable size of 400 to 500 grams decreases to four to five months." Assuming that the growing periods in the lake alternate between one of a maximum of five months and another of a maximum of seven, the claim of two harvests per annum in Laguna de Bay in the early days of fish culture may therefore be considered to be plausible.

LLDA (1978) analysed three fishpens, one over a ten-month period from October 1975 to August 1976, the other two only around the period of clear water conditions (mid-April to mid-June and mid-June to mid-August respectively). They also gave more precise details of stocking size and sampling dates. Fish were stocked in mid-October at 24g and grew to a maximum average of 510g in mid-August of the next year. Detailed sampling at intervals in the first pen revealed that the period of maximum growth started in mid-April when the fish had reached about 120g. The sampling in the other two pens largely confirmed these findings: fish grew from 100.0-182.8g from April-June and from 300.9-510.8g from June-August.

5. Major Uses of Laguna de Bay

Aside from fisheries and aquaculture, Laguna de Bay is used for a multitude of purposes, all of which conflict to a greater or lesser extent with the former two or each other. All areas of the lake are used by commercial passenger boats connecting the towns and villages around the shore. Since some local *barangays* (village, smallest administrative unit in the Philippines) are not connected to the road system, there is no way to access them other than by water and some of the motorised outrigger *bangkas* travel not only in coastal regions but will cross the major bays. This means that the fishpens in at least some parts of these bays have to be spaced so as to allow such boats to pass through. The almost constant boat traffic at some times of the day also prevents fishermen from setting some gears, such as gill

nets, especially in coastal areas which are often the only fishing locations available to them after the fishpens have occupied the central part of the lake bays.

Apart from passenger and private boating, the lake is used for transporting cargo. Smaller items for sale in the various *barangays* are usually carried by the same boats as are used for passengers. The most notable large-scale cargo vessels are the oil tankers carrying crude oil from Metro Manila via Diablo Pass to the refinery on the west shore of the Jala-Jala peninsula on the eastern side of Central Bay (Fig. 1).

While the western part of the catchment is heavily industrialized, the eastern and southern regions are predominantly agricultural, with rice fields and coconut plantations established in the floodplains. Consequently, a considerable amount of water is abstracted for cultivation purposes. Some water is also used by industry, e.g. as cooling water by the Muntinlupa power station. However, the most intense demands for water abstraction, not only in terms of quantity but also with respect to quality, come from the ever growing population, mainly of Metro Manila, for domestic purposes. While agriculture and industry are satisfied with the current water quality, at present Class C (Santos-Borja 1993), this would in theory have to be upgraded to Class A in order to meet the standards for human consumption. In practice, lake water is already used by the Metro Manilan Water Authority to supplement the previously utilised reserves which have by now fallen short of demand.

The plans for large-scale abstraction of Laguna de Bay water for domestic purposes are not new. The main hindrance to this scheme was the intrusion of saline water which unfortunately takes place in the dry season, i.e. just at that time of the year when demand is at its greatest. In order to overcome the problem, the government constructed a barrage along the Pasig River, the so-called Napindan Hydraulic Control Structure (NHCS), which could be raised to allow lake water to flow out to the sea or lowered to retain it or prevent seawater intrusion (Fig. 1). This structure was completed in 1984 and operated in subsequent years; however, the wild fishermen and aquaculturists united in their protests as they considered the lack of saline inflow responsible for high turbidity and consequent low fish production. Ultimately, the government consented and after 1988, the NHCS was left open to allow Manila Bay water to enter in the dry season. Nevertheless, there is today increasing pressure to re-operate the structure as originally planned in order to improve the water quality to meet the standards for human consumption.

A further threat to fishery and aquaculture, as well as to domestic water abstraction, is the fact that the lake is also used by industry and private users as a waste dump. Domestic

waste is largely non-toxic but helps to eutrophy the lake; in addition, large quantities of human sewage considerably raise the coliform count to levels endangering the potential of the water for human consumption. Industrial waste poses a greater hazard to aquaculture and fisheries with the main factors being metals, organochlorins and oil spillages. Cuvin-Aralar (1990) analysed water, sediment and a variety of fish from the lake and found concentrations in all of these to be within permissible limits. Set against this, Sly (1993) reported that only about a quarter of the industries around the lake reached acceptable standards for waste treatment and that substances such as cyanide, phenol and organochlorins are of concern in the discharges of others.

B. Fish Growth & Condition

1. Growth

The growth of fish, like that of any other organism, is achieved by the size increase and subsequent division of cells in the body. Assuming that all cells behave in a similar way, i.e. grow and divide at the same rate to each give rise to the same number of daughter cells, the total number of cells at any given point in time is dependent only on the number of cells at the start, the rate of division and the time that has elapsed. This demonstrates an important principle of growth, namely that unlimited growth of any kind proceeds exponentially. Mathematically, this may be summarised as follows:

$$dW/dt = g \times W \qquad (1)$$

which gives

$$W = W_0 \times e^{g \times t} \qquad (2)$$

(W = body weight, W_0 = weight at time t_0, g = growth rate, t = time elapsed since time t_0, e = Euler's number, base of the *logarithmus naturalis*)

Even the most superficial analysis of fish growth reveals that the above relationship, which implies that the absolute body mass increases continually and ever rapidly until the fish dies, does not hold for the entire life span of any fish species. Rather than this, the fish approaches some maximum size which is achieved by the growth rate slowing down more and more the closer the fish gets to this size limit. The mathematical implication of this is that the growth rate g starts at some maximum, G_0, from which it declines as the fish ages.

Of the various models of fish growth (for reviews, see Ricker 1979, Gamito 1998), the one which best incorporates this principle is that of Gompertz (1825), first used to describe the distribution of ages in the human population. This allows the growth rate g to decline at an exponential rate so that:

$$dg/dt = -k \times g \tag{3}$$

which gives

$$W = W_0 \times e^{G_0 \times (1 - e^{-k \times t})} \tag{4}$$

(k = rate of decline of growth rate g, G_0 = initial growth rate at time t_0, W_0 = initial weight of fish at time t_0)

The growth of fish is not only dependent on the age and size of the animal but also on a large number of environmental factors. These may be abiotic, such as temperature, light intensity, salinity and oxygen levels, or biotic, such as food availability, quality and digestibility. These factors will, no doubt, have several more complex aspects, e.g. food availability is governed by absolute food quantity, its dispersion in the environment and the presence of intra- and interspecific competitors. Furthermore, there may also be interactions between these factors. A review is given by Brett (1979).

Irrespective of the gradual decline in the growth rate g over time even when no factors are apparently limiting, this decline is too insignificant to affect an estimate of g over a short period of time. Nevertheless, it has to be acknowledged that growth is not linear but exponential, i.e. an increase in body weight is dependent on the absolute body size of the fish. This has led to the use of the growth rate g in the form of the Specific Growth Rate, SGR (Brown 1946) for the estimation of growth in short-term trials. This is normally calculated by rewriting Eqn. (2) and multiplying the result by a factor of 100 to permit quoting the result as a percentage, as follows:

$$\mathrm{SGR} = 100 \times g = 100 \times (\ln[W_t] - \ln[W_0])/t \tag{5}$$

(W_t = final weight of fish [g], W_0 = initial weight of fish [g], t = duration of the trial [days])

While the SGR compensates for the fact that the absolute weight increase is heavily dependent on fish size, it fails to account for the fact that, as stated above, the growth rate g declines with fish age. As mentioned previously, this change is too insignificant to affect the results of a short-term trial, but it will distort comparisons between SGRs obtained for fish of the same species but of different sizes. In order to compensate for this, Dabrowski *et al.*

(1986) proposed the use of the Metabolic Growth Rate, MGR. This also relates the growth increase over time to the body weight of the fish but uses the metabolic weight as its base. The rationale behind this is that body processes such as oxygen consumption under fasting conditions are related to this parameter rather than the absolute body weight. Since the metabolic quotient of fish is 0.8 (Winberg 1956), the MGR is calculated after the following formula (Kühlmann 1998):

$$\mathrm{MGR} = [(W_t - W_0)/([(W_t/1000)^{0.8} + (W_0/1000)^{0.8}]/2)]/t \qquad (6)$$

(MGR = Metabolic growth rate [g $kg^{-0.8}$ day^{-1}], W_0 and W_t = body weight at times t_0 and t respectively [g], t = time span between W_0 and W_t [days])

Although growth is usually measured simply in terms of the increase of body length or weight, the factors underlying it are rather more complex. Thus growth is usually divided into somatic and gonadic growth since the former represents a more or less permanent increase in weight (unless the fish is starved and has to fall back on its body tissues as an energy reserve) whereas the latter is, from the outset, destined to be lost when the fish reproduces. Somatic growth also has to be further qualified, depending on the nature of the tissues laid down. An excess of fat and protein in the diet merely leads to the storage of these substances, increasing the weight of the animal, but an increase in length is associated with the deposition of hard tissues and is therefore to a large extent irreversible. In phases of bad food availability or quality, there is no scope for a length increase and reserves even have to be used up for maintenance so that the fish remains the same length but weight is lost. This leads to considerable fluctuations in the relationship between body length and weight, which has given rise to the study of what is commonly known as fish condition.

2. Condition

The rationale behind fish condition is that improved food quality and/or quantity first gives rise to an increase in girth as a result of the deposition of material in the soft tissues before this is converted to an increase in length. Thus fish that have had more or better food are in the short term relatively more full bodied than their starved counterparts. The simplest length-weight relationship reflecting increasing body condition with improved feeding is the condition factor K of Fulton (1911):

$$K = 100 \times W/L^3 \qquad (7)$$

(W = body mass, L = body length)

The condition factor merely reflects the length-weight relationship of a fish without any direct relation to the factors affecting it. There are, however, a number of other reasons for fluctuations in this relationship, including gut fullness (Weatherley & Gill 1987) and gonad maturity. The former is most pronounced in species that show clear diel feeding periodicity and can be avoided by using gutted weights or analysing fish that have been caught at the same time of day. The latter affects only fish samples which include mature individuals but can lead to significant differences between the sexes so that these may have to be analysed separately. More problematic is the phenomenon of allometric growth since this is not as easy to eliminate from the estimation of condition. One of the best ways of testing for allometric growth is to plot the condition factors of a population of fish caught at the same time in the same location against body length. A clearly increasing or decreasing trend, such as that found by Weatherly (1959) in tench, *Tinca tinca* (L. 1758), is indicative of allometry. While the presence of allometry is not difficult to establish, its quantification can be more problematic. In principle, it is generally estimated as the deviation of the parameter b in the following relationship from the "ideal" value of 3.0:

$$W = a \times L^b \tag{8}$$

which has given rise to the following condition factor K', first proposed by Ricker (1975):

$$K' = 100 \times W/L^b \tag{9}$$

In practice, the accurate determination of b requires data on a considerable number of fish spanning a large range of body sizes, which are not always available. Large deviations in b from 3.0 may usually be attributed to insufficient data sets and should be regarded with suspicion. A further complication is the fact that the parameter b can change as the fish passes from one growth stanza to the next, as was demonstrated for brown trout, *Salmo trutta* L. 1758 (Bagenal & Tesch 1978) so that it is always specific to the data set being analysed. Jones *et al.* (1999) therefore proposed a new condition factor B based not only on body length and weight but also on height:

$$B = W/(L^2 \times H) \tag{10}$$

(W = body weight, L = body length, H = body height)

The rationale behind this factor was that the body height captured more of the variation in the length-weight relationship due to allometry and that the third dimension, body thickness, was difficult to measure easily and accurately. However, Richter *et al.* (2000) demonstrated an isometric relationship between body height and thickness for milkfish, *Chanos chanos* and showed that a better factor involving length, height and weight was consequently B':

$$B' = W/(L \times H^2) \qquad (11)$$

These considerations regarding allometric growth only affect condition estimations of fish of different sizes. Even in species in which growth is strongly allometric, fish of the same size and in the same condition would be expected to have similar values of K so that any variation in this condition factor does not include any variability due to allometry.

C. Stomach Content Modelling to Estimate Fish Daily Ration

1. General Principles

The estimation of food consumption from stomach contents in fish is based on the assumption that the stomach is a confined chamber with only one entrance and one exit. All ingested matter must enter through the former and leave through the latter. Unlike in the remainder of the digestive tract, no food is assimilated in the stomach so that all gains and losses may be respectively attributed to ingestion and evacuation. Just as the change in the stomach contents over a period of time reflects the balance between these two parameters, so the ingestion rate can be determined from a combination of the evacuation rate and the increase or decrease in stomach contents over time. The daily ration is then calculated by integrating the mathematical function describing the ingestion rate over that part of the day in which feeding took place.

2. Bajkov Model

The first approach to the subject was made by Bajkov (1935) who assumed that the fish were feeding more or less regularly so that the level of stomach fullness was fairly constant over time. His method was based on sampling fish at intervals over a period of time and then determining the food consumption from the average contents over this period and

the mean time interval required to evacuate this quantity from the stomach. The stomach evacuation time was derived independently, either in the laboratory or by retaining a subsample of the fish caught without food in the field for a known time interval before comparing their stomach contents with those sacrificed previously. The equation proposed by Bajkov (1935) was then:

$$D = A \times 1/n \times 24 \tag{12}$$

(D = food consumption over 24 hours, A = average stomach contents over the period analysed, n = number of hours taken to evacuate the stomach fully)

This formula was modified by Eggers (1979), who changed the stomach passage time (in the form of the number of hours to evacuate the stomach) to an evacuation rate which he assumed to be directly dependent on the level of stomach fullness. This rate therefore became the product of the stomach contents and an instantaneous evacuation rate, giving rise to the following formula ("modified Bajkov formula"):

$$\mathrm{d}S/\mathrm{d}t = -E \times S \tag{13}$$

(E = instantaneous evacuation rate, S = stomach contents)

Pennington (1985), however, demonstrated that this approach also holds true when the rate of evacuation is dependent on some other power of the stomach contents, so that the formula becomes as follows ("generalised Bajkov formula"):

$$\mathrm{d}S/\mathrm{d}t = -E \times S^{\beta} \tag{14}$$

where β is a constant. The daily ration is then the integral over 24 hours of the ingestion rate, which in those species without change in stomach fullness is equivalent to the rate of evacuation:

$$R_{\mathrm{d}} = \int_0^{24} E \times S^{\beta}.\mathrm{d}t = E \times S_{\mathrm{avg}}^{\beta} \times 24 \tag{15}$$

(R_{d} = daily ration, S_{avg} = average stomach contents over the 24 hour period)

The value of the parameter β, which determines the precise form of the model, has in the past been the matter of some debate. The most common models are the linear evacuation model (β = 0; the instantaneous evacuation rate E becomes the evacuation rate, Olson &

Mullen 1986), the square root model ($\beta = {}^1/_2$; Hopkins 1966), the surface area model ($\beta = {}^2/_3$; Fänge & Grove 1979) the simple exponential model ($\beta = 1$; Eggers 1977, Elliott & Persson 1978). Alternatively, β may be included as a true parameter (Temming & Andersen 1994). The question of which model is the most appropriate is not made any easier by the fact that a comparison cannot be made according to biological criteria, since these are poorly understood, but has to rely on fitting the various functions to a set of stomach content data and selecting the best fit. It is possible that no model applies universally and that different fish species or food types require different models. For the sake of simplicity and handling ease, the simple exponential model is usually applied since in most cases it gives a good enough approximation to the data set.

3. Elliott-Persson Model

While the Bajkov (1935) method works well for species with more or less constant levels of stomach fullness (i.e. those species feeding more or less continuously or having very slow evacuation rates), the main problem is that it can be very difficult to reliably estimate the average stomach contents if the fish show clear diel feeding periodicity unless many samples are taken over a 24-hour period. Eggers (1977) and Elliott & Persson (1978) therefore developed a new model based on a point-to-point approach with subsamples consisting of a number of fish being collected at regular intervals. These subsamples therefore define a series of phases, each subsample marking the end of one phase and the beginning of the next. The model assumes that stomach evacuation takes place at all times and is directly proportional to stomach fullness (simple exponential model). The feeding rate is assumed to be constant for any phase between successive sampling points; however, it should be pointed out that, by its nature, the so-called Elliott-Persson model allows for variations in the feeding rate between successive phases. The food consumption for any given phase is then described by:

$$C_t = (S_t - S_0 \times e^{-E \times t}) \times E \times t / (1 - e^{-E \times t}) \qquad (16)$$

(C_t = Amount of food consumed, S_0 and S_t = stomach fullness at the beginning and end of the phase analysed respectively, t = length of phase in hours, e = Euler's number, base of the *logarithmus naturalis*)

The daily ration is then the sum of the consumption estimates for all phases covering one 24-hour cycle. This model has been applied on numerous occasions on a variety of fish

species (Persson 1982, Worobec 1984, Brodeur & Pearcy 1987, Macdonald & Waiwood 1987, Mazzola *et al.* 1999).

In their application of the model to brown trout, *Salmo trutta* and perch, *Perca fluviatilis* L. 1758, Elliott & Persson (1978) still used laboratory derived estimates for the evacuation rates. Lane *et al.* (1979) developed this model one step further and estimated the evacuation rate of diamond turbot *Hypsopsetta guttulata* (Girard 1856) from field data by visually separating the data into two phases (feeding and non-feeding), linearizing the non-feeding phase and calculating evacuation rate E by linear regression. They then used the value obtained to linearize the feeding phase (possible if E is known) and further calculated a value for the ingestion rate. The two intersections between the curves gave estimates for the start and end of the feeding periods so that all the necessary parameters for the calculation of daily ration had been derived from the field data without need for laboratory experiments.

4. Sainsbury/MAXIMS models

Elliott & Persson (1978) presented a second model based on the same principle as the first, the only difference being that the ingestion rate was not constant between successive sampling points but was allowed to decrease as the stomach fullness increased to satiation level. Unfortunately, this model was unworkable in the form presented (there is no algebraic solution to their Eqn. 11, p. 981, to obtain their Parameter b) and has therefore never been applied in its original form. However, both of their models were adapted by Sainsbury (1986) who retained the basic assumptions of a constant or stomach fullness dependent ingestion rate and a simple exponential evacuation rate. The principal difference was that Sainsbury (1986), like Lane *et al.* (1979), assumed a strict division of the overall sampling period into one feeding and one non-feeding phase with each phase incorporating several of the subsamples collected. The point-to-point approach was therefore discarded in favour of nonlinear regression through the data in order to estimate the parameters, including the feeding rate which previously was calculated from the other parameters in the Elliott-Persson model (it is equivalent to C_t/t in Eqn. 16). The evacuation rate was estimated as a parameter from the phase in which fish were not feeding so that this approach was essentially the first to make an evacuation rate based on field data an integral part of the model assumptions. The daily ration was to be obtained by integrating the feeding rate over the period in which consumption takes place, thus making the model with the ingestion rate dependent on stomach fullness workable for the first time.

For both of the models presented by Sainsbury (1986), the general equation modelling the evacuation rate in the non-feeding phase is the same as in Eggers' (1979) approach (Eqn. 13) but with variable stomach contents, which may then be integrated to:

$$S = S_f \times e^{-E\times(t-T_f)} \tag{17}$$

(S_f = stomach contents at the start of the non-feeding period, t = time, T_f = time at the start of the non-feeding period)

As stomach evacuation is a continuous process, this factor must be incorporated into the equation modelling the feeding period which, if the ingestion rate is constant, then runs as follows:

$$dS/dt = J_1 - E\times S \tag{18}$$

(J_1 = ingestion rate)

This equation is integrated to:

$$S = S_r \times e^{-E\times(t-T_r)} + (J_1/E)\times(1 - e^{-E\times(t-T_r)}) \tag{19}$$

(S_r = stomach contents at the beginning of the feeding period, T_r = time at the beginning of the feeding period)

If, on the other hand, the rate of ingestion is inversely dependent on the stomach contents, the change in stomach contents during the feeding phase is defined by:

$$dS/dt = J_2 \times (S_m - S) - E\times S \tag{20}$$

(J_2 = instantaneous ingestion rate, S_m = theoretical maximum stomach contents at which ingestion is zero)

Note that the two ingestion rates J_1 and J_2 are not directly comparable to each other, even when the same data sets are analysed with the aid of the two different types of model. In practice, since the stomach is constantly being evacuated, the theoretical maximum stomach content value is never reached but the ingestion rate stabilises at an asymptotic content value where ingestion equals evacuation ($dS/dt = 0$) so that:

$$S_\infty = (J_2 \times S_m)/(J_2 + E) \tag{21}$$

(S_∞ = asymptotic stomach contents)

The integral to Eqn. 20 is then:

$$S = S_r \times e^{-(J_2+E)\times(t-T_r)} + S_\infty \times (1 - e^{-(J_2+E)\times(t-T_r)}) \qquad (22)$$

Sainsbury (1986) also tested both of his model versions by applying them to laboratory data on brown trout in which the evacuation rate was known and comparing the model predictions with the laboratory results. He concluded that the model accurately predicted the food uptake of this species.

In what represented only a slight modification of Sainsbury's (1986) approach, the International Centre for Living Aquatic Resource Management (ICLARM), developed a computer model which they named MAXIMS (Jarre-Teichmann *et al.* 1991, 1992). This fixed the length of one feeding cycle to 24 hours and also extended the Elliott & Persson (1978) models to include routines for fish species with two feeding periods per cycle. In this case, while the level of stomach fullness at the beginning of one 24-hour cycle matches that at the end of that cycle, stomach fullness at the beginning of one feeding period is not necessarily equal to stomach fullness at the beginning of the next feeding period. Each feeding period is then treated separately, but the ingestion and evacuation rates (J_1 or J_2; E) are assumed to be the same for both periods. As a result, the model is composed of four routines:-

Model 1.1 - one feeding period, constant ingestion rate

Model 1.2 - one feeding period, ingestion rate inversely proportional to stomach fullness

Model 2.1 - two feeding periods, constant ingestion rate

Model 2.2 - two feeding periods, ingestion rate inversely proportional to stomach fullness

Each routine divides the data into distinct phases according to the best mathematical fit, plotting curve sections that satisfy the relevant equations (feeding phase: Eqn. 19 for Models 1.1 & 2.1, Eqn. 22 for Models 1.2 & 2.2; non-feeding phase: Eqn. 17 for all models). The start and end of the feeding phase is determined from the intersections of the curve sections. Idealized model curves are given in Fig. 2. As previously, the daily ration may then be calculated from the integral of the ingestion rate over the feeding period:

Model 1.1 $$R_d = \int_{T_r}^{T_f} J_1.dt = J_1 \times (T_f - T_r) \quad (23)$$

Model 2.1 $$R_d = \int_{T_{r1}}^{T_{f1}} J_1.dt + \int_{T_{r2}}^{T_{f2}} J_1.dt = J_1 * (T_{f1} - T_{r1} + T_{f2} - T_{r2}) \quad (24)$$

Model 1.2 $$R_d = \int_{T_r}^{T_f} J_2 \times (S_m - S).dt = \int_{T_r}^{T_f} (S_\infty \times (J_2 + E) - J_2 \times S).dt$$

$$= E \times S_\infty \times (T_f - T_r) + \left((S_\infty - S_r)/\left(1 + \frac{E}{J_2}\right)\right) \times (1 - e^{-(J_2+E)\times(T_f - T_r)}) \quad (25)$$

Model 2.2 $$R_d = \int_{T_{r1}}^{T_{f1}} J_2 \times (S_m - S).dt + \int_{T_{r2}}^{T_{f2}} J_2 \times (S_m - S).dt$$

$$= \int_{T_{r1}}^{T_{f1}} (S_\infty \times (J_2 + E) - J_2 \times S).dt + \int_{T_{r2}}^{T_{f2}} (S_\infty \times (J_2 + E) - J_2 \times S).dt$$

$$= E \times S_\infty \times (T_{f1} - T_{r1} + T_{f2} - T_{r2})$$
$$+\left((S_\infty - S_{r1})/\left(1 + \frac{E}{J_2}\right)\right) \times (1 - e^{-(J_2+E)\times(T_{f1} - T_{r1})})$$
$$+\left((S_\infty - S_{r2})/\left(1 + \frac{E}{J_2}\right)\right) \times (1 - e^{-(J_2+E)\times(T_{f2} - T_{r2})}) \quad (26)$$

One major disadvantage in the software developed by ICLARM for fitting the various submodels to field data is that it fails to give confidence limits to the various parameters and the resulting daily ration estimate calculated from them. One of the drawbacks of nonlinear regression methods is that they are based on iteratively minimising the sum of squared residuals (SSR) value (or maximising the maximum likelyhood ratio) and there is always the chance of falling into a local rather than a global minimum (or maximum). The ICLARM programme is rather prone to doing this so that the best fit is difficult to find and several attempts, each with different starting values for the parameters, have to be made. The software also shows a remarkable reluctancy to deviate from the initial estimate for the end of the feeding period, T_f, and the final fit may be non-randomly distributed around the data points (Richter & Focken 1998). In order to overcome at least some of these problems, Richter *et al.* (1999) reprogrammed the model for SAS® for Windows 6.11 and presented subroutines for each of the submodels in an extensive review of the MAXIMS model. This also made it possible to use the data points for each individual fish rather than the averages

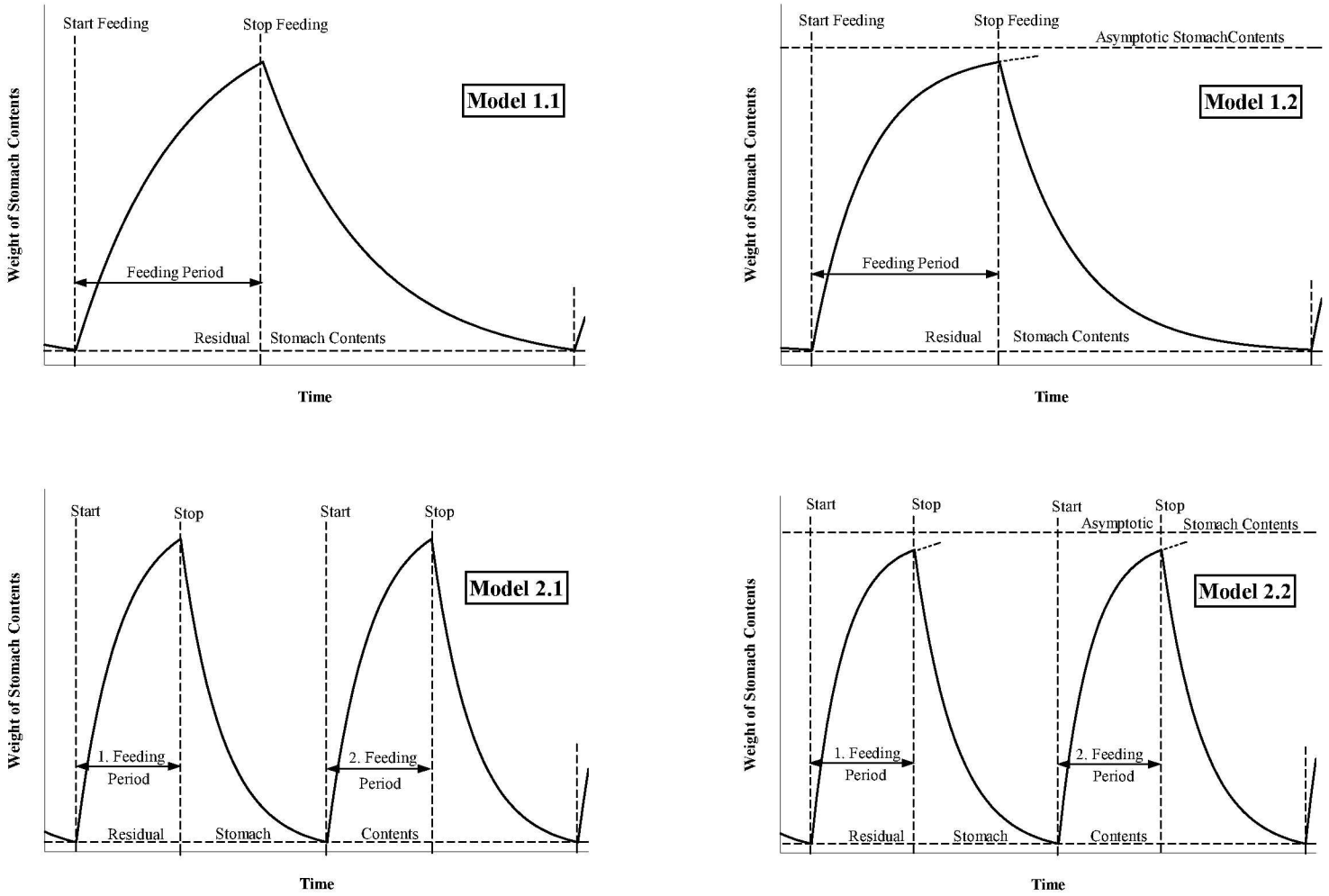


Figure 2. Idealized curves for the four MAXIMS Models 1.1, 1.2, 2.1 and 2.2. Models 1.1 and 2.1 with constant feeding rate, Models 1.2 and 2.2 with feeding rate inversely dependent on stomach fullness, all models with simple exponential stomach evacuation.

for the hourly subsamples. The disadvantage of using the latter is that these contain a certain measure of bias due to their non-normal distribution, particularly when most stomachs are empty, since it is not possible to have negative stomach contents (Olson & Mullen, 1986). By multiplying the matrix of partial derivatives with the covariance matrix (derived from the SAS® output) and further multiplying the product with the inverse matrix of partial derivatives (Rasch 1976), Richter *et al.* (1999) were able to develop a general method for the calculation of confidence limits to the daily ration estimate. The new SAS® version of the model also gives the user more flexibility and allows the development of more complex models to fit curves to more complex situations, such as multiple feeding periods in which the ingestion rates are not the same (Pinnegar 2000).

