Assessment and Management of South Asian Small Reservoir Fisheries: A Population Dynamics Approach

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Abstract

South Asian small reservoir fisheries are culture-based, i.e. reliant on the regular stocking of seed fish. In this study, an analytical model is developed that can be used to estimate the potential yield from such fisheries, and to explore options in their management.

Density-dependent growth and size-dependent mortality are the key biological processes in a culture-based fishery. Models for both processes are developed and tested on published data. The cost of seed fish and the selling price of produce from small reservoir fisheries are examined briefly, and are also modelled mathematically.

The sub-models for growth, mortality, costs and revenue are combined in a length-structured model of a small reservoir fishery. The model is then used to explore the effects of stocking density, size of seed fish, staggered harvesting, and multiple stocking on seasonal reservoir fisheries. The optimal stocking and harvesting of perennial reservoirs is also investigated. Management guidelines are developed.

Finally, it is discussed how the model, and the conceptual insights gained from it, can be used in the practical management of culture based reservoir fisheries.

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Contents

Chapter one

Introduction

Reservoirs are man-made water bodies that serve a variety of purposes. Large, "multipurpose" reservoirs serve hydroelectric power generation and water storage for irrigation and domestic use. Large reservoirs have only been built in South Asia since the last century, and are often associated with ecological, economic and social problems. Most of these problems and conflicts stem from two causes: large reservoirs lead to a large-scale redistribution of water resources and a disruption of seasonal flow patterns, and large areas of land are inundated and its inhabitants are displaced.

Small reservoirs serve mainly water storage for irrigation and domestic use. They affect the distribution of water on a local scale only and are not normally associated with ecological or social problems. Small reservoir construction dates back more than 2000 years in some areas of South Asia, like Sri Lanka (De Silva 1988) or Tamil Nadu in India (Nair 1992). At present there is a renaissance of small reservoir construction in many areas of the tropics, owing to the perceived immediate benefits of small reservoirs. Small reservoirs can be built and operated on a village scale, thus keeping villagers in control of irrigation. In addition, small reservoirs help to preserve ground water and mitigate soil erosion (Agarwal 1993).

The use of reservoirs for fish production is a very recent development, dating back only a few decades. Even in Sri Lanka with its 2000 year history of small reservoir construction, reservoir fisheries have only developed after 1950 (De Silva 1988). Fisheries aspects are only now beginning to be considered in the construction phase of reservoirs, but are still a low priority.

Natural fish production in tropical Asian reservoirs is often low, even under eutrophic conditions. The reason for this low fish production is an evolutionary one. With the exception of the African Rift Valley and some volcanic areas (e.g. Java), the tropics are essentially devoid of permanent lacustrine waters. Most economically important freshwater fish species live in rivers and depend on the floodplains for food and to complete their life cycle. Few species are able to complete their life cycle under lacustrine conditions (Fernando 1980, Lowe-McConnell 1987). Notable exceptions are the fishes of the great African lakes, in particular tilapia (*Oreochromis* spp., *Sarotherodon* spp.) and various small pelagic species (e.g. the "freshwater sardine" *Limnothrissa miodon*).

One possible answer to the lack of lacustrine fish species in tropical Asia is the introduction of African lake species, particularly tilapia. Such introductions have been performed on a large scale since 1950, and have often resulted in considerable increases in fish production and yield (Fernando 1980, Fernando & Holcik 1988, 1991). Tilapia is considered a cheap source of high quality protein for the poor. However, Indian major carp and Chinese carp are preferred to tilapia in many regions of South Asia (particularly India, Sreenivasan 1991), and command higher prices on the market. Like tilapia, these species have been introduced widely in South Asia outside their original area of distribution. Unlike tilapia, however, most of these cyprinids are unable to complete their life cycle in lacustrine waters, hence their populations have to be maintained by regular stocking of farm-produced seed fish. The introductions are controversial, but are on the whole regarded as beneficial (Welcomme 1988, Fernando & Holcik 1991, Sreenivasan 1991). At present, there is a tendency towards increased utilization of indigenous species in reservoir stocking programmes, and this involves a fair amount of aquaculture research to solve the technical problems of seed production.

Large reservoirs are formed by damming a major river, hence they are connected to a riverine environment and offer a variety of habitats for fish. Therefore they support self-perpetuating populations of various species and stocking only supplements natural fish production. In contrast, small reservoirs are fed by runoff water, are not connected to rivers and offer little diversity of habitats. Hence natural recruitment in small reservoirs is almost non-existent, and fisheries rely heavily on the regular stocking of seed material.

Small reservoir fisheries combine elements of aquaculture and capture fisheries, and are best referred to as culture-based fisheries. They are dependent on the regular stocking of seed fish, and the fish population structure can be controlled to a large extent. Most of the seed fish are now produced in hatcheries, although in India and Bangladesh some of the Indian major carp seed are still collected in rivers (Pillay 1990). Management of small reservoir fisheries is limited to stocking, harvesting and in some instances fertilization with manure or sewage Small reservoir fisheries are common or communal property resources, and may face similar problems (e.g. danger of "overfishing") as ordinary capture fisheries.

Culture-based inland fisheries are gaining in importance not only in reservoirs. In many regions (notably Bangladesh), flood control measures increasingly restrict the natural recruitment to fish populations in temporal water bodies (oxbow lakes and natural depressions, "beels") in the floodplains. Stocking of seed fish in such water bodies is practised in an attempt to alleviate the loss of natural recruitment. The contribution of culture-based fisheries to the total inland fish production is on the increase throughout the tropics, a tendency sometimes referred to as the intensification of inland fisheries. Hence, although this study is concerned primarily with small reservoir fisheries, its results are also relevant to an increasing number of other fisheries.

The following section summarizes briefly the limnological and fisheries characteristics of small reservoirs. Three small reservoir fisheries are introduced in more detail. The present practice of determining stocking and harvesting regimes for small reservoir fisheries is then reviewed briefly A lack of conceptual understanding of the dynamics of culture-based fisheries is identified as a key problem in their management. This study is an attempt to improve the understanding of the dynamics of culture-based fisheries. The last Section in this Chapter details the organization of this study.

1.1 WHAT IS A SMALL RESERVOIR?

Tropical small reservoirs are defined here as man-made lakes, the biological productivity of which is insufficiently utilized by natural fish populations so that the regular stocking of seed fish results in a noticeable increase of fish production. This definition comprises a wide range of different water bodies, without a clear boundary. The characteristics of South Asian small reservoirs are in many ways intermediate between those of fishponds, and of large reservoirs (Tab. 1.1).

Table 1.1: Characteristics of tropical fishponds, small reservoir and large reservoir fisheries.

	Fishpond	Small reservoir	Large reservoir
Surface area (ha)	< 1	1 - 100	> 100
Main purpose	Fish culture	Irrigation, various	Irrigation, power
Flushing rate	Very high	High	Low
Nutrient origin	Allochthonous	Allochthonous	Autochthonous
Production	Very high	High	Low
Macrophyte abundance	High	High	Low
Fish production based on stocking	100 %	> 90 %	20 %
Stocking density	Very high	High	Low
Risk	High	Intermediate	Low
Fertilization	Yes	Yes / no	No
Feeding	Yes	No	No
Predator & disease control	Yes	Yes / no	No
Stocking of carnivores	Yes / no	No	No
Ownership	Private	Communal	Common

Small reservoirs typically have a surface area of less than 100 ha. However, the above definition is not based on size explicitly, and it includes many reservoirs of surface areas above 100 ha. Water level and volume of most small reservoirs fluctuate considerably during the year, with the smaller ones drying up entirely (seasonal reservoirs or "tanks"). The seasonal-perennial distinction defines two classes of small reservoirs that are very different with respect to their production ecology and fisheries management.

The flushing rate (rate of water exchange) in tropical small reservoirs is usually very high. Small reservoirs often resemble running waters in terms of energy and matter flow, and biological production is mostly based on nutrients of allochthonous origin.

Productivity of small reservoirs is variable, depending largely on the allochthonous input of nutrients, but often very high (Marten & Polovina 1982, Jhingran 1992).

The rate of siltation in small reservoirs is often very high, a consequence of the high flushing rate. Hence the maintenance of small reservoirs usually involves regular digging.

Macrophytes contribute significantly to primary production in unmanaged small reservoirs, often channelling the bulk of production into the macrophyte-detritus chain. Macrophytes limit the availability of nutrients to phytoplankton, reduce light penetration and lower the water temperature (Gopal *et al.* 1984). They also create adverse physico-chemical conditions like strong fluctuations in pH and oxygen saturation (Bohl 1982). However, macrophytes may also be beneficial in breaking wave action on the shoreline and prevent shore erosion. The management of small reservoir fisheries usually involves some management of macrophyte vegetation.

The ecology and production of reservoirs changes rapidly during the first years after impoundment. At first, nutrient leeching from the newly inundated land results in very high primary production. However, this high primary production may not always transpire to higher trophic levels, simply because food webs are only just evolving. The initial phase of high production ("trophic surge") is followed by a trophic depression phase, before productivity stabilizes at an intermediate level (Craig & Bodaly 1988). This evolution of the reservoir ecosystem is typical for perennial reservoirs, but similar changes in productivity are known from seasonal reservoirs and fishponds (Huet 1973). Seasonal reservoirs may not show such a marked change in productivity, as they fall dry and are inundated periodically. The productivity of small reservoirs is strongly influenced by management, and the trophic depression phase can be avoided by fertilization.

Fish species stocked in tropical small reservoirs occupy a low trophic position, they feed mainly on plankton, macrophytes, and sometimes zoobenthos and detritus. Hence primary production is efficiently used for fish production, and the interaction between stocked species is limited to competition. Occasionally, predatory fish are stocked for regulatory purposes, e.g. to prevent stunting of tilapia populations.

Small reservoirs are often called "single purpose irrigation reservoirs" to differentiate them from larger "multiple purpose" reservoirs used mainly for irrigation and power generation. In fact, however, small reservoirs serve a wide variety of purposes like irrigation of fields and vegetable pads, drinking water supply, fisheries and fish culture, and watering of animals.

Small reservoir fisheries are often communal property resources, i.e. the use rights to the resource are "held by an identifiable community of users, who can exclude others and regulate use" (Berkes *et al.* 1989). Fisheries in larger reservoirs tend to be common property resources.

1.2 A CLOSER LOOK AT THREE SOUTH ASIAN SMALL RESERVOIR FISHERIES

This section gives a more detailed account of three South Asian small reservoir fisheries, covering biological, management, economic and social aspects. Although this study is mainly concerned with biological aspects of production, economic and social aspects are crucial in practical management and will be considered to some extent in later Chapters.

1.2.1 Village Fishponds in Northeast Thailand

Northeast Thailand (Esarn) is one of the poorest areas in this otherwise economically fast growing country. The main occupation of its rural inhabitants is paddy culture and tapioca growing.

Since about 1985, the Royal Thai Department of Fisheries (DOF) has been running a village fishpond (VFP) programme throughout Northeast Thailand. Under the programme, communal small reservoirs on a village level are constructed or rehabilitated for the development of a culture-based fishery. Village fishponds can be seasonal or perennial, usually cover an area between 2 to 20 ha, and are around 3 meters deep. Fig. 1.1 (top) shows such a village fishpond in Udorn Thani Province. Due to the stocking of grass carp, macrophyte abundance in the pond is very low. By contrast, the unmanaged swamp adjacent to the VFP is completely overgrown with macrophytes (Fig. 1.1 bottom).

The larger VFP's are perennial, but all are essentially managed as a seasonal fishery. Seed material is stocked in June/July, and ponds are harvested completely in March/April, during the dry season.

Stocked species comprise common carp (*Cyprinus carpio*), Chinese carp (bighead *Aristichthys nobilis*, and grass carp *Ctenopharyngodon idella*), Indian major carp (mrigal *Cirrhinus mrigala* and rohu *Labeo rohita*), nile tilapia (*Oreochromis niloticus*), and silver barb (*Puntius gonionotus*). Of these species, only silver barb is indigenous to Thailand. However, the potential for other indigenous species is currently being assessed and these may replace some of the introduced species in the longer run. The most important predators are snakehead (*Channa* spp.), which may cause heavy losses of seed fish. Pen nursing of seed

Fig. 1.1. Village fishpond in Northeast Thailand. **Top:** View of the village fishpond. The surface area of this pond is about 5 ha. **Bottom:** Dam of the village fishpond, with members of the fishpond committee. The unmanaged swamp to the left of the dam is overgrown by macrophytes.

to an advanced fingerling stage has proved successful in medium sized reservoirs in NE Thailand (Manni 1992), but is not yet practised in VFPs.

Total annual yield from VFPs is about 60 kg/ha on average, but can be up to 600 kg/ha in well-managed ponds. Stocked species contribute more than 90% to the total yield. The catch consists largely of small fish, about 0.2-0.3 kg in weight. There is a particularly high demand for fish in this size category, as the majority of the local population cannot afford to buy large fish.

The VFP is a communal resource, managed by a village fishpond committee, the members of which receive some relevant training in DOF courses. DOF provides 100% of the stocking material for free in the first year of operation, as opposed to 50% in the second and 25% in the third year. Thereafter, the village is expected to purchase all of the seed material, using revenue from the previous harvest. Harvesting is organized in various ways. Many villages sell "tickets" (licences) to the public, allowing the ticket holder to fish with a particular gear, often on only one "fishing day" per growing period. Other villages harvest the pond themselves, or sell exclusive rights to mobile harvesting teams, groups of professional fishermen. Fish are mostly sold at the local or provincial markets. On the whole, labour in the VFPs is low and occasional.

Little is known about the performance of village fishponds after withdrawal of DOF involvement. It appears that some are running successfully, while others are abandoned. The reasons for success or failure are currently being investigated by DOF. The objectives of the village fishpond programme are not only to increase the production of high quality protein by and for the rural poor, but also to encourage private aquaculture.

1.2.2 Calcutta Bheris, India

The wetland impoundments or bheris near Calcutta in West Bengal, India, support particularly productive culture-based fisheries. Bheris have been constructed since about 1940, and serve sewage treatment as well as food production. Today, the Calcutta bheris probably represent the world's largest wastewater-fed fishery (Ghosh & Sen 1987). Individual bheris usually cover a surface of about 100 ha, and are only 1 m deep. Domestic sewage is fed into the bheris through long canals that act as septic tanks, and bheri water is later used for the irrigation of vegetable fields.

Bheris are managed as continuous culture systems. Seed availability, hence also stocking, is linked to the reproductive season of the stocked species. Harvesting is continuous, but catches reflect the variations in stocking rate. Stocked species are Indian major carp (catla *Catla catla*, mrigal *C. mrigala* and rohu *L. rohita*), common Carp (*C. carpio*), and Chinese carp (silver carp *Hypophthalmichthys molitrix*, and grass carp *C. idella*), and nile tilapia (*O. nilotica*). The main predator is snakehead (*Channa* spp.), but its influence is reduced by stocking advanced fingerlings of more than 10 cm length.

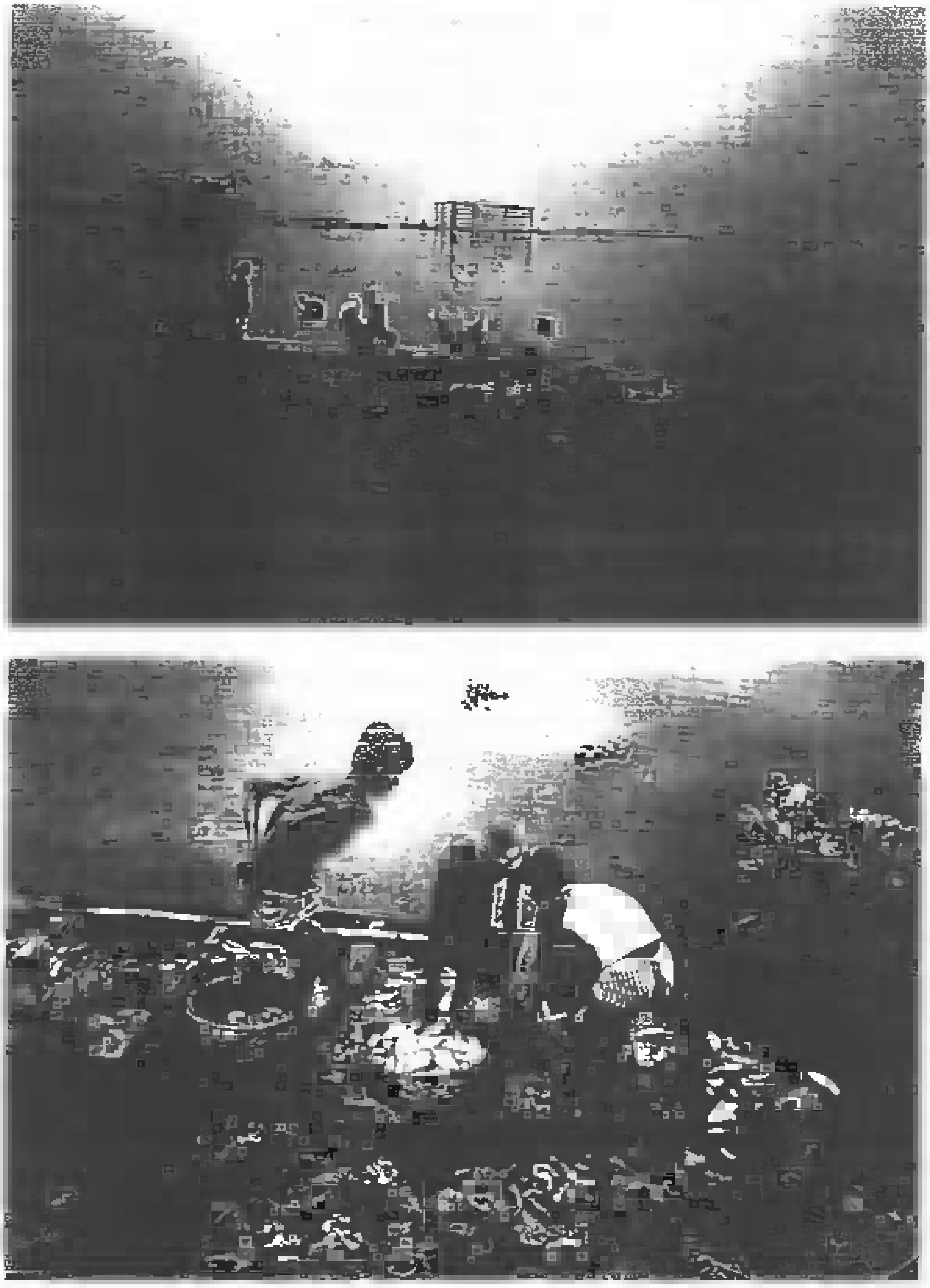

Fig. 1.2. Nalban bheri near Calcutta, India. Top. Harvesting with a seine net. A belt of water hyacinth (*Eichhornia crassiceps*) is seen in the foreground. Bottom. Landing the catch. Note the small size of the fish.

Annual yield from the bheris averages at 2500 kg/ha (Ghosh & Sen 1987), but may occasionally reach over 6000 kg/ha. Stocked species contribute more than 90% to the catch. Average weight of the fish at harvesting is low, usually 0.2 to 0.3 kg. Produce is sold at the Calcutta municipal market. Demand is high for small fish, due to the limited buying capacity of the poor. However, the occasional large fish are also marketable and command a higher price per unit weight.

Most bheris are managed by cooperative societies, and some by the West Bengal State Fisheries Commission. Seed material is usually purchased from state or private hatcheries and nursed in smaller ponds adjacent to the main bheris. Harvesting is effected in a highly organized way using seine nets. Labour in the bheri fisheries is high and continuous.

Fig. 1.2 shows the harvesting process in Nalban bheri, Salt Lake City, West Bengal. This bheri is managed by the West Bengal State Fisheries Development Corporation. A fine mesh seine net is used and larger fish for the market are selected by hand. A belt of water hyacinth (*Eichhornia crassiceps*) along the shore is protected from grass carp using a fence. The macrophyte belt breaks wave action and prevents shore erosion.

1.2.3 Irrigation Reservoirs in Karnataka, India

There are 54 irrigation reservoirs in Karnataka state, India, on average covering about 4000 ha, and 10 to 40 m deep. Hence most of these reservoirs do not strictly fall into the "small" category, but the culture-based component of reservoir fisheries is significant and is likely increase in the future. Stocking of reservoirs in the state started around 1980 and is carried out by the Karnataka Department of Fisheries.

The reservoirs are perennial, and are fished all year round, with a peak during the monsoon when stocked fish aggregate near the shore in an attempt to migrate into the (non-existent) floodplain. Stocked species are Indian major carp (catla *C. catla*, mrigal *C. mrigala* and rohu *L. rohita*), and common carp (*C. carpio*). The main predator is the catfish *Wallago attu*, but little information is available on losses.

Total annual yield from the reservoirs averages at 10 kg/ha (Devaraj & Mahadeva 1990). Currently only 20% of the yield is based on stocked species, while *W. attu* and various small "trash fishes" contribute 80%. Stocked species are caught at a relatively large size of 2 kg or more.

Access to the fishery is formally limited through a licensing system, operated by the fisheries department, but the licence fee is nominal and the number of licences unrestricted.

Fishing is not a traditional activity in inland Karnataka. Reservoir fishing is done by a small and ethnically distinct group of migrant fishermen, originating from the neighbouring states of Maharashtra, Andhra Pradesh and Tamil Nadu. The characteristic fishing craft are so-called coracles: small, light weight, circular boats made from bamboo and fertilizer bags.

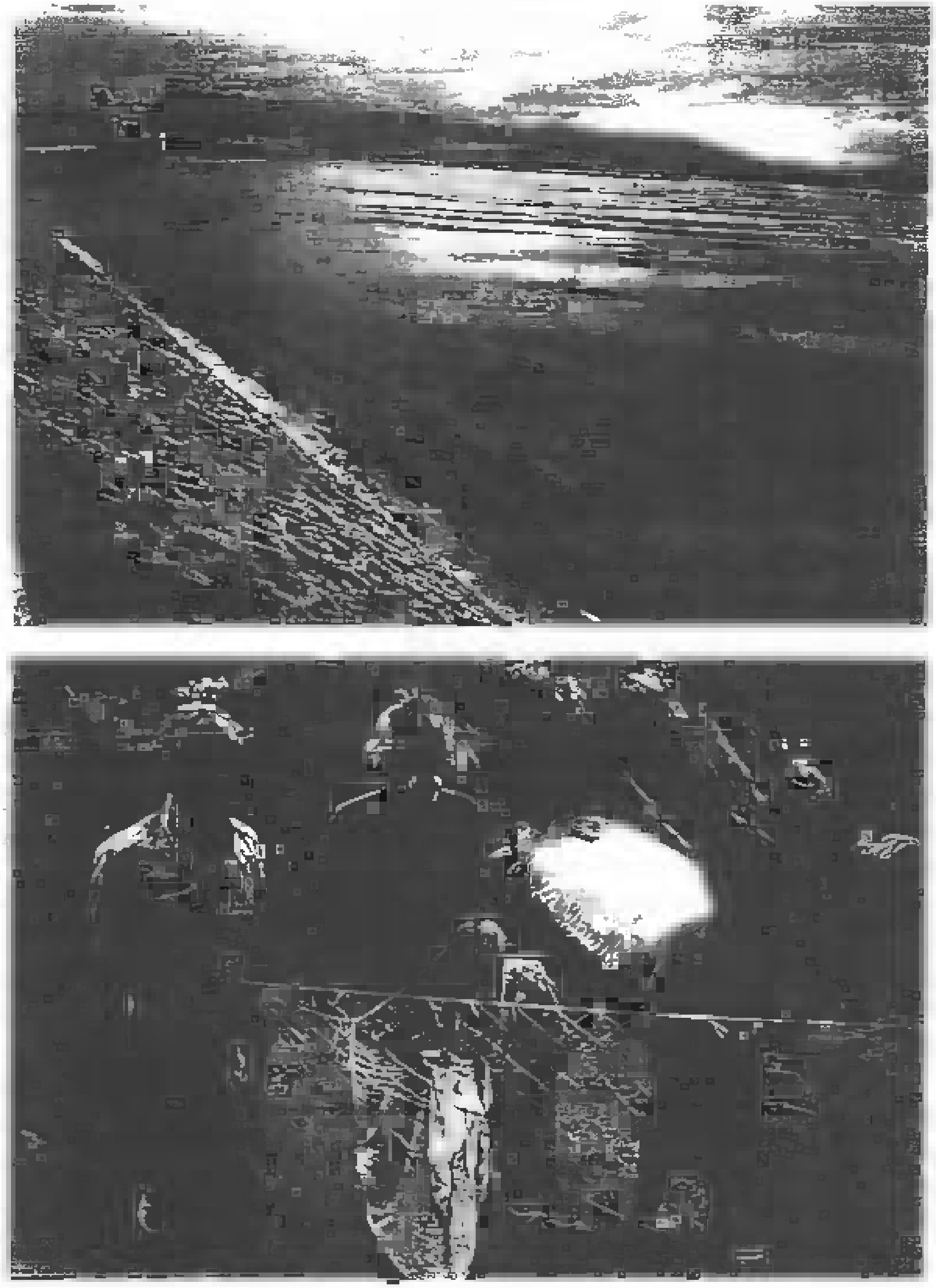

Fig. 1.3. Harangi reservoir, Karnataka, India. **Top.** View of the dam. Note coracles above the shoreline. **Bottom:** Migrant fishermen demonstrating a gillnet used to catch stocked carp. A coracle under construction can be seen in the background.

Locally, these fishermen are called *burde bestharu*, or "fishermen fishing with floats". The main fishing gear are gillnets, with some dragnets, castnets and longlines.

The marketing of fish varies locally and seasonally During the monsoon, reservoir catches are highest, and at the same time the landings of marine fish decline Reservoir fish are bought by middlemen at the landing sites, and distributed throughout the state. Outside the monsoon, catches are lower and less attractive for middlemen. Fish are then sold at local markets by women from the fishing communities.

Devaraj & Mahadeva (1990) consider the "economic backwardness" of the reservoir fishermen a serious limitation to reservoir fisheries development in the State.

The Karnataka Department of Fisheries encourages landless farmers to take up fishing in reservoirs as an occupation, and some have already done so.

Fig. 1.3 (top) shows the dam of Harangi reservoir in Karnataka, flooded in 1982. Coracles, the characteristic fishing crafts of the migrant fishermen, can be seen above the shoreline. In Fig. 1.3 (bottom), a migrant fisherman demonstrates a gillnet used to catch stocked carp and the catfish *W. attu*. A coracle under construction can be seen in the background, leaning against the house.

1.2.4 A Brief Comparison of the Fisheries

The three fisheries introduced here give a good indication of the variety of culture-based, "small reservoir" fisheries in South Asia (Tab. 1.2). Each of these fisheries could equally well be classified as either extensive pond culture (Thai village fishponds and Calcutta bheries), or a large reservoir fishery (Karnataka reservoirs). In the context of this study, the unifying feature of these fisheries is the fact that all are based on regular stocking to a large extent, and that management is limited to stocking, harvesting and sometimes fertilization

The bulk of fish production in small reservoirs is culture-based, while in the large Karnataka irrigation reservoirs, the culture-based production is relatively low.

The Thai Village fishponds are mostly seasonal, while both other systems are perennial.

Cyprinids figure prominently among the stocked species in all three fisheries, and this is a general feature of culture-based reservoir fisheries in South Asian.

Ownership of the small reservoirs (village fishponds and bheris) is communal: an identifiable community controls resource use, bears the cost of stocking and excludes others. The larger irrigation reservoirs in Karnataka are common property. The costs of stocking are born by the state, and access is open to all for a nominal licence fee.

Thai village fishponds and Karnataka reservoirs represent fisheries in an early state of development, while the Calcutta bheris are long established.

Tab 1.2: A comparison of village fishponds in NE Thailand, Calcutta bheris (India), and irrigation reservoirs in Karnataka (India).

	Village Fishponds	Calcutta bheris	Karnataka reservoirs
Surface area (ha)	1 - 20	100	> 1000
Depth (m)	1 - 4	1	10 - 40
Water regime	Seasonal	Perennial	Perennial
Average production (kg/ha/year)	600	2500	10
Culture-based	> 90 %	> 90 %	20 %
Fertilization	Yes / no (manure)	Domestic sewage	No
Species stocked	Cyprinids, tilapia	Cyprinids, tilapia	Cyprinids
Fishing gear	Various	Seine nets	Gill nets
Average weight of produce (kg)	0.2 - 0.3	0.2 - 0.3	> 2
Predators	Snakehead	Snakehead	Catfish
Labour input	Occasional	High, permanent	Low, permanent
Ownership	Communal	Cooperative or state	Common
Market	Local, provincial	Municipal	Local
Established	1985	1940	1980

1.3 HOW STOCKING AND HARVESTING REGIMES ARE DERIVED

Stocking and harvesting are the principal means of managing a small reservoir fishery. Hence the management of such a fishery is mostly within the realm of population dynamics. In contrast, more intensive forms of aquaculture rely heavily on feeding, and stocking policies are less crucial in determining production.

This section provides a brief review of current practice in determining stocking and harvesting regimes in culture-based fisheries. Here the term "stocking" always refers the release of young fish, to be recaptured at a larger size, without aiming at the establishment of a self-perpetuating population.

The aim of stocking in South Asian small reservoir fisheries is the optimal utilization of the productivity of the stocked water body. As fish production is essentially an economic activity, optimal utilization of productivity has both a biological and an economic aspect to it. Stocking policies, if they exist, are usually based on a mixture of theoretical reasoning and (mostly qualitative) past experience. Systematic analyses of stocking and catch data are rare.

The formulation of a management policy for a culture-based fishery involves decisions on a number of points:

(1) Selection of species for stocking;
(2) Size of seed fish;
(3) Stocking density;
(4) Temporal pattern of stocking;
(5) Timing, selectivity and intensity of fishing

The following sections give a brief overview of the considerations involved in making these decisions.

1.3.1 Selection of Species

Fish species stocked are mostly destined for human consumption, though some are chosen for their more indirect beneficial effects. Hence market demand is an important criterion in the selection of species for stocking. This, of course, is obvious and needs not be emphasized.

In terms of production ecology, the idea behind stocking of reservoirs (as well as pond polyculture) is to exploit "open niches" in the foodweb, in order to make full use of the biological production potential of the water body. Consequently, the selection of species should be based on an assessment of "open niches" in the reservoir. This procedure is not often followed explicitly, but some related considerations are very common: for example, the stocking of grass carp if macrophytes are abundant. Explicit considerations of niche requirements and availability are documented in Anon. (1989), for medium size reservoirs in NE Thailand.

Certain species are selected for stocking because they have some positive effect on the overall productivity of the water body or on certain populations. Examples are grass carp (*C. idella*), used to control macrophyte abundance, and the phytoplanktivorous silver carp (*H. molitrix*), stocked for its ability to utilize and control algal blooms (Pillay 1990). Predatory species are sometimes stocked to control the recruitment of tilapia in small water bodies, and to prevent stunting.

South Asian small reservoir fisheries are generally aimed at high protein production, rather than high value species. Hence the fish stocked occupy a position low in the food web.

1.3.2 Size of Seed Fish

The size of seed fish is an important consideration in a culture-based fishery. Predation mortality and escapement of fish into irrigation canals depend on the size of stocked fingerlings or fry Various minimum lengths for seed fish are recommended, usually between 4 and 15 cm (Jhingran 1986, Li 1988, Anon. 1992), but occasionally up to 26 cm (Tripathi 1971). Such recommendations are usually based on experience, and systematic investigations are very rare.

