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 911km² 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 2,900km² so that the area of the entire catchment (watershed plus lake) encompasses 3,800km². 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 $2C^{\circ}$ (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:

$$dW/dt = g \times W \tag{1}$$

which gives
$$W = W_0 \times e^{g \times t}$$
 (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

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

(*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:

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

 $(W_t = \text{final weight of fish [g]}, W_0 = \text{initial weight of fish [g]}, t = \text{duration of the trial [days]})$

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):

$$MGR = [(W_t - W_0)/([(W_t/1000)^{0.8} + (W_0/1000)^{0.8}]/2)]/t$$
(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):

$$K = 100 \times W/L^3 \tag{7}$$

(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':

$$B' = W/(L \times H^2) \tag{11}$$

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.

<u>C.</u> 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 periodanalysed, 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"):

$$dS/dt = -E \times S \tag{13}$$

(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"):

$$dS/dt = -E \times S^{\beta} \tag{14}$$

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:

$$R_{\rm d} = \int_{0}^{24} E \times S^{\beta} . \mathrm{d}t = E \times S^{\beta}_{\rm avg} \times 24$$
(15)

 $(R_d = \text{daily ration}, S_{\text{avg}} = \text{average stomach contents over the 24 hour period})$

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 ($\beta = 0$; 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:

$$C_{t} = (S_{t} - S_{0} \times e^{-E \times t}) \times E \times t/(1 - e^{-E \times t})$$
(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:

$$S = S_{\rm f} \times e^{-E \times (t - T_{\rm f})} \tag{17}$$

(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:

$$S = S_{\rm r} \times e^{-E \times (t - T_{\rm r})} + (J_1 / E) \times (1 - e^{-E \times (t - T_{\rm r})})$$
(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:

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

 $(J_2 = \text{instantaneous ingestion rate}, S_m = \text{theoretical maximum stomach contents at which ingestion is zero})$

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:

$$S = S_{\rm r} \times e^{-(J_2 + E) \times (t - T_{\rm r})} + S_{\infty} \times (1 - e^{-(J_2 + E) \times (t - T_{\rm r})})$$
(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
$$R_{\rm d} = \int_{T_{\rm r}}^{T_{\rm f}} J_1.{\rm d}t = J_1 \times (T_{\rm f} - T_{\rm r})$$
 (23)

Model 2.1
$$R_{\rm d} = \int_{T_{\rm r1}}^{T_{\rm f1}} J_1.{\rm d}t + \int_{T_{\rm r2}}^{T_{\rm r2}} J_1.{\rm d}t = J_1 * (T_{\rm f1} - T_{\rm r1} + T_{\rm f2} - T_{\rm r2})$$
 (24)

Model 1.2
$$R_{\rm d} = \int_{T_{\rm r}}^{T_{\rm f}} J_2 \times (S_{\rm m} - S) dt = \int_{T_{\rm r}}^{T_{\rm f}} (S_{\infty} \times (J_2 + E) - J_2 \times S) dt$$
$$= E \times S_{\infty} \times (T_{\rm f} - T_{\rm r}) + \left((S_{\infty} - S_{\rm r}) / (1 + \frac{E}{J_2}) \right) \times (1 - e^{-(J_2 + E) \times (T_{\rm f} - T_{\rm r})})$$
(25)

Model 2.2
$$R_{d} = \int_{T_{r1}}^{T_{r1}} J_{2} \times (S_{m} - S) dt + \int_{T_{r2}}^{T_{r2}} J_{2} \times (S_{m} - S) dt$$
$$= \int_{T_{r1}}^{T_{r1}} (S_{\infty} \times (J_{2} + E) - J_{2} \times S) dt + \int_{T_{r2}}^{T_{r2}} (S_{\infty} \times (J_{2} + E) - J_{2} \times S) dt$$

$$= E \times S_{\infty} \times (T_{f1} - T_{r1} + T_{f2} - T_{r2}) + ((S_{\infty} - S_{r1})/(1 + \frac{E}{J_2})) \times (1 - e^{-(J_2 + E) \times (T_{f1} - T_{r1})}) + ((S_{\infty} - S_{r2})/(1 + \frac{E}{J_2})) \times (1 - e^{-(J_2 + E) \times (T_{f2} - T_{r2})})$$
(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, $T_{\rm f}$, 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:

$$W(i)_{\text{avg}} = \left(M(i)_{\text{avg}} / T(i)_{\text{avg}} \right) \times \int_{0}^{t} f_{i}(t) dt$$
(27)

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

Since $M(i)_{avg}/T(i)_{avg}$ 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:

$$R_{\rm d} = 24 \times \sum_{i=1}^{i=N} W(i)_{\rm avg} / \int_{0}^{t} f_i(t) dt$$
(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 $0-158^{\circ}/_{oo}$, 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	Fertilization	Analytical	SGR	MGR
			Feeding		Period	(%)	(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 1.44-4.77g weight fish) for natural food and 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 $29^{\circ}/_{\circ\circ}$ (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 (1.03km²) 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.

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 40μ m 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.