5. Olson-Mullen model

The aforementioned models are largely unsuitable for determining daily ration in predatory fish. These fish ingest large prey items which, in the case of ambushers, are consumed at irregular intervals, even if feeding is clearly restricted to only part of the 24-hour cycle (e.g. at night when the chance of detection by the prey is low). The ingestion of even one prey item causes the stomach fullness level to rise dramatically within seconds and individual prey items can differ substantially in size. Furthermore, it has been shown that different food types can have different evacuation rates depending on digestibility, and that their evacuation models need not always be exponential. This means that the assumptions made by the aforementioned models are altogether not met. Olson & Mullen (1986) therefore developed a model which was based on partitioning the stomach contents into their various food types, each of which is modelled separately, with the results then combined over the period analysed. It was shown that the average weight of a given type of food in the stomach over an (extensive) period of duration t is:

$$W(i)_{\text{avg}} = \left(M(i)_{\text{avg}}/T(i)_{\text{avg}}\right) \times \int_0^t \text{f}_i(t).\text{d}t \qquad (27)$$

($W(i)_{\text{avg}}$ = mean weight of food type i in the stomach over the sampling period, $M(i)_{\text{avg}}$ = mean weight of items of food type i when ingested, $T(i)_{\text{avg}}$ = mean time interval between ingestion of individual items of food type i, $\text{f}_i(t)$ = evacuation function of food type i)

Since $M(i)_{\text{avg}}/T(i)_{\text{avg}}$ represents the mean hourly feeding rate on food type i (assuming evacuation is also expressed per hour), if the fish is feeding on N food types, the daily ration R_{d} may simply be calculated from:

$$R_d = 24 \times \sum_{i=1}^{i=N} W(i)_{avg} / \int_0^t f_i(t).dt \qquad (28)$$

The model was applied to data on yellowfin tuna, *Thunnus albacares* (Bonaterre 1788), feeding on four different food types (Pacific squid, *Loligo opalescens* Berry 1911; Japanese mackerel, *Scomber japonicus* Houttuyn 1782; surf smelt *Hypomesus pretiosus* (Girard 1854); nehu, *Encrasicholina purpurea* Fowler 1900). No attempt at a full verification of this approach by comparison of model predictions with known consumption rates has been made and the model does not seems to have been applied to any other fish species. Mergardt & Temming (1997) used a derivative of this method to analyse stomach contents in whiting, *Merlangius merlangus* (L. 1758), and were able to show that, despite more or less regularly filled stomachs throughout the 24-hour period, ingestion rates were at a distinct minimum around 9:00 hours.

D. Biology of Milkfish, *Chanos chanos* (Forsskål 1775)

1. Distribution & Environmental Tolerance

The milkfish is the only extant member of the family Chanidae; its distribution ranges throughout the marine waters of the Indo-Pacific region from the east coast of Africa (Longitude 40°E) to the west coast of the United States (Longitude 100°W) between Latitudes 40°N and 40°S (Schuster 1960). It is uncommon at the northern and southern extremities of this range where it is limited to waters warmer than 20°C (Bagarinao 1994). Inside these limits, the main centre of its distribution is the Southeast Asian region, especially Taiwan, Indonesia and the Philippines. It attains a length of about 1.5m and a maximum weight of about 15kg (Schuster 1960, Bagarinao 1994) and is characterized by its elongated body shape which is covered with numerous small, silvery, cycloid scales, its small mouth, its gelatinous eyelids and its long, deeply forked caudal fin. It is a catadromous species; the immature fish spend most of their life in coastal areas where they are mainly found in bays and mangrove swamps. They also migrate into brackishwater lagoons and estuaries where they spend most of their life in schools until they reach a size that can no longer be supported by such habitats. At this point, they migrate to the open sea where they mature. Spawning takes place in schools, close to small, oceanic islands coral reefs and atolls, which are thought to be chosen since the water there is deep enough for the eggs to avoid benthic predators but

close enough to larger land masses for the larvae to be transported to their nursery grounds (Bagarinao 1994).

One of the main features of environmental tolerance in the milkfish is the extreme euryhalinity of this species. Milkfish are able to survive in freshwater as well as in the sea and even in salinities in excess of this. Bagarinao (1994) mentions a range of 0-158‰, close to five times as concentrated as oceanic water. In contrast, it is adversely affected by low temperatures, its lower lethal temperature being around 12°C (Schuster 1960). On the other hand, while it is unlikely to encounter temperatures in excess of 30°C in the wild, it has been known to tolerate 40°C or more in shallow fishponds (Bagarinao 1994). The minimum oxygen requirements of milkfish were determined by Schröder (1997) who analysed the critical oxygen partial pressure (P_c) for fish ranging from 40-190g body mass and recorded values of 31.3 and 33.0 mm Hg (equivalent to 19.7 and 20.8% saturation) at 27.5 and 32.5°C respectively.

2. Growth & Culture Methods

Since the milkfish is a tropical species and fails to lay down clear growth rings in its otoliths, almost nothing is known about growth rates in the wild. Schuster (1960) pointed out that pond reared fish and fish that become landlocked fail to attain maturity which impairs their growth so that they eventually become stunted. Nevertheless, there is considerable data on growth of juvenile and sub-adult milkfish in captivity from several authors, their results being summarised in Table 1. Most of these studies were conducted to test the quality of different supplemental feeds (Coloso *et al.* 1988, Sumagaysay 1991, Sumagaysay & Chiu-Chern 1991, Sumagaysay *et al.* 1991) but some authors aimed to investigate the food intake and growth of this species under conditions typical of semi-intensive culture (Sumagaysay 1994, Kühlmann 1998). It is evident from these studies that natural food can be a good basis for milkfish production: some of the highest growth rates were recorded using the modular pond system with fertilisation but no feed supplementation (Agbayani *et al.* 1989). Furthermore, both Sumagaysay (1994) and Kühlmann (1998) showed that there were distinct differences in fish growth between the wet and dry seasons in the Philippines. These were attributed to harsher environmental conditions, in particular high salinities and temperatures in the latter season.

The culture of milkfish is practised mainly in the Philippines, Indonesia and Taiwan, where it has become a major industry. Indeed, so great is its importance in the Philippines,

Table 1. Specific (SGR) and Metabolic (MGR) Growth Rates of milkfish, *Chanos chanos*, recorded by various authors in laboratory experiments to test different types of food and/or feeding levels or for fish held under conditions typical of extensive and semi-intensive culture.

Authors	Location	Type of Culture	Supplemental Feeding	Fertilization	Analytical Period	SGR (%)	MGR (g $kg^{-0.8}$ day^{-1})
Chiu *et al.* 1987	-	Aquarium (Lab Trial)	Yes	-	6 weeks	1.1 - 2.3	3.1 - 5.6
Coloso et al. 1988	-	Aquarium (Lab Trial)	Yes	-	12 weeks	0.7 - 1.2	2.4 - 4.0
Agbayani *et al.* 1989	Philippines	Modular Pond System	No	Yes	90 days	2.8 - 4.2	13.0 - 15.4
Kühlmann 1998	Philippines	Brackishwater Ponds	Yes	Yes	31 days	1.2 - 5.8	6.9 - 23.9
Siriwardena 1986	Sri Lanka	Coastal Lagoon Pen Culture	No	No	185-195 days	1.2 - 1.3	5.3 - 5.6
Sumagaysay *et al.* 1990	Philippines	Brackishwater Ponds	Yes	Yes	3 months	4.5 - 4.7	13.8 - 14.2
Sumagaysay 1991	Philippines	Brackishwater Ponds	Yes	Yes	20 weeks	3.8 - 4.0	8.4 - 9.0
Sumagaysay &	Philippines	Brackishwater Ponds	No	Yes	97 days	0.9	4.9
Chiu-Chern 1991			Yes	No	97 days	1.2 - 1.3	6.4 - 6.9
Sumagaysay *et al.* 1991	Philippines	Brackishwater ponds	Yes	No	142 days	3.3 - 3.6	8.8 - 9.7
			No	Yes	142 days	3.1	8.3
Sumagaysay 1994	Philippines	Brackishwater Ponds	No	Yes	113-120 days	0.9 - 2.5	3.5 - 8.9
			Yes	Yes	113-120 days	1.8 - 3.2	7.5 - 11.3

that *bangus*, as it is known in the national language, has been given the status of national fish. Its culture has been carried out for centuries in saline, brackish- and freshwater ponds, with or without fertilizer to promote algal growth, or supplemental feeding to improve production rates more directly. The alternative method of culture has been to fence off part of an open body of water, such as a lagoon, lake or estuary and grow this species from fingerling to marketable size. While pond culture was attempted in the area around Laguna de Bay, the comparative scarcity of land for other uses in the area, as well as the availability of a large, highly productive body of water, meant that it was only natural that pen culture became the favoured method in Laguna Lake.

3. Feeding Ecology & Food Spectrum

The food of milkfish has been studied in detail at all stages in its life cycle and in all habitats. Milkfish are primarily filter feeders, ingesting mainly planktonic algae as well as some zooplankton, but older individuals are also known to feed on soft sediments, ingesting the associated benthic flora and fauna (Chandy & George 1960, Schuster 1960, Poernomo 1976). Milkfish cultured in ponds without supplemental feed have been found to survive mainly on algae (Vincencio 1964, Almazan 1970, Borlongan 1990), in particular the thick mats of blue-green algae, known locally in the Philippines as *lablab,* which form a scummy layer at the water surface and are associated with numerous species of diatoms and invertebrates. Trino & Fortes (1989) analysed the gut contents of wild milkfish from a mangrove lagoon in the central Philippines, with a size range (13-223g) very similar to that of cultured fish in Laguna de Bay. These fish ingested mostly detritus, dead plant material and fine sand; 64.5% of all fish sampled contained only these three food types. Food components which were probably alive when ingested included mainly filamentous green algae and benthic organisms. The authors concluded from these results that juvenile milkfish prefer detritus and that the other ingested material was consumed incidentally. Of particular interest to the present study is the work of Kumagai & Bagarinao (1981) who looked at milkfish collected in 1978 from a variety of mostly marine locations in the Philippines, as well as pen-cultured fish from Laguna de Bay and concluded that "detritus was found common to all samples, abundant in samples from Laguna de Bay". The other food components found were diatoms and animal elements (*sic*, probably zooplankton or benthic invertebrates) in fish from Laguna Lake and blue-green algae, diatoms and debris in marine fish. In summary, the natural food of this species consists mainly of planktonic and benthic

algae, zooplankton, benthic invertebrates and organic detritus. In captivity, milkfish will take formulated feeds (Chiu *et al.* 1987, Santiago *et al.* 1989, Sumagaysay *et al.* 1990) and the main reason why these are not given in penculture in Laguna de Bay even when primary production is low may probably be attributed to the impracticability of efficient distribution over such a large area as a fishpen.

Very little seems to have been done previously on feeding periodicity, evacuation rate and daily ration estimation in milkfish. Chiu *et al.* (1986) kept milkfish in canvas tanks and provided them with both natural and supplemental feed. No contents were found in the entire digestive tract between 22:00 and 2:00 hours from which Chiu *et al.* (1986) correctly deduced "the absence of feeding during this time and even earlier". Sumagaysay (1993), on the other hand, assumed from this that active feeding in this species takes place between 2:00-22:00 hours, which must be incorrect since the intestinal tract takes some time to empty completely after the cessation of feeding. Sumagaysay (1993) also determined the instantaneous rate of evacuation in fish of 122g average weight held in concrete tanks and given either natural food or supplemental feed; she recorded rather high values of 1.57 h^{-1} for natural food and 1.79 h^{-1} for supplemental feed. Since this parameter is measured as the proportion of the stomach contents evacuated per hour rather than a unit of absolute weight per hour, such high values reflect the relatively small storage capacity of the milkfish stomach. These evacuation rates were used to calculate daily rations by the method of Elliott & Persson (1978) and these were found to range from 0.4-0.67g $fish^{-1}$ day^{-1} (equivalent to 0.87-1.14% BME day^{-1}; percent body mass equivalent on a basis of dry weight food:wet weight fish) for natural food and 1.44-4.77g $fish^{-1}$ day^{-1} (equivalent to 2.01-4.10% BME day^{-1}) for supplemental feed.

The study conducted by Kühlmann (1998) on semi-intensively cultured milkfish also included information on feeding periodicity and daily ration, in this case obtained using the MAXIMS model, for several sampling occasions in the different seasons. His instantaneous evacuation rates are not comparable to those calculated by Sumagaysay (1993) since the entire digestive tract was analysed which naturally contains more food than just the stomach. Kühlmann (1998) also worked on fish with an extensive range of body weights so that, in order to compensate for the fact that larger fish eat less as a percentage of their body size than small ones (Jobling 1994), he quoted his food consumption figures in terms of grammes food per kilogram metabolic body weight per day (g $kg^{-0.8}$ day^{-1}, dry:wet basis). The feeding periodicity of the fish analysed by Kühlmann (1998) was rather shorter than the lengthy time

span quoted by Sumagaysay (1993). This was attributed to low dissolved oxygen values at night, particularly in the dry season, which would have resulted in the fish incurring too great a metabolic cost if feeding had taken place. Nevertheless, since the fish were provided with supplemental feed as well as natural food which, in addition, was enhanced by fertilizing, it is unlikely that food availability was limiting and this was reflected in the high daily rations of 16.2-34.7g $kg^{-0.8}$ day^{-1} (equivalent to 2.51-5.91% BME day^{-1} dry:wet basis).

4. Digestive Tract Anatomy

The alimentary tract of this species has previously been described in detail by Chacko (1945), Chandy (1956), Chandy & George (1960) and Ferraris *et al.* (1987) and bears a number of features characteristic of filter feeders. The mouth is relatively small, terminal and bears no teeth. The gill arches are equipped with gillrakers which interlock to filter particulate matter from the water passing through them. Poernomo (1976) states that these "though small, are numerous and joined together into an effective fine sieve." Immediately behind the pharyngeal cavity are a pair of pockets known as pharyngeal organs. These are also found in the Clupeids; microscopical studies have confirmed that these organs are involved in the process of collecting the food from the gillrakers and passing it to the oesophagus (Chandy & George 1960).

The oesophagus is unusual in milkfish on account of its elongation and the fact that the inner lining is composed of a series of spiral folds, each lined with minute papillae bearing numerous mucus glands. These apparently serve to lubricate the food and aid its passage to the stomach (Chandy 1956, Ferraris *et al.* 1987). The stomach is, in itself, peculiar, being divided into two portions, the cardiac stomach also known as the corpus or proventriculus, and a muscular pyloric stomach, also known as the pylorus or gizzard, on account of its similarity to this organ in birds (Chandy & George 1960). Ferraris *et al.* (1987) found mucous cells but no acid or enzyme secreting cells in this part of the stomach, suggesting that the pylorus is used mainly for grinding the food. Immediately following the stomach, a number of intestinal caecae, about 120-150 in total, adjoin the intestine. Chandy & George (1960) mention that their histological structure is similar to that of the intestine but did not comment on their possible function. The intestine is comparatively long; intestinal ratios of 4.1-5.9 times body length were found by Kumagai & Bagarinao (1981) in juveniles collected from marine waters in the Philippines. Poernomo (1976) recorded a specimen caught in Katang, measuring 100cm total length with a ratio of 7.1 and Bagarinao &

Thayaparan (1986) found values as high as 8.5 in oceanic milkfish captured off Sri Lanka. The comparatively long digestive tract is seen as an adaptation to a herbivorous or detritivorous existence. Ferraris *et al.* (1987) found little evidence of differentiation along the length of the intestine, but did mention that secondary folding occurred at seven months of age. They interpreted this as an adaptation to increase surface area without further lengthening this part of the digestive tract.

E. Biology of Nile Tilapia, *Oreochromis niloticus* (L. 1758)

1. Distribution & Environmental Tolerance

The Nile tilapia is a member of the family Cichlidae, a large family of freshwater fishes distributed throughout most of Africa and South and Central America. Its original distribution extends over most of northern Africa up as far as Israel, but due to its suitability for aquaculture, it has been spread from here to a great number of tropical countries, including southeast Asia. It was originally introduced to Japan from its native Egypt, from where it was spread to Thailand and later to the Philippines in 1972 (Pullin 1996). It is generally a fish of larger, slow-flowing or standing bodies of water and as such is found in many of the African rift valley lakes, such as Lakes Awasa and Zwai (Getachew 1987, 1989, Getachew & Fernando 1989), Lake Chamo (Getachew 1993), Lake George (Moriarty & Moriarty 1973) and Lake Rudolf (Harbott 1975), but may also be found in smaller lakes and ponds; as its name implies, it is also found in rivers such as the Nile (Abdelghany 1993). In addition, it has been introduced into and cultured in rice fields (Chapman & Fernando 1994), fishponds (Edwards *et al.* 1994a,b) and fishcages (Basiao & San Antonio 1986, Guerrero *et al.* 1987). It is capable of attaining a maximum length of about 60cm and a maximum weight in the region of 3.5kg (Trewavas 1983); there is little difference between the sexes in terms of size, shape and colouration.

Like the milkfish, the tilapia is very much a fish of warm waters. Caulton (1979, quoted in Caulton 1982) experimented with *O. niloticus* in a thermal gradient tank and recorded a preferred temperature of 31°C. Caulton (1982) also stated that growth practically ceases below 20°C and that long-term exposures to temperatures below about 12°C would be fatal. At the other extreme, the upper lethal temperature recorded for Nile tilapia is around 39-40°C (Bishai 1965). Although Nile tilapia will withstand some salinity and have been

known to survive up to 29‰ (Philippart & Ruwet 1982) they are not as tolerant in this regard as other members of the genus used for culture, such as *Oreochromis mossambicus*.

2. Growth & Culture Methods

The growth rate of Nile tilapia has been determined by various authors, mainly by way of analysing the effect of various feeding levels or compositions of feedstuff on this parameter under carefully controlled conditions (Wee & Wang 1987, Micha *et al.* 1988, Siddiqui *et al.* 1988, Tabthipwon *et al.* 1988, Wee & Tuan 1988, Ng & Wee 1989, Wee & Shu 1989, El-Sayed 1990, Hanley 1991, Omoregie & Ogbemudia 1993, Xie *et al.* 1998). Of greater significance to the present work are those studies on tilapia reared under lake conditions, particularly the works of Aquino & Nielsen (1983) and Basiao & San Antonio (1986). The former authors analysed this species in extensive cage culture in Sampaloc Lake, a small lake (1.03km^2) just south of Laguna Lake and in the latter's watershed. Sampaloc Lake is rather deeper (max. 27m) than Laguna de Bay so that turbidity due to the upwelling of sediment is not a problem. The maximum SGRs recorded were 7-8% for fish of mean weight between 5 and 20g when primary productivity was around 1.5gC m^{-3} day^{-1}. The lowest growth rates were recorded in August when algal production was at a minimum and growth was predicted to cease when primary productivity dropped below 0.5gC m^{-3} day^{-1}. Basiao & San Antonio (1986) carried out a similar study on Nile tilapia in Laguna de Bay in 1980-81, at a time when fish productivity had already declined significantly from its zenith in the early seventies. Their study pointed to high phytoplankton levels as being the prime reason for fast growth of this species in June and July, with the highest mean SGR and MGR recorded for this period being 3.45% and 9.96g kg$^{-0.8}$ day^{-1} respectively. Nevertheless, growth was significantly faster from August-November (mean SGR: 2.63%; mean MGR: 7.46g kg$^{-0.8}$ day^{-1}) than from December-April (mean SGR: 1.93%; mean MGR: 4.35g kg$^{-0.8}$ day^{-1}).

Since this species has a lower salinity tolerance than other tilapia species or milkfish, it has been cultured principally in fresh or brackish water. Where natural water bodies are available, cage culture in either floating or suspended cages is the method of choice, otherwise, it is generally grown in earth- or concrete-lined ponds. As in the case of milkfish, fertilizer and/or supplemental feed is often used if this practice is economically viable. This species tends to be fiercely territorial in nature so that it has to be stocked at high rates, particularly in clearer water, in order to avoid the domination of submissive fish by one or

few aggressive individuals which would lead to the loss of the former due to excessive harassment from the latter.

One of the main problems with this species in aquaculture concerns its reproductive biology. Tilapias are noted for the fact that they attain maturity at an early age, in the case of *O. niloticus* well within their first year of life, at which point they start to breed precociously, generally at the expense of somatic growth. Members of the genus *Oreochromis* are mouth brooders; the male keeps a territory in which he builds a nest and then attracts a female to lay her eggs into it. After fertilization, the eggs are taken into the mouth by the female and the male takes no further part in brood care. While the eggs, and later the larvae, are developing, the female is unable to ingest any food until the young have reached the postlarva stage, further depressing her growth rate. There is no clear spawning season in this species and spawning can take place several times a year, so that the reproductive effort of these fish can have significant long-term effects on growth.

3. Feeding Ecology & Food Spectrum

The food and feeding habits of this species have been studied extensively in almost all environments in which it has been found or introduced to. Bowen (1982) writes that "Practically every aquatic animal, vegetable and mineral small enough to pass through the esophagus has been found in the guts of these fish." While the fry and juveniles depend on small invertebrates (Bowen 1982), adult *O. niloticus* are essentially microherbivores (Hickley & Bailey 1987), feeding mostly on planktonic algae (Moriarty & Moriarty 1973, Harbott 1975, Getachew 1987, Getachew 1993). Zooplankton is also found frequently, but almost always in small quantities (Hickley & Bailey 1987, Abdelghany 1993); detritus is often recorded as well (Abdelghany 1993) and may in some cases even dominate the diet in environments where it is abundant, such as rice fields (Chapman & Fernando 1994). In some studies, Nile tilapia have been found to depend more on periphyton than plankton (Hickley & Bailey 1987, Dempster *et al.* 1993) and by constructing an energy budget model for this species, Dempster *et al.* (1995) demonstrated that it is not possible for *O. niloticus* to obtain enough sustenance from filtered material and that it has to rely on periphyton (microscopic algae, animals and associated detritus on stones and aquatic plants) in order to avoid weight loss.

The feeding periodicity and daily ration has been studied in somewhat more detail than that of milkfish, although here, the populations analysed were not cultured but living

wild in African rift valley lakes. Moriarty & Moriarty (1973) investigated Nile tilapia in Lake George, Uganda, and developed a method for determining daily ration different to that of the MAXIMS model and based on the separate analysis of stomach and intestine contents. Using this technique, they calculated daily rations for various size groups which ranged from 1.04-1.84% BME (dry matter food as a percentage of the wet body weight). Feeding activity was mainly restricted to the daylight hours with some fish starting as early as 4:00 hours most individuals ceasing around sunset. This method was also employed on tilapia by Harbott (1975) in Lake Rudolf (now Lake Turkana), Kenia, and Getachew (1989) in Lake Awasa, Ethiopia, both of whom also found that this species feeds principally during the day. The daily rations calculated by these authors were 0.94 and 0.59% BME (dry:wet basis) respectively.

4. Digestive Tract Anatomy

The anatomy of the digestive tract of Nile tilapia has been summarised by Bowen (1982) and described in more detail by Moriarty (1973), Northcott & Beveridge (1988) and Beveridge *et al.* (1988). The mouth is of moderate size and endowed with small teeth, used for scraping periphyton. The gills are equipped with short gillrakers on their upper surface which nevertheless interlock to form a tight network that filters particles from the water. There are also taste buds and mucous glands, the latter helping to entrap any potential food particles by a kind of aerosol mechanism (Northcott & Beveridge 1988). The pharyngeal pads carry large number of pharyngeal teeth, used to break up ingested matter. They are not as well developed as those of macrophagous tilapias, such as *Tilapia rendalli* (Boulenger 1897), reflecting the reduced need for grinding capability in a filter feeding fish (Bowen 1982).

The oesophagus is small and short, leading almost directly into the stomach. This organ is shaped more like a sac than an inflated tube and is remarkable for its capacity to secrete acid to a pH of well below 2.0; values of pH 1.4 are frequently encountered in the lower part (Moriarty 1973) which help considerably in the lysis of blue-green algal cells and diatoms. It has, however, been demonstrated that acid secretion does not start until the stomach is fairly full already, so that the first food ingested at the beginning of a feeding period is not utilised as efficiently as subsequently consumed material. Pepsinogen may also be found in the stomach wall cells with the resulting pepsin having an optimum pH of 2.1, but Moriarty (1973) found no obvious proteolytic activity in stomach juices. He

hypothesised that either the level of secretion is low or that pepsin plays a more important role at the juvenile stage when the fish is still feeding mainly on microinvertebrates. It therefore appears that these fish have almost entirely dispensed with enzymatic digestion in the stomach, relying solely on acid lysis.

Following on from the stomach is a strongly extended intestine which is separated from the former by a sphincter muscle. There is surprisingly little information available on intestinal length ratios in this species but Bowen (1982) pointed to the "the exceptional length of the intestine" in tilapias in general, quoting values of between 7:1 and 10:1 in *T. rendalli*, *Sarotherodon melanotheron* Rüppel 1852 and *O. mossambicus*, which were representative of the group in general. Just as in the milkfish, the enormously elongated intestine is assumed to be an adaptation to a diet of poor quality. Smith *et al.* (1999; cited in Tengjaroenkul *et al.* 1999) demonstrated that in Nile tilapia, the intestinal tract is histologically differentiated into five regions. The enzyme activities of these regions were investigated by Tengjaroenkul *et al.* (1999) who found mainly peptidases and non-specific esterases. Maltase and lipases were found at lower levels and it was concluded that the predominance of protein-digesting enzymes was in agreement with the low-fat, protein rich algal diet of these fish.

F. Natural Food of Filter-feeding Fish

1. General

As their name implies, filter-feeding fish generally strain particles from the water, although periphyton and *Aufwuchs* are also sometimes relied on. These particles are of three main types: phytoplankton, zooplankton and detritus. From the filter-feeder's point of view, one of the main differences between these is their respective size. Phytoplankton can form large colonies but most algal species have small representatives. Many zooplankters, on the other hand, feed on phytoplankton and exceed the average algal size, if only to be able to handle their food conveniently. The size of detrital particles can vary enormously depending on their nature and state of breakdown. Just as a fisherman will select the mesh size of a gillnet to suit the size of the fish he is trying to catch, filter-feeding fish have adapted to have either large or small gillrakers, depending on whether they feed mainly on phyto- or zooplankton. While there is some overlap in dietary niche between the two, these fish can therefore be grouped broadly into phyto- and zooplanktivores. In integrated aquaculture,

farmers will usually stock fish of both types in order to utilize the production of a body of water to the maximum possible extent (Lin 1969, Iwata *et al.* 1989, 1990, Takamura *et al.* 1994).

2. Phytoplankton

Phytoplankton is made up of a large number of algal groups, the main ones being the blue-green algae or Cyanobacteria, the diatoms or Bacillariophyceae and the green algae or Chlorophyta. These differ considerably in ecology, size and structure, which has implications for their suitability as food for phytoplanktivorous fish. In Laguna de Bay, the dominant taxa tend to be diatoms at times of turbid water, which are replaced by blue-greens and greens when the water clears. Occasionally, blooms of dinoflagellates (Dinophyta) are also recorded in the lake.

The blue-green algae are, as their scientific name implies, similar in structure to bacteria. They lack organelles and their cytoplasm is more of a soup composed of the essential chemicals. Structural complexity is achieved principally by the formation of colonies (e.g. *Microcystis*, *Oscillatoria*) which in some species are made up of more than one type of cell (e.g. *Nostoc*, *Anabaena*). These are often linked to a feature specific among the various phytoplanktonic groups to blue-green algae, namely the ability of some Cyanobacteria to fix atmospheric nitrogen into nitrate. Another characteristic is that some species are able to form gas vacuoles in their cells (van den Hoek *et al.* 1995). These features provide the basis for prolonged blooms of blue-green algae during calm weather and favourable conditions when other algal groups are prone to run out of nitrogen and/or sink because of a lack of wind to stir the water and return them to the surface.

The simple structure of blue-green alga generally makes them easily digestible to filter-feeding fish. In addition, their capacity to fix nitrogen makes them an ideal source of food. However, because they are little more than bacteria with chlorophyll, the size of the individual cells tends to be small, falling close to or even below the limit of the fish's ability to entrap them. Colonial groups, on the other hand, tend to encapsulate themselves in a thick coating of jelly which can be a hindrance to digestion. In addition, several groups have developed strains with powerful toxins which can be tasted by the fish and cause them to cease filter-feeding. The suitability of blue-green algae as a base for aquaculture production therefore depends on the species in question.

The diatoms dominate the marine phytoplankton but are also well-represented in freshwater. This group is divided into cycloid and pennate forms, the latter being mainly benthic so that they are primarily ingested with the periphyton. All have a siliceous shell consisting of two halves which are permeated by numerous pores. The main characteristic of this group is that they survive in lower light conditions than other algal groups. They generally have larger cells than the blue-green algae, which makes them easier for phytoplanktivorous fish to strain from the water. Their many cells pores allow for easy access of digestive juices to the cytoplasm which makes the organic part of the cell highly digestible. On the other hand, the siliceous shell makes up a large part of the dry matter of the cell and is completely indigestible so that a large amount of useless bulk has to be passed through the digestive tract by fish feeding mainly on members of this group. The heavy shell also makes diatoms considerably heavier than water so that blooms of these algae rely on windy conditions to stir the water and keep them in suspension.

The green algae are a diverse group, ranging in cell size from only a few nanometres (e.g. *Chlorella*) to almost a millimetre (e.g. *Closterium*). This algal group needs more light than the diatoms or blue-green algae (Prescott 1969) which may be the reason why they so rarely bloom in Laguna de Bay. Like the cyanobacteria, they are capable of forming colonies (e.g. *Pediastrum*) which in some cases are also encased in a jelly-like coat (e.g. *Botryococcus*). The one feature common to all green algae, however, is their cellulose cell wall. Since fish, like most higher animals, lack both cellulase and the microorganisms in their gut which manufacture this, they cannot break down this cell wall chemically and access the cell contents. In order to get at these, the cell therefore has to be first broken up mechanically which is generally not feasible in the case of smaller algae. As a result, these often pass through the digestive tract unharmed as long as they can withstand the low pH values found in fish such as tilapias and have even had the opportunity to benefit from their temporary stay in a nutrient-rich environment (McDonald 1985a). This generally makes green algae rather poor food for phytoplanktivorous fish (Juario & Storch 1984, McDonald 1985b).