Stocking of large fingerlings provides better returns than stocking of small fingerlings or fry, but there is a tradeoff with the production costs for fingerlings, which is seldom considered explicitly.

Small seed fish are dependent on a narrow range of food organisms. Hence small seed fish are more likely than larger ones to suffer from starvation due to lack of appropriate food

In practice, seed fish are often smaller than the recommended minimum size, due to limited nursing facilities

1.3.3 Stocking Density

Various approaches are used to determine stocking density. These include fixed guidelines, experience, and a simple model that is used in conjunction with either past experience or a yield predictive model. In practice, stocking densities have often been determined by the availability of seed material, but this constraint is becoming less and less important.

Fixed guidelines exist for stocking densities in Thai reservoirs (Chookajorn, pers. comm). These are based on experience in a limited number of water bodies, and on some theoretical considerations. Because the productivity of reservoirs tends to increase with decreasing size, and small reservoirs support fewer natural fish populations, the recommended stocking densities are highest for small reservoirs. The problem in using such guidelines is that they do not account for the unique characteristics of any particular water body.

The Schäperclaus-Huet formula

In most cases, stocking densities are based on experience, particularly of the fishery has been in operation for some time. Pond culturists (Schäperclaus 1949, 1961, Huet 1973) have suggested the following formula to determine the stocking rate of ponds:

$$\text{Stocking density} = \frac{\text{Production}}{\text{Individual weight gain}} + \text{Expected loss} \qquad (1.1)$$

where stocking density (numbers), expected loss (numbers), and production (weight) refer to the same unit area. Schäperclaus and Huet proposed this formula to be used if the total production and losses of a particular pond are known from experience. The desired harvesting weight (growth target) of the fish is chosen, and the stocking rate calculated.

The formula is widely used to calculate stocking densities for reservoirs in India, where potential production is assessed using empirical yield models (Jhingran 1986, Jhingran & Sugunan 1990).

Empirical yield models

Empirical yield models predict fish yield (production) as a function of physico-chemical, biological or fishery data. Such yield estimates may be combined with Equation (1.1) to calculate stocking densities.

The selection of explanatory variables in yield predictive models is often based on some theoretical considerations, but the empirical model itself only makes predictions without attempting to "explain" anything.

To derive an empirical model for a certain type of water body, the model is fitted to data from a number of water bodies that display some variation in the explanatory variables, but are as uniform as possible with regard to all other parameters. The fitted model may then be used to predict the yield in similar water bodies that did not form part of the initial data set. At present, there is no set of well-studied tropical small reservoirs upon which an empirical model might be based. The application of existing models for other types of water body to small reservoirs does, strictly speaking, violate the very principles of empirical modelling (Rigler 1982).

The following paragraphs provide a very brief review of some yield predictive models and their applicability to small reservoir fisheries.

The most widely used of the yield predictive models is the morphoedaphic index (MEI), proposed by Ryder (1965) and reformulated into a multivariate regression model by Rempel & Colby (1991). The morphoedaphic index is defined as the ratio of total dissolved solids (TDS) to mean depth of the water body (Ryder 1965, 1982). Hence it comprises a morphometric factor (mean depth) relating to energy and nutrient dilution and a partial unidirectional sink for these two variables (Ryder 1978), and an edaphic factor (TDS) relating to nutrient levels. Small reservoirs are characterized by very high rates of water exchange, and nutrients are predominantly of allochthonous origin. Hence the morphoedaphic index is not generally applicable to small reservoirs, except those with a relatively low flushing rate.

Hanson & Leggett (1982) have shown that total phosphorus can be a powerful predictor of fish yield in lakes, and this may also apply to small reservoirs with a high flushing rate.

Various attempts have been made to estimate fish production or biomass from the production or biomass at lower trophic levels. As Oglesby (1977) has pointed out, such models are inherently more accurate and subject to fewer exceptions than those related to morphoedaphic factors. Regression models have been developed to predict fish yield from gross photosynthesis (Melack 1976, McConnell *et al.* 1977, Jhingran 1986), phytoplankton biomass (Oglesby 1977) and primary production (Liang *et al.* 1981, Moreau & De Silva 1991).

Some models have been developed to predict yield as a function of fishing effort (Moreau & De Silva 1991) and/or stocking density (De Silva *et al.* 1992). The latter models have the advantage that they can predict optimal stocking densities directly, given that other parameters remain constant. Also, these are the first models to use stocking and catch data directly in the optimization of stocking densities.

Most empirical models require extensive limnological sampling to produce results of reasonable accuracy. This is clearly not feasible in small reservoirs. Stocking and catch data, on the other hand, are often collected as part of routine management. This information is also likely to give the best indication of possible improvements in stocking densities, and methods that utilize such data hold a strong potential for management.

1.3.4 Temporal Pattern of Stocking

In seasonal reservoir fisheries, stocking is done shortly after flooding, i.e. its timing is linked to the water regime. The temporal pattern of stocking in perennial reservoirs is largely determined by the availability of seed material, i.e. mostly linked to the reproductive cycle of the species. Although some species can now be induced to spawn all-year round, seed availability remains seasonal in many regions.

Small fish are dependent on a very narrow range of food organisms, hence their stocking success is dependent on the successional stage of the plankton community. Larger fingerlings are less specific in their food requirements, and can be stocked all year round.

1.3.5 Timing, Selectivity and Intensity of Fishing

In seasonal small reservoirs, the timing and selectivity of harvesting is restricted by the physical environment. Often, seasonal reservoirs are harvested completely during a short time before they fall dry. Staggered harvesting, i.e. the selective harvesting of large fish during the growing season, is practised in some reservoirs to improve the growth of the remaining fish and to supply markets with fish of relatively uniform size (De Silva 1988).

In perennial reservoirs, few physical restrictions exist concerning the choice of fishing patterns. Usually, gear selectivity is tuned to market demand for fish of certain size classes Small fish are in high demand in South Asia and this is reflected in the choice of gear. Temporal distribution of fishing effort can be fairly uniform if the fishery is dominated by full-time fishermen. Often, however, there is an interaction with the demand for labour in other activities (e.g. agriculture) or the demand for fish products, so that effort fluctuates in response to factors external to the fishery. Finally, effort may be linked to characteristics of the fishery, e.g. increased catchability of fish during certain times of the year which makes fishing more attractive.

Small reservoir fisheries are often communal property resources, in which case access to the fishery is limited. Some fisheries, particularly in larger reservoirs stocked by the government, are essentially open access and may be in danger of overfishing.

1.4 DEFINING THE PROBLEM

The dynamics of culture-based fisheries are poorly understood There are various concepts and rules pertaining to particular aspects of culture-based fisheries, but no unifying framework that would allow an understanding of their interaction

Consequently, there is also a lack of appropriate assessment methodology for such fisheries. Assuming that some past stocking and catch data are available for a particular fishery: how can such data be utilized to devise improvements in management, and what is the yield likely to be under improved management? If the fishery is currently making a net economic loss, is it possible at all to change stocking and harvesting policies so that a net profit will result? Such crucial questions are difficult to answer using the present, limited assessment tools.

This study attempts to improve the conceptual understanding of culture-based fisheries, and to develop tools for the assessment of such fisheries on the basis of stocking and catch data An analytical population model for a culture-based fishery is being developed, and the dynamics of the fishery are explored. Some qualitative guidelines for stocking and harvesting are derived, and an adaptive approach to the assessment of culture-based reservoir fisheries is outlined

1.5 ORGANIZATION OF THE TEXT

This study explores the dynamics of culture-based small reservoir fisheries using mathematical modelling. Some contributions are made to the development of assessment methodology and management strategies.

Chapter 2 deals with the key processes in the population dynamics of culture-based fisheries: density-dependent growth, and size- and density-dependent mortality. Mathematical representations are proposed for these processes and tested on data sets from the literature.

Some economic considerations in small reservoir fishery management are introduced in Chapter 3. The intentions of this chapter are very limited, it only includes considerations directly relevant to the choice of a stocking and harvesting regime. Of particular importance in this respect are price-size relationships for seed fish and produce. These relationships are investigated in examples, and simple models are proposed which will be used in Chapter 4.

In Chapter 4, a general size-structured model for a culture-based fishery is developed. It incorporates the sub-models for density-dependent growth and size-dependent mortality proposed in chapter 2. The model is used to explore the dynamics of small reservoir fisheries, and to derive qualitative guidelines for stocking and harvesting.

Chapter 5 deals with the management process. It is discussed how the model developed in Chapter 4 and its results can be used in practical management, and how an adaptive approach to management can lead to a better understanding of the fishery, and in turn to better stocking and harvesting.

Chapter two

Growth and Mortality in Culture-Based Fisheries

In order to manage culture-based fisheries rationally, it is crucial to understand the population processes of density-dependent growth, of size and density-dependent mortality, and their interactions. Standard analytical ("dynamic pool") fisheries models usually assume growth and mortality to be constant in the recruited population, with density, size and environmental effects considered to act primarily on the pre-recruits. All processes which determine the number of recruits are lumped into an overall "stock-recruitment relationship".

A stock-recruitment relationship, if it can be determined from empirical data, is a useful tool in the management of natural fish populations, as recruitment is mostly beyond the control of the manager. In a culture-based fishery, the manager can choose the size and number of seed fish, and the time of stocking. Recruitment can therefore be controlled by the manager if the density- and size-dependent mechanisms determining recruitment are understood. This is, of course, subject to the variation and predictability of (density-independent) environmental effects.

Density-dependence in growth is the result of intraspecific competition. Competition is inevitable if resources are limited, and the feedback is instantaneous

Size-dependent mortality, i.e. the decrease of the instantaneous mortality rate of fish with increasing size, is often attributed to the effects of predation, but may also result from parasitism.

Density-dependent mortality can be caused by various biological mechanisms, and it is proposed here to distinguish between "competition-mediated" and "predation-mediated" density-dependence in mortality.

Competition-mediated density-dependence in mortality results from the interaction of density-dependent growth and size-dependent mortality. If mortality decreases with increasing size, then dense, slow growing fish populations suffer higher losses than thin, fast growing populations. Hence mortality within the population is density dependent, although the mortality rate at any particular size is independent of density. Competition-mediated density-dependence in mortality results from density-dependent growth, and is thus equally instantaneous and inevitable

Predation-mediated density-dependence results if mortality at size changes with population density. Such a change of mortality for a certain size group requires a functional or numerical response of the predators to the population density of the prey. A numerical response (increase in the predator population density) involves a substantial time lag, and can be mitigated by predator control measures. Density-dependent mortality of the predation-mediated type may also result from parasitism.

The following sections deal with density-dependent growth, and size and density-dependent mortality. All sections are organized in a similar way. At first, empirical evidence is reviewed, and biological mechanisms are identified. A mathematical model for the process is then proposed, tested on an example, and some of its implications are explored.

2.1 DENSITY-DEPENDENT GROWTH

Density-dependent growth has often been described in wild populations, and Beverton & Holt (1957) consider it "perhaps the best established of the density-dependent effects". Early published evidence includes Petersen (1894), Hile (1936), and Le Cren (1958). Backiel & Le Cren (1978) conclude that, in the absence of strong predation pressure, freshwater fish populations will often move towards the state of a dense, slow growing population. This effect is well-known in the pond culture of some species, notably tilapia (Pillay 1990). Hanson and Leggett (1985) have shown that intraspecific and interspecific competition is intense at natural densities in the littoral zone of Canadian lakes, leading to growth rates not significantly different from zero during 14 day experiments

Fish farmers of course have been aware of density-dependent growth for long, and have taken account of this in their culture practices. Scientific experiments on density-dependent growth in pond culture have been conducted by Walter (1934) on common carp (*C. carpio*) and tench (*Tinca tinca*) in Germany, and by Swingle & Smith (1942) on bluegill (*Lepomis macrochirus*) in the United States.

Biological mechanisms causing density-dependence in growth

Although density-dependent growth is well known, its mechanisms are poorly understood. In wild populations, density-dependence in growth is often attributed to competition for food (e.g. Beverton & Holt 1957). Increasing density obviously means that a smaller share of a limited food resource is available to each individual. Fish can partially compensate for this effect by diversifying their food base, i.e. feeding on items they would disregard under less competition (Contag 1931, Ivlev 1961).

The food resource itself will respond to increased grazing or predation pressure, usually with lower density and increased production. The response of the food resource is little understood, although Beverton & Holt (1957) have considered it theoretically in some detail, likening it to the exploitation of a fish population. Ball & Hayne (1952), Crowder & Cooper (1982) and Post & Cucin (1984) present empirical evidence that a decrease in fish density leads to an increase in invertebrate prey density in lakes. No such evidence was found by Hall *et al.* (1970) and Hanson & Leggett (1986), who also suggested that the results of Post & Cucin (1984) may reflect behavioral responses of food organisms rather than true changes in their population density

Competition for space might lead to density-dependent growth in some species. However, competition for space is primarily known from territorial species, where it appears to act on mortality rather than on growth (Le Cren 1973, Elliott 1985, 1993).

Other density effects are probably important at very high densities not normally attained in natural populations or extensive aquaculture. Shireman *et al.* (1977) have demonstrated that low oxygen availability due to high population density depresses the growth of grass carp (*C. idella*) even if fish are fed to satiation. Some cyprinids (*Carassius carassius* and *C. carpio*) are known to release a growth-suppressing pheromone ("crowding factor") when kept at high densities (Pfuderer & Francis 1972).

Several of these effects will usually interact to cause a density response in growth. If density changes by a moderate amount, the change in growth will be mainly quantitative, while large changes in density are likely to have a qualitative effect. different processes may become dominant in shaping the growth response. For example, a population originally limited by food supply may suffer from oxygen depletion at very high densities.

Before moving on to the mathematical modelling of density-dependent growth, a crucial question has to be asked: what density does density-dependence depend on? In other words, is a fish competing with all its conspecifics in the population, or with only some of them? The answer depends on the mechanism dominating the density-dependent response. In natural populations, competition for food is probably most important. In species which undergo major ontogenic changes in diet (e.g. predators), a population may consist of two or more sub-populations, with individuals competing within, but not between the sub-populations. In species not undergoing major ontogenic diet changes, all individuals (with the exception of early life-history stages) can be regarded as competitors.

Surprisingly little work has been done on the mathematical description of density-dependent growth since Beverton & Holt (1957) There is no standard way of modelling density-dependent growth. Two models are presented here: an empirical model, and a model based on the von Bertalanffy theory of growth. Both models use biomass density, i.e. biomass per unit area, as a measure of population density.

Walter's experiments

Walter (1934) conducted a large number of stocking experiments on both mixed age populations and single cohorts. The results of Walter's experiments are used in this study to test the models for density-dependent growth.

In one set of experiments, Walter stocked populations of one to four year old carp in unfertilized ponds and ponds fertilized with inorganic phosphate and liquid manure, at two different densities. Mean weights at stocking and harvesting were calculated for each age group of fish, from data given in Tab. 6 in Walter (1934).

In another set of experiments, Walter stocked single cohorts of one and two year old carp at various densities in ponds fertilized with inorganic phosphates. Numbers and mean weights at stocking and harvesting are given in Tabs. 34 and 35 in Walter (1934).

The experiments were conducted over periods of about six months, which represent the full annual growth period under German conditions.

2.1.1 An Empirical Model for Density-Dependent Growth

An empirical model is proposed here to describe the length increments ΔL of fish over short production periods Δt, as a function of the initial biomass density B_0. The model is given by

$$\Delta L_{\Delta t} = \alpha - \beta \ \ln(B_0) \tag{2.1}$$

where α is the length increment at unit biomass density, and β is a coefficient describing the response of length increment to initial biomass density.

The biomass density at which growth increments are zero is equal to the carrying capacity B_∞ of the water body and is given by:

$$B_\infty = e^{\frac{\alpha}{\beta}} \tag{2.2}$$

If only data on weight are available, the cubic root of weight can be used as a substitute for length, assuming that fish grow isometrically.

Application of the model to Walter's data

The empirical model is applied to Walter's single cohort stocking experiments. The cubic root of initial and final weight is used to calculate length increments (in units of $kg^{1/3}$).

In Fig. 2.1, length increments are plotted against the logarithm of initial biomass, resulting in a linear relationship. The parameter estimates of the regression line are α=7.16 $kg^{1/3}$ and β=-2.73 $kg^{1/3}$/ln(kg/ha), with a coefficient of determination r^2 of 0.93.

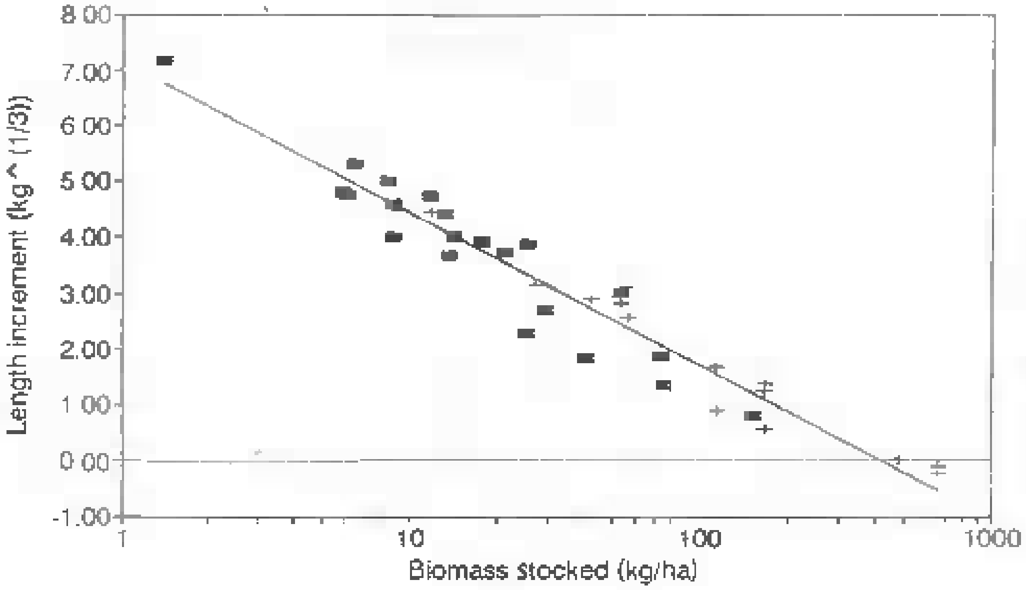

Fig. 2.1. Length increment of carp in Walter's experiments, plotted against the initial biomass stocked on a logarithmic scale. Carp in their first (■) and second (+) summer.

2.1.2 A Model Based on the von Bertalanffy Theory of Growth

Beverton & Holt (1957) have studied density-dependent growth within the framework of the von Bertalanffy growth function (VBGF), and proposed a model briefly summarized below.

The VBGF was deduced by von Bertalanffy on the basis of the action of anabolism and catabolism. In the form of the VBGF commonly used in fisheries,

$$\frac{dL}{dt} = -K(L - L_\infty) \qquad (2.3)$$

the parameter K is a measure of catabolic activity, while the infinite length L_∞ is related to anabolic activity. Catabolic activity, the breakdown of body materials, is assumed to be independent of food consumption. Anabolism, hence L_∞, is clearly dependent on food consumption. Competition for food is thus expected to influence L_∞, but not K. Therefore, in order to model density-dependent growth, L_∞ is expressed as a function of density.

Beverton & Holt assumed food supply to be the main limiting factor for fish growth. They considered the effects of fish grazing on the production of their prey populations, and concluded that given such a predator-prey system in an equilibrium situation, the infinite length L_∞ in the fish (predator) population will be a linear function of its density, over some, range of densities. Beverton & Holt point out that this conclusion is subject to certain constraints: It applies to an equilibrium situation only, and the linear relationship will break down if there are large changes in population structure. Beverton & Holt argue that density in numbers will yield a better relationship than biomass density

Formulation of the model

Beverton & Holt's density-dependent VBGF growth model can be generalized so that it can be applied to certain situations not considered by Beverton & Holt. The generalization is based on the propositions that (1) the linear relationship between L_∞ and density also holds for certain non-equilibrium situations, and (2) biomass density is an appropriate measure of density, even in non-equilibrium situations.

The density-dependent infinite length $L_{\infty B}$ can be defined as a function of instantaneous biomass B:

$$L_{\infty B}=L_{\infty L}-d\ B \qquad (2.4)$$

where $L_{\infty L}$ is the limiting infinite length, which fish would approach in the absence of competition. The coefficient d is the slope of the linear relationship between infinite length and biomass density. The equivalent expression for infinite weight $W_{\infty B}$ as a function of biomass is:

$$W_{\infty B}=(W_{\infty L}^{1/3}-c\ B)^3 \qquad (2.5)$$

The coefficient c of the weight equation is related to d by

$$c=d\ a^{1/3} \qquad (2.6)$$

where a is the coefficient of the isometric length-weight relationship:

$$W=a\ L^3 \qquad (2.7)$$

Introduction of these terms into the differential form of the VBGF results in the following models, which give the instantaneous rates of length and weight growth of fish as a function of individual size and population biomass density B_t for length:

$$\frac{dL_t}{dt}=-K(L_t-L_{\infty L}+d\ B_t) \qquad (2.8)$$

and for weight:

$$\frac{dW_t}{dt}=-3\ K\ W_t\left(1-\frac{W_{\infty L}^{1/3}-c\ B_t}{W_t^{1/3}}\right) \qquad (2.9)$$

The parameters $L_{\infty L}$ and $W_{\infty L}$ are dependent on the productivity of the water body, they have no physiological significance outside the particular environment in which they were measured. A somewhat paradoxical situation arises if the model is applied to a single fish: since the biomass density of a population consisting of one fish is still greater than zero, that single fish cannot reach the infinite limiting size unless the coefficients c and d are zero. One possible way of solving this problem would be to define B_t as the biomass of competitors of the individual whose growth is being modelled, so that B_t equals zero for a single fish. However, the predicted growth would then depend on the unit area on which the biomass density is defined, because removing one fish makes a much bigger difference if the unit area is small than if it is large. Hence this would effectively introduce another parameter into the growth model. Fortunately, the whole problem is of little practical significance, and needs not to be considered further.

Another problem occurs when some fish are greater than $W_{\infty B}$ or $L_{\infty B}$. According to the model, such individuals would shrink in length and weight. While fish can loose weight, they are unlikely to shrink in length. Hence weight loss occurs as a loss of condition, and represents a strong departure from isometric growth. The VBGF model is based on the assumption of isometric growth, and can not represent changes in condition adequately.

The growth model as formulated above can be used in two situations: One is in the case considered by Beverton & Holt of a population near equilibrium, when the population structure is approximately stable. The other case is that of a single cohort, i.e. when all fish are of approximately the same size.

In the near-equilibrium situation in a multi-cohort population, biomass is constant and the growth of fish is described by the standard integrated form of the VBGF, with the infinite length $L_{\infty B}$ weight $W_{\infty B}$.

A single cohort is about as far away from the equilibrium situation as can be. Consider small fish stocked into a pond or a lake at moderate density. At first, there is little competition and growth is fast. Biomass increases rapidly and competition gains in intensity, so that $L_{\infty B}$ and $W_{\infty B}$ decrease quickly with increasing individual size in the cohort. Hence the growth of a single cohort can not be described by the standard integrated version of the VBGF, which assumes a constant infinite length or weight. The biomass density of a cohort is simply its density in numbers N_t times the mean weight of individuals W_t, hence the weight growth rate is given by:

$$\frac{dW_t}{dt} = -3\ K\ W_t \left(1 - \frac{W_{\infty L}^{1/3} - c\ N_t\ W_t}{W_t^{1/3}}\right) \qquad (2.10)$$

Unfortunately, this Equation can not be integrated explicitly to give weight as a function of time. It can only be solved numerically (see Appendix B). The equivalent expression to (2.10) for length growth is derived in a similar way, by substituting N_tW_t for B_t in Equation (2.8).

The infinite weight $W_{\infty N}$ that is approached by individuals in a cohort of density N is obtained by setting Equation (2.10) to zero:

$$W_{\infty N}^{1/3} + c\ N\ W_{\infty N} = W_{\infty L}^{1/3} \qquad (2.11)$$

This equation has several solutions, which can be calculated from rather awkward formulae However, there is only one solution for which $0 < W_{\infty N} < W_{\infty L}$, which is best determined numerically.

Limits to the applicability of the VBGF model

Under which conditions can the model be expected to provide a good description of field and experimental data? The central consideration here is that of the food populations preyed upon by the fish population. Fish of different size will often have preferences for different food organisms. This is particularly pronounced in gape-limited predators, while overlap is likely to be larger for omnivorous bottom feeders, and still larger for plankton feeders. When there is little overlap, competition for food at a given biomass of fish is much smaller if the population comprises fish of various sizes, than if all fish are of a similar size and rely on the same food resource. Hence the competition coefficient c will be different between population structures. If overlap is large, competition at a given biomass is almost independent of population structure, and a single value of c might apply to virtually all population structures. The growth of a single cohort can be described by the model if either food preference does not change with size, or the various food populations utilized during the growth period are of roughly similar productivity.

However, the mechanistic foundation of the model given by Beverton & Holt (1957) should not be overstressed. The main criterion for the applicability of the model to a particular population is whether it provides an adequate description of the available data

Fitting the model

Fitting the model involves the numerical solution of the growth equation (Equation 2.8 or 2.9), and estimation of parameters of the non-linear model (Appendix B). The technique employed here is as follows: Mortality is assumed to be an exponential process independent of size, and mortality rates are calculated for each experiment from the numbers of fish stocked and harvested. The weight of fish at stocking is taken as the independent variable, and the weight at harvesting is predicted using the growth equation and exponential mortality. The parameters of the growth function are estimated as the combination which minimizes the difference between predicted and observed weight at harvesting. The objective function is the sum of squared differences of the log transformed predicted and observed weight. The logarithmic transformation is applied in order to ensure homogeneity of variance. The goodness of fit is assessed on the basis of residual plots, as only aggregated data (mean weight) are available for most experiments.

In this fitting procedure, the weights at stocking are taken as independent variables and are assumed to be known without error. This may give rise to some bias in the parameter estimates. A simple way of assessing the magnitude of this bias is to run the estimation "backwards", i.e. to take the weight at harvesting as the independent variable, and the stocking weight as the dependent variable. The bias in the parameter estimates is smaller than the difference between the "forward" and the "backward" estimates

Results: Walter's experiments

The model for density-dependent growth is based on the von Bertalanffy growth function, hence a condition for its applicability to a mixed age population near equilibrium is that the growth of fish can be described by a standard VBGF. A simple, visual test for this criterion is provided by the Ford-Walford plot (Ricker 1973). For each population, a plot of the cubic root of final weight against the cubic root of initial weight for all age groups is expected to give a straight line, if growth follows a VBGF. Fig. 2.2 shows such plots for the fertilized and unfertilized ponds. The data for high and low stocking density are given in the same graphs. Lines were fitted by eye, subject to the constraint that their slopes (i.e. the value of K) should be the same for both stocking densities. Infinite weight W_∞, the intercept of the fitted line and the line of slope 1, is higher at low density in both fertilized and unfertilized ponds. In the unfertilized pond at high density, the four year old carp are larger than W_∞ and consequently suffer a loss of weight, while younger carp show positive growth. On the whole the data are well described by a VBGF, but there are some systematic departures, which will be referred to as "outliers" in the following paragraphs. The growth of three year old carp is always exceptionally high. Negative weight growth is incompatible with the isometric growth assumption of the VBGF, hence the four year old carp in the high density, unfertilized pond should be excluded from the analysis for principal reasons.

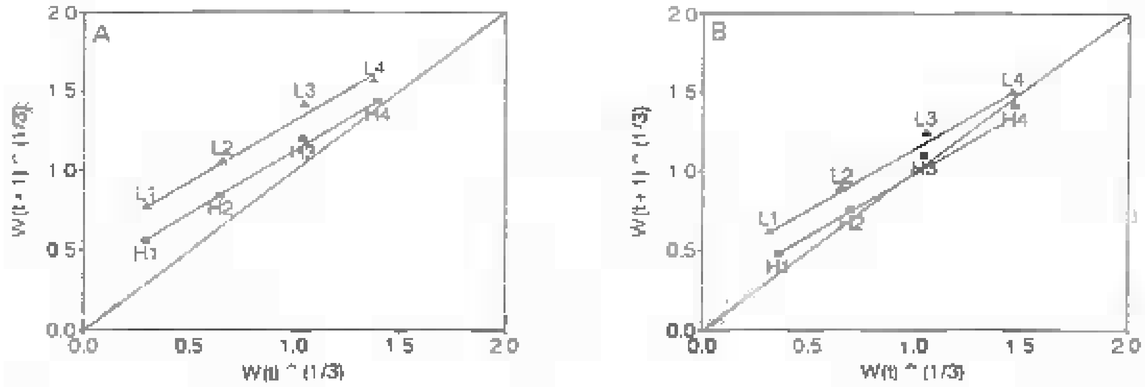

Fig. 2.2. Ford-Walford plots of Walter's mixed age stocking experiments. The cubic root of final mean weight is plotted against the cubic root of initial mean weight for each age group. (A) Fertilized ponds. (B) Unfertilized ponds. Labels denote high or low stocking density (H, L) and the age group of carp (1 to 4 summers).

Using the technique outlined above, the model was fitted to data from Walter's mixed age and single cohort experiments. The time interval between stocking and harvesting was assumed to be one year, thereby averaging out seasonality in growth. The setting of the time interval only affects the estimate of K. If a half year interval (the true duration of the experiments) was assumed, K would be twice the annual value, and would describe growth during the summer period only.

Parameter values estimated form the data both including and excluding "outliers" (see below) are given in Tab. 2.1. All parameter values are different between the experiments, partly because the VBGF parameters are highly correlated, i.e. various combinations of the parameters K and W_∞ fit the data about equally well. This problem can be overcome by fixing the one parameter that is not expected to vary between experiments at some sensible value, so that variations in the other parameters can be interpreted. $W_{\infty L}$ is related to the productivity of the water body, and c is dependent on the population structure, hence only K is expected to be the same in all experiments. Estimates of K vary between 0.19 and 0.27 y^{-1} (Tab. 2.1), and K is fixed at 0.25 y^{-1}.

Tab. 2.1 Parameters of the density-dependent VBGF growth model, estimated from Walter's experiments. All three parameters estimated.

	Full data set			"Outliers" excluded		
	K (y^{-1})	$W_{\infty L}$ (kg)	c (ha $kg^{-2/3}$)	K (y^{-1})	$W_{\infty L}$ (kg)	c (ha $kg^{-2/3}$)
Fertilized	0.23	44.10	0.0068	0.23	43.47	0.0069
Unfertilized	0.19	22.92	0.0073	0.26	12.40	0.0063
Cohort	0.22	31.49	0.0083	0.27	23.60	0.0096

The estimation procedure is repeated with fixed K, and the new parameter estimates are given in Tab. 2.2. Residual plots are shown in Fig. 2.3 for the mixed age experiments and in Fig. 2.4 for the cohort experiments.

Tab. 2.2. Parameters of the density-dependent VBGF growth model, estimated from Walter`s experiments. The value of K is fixed at 0.25.