3. Zooplankton

Freshwater zooplankton is made up principally of Rotifers (Rotifera), water fleas (Cladocera) and copepods (Copepoda). Other groups such as the Ostracoda and unicelled animals (Protista) tend to be benthic or epiphytic, although some protists, especially ciliates,

can be found in large numbers in the plankton. The rotifers are among the smallest plankters, mostly ranging from about 40µm up to 1mm (Streble & Krauter 1988). The copepods and cladocerans, both crustaceans, are larger (up to several mm) and are capable of swimming powerfully with the aid of elongated antennae. All three groups have an outer skeleton, in the case of the rotifers made of proteins with some acidified polysaccharides (Hartwich 1984), in the case of the other two groups made of chitin, a nitrogen-containing polysaccharide (Gruner 1993). In no group is the entire body covered by this skin without gaps or holes so that it does not give as much protection from digestive juices as, for example, the cellulose cell wall of green algae.

Zooplankton constitutes the main food of most fish species when these are at their postlarval stage. One of the major reasons why larger fish abandon this food source is that it becomes too small relative to their body size and is too dispersed in the water to be profitable. Practically the only way for larger fish to obtain sufficient quantities is by filter feeding (e.g. bighead carp). Nevertheless, the larger plankters are normally scarce in or absent from the diets of phytoplanktivorous fish such as milkfish and tilapia. This is because these fish move more slowly through the water when filtering than zooplanktivores do, allowing the larger plankton to take evasive action. In spite of this, zooplankton is probably a very good potential source of food for fish, as shown by the rapid growth rates of those fish which rely on it.

4. Detritus

Detritus is defined as any dead organic matter, ranging from tree trunks to ultrafine particles. This material was once believed to constitute a dead end of the trophic network but it is now thought that it supports over half the higher animal production in most ecosystems. Intensive research has revealed that there are two detrital paths by which large items of dead organic matter are reduced to ultrafine particles in aquatic ecosystems. In the "fragmentation" pathway, the insoluble matter is physically broken up to an increasing degree by erosion or the chewing action of detritivores. Soluble substances, including amino acids from the breakdown of proteins, are often not fully utilised but are quickly lost by leaching. These substances are to some extent mineralised by microbial action but a surprisingly large proportion is recomplexed by adsorption onto mineral particles or secretion as bacterial slime. By this method, detritus is formed along the "dissolved organic matter" pathway. The two types of detritus formed are quite different and may be easily distinguished from each

other. The former tends to be fibrous, especially if derived from plant matter in which case the cellulose cell wall defines the former cell shape even after the cells have been destroyed, allowing the material to be identified. The latter, on the other hand, tends to have a uniform fine-grained structure and is generally termed "amorphous" detritus. Useful reviews may be found in Pomeroy (1980) and Bowen (1987).

Because detritus is dead material to which hardly anything is added and rather more taken away by detritivores, its nutritional value tends to decline with time. Highly nutritional substances that are easily utilised tend to be the first to be removed by such organisms and anything not taken up is soon lost through the leaching process. As a result, protein and non-protein nitrogen content is usually low, often less than 10% of ash-free dry matter (Bowen 1987). Surprisingly, this is also the case in amorphous detritus, despite the fact that this material is at least partly derived from exactly the highly nutritional substances that were so quickly leached out of the fibrous detritus. The gross energy content, on the other hand, tends to be comparatively high, often exceeding 10kJ g^{-1} dry matter, although in the case of fibrous detritus, a large proportion of this may be in the form of cellulose which is indigestible to fish. Both types of detritus tend to be colonised by microorganisms which break down the organic material and it has been suggested that these constitute the main source of nutrients for detritivores ingesting detrital particles. The microbial biomass has, however, been found to be invariably low (around 1%, Bowen 1987) and only the smallest detritivores can select the microbes from the other material. As a result, the main limitation for growth in larger animals feeding on detritus is usually the total protein and amino acid content of the food, the speed at which this can be processed and the energetic cost of doing so.

III Materials & Methods

A. Sampling of Milkfish & Nile Tilapia at Commercial Setups

1. Monthly Changes in Phytoplankton Biomass & Composition

In order to be able to compare the food intake and composition of the cultured fish with the food availability at different times of the year, it was necessary to monitor the algal biomass throughout the study period. As mentioned previously, however (cf. Introduction), this study was part of a larger project to set up a management plan for Laguna de Bay, carried out by several institutions. The task of monitoring the limnology and water quality of the lake was assigned to SEAFDEC AQD and presented in the communal annual report to the funding agency, the European Union (SEAFDEC 1996, 1997, 1998). The work discussed in this section is essential to this dissertation insofar that it gives information on the changing availability of natural food for milkfish and tilapia and has been included as original work, since it was collected by an institution directly involved in the overall project.

Monthly water samples were collected at four stations in the lake (Station W: West Bay; Station C: Central Bay; Station S: South Bay; Station P: Fishpen; Fig. 3) from April-December 1995. After a project re-evaluation, Station C was dropped in 1996 and 1997. Each station was sampled once a month with the sampling time falling around midday on each occasion. Stations W&P were sampled one day and Station S (and C in 1995) the next day. On each occasion, integrated water samples (one per station in 1995, three in 1996-1997) were taken with a 3*l* modified Schindler type water sampler at 0.5m depth intervals throughout the water column with two samplers collected at each depth. The entire sample was pooled in a PVC container, a 1*l* subsample taken for the estimation of algal biomass and the remainder filtered for zooplankton analysis (not relevant here). The phytoplankton sample was preserved in Lugol's solution and analysed at a later date. For this purpose, a 10m*l* aliquot was concentrated to 1m*l* by centrifugation and resuspension and the phytoplankton identified and counted on a haemacytometer. The wet biomass was estimated by shape approximation assuming a relative density of 1.0 for all plankton groups. Each phytoplankton sample was analysed in triplicate and the results averaged.

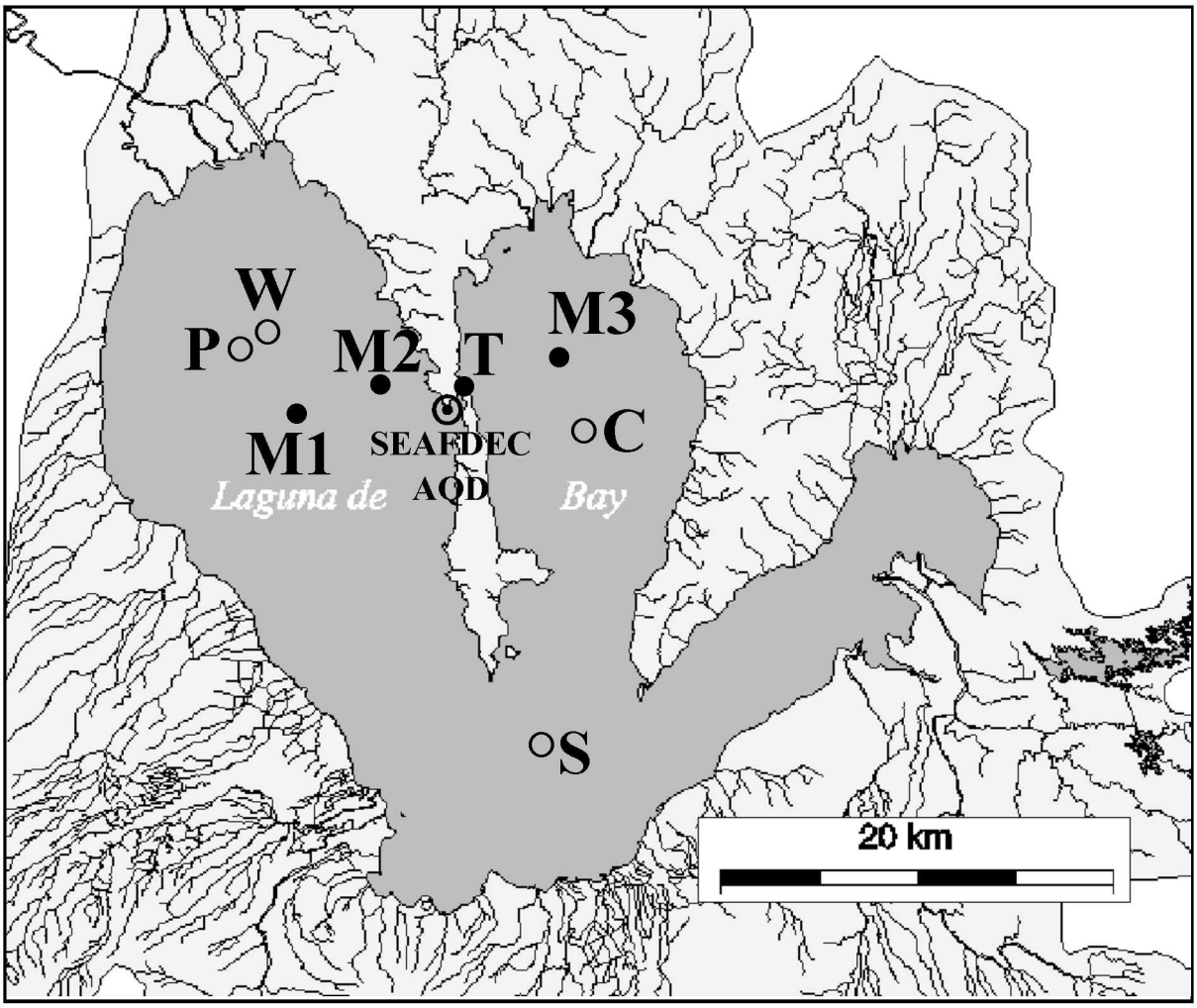


Figure 3. Map of Laguna de Bay and its watershed, showing the SEAFDEC water quality monitoring stations (○) and the location of the fishpens and -cages (●) at which fish sampling was carried out. SEAFDEC Stations: W (West Bay), P (Fishpen), C (Central Bay) and S (South Bay). Fish sampling sites: T: fishcages used for all tilapia samplings; M1: fishpen used for June and August 1995 milkfish samplings; M2: fishpen used for October 1996 and February and April 1997 milkfish samplings; M3: fishpen used for June and August 1997 samplings. SEAFDEC AQD, at which laboratory work was carried out, is included for reference (⊙). Diagram by courtesy of the University of Hamburg

2. Milkfish

a) General Sampling Procedure

Milkfish were sampled on several occasions throughout the study period with the primary intention of assessing their food composition and daily ration. Length and weight data were also taken on these occasions to estimate growth rates and condition and the gutted carcasses were also used for the analysis of body composition. In accordance with the

general requirements for estimating daily ration by stomach content modelling, the subsamples were spread more or less evenly over the 24-hour cycle. In 1995, eight subsamples of ten fish were collected at three-hour intervals but subsequent analysis demonstrated that the data gained from this sampling regime failed to meet the lower limit required for a reliable daily ration estimate. In the 1996-97 samplings, subsamples were therefore spaced at hourly intervals as far as the sampling circumstances allowed and the number of fish per subsample reduced to five.

Fish were obtained from a commercial operator on all sampling occasions so that they were cultured according to the practices commonly used in Laguna de Bay. In the case of milkfish, it was not possible to cooperate with the same fishpen owner over the entire study period. The first (sampled in June and August 1995) was put out of business by a severe typhoon towards the end of 1995 and the second (sampled October 1996, February and April 1997) increasingly came to regard the sampling days as disruptive until he refused to cooperate further so that a third fishpen had to be visited (sampled in June and August 1997). As a result, some differences with respect to fishpen size (100, 25 and 60 hectares respectively) and location (Fig. 3) had to be taken into account, but in all three cases, the fish were stocked at the same rate (ca. 5 fish m^{-2}) and kept without supplemental feed.

The general analytical procedure is summarised in Fig. 4. Due to the size of the fishpen, the only acceptable method of catching milkfish was by gillnetting. Milkfish in a particular pen are stocked on the same day and no fish are added or removed until they are harvested. At any one time, all the fish in the pen would therefore be expected to be approximately the same size. The mesh size of the gillnet was thus chosen accordingly after interviewing the fishpen operators as to what size of fish could be expected. After sampling, the fish were immediately killed and processed in the field. Standard lengths (nearest mm) and total and gutted weights (nearest g) were measured, the inner organs (liver, kidney, intestinal tract, gall bladder) were removed and placed in preweighed containers, after which gutted fish and innards were kept on ice until the return to the laboratory. Here, the fish were frozen until subjected to proximate analysis and the innards weighed (nearest 0.01g) and preserved in 70% ethyl alcohol until the stomach content analysis was carried out.

b) Growth Rates

The fact that milkfish in Laguna de Bay are stocked in empty fishpens and no fish are added or removed until harvesting makes it possible to estimate the growth rates of this

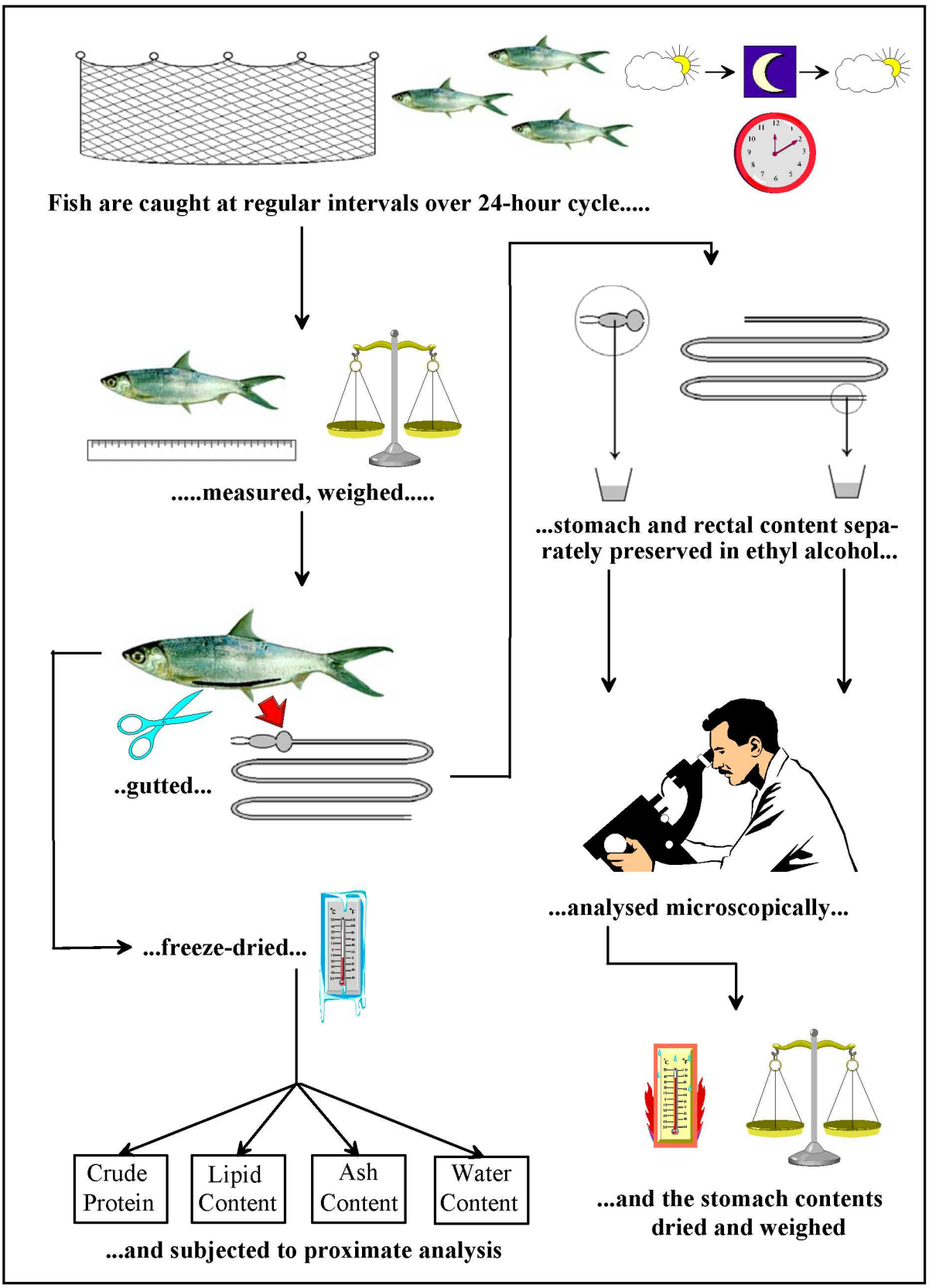


Figure 4. Schematic representation of the procedure by which milkfish and Nile tilapia and their stomach contents were analysed.

species for different times of the year provided that the same fishpen is visited twice and no harvesting has taken place in the time interval between sampling. The population Specific Growth Rates (SGR; %) and Metabolic Growth Rates (MGR; g $kg^{-0.8}$ day^{-1}) were therefore calculated for milkfish for those phases of the study period for which these conditions could be satisfied. The following formulae were used:

$$SGR = 100 \times (\ln[W_b] - \ln[W_a])/t \quad (29)$$

and

$$MGR = ((W_b - W_a)/[((W_a/1000)^{0.8} + (W_b/1000)^{0.8})/2])/t \quad (30)$$

(W_a = Average Total Fresh Body Weight at First Sampling (g); W_b = Average Total Fresh Body Weight at Second Sampling (g); t = Number of Days between First and Second Sampling)

c) Condition

The condition of milkfish was assessed by calculating the condition factor for each individual fish using the formula of Ricker (1975):

$$K' = 100 \times GW/SL^b \quad (31)$$

(GW = Gutted body weight, fresh (g); SL = Standard length (cm); b = Coefficient of the regression between log[SL] and log[GW] for all fish from all sampling days)

Since milkfish were found to show pronounced diel feeding periodicity (cf. Results), the condition factors were based on gutted weights in order to avoid having this parameter influenced by differences in food consumption related factors, such as feeding intensity and length of the feeding period, between sampling days.

d) Body Composition

A sample of 24 of the gutted fish (one from each hourly subsample) was later homogenized and analysed for moisture, crude protein, total lipid, and ash content. Water content was assessed by loss of weight after freeze-drying and heating to constant weight at 105°C to remove residual water. Crude protein was estimated as total Kjeldahl nitrogen x 6.25, total lipid as the ether-soluble extract and subsamples were combusted at 500°C to determine ash content.

e) Food Composition

The preserved stomachs were opened by a longitudinal incision, the contents flushed out into preweighed containers and preserved in 70% ethyl alcohol until microscopic analysis. For this purpose, the stomach contents were fully mixed and a small subsample, sufficient to comfortably fit under a cover slip without air bubbles being trapped or excess sample to ooze out, transferred to a microscope slide. The entire subsample thus obtained was analysed, all taxa identified as far as possible and the percentage contribution of the major components (phyto- and zooplankton, benthic algae, benthic crustaceans) estimated visually according to their level of coverage. Components found only at trace levels were assigned a nominal 1%. The relative simplicity of the method and the homogeneity of the samples ensured that the analysis of one such subsample was sufficient; no discernible differences were found between replicates analysed for the earlier samples and the analysis quickly showed that the assessment of even a portion of the subsample under the cover slip would have sufficed. All unidentifiable material was attributed to detritus. This was present in abundance (cf. Results) but almost always as amorphous detritus (Bowen 1987). A rectal sample was also collected from the last few cm of the intestinal tract in order to be able to judge the state of digestion of those components observed in the stomach contents. After analysis under the microscope, the material on the slide was recombined with the remainder of the stomach contents of that fish. These were then dried at 70°C in the preweighed containers and the dry weights measured (nearest 0.01g) for the MAXIMS analysis.

f) Feeding Periodicity & Daily Ration

In order to compensate for the fact that larger fish are logically able to consume more and that the fish collected on any one sampling day were not of the same size, the dry weights of the stomach contents were standardised for the purpose of the MAXIMS analysis by converting them to percentages of the fresh weight of the fish (% Body Mass Equivalent, hereafter referred to as % BME).

The MAXIMS curves for any particular sampling day were calculated using the model in the version programmed for SAS® 6.11 for Windows (Richter *et al.* 1999). Since milkfish, as filter feeders, are more likely to have relatively constant ingestion rates, the MAXIMS Model 1.1 was used in all cases for this species. The SAS® routines used to model the milkfish samplings are given in Appendix 1. In all cases, the data points gained from the individual fish rather than the averages for the subsamples were used. Several different sets

of starting estimates were used and the fit with the lowest Sum of Squared Residuals (SSR) value selected. Using the SAS® output, the daily rations were calculated according to Eqn. 23 from the integrals of the feeding rate over the feeding phase.

The standard errors to the parameter estimates were taken directly from the SAS® output. The standard error to the daily ration was calculated by the method described in Richter *et al.* (1999) using the parameter estimates, their standard errors and their correlation coefficients (all given by the SAS® output). This involved the multiplication of the partial derivatives matrix with the covariance matrix and multiplying the resulting product with the inverse of the partial derivatives matrix, as described by Rasch (1976). An example of this procedure is given in Appendix 3. The equivalent parameter and daily ration estimates obtained for different sampling months were compared statistically using the Tukey-Kramer test for unplanned comparisons (Sokal & Rohlf 1995) at a significance level of $p \leqslant 0.05$.

3. Nile Tilapia

a) General Sampling Procedure

The analysis of tilapia proceeded on rather similar lines to that of milkfish, the main difference being that, since the commercial farm from which Nile tilapia were obtained was located inshore and close to the Binangonan Freshwater Station of the Aquaculture Department, Southeast Asian Fisheries Development Centre (SEAFDEC AQD; Fig. 3), it was possible to analyse the fish in the laboratory of this station and slightly simplify the procedure. The tilapia were kept in shallow water in small, closed-bottomed cages which measured about 3x6m and which were sufficiently deep to reach the bottom sediments. The stocking rates were approximately 50 fish m^{-2}, which is not excessive considering that this species is supplemented for large parts of the year; fingerlings are stocked at up to 200 m^{-2} (Guerrero et al 1987). Sampling was carried out in May and August 1995, March, May, July and September 1996 and January 1997. In May 1995, the fishcage contained two groups of fish of distinctly different sizes and both size classes were analysed separately. On each sampling occasion, fish were collected by manually lifting the net until a small enclosure was formed and randomly extracting the desired number of fish. These were immediately killed by immersion in iced water and brought to the station for analysis. Standard lengths (nearest mm) and total and gutted weights (nearest 0.01g) were measured, the inner organs (intestinal

tract, liver, kidney, gall bladder, gonads) removed, weighed (nearest 0.01g) and preserved in 70% ethyl alcohol. The fish were frozen until further analysis for body composition.

Supplemental feed (Robina Starfeeds, Universal Robina Corporation) was given in August 1995, September 1996 and January 1997; on the latter two sampling occasions, two sets of fish from different fishcages were analysed, one with and the other without supplementation in order to compare the two. In August 1995, the fish were offered pellets in one dose in the morning whereas in September 1996 and January 1997, powdered feed was given (one dose in 1996, two in 1997). This change reflected the economic situation of the operator: in November 1995, a strong typhoon destroyed practically all aquaculture structures in the lake so that even a year later, the farmer could not afford to buy pelleted feed but had to rely on stocks which were made up only of starter crumble. The level of supplementation was left to the discretion of the fishfarmer and therefore varied between sampling days. The quantity of feed commonly given to tilapia in Laguna de Bay ranges between around 6-12% Body Mass Equivalent (% BME) and partly depends on the financial situation of the fishcage operator. In our case, subsequent discussion revealed that the fish were given 6.5% BME in August 1995 and 8% BME in September 1996 (wet:wet ratio) in one dose in the morning. Due to a calculating error by the fishfarmer, the supplementation level was disproportionately high in January and the fish received nearly 40% BME in two doses, so that the fish can be regarded to have been fed to excess on that occasion.

b) Growth rates

These growth rates of this species were not calculated using the data from the fish sampled at commercial operations since on account of the culture method, it is easy and therefore apparently common practice in Laguna de Bay to check these fish and remove those that have reached a marketable size and/or add new fish. This would have distorted any population growth rates determined. In addition, the fact that these fish were given supplemental feed for at least part of the study period would have made it difficult to interpret the growth rates in relation to water quality and natural food availability. The growth rates were instead determined by keeping fish in cages at the SEAFDEC station over eight months in 1997 without supplementation (cf. Section B, Tilapia Growth & Water Quality Study).

c) Condition

The body weight range of the tilapia collected in this part of the study was rather less than two orders of magnitude so that any allometry in the growth of this species would not be expected to have much of an effect in the determination of condition of the fish sampled here. When assessing the condition of this species, Fulton's (1911) condition factor was therefore used:

$$K = 100 \times GW/SL^3 \qquad (32)$$

(GW = Gutted body weight, fresh [g]; SL = Standard length [cm])

The data for May 1995 (large and small fish) were combined since these had been kept under the same conditions, whereas the data for supplemented and unsupplemented fish collected in September 1996 and January 1997 were analysed separately. This was because fish kept with and without compound feed had been on these feeding regimes for about a month prior to sampling in order to allow them to acclimatize to the presence/absence of feed in their diet well in advance. As in the case of milkfish, distinct feeding and non-feeding periods were found over the 24-hour cycle (cf. Results) so that the gutted weights were used in the analysis of condition.

d) Body Composition

The proximate analysis of tilapia proceeded on the same lines as that for milkfish. The supplemental feed provided in August 1995, September 1996 and January 1997 was analysed in the same manner, although for this substance, total fibre was also determined.

e) Food Composition

The stomach contents of tilapia were also analysed in a similar manner to those for milkfish. When supplemental feed was given, this was distinguished from detritus on the basis of the amorphous nature of the latter. The fishfeeds used in the Philippines contain substantial proportions of plant material which retain their cell structure even when ground and there was no mistaking the characteristic, fine-grained detritus for supplemental feed.

f) Feeding Periodicity & Daily Ration

The dry stomach content weights of tilapia were transformed to % BMEs and analysed with the aid of the MAXIMS model (SAS® 6.11 Version) in order to investigate

feeding periodicity and food uptake. One problem in the case of this species was that only the fresh weights of the stomach contents were recorded for the 1995 samples, making a comparison with the data from subsequent samplings difficult. In addition to the dry weights, the alcohol-preserved weight of the stomach contents as well as the fresh weight of the digestive tract were taken for each fish in 1996 and 1997. This permitted an estimation of the fresh weight of the contents for the 1996 and 1997 by the following formula (adapted from Kühlmann 1998, his Eqns. 9&10):

$$FrWC=(FrWI \times AlcWC)/AlcWI \qquad (33)$$

(*FrWC* = Fresh Weight of Contents; *FrWI* = Fresh Weight of Full Innards; *AlcWC* = Alcohol preserved Weight of Contents; *AlcWI* = Alcohol preserved Weight of Full Innards)

These estimated fresh weights were then regressed against the respective dry weight for that fish by means of a Model II (geometric mean) regression (Sokal & Rohlf 1995). The regression coefficients for each sampling day were then averaged and used to convert the results of the 1995 samplings to estimated dry weights.

The main problem in applying the MAXIMS model to the data was that the basic assumption of a constant ingestion rate in the feeding period was seriously violated in several of the data sets collected. This mainly happened when supplemental feed was given since this component was ingested far more easily than natural food, but other reasons for this were also found (cf. Results). Irrespective of the causes of this phenomenon, none of the normal MAXIMS routines could be applied and another solution had to be found.

By analysing not only the total weight of the stomach contents over time but also their composition, it was possible to determine when one food component (e.g. supplemental feed) started to increase or decline relative to the other components. These time points were taken to mark a change in the feeding pattern and the feeding period was split into several subphases on the basis of this information. Each subphase was assumed to have a constant ingestion rate (equivalent to the MAXIMS Models 1.1 & 2.1 assumption) but different subphases were allowed to differ with respect to this parameter. The instantaneous evacuation rate was assumed to be constant throughout the 24-hour cycle. The entire analytical period was then remodelled by writing more complex models on the basis of the above assumptions.

All special models incorporated the same assumption concerning stomach evacuation common to all MAXIMS models, namely that stomach evacuation takes place at all times

and is directly dependent on the level of stomach fullness in combination with a constant instantaneous evacuation rate. A second common assumption was that the analytical cycle lasted 24 hours and that the level of stomach fullness at the start was equal to that 24 hours later. One vital prerequisite was that the fish ceased feeding for at least part of the study period so that the model was able to calculate the instantaneous evacuation rate. The SAS® routines written for tilapia are presented in Appendix 2; further details of the individual models are presented in Section III: Results. Again, the individual data points were used rather than the subsample averages and the best fit was chosen on the basis of the lowest SSR value. The daily rations were again calculated by integrating the ingestion rate(s) over the (respective) feeding phase(s) analogous to Eqn. 23 & 24. The confidence limits to the daily ration and the comparison of parameter and daily ration estimates were calculated according to the same principles as for milkfish.

B. Tilapia Growth & Water Quality Study

1. Water Quality Sampling

a) General Sampling Procedure & Secchi Depth

Between March and November 1997, water samples were collected at weekly intervals for particulate organic and inorganic matter (POM, PIOM), Chlorophyll-a (Chl-a) and zooplankton biomass at the SEAFDEC station. The Secchi depth was also measured on these occasions. Integrated water samples were taken with the aid of a 3*l* water sampler (modified Schindler type) at depth intervals of 0.5m starting at the surface; two full samplers were collected at each depth interval. All water thus obtained was pooled in a large PVC container and filtered first through a 50µm, then a 15µm plankton net. The residues were resuspended in 300m*l* distilled water and a quantity of the filtrate sufficient for further analysis retained so that three size fractions (<15µm, 15-50µm and >50µm; hereafter referred to as the small, middle and large size fraction respectively) were collected. This procedure was repeated twice so that triplicate samples were collected for all size fractions, which were kept refrigerated until further analysis on the same day as the samples were taken.

b) Chlorophyll-a

100m*l* of each sample (replicate and size fraction) was filtered onto cellulose nitrate filters and crushed in 10m*l* acetone (90% concentration) to extract the photosynthetic pigments. The sample was centrifuged and a spectrophotometric reading taken at 665nm. The Chl-a concentration in the water was calculated from the following formula, adapted from Golterman *et al.* (1978):

$$Chl-a = SR \times 11.9 \times v/V \qquad (33)$$

(*Chl-a* = chlorophyll-a concentration [mg l^{-1}]; *SR* = spectrophotometric reading at 665nm; *v* = volume of acetone used for extraction [m*l*]; *V* = volume of water sample filtered [m*l*])

When conducting this calculation for the middle and large size fractions, the degree to which these had been concentrated by the filtering process was taken into account.

c) Particulate Organic & Inorganic Matter

A further 100m*l* of each sample (replicate and size fraction) was filtered through preweighed Whatman GF/C glassfibre filter papers to assess the concentration of suspended solids. The filters were dried at 70°C after filtration, weighed (nearest mg), ashed at 550°C and weighed once more (nearest mg). The difference between weight after ashing and initial filter weight was taken as the level of PIOM; the difference between weight after drying and weight after ashing as the level of POM.

d) Zooplankton

A further three replicate water samples were collected for zooplankton analysis. These were filtered through a 50µm plankton net; it was assumed that all zooplankton was large enough to be retained by this mesh size. While this was not strictly true for some of the smaller rotifers, it is certainly true that all the copepod and cladoceran species would not pass through this pore size so that most of the zooplankton may be assumed to have been included in the sample. The residues were resuspended in 10% methanaldehyde (formalin) solution to preserve them until further analysis. At a later date, a representative portion was analysed under the microscope, the zooplankton counted and its biomass estimated by shape approximation assuming a relative density of 1.0 and a wet:dry mass ratio of 10:1 (Schwoerbel 1980).

2. Tilapia Growth Rates

Since it had not been possible to calculate the growth rates of Nile tilapia from the fish used for stomach content analysis on account of their culture method, growth rates for this species were obtained by keeping fish in cages in the lake. This was done at the SEAFDEC Station during the same time period as the water samples for Chl-a, zooplankton, POM and PIOM were collected. No supplemental feed was given and the standard length and total weight of the fish were determined twice a month. Four replicate cages, each measuring 5x5x4m, were used and the initial stocking density was 25 fish per cage. This figure is rather lower than the 50 fish m^{-2} normally stocked in the case of this species but it should be remembered that in this study no supplemental feed was given. The fish were collected for analysis at around 8:00 hours on all measuring/weighing days and kept in clear water so that substantial differences in weight and condition between different sampling days due to different levels of gut fullness were not to be expected. The fish were blotted dry and the water drained from the oral cavity to minimise sampling error; this practice also helped determine whether any of the fish were mouthbrooding and thereby prevented from feeding. The fish were not tagged so that it was not possible to monitor the growth of individuals; nevertheless, all fish were measured and weighed individually. Following analysis, the fish were returned to their cages. Dead fish were not replaced in order to simplify the calculation of population growth rates between samplings. Stocking took place on 26. March 1997 and the last analysis was carried out on 20. November 1997.

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

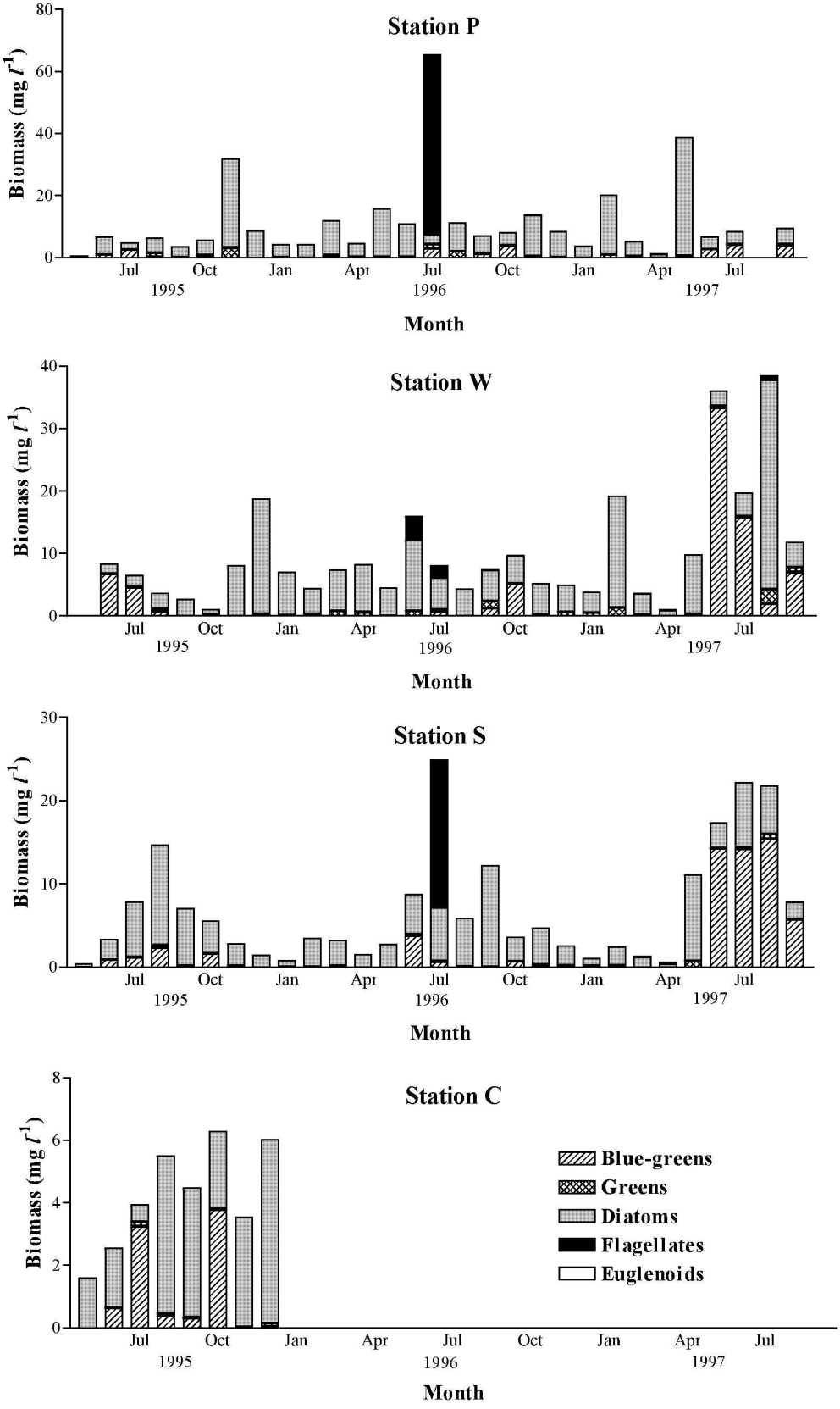


Figure 5. Phytoplankton biomass in a fishpen (Station P), in West Bay (Station W), South Bay (Station S) and Central Bay (Station C) from May 1995 to September 1997 inclusive. No sampling at station C throughout 1996 and 1997 or at Station P in August 1997). Common legend shown at Station C. Note different 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 ± 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 ± 1.1	45.8 ± 11.6	37.9 ± 9.7
7.-8. August 1995	M1	80	21.9 ± 1.3	200.5 ± 34.9	182.4 ± 32.6
3.-4. October 1996	M2	120	11.3 ± 1.9	26.5 ± 15.3	22.0 ± 13.5
6.-7. February 1997	M2	86	14.1 ± 2.3	44.7 ± 30.3	40.4 ± 26.0
29.-30. April 1997	M2	85	14.7 ± 2.8	48.6 ± 28.0	44.2 ± 25.9
19.-20. June 1997	M3	99	22.8 ± 1.5	220.9 ± 50.2	194.8 ± 44.5
21.-22. August 1997	M3	88	30.5 ± 1.4	528.0 ± 66.7	495.8 ± 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

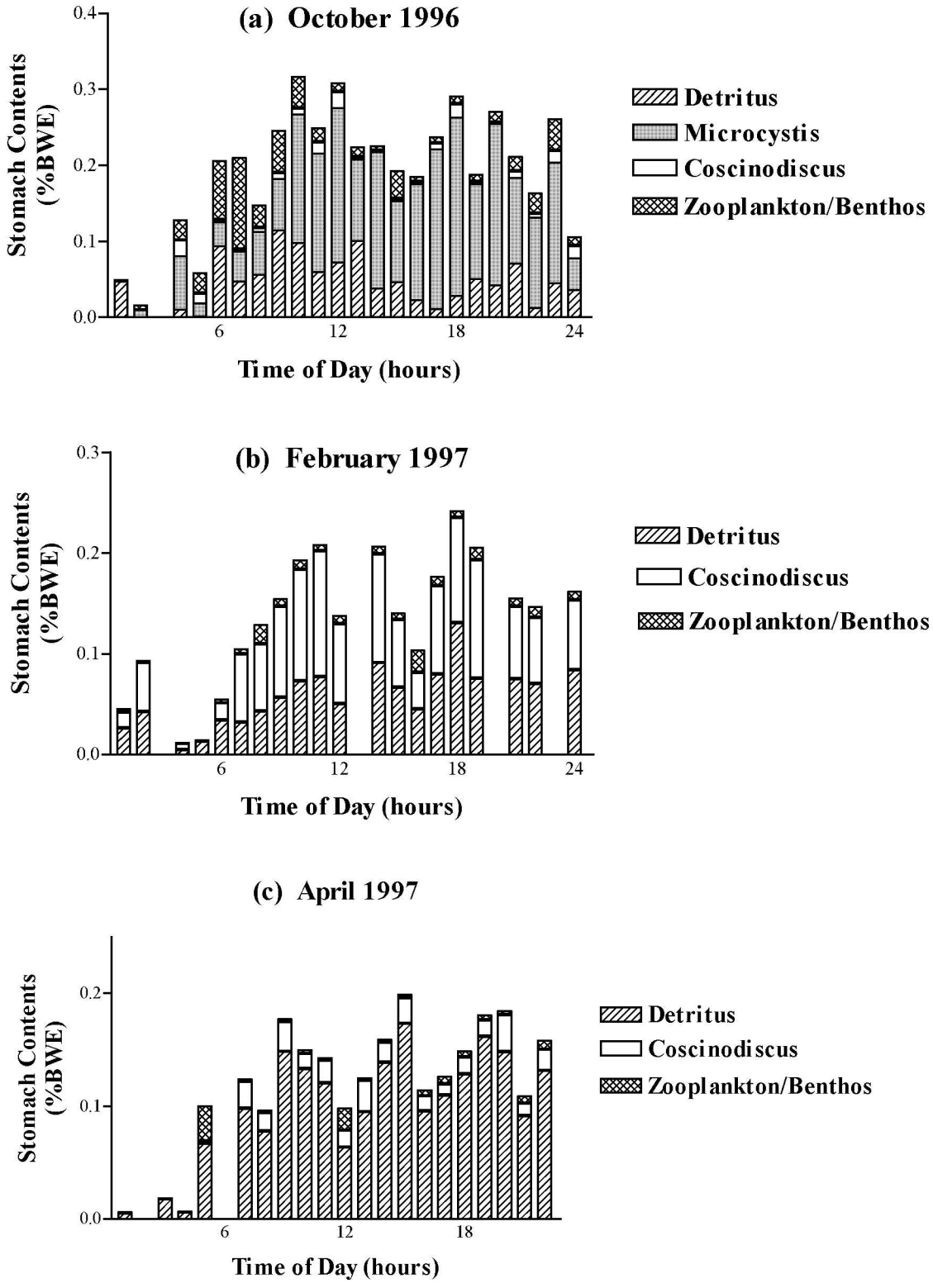


Figure 6. Stomach content composition of milkfish sampled throughout the project. Each bar represents the average of up to five fish. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Note different Y-axis scales. (a)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

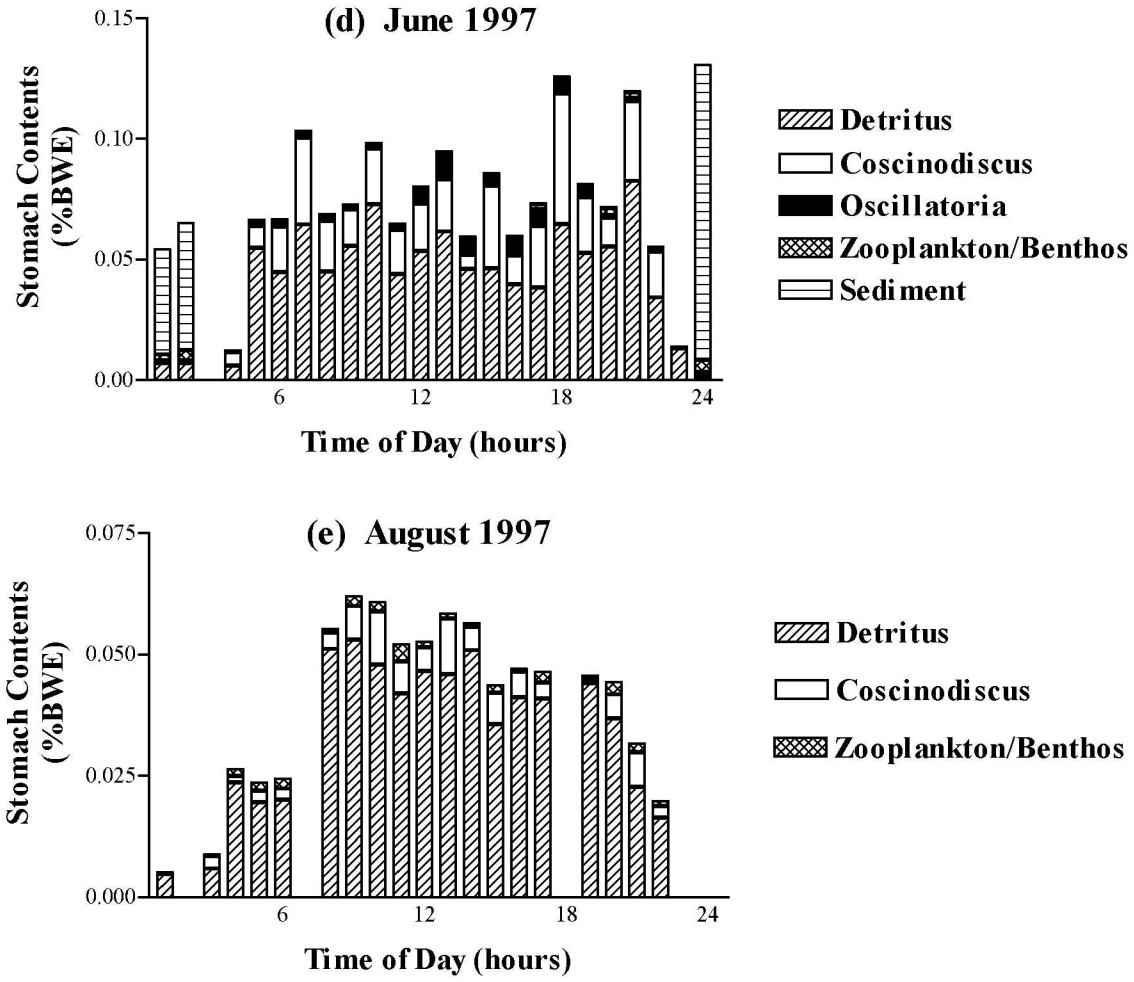


Figure 6 (cont.). Stomach content composition of milkfish sampled throughout the project. Each bar represents the average of up to five fish. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Note different Y-axis scales. (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 g[food] kg[body-mass]$^{-0.8}$ 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 (g $kg^{-0.8}$ 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 (g $kg^{-0.8}$ h^{-1})	0.74	0.64	0.69	0.61	0.23
Daily Ration (g $kg^{-0.8}$ 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.

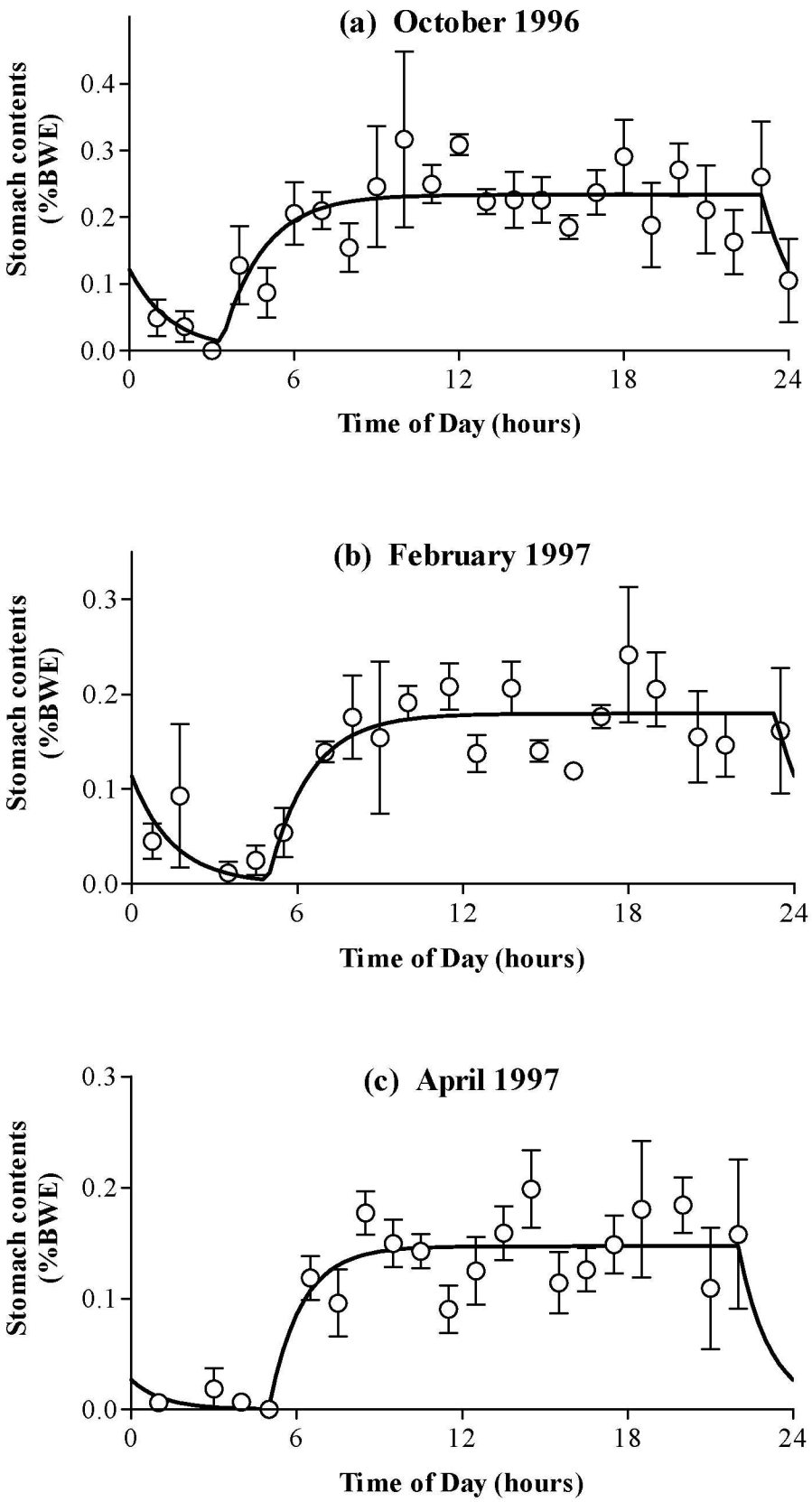
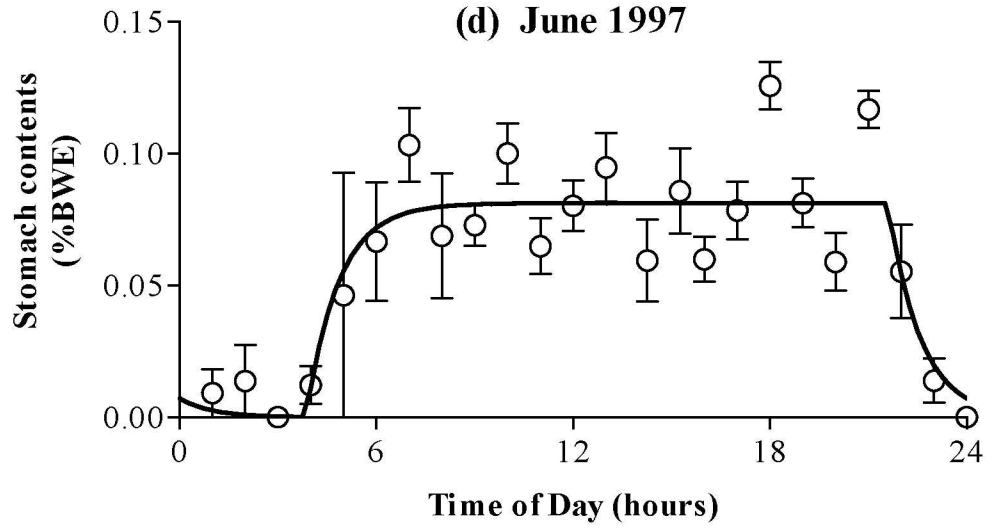


Figure 7. Mean observed stomach contents ± standard deviations (◯) and MAXIMS curves (—) for milkfish sampled throughout the project. Each data point represents the average of up to five fish. Note different Y-axis scales. (a) October 1996 (b) February 1997 (c) April 1997



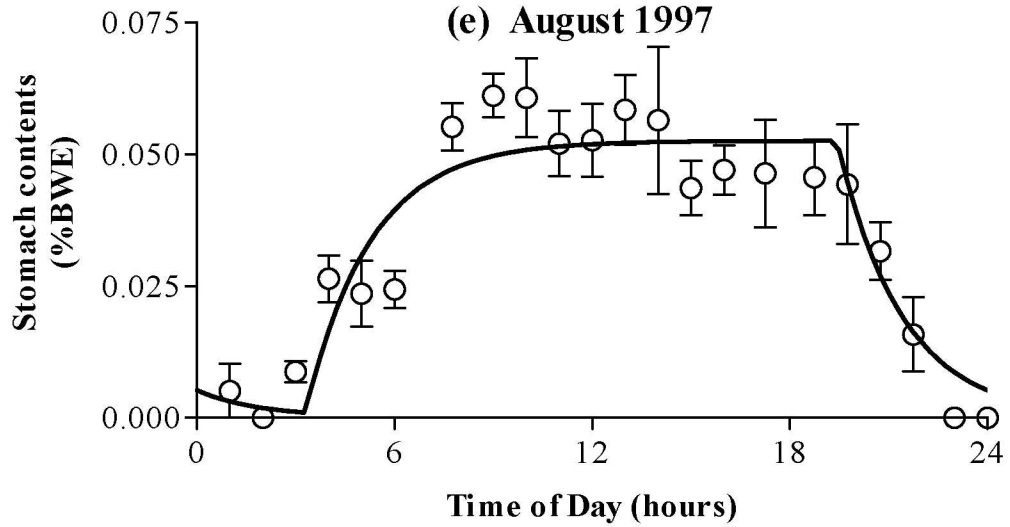


Figure 7 (cont.). Mean observed stomach contents ± standard deviations (◯) and MAXIMS curves (—) for milkfish sampled throughout the project. Each data point represents the average of up to five fish. Note different Y-axis scales. (d) June 1997 (e) August 1997

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 ± 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 ± 0.53	31.5 ± 6.01	27.7 ± 5.37
- Small Fish	40	6.14 ± 0.62	9.8 ± 3.58	8.4 ± 2.89
4-5. August 1995	80	12.21 ± 1.20	81.7 ± 23.83	71.6 ± 21.31
19-20. March 1996	120	10.04 ± 1.28	41.0 ± 11.37	35.3 ± 9.77
16-17. May 1996	120	9.07 ± 1.70	30.5 ± 14.30	26.8 ± 12.67
17-18. July 1996	110	8.97 ± 1.47	32.5 ± 14.99	27.8 ± 12.9
26-27. Sept. 1996				
- Supplemented Fish	120	8.41 ± 1.20	25.1 ± 8.13	21.0 ± 7.00
- Unsupplemented Fish	120	8.59 ± 0.92	25.3 ± 8.27	21.6 ± 7.18
14-15. Jan. 1997				
- Supplemented Fish	120	7.53 ± 0.78	15.4 ± 5.54	13.2 ± 4.84
- Unsupplemented Fish	120	7.52 ± 0.73	14.8 ± 4.95	13.0 ± 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 *K*	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

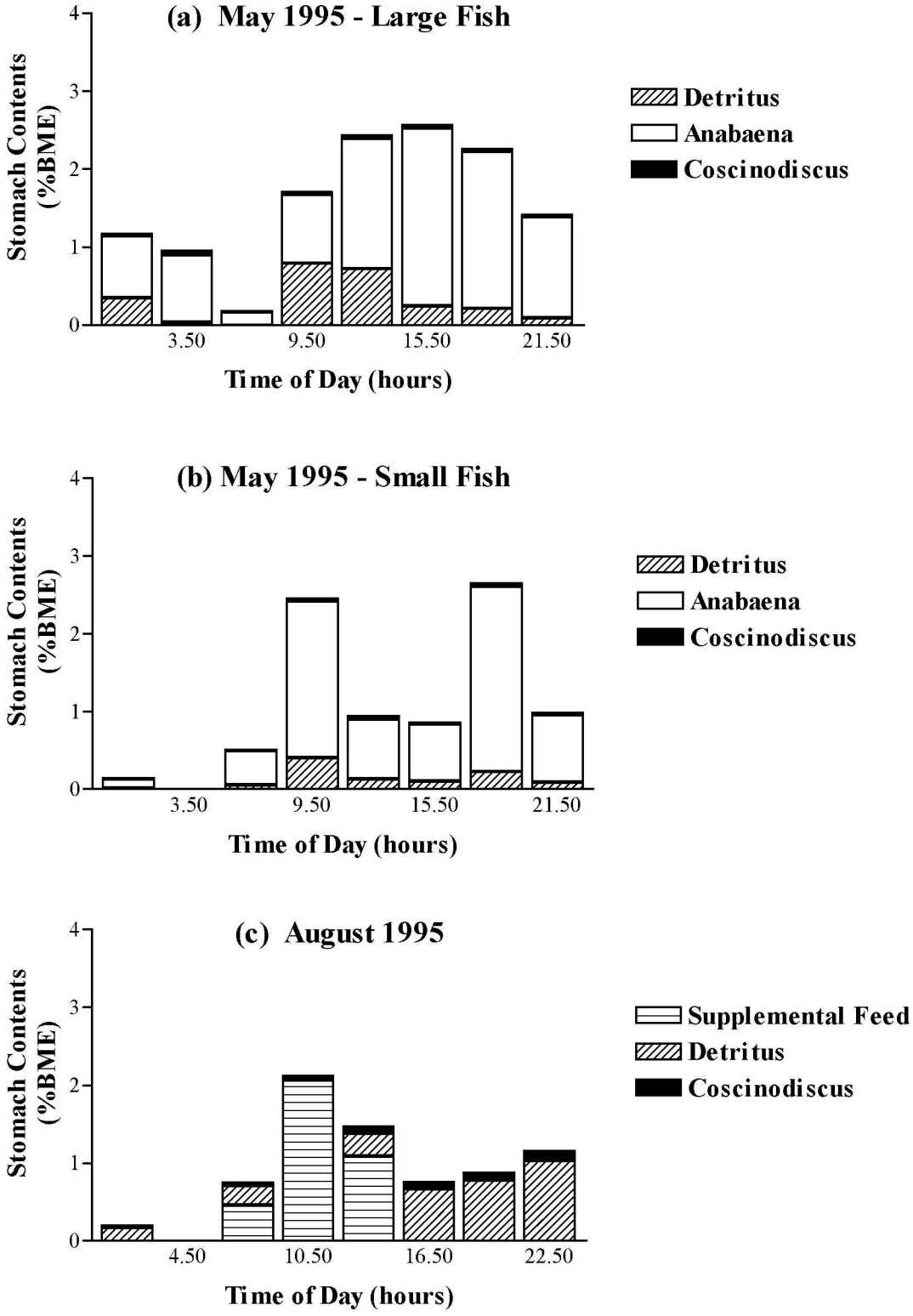


Figure 8. Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish (all other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