	Full data set			"Outliers" excluded		
	K (y^{-1})	$W_{\infty L}$ (kg)	c (ha $kg^{2/3}$)	K (y^{-1})	$W_{\infty L}$ (kg)	c (ha $kg^{-2/3}$)
Forward fit						
Fertilized	0.25	35.7	0.0063	0.25	36.1	0.0065
Unfertilized	0.25	12.8	0.0059	0.25	12.9	0.0064
Cohort	0.25	24.8	0.0075	0.25	28.5	0.0095
Backward fit						
Fertilized	0.25	34.3	0.0058	0.25	34.2	0.0058
Unfertilized	0.25	11.4	0.0049	0.25	11.3	0.0049

In the mixed age experiments (Fig. 2.3), the data points identified as potential "outliers" on the basis of the Ford-Walford plots do indeed account for the largest residuals of the density-dependent model. Hence these residuals reflect a problem of the basic VBGF, rather than its density-dependent extension. If the outliers are excluded, residuals still show a systematic pattern in both the fertilized and unfertilized ponds. However, the residuals are so small that this pattern can be ignored here. The exclusion of "outliers" from the mixed age experiments has a negligible effect on parameter estimates (Tab. 2.2), hence there is no need to examine the "outliers" further.

In Fig. 2.4, residuals for the cohort experiments are plotted against the biomass stocked, and against the predicted weight. It can be seen that the residuals are small and apparently random over a wide range of biomass. Experiments at the extremes of biomass are not described well by the model (i.e. they are "outliers" in this sense) and should be excluded from parameter estimation. If these extremes are excluded, the model provides a very good fit to the experimental data over the remaining range of densities. Exclusion of extreme densities in the cohort experiments does change the parameter estimates. All further analysis of the results is conducted on the estimates obtained when outliers are excluded.

"Backward fit" estimates have been obtained for mixed age experiments only. In the cohort experiments, weight at stocking is often very low, and weight at harvesting shows high stochastic variation. Hence the prediction of weight at stocking from weight at harvesting frequently resulted in negative values.

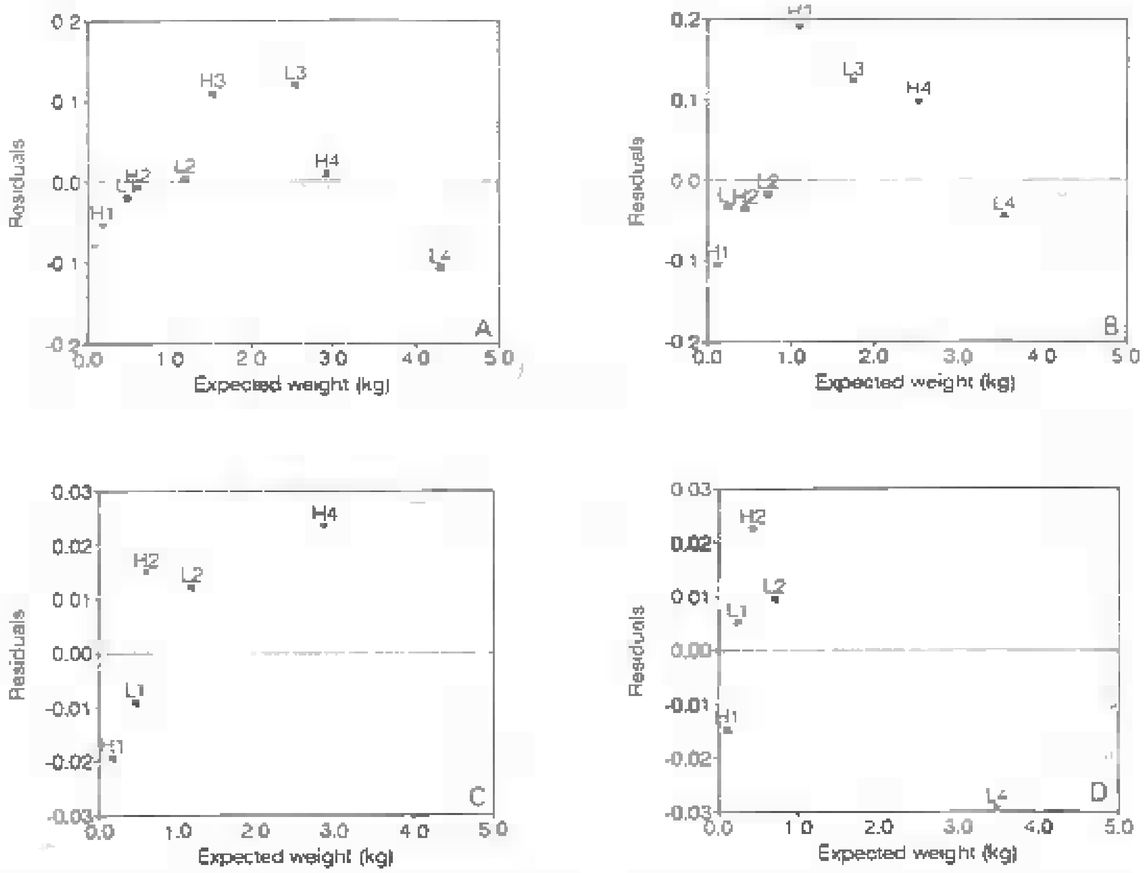

Fig. 2.3. Residuals (Log observed minus log expected weight) of the VBGF growth model fitted to Walter's mixed age data. Using the complete data for (A) fertilized ponds, and (B) unfertilized ponds. After removal of "outliers" (see text) for (C) fertilized ponds and (D) unfertilized ponds. Labels denote high or low stocking density (H, L) and the age group of carp (1 to 4 summers).

"Backward fit" estimates of $W_{\infty L}$ and c for the mixed age experiments are consistently lower than the "forward fit" estimates. The difference is below 10% in all parameters for the fertilized ponds, but 22% in c for the unfertilized ponds. The true values of the parameters are likely to lie in between the two estimates, and closer to the "forward fit" estimates. Hence the "forward fit" estimates are probably biased moderately upwards, by not more than 10%

The estimated value of $W_{\infty L}$ is highest for the fertilized ponds and lowest for the unfertilized ponds used in the mixed age stocking experiments, while value of $W_{\infty L}$ for the single cohort experiments is in between the two. $W_{\infty L}$ reflects the productivity of the ponds, and the estimated values are in good agreement with the fertilizer input received by the ponds (phosphate and manure, phosphate only, and no fertilizer at all).

The competition coefficient c is very similar for the mixed age stocking experiments, the difference in c between fertilized and unfertilized ponds being below 7%. In contrast, the competition coefficient for the single cohort experiments is about 50% higher than that for mixed age stocks.

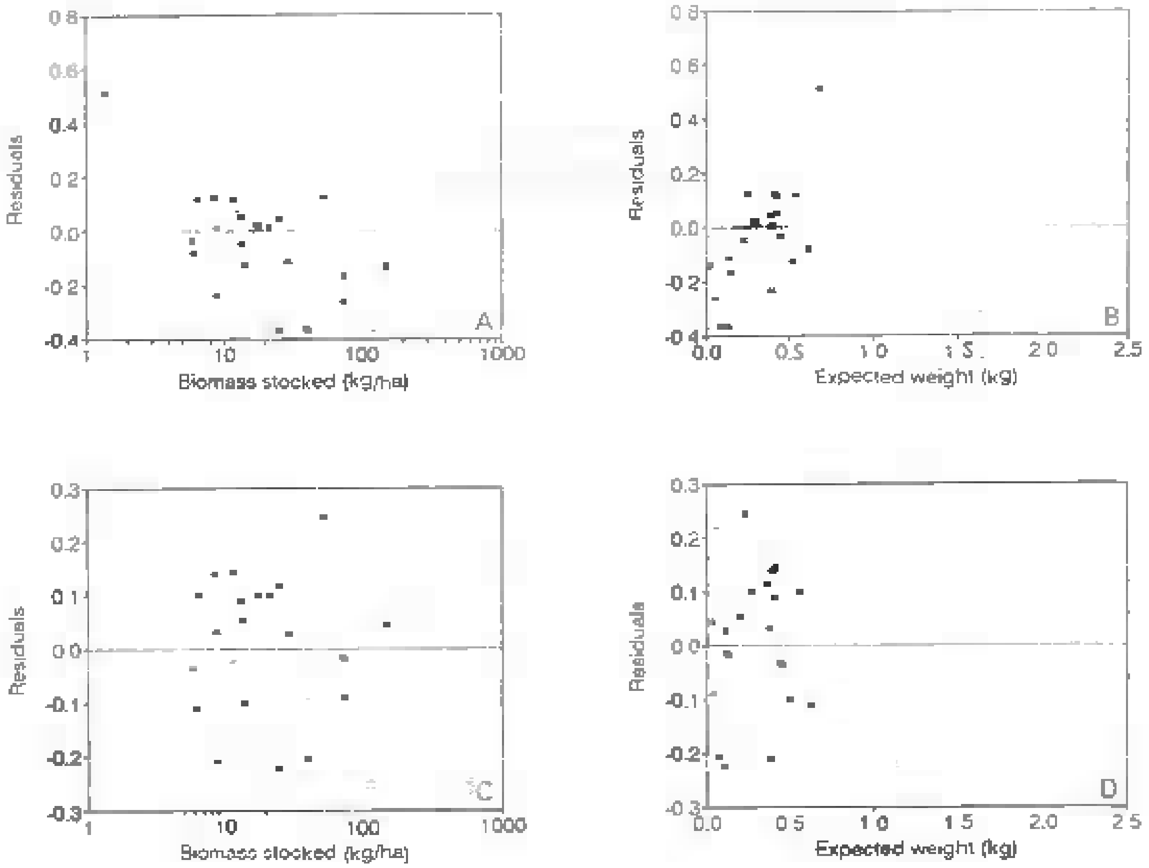

Fig. 2.4. Residuals (Log observed minus log expected weight) of the VBGF growth model fitted to Walter's single cohort stocking data Using the complete data, and plotted against (A) biomass stocked and (B) expected weight. After removal of the experiments at extreme densities, plotted against (C) biomass stocked and (D) expected weight. Carp in their first (■) and second (□) summer

Further exploration of the growth model

In the preceding Sections, it has been shown that the proposed model can give a good representation of some experimental data on density-dependent growth in carp. Here, the model and some of its consequences are examined in more detail, with particular reference to a single cohort The parameter values estimated from the single cohort carp populations in Walter's experiments are used as an example.

The growth response to stocking density in single cohorts is illustrated in Fig. 2.5, which shows the predicted individual weight growth in a single cohort of carp as a function of stocking density, for no mortality. All fish are stocked at time 0, at an individual weight of 0.05 kg. Individual weights after 6, 12 and 24 months are shown, together with $W_{\infty N}$. Both density and weight are displayed on logarithmic scales, a procedure common in plant yield-density studies (Kira *et al.* 1953, Harper 1977). At very low density, growth is primarily limited by the physiological growth potential of the fish, and almost independent of density. At higher densities, weight at age decreases rapidly with increasing density. All weight at age curves in the log-log plot approach a straight line of slope -1 at very high density. This means that under strong competition, individual weight is inversely proportional to cohort density, and total biomass is constant. Fig. 2.5 (B) supports this model prediction:

it shows that the weight reached by C1 at the end of the growth period approaches the -1 line at high density, but departs from it at densities below 1000 fish/ha.

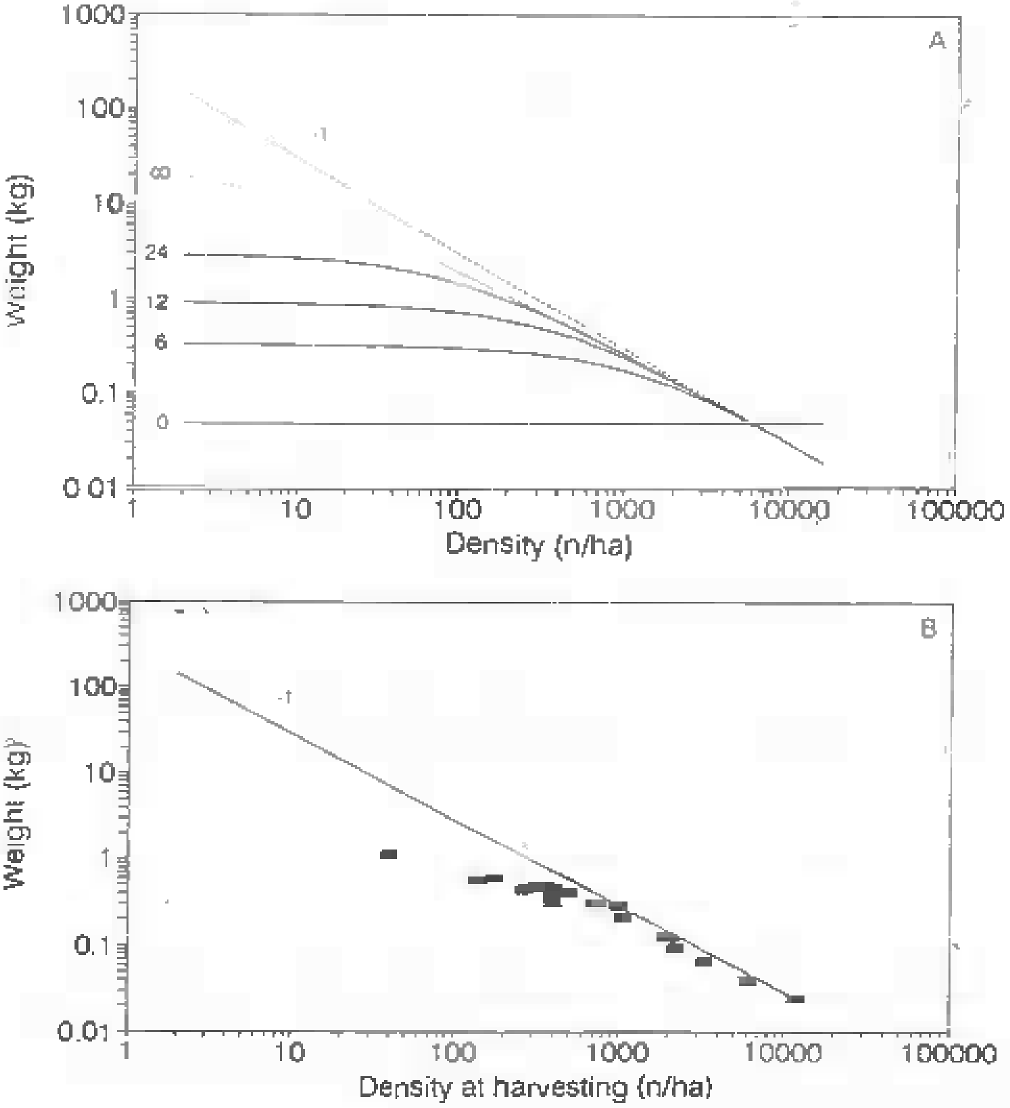

Fig. 2 5. (A) Predicted weight of carp, after 6, 12, and 24 months, and W_∞ as a function of stocking density Initial weight at time 0 is 0.05 kg. No mortality. Note logarithmic scaling on both axes. A straight line of slope -1 denotes constant final biomass. Parameter values: $K=0.25\ y^{-1}$, $W_{\infty L}=28.5$ kg, $c=0.0095$ ha kg$^{-2/3}$. (B) Weight at harvesting of one year old carp in Walter's experiments, plotted against the density at harvesting The axes are the same as in (A).

Growth trajectories (weight at time after stocking) are shown in Fig. 2.6 for cohorts of various densities. As mentioned earlier, under the density-dependent growth model proposed, growth of single cohorts does not follow a standard VBGF pattern. However, cohort growth trajectories can be approximated by a standard VBGF. If a standard VBGF is used to approximate the growth of a single cohort, W_∞ equals the $W_{\infty N}$ derived from the density-dependent model, which decreases with increasing density. The higher the initial stocking density (hence biomass), the less time it will take the fish to reach their final weight. Thus, K will increase with increasing density. This is shown in Fig. 2.6: at the highest density (1024 fish/ha), fish reach their final weight in less than a year, while at lower densities they still grow at the end of their second year.

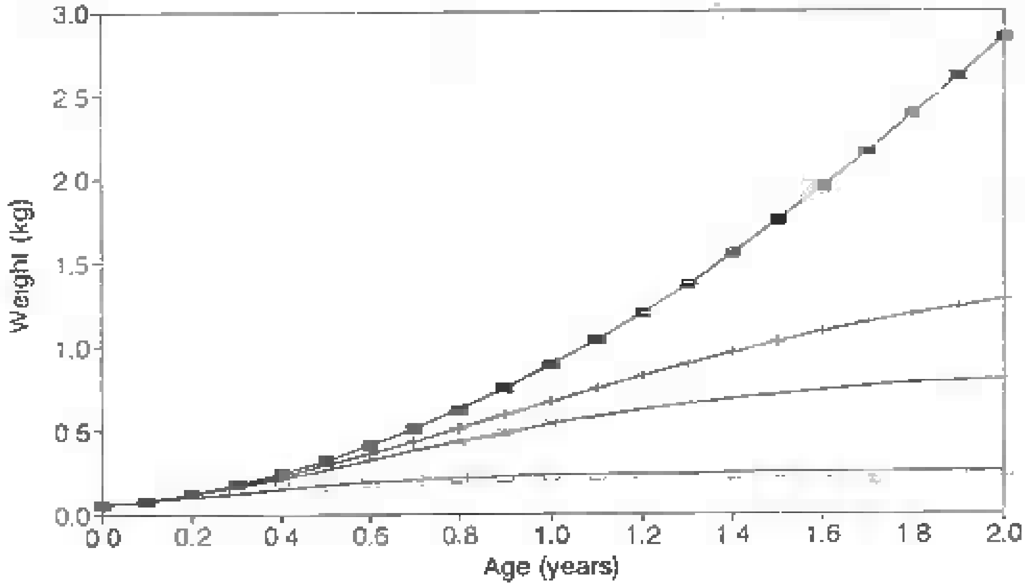

Fig. 2.6 Growth trajectories (weight at time after stocking) for single cohorts of carp at various stocking densities. Initial weight 0.05 kg. No mortality. Densities are 2 (■), 128 (+), 256 (*) and 1024 (□) fish per hectare. Parameter values: $K=0.25\ y^{-1}$, $W_{\infty L}=28.5$ kg, $c=0.0095$ ha $kg^{-2/3}$.

Various indices have been developed for the comparison of fish growth performance between species and between culture systems (Pauly 1981, 1985, Moreau *et al.* 1986, Pauly *et al.* 1988). These indices are based on the standard VBGF parameters estimated from experimental data, and do not take account of stocking density explicitly (although density is an implicit trait of the particular culture system).

To explore the effect of stocking density in single cohort culture, a standard VBGF is fitted to simulated growth trajectories for various densities, including those depicted in Fig. 2.6. W_∞ is calculated as $W_{\infty N}$ from Equation (2.11), and corresponding values of K are calculated for each 0.1 year time-step over the first two years after stocking. As growth does not strictly follow a VBGF pattern, estimated K values increase with time after stocking (i.e. increasing competition) and the arithmetic mean of the values is used in the assessment of growth performance.

The estimated VBGF growth parameters for a range of densities are plotted in the auximetric grid in Fig. 2.7. The auximetric grid (a plot of K against W_∞ on logarithmic scales) was introduced by Pauly (1979) for the comparison of growth performance between fish populations that differ in both VBGF parameters. In the auximetric grid, lines of slope -

1 are isolines of growth performance (i.e. all fish on one such line have the same growth performance). Each line corresponds to a particular value of the index P of growth performance:

$$P=\log_{10}(W_\infty K) \qquad (2.12)$$

The index P is related to the maximum growth rate the fish of a certain population attain during their life, at the inflection point of the weight growth curve (Pauly 1979).

Fig 2.7 shows a clear progression towards lower W_∞ and higher K with increasing density. The growth performance P decreases from 3.8 to 2.7 when stocking density is increased by three orders of magnitude.

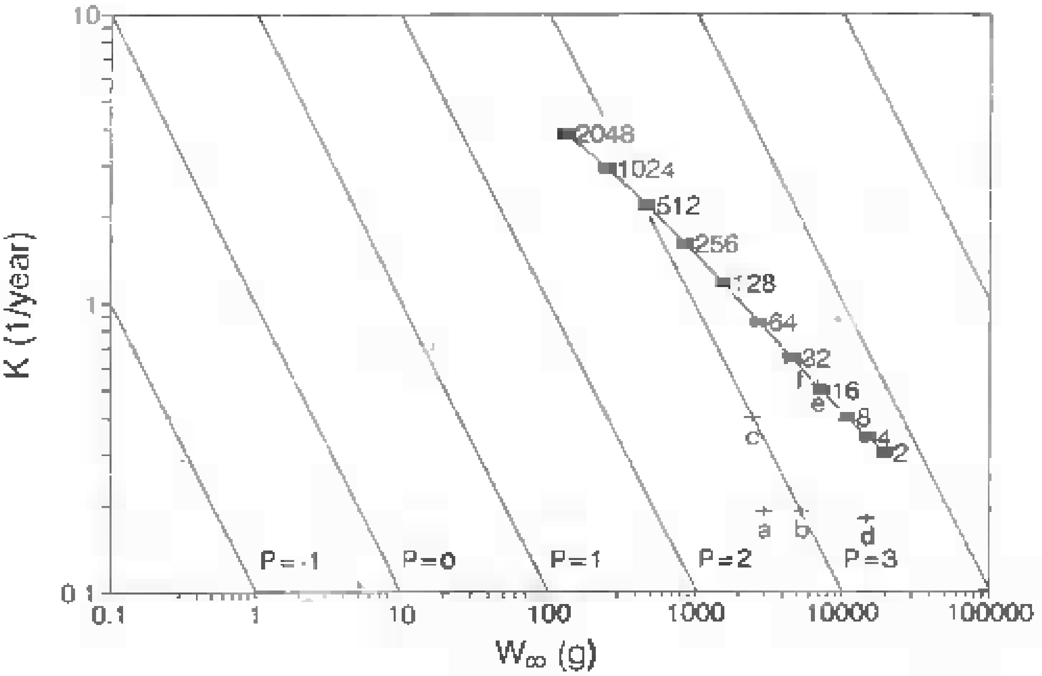

Fig. 2.7. Position of carp in the auximetric grid. (●) Predictions of the growth model for single cohorts at various stocking densities. Labels indicate stocking density. Parameter values: $K=0.25\ y^{-1}$, $W_{\infty L}=28.5$ kg, $c=0.0095$ ha $kg^{-2/3}$. (+) Wild populations of common carp. (a) Camargue, (b) Lake Aral (c) natural and (b) stocked populations in the Neusiedlersee, (e) females and (f) males in Clear Lake, Ohio. Growth parameters from Tab. 2.3.

For comparison, VBGF growth parameters have been estimated from published data for some carp populations in temperate waters (Tab. 2.3).

Tab. 2.3. VBGF growth parameters for some populations of common carp in temperate waters.

Population	K (y^{-1})	W_∞ (kg)	Source of data
Camargue	0.19	3.00	Crivelli 1981
Lake Aral	0.19	5.27	Nikolskii 1940
Neusiedlersee			
natural	0.40	2.48	Unterüberbacher 1963
stocked	0.18	14.82	
Clear Lake			
females	0.52	6.98	English 1952
males	0.63	5.21	

The growth parameters of these populations are also shown in Fig. 2.7. The growth performance of these populations is within the range of values predicted by the model for extensive pond culture under various densities.

2.1.3. Discussion

The empirical model

Various workers concerned with the analysis of pond stocking experiments or the growth of juvenile fish have found that observed weight increments decrease linearly with increasing logarithm of population density in numbers (Le Cren 1958, Johnson 1961, Brocksen *et al.* 1970, Backiel & Le Cren 1978). The empirical model presented in Section (2.1.1) is both a modification and a generalization of this relationship. Length increment is substituted for weight increment, and initial biomass density is used instead of density in numbers. The advantage of using biomass density is that a single model can be used for fish of various sizes at stocking.

The empirical model provides an excellent description of the growth of both one and two year old carp in Walter's single cohort experiments. This indicates the value of biomass as a predictor of growth.

The empirical model implicitly makes a number of unrealistic assumptions, which limit its applicability. First, all fish are assumed to grow by the same length increment at a given density, no matter how large they are at the time of stocking. Second, decreasing density always leads to increasing growth increments, there is no physiological or environmental limit to fish growth. Third, all fish (independent of their size) cease to grow at the same biomass density B_∞ of the population. This is at odds with the von Bertalanffy theory of growth, where the growth rate approaches zero only for fish that are close to the infinite maximum size, while smaller fish continue to grow. Walter's mixed age stocking experiments in unfertilized ponds clearly demonstrate that small fish in a population can still grow, even if large fish in the same population loose weight due to food limitation (Fig. 2.2). This result lends support to the von Bertalanffy theory of growth, and pinpoints the limitations of the empirical model.

The VBGF-based model

The VBGF-based model for density-dependent growth provides an extremely good description of Walter's carp growth experiments over a wide range of densities. Only a part of this range is of practical interest in culture-based fisheries.

The "forward fit" estimates of the parameters are likely to have a smaller bias than the "backward fit" estimates, because the stocking weight is usually known with a smaller error than the harvesting weight. Hence the bias of the "forward" estimates is probably smaller than half of the difference between the "forward" and "backward" estimates. Moreover, the main purpose of the model is the prediction of harvesting weight from stocking weight, and Krutchkoff (1967) has argued that for this purpose, its parameters should be estimated in the same way (i.e. taking stocking weight as the independent variable and harvesting weight as the dependent variable). This matter is, however, still controversial (Lwin & Maritz 1982).

The estimated value of the VBGF parameter K is in good agreement with estimates from wild populations of common carp in temperate areas (Tab. 2.3). This is reassuring of the model. It also suggests the possibility that K values estimated from natural populations can be used in the density-dependent model, thus reducing the number of parameters to be estimated for a particular fishery to two.

The competition coefficients estimated from the mixed age experiments are very similar, despite a large difference in the productivity of the ponds. If this was generally the case, such competition coefficients for particular species and population structures could be established in experiments, and then used to model the growth of similar populations in other water bodies.

The competition coefficient for single cohorts is much higher than that for the mixed age populations. This is in agreement with expectations: For a given biomass, competition is more intense if this biomass is made up of fish of roughly the same size, than if it is made up of fish of different sizes, exploiting a wider range of food organisms The model gives a very good description of density-dependent growth for each population structure separately. However, it cannot accurately predict the growth response under changing population structure.

The growth model as proposed here does not account explicitly for seasonality in growth A seasonal term could be introduced into the model, but this would also mean the introduction of at least one additional parameter. Hence the non-seasonal model as presented here is the best choice in all situations where there is no need to consider seasonality explicitly. If the growth period is predefined and constant, the seasonal effect on growth is always the same, and it does not affect the model predictions. This is the case in Walter's growth experiments.

The density-dependent VBGF model predicts that single cohorts in extensive culture (without feeding) do not strictly follow a standard VBGF pattern of growth. Nevertheless, their growth trajectories can well be approximated by a VBGF, the parameters of which are dependent on the stocking density. The higher the density, the lower W_∞, and the higher K. Prein (1990) has noted that tilapia in extensive culture grow to a small W_∞ at a high K, while intensively grown tilapia grow to a higher W_∞ at a lower K. This observation is in perfect agreement with the predictions of the density-dependent VBGF. In intensive culture, fish are fed according to their requirements, and growth is limited by physiological constraints rather than competition for food.

Growth performance in extensive culture is dependent on stocking density. This should be borne in mind if the index P of growth performance is used to compare culture systems or species.

The growth performance of carp in temperate waters is generally similar to or slightly higher than that of tilapia in the tropics (Pauly *et al.* 1988).

2.2 SIZE AND DENSITY EFFECTS ON MORTALITY

The relationship between size and mortality of fish is of particular interest in a culture-based fishery, because it pertains directly to the optimal size of seed fish. Moreover, size-dependent mortality and density-dependent growth interact to cause competition-mediated density-dependent mortality. Competition-mediated density-dependent mortality does not involve a change in mortality with population density for any given size group. Conversely, "predation-mediated" density-dependent mortality occurs when the mortality rate for a given size of fish changes with population density.

2.2.1 Size-Dependent Mortality

There is strong evidence for size-dependent mortality on the level of fish populations (Pearcy 1962, Ware 1975, Craig 1982, Werner 1986), as well as communities and whole ecosystems (Peterson & Wroblewski 1984, McGurk 1986). In culture-based fisheries, the principal interest is in the mortality-size relationship within populations.

Biological basis of size-dependent mortality

Size-dependence in mortality of fish is primarily attributed to predation (Craig 1982, Peterson & Wroblewski 1984, Werner 1986, McGurk 1986). Peterson & Wroblewski (1984) use the theory of biomass size spectra and predation to deduct a theoretical relationship between predation mortality and size.

Parasitism is also potentially an important source of size-dependent mortality. Fish culture research has shown that young fish are particularly vulnerable to many viral, bacterial and protozoan infections (Sinderman 1986). There is, however, little information on mortalities caused by such infections in the natural environment.

Young, small fish are more specific in their food requirements than larger ones, and at the same time they are less able to withstand periods of starvation (Wootton 1990). Hence a shortage of adequate food may also give rise to size-dependent mortality.

The model

Peterson & Wroblewski (1984) have argued on theoretical grounds that mortality can be described as a power function of weight. They also presented some empirical evidence for such relationship, as did McGurk (1986, 1987). Therefore, the following model is proposed to describe mortality as a function of weight:

$$M_W = M_r \left(\frac{W}{W_r} \right)^{-\varrho} \qquad (2.13)$$

Here M_W is the mortality rate at weight W, W_r is a reference weight at which fish are subject to mortality M_r, and the negative exponent ϱ describes the change of mortality rate with weight. This model is a slight modification of the one proposed by Gulland (1987) The corresponding model for length is

$$M_L = M_r \left(\frac{L}{L_r} \right)^{-3\varrho} \qquad (2.14)$$

where M_L is the mortality rate at length L, L_r is the reference length, and M_r is the mortality rate at reference length The exponent -3ϱ is based on the assumption of isometric growth.

If the instantaneous mortality rate is a function of weight as defined by Equation (2.13), then the mean mortality rate $M_{1,2}$ suffered by a cohort during the time period $[t_1, t_2]$

is given by

$$M_{1,2} = M_r W_r^{\varrho} \int_{t_1}^{t_2} W_t^{-\varrho} = -\ln (N_2/N_1) \qquad (2.15)$$

where N_1 and N_2 are the numbers in the cohort at times t_1 and t_2, respectively.

Estimation of the parameter ϱ

If estimates of the instantaneous mortality rate at size are available, the parameter ϱ can be determined by linear regression of log mortality against log weight (or length). Estimates of instantaneous mortality rates can be obtained by following the decline in population numbers over a very short time span, so that the influence of growth is negligible. This approach requires a high sampling effort, and few such data sets exist.

Mean mortality rates over a longer period are more readily available, together with weights at the beginning and at the end of the period. The mean mortality rate during a time period $[t_1, t_2]$ is the integral of the instantaneous mortality rates over the period (Equation 2.15), i.e. it depends on the growth pattern as well as on the mortality-size relationship hence the estimation of ϱ from mean mortality rates requires information on the growth pattern during the period over which the mean mortality $M_{1,2}$ was measured. In the absence of such information, an approximate estimate of ϱ can be obtained by linear regression of the log of mean mortality against the log of weight at mean length:

$$\ln(M_{1,2}) = \ln(M_r) - \varrho \ln(W^*_{1,2}) \qquad (2.16)$$

where $W^*_{1,2}$ is the weight at mean length during the period $[t_1, t_2]$:

$$W^*_{1,2} = \left(\frac{W_1^{1/3} + W_2^{1/3}}{2}\right)^3 \qquad (2.17)$$

If length data are available, mean length can be used directly to estimate 3ϱ

A simulation study summarized in Appendix C indicates that estimates of ϱ obtained from this regression are insensitive to the growth pattern, and are likely to have a slight downward bias of less than 10%.

The use of mean weight or initial weight instead of weight at mean length in the regression can lead to grossly inaccurate estimates of ϱ.

Testing the model

Logan (1985) has compiled data on mortality in relation to mean length of juvenile striped bass (*Morone saxatilis*) in the Hudson River, from Saila & Lorda (1977) and Dey (1981). Predictive linear regression was used to estimate the value of ϱ from this data set. Fig. 2.8 shows mortality as a function of length, together with the fitted regression line of slope -1.68 (corresponding to ϱ =0.56).

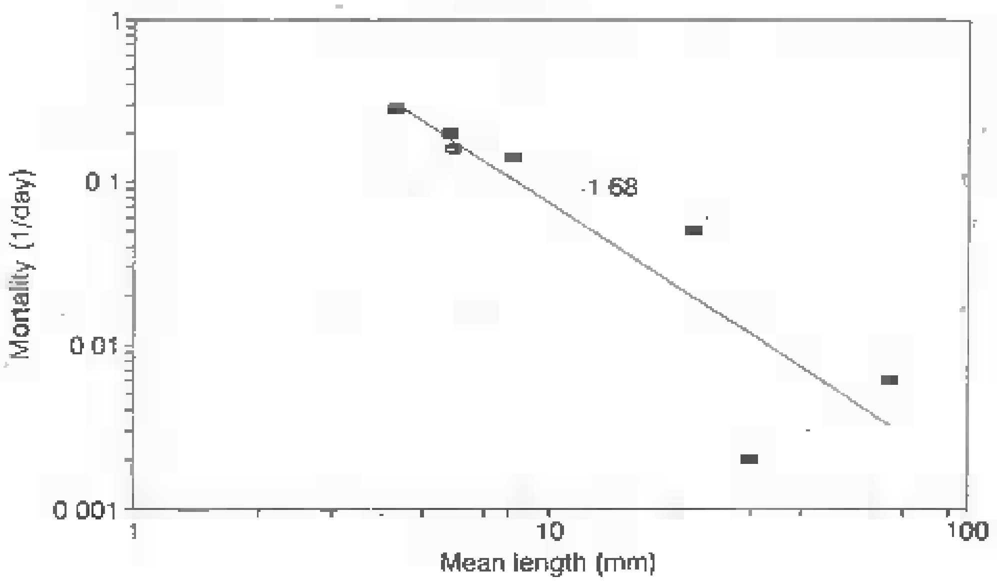

Fig. 2.8 Mortality rate at mean length for striped bass (*Morone saxatilis*) in the Hudson River. The slope of the fitted regression line is -1.68, corresponding to ϱ =0.56. (Data from Saila & Lorda 1977 and Dey 1981, compiled by Logan 1985).

Several textbooks of fish culture (Schäperclaus 1949, Huet 1973, Bohl 1982, Horvath *et al.* 1984) provide figures for expected losses in the pond culture of cyprinids of various sizes, based on extensive experience. Mean mortality rates and weight at mean length were calculated from the loss and weight figures given in the textbooks. The values of ϱ estimated from these data using predictive linear regression are given in Tab. 2.5. The estimates of ϱ lie between 0.36 and 0.98. In Fig. 2.9, mean mortality in the pond culture of common carp is shown as a function of weight at mean length.

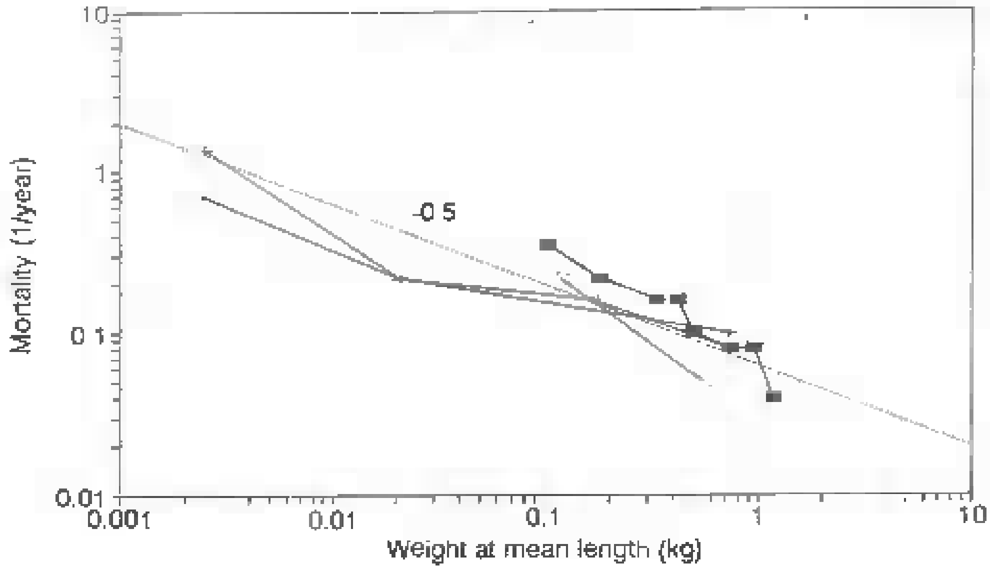

Fig. 2.9. Mortality rates in the pond culture of common carp, in relation to weight at mean length during the growth period. The straight line indicates a slope of -0.5 (ϱ=0.5). Mortality rates have been calculated from information on expected losses given in (*) Bohl (1982), (■) Horvath *et al.* (1984), (+) Huet (1973), and (□) Schäperclaus (1949)

Table 2.5: Estimates of the exponent ϱ of the mortality-weight relationship for striped bass (*Morone saxatilis*) in the Hudson River, and various carp species in pond culture.

Species	Environment	ϱ	Source of data
Morone saxatilis	Hudson River, USA	0.56	Logan 1985
C. carpio	Fishpond, Europe	0.36	Bohl 1982
"	"	0.44	Huet 1973
"	"	0.96	Schäperclaus 1949
"	"	0.79	Horvath *et al.* 1984
C. idella	"	0.82	Horvath *et al.* 1984
H. molitrix	"	0.90	Horvath *et al.* 1984
A. nobilis	"	0.98	Horvath *et al.* 1984

Further exploration of the mortality model

To illustrate the effects of size-dependent mortality, let us consider a cohort of fish, growing according to a standard VBGF with parameters $W_\infty = 1.0$ kg and $K = 0.5\ y^{-1}$. At the beginning, the cohort consists of 1000 fish, each weighting 0.05 kg. After two years, 500 fish have died. How did population numbers develop during these two years, given different degrees of size-dependence in mortality? Fig. 2.10 shows the development of the cohort for values of the exponent ϱ ranging from 0 to 0.75. As expected, the logarithm of numbers over time follows a straight line if $\varrho = 0$, i.e. mortality is independent of size. The slope of this line equals the constant mortality rate, which is also the mean rate of mortality for any value of ϱ. If ϱ is greater than 0, mortality is higher than the mean rate at the beginning of the period when fish are small, and lower than the mean at the end of the period when fish are large.

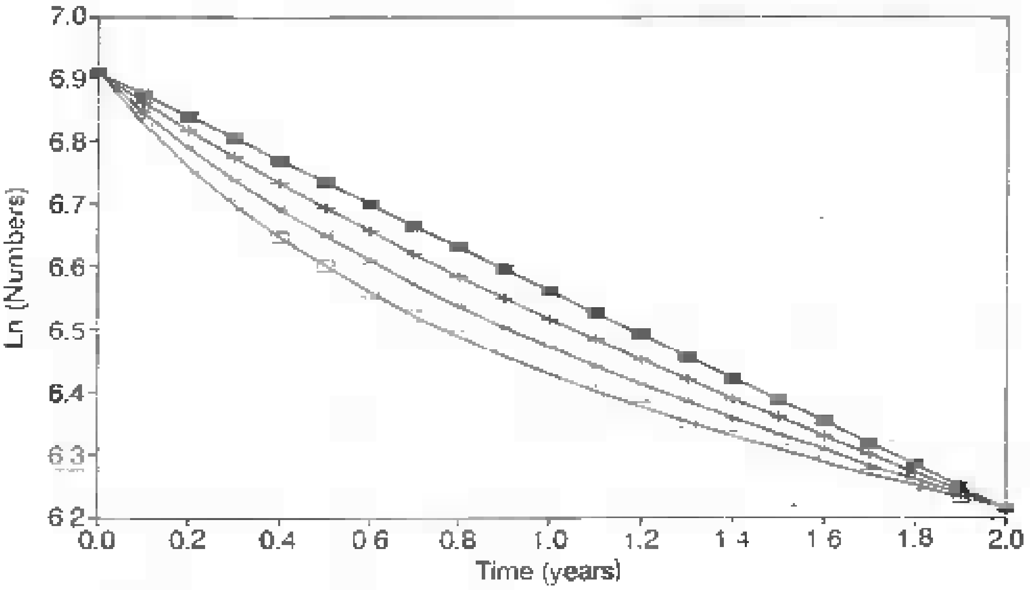

Fig. 2.10. Development of the logarithm of population numbers over a two year period, for a constant mean mortality rate, and varying degrees of size-dependence. (■) $\varrho = 0$ (constant mortality), (+) $\varrho = 0.25$, (*) $\varrho = 0.5$, and (□) $\varrho = 0.75$. Growth parameters: $K = 0.5 y^{-1}$, $W_\infty = 1.0$ kg, Initial weight 0.05 kg.

If mortality is size-dependent, the individual growth rate of fish has a strong bearing on the mortality suffered by the population. This is well illustrated in Fig. 2.11, which shows the development of a cohort of initially 1000 fish over a two-year period. Mortality is size-dependent with $\varrho = 0.5$, and fish grow according to a VBGF with $W_\infty = 1.0$ kg. The growth rate K varies between 0.25 and 1.0 y^{-1} The higher the growth rate, the more fish survive the two-year growth period. This is the basis of competition-mediated density-dependence.

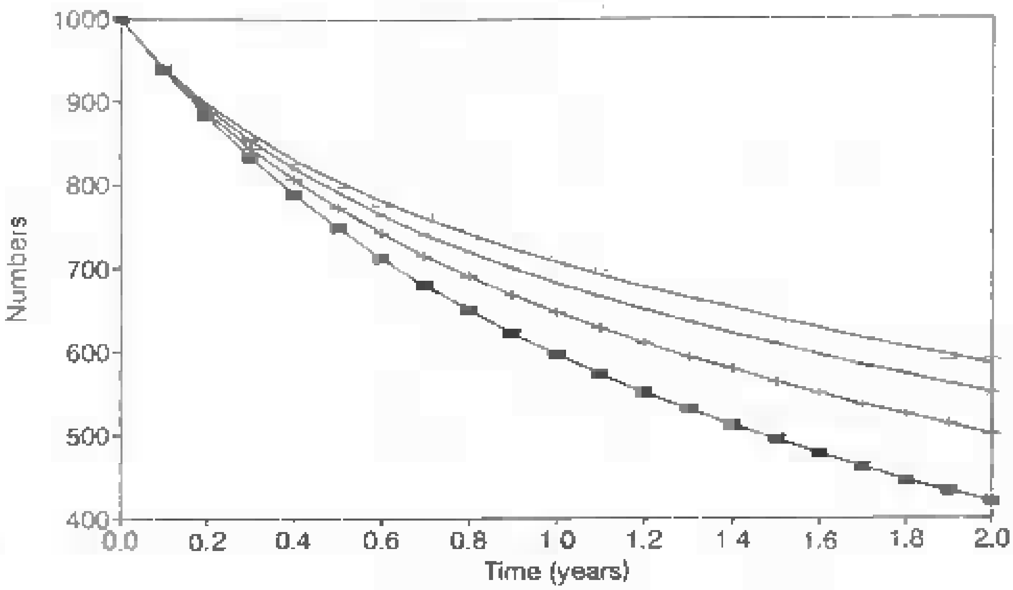

Fig. 2.11. Influence of the growth rate on mortality, if mortality is size-dependent ($\varrho = 0.5$). Development of population numbers over a two year period for (■) $K = 0.25$, (+) $K = 0.5$, (*) $K = 0.75$, (□) $K = 1.0$; $W_\infty = 1.0$ kg, initial weight 0.05 kg.

2.2.2 Density-Dependent Mortality

As pointed out in the beginning of this Chapter, it is distinguished here between two types of density-dependent mortality, called "competition-mediated" and "predation-mediated" density-dependence.

Competition-mediated density-dependence

Competition-mediated density-dependent mortality is defined as the interaction of density-dependent growth and size-dependent mortality. There is strong empirical evidence for the occurrence of both density-dependent growth and size-dependent mortality, and density-dependent mortality of the competition-mediated type is inevitable if the two processes operate.

Mathematically, competition-mediated density-dependent mortality is described by linking the models for density-dependent growth and size-dependent mortality into a single population model, as is done in Chapter 4.

Predation-mediated density-dependence

Density-dependent mortality of the predation-mediated type occurs when mortality-at-size changes in response to population density. This requires a functional or numerical response of the predator population, i.e. a change in either its feeding activity or its abundance.

Evidence for density-dependent mortality of the predation-mediated type in juvenile and adult fish is rare. Where it is known to occur, it is often attributable to cannibalism (Cook & Armstrong 1986, Wright 1990). As Ricker (1954) has noted, "of all the methods of population regulation (...), cannibalism is the one in which abundance of the control agent is most closely and inseparably allied to that of the population controlled".

Density-dependent mortality of the predation-mediated type can also result from parasitism (Anderson & May 1978, Dobson & May 1986), but field evidence is scarce (Sinderman 1986).

In theory, extreme competition for food can lead to starvation, and consequently density-dependent mortality of the predation-mediated type. However, the unique growth plasticity of fish, their ability to lay down reserves of lipids and to survive long periods of starvation means that starvation-induced mortality rarely occurs (Wootton 1990).

Density-dependent mortality of the predation-mediated type is well known from populations of young salmonids (Le Cren 1973, Elliott 1985). This mortality is related to competition for space in territorial animals, and is further examined in Section 2.2.3.

A common way of representing density-dependent mortality mathematically is to model the mortality rate as a linear function of the logarithm of density (Begon, Harper & Townsend 1986).

2.2.3 Self-Thinning

As individuals within a cohort grow, their demand for resources increases and competition becomes more severe. In some species, resource limitation affects all individuals to a similar degree and results in depressed growth, but has little effect on mortality. In other species, competition is asymmetric, i.e. some individuals outcompete others which will finally die. The latter mechanism is commonly referred to as self-thinning (Harper 1977). Under certain conditions, it results in a very simple and predictable pattern of mortality in a growing cohort.

Self-thinning was first observed in cohorts of plants sown at high density (Yoda *et al.* 1963). If the mean weight of growing plants in the cohort is plotted against cohort density, both on logarithmic scales, successive points tend to approach and then follow a line of slope -3/2. This weight-density relationship is fairly universal in dense plant populations (although the slope may vary slightly), and is referred to as the "self-thinning rule" or "Yoda's rule" (Yoda *et al.* 1963, Harper 1977). Although the precise reason for the -3/2 slope is still a matter of debate (White 1981, Lonsdale 1990), its heuristic explanation is that the biomass of plants (dimensions to the power 3) is supported by a light intercepting canopy area (dimensions to the power 2).

Begon, Firbank & Wall (1986) have discussed the potential occurrence of self-thinning in animal populations, and concluded that a general law is likely to exist for sessile animals. They argue that if such a law existed for mobile animals, the weight-density relationship is likely to follow a power of –4/3. The metabolic rate of individual animals is often proportional to their weight to the power 4/3 (Schmidt-Nielsen 1983), hence the metabolic rate of the whole cohort should scale with the same power of mean individual weight. On the other hand, the metabolic rate of the cohort is expected to be proportional to its food consumption. If food is limited and its total consumption remains constant, the animals can only grow if their population density declines with their individual weight to the power of –3/4. During the self-thinning process, weight is then proportional to density to the power of –4/3.

Elliott (1993) has shown that the self-thinning rule for mobile animals as proposed by Begon, Firbank & Wall (1986) can be applied to populations of juvenile sea-trout (*Salmo trutta*) in a Scottish stream.

Does self-thinning occur in carp populations?

Carp species predominate in the culture-based fisheries of South Asian reservoirs. Does self-thinning occur in such carp populations?

The occurrence of self-thinning in common carp can be investigated using the results of Walter's single cohort stocking experiments. If self-thinning operates in cohorts of carp, weight at harvesting should scale with density at harvesting to the power -4/3.

The development of density and individual weight of cohorts in Walter's experiments is shown in Fig. 2.12. Each solid line corresponds to one experiment. Stocking density and individual weight are indicated by filled squares, while the opposite end of the line indicates density and weight at harvesting. Note the logarithmic scales on both axes. The dashed line indicates a slope of -1. Final weight at high density (above 300 fish/ha) can be seen to scale with density to the power of -1. There is no indication of a slope -4/3 relationship as predicted by the self-thinning rule.

The slopes of the lines describing individual experiments indicate the mortality suffered by that particular cohort. Vertical lines indicate no change in density, i.e. no mortality. The more inclined a line is to the left, the higher the mortality during the growth period. The highest mortalities occur in the bottom right hand corner of the diagram, in the dense, slow growing cohorts. Obviously, density has some bearing on mortality, through either competition- or predation-mediated density-dependent mortality. However, density-dependent mortality is not adequately described by the self-thinning rule of Begon, Firbank & Wall (1986).

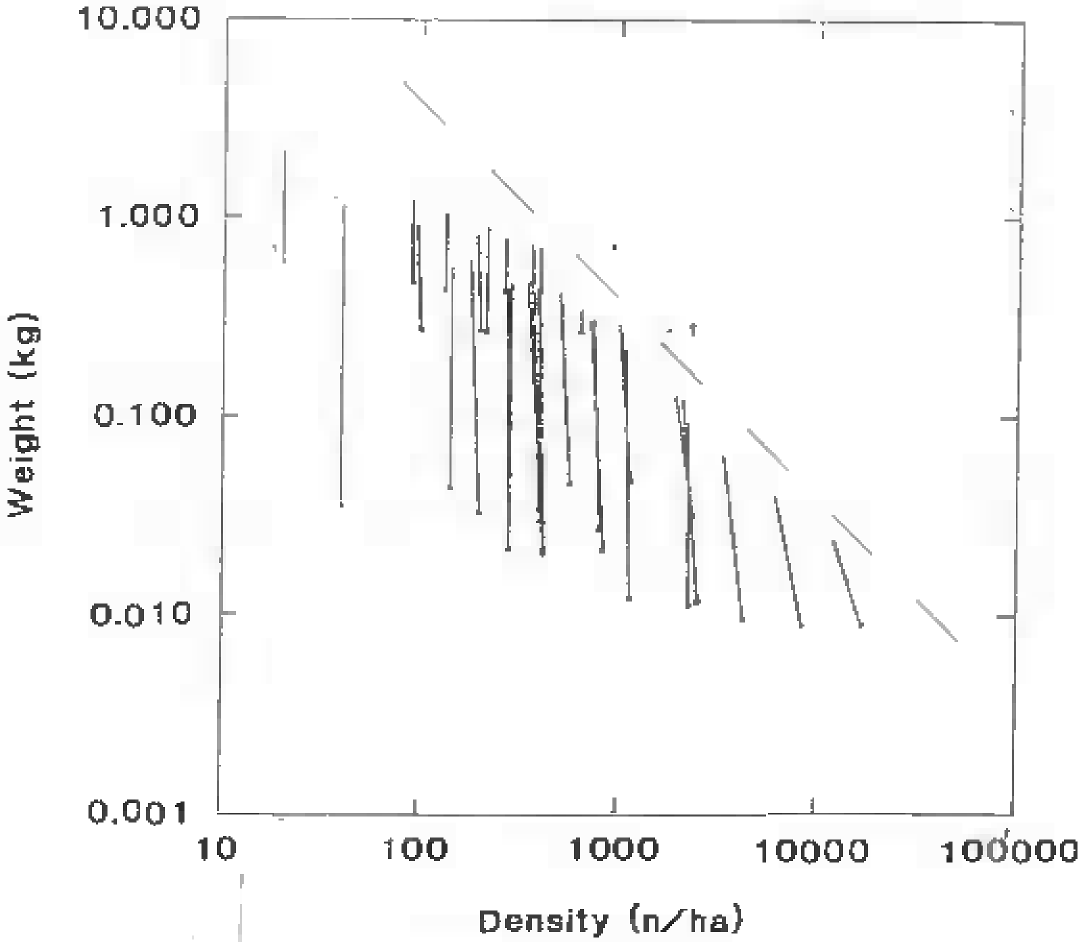

Fig. 2.12. Development of population density and individual weight in Walter's cohort experiments. Density and weight at stocking are indicated by a filled square. Note logarithmic scales on both axes. The dashed line denotes slope -1.

2.2.4 Discussion

Mortality-size relationship

Peterson & Wroblewski (1984) have shown that the mortality rates of many pelagic organisms, from invertebrates to whales, scale with the mean weight of the organisms during their lifetime to the power of -0.25. The existence of a relationship between the mean weight of organisms during their lifetime, and their mortality rate is not surprising. The intrinsic rate of natural increase of all organisms from bacteria to whales is closely related to their mean body mass (Fenchel 1974), and a similar relationship must exist for mortality, if populations are to persist as they apparently do. Fenchel (1974) found that the intrinsic rate of increase scales with body mass to the power of -0.275.

Here, however, the question is how the mortality rate of organisms within a single population changes with their size during ontogenic development. McGurk (1986) has addressed this question in the context of the early life stages of marine fish. He has shown that fish eggs and larvae tend to have a higher mortality rate than predicted from their weight, and suggested that this can be explained by their highly aggregated (patchy) distribution. The early life stages of fish are of little interest to culture-based fisheries. The question remains, however, whether there exists a genuine relationship between size and mortality during the ontogenic development of a fish from fingerling to adult stage.

McGurk (1986, 1987) noted that within taxa, the exponent of the weight-mortality relationship can differ significantly from the -0.25 describing the relationship in the ecosystem (Peterson & Wroblewski 1984). McGurk (1987) compared mortality and weight between a number of marine fish populations, and estimated an exponent of -0.4 using functional regression, while Gulland (1987) obtained an "eye fit" estimate of -0.5 from the same data set.

In this study, it was attempted to establish a relationship between mortality and size within populations. Mortality of juvenile striped bass in the Hudson River is well described by the proposed model, with an exponent ϱ of 0.56. The model also provides a good description of the mortality-size relationship in European carp pond culture, with the exponent ϱ varying between 0.36 and 0.98.

The mortality-size relationship in a pond fish population appears to be strikingly similar to that of fish in rivers or in the oceans. This is surprising because the sources of mortality in these ecosystems must be quite different. Predation is likely to play a major role in natural environments, but can be virtually ruled out in a fishpond. Mortality-size relationships within populations deserve further attention, for the sake of basic ecology as well as fisheries management.

The mortality-size relationship is of crucial importance in culture-based fisheries, because it pertains directly to the optimal size of seed fish, and to the stocking density. Often, no specific information will be available on the mortality-size relationship in a particular fishery. The analysis conducted here indicates that assuming $\varrho = 0.5$ will often be a good initial guess, as was suggested by Gulland (1987).

Methods for the estimation of parameters of the mortality-size relationship need to be developed further. The method used here has been shown to give reasonable estimates of ϱ in simulations (Appendix C). However, it needs to be examined further and can almost certainly be improved.

Density-dependent mortality

It was proposed to distinguish between two types of density-dependent mortality, referred to as "competition-mediated" and "predation-mediated" density-dependence.

Competition-mediated density-dependent mortality occurs as a consequence of density-dependent growth and size-dependent mortality. This type of density-dependent mortality is the basis of stock-recruitment models proposed by Ricker & Foerster (1948) and Shepherd & Cushing (1980), and has been reviewed by Anderson (1988). There is solid evidence for density-dependent growth and size-dependent mortality in wild populations, as well as in pond culture. The combination of both processes inevitably leads to density-dependent mortality of the competition-mediated type, which is therefore certain to occur in natural populations as well as in culture-based fisheries.

Predation-mediated density-dependent mortality, i.e. a response in mortality-at-size to population density, is less well supported by empirical evidence. This may be partly due to the inherent difficulties of detecting density-dependence (Hassell *et al.* 1989, Solow & Steele 1990). If density-dependence of this type occurs, it is likely to involve a substantial time-lag in the order of the predator's generation time. Hence in the management of culture-based fisheries, it will be sufficient to adjust the natural mortality rate in successive production periods, while mortality during the period can be regarded as constant. In small water bodies, a numerical response of predator abundance to prey density can also be mitigated by selective fishing for predators using traps, longlines etc. (Bhukaswan 1983).

Summing up, density-dependent mortality of the competition-mediated type must be taken into account in the management of a culture-based fishery, and this is done automatically if density-dependent growth and size-dependent mortality are considered together. Predation-mediated density-dependent mortality is of lesser interest in short-term management, and does not need to be included in population models for small reservoir fisheries.

Self-thinning

There is no indication of self-thinning in cohorts of common carp. This does not rule out self-thinning in other carp species, but its occurrence is unlikely.

The juvenile sea-trout that exhibited self-thinning in Elliott's (1993) study are territorial. Larger individuals are likely to be able to claim larger territories, thereby introducing an element of asymmetry into competition. Carp are not territorial, and there is no indication of asymmetric competition within a cohort.

Size-dependence or density-dependence?

Size and density effects on mortality are often confounded in experimental and field data from individual populations, due to the action of density-dependent growth. This is well illustrated by Walter's experiments, as shown in Fig. 2.12. Cohorts stocked at high density suffer a higher mortality rate, but it is impossible to conclude whether this is due to predation-mediated or due to competition-mediated density-dependence in mortality.

For practical purposes, it may be best to consider only density-dependent growth and size-dependent mortality (i.e. competition-mediated density-dependent mortality), unless there is strong evidence of predation-mediated density-dependent mortality

Chapter three

Some Economic Considerations with Respect to Stocking and Harvesting

The viability of small reservoir fisheries is ultimately determined by economic and socio-economic factors, which are largely beyond the scope of this study. This chapter briefly examines only those economic aspects that pertain directly to the optimal stocking and harvesting of a fishery.

Small reservoirs or the fishing rights therein are often communal property of villages or cooperative societies. Hence the production process in small reservoir fisheries lies in the hands of a single production unit (village, cooperative), which forms the basis of this economic analysis

3.1 ECONOMIC OBJECTIVES IN SMALL RESERVOIR FISHERIES

A production unit may adopt various objectives in running a small reservoir fishery. Only two, conceptionally simple objectives are considered here:

(1) Maximization of biological production, or

(2) Maximization of profit.

Maximization of biological production may be adopted if maximum food production is given priority over the economics of the production unit. Such may be the case in government owned or subsidized units. Maximization of profit can be expected of private sector units in a free market environment, unless production is mainly for subsistence.

Biological production is completely within the realm of biology, while profit requires consideration of costs and prices, which are examined below.

3.2 REVENUE, COSTS, AND PROFIT

The total profit (TP) received is the difference between total revenue (TR) from the sale of fish and the total costs (TC) involved in producing them:

$$TP = TR - TC \tag{3.1}$$

Total revenue is determined by the total volume, and the individual size of the fish produced.

Costs can be divided into fixed costs and variable costs. Fixed costs are independent of the production level, and usually comprise interest on capital, purchase or lease of land, capital depreciation and some operation costs. Variable costs are dependent on the production level, and include the costs of seed fish, and some operating costs.

Most small reservoirs are maintained primarily for purposes other than fish production, hence fixed costs in small reservoir fisheries tend to be exclusively operating costs. Operating costs in turn are primarily labour costs due to the extensive nature of small reservoir fish production. For simplicity, all labour costs are regarded as fixed in this study. The principal variable costs are those of the seed material, which are dependent on the quantity and size of the seed fish.

Only the total revenue and the variable costs are of interest in the optimization of stocking and harvesting for a given fishery. Fixed costs merely reduce the profit by a constant amount. They may be crucial to the viability of the fishery, but have no bearing on the optimal stocking and harvesting.

Sales revenue is often dependent on the individual size of the fish produced, and seed costs always increase with the size of fingerlings. A brief empirical examination of these relationships is presented in Sections (3 2.1) and (3.2 2).

3.2.1 Price-Size Relationship for Produce

Fish produced in the Calcutta bheris owned by the West Bengal State Fisheries Development Corporation (WBSFDC) are sold at the municipal market, for prices fixed monthly by the Corporation. The produce is graded by individual weight, and different prices per unit weight apply to different weight categories. The Corporation's selling prices for November 1992 are used here as an example of producer's price-size relationships.

The producer's price per kg for various species is plotted against the median weight of the size category in Fig. 3.1. Indian major carp generally fetch the highest prices, followed by grass carp, common carp, and silver carp. The relationship between price per unit weight and individual weight is different for each species or species group, but it can usually be approximated by a straight line.

For the length-based model to be developed in Chapter 4, it is necessary to express the price per piece of fish as a function of its length. Price per piece is calculated from price per unit weight, and the cubic root of median weight is used as a substitute for length. Fig. 3.2 shows price per piece plotted against the cubic root of median weight (times a scaling

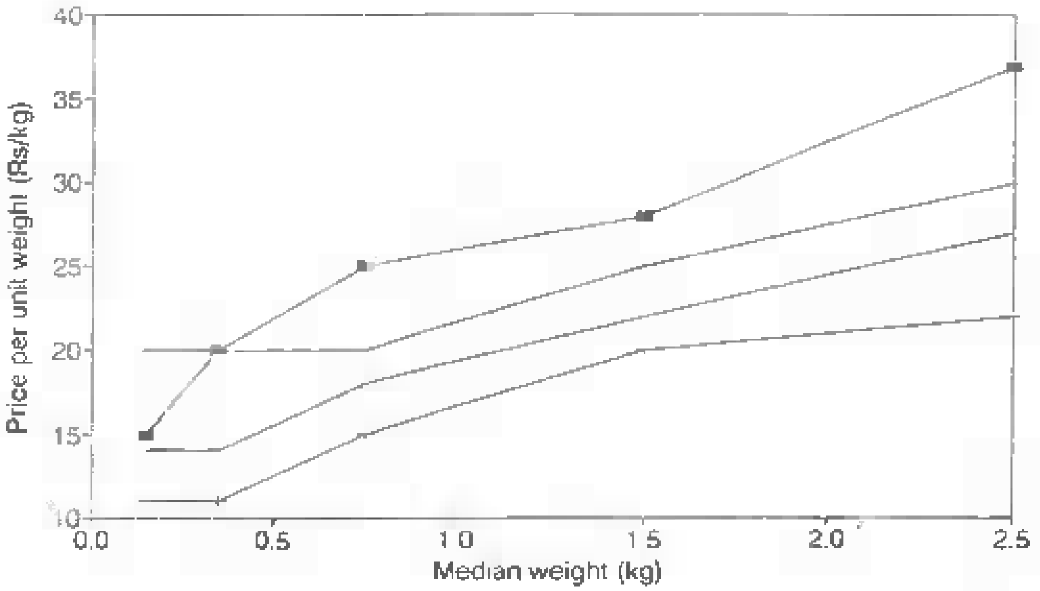

Fig. 3.1. Price per unit weight as a function of individual weight, for various cyprinids produced in the bheris of the West Bengal State Fisheries Development Corporation. (■) Indian major carp, (*) grass carp, (□) common carp, and (+) silver carp.