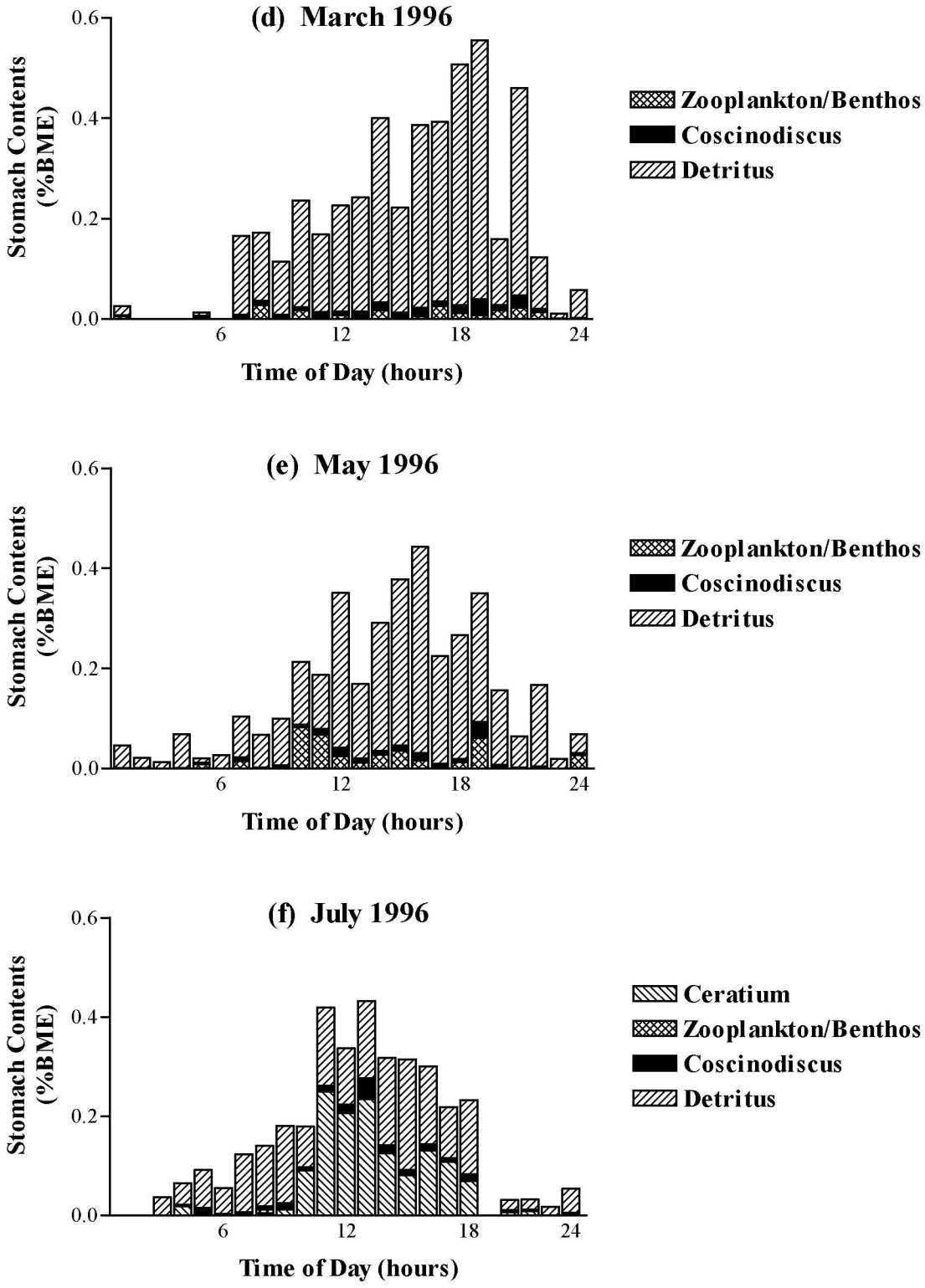


Figure 8 (cont.). Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish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

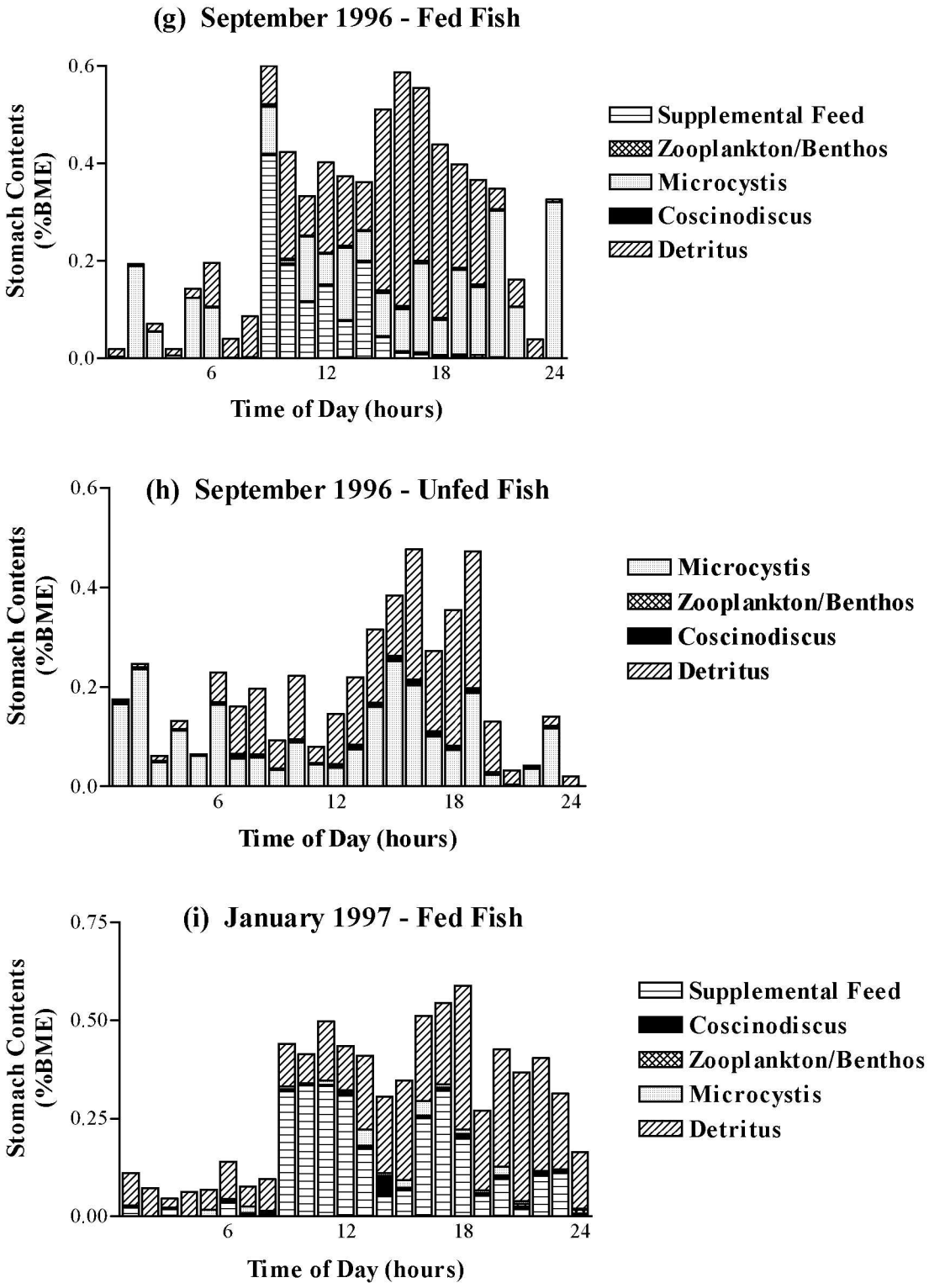


Figure 8 (cont.). Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish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

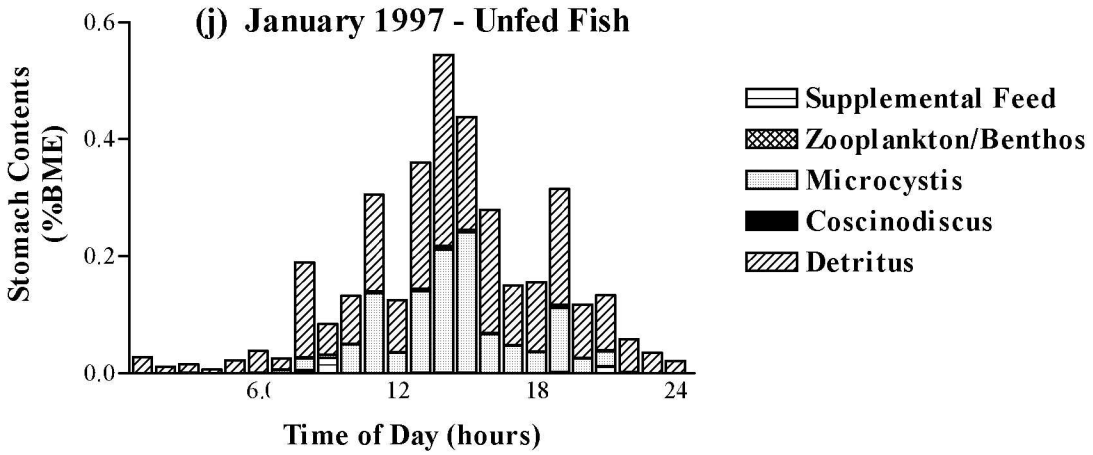


Figure 8 (cont.). Stomach content composition of Nile tilapia sampled throughout the project. Phytoplankton species not specifically listed were present only at trace level and have been grouped into the category *Coscinodiscus*. Each bar represents the average of ten fish (August 1995) or five fish (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

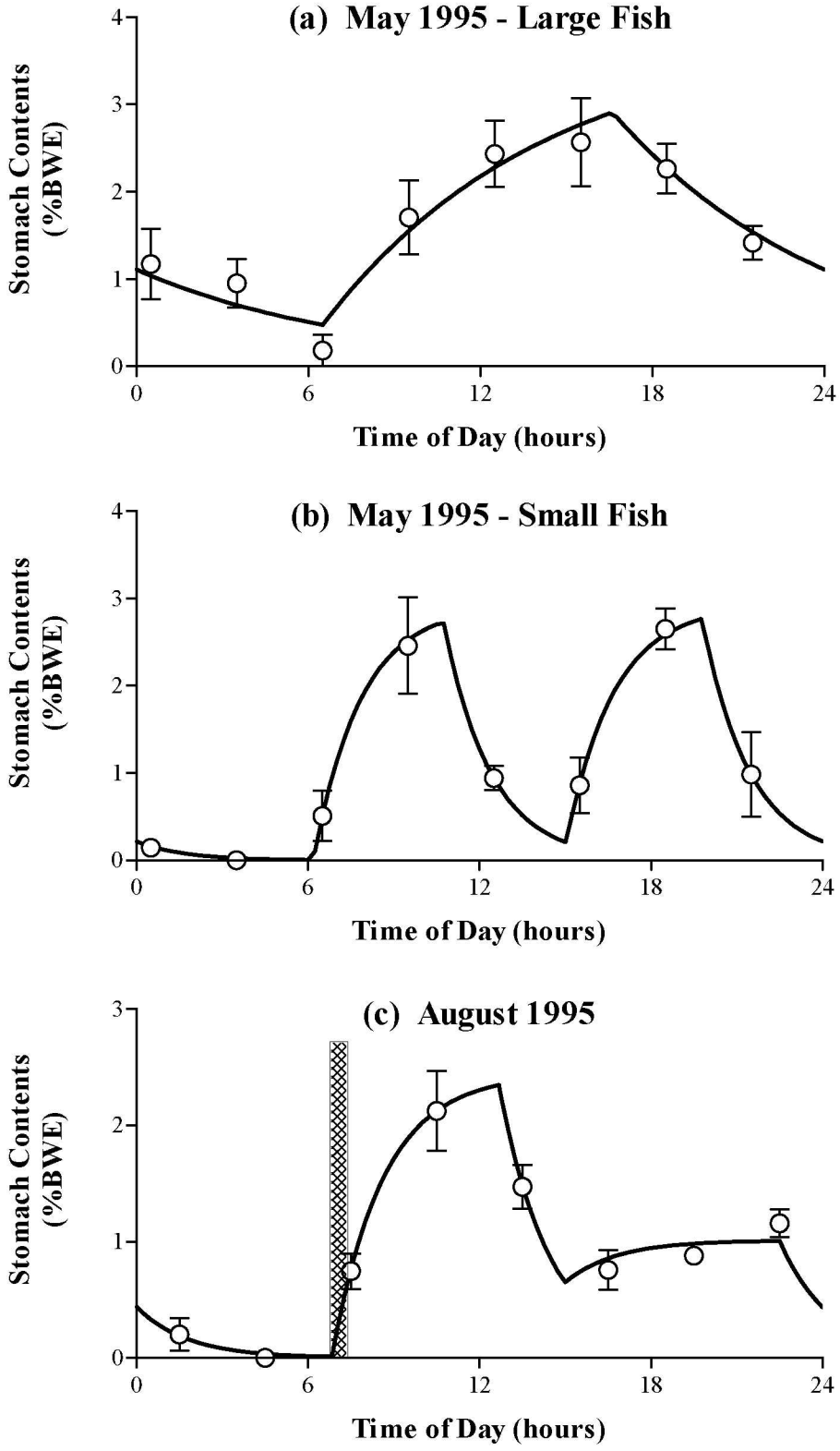


Figure 9. Mean observed stomach contents ± standard deviations (◯) and MAXIMS curves (—) for Nile tilapia sampled throughout the project. Each data point represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (a) May 1995 - large fish b) May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

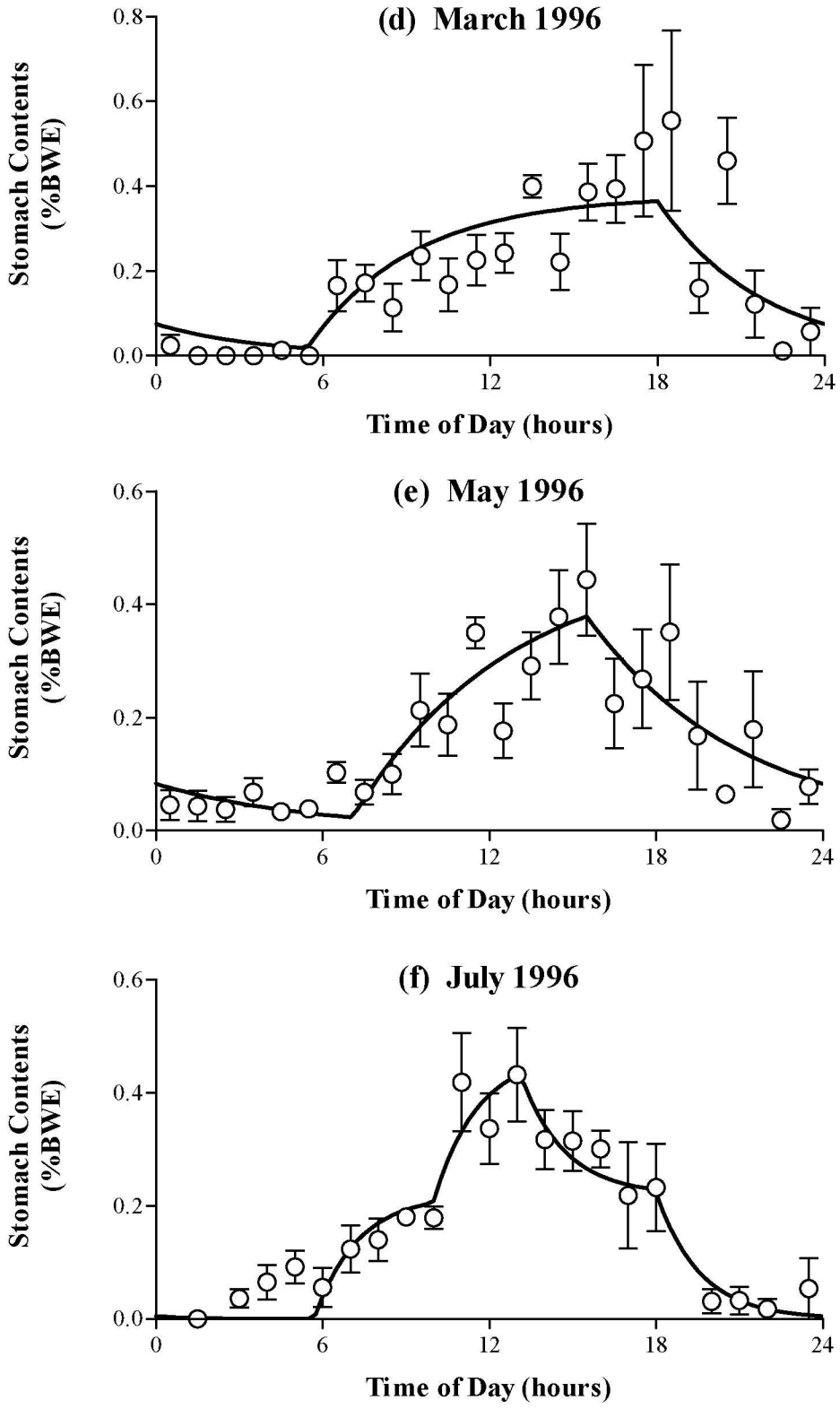


Figure 9 (cont.). Mean observed stomach contents ± standard deviations (◯) and MAXIMS curves (—) for Nile tilapia sampled throughout the project. Each data point represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (d) March 1996 (e) May 1996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

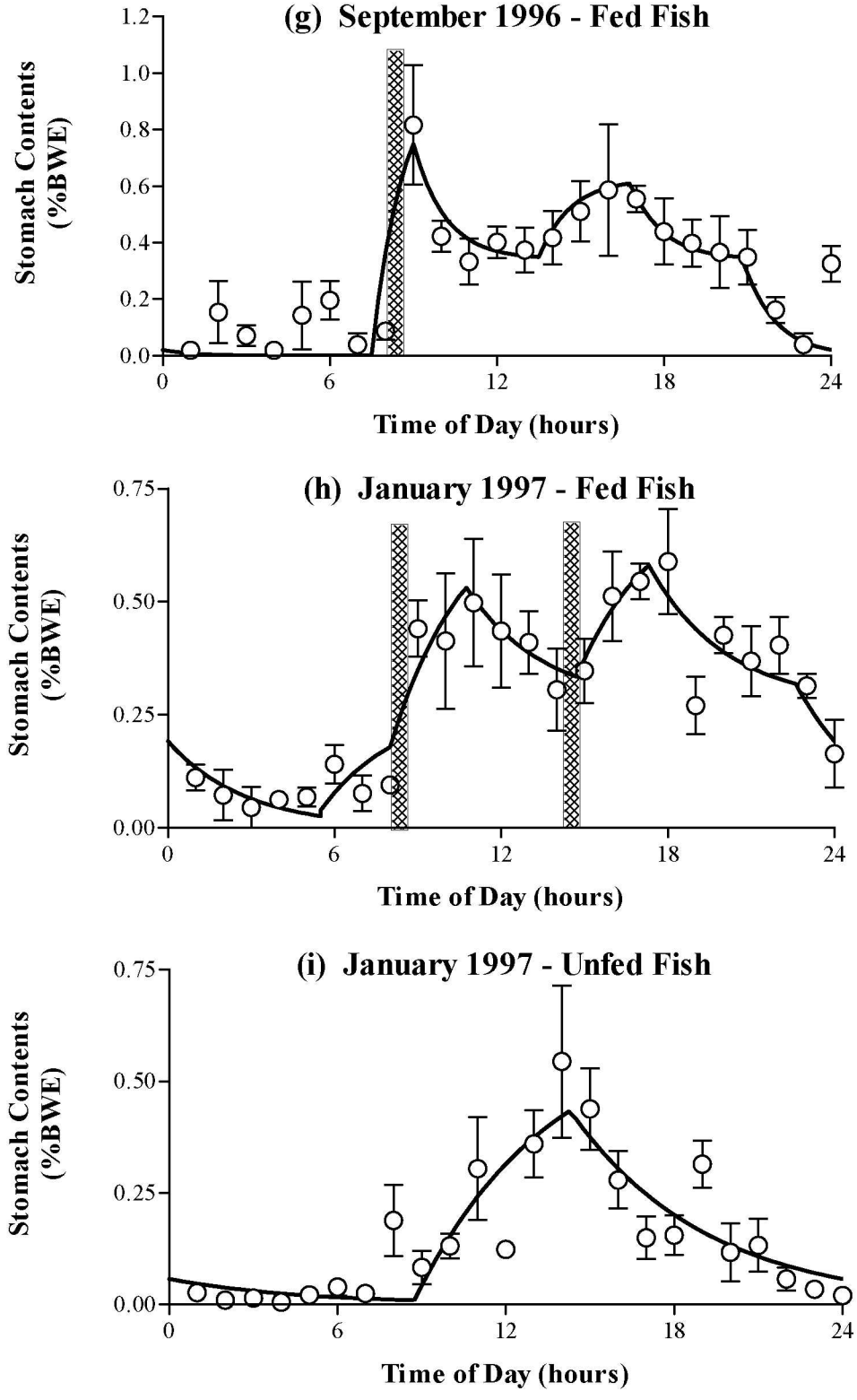


Figure 9 (cont.). Mean observed stomach contents ± standard deviations (◯) and MAXIMS curves (—) for Nile tilapia sampled throughout the project. Each data point represents the average of ten fish (August 1995) or five fish (all other samplings). Note different Y-axis scales. (g) September 1996 - supplemented 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_1, 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	-	-	-	-	-	-
F_b-feed 1	-	-	23mins)	-	-	-	7:55 (7mins)	8:00 (55mins)	-
F_b-feed 2	-	-	6:50 (15mins)	-	-	-	-	14:43 (33mins)	-
F_b-*Ceratium*	-	-	-	-	-	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	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)	20mins) -	-	-	-	-	-
F_s-feed 1	-	-	12:41 (3mins)	-	-	-	8:54 (45mins)	10:44 (33mins)	-
F_s-feed 2	-	-	-	-	-	-	-	17:19 (41mins)	-
F_s-*Ceratium*	-	-	-	-	-	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})									
J_1-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)
J_1-feed	-	-	0.227 (0.058)	-	-	-	1.130 (0.822)	0.268 (0.082)	-
J_1-*Ceratium*	-	-	-	-	-	0.299 (0.077)	-	-	-
J_1-detritus	-	-	-	-	-	-	0.448 (0.263)	-	-
Evacuation Rate (h^{-1})									
E	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})									
R_d - Natural Food	0.836	2.738	0.715	1.255	0.723	2.220	3.359	1.167	0.728
R_d - Supplemental Feed	-	-	1.325	-	-	-	1.101	1.428	-
R_d - 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.

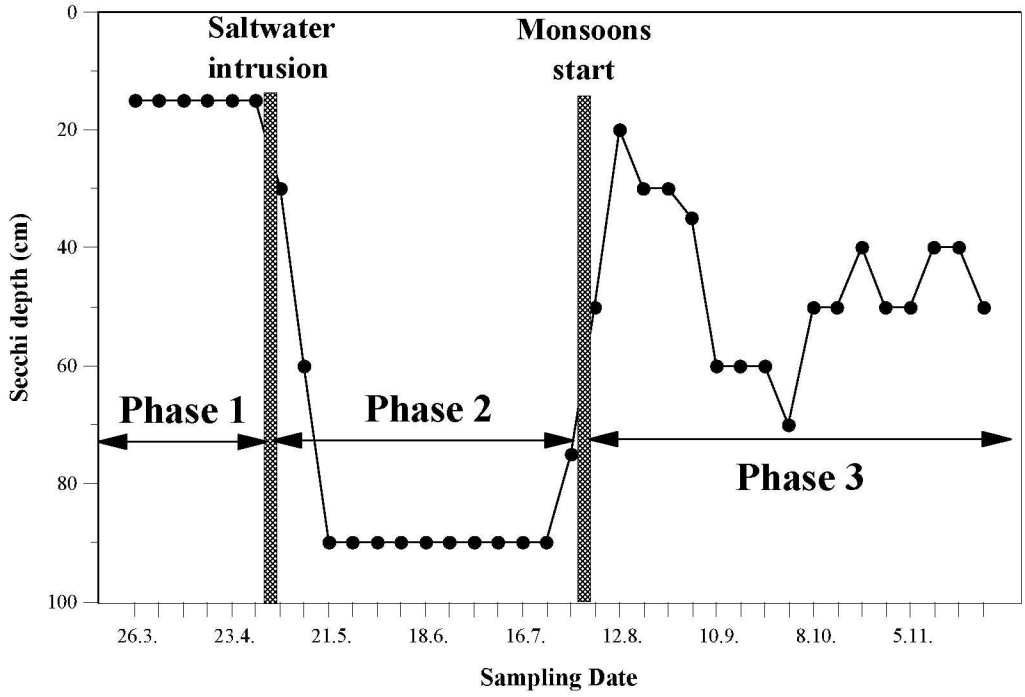


Figure 10. Secchi depth between March and November 1997, showing the three-phase pattern demarcated by the arrival of saltwater intrusion and the start of the monsoon winds

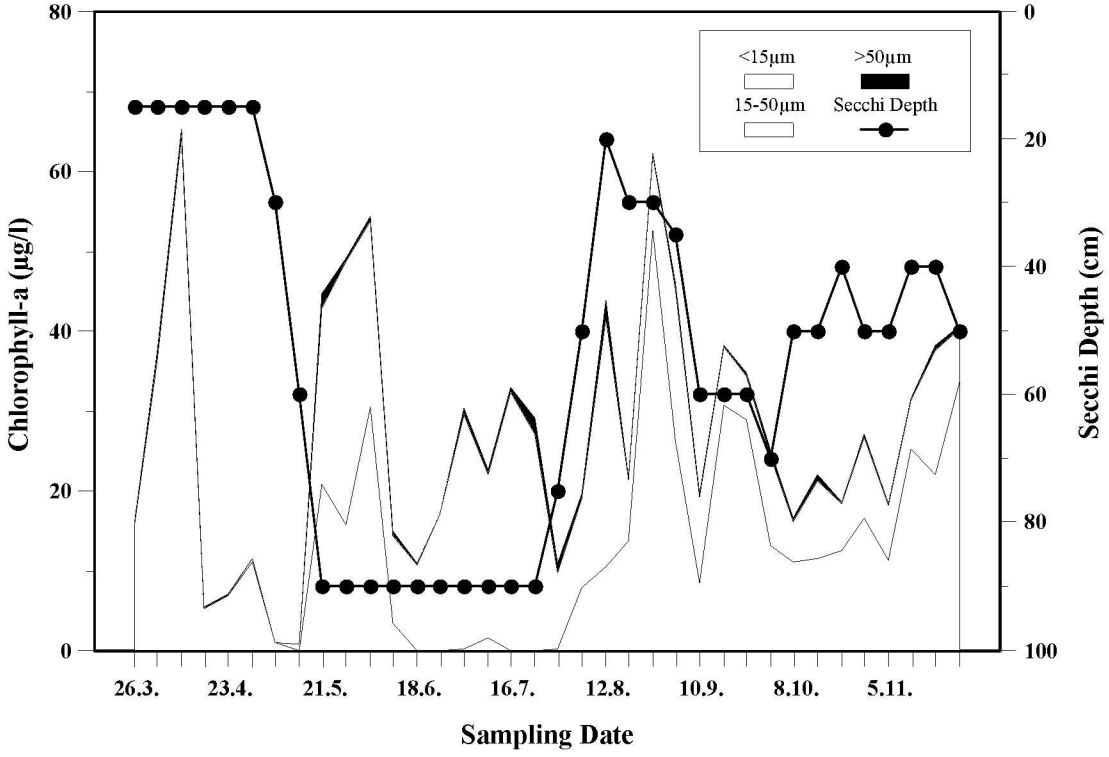


Figure 11. Chlorophyll-a concentrations in three size fractions between March and November 1997. Secchi depth is included to demarcate the three study phases (see text)

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 <15μm 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

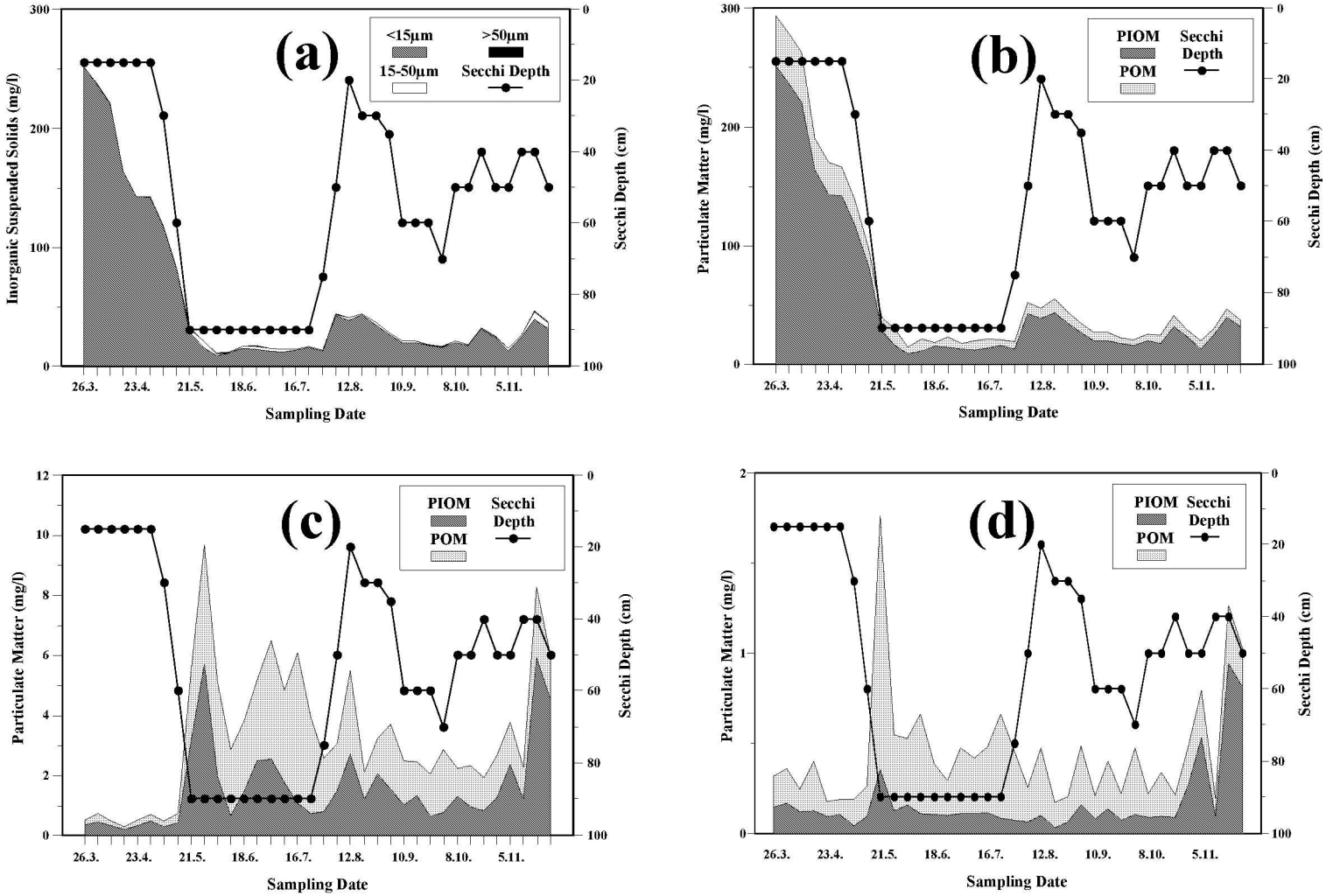


Figure 12. Concentration of total suspended solids in the three size fractions (a) and of particulate organic and inorganic matter in the small (b), middle (c) and large (d) size fractions between March and November 1997. Secchi depth is included in each case to demarcate the three study phases