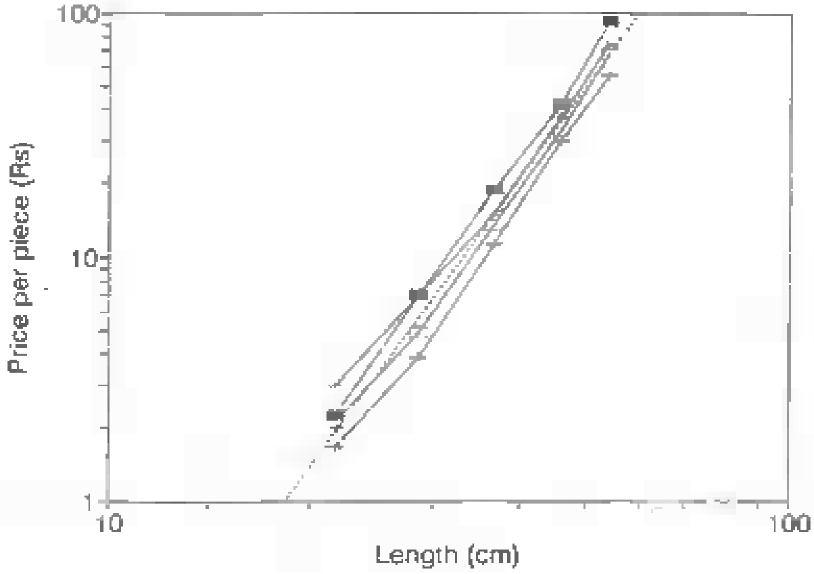

Fig. 3.2. Price per piece as a function of length, for the produce of the West Bengal State Fisheries Development Corporation. (■) Indian major carp, (*) grass carp, (□) common carp, and (+) silver carp. The dotted line indicates a slope of 4

factor), on logarithmic scales. Price per piece can be described by a power function of length:

$$p_L=p_0\ L^{p_1} \tag{3.2}$$

Here, p_L is the producer's price of a fish of length L, p_0 is a scaling factor, and p_1 is the exponent of the price-length relationship. As indicated in Fig. 3.2, the price-length relationships for produce of the WBSFDC are well described by an exponent p_1 of 4

3.2.2 Cost-Size Relationship for Seed Fish

Data on the cost of seed fish in relation to size are available from various sources. The WBSFDC has fixed selling rates for seed fish of different length categories. Similar data for Yasothon Province in Northeast Thailand are given in Anon. (1992). Bohl (1982) gives the cost of pre-nursed, and one summer old common carp in Germany.

Cost per fingerling has been calculated from this information, for individual species or mixed fingerlings of Indian major carp. Fig. 3.3 shows the natural logarithm of cost per fingerling as a function of length. Costs are in three different currencies, so the absolute costs are not comparable. For each single species and market, the logarithm of cost per fingerling is approximately proportional to length. Hence cost increases exponentially with length, and can be described by a function of the form

$$c_L = c_0 \ e^{c_1 L} \tag{3.3}$$

where c_L is the cost of a fingerling of length L, c_0 is a scaling factor, and c_1 is a factor in the exponent of the cost-length relationship.

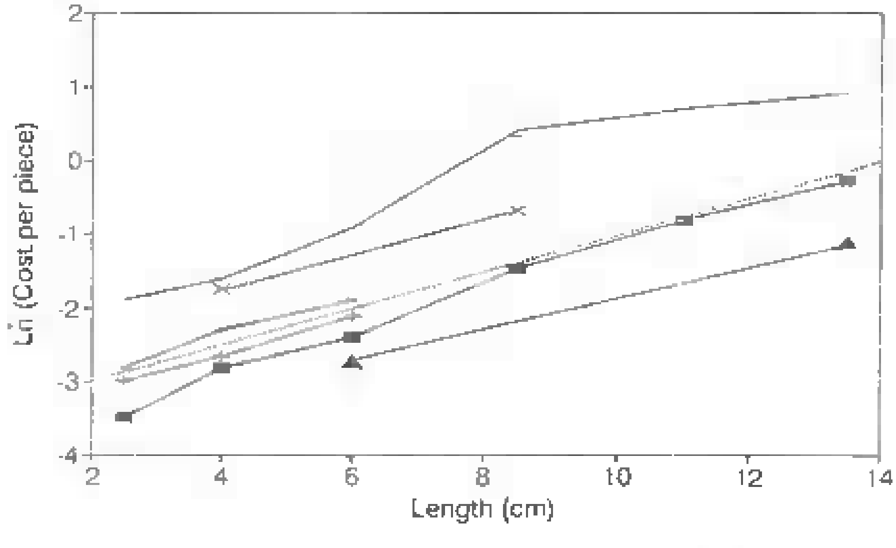

Fig. 3.3. Logarithm of the cost (various currencies) per piece of seed fish as a function of length. (■) Indian major carp, (+) silver carp, (*) grass carp and (O) common carp seed selling prices of the West Bengal State Fisheries Development Corporation in 1992. (▲) Indian Major carp in Northeast Thailand. (×) Common carp in Germany. The dotted line indicates a slope of 0.25.

The slopes of the relationships between the logarithm of cost and length are equal to the factor c_l. These slopes are fairly similar in all the data examined (Fig. 3.3), with c_l varying between 0.21 and 0.32 cm^{-1} (average 0.26 cm^{-1}). The dashed line in Fig. 3.3 denotes a slope of 0.25 cm^{-1} for reference.

3.3 DISCUSSION

Property rights and the production unit

Small reservoir fisheries are here regarded as communal property resources, i.e. they are "held by an identifiable community of users, who can exclude others and regulate use" (Berkes *et al.* 1989). If the community of users regulates both stocking and harvesting of the fishery, it constitutes a production unit in the economic sense.

Culture based fisheries in larger reservoirs are usually common property resources. Stocking is carried out by the government, and access to the fishery is often unrestricted, although a nominal licensing system may be in operation. Such culture-based fisheries cannot be regarded as a single production unit. They are more complex, and may be subject to typical common property problems like rent dissipation and biological over-exploitation (Hardin 1968, Berkes *et al.* 1989).

Economic objectives of the production unit

Economic objectives of small reservoir production units are not always stated explicitly. In Chapter 4, it will be shown that the stocking and harvesting regime that maximizes biological production is often different from the regime that maximizes profit. Hence it is important to clarify the objectives of the production unit, in order to optimize management.

In reality, economic objectives are likely to be more complex than simply the maximization of production or profit. However, the study of optimal management with respect to these simple objectives can provide a basis for management aimed at attaining more complex objectives.

Revenue and costs

The price-size relationship for produce established here is by no means universal. An increase in price per unit weight with increasing weight is to be expected if the marketing and distribution system is well developed, and large fish can reach customers of the appropriate buying capacity. This is the case in the Calcutta bheris, where produce is taken to the municipal market. Small reservoir fisheries in rural areas may not have access to well-developed markets, and the price per unit weight may be essentially constant. Indeed, it may be difficult to sell large produce if consumers are of low buying capacity, and prefer to buy whole fish.

Labour costs are usually regarded as partly fixed and partly variable (Cunningham *et al.* 1985). Here, all labour costs are taken to be fixed for simplicity.

The costs of seed fish always increase with size, reflecting production costs. A brief analysis of the available data indicates that costs often increase exponentially with length. The factor c_1 in the exponent lies within a narrow range for all data sets examined.

The price-size relationships established here serve as examples, and will be used as such in Chapter 4. The functional form of these relationships has no further relevance. In practical management, the price-size relationships must be established in each particular case. General models are neither possible, nor are they necessary, given that actual price-size information can easily be acquired.

Chapter four

Dynamics of Culture-Based Reservoir Fisheries: a Length-Structured Model

In Chapters 2 and 3, the key biological processes and some economic considerations relevant to culture-based small reservoir fisheries have been identified. In this Chapter, the models for individual processes are linked together in a general, analytical model for culture-based fisheries. The model is then used to explore various management options for such fisheries, and to derive some management guidelines.

4.1 THE GENERAL MODEL

A length-structured, discrete time, projection matrix model for culture-based fisheries is developed here. The model is based on explicit sub-models for density-dependent growth and size-dependent mortality, and it can accommodate any stocking and harvesting policy. Hence the model is suitable for a general exploration of management policies in culture-based fisheries.

4.1.1 Population and Catch Equations

The fish population is divided into m length classes of equal width dL, with lower length bounds L_i, for $i=1,\ldots,m$. The population at time t is then represented as a vector n_t of numbers in the length classes. The mid-length of class i is denoted L_i^*, and W_i^* is the weight at L_i^*.

The population equation

The population n_{t+dt} at time $t+dt$ is projected from n_t using the matrix equation

$$n_{t+dt}=G_t\ S_t\ (n_t+u_t) \tag{4.1}$$

Here G_t is the growth projection matrix describing the transition of fish between length classes during the time interval dt, and S_t is the (diagonal) survival matrix describing the survival of fish in the individual length classes during dt. The vector u_t gives the numbers of fish stocked at time t.

The actual structure of the above model is easier to comprehend if expressed in matrix notation:

$$\begin{bmatrix} n_{1t+dt} \\ n_{2t+dt} \\ \cdot \\ n_{mt+dt} \end{bmatrix} = \begin{bmatrix} g_{11} & g_{21} & \cdot & g_{m1} \\ g_{12} & g_{22} & \cdot & g_{m2} \\ \cdot & \cdot & \cdot & \cdot \\ g_{1m} & g_{2m} & \cdot & g_{mm} \end{bmatrix} \times \begin{bmatrix} s_{11} & 0 & \cdot & 0 \\ 0 & s_{22} & & 0 \\ \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & \cdot & s_{mm} \end{bmatrix} \times \left(\begin{bmatrix} n_{1t} \\ n_{2t} \\ \cdot \\ n_{mt} \end{bmatrix} + \begin{bmatrix} u_{1t} \\ u_{2t} \\ \cdot \\ u_{mt} \end{bmatrix} \right).$$

The catch equation

The catch taken from the population during the time period from t to t+dt is given by

$$c_t=G_t\ H_t\ (n_t+u_t) \tag{4.2}$$

where c_t is the catch at length vector, and H_t is the harvesting matrix. The size distribution of the catch corresponds to time t+dt, i.e. the catch is effectively taken at the end of the period.

4.1.2 Construction of the Matrices

All the three matrices G_t, S_t and H_t may vary over time, G_t because of density-dependence in growth, and S_t and H_t because of variation in the fishing mortality rate and gear selectivity. The matrices are constructed as follows.

The growth projection matrix

The growth projection matrix was introduced by Shepherd (1987), who also devised the following algorithm for its construction.

In the model developed here, growth is described by the density-dependent VBGF introduced in Chapter 2. If the time interval dt is sufficiently short, biomass can be regarded as constant during the interval. Growth during the interval then follows a standard VBGF with constant a $L_{\infty B}$ given by

$$L_{\infty B} = L_{\infty L} - d\ B \tag{4.3}$$

where B_t is the biomass at time t

$$B_t = \sum_{i=1}^{m} n_{it}\ W_i^* \tag{4.4}$$

The basic idea behind the projection matrix is that at time t+dt, the length interval $[L_i, L_{i+1}]$ contains the surviving individuals that at time t were within the interval $[L'_i, L'_{i+1}]$, defined by the back-calculated lengths of the current bounds. The back-calculated length L'_i of bound L_i is given by:

$$L_i' = \frac{L_i - L_{\infty B}\ (1 - e^{-K\,dt})}{e^{-K\,dt}} \tag{4.5}$$

This is the Ford-Walford equation (Ricker 1975) solved for the length at the beginning of the growth period.

Once the former bounds of the length classes have been calculated, the elements g_{ij} of the growth projection matrix are determined using the following algorithm:

if $L_j < L'_i < L_{j+1}$ then $g_{ij} = (L_{j+1} - L'_i)/dL$
if $L_j < L'_{i+1} < L_{j+1}$. then $g_{ij} = (L'_{i+1} - L_j)/dL$

if $L'_i < L_j$ and $L_{j+1} < L'_{i+1}$ then $g_{ij} = 1.0$

if $L'_{i+1} < L_j$ then $g_{ij} = 0$
if $L'_i > L_{j+1}$ then $g_{ij} = 0$

and, if the highest length class is a plus group,

if $L'_m < L_j$ then $g_{mj} = 1.0$

The element g_{ij} of the projection matrix is simply the proportion of the initial length class j that contributes to the final class i.

Most elements of the projection matrix are zero, and the non-zero elements are situated in a narrow band near, but not parallel to the main diagonal. This band crosses the main diagonal at the length class containing L_∞. Length classes above L_∞ are projected to lower lengths, i.e. individuals shrink. In a culture-based fishery with density-dependent growth, $L_{\infty B}$ may assume low values at high biomass densities, and may well be below the highest length class in the model.

The survival matrix

The survival matrix S is a diagonal matrix, i.e. all its elements are zero, except for those on the main diagonal. The element s_{jj} on the main diagonal equals the proportion of individuals present in length class j at time t that survives to time t+dt. The survival s_{jj} is a function of the natural mortality rate M_j, the fishing mortality rate F, and the gear selectivity v_j. Natural mortality in length class j is given by Equation (2.14), applied to the mid-length L_j^*:

$$M_j = M_r \left(\frac{L_j^*}{L_r} \right)^{-3e} \tag{4.6}$$

where M_r is the mortality rate at reference length L_r.
The survival rate s_{jj} of fish in length class j is then given by:

$$s_{jj} = e^{-(M_j + Fv_j)\ dt} \tag{4.7}$$

The harvesting matrix

The harvesting matrix H is diagonal, like the survival matrix. Its element h_{jj} on the main diagonal is the proportion of fish in length class j that is harvested during the time interval [t, t+dt]. Using the parameters defined above, the elements on the main diagonal of the harvesting matrix are given by:

$$h_{jj} = \frac{Fv_j}{M_j + Fv_j} \left(1 - e^{-(M_j + Fv_j)\, dt}\right) \tag{4.8}$$

4.2 SIMULATION OF CULTURE-BASED RESERVOIR FISHERIES

In Sections 4.3. and 4.4, the general population model developed above is used for simulations, to explore the dynamics of culture-based reservoir fisheries. This section explains how stocking is simulated, and how the aggregated variables (mean weight, production, profit) are calculated. The standard parameter values used in the simulation are defined and explained.

4.2.1 Stocking

The length of seed fish stocked in the simulations is assumed to be normally distributed with a standard deviation of 1 cm. By default, the mean length of seed fish is 5 cm, but sometimes 3, 7 or 9 cm are assumed to explore the effects of seed size on production.

The proportion of seed fish that falls into a certain length class is given by the cumulative normal distribution with 1 cm standard deviation. For a mean length of 5 cm, 34.13% of the seed fish fall into each length classes 5 and 6, 13.59% into each length classes 4 and 7, and 2.28% into each classes 3 and 8. For other mean lengths, the whole distribution is shifted accordingly.

4.2.2 Aggregated Variables

Mean weight in the catch, total production, and profit are aggregated variables, i.e. they summarize the results of the length-structured model simulations. The aggregated variables are calculated as follows:

Mean weight in the catch

The mean weight WC_t^* of fish in the catch during time step t equals the biomass harvested, divided by the number harvested:

$$WC_t^* = \frac{\sum_{i=1}^{m} c_{it} \, W_i^*}{\sum_{i=1}^{m} c_{it}} \tag{4.9}$$

The mean weight of the catch over several time steps is calculated in the same way, as the total biomass harvested divided by the total harvested.

Production

The production Pr during a period $[t_1, t_2]$ equals the total biomass harvested, minus the total biomass stocked during the period:

$$Pr_{t_1,t_2}=\sum_{t=t_1}^{t_1}\sum_{i=1}^{n}(n_{it}-u_{it})\,W_i^* \tag{4.10}$$

Profit

Profit always refers to gross profit GP, which is defined here as the total revenue minus the cost of seed fish. All other costs are neglected. Gross profit during the time interval $[t_1, t_2]$ is given by:

$$GP_{t_1,t_2}=\sum_{t=t_2}^{t_2}\sum_{i=1}^{m}(n_{it}\,p_i-u_{it}\,c_i) \tag{4.11}$$

Where p_i and c_i are the producer's price and cost of an individual fish in class i.

Profit is calculated for two different price structures: constant price per unit weight, and size-dependent prices. For constant price per unit weight, p_i equals W_i^* times the price per unit weight. For size-dependent prices, p_i is calculated from Equation (3.2). The cost of seed fish c_i is always calculated from Equation (3.3)

4.2.3 Standard Parameter Values

A set of standard parameter values for the simulations is defined in Table 4.1, and explained below.

Fish are assumed to grow isometrically, i.e. in the weight-length relationship,

$$W=a\ L^{b} \tag{4.12}$$

the exponent b equals 3.0. The coefficient a has been chosen so that a fish of 20 cm length weights 0.2 kg.

The limiting infinite length of the density-dependent VBGF $L_{\infty L}$ is 100 cm, and the length-based competition coefficient d is 0.5 cm x ha / kg. Hence $L_{\infty B}$ equals 50 cm at a biomass density of 100 kg/ha, and $L_{\infty B}$ is zero at a biomass density of 200 kg/ha.

Both constant (size-independent) and size-dependent mortality are considered in the simulations. Constant annual mortality rates are integers from zero to three. By default, mortality is assumed to be size-dependent with an exponent ϱ of 0.5 (Equation 4.6). The values of mortality at reference length (M_r) have been standardized so that the mean size dependent mortality rates in a cohort stocked at 1000 fish/ha, during a 6 months growth period, are equal the corresponding constant rates. For example, a size-dependent mortality rate of 1.292 per year at reference length $L_r = 20$ cm means that 223 out of 1000 fish survive a half year growth period. This corresponds to a constant mortality rate of 3.0 per year. The effects of a higher degree of size-dependence are also explored, using $\varrho = 1.0$ and $M_r = 0.361\ y^{-1}$, corresponding to a constant $M = 3.0\ y^{-1}$ at a stocking density of 1000 fish/ha.

Table 4.1: Parameter values used in the simulations. Default values are printed in bold.

Parameter	Value(s)
Weight-length relationship	
a	2.5×10^{-5} kg / cm^3
b	3.0
Density-dependent VBGF	
$L_{\infty 1}$	100 cm
K	0.5 y^{-1}
d	**0.45**, 0.5, 0.4 cm x ha kg^{-1}
Constant mortality	
M	**0.0**, 1.0, 2.0, 3.0 y^{-1}
Size-dependent mortality	
ϱ	**0.5** (1.0)
L_r	20 cm
M_r	0.0, 0.406, 0.840, **1.292** (0.361) y^{-1}
Cost-length relationship	
c_0	0.02865 cu
c_1	0.25 cm^{-1}
Constant price per kg	10 cu kg^{-1}
Price-length relationship	
p_0	1.25×10^{-5} cu
p_1	4.0

For the economics sub-model, parameters have been chosen so that they correspond to the selling rates of the West Bengal State Fisheries Development Corporation. Costs and prices are expressed in arbitrary currency units (cu).

The factor c_1 in the exponent of the cost-length relationship is set to 0.25 cm^{-1}, in accordance with the empirical relationship found in Chapter 3. The parameter p_0 is set so that a 5 cm long seed fish costs 0.1 cu.

The price of produce is usually assumed to be constant at 10 cu/kg. When size-dependent prices are considered, p_1 is set to 4 in accordance with the empirical relationship found in Chapter 3, and p_0 is set so that the price of a 20 cm long fish is 2 cu. Such a fish weighs 0.2 kg, and consequently the price per kg for fish of this size is 10 cu.

4.2.4 Length of Time Steps

Care has to be taken in selecting the length of time steps in the simulations. Biomass density is assumed to be constant during the time step, and equal to the value at the beginning of the step. Hence the density-dependent growth rate is also constant and equal to that at the beginning of the step. If biomass density changes rapidly due to fast growth or heavy mortality (e.g. in a single cohort), long time steps lead to a misrepresentation of growth. If the biomass dynamics is slow (e.g. in populations consisting of several cohorts), relatively long time steps can be chosen.

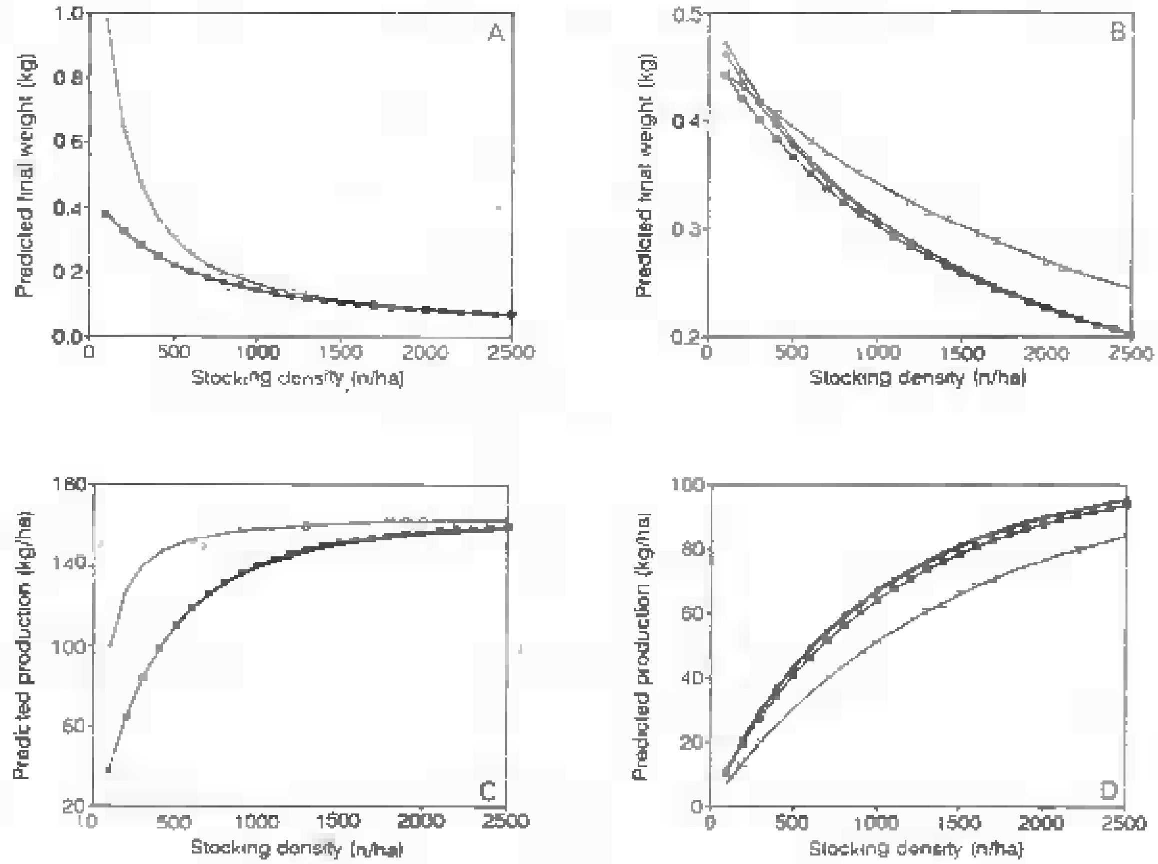

Fig. 4.1. Influence of the length of the time step on model predictions. (A) Predicted final weight for $M=0$. (B) Predicted final weight for $M_r=1\ 292\ y^{-1}$, $\rho=0.5$. (C) Predicted production for $M=0$. (D) Predicted production for $M_r=1\ 292\ y^{-1}$, $\rho=0.5$. Time steps are (□) 1 month, (■) 1 week, (+) 0.5 weeks, (*) 0.25 weeks

The most appropriate length of time steps can be found empirically, by observing the effect of different time steps on model predictions. Such an example is given in Fig. 4.1, for the parameter values defined in Section (4.2.3), and time steps of 1 month, 1 week, 0.5 weeks and 0.25 weeks. In Figs. 4.1. (A) and (B), the predicted final weights of fish after a six months growth period are shown as a function of stocking density, for no mortality (A), and size-dependent mortality ($M_r = 1.292\ y^{-1}$, $\varrho = 0.5$) (B). Also shown is the total production during the growth period, for no mortality (Fig. 4.1 C), and size-dependent mortality (Fig. 4.1.D). The predictions obtained for time steps of 1, 0.5 and 0.25 weeks are generally very close or identical. Predictions based on time steps of one month differ widely from those obtained using 1 week or shorter steps. Time steps of one week are used in all subsequent simulations.

4.3 DYNAMICS OF A SEASONAL RESERVOIR FISHERY

In a seasonal reservoir fishery, the growth period is limited by the physical environment. In tropical small reservoirs, this period usually starts with the monsoon, and ends when the reservoir is emptied or dries out during the dry season.

Three stocking and harvesting options are available for seasonal small reservoir fisheries. The most common is to stock the reservoir once at the beginning of the growth period, and to harvest it completely at the end. A more elaborate method sometimes practised is staggered harvesting, thereby "thinning" the population during the growth period, and increasing the growth rate of the remaining individuals. Finally, multiple stocking may be practised. All three management options are considered separately below.

Unless stated otherwise, all simulations in this section are done for a six month growth period, using the standard parameter values defined in Section 4.2 (Tab. 4.1).

4.3.1 Single Stocking and Single Harvesting: Optimal Density and Size of Seed Fish

Single stocking and complete harvesting in one instant is the simplest regime to be considered. Management decisions are limited to two variables: stocking density, and size of seed fish.

At first, stocking density in the absence of mortality is considered. Then, the influence of constant and size-dependent mortality on production and profit, and their implications for the optimal stocking density are investigated. Finally, the question of the optimal size of seed fish is addressed.

No mortality

The assumption of no mortality provides a good starting point to explore the consequences of density-dependent growth for production.

The length structure of the model population is illustrated in Fig. 4.2, which shows monthly length frequency distributions of a cohort stocked at a density 2500 fish/ha The length distribution at month 1 is that of the stocked fingerlings, subsequent distributions are projected by the model. Growth is rapid at first, but soon slows down due to intense competition Growth virtually ceases after four months, so that the last two months contribute little to production.

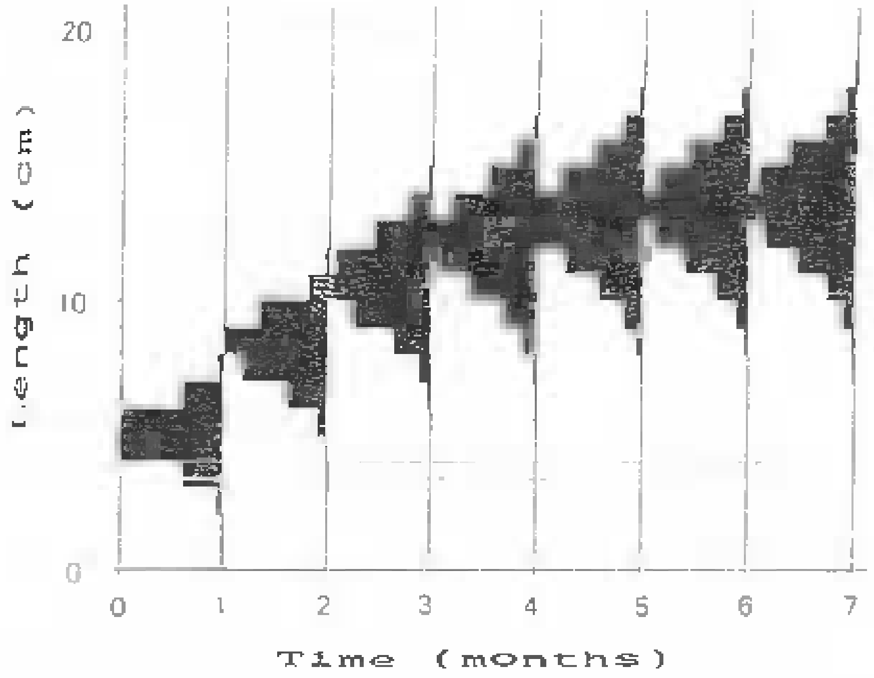

Fig. 4.2. Length frequency distributions of a growing cohort, at monthly intervals during a six month growth period. Stocking density 2500 fish per hectare. Standard parameter values No mortality

The effects of stocking density on growth, production and profit are explored using aggregated variables (Fig. 4.3): average weigh of produce, production, and profit

The average weights of fish at the end of the six month growth period are shown in Fig. 4.3 (A). Final weight decreases rapidly with increasing stocking density.

Yield (biomass harvested), biomass stocked and production are shown in Fig. 4.3 (B). Yield increases sharply with increasing density at first, but changes very little at high densities. Asymptotically, yield approaches 200 kg/ha, the biomass density at which $L_{\infty B}$ is zero. The biomass stocked is a linear function of stocking density, and production is simply the difference between biomass harvested and biomass stocked. Consequently, production increases with stocking density as long as the slope of the yield curve is higher than that of

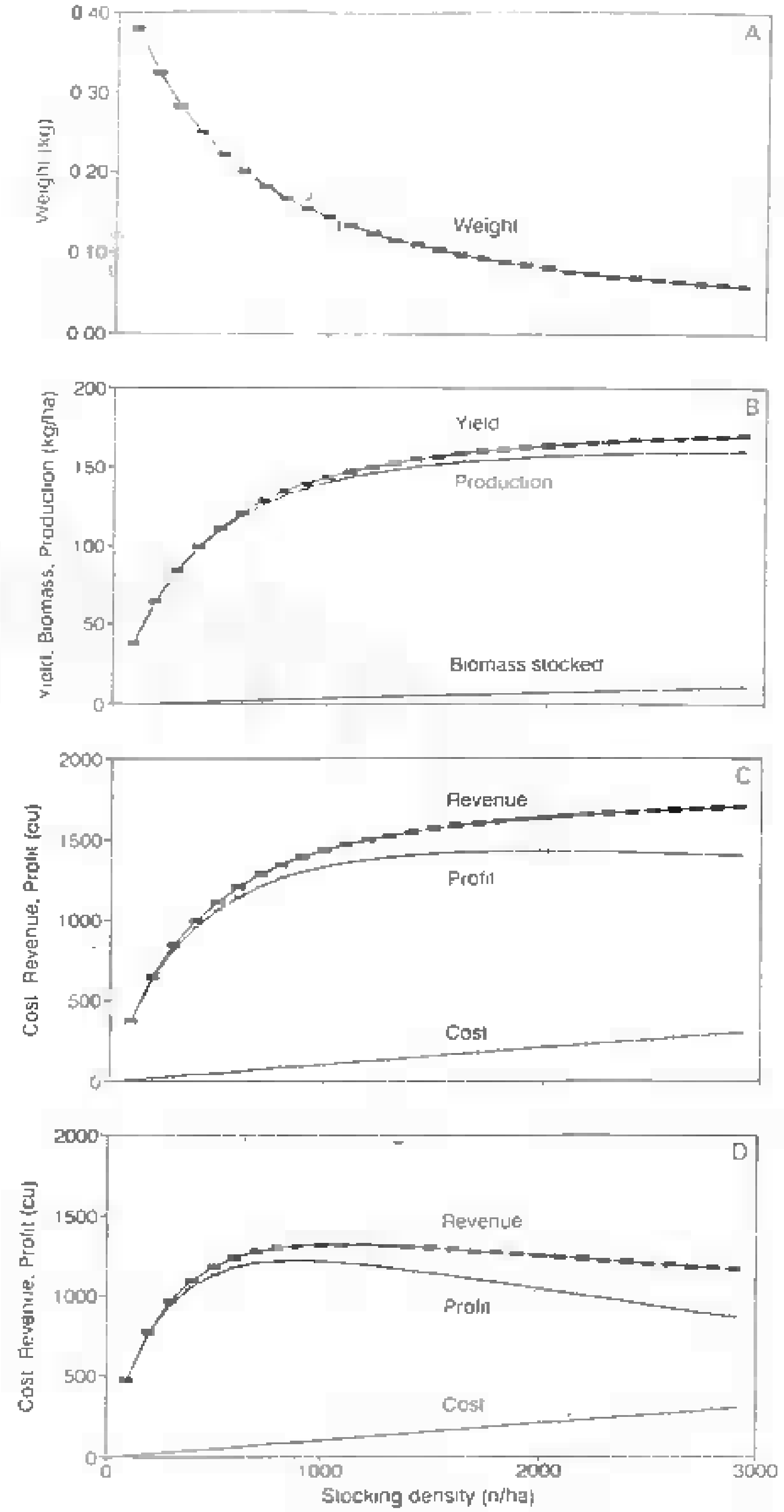

Fig. 4.3. Influence of stocking density on various aspects of production in a seasonal reservoir. (A) Average individual weight at harvesting. (B) Yield, biomass stocked and production. (C) Revenue, seed cost and profit for constant prices per unit weight of produce. (D) Revenue, seed cost and profit for size-dependent prices of produce.

the stocked biomass curve. Maximum production is reached where the slopes of the two curves are equal, in this case at a density of about 2900 fish/ha.