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

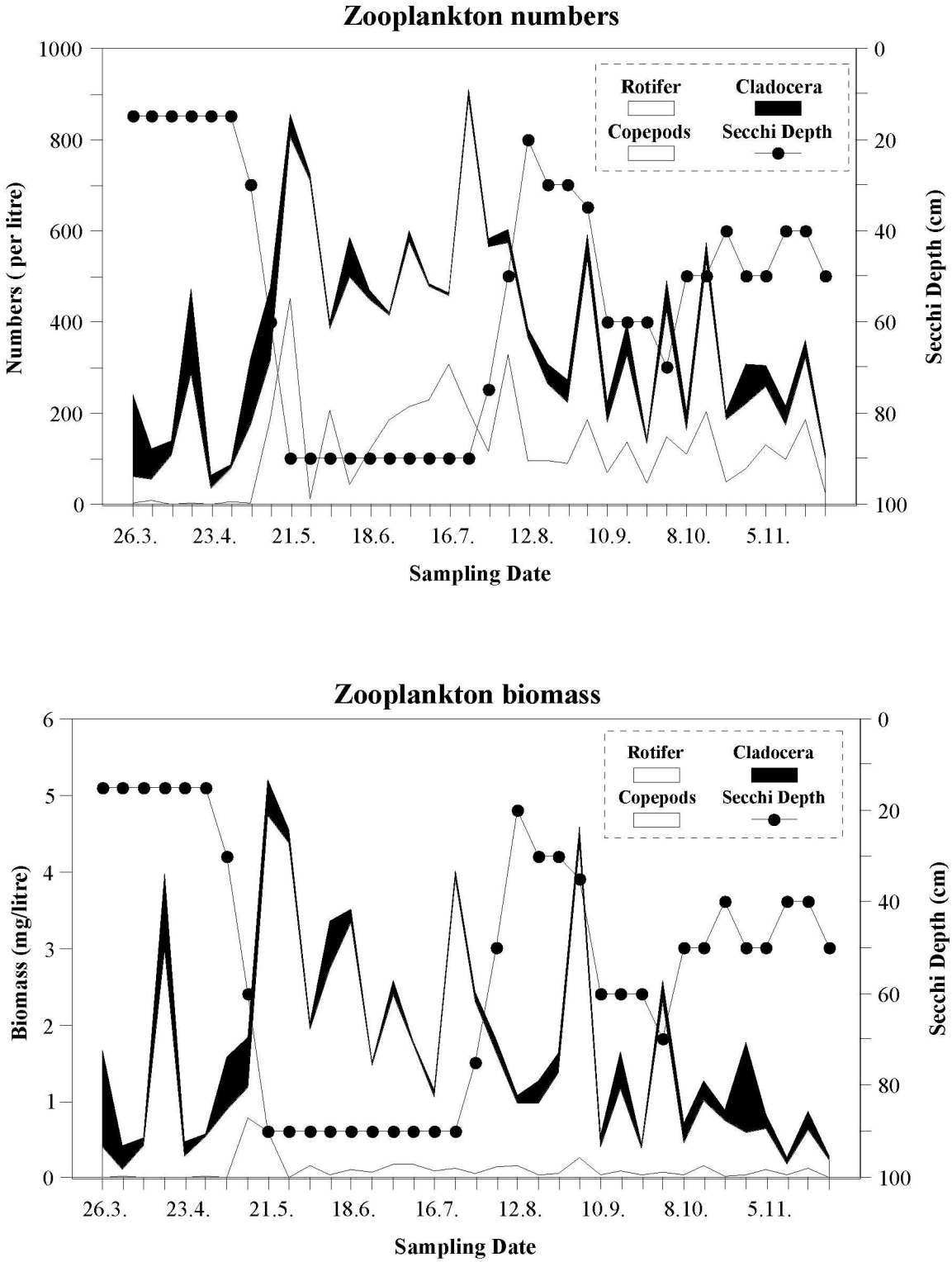


Figure 13. Zooplankton numbers and biomass between March and November 1997. Secchi depth is included for comparison

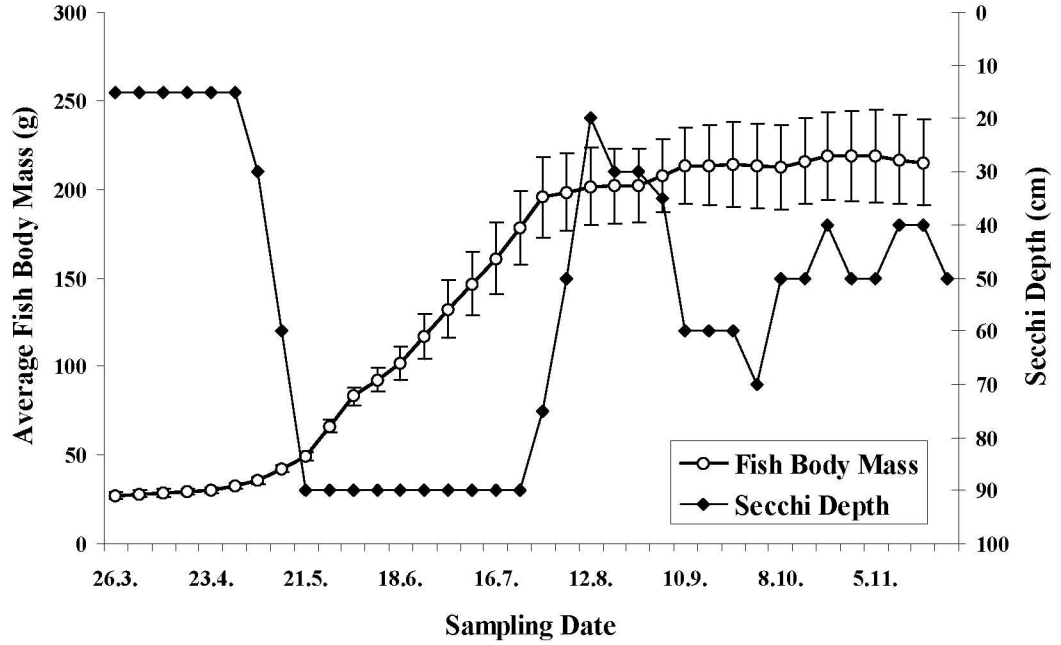


Figure 14. Secchi depth and body mass of Nile tilapia (Mean ± St. Dev. of four cages) between March and November 1997. Secchi Depth is included to demarcate the three study phases (see text)

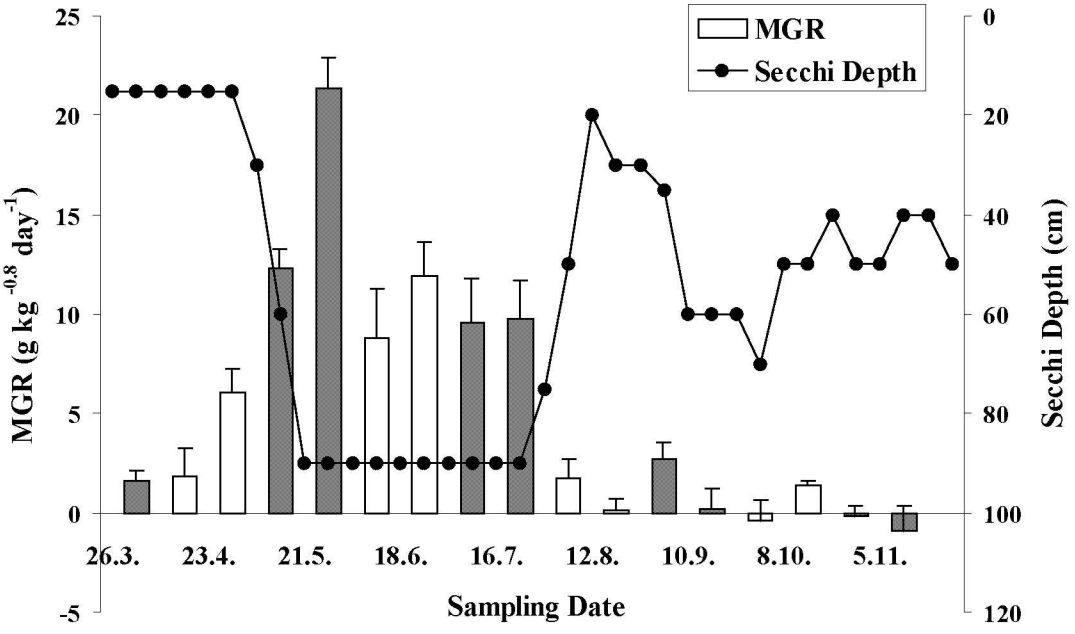


Figure 15. Metabolic Growth Rates (MGR; Mean ± St. Dev. of four cages) of Nile tilapia between March and November 1997. Secchi Depth is included to demarcate the three study phases (see text)

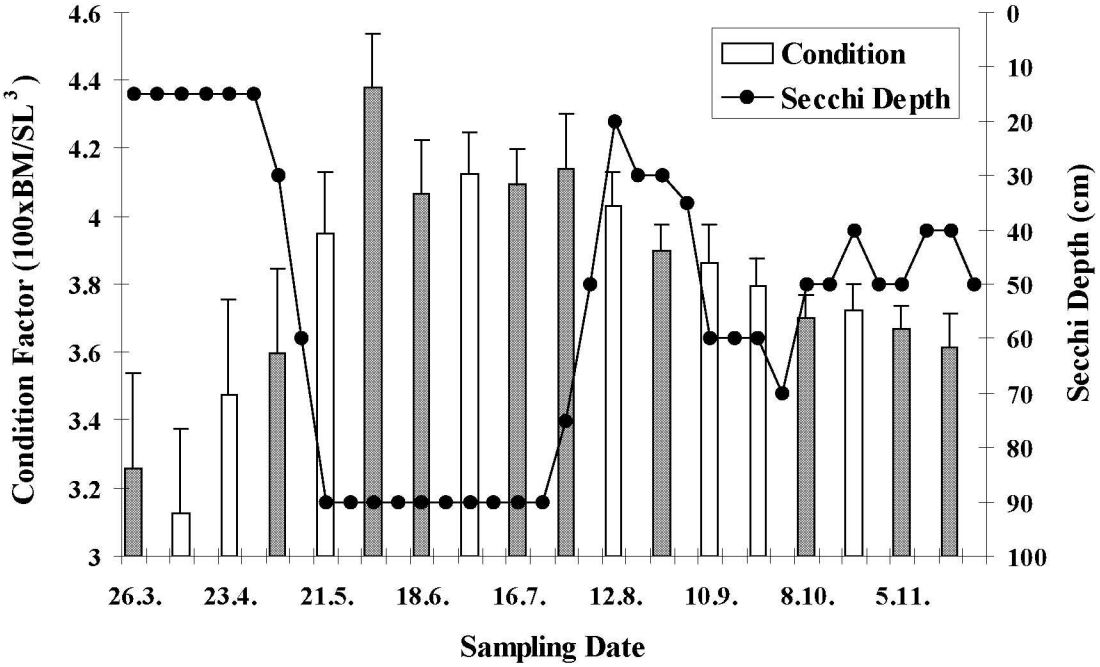


Figure 16. Condition factors *K* of Nile tilapia between March and November 1997. Secchi Depth is included to demarcate the three study phases (see text)

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 m^3 $fish^{-1}$ when the water depth was at a minimum of 1.5m), it is

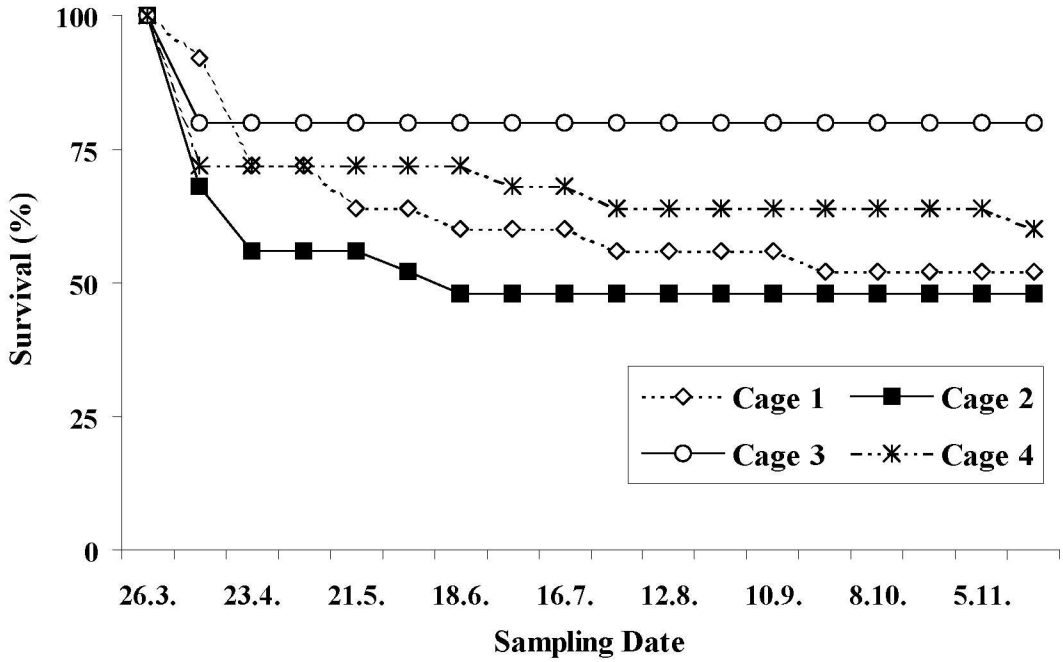


Figure 17. Survival of Nile tilapia in four different experimental cages between March and November 1997

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}:

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

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

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:

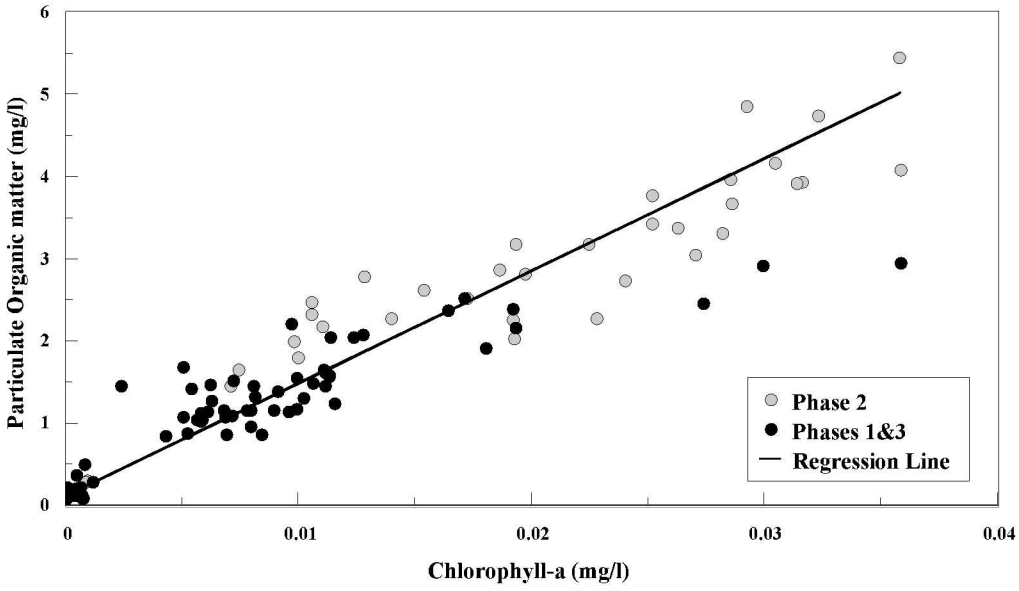


Figure 18. Relationship between Chlorophyll-a and Particulate Organic Matter (POM) in the middle size fraction (15-50µm) in Phase 2 (11.5.-2.8.1997) and Phases 1 (26.3.-10.5.1997) and 3 (3.8.-26.11.1997) of the water quality study period (March-November 1997). Geometric mean regression line is included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

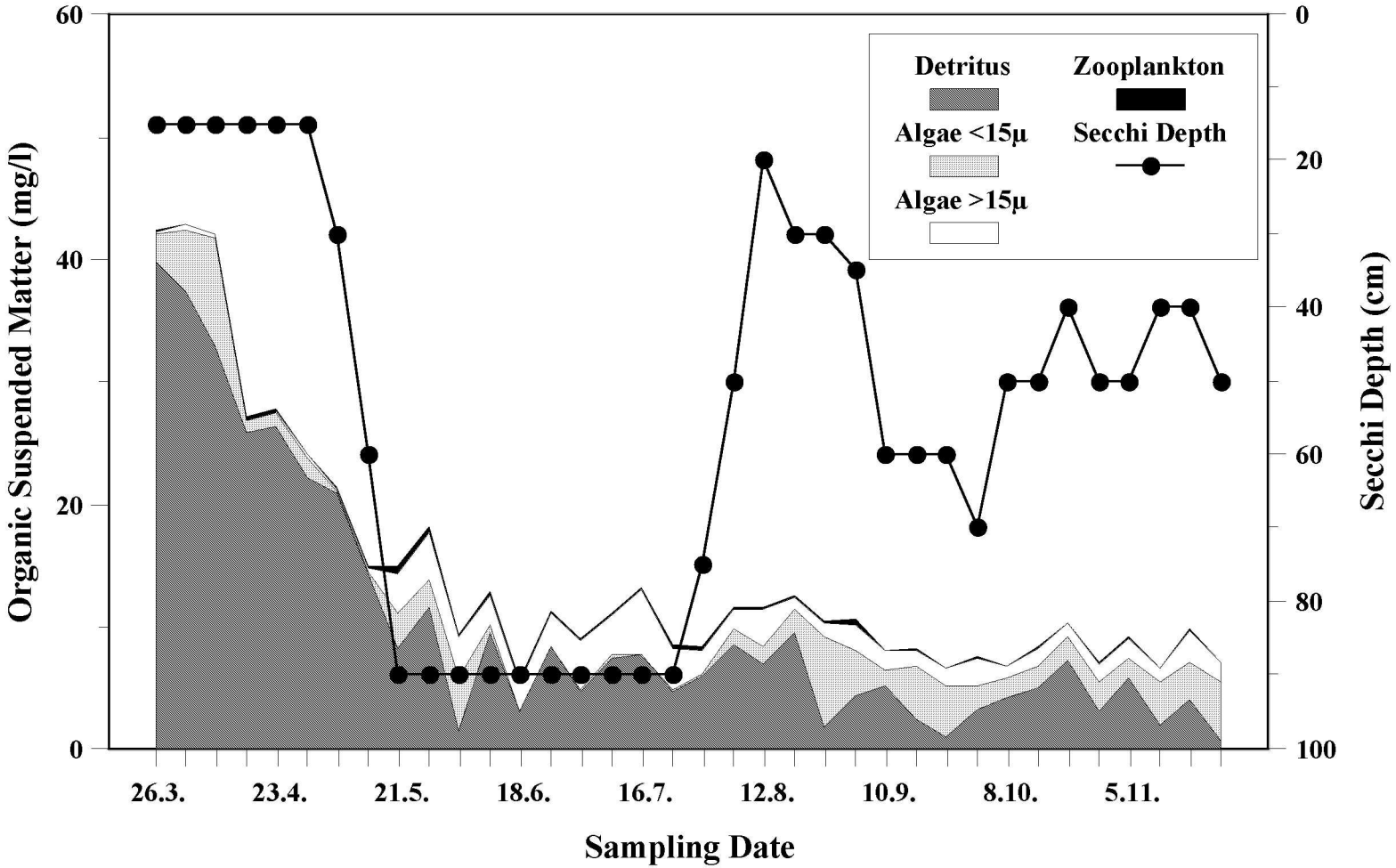


Figure 19. Estimated composition of Particulate Organic Matter (POM) in the three size fractions on the basis of the geometric mean regression between Chlorophyll-a and POM in the middle size fraction over the water quality study period (March-November 1997). Secchi depth is included to demarcate the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

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 JI (%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.

VII Summary

Laguna de Bay, the largest lake in the Philippines and located immediately southeast of the national capital Manila, has been fished extensively for centuries to provide food for the local population. The lake covers 911 square kilometres at an annual mean depth of only 2.8 metres and is mostly freshwater. Due to its close horizontal and vertical proximity to the sea, there is some intrusion of saltwater via the Pasig River, the only link with Manila Bay, when the lake level lowers sufficiently during the dry season (March-June). The water is normally turbid (Secchi depth <30 cm) but the inflowing saline water flocculates and settles the suspended clay particles, clearing the water (Secchi depth >100 cm) and causing blooms of nitrogen-fixing blue-green algae until the return of the rainy season and the monsoon winds around August.

The lake has also been used for aquaculture since the early 1970s when milkfish, *Chanos chanos* (Forsskål), started to be grown in large netpens (max. 2000 ha) and Nile tilapia, *Oreochromis niloticus* (L.) in smaller, closed-bottomed netcages (max. 200 m^2). In the first years of the practice, it was possible to grow fish from fingerling (ca. 10 g) to marketable (ca. 200 g) size in as little as three months when algal blooms prevailed after saltwater intrusion, making two harvests a year without the use of supplemental feed feasible. By the early eighties, this was no longer possible and this was attributed to the excessive expansion of the netpen industry to over a third of the total lake area in 1984, as well as to high stocking rates, both of which were regarded to result in the overexploitation of the primary production of the lake. Tilapia producers circumvented the problem by giving supplemental feed at times of turbid water but due to the immense size of the netpens, leading to significant feed wastage, this option was not available to milkfish growers.

Since the mid-eighties, the total netpen coverage in the lake has fluctuated but has, at times, fallen to the generally recommended value of about 10 % of the lake area. In spite of this, it has not been possible to achieve two harvests a year of milkfish, still the main culture species, as was the case in the early 1970s. This study was therefore carried out to quantify the seasonal growth rates, feed intake and food spectrum of milkfish and tilapia in the lake in order to determine the factors limiting fish growth more precisely.

Between May 1995 and August 1997, milkfish were sampled on seven and tilapia on eight occasions in commercial aquaculture operations in the lake. On each occasions, up to ten fish were collected at 1-3 hour intervals over the daily cycle. The fish were sacrificed,

measured, weighed, gutted and both the fish and the intestinal tracts preserved until further analysis. The fish were freeze-dried, homogenized and investigated for dry matter, crude protein, lipid, and ash content, whereas the stomach contents were flushed into preweighed vials using 70 % ethanol and examined microscopically to determine the main components. Following this, they were dried and the dry weights obtained by difference between the full and empty vial weights. In the case of tilapia, a sample of supplemental feed, when this was given, also underwent proximate analysis with crude fibre also determined.

Since all milkfish in a given pen are stocked on a particular date and no fish are added or selectively removed until harvesting, it was possible to estimate the growth rates of this species at different times of the year from the average sizes of fish in a pen. The lengths and weights were also used to estimate fish condition. The stomach contents were analysed over the daily cycle with the feeding model MAXIMS and daily food consumption determined for the different sampling days. These parameters were also estimated for tilapia except fish growth which, because of the common practice of partial harvesting and adding smaller fish in a cage at intervals, could not be calculated reliably. Since tilapia were supplemented when growth would otherwise be slow, calculated growth rates would, in any case, have been meaningless.

Tilapia growth rates were instead determined by keeping fish in cages without feed from March to November 1997 and measuring and weighing at two-weekly intervals. At the same time, integrated water samples were collected weekly and analysed for particulate organic (POM) and inorganic (PIOM) matter, zooplankton biomass and chlorophyll-a (Chl-a). Before analysis, the samples were split into different size fractions (small: <15 μm; medium: 15-50 μm; large: >50 μm) by filtering through appropriately meshed nets. Secchi depth was also recorded on these occasions.

Milkfish grew faster in June and July when the water was clear (Metabolic Growth Rate, MGR: 10.9-16.5 g $kg^{-0.8}$ day^{-1}) than at other times of the year (MGR: 0.6-1.1 g $kg^{-0.8}$ day^{-1}). Condition and body lipid levels were also highest in August towards the end of the season of clear water than on other sampling occasions. At the same time, the daily rations calculated by the MAXIMS model were no higher in June 1997 when the water was clear (1.46 % Body Mass Equivalent, %BME, [dry mass food]:[wet mass fish] basis) than at other sampling times (0.43-3.02 % BME). The main component found in the stomachs of this species was amorphous organic detritus with the remainder made up of algae, particularly at times of phytoplankton bloom.

Nile tilapia were also in better condition and had higher body lipid levels in August after saltwater intrusion than at other times despite receiving supplemental feed when the water was turbid. This was reflected in the fact that even when feed was given did natural food contribute substantially towards overall food consumption (35-75 %). At the same time, the highest daily rations were generally recorded when the fish were supplemented (1.9-4.5 %BME) and these were matched by unsupplemented fish only at times of algal bloom. As was the case for milkfish, the stomach contents generally contained large proportions of amorphous detritus; algae were found in large numbers only when they were in bloom and supplemental feed featured when this was given.

The water samples collected from March-November 1997 clearly reflected the annual water quality cycle. Secchi depth was low (10 cm) until mid-May, after which it rose to 90cm until August due to saltwater intrusion. The return of the monsoon thereafter lowered Secchi depth to moderate levels (40-60 cm). Throughout the study period, levels of total Chl-a fluctuated without showing a particular pattern but this was present only in the small size fraction in Phase 1, only in the middle size fraction in Phase 2 and in both these in Phase 3, but then mostly in the smaller fraction. After converting Chl-a to algal biomass, it was possible to estimate the suspended detritus mass. This material was found to be present at all times, mostly occurring in the small size fraction. The growth rates of tilapia followed the three-phase pattern closely in the first two phases: practically no growth was observed until mid-May and high growth rates (MGR: 8.8-21.4 g $kg^{-0.8}$ day^{-1}) recorded thereafter until the start of August. In the third phase, however, despite moderate Secchi depths, growth rates declined to levels even lower than those recorded in the first phase and weight loss was even observed between some successive samplings.

The growth rates obtained here for milkfish and tilapia confirm that it is no longer possible achieve two harvests a year without supplementation. On the other hand, the discrepancies in food intake in unsupplemented fish between those times of the year when growth is rapid or slow hardly suffice to explain these differences in growth rate. If the pattern of fish growth cannot be explained by dietary quantity, it must be linked to dietary quality. This is supported by the fact that the stomach contents of milkfish or unsupplemented tilapia when the water is turbid consist mainly of detritus, which has frequently been found to be of poor nutritional quality. Phytoplankton is apparently ingested in significant quantities only at times of an algal bloom which takes place mainly, although not exclusively, after saltwater intrusion.

The water samples collected in 1997 demonstrate, however, that fish growth rates are controlled not only by total phytoplankton biomass but also by the size of the dominant algae. Rapid fish growth is linked to the occurrence of larger algae which dominate after the inflow of saline water. Since filter-feeding fish such as milkfish and tilapia are generally unable to discriminate between potential food items other than on the basis of size, the cultured fish can obviously selectively ingest larger algae when these are in bloom but cannot select smaller algae from the fine algal-detrital mixture of particulate matter when large phytoplankton is absent. The decline in cultured fish production since the mid-1970s is therefore linked at least partly to a shift in the relative proportions of small phytoplankton and detritus in favour of the latter. This helps to explain why it has not been possible to restore fish production rates by lowering stocking and netpen expansion rates, so far the main factors attributed with causing the slump in the aquaculture industry. An improvement in fish production can only be achieved through either raising the levels of blue-green algae by clearing the water, or by lowering the input of detrital material into the lake.

VIII Zusammenfassung

Laguna de Bay, der größte philippinische See, der südwestlich an die Hauptstadt Manila angrenzt, wurde schon seit Jahrhunderten extensiv befischt, um den Nahrungsbedarf der lokalen Bevölkerung zu decken. Der See breitet sich über 911 km^2 bei einer mittleren Tiefe von nur 2,8m aus und ist hauptsächlich ein Süßwassersee. Aufgrund seiner Nähe zum Meer kommt es in der Trockenzeit (März-Juni) zum Eindringen salzhaltigen Wassers durch den Pasig River, normalerweise der einzige Abfluß, wenn der Wasserspiegel unter den des Meeres fällt. Das Wasser ist normalerweise sehr trüb (Secchitiefe <30 cm), aber durch das einfließende Salzwasser werden die suspendierten anorganischen Partikel flokkuliert, sodaß sie ausfallen und sich das Wasser klärt (Secchitiefe >100 cm), was bis zum Ende der Trockenzeit zur Bildung von Blüten stickstoffixierender Blaualgen führt.

Der See ist seit Anfang der Siebziger Jahre des letzten Jahrhunderts für die Kultur von Milchfischen, *Chanos chanos* (Forsskål) in großen Umzäunungen (max. 2000 ha) und Niltilapien, *Oreochromis niloticus* (L.) in kleineren Netzkäfigen (max. 200 m^2) benutzt worden. In den frühen Jahren der Aquakultur war es nach dem Salzwassereindringen möglich, Fische ohne Zugabe von Supplementfutter in drei Monaten von der Besatzgröße (ca. 10 g) zur Marktreife (ca. 200 g) zu züchten, was zwei Ernten im Jahr möglich machte. Anfang der Achtziger war dies nicht mehr der Fall, was auf die übermäßige Ausbreitung der Aquakultur auf mehr als ein Drittel der Seefläche anno 1984, sowie den hohen Besatzdichten zurückgeführt wurde. Die Tilapienzüchter lösten das Problem durch den Einsatz von Supplementfutter bei trübem Wasser, aber dies war bei Milchfischen nicht praktikabel, da es aufgrund der immensen Größe der Umzäunungen zu erheblichen Futterverlusten geführt hätte.

Seit Mitte der Achtziger Jahre schwankte die Flächendeckung der Aquakultur und fiel zuweilen auf 10 % der Gesamtfläche des Sees, was allgemein als eine nachhaltige Ausdehnung akzeptiert wird. Dennoch war es seitdem nicht mehr möglich, wie in den frühen Jahren der Aquakultur zwei Ernten im Jahr zu erreichen. Diese Studie wurde daher ausgeführt, um das Wachstum, die Futteraufnahme und die Futterzusammensetzung der Milchfische und Tilapien in den unterschiedlichen Jahreszeiten, und daraus die Faktoren, die das Fischwachstum begrenzen, zu ermitteln.

Von Mai 1995 bis August 1997 wurden in kommerziellen Aquakulturunternehmen im See siebenmal Milchfischproben und achtmal Tilapienproben gezogen. Dabei wurden bis zu

zehn Fische in Abständen von 1-3 Stunden über einen 24-Stundenzyklus gefangen, geschlachtet, gemessen, gewogen, die Eingeweide entnommen und Fisch und Eingeweide separat konserviert. Die Fische wurden homogenisiert, gefriergetrocknet und auf ihren Gehalt an Trockensubstanz, Rohprotein, Rohfett, Asche analysiert. Die Mageninhalte wurden mit 70 % Alkohol in vortarierte Behälter gespült und die wesentlichen Bestandteile mikroskopisch bestimmt. Danach wurden sie getrocknet und ihr Gewicht als Unterschied des vollen und leeren Behältergewichtes ermittelt. Falls Tilapien Supplementfutter bekamen, so wurde davon eine Probe ebenfalls einer Schlachtkörperanalyse unterzogen, wobei hier auch die Rohfaser bestimmt wurde.

Da alle Milchfische einer Umzäunung am gleichen Tag eingesetzt werden und bis zur Ernte keine weiteren Fische hinzukommen oder Fische selektiv entfernt werden, war es möglich für diese Art aus den mittleren Fischgewichten die Wachstumsraten in einer Umzäunung zu unterschiedlichen Jahreszeiten zu bestimmen. Die Fischkondition wurde ebenfalls aus den Fischlängen und -gewichten geschätzt. Die Mageninhalte wurden über den Tagesverlauf mit dem Freßmodell MAXIMS analysiert und die Tagesration für die verschiedenen Probennahmen ermittelt. Außer der Wachstumsrate wurden diese Parameter auch für Tilapien bestimmt, da diese durch die geläufige Praxis der selektiven Ernte von größeren und Besatz von kleineren Fische in Netzkäfigen nicht zuverlässig bestimmt werden konnte. Da die Tilapien Supplementfutter bekamen, wenn andernfalls geringe Wachstumsraten zu erwarten waren, wäre eine solche Schätzung ohnehin bedeutungslos.

Das Wachstum der Tilapien wurde statt dessen anhand eigens gehaltenen Fischen ermittelt, die von März bis November 1997 ohne Supplementierung in Käfigen gezogen und in Abständen von zwei Wochen gemessen und gewogen wurden. Gleichzeitig wurden wöchentlich integrierte Wasserproben gezogen und auf suspendierte organische (POM) und anorganische (PIOM) Partikel, Zooplanktonbiomasse und Chlorophyll-a (Chl-a) Gehalt untersucht. Vor der Analyse wurden die Proben mit Hilfe entsprechender Planktonnetze in drei Größenfraktionen (klein: <15 µm; mittel: 15-50 µm; groß: >50 µm) geteilt. Die Secchitiefe wurde während dieser Probennahmen ebenfalls gemessen.

Milchfische wuchsen im Juni und Juli zur Zeit des klaren Wassers schneller (Metabolische Wachstumsrate, MGR: 10,9-16,5 g $kg^{-0.8}$ d^{-1}) als zu anderen Jahreszeiten (MGR: 0,6-1,1 g $kg^{-0.8}$ d^{-1}). Kondition und Körperfettgehalt waren ebenfalls im August gegen Ende der Trockenzeit am höchsten. Andererseits waren die Tagesrationen, die mit dem MAXIMS-Modell für Juni, die Zeit klaren Wassers, errechnet wurden, nicht höher (1,46 %

Körpermassenäquivalent, % BME, Futtertrockenmasse:Fischfeuchtmasse) als die für andere Jahreszeiten (0,43-3,02 %BME). Die Nahrung dieser Tiere bestand hauptsächlich aus amorphen, organischen Detritus, der Rest setzte sich, besonders zu Zeiten einer Phytoplanktonblüte, aus Algen zusammen.

Niltilapien waren ebenfalls im August nach einem Salzwassereinfluß in besserer Kondition und hatten einen höheren Körperfettgehalt, obwohl sie zu Zeiten trüben Wassers Supplementfutter bekamen. Dies spiegelte sich darin wieder, daß die Nahrung selbst bei Zugabe von Supplementfutter zu 35-75% aus Naturnahrung bestand. Dennoch wurden die höchsten Tagesrationen an gefütterten Fischen gemessen (1,9-4,5 %BME), was von ungefütterten Fischen nur zu Zeiten von Algenblüten erreicht wurden. Wie bei Milchfischen bestanden die Mageninhalte hauptsächlich aus Detritus; größere Mengen von Algen wurden nur bei Phytoplanktonblüten, sowie Supplementfutter bei der Zufütterung gefunden.

Die von März bis November 1997 gezogenen Wasserproben reflektierten den jährlichen Wasserqualitätszyklus. Bis Mitte Mai war die Secchitiefe gering (ca. 10 cm), stieg aber danach bis August aufgrund einfließendem Salzwasser auf 90 cm an. Die darauffolgenden Monsunwinde trübten das Wasser bis zu moderaten Secchitiefen (40-60 cm). Der Gesamtgehalt an Chl-a im Wasser schwankte während der Studie ohne ein erkennbares Muster aufzuweisen, aber bis Mitte Mai (Phase 1) wurde alles Chl-a in der kleinen, Mitte Mai bis Anfang August (Phase 2) in der mittleren und ab August (Phase 3) in der kleinen und mittleren, aber dann hauptsächlich der kleinen Größenfraktion, gefunden. Nachdem die Chl-a-konzentration in Algenbiomasse umgewandelt worden war, war es möglich die Detrituskonzentration im Wasser zu schätzen. Dieses Material war in allen drei Phasen vorhanden und wurde hauptsächlich in der kleinen Fraktion gefunden. Das Wachstum der Tilapien reflektierte dieses Schema nur in den ersten zwei Phasen: bis Mitte Mai war fast kein Wachstum zu verzeichnen während danach bis Anfang August die Wachstumsraten auf bis zu 21,4g $kg^{-0,8}$ Tag^{-1} (metabolische Basis) anstiegen. In der dritten Phase gingen die Wachstums- raten trotz der mittelmäßigen Secchitiefe auf ein Niveau unter dem der ersten Phase zurück und zeitweilig wurden sogar Gewichtsverluste beobachtet.

Die hier an Milchfischen und Niltilapien gemessenen Wachstumsraten bezeugen, daß es nicht mehr möglich ist, ohne Supplementfutterzugabe zwei Fischernten im Jahr zu erreichen. Andererseits reichen die Unterschiede in der Futtermenge von unsupplementierten Fischen zu Zeiten schnellen und langsamen Wachstums nicht aus, um diese Unterschiede in der Wachstumsrate zu erklären. Dies deutet darauf hin, daß das Fischwachstum eher durch

die Futterqualität limitiert wird, was auch dadurch unterstützt wird, daß der Mageninhalt dieser Fische bei trübem Wasser hauptsächlich aus Detritus, einer nachweislich minderwertigen Futterkomponente, besteht. Größere Mengen Phytoplankton werden nur zu Zeiten von Algenblüten, die hauptsächlich aber nicht ausschließlich nach dem Eindringen salzhaltigen Wassers auftreten, gefressen.

Die 1997 gezogenen Wasserproben zeigten jedoch, daß das Fischwachstum nicht nur von der Gesamtbiomasse der Algen abhängig ist, sondern auch vom Größenspektrum der dominierenden Algenarten. Ein schnelles Wachstum hängt mit dem Auftreten größerer Blaualgen zusammen, die nach dem Einfluß salzigem Wassers dominieren. Da Fische, die ihre Nahrung aus dem Wasser filtrieren, ihr Futter nur auf der Basis seiner Größe selektieren können, ist es den hier gezüchteten Fischen nur möglich, größere Algen aber nicht die kleineren Algenarten aus dem Gemisch von Phytoplankton und feinkörnigen Detritus herauszuselektieren. Der Rückgang im Fischwachstum seit den siebziger Jahren des vorigen Jahrhunderts hängt daher zumindestens teilweise mit einer Verschiebung der relativen Proportionen der kleinen Algen und des Detritus zugunsten des letzteren zusammen. Dies erklärt auch, warum es bisher nicht möglich war, die Fishproduktion wieder durch eine Verringerung von Besatzdichte sowie Ausdehnung der Aquakultur zu steigern, obwohl die Steigerung dieser beiden Faktoren bisher als die Hauptgründe für den Rückgang der Industrie angesehen wurden. Eine Steigerung der Produktion würde voraussetzen, daß das Wachstum der größeren Blaualgenarten durch verminderte Wassertrübung gefördert oder die Zugabe von Detritus verringert wird.

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Appendix 1

SAS® Routines to determine

MAXIMS curves for milkfish

October 1996

```
data a ;
   input X Y ;
   cards ;
6.00    0.685958  6.00    1.355671  6.00    1.545187  6.00    0.448360
6.00    0.723689  7.00    0.790480  7.00    0.817858  7.00    0.853679
7.00    1.520441  7.00    0.941053  8.00    0.664794  8.00    1.048153
8.00    0.318375  8.00    0.962518  8.00    0.677836  9.00    1.411580
9.00    0.413058  9.00    0.000000  9.00    1.497342  9.00    1.914338
10.00   0.000000  10.00   2.914340  10.00   2.934162  10.00   0.633297
10.00   0.899247  11.00   0.823592  11.00   0.981562  11.00   1.091192
11.00   1.451481  11.00   1.441534  12.00   1.736222  12.00   1.525285
12.00   1.492565  12.00   1.569260  12.00   1.166655  13.00   0.893953
13.00   1.013550  13.00   1.268239  13.00   0.994737  13.00   1.302000
14.00   0.967995  14.00   0.997912  14.00   0.918285  14.00   1.793440
14.00   0.714691  15.00   0.329568  15.00   1.023475  15.00   0.921878
15.00   1.412936  15.00   1.369661  16.00   1.108429  16.00   1.138862
16.00   0.631014  16.00   1.013094  16.00   0.645469  17.00   0.750655
17.00   1.193676  17.00   1.099498  17.00   1.600568  17.00   0.858612
18.00   1.406837  18.00   1.025892  18.00   2.133550  18.00   1.308159
18.00   0.653525  19.00   0.245606  19.00   2.157529  19.00   0.918344
19.00   0.736479  19.00   0.528271  20.00   1.827478  20.00   1.483064
20.00   0.753057  20.00   1.095328  20.00   1.046202  21.00   1.949515
21.00   0.812212  21.00   0.000000  21.00   1.254972  21.00   0.921993
22.00   0.000000  22.00   0.879599  22.00   1.406837  22.00   0.853679
22.00   0.659699  23.00   1.631399  23.00   0.000000  23.00   0.812212
23.00   1.456078  23.00   2.286525  24.00   0.769544  24.00   0.315984
24.00   1.640008  24.00   0.000000  24.00   0.000000  1.00    0.000000
1.00    0.680519  1.00    0.193755  1.00    0.249872  1.00    0.000000
2.00    0.000000  2.00    0.543877  2.00    0.000000  2.00    0.000000
2.00    0.322734  3.00    0.000000  3.00    0.000000  3.00    0.000000
3.00    0.000000  3.00    0.000000  4.00    0.586997  4.00    0.000000
4.00    0.000000  4.00    1.059331  4.00    1.409633  5.00    0.000000
5.00    0.486735  5.00    0.883574  5.00    0.672540  5.00    0.000000
;
proc nlin method=dud ;
   parms  J=0.705  E=0.645  T1=3.33  T2=23 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

February 1997

```
data a ;
   input X Y ;
   cards ;
7.00    0.775288  7.00    0.625545  7.00    0.000000  7.00    0.672540
8.00    1.299466  8.00    0.600292  8.00    0.849281  8.00    1.416489
8.00    0.623301  9.00    1.301542  9.00    0.000000  9.00    0.886358
10.00   0.938094  10.00   1.226351  10.00   0.903781  10.00   0.685101
10.00   0.978446  11.50   1.203738  11.50   1.002761  11.50   1.227465
11.50   0.664619  11.50   1.263958  12.50   0.980566  12.50   0.942752
12.50   0.454012  12.50   0.635843  12.50   0.682155  13.75   1.564232
13.75   1.413077  13.75   0.884892  13.75   0.789263  13.75   0.889179
14.75   0.577391  14.75   0.691425  14.75   0.776455  14.75   0.865035
14.75   0.793125  16.00   0.843188  16.00   0.447770  16.00   0.604037
17.00   0.940834  17.00   1.098561  17.00   0.878848  18.00   0.662378
18.00   1.160236  18.00   0.413093  18.00   2.483404  18.00   1.876566
19.00   1.832273  19.00   0.669876  19.00   1.008323  19.00   1.281623
20.50   0.000000  20.50   0.466321  20.50   1.118223  20.50   1.056906
20.50   1.499713  21.50   0.847204  21.50   0.396251  21.50   0.926811
21.50   0.462896  21.50   1.414795  23.50   0.617037  23.50   1.426132
23.50   0.386254  0.75    0.000000  0.75    0.000000  0.75    0.330623
0.75    0.387787  0.75    0.438396  1.75    0.220565  1.75    0.000000
1.75    1.116545  3.50    0.000000  3.50    0.000000  3.50    0.000000
3.50    0.215799  4.50    0.000000  4.50    0.378898  4.50    0.000000
4.50    0.301003  4.50    0.000000  5.50    0.250690  5.50    0.592860
5.50    0.000000  5.50    0.243370
;
proc nlin method=dud ;
   parms  J=0.6  E=0.6  T1=4.5  T2=23 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

April 1997

```
data a ;
   input X Y ;
   cards ;
6.50    0.926417  6.50    0.656632  6.50    0.796928  6.50    0.431506
7.50    0.505391  7.50    0.437101  7.50    0.829418  7.50    0.000000
7.50    0.581863  8.50    0.755378  8.50    0.991856  8.50    0.912142
8.50    0.961122  8.50    1.215903  9.50    0.407884  9.50    0.998099
9.50    0.862795  9.50    0.925556  9.50    0.971715  10.50   0.968892
10.50   0.972455  10.50   0.593370  10.50   0.643788  11.50   0.789896
11.50   0.715830  11.50   0.351690  11.50   0.354457  12.50   0.271372
12.50   0.853996  12.50   1.216189  12.50   0.337346  12.50   0.525306
13.50   0.725688  13.50   1.104476  13.50   0.865997  13.50   0.961231
13.50   0.405370  14.50   1.610551  14.50   0.798515  14.50   1.050611
14.50   0.637633  15.50   0.970219  15.50   0.865035  15.50   0.848864
15.50   0.242489  15.50   0.223309  16.50   0.785559  16.50   1.025375
16.50   0.787958  16.50   0.593630  16.50   0.368409  17.50   0.538992
17.50   0.646748  17.50   0.971641  17.50   1.107263  18.50   0.375327
18.50   1.951077  18.50   0.627223  18.50   1.004657  20.00   0.915445
```

```
20.00    0.997647  20.00    1.365925  20.00    0.611812  21.00    1.042664
21.00    0.000000  21.00    0.871880  22.00    0.433118  22.00    0.925736
22.00    1.673849  22.00    0.000000  1.00     0.128507  1.00     0.000000
1.00     0.000000  1.00     0.000000  3.00     0.000000  3.00     0.000000
3.00     0.389314  3.00     0.000000  4.00     0.000000  4.00     0.188636
4.00     0.000000  4.00     0.000000  4.00     0.000000  5.00     0.000000
5.00     1.261915
;
proc nlin method=dud ;
   parms  J=0.6  E=0.75  T1=4  T2=22 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

June 1997

```
/* ALL DATA POINTS PUT 1.5 HOURS EARLIER (X'=X-1.5) TO */
/* ALLOW FOR LONGER FEEDING PERIOD PAST MIDNIGHT       */
/* RECALCULATE TIMES (X-VALUES) AFTER ANALYSIS         */|

data a ;
   input X Y ;
   cards ;
4.5      0.384520  4.5    0.489895    4.5    0.546357    4.5    0.000000
4.5      1.004588  5.5    0.757261    5.5    0.897840    5.5    0.486543
5.5      0.907937  6.5    0.756127    6.5    0.777309    6.5    0.000000
6.5      0.518304  7.5    0.616551    7.5    0.555162    7.5    0.420788
8.5      0.707842  8.5    0.722233    8.5    0.671571    8.5    0.546625
8.5      0.940757  9.5    0.565292    9.5    0.315323    9.5    0.388910
9.5      0.657953  10.5   0.468671    10.5   0.374434    10.5   0.756931
10.5     0.740074  10.5   0.591129    11.5   0.820425    11.5   0.782086
11.5     0.532449  12.75  0.647658    12.75  0.244148    12.75  0.408103
13.75    0.498608  13.75  1.098548    13.75  0.528803    13.75  0.460710
13.75    0.547105  14.5   0.380536    14.5   0.628089    14.5   0.550868
14.5     0.304117  14.5   0.427779    15.5   0.610620    15.5   0.765863
15.5     0.746770  15.5   0.624051    15.5   0.373995    16.5   1.046625
16.5     0.771423  16.5   0.950588    17.5   0.542391    17.5   0.458889
17.5     0.522856  17.5   0.613761    17.5   0.835582    18.5   0.444360
18.5     0.561063  18.5   0.498590    18.5   0.934349    18.5   0.193274
19.5     0.822573  19.5   0.926251    19.5   0.875761    20.5   0.607269
20.5     0.631683  20.5   0.188388    20.5   0.598043    20.5   0.000000
21.5     0.000000  21.5   0.090368    21.5   0.209110    22.5   0.848751
22.5     2.251614  22.5   0.000000    23.5   0.270301    23.5   1.782448
23.5     0.000000  23.5   0.000000    23.5   0.000000    0.5    0.224253
0.5      0.000000  0.5    0.624832    0.5    1.207979    1.5    0.000000
1.5      0.000000  1.5    0.000000    2.5    0.201838    2.5    0.000000
2.5      0.000000  2.5    0.155022    3.5    0.000000    3.5    0.712605
3.5      0.841286  3.5    0.447255    3.5    0.400683
;
proc nlin method=dud ;
   parms  J=0.7  E=0.8  T1=2.2  T2=22.5 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
```

```
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

August 1997

```
data a ;
   input X Y ;
   cards ;
7.75    0.04818   7.75  0.06357     9.00  0.07079     9.00  0.06501
9.00    0.05599   9.00  0.05273     10.00 0.06096     10.00 0.07577
10.00   0.03341   10.00 0.07241     10.00 0.06130     11.00 0.04384
11.00   0.05788   11.00 0.06657     11.00 0.04002     12.00 0.04976
12.00   0.07273   12.00 0.04132     12.00 0.04690     13.00 0.04429
13.00   0.07582   13.00 0.05425     13.00 0.05941     14.00 0.08191
14.00   0.03368   14.00 0.05386     15.00 0.05428     15.00 0.03083
15.00   0.04014   15.00 0.04917     16.00 0.03833     16.00 0.04850
16.00   0.05434   17.25 0.03351     17.25 0.04524     17.25 0.07555
17.25   0.03125   18.75 0.03846     18.75 0.05281     19.75 0.05830
19.75   0.07932   19.75 0.04342     19.75 0.02029     19.75 0.02018
20.75   0.02691   20.75 0.05328     20.75 0.02545     20.75 0.02402
20.75   0.02842   21.75 0.02943     21.75 0.03540     21.75 0.01002
21.75   0.00431   23.00 0.00000     23.00 0.00000     23.00 0.00000
23.00   0.00000   23.00 0.00000     24.00 0.00000     24.00 0.00000
24.00   0.00000   24.00 0.00000     24.00 0.00000     1.00  0.01534
1.00    0.00000   1.00  0.00000     2.00  0.00000     2.00  0.00000
2.00    0.00000   2.00  0.00000     3.00  0.01196     3.00  0.00500
3.00    0.00931   4.00  0.01633     4.00  0.03457     4.00  0.03296
4.00    0.02177   5.00  0.00000     5.00  0.03527     5.00  0.02273
5.00    0.03080   5.00  0.02899     6.00  0.03393     6.00  0.02372
6.00    0.01320   6.00  0.02182     6.00  0.02924
;
proc nlin method=dud ;
   parms  J=0.05  E=0.5  T1=3.25  T2=19.4 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

Appendix 2

SAS® Routines to determine

MAXIMS curves for Nile tilapia

May 1995 - large fish

```
data a ;
   input X Y ;
   cards ;
    9.5     3.027719        9.5     1.449664        9.5     1.279772
    9.5     0.566667        9.5     2.205882       12.5     1.275343
   12.5     2.116402       12.5     2.340892       12.5     2.876481
   12.5     3.559436       15.5     1.662313       15.5     3.613726
   15.5     3.471553       15.5     1.078626       15.5     3.010552
   18.5     2.571861       18.5     3.024417       18.5     2.328373
   18.5     2.066487       18.5     1.330724       21.5     0.853298
   21.5     1.305622       21.5     1.898734       21.5     1.222494
   21.5     1.794872        0.5     1.913394        0.5     0.528402
    0.5     1.308615        0.5     2.119527        0.5     0.000000
    3.5     0.665509        3.5     1.290323        3.5     1.581990
    3.5     0.000000        3.5     1.225667        6.5     0.000000
    6.5     0.904977        6.5     0.000000        6.5     0.000000
    6.5     0.000000
;
proc nlin method=dud ;
   parms  J=0.5  E=0.15  T1=6  T2=17 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

May 1995 - small fish

```
data a;
   input X Y ;
   cards ;
    9.5     2.356021        9.5     1.823154        9.5     0.837989
    9.5     3.275862        9.5     4.000000       12.5     1.229896
   12.5     1.277683       12.5     0.956522       12.5     0.595238
   12.5     0.655022       15.5     0.311526       15.5     1.434978
   15.5     0.865052       15.5     1.688312       15.5     0.000000
   18.5     2.308961       18.5     2.560000       18.5     2.748626
   18.5     2.147577       18.5     3.488372       21.5     2.500000
   21.5     1.622248       21.5     0.000000       21.5     0.794702
   21.5     0.000000        0.5     0.400000        0.5     0.000000
    0.5     0.000000        0.5     0.318134        0.5     0.000000
    3.5     0.000000        3.5     0.000000        3.5     0.000000
    3.5     0.000000        3.5     0.000000        6.5     0.469484
```

```
    6.5     0.000000        6.5     1.564537        6.5     0.000000
    6.5     0.515464
;
proc nlin method=dud ;
   parms  J=1.5  E=0.5  T1=6  T2=10.5  T3=15  T4=19.5 ;
   file print ;
   Sra=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T4))*(1-exp(-E*(T4-T3))*
        (1-exp(-E*(T3-T2))*(1-exp(-E*(T2-T1))))) ;
   Sfa=Sra*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   Srb=Sfa*exp(-E*(T3-T2)) ;
   Sfb=Srb*exp(-E*(T4-T3))+(J/E)*(1-exp(-E*(T4-T3))) ;
   So=Sfb*exp(-E*(24-T4)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sra*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=T3 then do ;
      model Y=Sfa*exp(-E*(X-T2)) ;
   end ;
   else if T3<X<=T4 then do ;
      model Y=Srb*exp(-E*(X-T3))+(J/E)*(1-exp(-E*(X-T3))) ;
   end ;
   else if T4<X<=24 then do ;
      model Y=Sfb*exp(-E*(X-T4)) ;
   end ;
   run ;
```

August 1995

```
data a ;
   input X Y ;
   cards ;
10.5    1.779399  10.5    3.253549  10.5    1.320132  10.5    1.385189
10.5    3.062803  10.5    2.210229  10.5    2.880000  10.5    1.799763
10.5    3.537432  10.5    0.000000  13.5    2.927928  13.5    1.035570
13.5    1.669471  13.5    1.538462  13.5    1.564572  13.5    0.733272
13.5    1.063516  13.5    1.514387  13.5    1.213172  13.5    1.450610
16.5    0.878416  16.5    0.525977  16.5    1.794669  16.5    0.805902
16.5    1.205396  16.5    0.236904  16.5    0.647634  16.5    1.195730
16.5    0.278094  19.5    0.836623  19.5    0.680052  19.5    0.909720
19.5    1.237191  19.5    0.784626  19.5    0.827690  19.5    0.628931
19.5    0.682109  19.5    1.254657  19.5    0.939387  22.5    1.178034
22.5    1.314060  22.5    1.583873  22.5    0.558914  22.5    0.799087
22.5    0.800500  22.5    0.984081  22.5    1.444992  22.5    1.754109
22.5    1.157184  1.5     0.000000  1.5     0.000000  1.5     0.000000
1.5     0.000000  1.5     0.751295  1.5     0.000000  1.5     0.000000
1.5     1.275964  1.5     0.000000  1.5     0.000000  4.5     0.000000
4.5     0.000000  4.5     0.000000  4.5     0.000000  4.5     0.000000
4.5     0.000000  4.5     0.000000  4.5     0.000000  4.5     0.000000
4.5     0.000000  7.5     0.847336  7.5     0.610842  7.5     0.838619
7.5     0.607287  7.5     0.000000  7.5     0.606469  7.5     1.689189
7.5     0.142399  7.5     0.991543  7.5     1.116838
;
proc nlin method=dud ;
   parms  J1=1.25  J2=0.48  E=0.48  T1=7.1  T2=11.75  T3=12.6  T4=22.5  ;
   file print ;
   Sr1=(J1/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1)))+
((J2/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T3-T4))*(1-exp(-E*(T4-T3)))*
exp(-E*(T4-T3))+(J2/E)*(1-exp(-E*(T4-T3))))*exp(-E*(24+T1-T4))  ;
   Sf1=Sr1*exp(-E*(T2-T1))+(J1/E)*(1-exp(-E*(T2-T1))) ;
   Sr2=Sf1*exp(-E*(T3-T2)) ;
   Sf2=Sr2*exp(-E*(T4-T3))+(J2/E)*(1-exp(-E*(T4-T3))) ;
   So=Sf2*exp(-E*(24-T4)) ;
   if 0<=X<=T1 then do ;
```

```
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr1*exp(-E*(X-T1))+(J1/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=T3 then do ;
      model Y=Sf1*exp(-E*(X-T2)) ;
   end ;
   else if T3<X<=T4 then do ;
      model Y=Sr2*exp(-E*(X-T3))+(J2/E)*(1-exp(-E*(X-T3))) ;
   end ;
   else if T4<X<=24 then do ;
      model Y=Sf2*exp(-E*(X-T4)) ;
   end ;
   run ;
```

March 1996

```
data a ;
   input X Y ;
   cards ;
6       0.267329  6       0.302656  6       0.041824  6       0.213010
6       0.002711  7       0.130405  7       0.313127  7       0.076235
7       0.107379  7       0.230957  8       0.032713  8       0.039068
8       0.282034  8       0.216609  8       0.000000  9       0.379533
9       0.111829  9       0.270133  9       0.181444  10      0.000000
10      0.178507  10      0.000000  10      0.324228  10      0.196466
11      0.060309  11      0.257378  11      0.311226  11      0.109436
12      0.279141  12      0.202338  12      0.131572  12      0.404315
12      0.195076  13      0.372037  13      0.318499  13      0.392267
13      0.465272  13      0.449927  14      0.186073  14      0.322776
14      0.421281  14      0.068202  14      0.109160  15      0.309221
15      0.574899  15      0.384615  15      0.276701  16      0.384570
16      0.281215  16      0.285598  16      0.623575  17      1.139122
17      0.062758  17      0.316504  17      0.453619  17      0.562117
18      0.337086  18      0.577953  18      0.164175  18      1.140608
19      0.209903  19      0.151960  19      0.000000  19      0.276890
20      0.583897  20      0.524094  20      0.575222  20      0.156686
21      0.000000  21      0.385249  21      0.000000  21      0.000000
21      0.223450  22      0.000000  22      0.057794  22      0.000000
22      0.000000  22      0.000000  23      0.000000  23      0.000000
23      0.000000  23      0.227348  24      0.000000  24      0.000000
24      0.000000  24      0.000000  24      0.122577  1       0.000000
1       0.000000  1       0.000000  1       0.000000  1       0.000000
2       0.000000  2       0.000000  2       0.000000  2       0.000000
2       0.000000  3       0.000000  3       0.000000  3       0.000000
4       0.000000  4       0.066462  4       0.000000  4       0.000000
4       0.000000  5       0.000000  5       0.000000  5       0.000000
5       0.000000  5       0.000000
;
proc nlin method=dud ;
   parms  J=0.1  E=0.3  T1=5  T2=18.2 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run  ;
```