The sales revenue at constant prices per unit weight, the cost of seed fish, and gross profit are shown in Fig. 4.3 (C). Revenue equals yield multiplied by the constant price per unit weight, hence the revenue curve has the same shape as the yield curve. The total costs of seed fish increase linearly with stocking density. Profit is the monetary equivalent of biological production. Maximum profit occurs where the slopes of the revenue and cost curves are equal. The cost per unit weight of seed fish is much higher than the revenue per unit weight of produce. Hence the slope of the cost curve is comparatively high, and maximum profit is reached at a stocking density lower than for maximum production. For constant prices, maximum profit is reached at a density of 1900 fish/ha

Revenue, cost and profit for size-dependent prices are shown in Fig. 4.3 (D). The average weight of produce declines with increasing stocking density, and so does the revenue obtained per unit weight. Hence the revenue curve reaches a maximum at a relatively low stocking density. Consequently, maximum profit is also reached at a low stocking density of only 900 fish/ha (where the slope of the revenue curve equals that of the cost curve)

The above optima of stocking density with respect to various objectives have been derived without considering the fact that there is often a minimum marketable size for produce. If stocking density is optimized for production, or profit at constant price per unit weight, the average weight of produce is well below 0.1 kg. Although small fish are readily accepted on many markets in South Asia, there is nevertheless a lower size limit. If this limit is at 0.1 kg, for example, stocking density must not exceed 1600 fish/ha (Fig. 4.3 A). Production, and profit at constant prices, are still increasing beyond this density, but 1600 fish/ha is the optimal stocking density given the constraint of a lower limit size. If prices are size-dependent, it is advantageous to produce fish bigger than the lower limit size of 0.1 kg.

If the lower limit is 0.15 kg, the maximum stocking density is 800 fish/ha (Fig. 4.3 A). This is also the optimal density by any criterium, given the constraint of a 0.15 kg minimum size.

Constant and size-dependent mortality

The implications of constant and size-dependent mortality for stocking and harvesting are now examined.

The relative survival of the stocked fish to the end of the growth period is shown in Fig. 4.4, for constant and size-dependent mortality. If mortality is constant, i.e. independent of size, survival is the same for all stocking densities. If mortality is size-dependent, survival decreases with increasing stocking density, because fish remain smaller, and consequently are subject to higher mortality. The result is competition-mediated density-dependent mortality as defined Chapter 2. As mentioned in Section 4.2, the size-dependent mortality

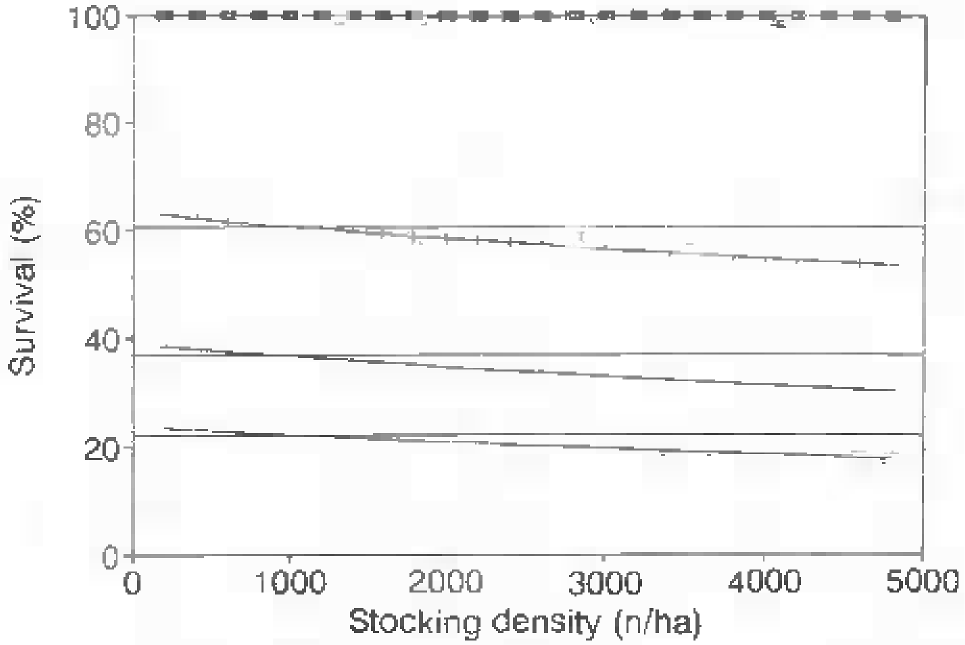

Fig. 4.4. Influence of stocking density on survival under size-dependent and constant mortality. (■) $M_r = 0.0$ y^{-1}, (+) $M_r = 0.406$ y^{-1}, (*) $M_r = 0.840$ y^{-1}, and (□) $M_r = 1.292$ y^{-1}; always for $\varrho = 0.5$ and $L_r = 20$ cm. Horizontal lines indicate constant survival, corresponding to constant mortality rates of 0.0, 1.0, 2.0, and 3.0 y^{-1}. These constant mortality rates equal the average size-dependent mortality rate at a stocking density of 1000 fish per hectare.

rates have been standardized so that at a stocking density of 1000 fish/ha (5 cm mean length), the mean size-dependent mortality equals a predefined constant mortality rate. Hence the survival curves for size-dependent mortality in Fig. 4.4 cross the corresponding constant mortality lines at a stocking density of 1000 fish/ha.

Weight, production and profit are shown in Fig. 4.5 for various levels of constant and size-dependent mortality. Zero mortality does, of course, lead to the same pattern in both cases, and can be used as a reference when comparing the graphs.

Final weight (Fig. 4.5 A and B) follows the familiar pattern of decline with increasing density, at all mortality rates. Final weight always increases with increasing mortality, because mortality eases competition between the survivors and increases their growth rate. This effect is more marked under size-dependent than under constant mortality. Under size-dependent mortality, the bulk of losses occurs at a small size, early in the growth period. Hence the survivors have time to compensate the loss of biomass by increased individual growth.

Production (Fig. 4.5 C and D) always decreases with increasing mortality. The loss in numbers is not fully compensated by increased individual growth. The stocking density at which maximum production is achieved increases with mortality, but increased stocking density can not compensate for the production losses due to mortality. Production is the difference between stocked and harvested biomass, and an increase in stocking density is always an increase in stocked biomass. However, density-dependent growth provides some

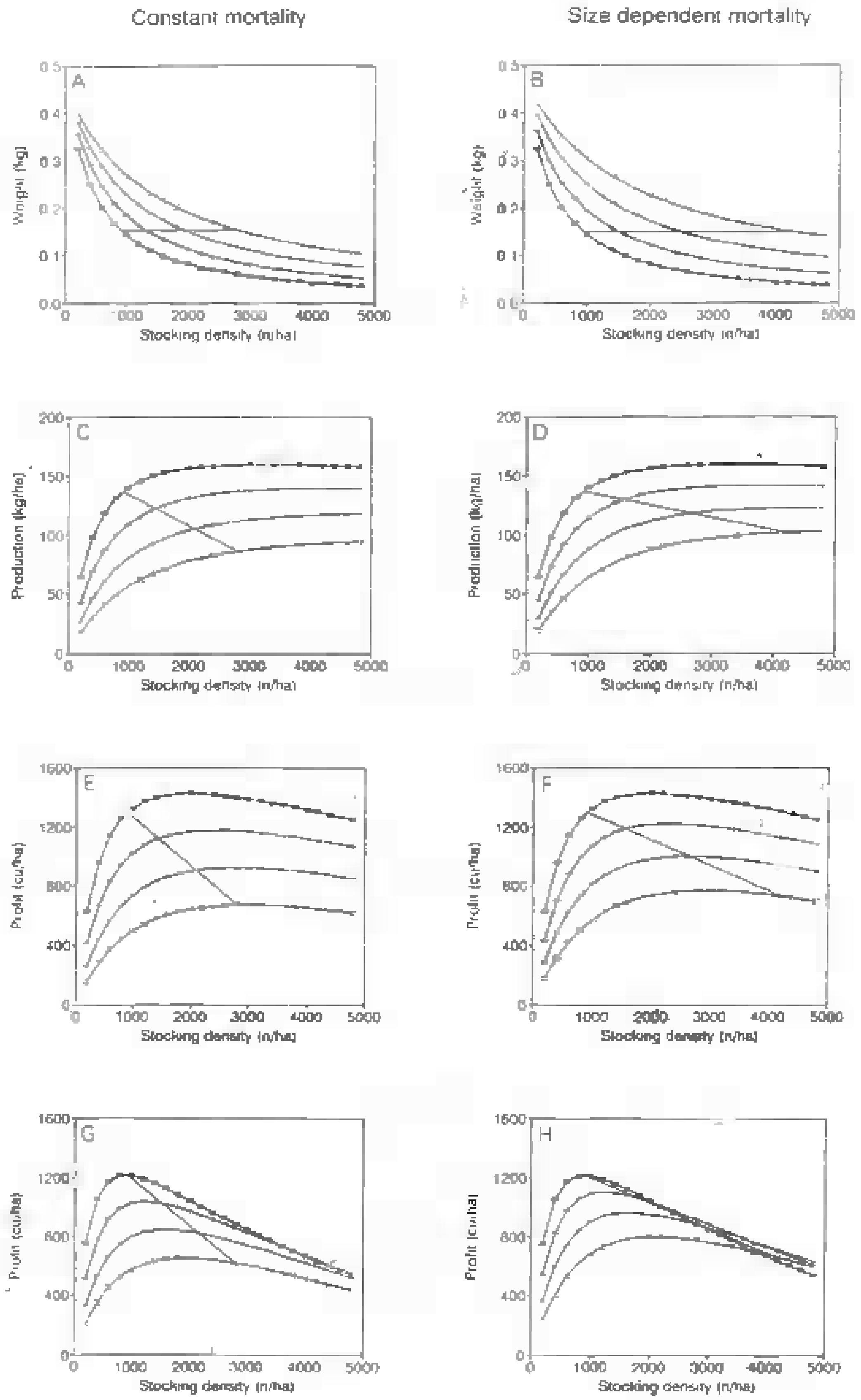

Fig. 4.5. Effects of constant mortality (left hand side) and size-dependent mortality (right hand side) on various aspects of production. (A), (B) Individual size at harvesting. (C), (D) Production. (E), (F) Profit for constant prices per unit weight. (G), (H) Profit for size-dependent prices. (■) $M = 0.0\ y^{-1}$ and $M_s = 0.0\ y^{-1}$, (+) $M = 1.0\ y^{-1}$ and $M_s = 0.406\ y^{-1}$, (*) $M = 2.0\ y^{-1}$ and $M_s = 0.840\ y^{-1}$, (□) $M = 3.0\ y^{-1}$ and $M_s = 1.292\ y^{-1}$. The solid straight lines indicate an average weight of 0.15 kg at harvesting.

compensation for mortality, so that the loss of production is always relatively less than the loss in numbers.

Production under size-dependent mortality (Fig.4.5 D) is slightly higher than under the corresponding constant mortality, due to the growth compensation described above. At a stocking density of 1000 fish/ha, 223 fish/ha survive at an average mortality rate of 3.0 y^{-1}. If mortality is constant, the fish attain an average weight of 0.270 kg, and the biomass harvested is 60 kg/ha. If mortality is size-dependent, the average weight is 0.303 kg and consequently the biomass harvested is 65 kg/ha. At this particular stocking density, survival under both mortality regimes is equal, and the difference in yield simply reflects the difference in growth. At higher densities, survival is lower under size-dependent mortality than under constant mortality. However, production under size-dependent mortality still exceeds slightly that under constant mortality. The decrease in survival with increasing density is more than compensated by growth.

Profits (Fig. 4.5 E, F, G and H), like production, decrease with increasing mortality. For a given level of mortality, maximum profit at constant prices is reached at a density below that of maximum production, and maximum profit at size-dependent prices is reached at still lower density. This can be taken as a general rule, which is valid as long as the cost per unit weight of stocking material is higher that the revenue per unit weight of produce.

If there is a minimum marketable size for produce, this size may be reached at a stocking density below the optimal densities with respect to profit or production. In this case, stocking densities are chosen so as to produce fish that average at the minimum marketable size. In Fig. 4.5, solid lines indicate the stocking densities at which a weight of 0.15 kg is reached. If 0.15 kg is the minimum marketable size, stocking densities above those indicated by the line must be avoided.

Size of seed fish

Up to now, no consideration has been given to the optimal size of seed fish. If a range of sizes of seed fish is available, which size should be used for stocking?

Both density-dependent growth and size-dependent mortality have an influence on the optimal size of seed fish. In order to disentangle the two, results are presented in Fig. 4.6 both for no mortality, and for high size-dependent mortality ($\varrho=0.5$, $M_r=1.292$).

In the absence of mortality, the implications of density-dependent growth alone for the optimal size of seed fish are demonstrated. The average weight of produce, production and profit at no mortality are shown in Fig. 4.6 (A, C, E, and G), for mean lengths of seed fish ranging from 3 cm to 9 cm.

Weight at harvesting is shown in Fig. 4.6 (A). At low stocking density, larger seed fish give rise to larger produce. However, the difference in size diminishes with increasing stocking density. Above 1500 fish/ha, the final weights are virtually identical, independent of the size of seed fish.

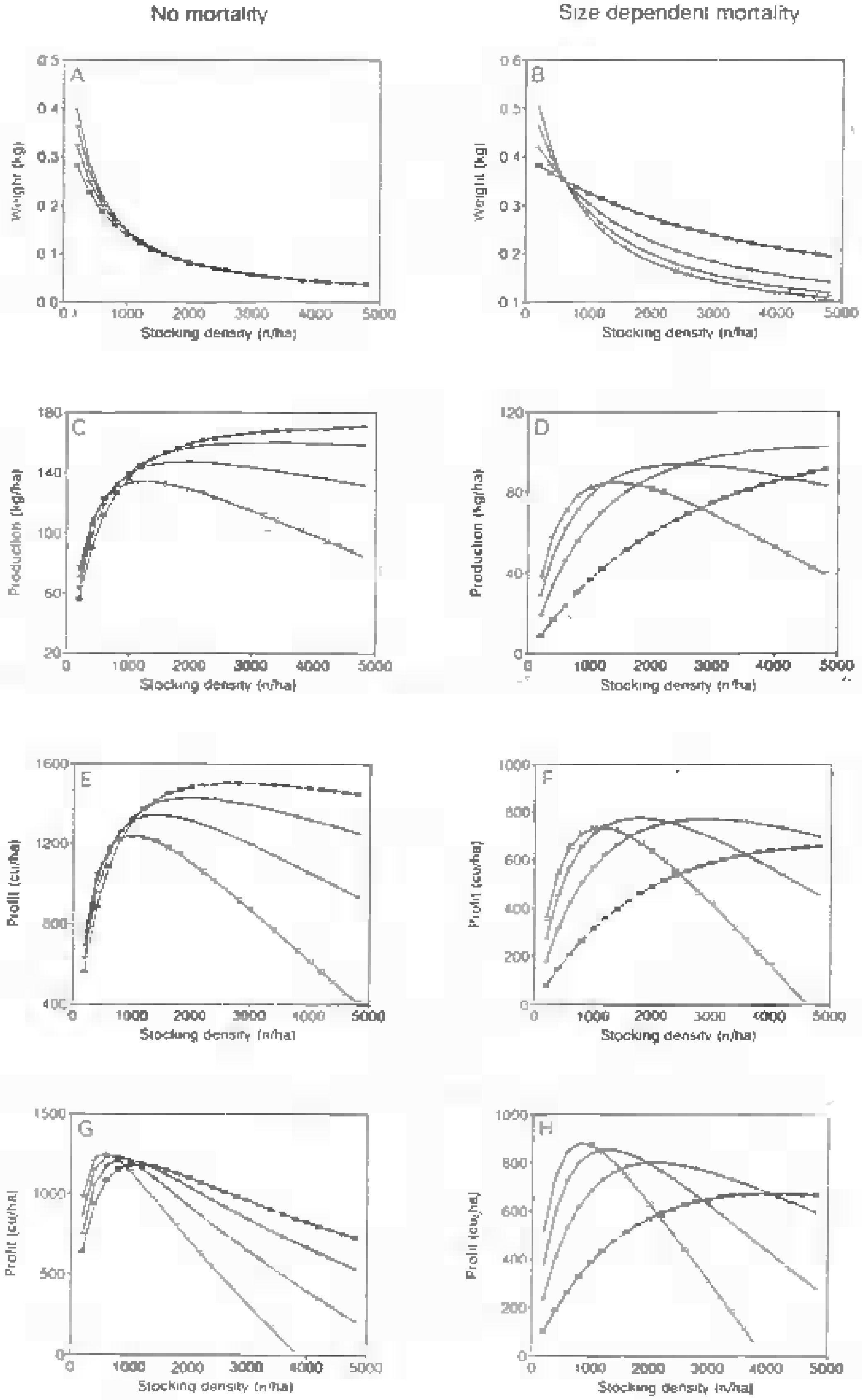

Fig. 4.6. Influence of the size of seed fish on various aspects of production, for no mortality (left hand side) and a size-dependent mortality (right hand side) of $M_r = 1.292\ y^{-1}$ with $\rho = 0.5$. (A), (B) weight at harvesting (C), (D) Production. (E), (F) Profit for constant prices per unit weight. (G), (H) Profit for size-dependent prices. The average length of seed fish is (■) 3 cm, (+) 5 cm, (*) 7 cm, and (□) 9 cm.

Production (Fig. 4.6 C) reflects the influence of seed fish size on growth. At low density, there is a slight advantage in stocking large fingerlings of 9 cm length. The optimal size then decreases with increasing density: consecutively 7 cm, 5 cm, and finally 3 cm is the optimal length. The difference in production between the various seed fish sizes is greatest at very high stocking density. The final weight, and hence yield, obtained at high density is independent of the size of seed fish. The differences in production are solely due to the difference in biomass stocked. If large fingerlings are stocked, the initial biomass is already high, and production is accordingly low. The highest overall production is achieved by stocking small fingerlings at a high density.

Profit at constant prices per unit weight of produce (Fig. 4.6 E) behaves in very much the same way as production, but maximum profit is reached at lower stocking densities than maximum production. If prices are size-dependent (Fig. 4.6 G), the picture changes in both quantitative and qualitative terms. It becomes more advantageous to stock large fingerlings at a low density, and this effect is so pronounced that the overall profit maximum is achieved by stocking 9 cm long fingerlings at a density of 500 fish/ha. However, it is possible to achieve almost the same profit by stocking smaller fingerlings at a higher density.

When stocking large fingerlings, optimal production or profit are achieved over a relatively narrow range of stocking densities. Small seed fish yield good results over a wider range of stocking densities, because the biomass stocked and the cost of seed fish are relatively low, even at high densities.

These results are affected by mortality. Constant mortality results in a general decrease of yield and profit, but does not affect the relative performance of the various seed sizes.

Size-dependent mortality yields qualitatively different results (Fig. 4.6 B, D, F, and H). At low stocking density, larger seed fish give rise to larger produce (Fig. 4.6 B), just as in the case of zero mortality. However, this pattern reverses at higher stocking densities, where the smallest seed fish give rise to the largest produce. This qualitative change is the result of size-dependent mortality. Small seed fish suffer a high mortality early in the growth period, so that competition between the survivors is low. Large seed fish are less affected by mortality, even at high density. Hence their density at harvesting is still comparatively high, and their average size is accordingly low.

Production (Fig. 4.6 D) demonstrates the compensatory role of density-dependent growth and size-dependent mortality. Similar levels of production can be achieved with any size of seed fish. The smaller the seed fish, the higher the stocking density required to reach maximum production. The highest production is achieved by stocking small seed fish at high density, but the advantage over larger fingerlings stocked at lower density is only marginal.

Profit at constant prices per unit weight of produce (Fig. 4.6 F) can also reach a similar level for any size of seed fish. Here, the highest profit is achieved by stocking 7 cm long fingerlings at a density of 1700 fish/ha. Hence there is an intermediate optimal size, but the advantage of this size group over others is only marginal.

If prices of produce are size-dependent (Fig. 4.6. H), maximum profit is obtained by stocking large fingerlings at a low density, and the difference in maximum profit between the size groups is more pronounced.

As in the absence of mortality, production and profit are very sensitive to stocking density for large fingerlings, while small fingerlings yield good results over a wide range of densities.

In Fig. 4.7, production is shown as a function of biomass stocked, for different sizes of seed fish, and for no mortality and high size-dependent mortality. In the absence of mortality, the smallest fingerlings give rise to the highest production, and they need to be stocked at a low biomass only. Larger fingerlings must be stocked at a higher biomass to yield maximum production. This rule also applies regardless of the level of production: the larger the seed fish, the higher the biomass of them that must be stocked to attain a certain level of production. In the absence of mortality, a production of 130 kg/ha can be achieved by stocking 1 kg of 3 cm, 3 kg of 5 cm, 6 kg of 7 cm, or 15 kg of 9 cm fingerlings. As shown in Fig. 4.6 (C), the stocking density of 3 cm fingerlings necessary to achieve a production of 130 kg/ha (at no mortality) is less than two times the necessary density of 9 cm fingerlings. Yet the average weight of a 9 cm fingerling is 27 times that of a 3 cm fingerling. Hence the biomass to be stocked of 9 cm fingerlings is about 15 times that of 3 cm fingerlings.

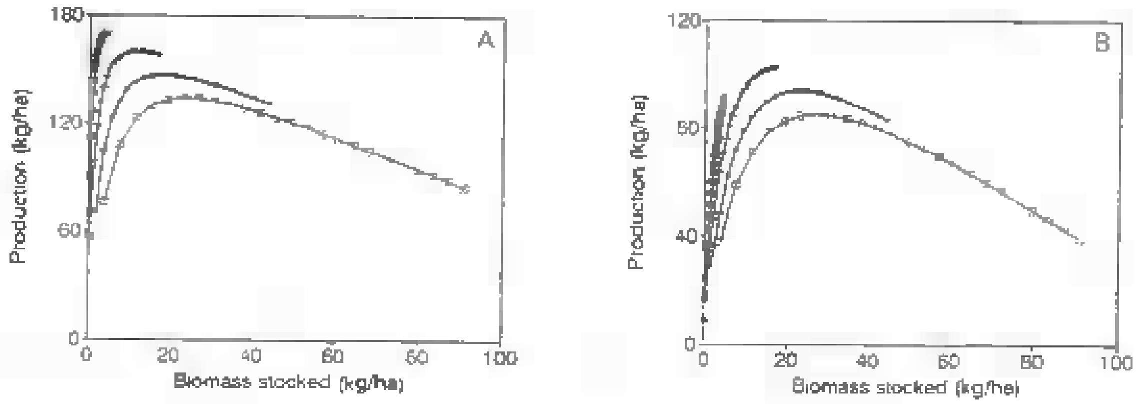

Fig. 4.7. Production as a function of stocked biomass, for different sizes of seed fish (A) No mortality (B) Size-dependent mortality ($M_r = 1.292\ y^{-1}$, $\varrho = 0.5$). The average length of seed fish is (■) 3 cm (+) 5 cm, (*) 7 cm, and (□) 9 cm

The results for size-dependent mortality (Fig. 4.7 B) are similar, the biomass to be stocked for optimal production increases sharply with the size of fingerlings As has been shown earlier, the overall maximum production under size dependent mortality is achieved by stocking 5 cm long fingerlings.

The influence of the degree of size-dependence in mortality on the optimal size of seed fish is demonstrated Fig. 4.8, where results are shown for different values of the parameter ϱ ($\varrho = 0.5$, and $\varrho = 1.0$). The survival of fish during the growth period is shown in Figs. 4.8 (A) and (B). As expected, the difference in survival between length groups of seed fish increases with increasing degree of size-dependence of mortality. The survival of large seed fish is highly dependent on stocking density, while this effect is less marked for smaller seed fish. The stocking of large seed fish results in strong competition, and consequent competition-mediated density-dependent mortality. Small seed fish stocked at the same density are subject to less competition and to higher mortality, so that competition-mediated density-dependence is less pronounced.

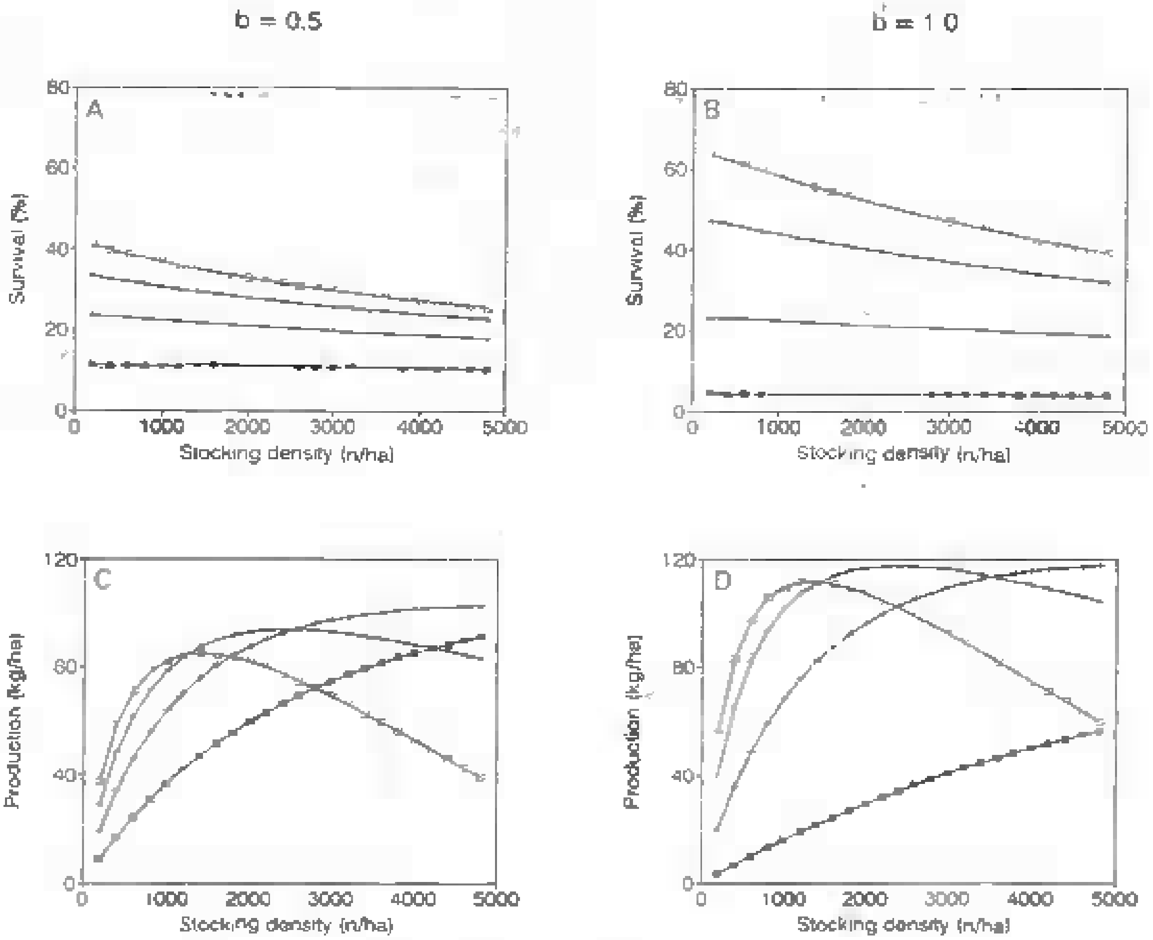

Fig. 4.8. Influence of the degree of size-dependence in mortality on survival and production of different size groups of seed fish. Left hand side: $\varrho = 0.5$, right hand side: $\varrho = 1.0$. (A) Survival for $\varrho = 0.5$. (B) Survival for $\varrho = 1.0$. (C) Production for $\varrho = 0.5$. (D) Production for $\varrho = 1.0$. The average lengths of seed fish are (■) 3 cm, (+) 5 cm, (*) 7 cm, and (○) 9 cm.

The survival of 5 cm long seed fish is about the same for both degrees of size dependent mortality. For larger fingerlings, survival is higher under strong size-dependence in mortality, while survival of smaller fingerlings (3 cm) is much lower. Production (Figs. 4.8 C and D) reflects the influence of the degree of size-dependence in mortality on survival. Fingerlings of 5 cm or larger produce more if size-dependence is stronger, while 3 cm fingerlings produce less.

The higher the degree of size-dependence in mortality, the larger the optimal size of seed fish. However, while very small seed fish are a definite disadvantage, the difference between larger seed fish is marginal.

Summary of management implications

(1) It is usually optimal to produce fish at or only slightly above the minimum marketable size. This determines the optimal stocking density.

(2) Maximum profit is reached at a lower, or at the same stocking density as maximum production.

(3) If revenue per unit weight of produce is size-dependent, it may be optimal to produce fish slightly larger than the minimum size, by stocking at a lower density. However, it is never optimal to produce very large fish.

(4) Mortality is always limiting production and profit. A high stocking density can not compensate for high mortality.

(5) The optimal stocking density increases with increasing mortality.

(6) Similar levels of production or profit can be reached by stocking various sizes of seed fish.

(7) If mortality is low and/or weakly size-dependent, it is optimal to stock small seed fish at a high density. At high, strongly size-dependent mortality, there is a well defined minimum size, but similar levels of production or profit are reached over a range of larger sizes

(8) The biomass that must be stocked to attain a certain level of production increases with increasing individual size of seed fish.

(9) Production and profit are more sensitive to stocking density for large fingerlings than for small fingerlings. Large fingerlings are easily overstocked, resulting in a loss of production and profit.

4.3.2 Staggered Harvesting

Staggered harvesting refers to a regime where harvesting is effected over a certain time span, rather than limited to the end of the production period. Fish that have reached a marketable size are being harvested continuously, thereby thinning the population and increasing the growth rate of the remaining individuals.

The utility of staggered harvesting is explored here in relation to stocking density and minimum marketable size. The results in the previous Section suggest that it is often optimal to produce fish at, or only slightly above the minimum marketable size. Therefore, the selectivity of gear used in staggered harvesting will normally be such that the average size in the catch is close to the minimum marketable size.

In the simulations, knife-edge selection is assumed at length l_c, i.e. no fish are caught below this length, while all larger fish are subject to 100% selection by the fishing gear. Fishing mortality is assumed to be infinitely high, i.e. all fish larger than l_c are caught within one time step after reaching l_c. The total yield consists of the larger fish caught during the production period, and all fish remaining in the reservoir and harvested at the end of the period.