May 1996

```
data a ;
   input X Y ;
   cards ;
6     0.075815    6     0.069396    6     0.172340    6     0.107488
6     0.091033    7     0.045725    7     0.069735    7     0.127226
7     0.000000    7     0.098232    8     0.000000    8     0.133038
8     0.067249    8     0.086580    8     0.214500    9     0.336875
9     0.188561    9     0.360082    9     0.000000    9     0.180126
10    0.090212    10    0.073314    10    0.352645    10    0.279525
10    0.141343    11    0.302480    11    0.303951    11    0.448430
11    0.369276    11    0.327225    12    0.361882    12    0.287632
12    0.166945    12    0.107296    12    0.328330    13    0.061162
13    0.311333    13    0.385604    13    0.376176    13    0.321932
14    0.085763    14    0.522193    14    0.545171    14    0.397614
14    0.338696    15    0.735294    15    0.532351    15    0.131148
15    0.383772    15    0.436999    16    0.109981    16    0.362450
16    0.455005    16    0.031878    16    0.165563    17    0.259628
17    0.168527    17    0.458872    17    0.000000    17    0.453515
18    0.782949    18    0.278834    18    0.046937    18    0.338066
18    0.308166    19    0.048065    19    0.450362    19    0.062637
19    0.111607    20    0.064837    21    0.565327    21    0.000000
21    0.208623    21    0.062344    21    0.059207    22    0.000000
22    0.000000    22    0.000000    22    0.000000    22    0.094162
23    0.185014    23    0.000000    23    0.088355    23    0.045579
23    0.071582    24    0.142891    24    0.041929    24    0.043113
24    0.000000    24    0.000000    1     0.000000    1     0.104676
1     0.000000    1     0.112676    1     0.000000    2     0.074553
2     0.000000    2     0.038730    3     0.000000    3     0.044222
3     0.118427    3     0.048638    3     0.130492    4     0.049546
4     0.054555    4     0.031447    4     0.000000    5     0.046168
5     0.054805    5     0.043917    5     0.048008    5     0.000000
;
proc nlin method=dud ;
   parms  J=0.1  E=0.2  T1=5  T2=16.5 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

July 1996

```
data a ;
   input X Y ;
   cards ;
6     0.026110    6     0.146056    6     0.000000    6     0.076687
6     0.000000    7     0.088810    7     0.148258    7     0.121581
7     0.258131    7     0.000000    8     0.081588    8     0.181406
8     0.117096    8     0.265675    8     0.053619    9     0.168549
9     0.207156    9     0.178359    9     0.167616    10    0.118378
10    0.220629    10    0.150565    10    0.187793    10    0.217746
11    0.219386    11    0.742532    11    0.409218    11    0.351351
11    0.371471    12    0.173581    12    0.376851    12    0.405954
12    0.510687    12    0.216732    13    0.200240    13    0.552196
```

```
13    0.550122    13    0.425254    14    0.455032    14    0.414869
14    0.308642    14    0.196323    14    0.210600    15    0.471563
15    0.256279    15    0.284669    15    0.246548    16    0.294811
16    0.294166    16    0.414610    16    0.289169    16    0.210526
17    0.134202    17    0.164054    17    0.589910    17    0.134641
17    0.069767    18    0.202293    18    0.000000    18    0.407166
18    0.155763    18    0.397141    20    0.000000    20    0.000000
20    0.045496    20    0.109469    20    0.000000    21    0.038329
21    0.000000    21    0.123916    21    0.000000    21    0.000000
22    0.000000    22    0.088378    22    0.000000    22    0.000000
22    0.000000    23.5  0.000000    23.5  0.000000    23.5  0.000000
1.5   0.000000    1.5   0.000000    1.5   0.000000    1.5   0.000000
1.5   0.000000
;
proc nlin method=dud ;
   parms  J1=0.05  J2=0.3  E=0.3  T1=5.5  T2=10  T3=13  T4=16.5  ;
   file print ;
   Sr1=(J1/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T4))*(1-exp(-E*(T4-T1)))+
(((J2-J1)/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T2-T3))*(1-exp(-E*(T3-T2)))*
exp(-E*(T3-T2))+((J2-J1)/E)*(1-exp(-E*(T3-T2))))*exp(-E*(24+T1-T3))  ;
   Sr2=Sr1*exp(-E*(T2-T1))+(J1/E)*(1-exp(-E*(T2-T1))) ;
   Sf1=Sr2*exp(-E*(T3-T2))+(J2/E)*(1-exp(-E*(T3-T2))) ;
   Sf2=Sf1*exp(-E*(T4-T3))+(J1/E)*(1-exp(-E*(T4-T3))) ;
   So=Sf2*exp(-E*(24-T4)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr1*exp(-E*(X-T1))+(J1/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=T3 then do ;
      model Y=Sr2*exp(-E*(X-T2))+(J2/E)*(1-exp(-E*(X-T2))) ;
   end ;
   else if T3<X<=T4 then do ;
      model Y=Sf1*exp(-E*(X-T3))+(J1/E)*(1-exp(-E*(X-T3))) ;
   end ;
   else if T4<X<=24 then do ;
      model Y=Sf2*exp(-E*(X-T4)) ;
   end ;
   run ;
```

September 1996 - supplemented fish

```
data a ;
   input X Y ;
   cards ;
6       0.203607  6       0.393959  6       0.000000  6       0.109409
6       0.274725  7       0.158443  7       0.000000  7       0.000000
7       0.000000  8       0.102249  8       0.157563  8       0.037425
8       0.000000  8       0.137552  9       1.446718  9       0.492005
9       1.205757  9       0.452944  9       0.485437  10      0.285714
10      0.417141  10      0.337079  10      0.477327  10      0.596910
11      0.174390  11      0.379795  11      0.445576  12      0.392003
12      0.557103  12      0.281426  12      0.495495  12      0.283286
13      0.178571  13      0.380785  13      0.257922  13      0.406504
13      0.645482  14      0.394945  14      0.770328  14      0.278164
14      0.416667  14      0.226757  15      0.339982  15      0.433369
15      0.868167  15      0.622877  15      0.290192  16      1.186376
16      0.159299  16      0.211149  16      1.122544  16      0.251889
17      0.690938  17      0.462072  17      0.611829  17      0.443319
17      0.563380  18      0.814076  18      0.077280  18      0.400400
18      0.481696  18      0.420610  19      0.157092  19      0.436840
19      0.472519  19      0.639205  19      0.284091  20      0.051697
20      0.288600  20      0.648607  20      0.674624  20      0.167973
21      0.449775  21      0.331263  21      0.644607  21      0.240096
21      0.076570  22      0.180701  22      0.042159  22      0.124585
```

```
22      0.324675  22      0.137112  23      0.195791  23      0.000000
23      0.000000  23      0.000000  23      0.000000  24      0.364409
24      0.315126  24      0.461023  24      0.162338  1       0.030257
1       0.045746  1       0.000000  1       0.000000  2       0.211149
2       0.000000  2       0.000000  2       0.561167  2       0.000000
3       0.127348  3       0.000000  3       0.183554  3       0.045434
3       0.000000  4       0.000000  4       0.000000  4       0.098912
4       0.000000  4       0.000000  5       0.000000  5       0.501630
5       0.025170  5       0.045106
;
proc nlin method=dud ;
   parms  J1=0.15  J2=1.7  J3=0.35  E=0.7  T1=7.8  T2=9.1  T3=13.5  T4=16
      T5=21  ;
   file print ;
   Sr1=(J1/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T5))*(1-exp(-E*(T5-T1)))+
((J2-J1)/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1)))+
(((J3-J1)/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T3-T4))*(1-exp(-E*(T4-T3)))*
exp(-E*(T4-T3))+((J3-J1)/E)*(1-exp(-E*(T4-T3))))*exp(-E*(24+T1-T4))  ;
   Sf1=Sr1*exp(-E*(T2-T1))+(J2/E)*(1-exp(-E*(T2-T1))) ;
   Sf2=Sf1*exp(-E*(T3-T2))+(J1/E)*(1-exp(-E*(T3-T2))) ;
   Sf3=Sf2*exp(-E*(T4-T3))+(J3/E)*(1-exp(-E*(T4-T3))) ;
   Sf4=Sf3*exp(-E*(T5-T4))+(J1/E)*(1-exp(-E*(T5-T4))) ;
   So=Sf4*exp(-E*(24-T5)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr1*exp(-E*(X-T1))+(J2/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=T3 then do ;
      model Y=Sf1*exp(-E*(X-T2))+(J1/E)*(1-exp(-E*(X-T2))) ;
   end ;
   else if T3<X<=T4 then do ;
      model Y=Sf2*exp(-E*(X-T3))+(J3/E)*(1-exp(-E*(X-T3))) ;
   end ;
   else if T4<X<=T5 then do ;
      model Y=Sf3*exp(-E*(X-T4))+(J1/E)*(1-exp(-E*(X-T4))) ;
   end ;
   else if T5<X<=24 then do ;
      model Y=Sf4*exp(-E*(X-T5)) ;
   end ;
   run ;
```

January 1997 - supplemented fish

```
data a ;
   input X Y ;
   cards ;
1       0.083667  1       0.100400  1       0.195708  1       0.065712
2       0.288880  2       0.074586  2       0.000000  2       0.000000
2       0.000000  3       0.000000  3       0.000000  3       0.227514
3       0.000000  3       0.000000  4       0.057456  4       0.102037
4       0.060746  4       0.032430  4       0.061381  5       0.126512
5       0.013131  5       0.030435  5       0.091863  5       0.080900
6       0.032279  6       0.258238  6       0.206165  6       0.062867
6       0.142546  7       0.038505  7       0.000000  7       0.163882
7       0.180982  7       0.000000  8       0.124588  8       0.131837
8       0.091661  8       0.056435  8       0.071905  9       0.338260
9       0.434855  9       0.547096  9       0.607066  9       0.274190
10      0.744097  10      0.201700  10      0.066735  10      0.801138
10      0.253100  11      0.328561  11      0.553527  11      0.975227
11      0.123565  11      0.507816  12      0.546604  12      0.866272
12      0.355771  12      0.228402  12      0.179049  13      0.231309
13      0.264233  13      0.564736  13      0.535522  13      0.454491
14      0.152534  14      0.164882  14      0.283827  14      0.653117
14      0.273726  15      0.303730  15      0.417645  15      0.111308
```

```
15      0.546936  15      0.355832  16      0.873120  16      0.553230
16      0.400770  16      0.305863  16      0.425720  17      0.566199
17      0.534352  17      0.546651  17      0.414718  17      0.661953
18      0.743916  18      0.827147  18      0.756518  18      0.267456
18      0.348550  19      0.387121  19      0.188156  19      0.134233
19      0.456211  19      0.187034  20      0.387699  20      0.571824
20      0.363495  20      0.450822  20      0.356168  21      0.407464
21      0.505034  21      0.230179  21      0.549802  21      0.148347
22      0.287163  22      0.543883  22      0.532246  22      0.420887
22      0.235259  23      0.348115  23      0.331642  23      0.368095
23      0.305319  23      0.216871  24      0.237340  24      0.078420
24      0.424078  24      0.023083  24      0.054827
;
proc nlin method=dud ;
   parms  J1=0.1  J2=0.27  E=0.365  T1=5.5  T2=8  T3=10.75  T4=14.75
T5=17.4  T6=22.67 ;
   file print ;
   Sr1=(J1/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T6))*(1-exp(-E*(T2-T1)))+
(((J2-J1)/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T3-T4))*(1-exp(-E*(T5-T4))*
(1-exp(-E*(24+T2-T5))*(1-exp(-E*(T3-T2)))))*exp(-E*(T5-T4))+((J2-J1)/E)*
(1-exp(-E*(T5-T4))))*exp(-E*(24-T5)) ;
   Sr2=Sr1*exp(-E*(T2-T1))+(J1/E)*(1-exp(-E*(T2-T1))) ;
   Sf1=Sr2*exp(-E*(T3-T2))+(J2/E)*(1-exp(-E*(T3-T2))) ;
   Sr3=Sf1*exp(-E*(T4-T3))+(J1/E)*(1-exp(-E*(T4-T3))) ;
   Sf2=Sr3*exp(-E*(T5-T4))+(J2/E)*(1-exp(-E*(T5-T4))) ;
   Sf3=Sf2*exp(-E*(T6-T5))+(J1/E)*(1-exp(-E*(T6-T5))) ;
   So=Sf3*exp(-E*(24-T6)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr1*exp(-E*(X-T1))+(J1/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<=X<T3 then do ;
      model Y=Sr2*exp(-E*(X-T2))+(J2/E)*(1-exp(-E*(X-T2))) ;
   end ;
   else if T3<=X<T4 then do ;
      model Y=Sf1*exp(-E*(X-T3))+(J1/E)*(1-exp(-E*(X-T3))) ;
   end ;
   else if T4<=X<T5 then do ;
      model Y=Sr3*exp(-E*(X-T4))+(J2/E)*(1-exp(-E*(X-T4))) ;
   end ;
   else if T5<=X<T6 then do ;
      model Y=Sf2*exp(-E*(X-T5))+(J1/E)*(1-exp(-E*(X-T5))) ;
   end ;
   else if T6<X<=24 then do ;
      model Y=Sf3*exp(-E*(X-T6)) ;
   end ;
   run ;
```

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```
data a ;
   input X Y ;
   cards ;
1     0.000000    1     0.060091    1     0.000000    1     0.018318
1     0.055668    2     0.022144    2     0.000000    2     0.000000
2     0.029800    2     0.000000    3     0.000000    3     0.000000
3     0.034642    3     0.039488    3     0.000000    4     0.000000
4     0.000000    4     0.029086    4     0.000000    4     0.000000
5     0.000000    5     0.072523    5     0.036726    5     0.000000
5     0.000000    6     0.000000    6     0.000000    6     0.048059
6     0.102421    6     0.047098    7     0.012333    7     0.042549
7     0.000000    7     0.052599    7     0.019086    8     0.436791
8     0.072311    8     0.318276    8     0.032116    8     0.083968
9     0.062692    9     0.141428    9     0.195380    9     0.018252
```

```
9     0.000000    10    0.204863    10    0.067972    10    0.144459
10    0.172762    10    0.067934    11    0.354608    11    0.076151
11    0.231506    11    0.724788    11    0.137532    12    0.108915
12    0.132630    12    0.142806    12    0.068397    12    0.167802
13    0.191545    13    0.230974    13    0.295847    13    0.550194
13    0.532323    14    0.190861    14    0.243283    14    0.664061
14    1.132808    14    0.490785    15    0.125829    15    0.587737
15    0.491036    15    0.632411    15    0.353745    16    0.155654
16    0.159051    16    0.501368    16    0.336813    16    0.244220
17    0.200645    17    0.115785    17    0.061511    17    0.060227
17    0.311610    18    0.105150    18    0.019050    18    0.203525
18    0.173385    18    0.277696    19    0.386161    19    0.117110
19    0.312434    19    0.335873    19    0.422115    20    0.014601
20    0.021218    20    0.000000    20    0.246499    20    0.303642
21    0.011078    21    0.028918    21    0.140634    21    0.345855
21    0.137893    22    0.025004    22    0.093584    22    0.029800
22    0.000000    22    0.139817    23    0.000000    23    0.056346
23    0.040982    23    0.031191    23    0.046123    24    0.000000
24    0.029385    24    0.042399    24    0.032826    24    0.000000
;
proc nlin method=dud ;
   parms  J=0.13  E=0.21  T1=8.75  T2=14.25 ;
   file print ;
   Sr=(J/E)*(1/(1-exp(-24*E)))*exp(-E*(24+T1-T2))*(1-exp(-E*(T2-T1))) ;
   Sf=Sr*exp(-E*(T2-T1))+(J/E)*(1-exp(-E*(T2-T1))) ;
   So=Sf*exp(-E*(24-T2)) ;
   if 0<=X<=T1 then do ;
      model Y=So*exp(-E*X) ;
   end ;
   else if T1<X<=T2 then do ;
      model Y=Sr*exp(-E*(X-T1))+(J/E)*(1-exp(-E*(X-T1))) ;
   end ;
   else if T2<X<=24 then do ;
      model Y=Sf*exp(-E*(X-T2)) ;
   end ;
   run ;
```

Appendix 3

Calculation of confidence limits to the daily ration

Sainsbury (1986) in his further presentation of the Elliott & Persson (1978) model, which was the basis for the development of the MAXIMS model, gave a formula for the calculation of confidence limits to the daily ration in Model 1.1. He himself pointed out that the determination of confidence limits in the inversely dependent models was not possible by straightforward means since the formula for these include exponential functions so that a jackknife method would have to be applied. The general principle behind the calculation for constant ingestion models was summarised by Rasch (1976) and may be demonstrated here with the aid of the formula for the daily ration to the MAXIMS Model 2.1. This involves three steps:

1. Determination of the partial derivatives matrix from the daily ration formula

2. Determination of the covariance matrix from the parameter correlation coefficients and standard errors

3. Multiplication of the first matrix with the second matrix and then multiplying the product with the inverse of the first matrix.

1. Partial derivatives matrix

For the sake of example, the formula for the calculation of the daily ration to the MAXIMS model 2.1 (Eq. (24)) will be treated here. The daily ration is calculated as:

$$R_d = J \times (T_{f1} - T_{r1} + T_{f2} - T_{r2})$$

From this, the partial derivatives are obtained by differentiating R_d with respect to each parameter as follows:

$$dR_d/dJ_1 = T_{f1} - T_{r1} + T_{f2} - T_{r2}$$

$$dR_d/dT_{r1} = J_1$$

$$dR_d/dT_{f1} = J_1$$

$$dR_d/dT_{r2} = J_1$$

$$dR_d/dT_{f2} = J_1$$

2. Covariance matrix

The covariances are calculated from the correlation coefficients and the standard errors, both included in the SAS output, in the following manner:

$$Cov_{[A,B]} = SE_{[A]} \times SE_{[B]} \times CC_{[A,B]}$$

($Cov_{[A,B]}$ = covariance between parameters A and B, $SE_{[A]}$ & $SE_{[B]}$ = standard errors for A and B respectively, $CC_{[A,B]}$ = correlation coefficient between A and B

Naturally, the covariance between a parameter and itself is merely the variance of that parameter.

3. Matrix calculation

The variance of the daily ration is then calculated as follows:

$$Var_{[R_d]} = \begin{pmatrix} T_{f1} - T_{r1} + T_{f2} - T_{r2} & J_1 & J_1 & J_1 & J_1 \end{pmatrix} \times$$

$$\begin{pmatrix} Var_{[J_1]} & Cov_{[J_1,T_{r1}]} & Cov_{[J_1,T_{f1}]} & Cov_{[J_1,T_{r2}]} & Cov_{[J_1,T_{f2}]} \\ Cov_{[T_{r1},J_1]} & Var_{[T_{r1}]} & Cov_{[T_{r1},T_{f1}]} & Cov_{[T_{r1},T_{r2}]} & Cov_{[T_{r1},T_{f2}]} \\ Cov_{[T_{f1},J_1]} & Cov_{[T_{f1},T_{r1}]} & Var_{[T_{f1}]} & Cov_{[T_{f1},T_{r2}]} & Cov_{[T_{f1},T_{f2}]} \\ Cov_{[T_{r2},J_1]} & Cov_{[T_{r2},T_{r1}]} & Cov_{[T_{r2},T_{f1}]} & Var_{[T_{r2}]} & Cov_{[T_{r2},T_{f2}]} \\ Cov_{[T_{f2},J_1]} & Cov_{[T_{f2},T_{r1}]} & Cov_{[T_{f2},T_{f1}]} & Cov_{[T_{f2},T_{r2}]} & Var_{[T_{f2}]} \end{pmatrix} \times \begin{pmatrix} T_{f1} - T_{r1} + T_{f2} - T_{r2} \\ J_1 \\ J_1 \\ J_1 \\ J_1 \end{pmatrix}$$

The variance may then be used to calculate confidence limits using Student's t-distribution, the degrees of freedom being the number of data points used less the number of parameters in the model.

Contents

Appendices

Abbreviations

ACA - Agricultural Credit Administration

ACCFA - Agricultural Credit and Co-operative Financing Administration

AFP - Armed Forces of the Philippines

AMA - *Aniban ng mga Manggagawa sa Agrikultura* (Association of Agricultural Workers)

AMC - area marketing cooperative

ARRD - agrarian reform and rural development

ATMA - alternative trading marketing association

BARC - *barangay* agrarian reform council

BCOD - Bureau of Cooperative Development

BoD - Board of Directors

CARL - Comprehensive Agrarian Reform Law

CARP - Comprehensive Agrarian Reform Program

CAT - *Central Azucarera de Tarlac* (also referred to as *Central*)

CDA - Cooperative Development Agency

CDF - Countrywide Development Fund

CEBEMO - Catholic Organization for Development Cooperation

CETF - Cooperative Education Training Fund

CfP - Coops for the Poor program

CfP2 - Coops for the Poor program phase 2

CFPI - Cooperative Foundation of the Philippines Inc.

CLDP - Central Luzon Development Plan

CLT - Certificate of Land Transfer
CRB - Credit Rural Bank

CPP - Communist Party of the Philippines

CUP - Cooperative Union of the Philippines

DA - Department of Agriculture

DAP - Development Academy of the Philippines

DAR - Department of Agrarian Reform

DENR - Department of Environment and Natural Resources

dKMP - *demokratikong* Kilusang Mambubukid ng Pilipinas (democratic Alliance of Filipino Farmers)

DOLE - Department of Labor and Employment

DRDAP - Dutch Rural Development Assistance Program

DTI - Department of Trade and Industry

E.O. - Executive Order

EP - Emancipation Patent

FACOMA - Farmers' Cooperative Marketing Associations

GO - government

ICA - International Cooperative Alliance

ICCO - Inter-Church Coordination Committee for Development

IPD - Institute for Popular Democracy

IPM - Integrated Pest Management

LBP - Land Bank of the Philippines

LGC - local government code

LGU - local government unit

MARO - municipal agrarian reform officer

MDC - municipal development council

MOA - memorandum of agreement

MPCI - multi-purpose cooperative inc.

NATCCO - National Confederation of Cooperatives

NAMAFRA - *Nagkaisang Magsasaka ng Frances* (United Farmers of Frances) which is composed of the *Kaunlaran* MPCI, the *Samahang Nayon* cooperative in *Barangay* Frances and the *Samahan ng mga Irrigayson sa Frances* (Irrigation Association of Frances)

ND - national democrat

NDF - National Democratic Front

NFA - National Food Authority

NGO - non-governmental organization

NPA - New People's Army

OCW - overseas contract worker

PAIDO - Provincial Agro-Industrial Development Office

PARO - provincial agrarian reform officer

PARRDS - Partnership for Agrarian Reform and Rural Development Services Inc.

PCIC - Philippine Crop Insurance Company

PD - presidential decree

PEACE - Partnership for Ecumenical Action and Community Empowerment

PET - Provincial Education Training

PHFs - post-harvest facilities

PKP - *Partido Komunista ng Pilipinas* (old Communist Party of the Philippines)

PLF-TILCO - People's Livelihood Foundation Inc.- Tarlac Integrated Livelihood Cooperative Inc.

PMES - pre-membership education seminar
PnB - *Partido ng Bayan*

PO - people's organization

popdems - popular democrats

PRRM - Philippine Rural Reconstruction Movement

RA - "reaffirm" faction of the Communist Party of the Philippines

R.A. - Republic Act

RJ - "rejectionist" faction of the Communist Party of the Philippines

SHG - self-help group

SJPMPC - San Jose Primary Multi-Purpose Cooperative Inc.

SN - *Samahang Nayon*

TLRC - Technology and Livelihood Resource Center

Preface

The 1986 February People Power Revolution which led to the downfall of the Marcos dictatorship gave much hope to the Filipino people that the restoration of democracy would eventually pave the way for socio-economic development and the alleviation of mass poverty which continues to pervade Philippine society. For more than a decade, since its former president Ferdinand Marcos declared martial law in 1972, one witnessed the country's rapid economic decline. In the 1950s, the Philippine economy was considered as the most vibrant only second to Japan in Asia. Within two decades, however, the nation had been transformed into one of the region's beggar economies. The nation's dire economic situation has been blamed on the pursuit of a path of development benefitting only a few, a situation which was heightened under the corrupt Marcos authoritarian regime. The repercussions of this are still in evidence today as the country's elite, composing around ten per cent of the population continue to control 70% of the nations' wealth. This elite also happens to dominate Philippine politics. Out of the 200 members of the House of Representatives of the Philippine Congress, 145 belong to the decade's old political clans and oligarchic families. (Tiglao:1994, p 25)

It is not surprising, therefore, that the country produced one of the most dynamic as well as the only active communist insurgency in the Southeast Asian region since the 1980s. The Marxist-Leninist-Maoist Communist Party of the Philippines (CPP), which was formed in the 1960s as a breakaway faction from the old Communist Party of the Philippines (which is better known as the *Partido Komunista ng Pilipinas* or PKP) grew in numbers due to the increasing gravity of the political and economic abuses of the Marcos authoritarian regime. As political analysts observed, Marcos was the CPP's biggest recruiter to the insurgency. Together with its military arm, the New People's Army (NPA) and its underground united front

movement, the National Democratic Front (NDF) which cuts across all sectors of society, i.e., from workers to professionals, the CPP-NPA-NDF, also referred to as the mainstream left composed almost 80% of the nations' popular movement and was the staunchest opposition to the dictatorship.

The shift from an authoritarian regime to a liberal bourgeois democracy

The ushering in of a liberal bourgeois democracy after the 1986 February People Power Revolution, under the initially very popular government of Mrs. Corazon Aquino, opened up a Pandora's box in the Philippine communist movement. A faction of the left identified with the current CPP leadership of Jose Ma. Sison argues that no change has occurred at all in Philippine society, i.e., the same political and economic elite continue to dominate the country. The only recourse to correct the situation, therefore, is still through armed struggle. This faction is referred to as the "reaffirms" or RAs because they seek to reassert the old line of the movement, i.e., socio-economic equality can only occur with the overthrow of the system which is dominated by the elite.

Another faction is called the "rejectionists" or RJs which believes that the present political dispensation does not currently warrant armed struggle. The "rejectionists" argue that the country is presently enjoying a "democratic space" which was not there during the dictatorship's dark years. A dominant issue is the need to focus on development work, i.e. there is much more room now to organize the marginalized communities to engage in economic projects with the end goal of self-reliance and self-sufficiency. In this way, members of the "rejectionist" camp argue, people will learn to chart their own economic destinies and to fight for this if challenged by adverse societal forces. This is one way, they contend, of enlarging the windows for self-governance. Such development efforts have also been pursued by the

mainstream left in the past but it has always been subsumed under the primacy of armed struggle. The RJs are now arguing that socio-economic endeavors should no longer be treated as only secondary but the primary strategy by which to improve the situation of the dispossessed sectors of society. The gravity of such a debate, together with other issues, led to the split of the Communist Party of the Philippines (CPP) on December 1992 between the "reaffirms" and the "rejectionists". (Among the "rejectionists" there are also divisions but a unifying factor for them is that they believe that it is currently possible to work within the system to bring about substantial changes.)

The NGO approach to development work

This study focuses on that faction of the rejectionist camp which has sought to pursue development work as a means of bringing about socio-economic changes in Philippine society. A popular vehicle for these "rejectionists" are the non-governmental organizations (NGOs). NGOs are defined as private, non-profit volunteer organizations that are committed to the task of what is broadly termed as "development". These NGOs usually are intermediary organizations which service communities. NGOs, on the other hand, whose members and constituents are also its beneficiaries are called grassroots NGOs. These are also referred to as people's organizations (POs). (Garilao:1987, p. 115)

Most of these NGOs stress that their engagement in socio-economic activities is not an end in itself but emanates from a political vision, i.e., their economic activities are seen as a step towards both the economic and political emancipation of Philippine society's marginalized sectors. Thus, it is not rare for these NGOs to also engage in advocacy work. They argue that this is because of the continuous existence of societal structures which

prevent the attainment of the people's economic advancement. These adverse forces, they contend, will have to be confronted in a political manner.

The NGO development trend in the Philippine popular movement which was heightened with the shift to a liberal bourgeois state brings to light the various economic experiments which have been initiated in an attempt to bring about prosperity. In the Philippines, the same issues of underdevelopment which existed under the Marcos regime continue to persist particularly in the agrarian sector, i.e., poverty, unemployment and inequality. As pointed out by Dudley Seers, if these problems endure, irrespective of per capita income, one cannot say that 'development' has occurred. (Slater:1993, p. 105)

This study, therefore, focuses on the attempts of two left personalities associated with the "rejectionist" camp, i.e., Bernabe Buscayno, more popularly known as *Kumander* Dante, founder of the New People's Army (NPA) and Horacio "Boy" Morales, erstwhile head of the National Democratic Front (NDF), to address the persistent issue of underdevelopment in Philippine society through the establishment of NGO-assisted cooperatives. For Buscayno, this is the People's Livelihood Foundation-Tarlac Integrated Livelihood Cooperative (PLF-TILCO) which he initiated in his NPA mass base in Tarlac. Morales, on the other hand, rejuvenated the Cooperative Foundation of the Philippines Inc., a former quasi-government agency, which has established and assisted cooperatives all over the country. The development efforts of the PLF-TILCO and the CFPI will hopefully provide relevant insights into the factors which have enhanced as well as hindered grassroots efforts in providing for a more humane existence for the majority of the Filipino people.