The effects of staggered harvesting are illustrated in Fig. 4.9. The length structure of the population and of the catch are shown for a cohort stocked at 2500 fish/ha, with and without staggered harvesting at $l_c = 18$ cm, in the absence of natural mortality. For a single harvesting event, Fig. 4.9. (A) shows the length distribution of the population in monthly intervals, and Fig. 4.9 (C) shows the length distribution of the catch taken at the end of the

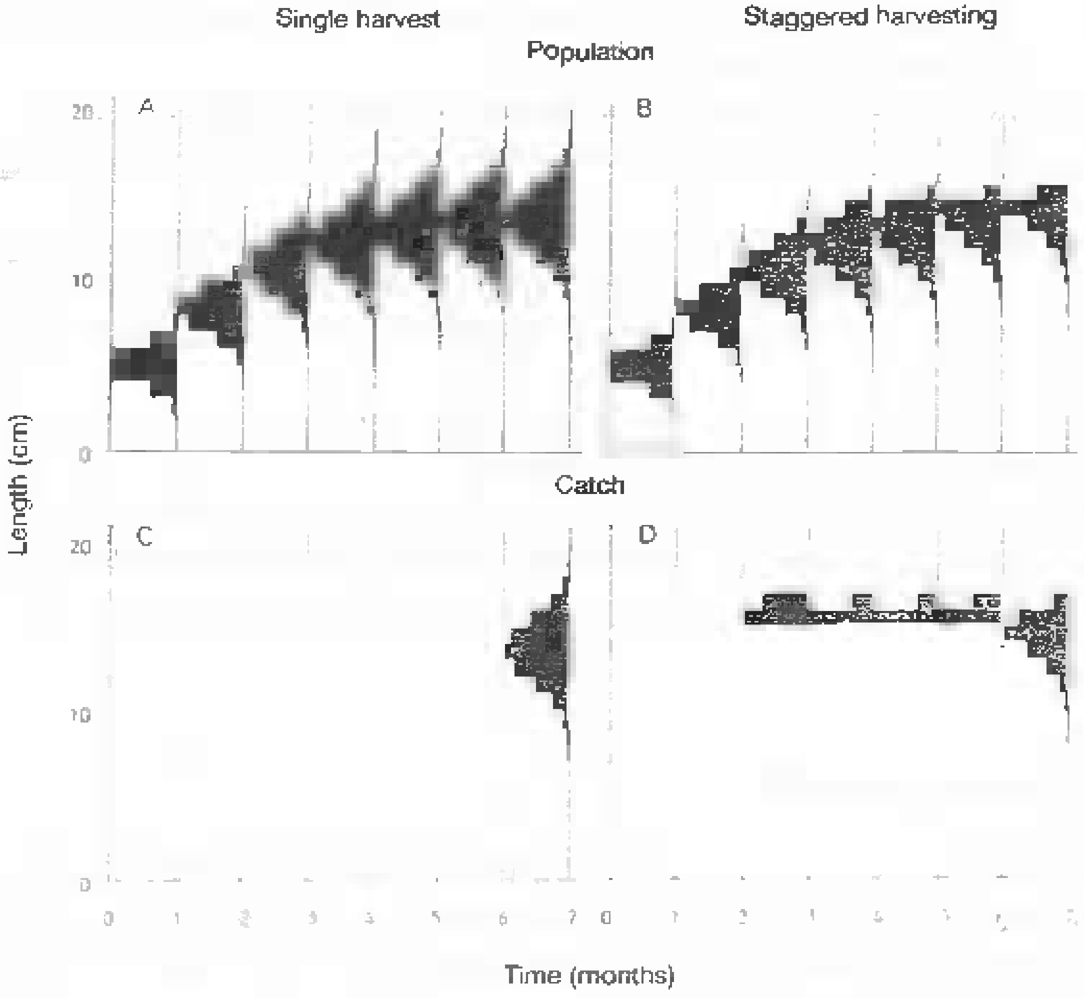

Fig. 4.9. Influence of staggered harvesting on population and catch length structure. (A) Length frequency distribution of a cohort over a six months growth period (Stocking density 2500 fish per hectare, no mortality). (B) Length frequency distribution of the same cohort in the case of staggered harvesting at a selection length $l_c = 18$ cm. (C) Length frequency distribution of the catch taken from the cohort displayed in (A). (D) Length frequency distributions of the catch taken under staggered harvesting (from the cohort shown in B).

growth period. Length distributions of the population and of the catch under staggered harvesting are shown in Figs 4.9 (B) and (D), respectively. Staggered harvesting has three main effects: the catch is obtained over a longer time span, the average size of produce is larger, and the size of produce is more uniform. The selective removal of large fish has a strong effect on biomass, and the improved growth in the remaining population is clearly visible in Fig. 4.9 (B).

Staggered harvesting presents an advantage over a single harvest under certain conditions. In Fig. 4.10, average weight of produce, production, and profit are shown as a function of stocking density, for staggered harvesting at gear selection lengths l_c of 15, 18, and 20 cm, and for single harvesting at the end of the production period. No mortality, and size-dependent mortality ($M_T = 1.292\ y^{-1}$, $\varrho = 0.5$) are examined.

Average weight (Fig. 4.10 A) in the absence of staggered harvesting follows the familiar pattern of decline with increasing stocking density. At low stocking density, fish grow much larger than the gear selection lengths. Under staggered harvesting, these fish are caught soon after reaching l_c (15, 18, or 20 cm). Hence, at low stocking density, the average weight under staggered harvesting is almost constant, and lower than the weight reached under single harvesting. Staggered harvesting is clearly not beneficial at low stocking densities. The average weight under single harvesting declines with increasing density, and at some density falls below the average weight under staggered harvesting at any given l_c. Above this stocking density, staggered harvesting is advantageous because it increases the average size of the produce and hence production with respect to single harvesting. If density is increased further, the average weight under staggered harvesting approaches that under single harvesting. Hence staggered harvesting leads to an increase in the average weight of produce over some limited range of stocking densities. This pattern is similar for all three selection lengths l_c, but the benefit of staggered harvesting is greatest at low l_c, i.e. when fish are harvested at a small size.

If fish of a certain size are to be produced under single harvesting, this is achieved by stocking at such a density that the desired average size is reached at the end of the production period. When fish are stocked at a higher density, they do not reach the desired average size. However, because a cohort comprises fish of a range of sizes, some fish at least are growing to the desired size before the end of the period. The harvesting of such individuals eases competition within the remaining population, and allows smaller fish to reach the desired size. Hence the average size of produce is increased with respect to single harvesting at the same stocking density. At very high stocking densities, very few or no fish will reach the desired size, and staggered harvesting can not take effect.

Production under staggered harvesting, at no mortality, is shown in Fig. 4.10 (B). Staggered harvesting increases production relative to single harvesting at those stocking densities where it increases the average size of produce. For any selection length l_c, there is a certain range of stocking densities at which staggered harvesting is beneficial. The smaller l_c, the greater is the advantage of staggered harvesting, at the corresponding optimal stocking

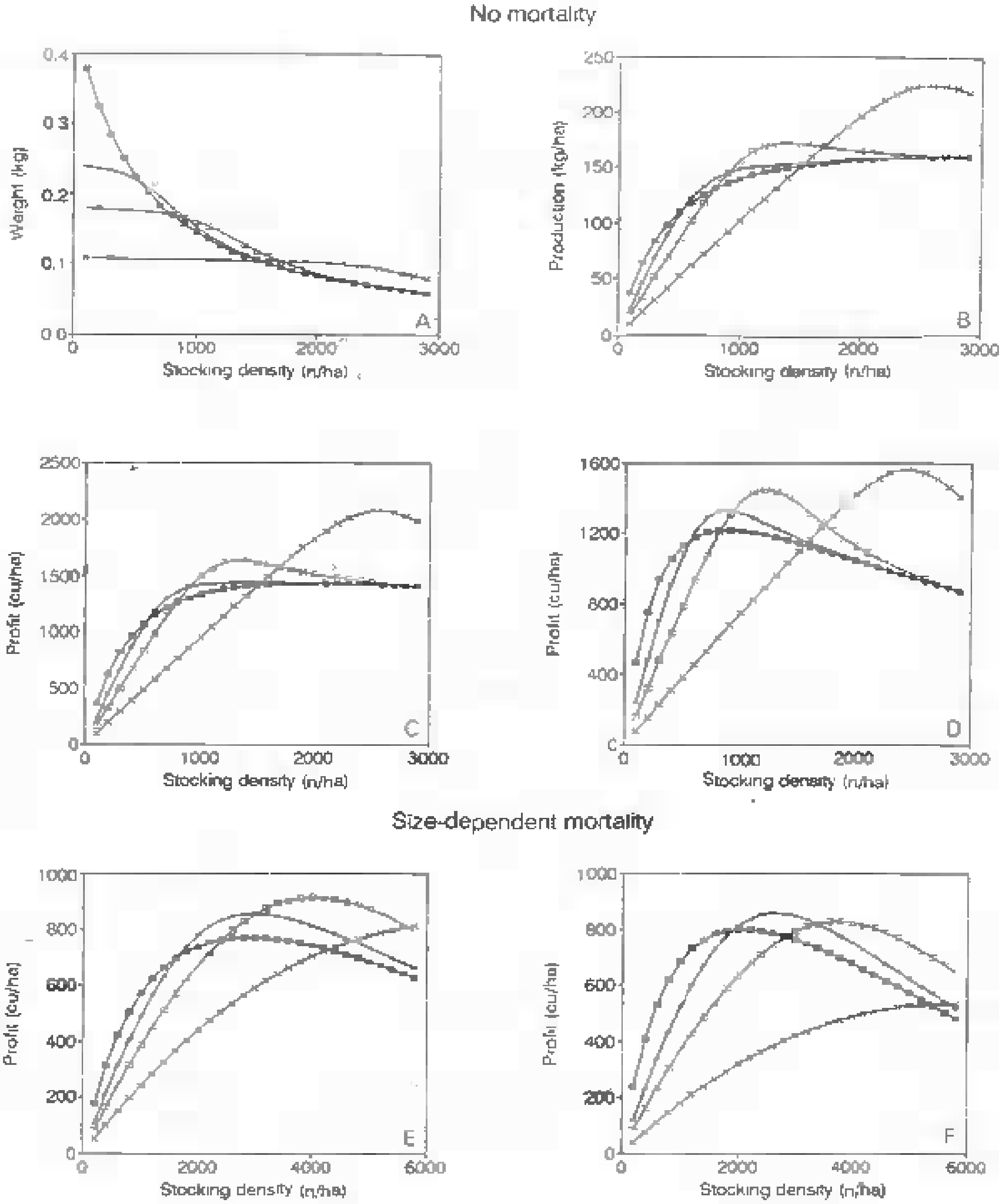

Fig. 4.10. Effects of staggered harvesting in relation to stocking density. (A, B, C, D) No mortality, and (E, F) size-dependent mortality ($M_r = 1.292$, $\varphi = 0.5$). Note different scales on both axes. Standard parameter values and a six months growth period. (A) Average weight of produce, no mortality. (B) Production, no mortality. (C) Profit for constant prices per unit weight, no mortality. (D) Profit for size-dependent prices, no mortality. (E) Profit for constant prices, size-dependent mortality. (F) Profit for size-dependent prices, size-dependent mortality. (■) No staggered harvesting, (*) $l_c = 20$ cm, (□) lc = 18 cm, and (+) lc = 15 cm.

density. The optimal stocking density for producing fish of a certain size under staggered harvesting is always higher than the density at which the same average size is reached under single harvesting. For example, an average size of 0.15 kg is reached at a stocking density of 900 fish/ha under single harvesting. The same average size is reached under staggered harvesting at $l_c=18$ cm, at a stocking density of 1200 fish ha. Hence the optimal stocking density under this staggered harvesting regime is about 30% higher than under single harvesting.

Profit for constant price per unit weight (Fig. 4.10 C) behaves in a way similar to production, but maximum profit is always reached at a slightly lower stocking density than maximum production.

If prices of produce are size-dependent (Fig. 4.10 D), maximum profit is reached at still lower stocking densities. Staggered harvesting is comparatively less advantageous for size-dependent prices than it is when prices are constant. As demonstrated above, staggered harvesting is most effective in terms of production if fish are harvested at a small size, but such fish are of a low value if prices are size-dependent.

Mortality has an important bearing on the potential benefits of staggered harvesting. Fig 4.10 (E) and (F) show profit for constant and size-dependent prices respectively, at size-dependent mortality ($M_r=1.292\ y^{-1}$, $\varrho=0.5$). The production of small fish under staggered harvesting looses its advantage, because the dense, slow growing population is subject to very high losses. If prices are constant (Fig. 4.10 E), staggered harvesting at higher selection lengths can still increase profits over those from single harvesting. If prices are size-dependent (Fig. 4 10 F), the benefit of staggered harvesting is at best marginal. Staggered harvesting at low selection length l_c even incurs a substantial loss of profit.

The benefit of staggered harvesting is highly dependent on the duration of the production period. In Fig. 4 11, maximum production with and without staggered harvesting at $l_c=18$ cm is shown in relation to the duration of the production period; for no mortality (Fig. 4.11 A), and size-dependent mortality (Fig 4 11 B) ($M_r=1.292\ y^{-1}$, $\varrho=0.5$). Maximum production is subject to the constraint of a minimum average size of produce of 0.15 kg.

In the absence of mortality (Fig. 4.11 A), the absolute and relative benefit of staggered harvesting increases with the duration of the production period. During a 4 month period, staggered harvesting incurs a production loss, but at 6 months there is a gain of 20%, which rises to 44% for a 12 months period.

At high, size-dependent mortality (Fig. 4.11 B), the picture is somewhat different. Production under both harvesting regimes increases initially with the duration of the period, but is about constant for periods of 8 months or longer. Staggered harvesting again incurs a loss of production during a 4 months period, but is beneficial if the production period is longer. However, neither production, nor the benefit of staggered harvesting are increasing for periods longer than 8 months. At high, size- dependent mortality, the cohort is

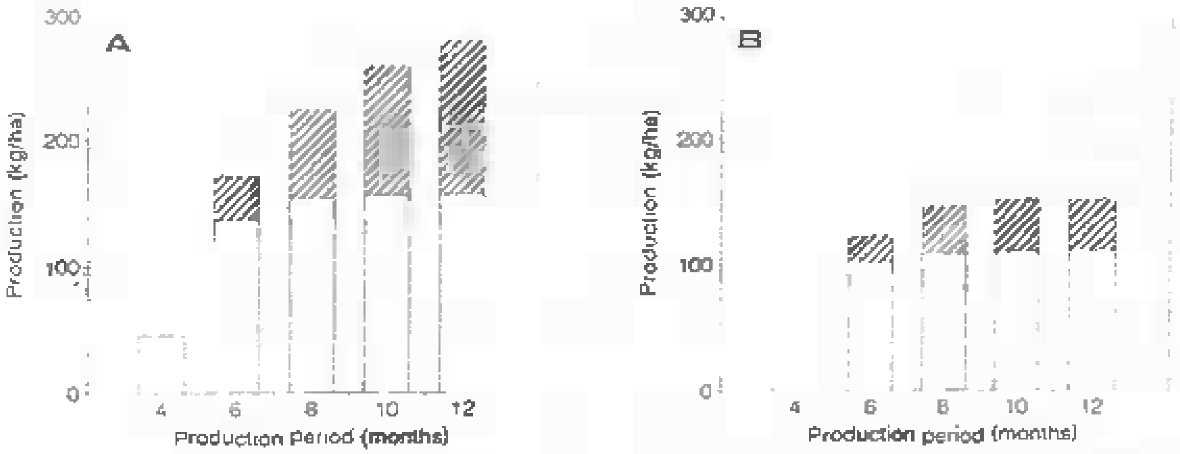

Fig. 4.11. Influence of the length of the production period on production, under single and staggered harvesting. Hatched bars denote production gained by staggered harvesting. (A) No mortality (B) Size-dependent mortality ($M_r = 1\ 292\ y^{-1}$, $\varrho = 0.5$).

thinned naturally early in the growth period, and an increase in stocking density is compensated by increasing mortality. The number of fish surviving to reach harvesting size is about constant, and their growth rate is relatively high because of low competition. Hence the thinning effect of staggered harvesting is limited.

Summary of management implications

(1) Under staggered harvesting, the yield is obtained over a longer time period, production is higher, and the produce is larger and more uniform in size than under single harvesting, provided that the optimal stocking density is maintained

(2) Optimal stocking density under staggered harvesting is higher than under single harvesting.

(3) Staggered harvesting at low stocking density incurs a loss of production.

(4) Staggered harvesting is most effective if natural mortality is low, and if fish are harvested at a small size. If mortality is high, fish should be harvested at a larger size but staggered harvesting is less effective as a means of increasing production

(5) The absolute and relative gain in yield due to staggered harvesting increases with the duration of the growth period, but approaches a constant value for long periods

(6) If natural mortality is high, long production periods offer no advantage. This applies to staggered as well as to single harvesting

4.3.3 Multiple Stocking

In the previous Sections, stocking has been limited to one instance at the beginning of the growth period. Under some conditions, it may be advantageous to stock several times during the growth period. Two modes of multiple stocking are considered here. The first approach is to split the growth period into two or more discrete production cycles with one stocking and one harvesting event in each. The other approach is to combine multiple stocking with staggered harvesting, during a single production cycle.

Several production cycles

The feasibility of splitting the growth period into several discrete production cycles is easily investigated. Maximum production is calculated for various growth periods. A long growth period can be split up into two or three short cycles, in which case the total production during the period equals two or three times the production achieved during one short cycle.

In this analysis, maximum production is calculated subject to the constraint of a minimum marketable size of 0.15 kg. The total production and production per month that can be achieved during cycles of 4 to 12 months are given in Tab. 4.2, for no mortality and size-dependent mortality ($M_r=1.292\ y^{-1}$, $\varrho=0.5$). Cycles shorter than 4 months are not included, because fish fail to reach the minimum size even at low stocking density. Total production increases sharply with increasing length of the period at first, but then approaches a constant value for long periods. Obviously, there is no advantage in very long production cycles. Production per month reaches a maximum for cycles of 5 to 6 months, under both mortality regimes. Hence the optimal length of a production cycle is 5 to 6 months.

In Fig. 4.12, total production in the absence of mortality is shown for periods of 4 to 12 months, managed as one, two, or three discrete production cycles. For periods of up to 6 months, a single production cycle is the only feasible option. An 8 months period could be split into two 4 months cycles, but this would result in a loss of production. Conversely, the production during a 10 or 12 months period is greatly increased by splitting it up into two cycles of 5 or 6 months. This ties in with the result that 5 to 6 months is the optimal duration of the production cycle. A 12 months period could also be split into three 4 months cycles, but production would be lower than during two 6 months cycles.

The relative benefit of producing in two cycles increases with increasing natural mortality: the gain in production is 50% and 73% during 10 and 12 months periods at no mortality, and 56% and 85%, respectively, at high size-dependent mortality ($M_r=1.292\ y^{-1}$, $\varrho=0.5$) A shorter production cycle reduces the loss due to mortality, and this effect is most noticeable if mortality is high

Tab. 4.2: Maximum production achieved during different growth periods, subject to a minimum average weight at harvesting of 0.15 kg. Also given are the stocking densities at which maximum production is achieved.

	No mortality ($M = 0$)			Size-dependent mortality ($M_r = 1.292\ y^{-1}$, $\varrho = 0.5$)		
Period (m)	Stocking density (n/ha)	Production (kg/ha)	Production (kg/ha/m)	Stocking density (n/ha)	Production (kg/ha)	Production (kg/ha/m)
4	300	45	11	1100	42	11
5	800	117	23	2700	85	17
6	900	136	23	4200	102	17
8	1000	153	19	3900	108	14
10	1000	156	16	3400	109	11
12	1000	157	13	2900	110	9

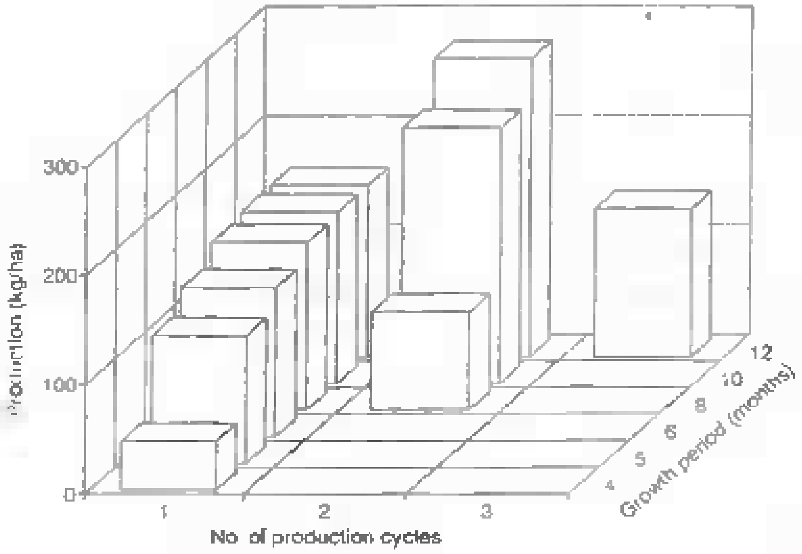

Fig. 4.12. Total production as a function of the length of the growth period and the number of production cycles during the period. No mortality

Multiple stocking and staggered harvesting

In Section (4.3.2), it has been shown that staggered harvesting can often yield a higher production than single harvesting. Instead of splitting a production period into several discrete cycles, multiple stocking can be combined with staggered harvesting during a single cycle. This option is explored here for a ten months growth period.

Various stocking patterns were simulated, always for staggered harvesting at an l_c of 18 cm (resulting in an average weight of produce of about 0.15 kg). Only one multiple stocking pattern was found to offer an advantage over single stocking with staggered harvesting, or several discrete production cycles. This pattern was continuous stocking during the first 6 months of the period.

Production under various stocking and harvesting regimes is given in Tab. 4.3. At no mortality, the highest production is achieved with a single stocking and staggered harvesting, followed by continuous stocking over 6 months, and two discrete cycles. At high size-dependent mortality, the picture is quite different. Continuous stocking over the first 6 months is best, closely followed by two discrete cycles. A single stocking with thinning does worse, because fish stay in the reservoir for a long time and suffer high losses. At high mortalities, there is a strong advantage in reducing the time span that fish stay in the reservoir

Under certain conditions, there may be a slight advantage in multiple stocking with thinning over other stocking and harvesting regimes.

Tab. 4.3: Effect of various stocking and harvesting regimes on total production during a ten months growth period. Maximum production is given, subject to the constraint of a minimum average weight of 0.15 kg. The management patterns are: single and double cycles with complete harvesting at the end of cycle; and single stocking, continuous stocking over 10 months and continuous stocking over the first 6 months, all with staggered harvesting at l_c = 18 cm and infinite fishing mortality.

	$M = 0$		$M_r = 1.292\ y^{-1}$, $\varrho = 0.5$	
Regime	Production (kg/ha)	Stocking density (n/ha)	Production (kg/ha)	Stocking density (n/ha)
Single cycle (10 months)	156	1000	109	3400
Two cycles (5 months each)	234	1600	170	5400
Single cycle with staggered harvesting	**259**	1600	150	8000
Continuous stocking (first 6 months), staggered harvesting	**250**	1700	184	8600

Summary of management implications

(1) If the growth period is sufficiently long, multiple stocking will often lead to an increase in production.

(2) The simplest mode of multiple stocking is to split the growth period into two (or three) discrete production cycles. This will lead to a strong increase in yield when growth periods are long, and particularly if mortality is high. If mortality is low, single stocking with staggered harvesting yields better results than two discrete cycles.

(3) More complex multiple stocking patterns, combined with staggered harvesting during a single production cycle may under some circumstances yield slightly better results than two discrete cycles or a single cycle with staggered harvesting. However, the gain is unlikely to be substantial.

(4) Two discrete production cycles or one cycle with staggered harvesting are the principal management options to be considered if a long growth period is available. Two cycles are optimal if natural mortality is high, while a single cycle with staggered harvesting is optimal at low mortality.

4.4 DYNAMICS OF A PERENNIAL RESERVOIR FISHERY

In a perennial reservoir fishery, the length of the production cycle is not limited by physical constraints as in seasonal reservoirs. The production cycle (time between stocking and harvesting of a cohort) may be completed after a few months, or extend over several years. The actual length of the cycle is determined by stocking density and fishing patterns.

Section (4.4.1) explores the dynamics of a perennial reservoir fishery under continuous stocking and harvesting. The implications of discontinuous stocking, as is practised in most reservoir fisheries, are examined in Section (4.4.2).

All simulations of perennial reservoir fisheries are done for a moderately high, size-dependent mortality ($M_r = 1.292\ y^{-1}$, $\varrho = 0.5$). This is likely to be a good approximation to the conditions found in many perennial tropical reservoir fisheries.

4.4.1 Continuous Stocking

If a perennial reservoir is stocked and harvested continuously, with constant stocking density, fishing mortality and gear selectivity, then the fish population is in a state of demographic equilibrium. The population biomass is constant, and the size structure stable. Hence fish grow according to a standard VBGF, with a constant $L_{\infty B}$ determined by the population biomass. The yield obtained from the fishery is also constant over time.

Population biomass, production and the time span needed by an average seed fish to reach the gear selection length are shown in Fig. 4.13, as a function of stocking density. The fishery is harvested continuously at a selection length L_c of 18 cm, with infinitely high fishing mortality. Population biomass increases almost linearly with stocking density over the simulated range of densities. Hence L_∞ decreasing linearly with biomass, and the time it takes a seed fish to grow to the gear selection length increases from about 0.3 to 0.6 years over the density range explored. Annual production reaches its maximum of 265 kg/ha at a stocking density of 11000 fish/ha/year. The population biomass then is 67 kg/ha, so that the annual P/B-ratio is 4:1. An average seed fish needs about half a year to grow to the selection length.

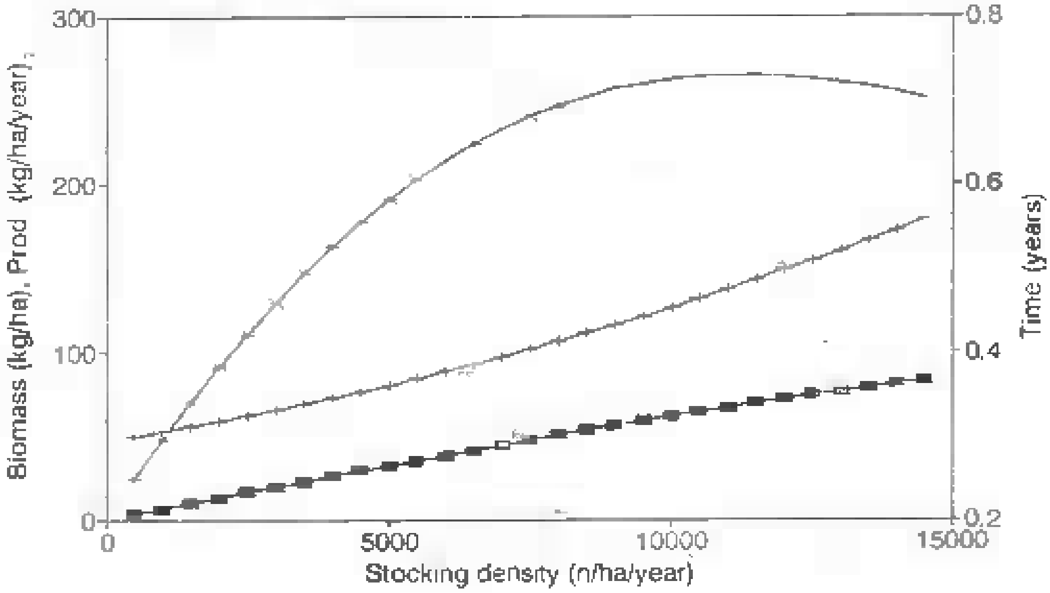

Fig. 4.13. Aspects of production in a perennial reservoir fishery, stocked continuously and harvested continuously with a selection length of L_c = 18 cm and very high fishing mortality. (■) Biomass of the population, (*) Production per year, and (+) Time span needed by an average seed fish to grow to the selection length L_c.

Comparison of production under a limited cycle and continuous culture

Some small reservoirs are perennial, but are nevertheless managed as a seasonal fishery. If such a fishery is changed to a continuous mode of operation, the result will be a production increase, which can be predicted using the model. One potential problem, however, is the change in population structure brought about by a change in stocking patterns. As discussed in Chapter 2, competition at a given biomass is usually less intense in a population comprising several cohorts (hence a wide range of size groups), than in a single cohort. Hence the competition coefficient d is expected to decrease if production is changed from single cycles to continuous mode.

The influence of the value of d on production in a continuous system is shown in Fig 4.14, for l_c=18 cm and infinite fishing mortality (as in Fig. 4.11). As d decreases from 0.5 to 0.45 and 0.4 cm ha y^{-1}, production increases and the maximum is reached at higher stocking densities.

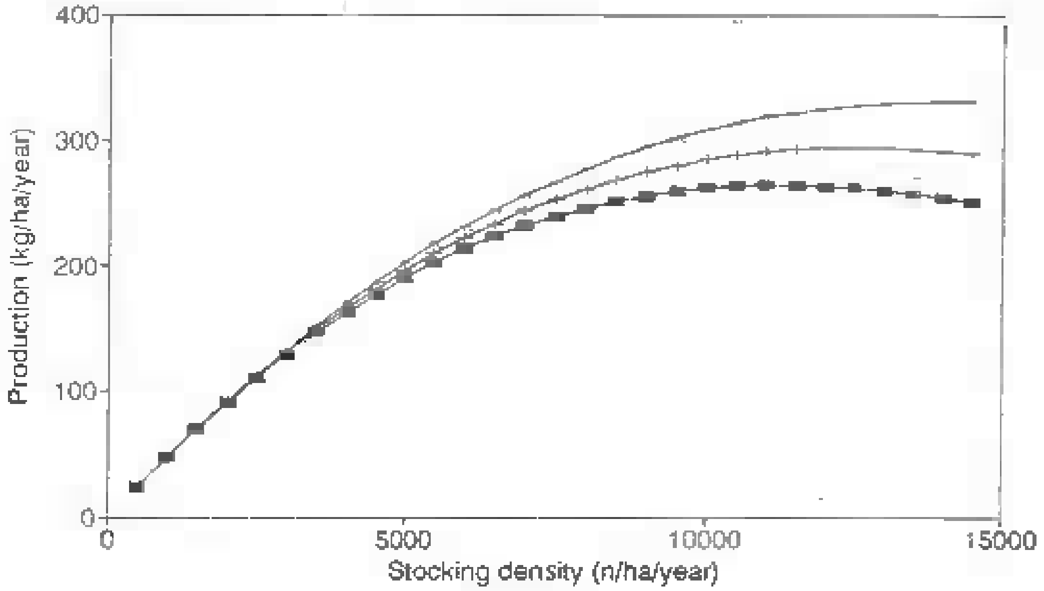

Fig. 4.14. Effect of a change in the competition coefficient d on total production in a perennial reservoir (continuous stocking and harvesting, l_c=18 cm). Values of d are (▪) 0.5, (+) 0.45 and (*) 0.40 cm ha kg^{-1}.

Tab. 4.4 lists the maximum production per month achieved in a fishery managed as discrete production cycles, and as a continuous system. The figure for discrete cycles refers to an optimal cycle of 5 to 6 months (Tab. 4.2).

Tab. 4.4. Maximum production per month of growth period, attainable under discrete cycles and continuous production. Standard parameter values, size-dependent mortality (M_r=1.292 y^{-1}, ϱ=0.5), gear selection length l_c= 18 cm and infinite fishing mortality.

Regime	d (cm ha y^{-1})	Production (kg/ha/month)
Discrete cycles	0.50	17
Continuous	0.50	22
"	0.45	25
"	0.40	28

Continuous production always offers an advantage over discrete cycles, even if the change in population structure does not reduce the intensity of competition. In the likely case that continuous stocking reduces the intensity of competition, the advantage is even greater.

Gear selection and optimal size at harvesting

The optimal size at harvesting in a perennial culture-based fishery is dependent on the stocking density. In this paragraph, fishing mortality is assumed to be infinitely high, so that fish are caught immediately after reaching the selection length. Fig. 4.15 shows production for different gear selection lengths as a function of stocking density. If stocking density is low, maximum production is achieved at high selection lengths, i.e. by harvesting large fish. As stocking density increases, it becomes advantageous to decrease the selection length, i.e. to harvest smaller fish. If there is no limitation on the number of seed fish that can be stocked, it is best stock at a high density, and to harvest fish as soon as they reach the minimum marketable size. If the availability of seed is limited, the harvesting of small fish will lead to growth overfishing.

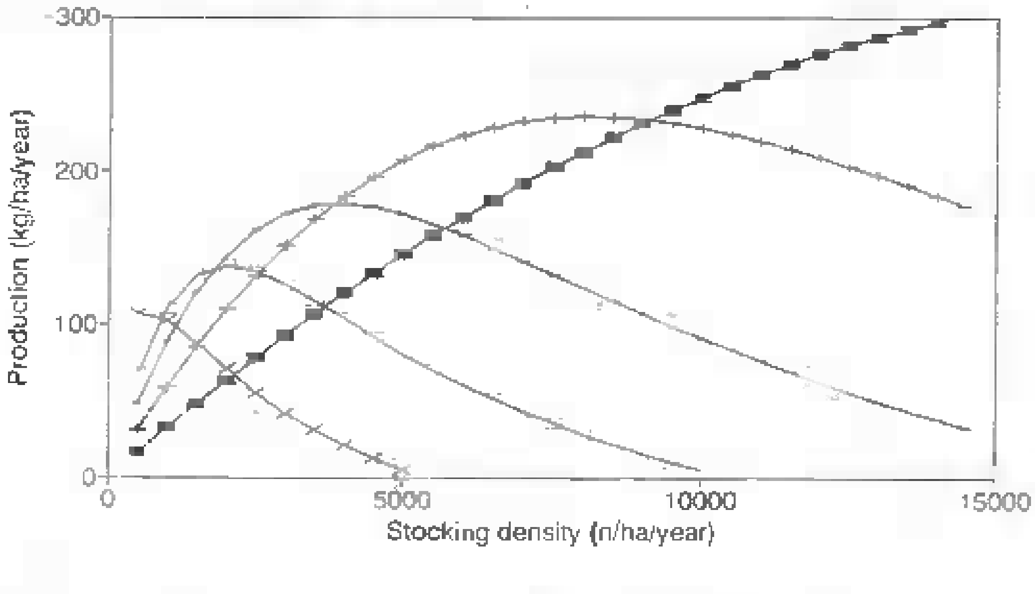

Fig. 4.15. Effect of the gear selection length (at very high fishing mortality) on production in a perennial reservoir. Selection lengths l_c are (■) 15 cm, (+) 20 cm, (*) 25 cm, (□) 30 cm, (×) 35 cm.

Fishing mortality

The influence of different fishing mortality rates on the average weight of produce, at selection lengths l_c of 15 cm and 25 cm, is shown as a function of stocking density in Fig 4.16. The higher the fishing mortality rate, the sooner the fish are caught after reaching the selection length, and the smaller the average weight in the catch. Stocking density also has a strong influence on the average size, because it determines the growth rate of the fish. For each value of the fishing mortality coefficient, the average time a fish will live after reaching the selection length is constant, independent of the stocking density. During this time, however, fish are growing much faster at low density.

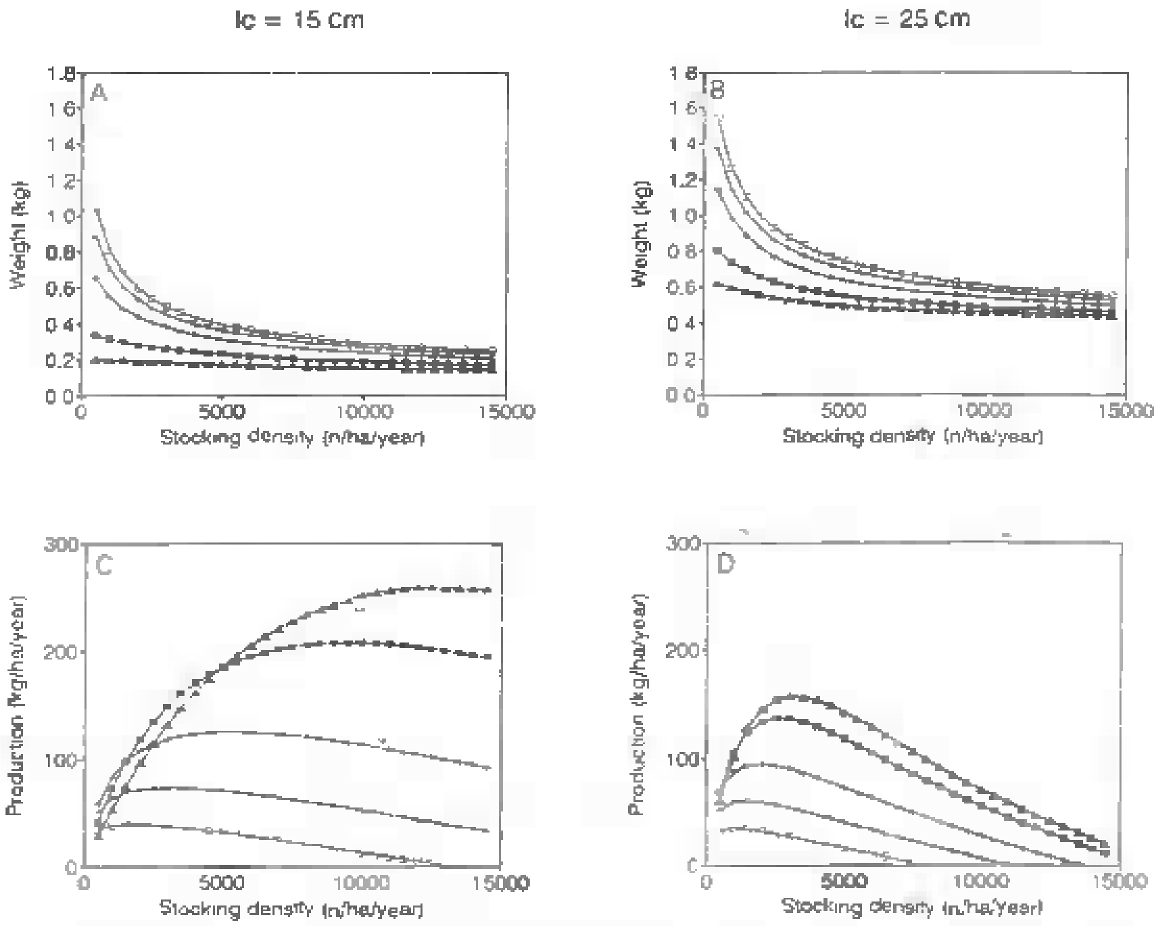

Fig. 4.16. Effects of fishing mortality on the average weight of produce and total production for selection lengths l_c of 15 cm (left hand side) and 25 cm (right hand side). Annual fishing mortality rates are (▲) 10, (■) 5, (+) 2, (^) 1 and (○) 0.5.

Production (Fig. 4.16 C, D) is usually highest at the highest level of fishing mortality, with the exception of very low stocking densities. At low stocking densities, growth overfishing may occur if the gear selection length is low and fishing mortality is high. The highest production is achieved at high stocking densities, high fishing mortality, and low selection length. If fishing mortality is low, the optimal stocking density is also lower. This result has important management implications: if fishing pressure on a reservoir population is low, high stocking densities must be avoided to prevent stunting of the population.

Interaction of gear selection and fishing mortality

Gear selection, fishing mortality and stocking density are the main traits of a reservoir fishery that can be influenced by the manager. In Fig. 4.17, production is shown as a function of gear selection and fishing mortality, for three different stocking densities. As stocking density and stocked biomass are constant in each of the diagrams, yield, and yield per fingerling contours are similar to the production contours. Each contour graph looks similar to the yield per recruit contours obtained from standard dynamic pool models (Beverton & Holt 1957). Here, however, yield per fingerling is dependent on the stocking density (i.e. the number of fingerlings). The optimal harvesting of the population is dependent on its density, a consequence of density-dependent growth.

At low stocking density (Fig. 4.17 A), it is best to harvest at a high selection length, and high fishing mortality. If the gear selection length is low, fishing mortality should also be lower. At higher stocking densities (Fig. 4.17 B, C), a higher fishing pressure can be sustained, in terms of both higher mortality and lower selection length. These results are essentially the same as those obtained in the previous section for infinite fishing mortality and various values of L_c: the higher the stocking density, the smaller the fish should be harvested and vice versa.

If growth overfishing occurs, it can be alleviated by an increase in stocking density. This result can be understood within the framework of classical yield per recruit models: an increase in stocking density causes a decrease in $L_{\infty g}$, which is essentially the same as increasing the gear selection length in a density-independent population.

Summary of management implications

(1) In a perennial reservoir, continuous stocking and harvesting yields higher production and profit than any regime involving discrete cycles.

(2) Optimal production and profit are achieved by a combination of high stocking density, low gear selection length and high fishing mortality.

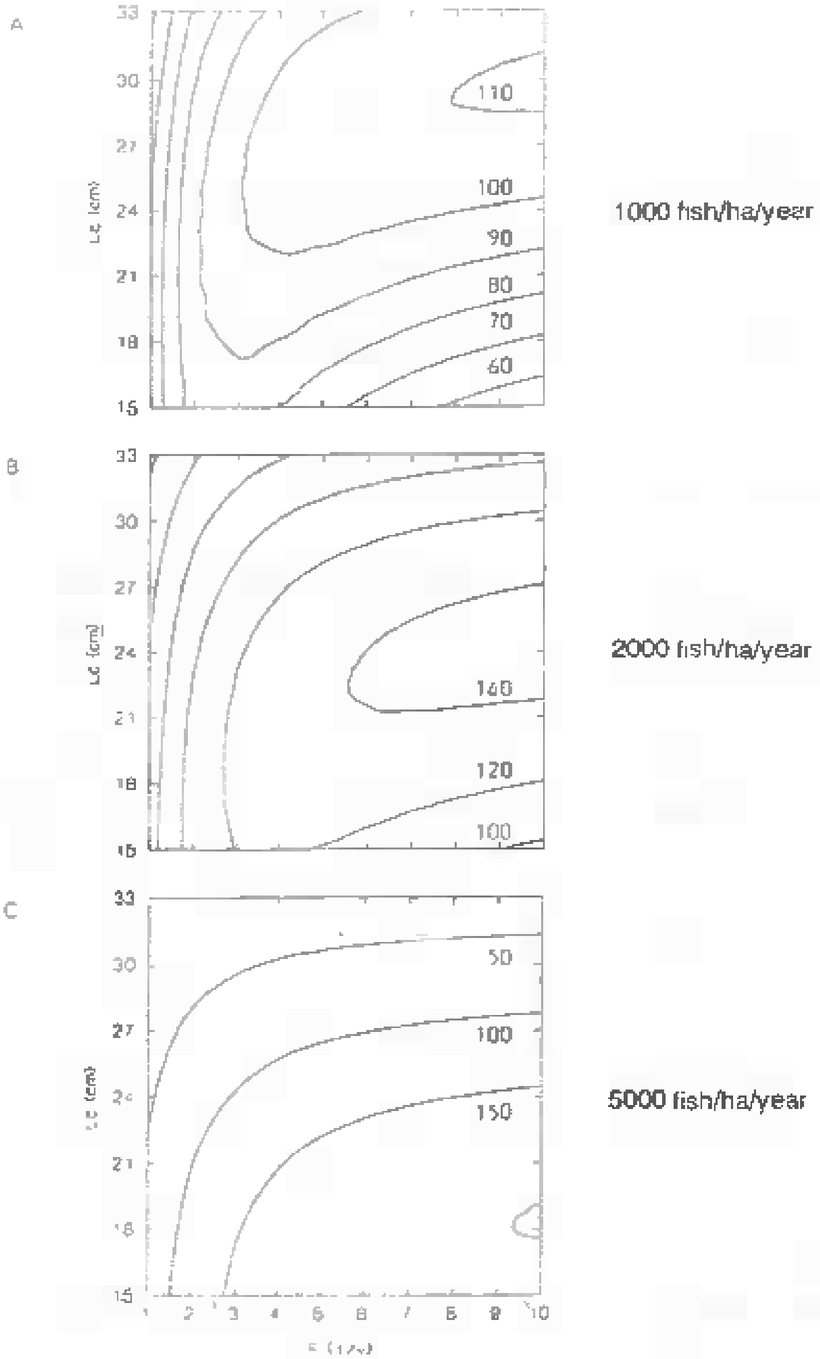

Fig. 4.17. Total production as a function of fishing mortality F and gear selection length L_c for a perennial reservoir fishery at three different stocking densities. Stocking densities are (A) 1000 fish/ha/year, (B) 2000 fish/ha/year, (C) 5000 fish/ha/year. Figures near the contour lines indicate production in kg per hectare per year.

(3) If seed availability limits stocking density, growth overfishing may result from low gear selection length and/or high fishing mortality.

(4) Growth overfishing can be averted by an increase in stocking density.

(5) If fishing effort, and hence fishing mortality, are low (e.g. in a developing fishery), care must be taken to avoid overstocking.

(6) In a developing fishery, increases of fishing mortality and stocking rate should go hand in hand.

4.4.2 Discrete Stocking

Most perennial reservoirs are stocked several times during a year, but not continuously. Hence it is necessary to explore how the results obtained for continuous stocking are affected if stocking is discontinuous.

The effect of different stocking patterns on population biomass and weekly yield over a one year period is shown in Fig. 4 18, always for the same total stocking density of 5000 fish/ha/year, a gear selection length l_c=20 cm, and very high fishing mortality.

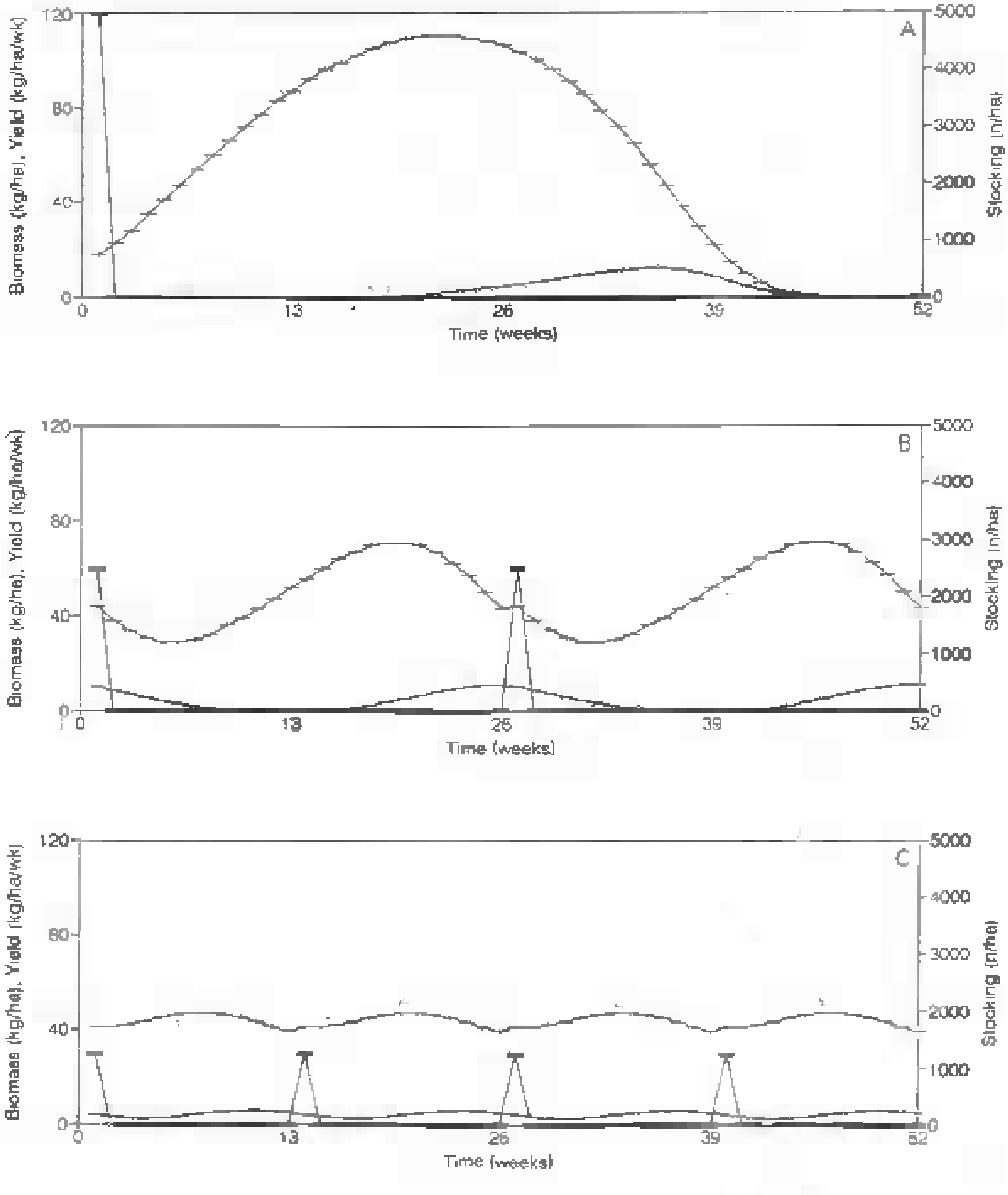

Fig. 4 18. Discrete stocking in a perennial reservoir (A) One, (B) two, and (C) four stocking events per year (■) Numbers stocked (+) Biomass of the population, (*) weekly yield Total annual stocking is 5000 fish/ha. l_c=20 cm very high F.

If all fish are stocked in a single event (Fig. 4.18 A), population biomass builds up rapidly to reach a maximum of 110 kg/ha after 22 weeks. By this time, more and more fish reach the selection length and are being harvested, so that biomass declines. Most of the yield is obtained during the third quarter of the year. During the fourth quarter, the reservoir is virtually fished out and its production potential is unutilized.

If the same number of fish is stocked in two events six months apart (Fig. 4.18 B), the picture is different. Population biomass fluctuates within a more narrow band, it neither reaches high values, nor does it decline to zero as in the case of single stocking. Hence the production potential of the water body is utilized throughout the year. There are now two peak harvesting periods, each about half a year after the stocking of the respective cohort. Fish take less time to grow to the selection length than after a single stocking event, because biomass remains lower and growth rate higher. A staggered stocking over four events (Fig. 4.18 C) results in almost constant biomass and yield.

The total annual production reached under various stocking densities and regimes is shown in Fig. 4.19. Stocking twice a year gives rise to the same production as continuous stocking, and so does any frequency of stocking above two events per year. Production obtained from a single stocking event is substantially lower. A single stocking event is insufficient (under the given harvesting regime) to fully utilize the production potential of the water body.

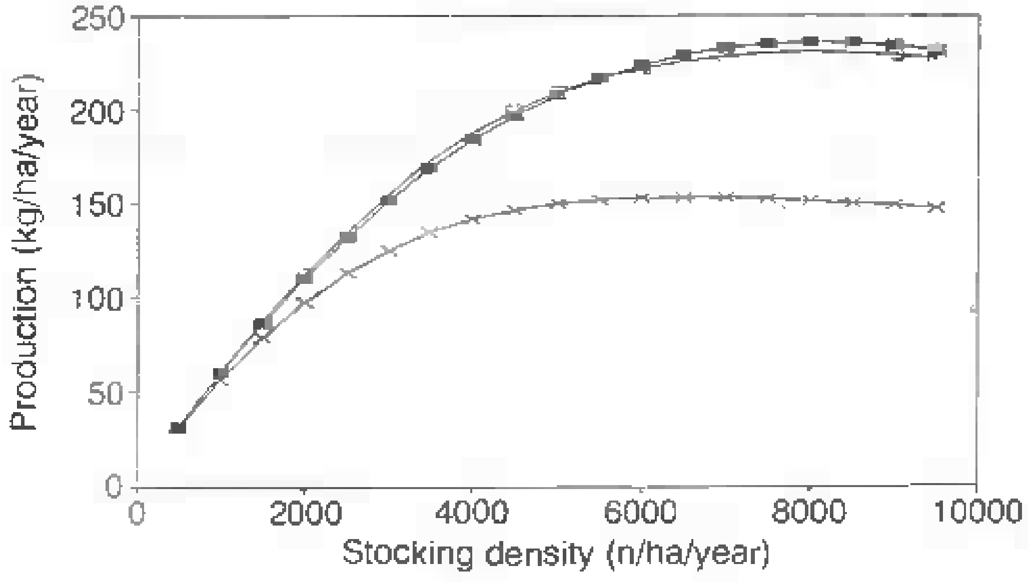

Fig. 4.19. Influence of the frequency of stocking on production. Stocking (■) once a week (□) twice a year and (×) once a year at the same annual stocking density Standard parameter values, $L_c = 20$ cm.

Summary of management implications

(1) The management implications listed in Section 4.4.1 also apply to discrete stocking.
(2) The temporal pattern of stocking has little influence on the total annual production of a fishery under continuous harvesting, provided that a sufficient level of biomass is maintained throughout the year.
(3) The total annual stocking density resulting in optimal production is independent of the temporal pattern of stocking, provided that a sufficient level of biomass is maintained throughout the year.
(4) Frequent stocking reduces temporal variability in biomass and yield.

4.5 DISCUSSION

This discussion is structured in three Sections. Section (4.5.1) discusses the model itself, its advantages and limitations, and ways of simplifying it. Sections (4.5.2) and (4.5.3) discuss the results and management implications of the model for seasonal and perennial reservoir fisheries, respectively.

4.5.1 The Model

The length-structured matrix population model developed for this study is most general in the sense that it allows all possible stocking and harvesting regimes to be investigated. It can be used to explore the dynamics of culture-based fisheries and derive qualitative management guidelines, as demonstrated in this Chapter. The model can also be used in the management of specific fisheries to make quantitative predictions. Finally, the model can be used in the estimation of parameters from stocking and catch data, if combined with a minimization algorithm.

The growth projection matrix was first proposed by Shepherd (1987), who also devised the algorithm for its construction used in Section 4.1.2. Sullivan *et al.* (1990) constructed the matrix using a stochastic growth model based on the VBGF. The matrix used here is unusual in that it extends to length groups above $L_{\infty B}$. Also, it needs to be re-evaluated at every time step to account for the density effect on growth.

Care must be taken in selecting the width of the length groups in the model. Individuals are assumed to be evenly distributed within any length group, to grow by the same length increment, and to be subject to the same mortality. These assumptions are realistic if length intervals are small, but can lead to serious distortions if the chosen length intervals are too large. Hence the smaller the length intervals, the better the precision of the model becomes. However, computing time and memory requirements increase roughly with the square of the number of length groups (because of the matrix operations involved). In practice, a balance must be sought between the need for small length groups, and the need to limit computing time.

The model presented here is most general in that it allows for any possible stocking and harvesting regime. Its analysis has shown, however, that usually only two special cases need to be considered in the assessment of fisheries: a single cohort in seasonal reservoirs, and a population at demographic equilibrium (continuous stocking and harvesting) in perennial reservoirs. Both special cases can be investigated using simple, differential equation models like the one used to estimate growth parameters in Section 2.1.2 (see Appendix B). Such models are not only more simple, but also much faster to simulate on a computer. Hence it is possible to use such models in computer-intensive-methods to obtain parameter estimates or predictions with confidence limits (Efron 1982, Restrepo & Fox 1988).

4.5.2 Seasonal Reservoirs

As a rule of thumb, seasonal reservoirs should be stocked at a density such that the produce is of the minimum marketable size, or only slightly larger. This rule has also been derived experimentally for European carp pond culture by Schäperclaus (1949, 1961). A small reservoir fishery producing large fish is likely to be understocked, and its production can be increased by increasing the stocking density.

The production potential of small reservoir fisheries is best utilized by producing small fish at a high density, if such fish are accepted on the market. A preference for large fish limits the total production that can be achieved from culture-based small reservoir fisheries.

The optimal stocking density with respect to profit is often lower than the optimal density with respect to biological production. Hence it is important to clarify the economic objectives of the fishery. Management for optimal production often results in sub-optimal profit, and vice versa. This conflict between the two objectives is not always intuitive. Maximum production is often implicitly taken as an objective, even if the manager is more interested in profit.

Mortality is always a limiting factor for production. At very high mortality, production is virtually nil. Reduction of mortality by predator or parasite control should be considered if mortality is high. The implications of these options can be explored quantitatively using the model.

Mortality might also be a source of variation in empirical models relating fish yield or production to other biotic or abiotic parameters. For given levels of nutrient loads, primary production etc., fish yield always declines with increasing mortality.

The optimal size of seed fish is the subject of much speculation, little hard evidence, and various rules. The model results indicate that there is an optimal intermediate size range for seed fish, and that this range is often fairly wide. Within this range, the optimal stocking density declines as size increases, while the production or profit obtained are about constant. If spawn availability is limited, but sufficient nursing facilities are available, large fingerlings can be stocked. If spawn availability is high, but nursing facilities are limited, small fingerlings can be stocked at a higher density. An alternative option in the latter case is to set part of a reservoir aside for pen or bay nursing. Seed fish are nursed to advanced fingerling stage in the pen or bay, and are partly released into the reservoir, and partly cultured intensively in the pen, or sold to private fish farmers. This approach has been successfully implemented as a pilot project in NE Thailand (Manni 1992), and is also recommended for Indian reservoirs (Jhingran & Unnithan 1990). The feasibility of pen or bay nursing depends mostly on local economic conditions.

Large seed fish must be stocked at a much higher biomass than small seed fish to achieve a similar level of production. Hence there is no optimal stocked biomass independent of the size of seed fish. If a certain biomass is known to be optimal for large fingerlings, stocking of the same biomass of smaller seed will result in overstocking.

An important consideration with respect to the optimal size of seed fish is the fact that production and profit are most sensitive to stocking density if seed fish are large. If large fingerlings are to be stocked, it is essential to have a good knowledge of growth and mortality in the population, in order to avoid losses due to over- or understocking. If small seed fish are used, stocking density is far less critical

Staggered harvesting is considered an important management measure in seasonal reservoir fisheries by De Silva (1988). The modelling results suggest that staggered harvesting may indeed increase production, raise the average size of produce, and result in a more uniform size of produce. As harvesting is spread over a longer time period, staggered harvesting also prevents a temporal oversupply of the market, with an associated drop in prices. The modelling results give a good indication of the conditions under which staggered harvesting is successful. Stocking density must be higher than optimal density in the absence of staggered harvesting. Staggered harvesting is most effective if growth periods are long, and mortality is low. If natural mortality is high, and the growth period is long, it may be more effective to operate the fishery with two discrete production cycles and without staggered harvesting.

Multiple stocking can increase production of seasonal reservoir fisheries if the growth period (season) is sufficiently long. The simplest mode of multiple stocking is to split the growth period into two (or three) discrete production cycles, with a single stocking and single harvesting in each. Other modes of multiple stocking are unlikely to offer substantial improvements over discrete cycles, and need not normally be considered. Short production cycles are common in tropical aquaculture (Pillay 1990).

In a seasonal reservoir fishery, two management options should be explored if the growth period is long: staggered harvesting during a single production cycle, or multiple production cycles. The choice depends mainly on the natural mortality rate. If mortality is low, staggered harvesting during a single cycle is best. If mortality is high, two or three short cycles are better. The model can be used to obtain predictions of yield and optimal stocking density under these management options, provided that sufficient data are available to estimate parameters.

4.5.3 Perennial Reservoirs

Perennial reservoirs are best managed as continuous culture systems, since discrete production cycles in perennial water bodies always yield a lower production.

Many results obtained for seasonal reservoirs (e.g. concerning the size of seed fish, influence of mortality, etc.) apply equally to perennial reservoir fisheries, and are not discussed again here.

Maximum production in perennial reservoirs is achieved at high stocking density, and harvesting at small sizes. This is similar to seasonal reservoir fisheries. However, the size of produce alone does not indicate whether a perennial fishery is managed optimally or not. This can only be assessed if information on growth is available. If growth is rapid and stocking density is low, then small produce indicates growth overfishing. Stocking densities in large tropical reservoirs are often low due to limited availability of seed (Bhukaswan & Chookajorn 1988, Pathak 1990). High fishing pressure on such reservoirs results in growth overfishing.

Growth overfishing in a culture-based fishery can be averted by increasing the selection length of the gear, decreasing fishing effort, or increasing stocking density. If seed material is available, an increase in stocking density is usually the best option, because it increases yield substantially, and does not involve the social costs of limiting fishing effort.

At high stocking density, it is not necessary to impose a size limit above the minimum marketable size. If a high size limit is imposed, stunting will result and the total yield as well as the yield of larger fish is likely to decline. This has been observed in temperate reservoir fisheries (Craig & Bodaly 1988).

In some cases, for example the Karnataka irrigation reservoirs, fishing effort is relatively low and the produce is very large. An increase in fishing effort is an important step towards increasing yield, as has been pointed out by Devaraj & Mahadeva (1990).

In a developing culture-based reservoir fishery, fishing effort and stocking density must be increased together, to obtain optimal production. This result has also been obtained experimentally in culture-based coregonid fisheries in Northern Europe (EIFAC 1992).

At constant stocking density and fishing pattern, individual growth in a multi-cohort fishery is described by a standard VBGF. A standard yield per recruit analysis can be used to evaluate the fishing regime and to detect growth overfishing, for any given stocking density. A change in stocking density, or a large change in fishing patterns, will affect the biomass and hence the growth of fish. Hence this yield per recruit analysis is only valid for a constant number of recruits. The same applies, strictly speaking, to yield per recruit analysis of any wild population.

Annual total production is not affected by the frequency of stocking, as long as the frequency is sufficient to guarantee a substantial level of biomass in the reservoir. The compensatory mechanism of density-dependent growth ensures that periods of low density are efficiently utilized via increased production of the remaining population. This result is based on the assumption that the competition coefficient is independent of population structure, i.e. all individuals in the population compete for the same resources. If fish undergo significant ontogenic changes in resource requirements, production will be highest if all resources are utilized, i.e. the full size spectrum is occupied at all times. Frequent stocking will then yield higher production than infrequent stocking.

In intensive aquaculture, artificial feeding results in density-independent growth (except at very high densities, when oxygen consumption and accumulation of waste products may become limiting). If growth is density-independent, production is maximised by constantly operating the aquaculture plant at the highest biomass density it can sustain. The only way to avoid fluctuations in biomass during the production process is continuous stocking (Watten 1992). However, the benefits of this policy may in practice be outweighed by technical difficulties and increased labour demand.

All results are presented and discussed here for fisheries which are entirely culture-based. In larger perennial reservoirs, stocked species may establish self-perpetuating populations (Jhingran 1986). In such reservoirs, stocking may still be practised to enhance yield. The management of such fisheries is more complex, and beyond the scope of the present study.

Chapter five

Adaptive Management of Culture-Based Small Reservoir Fisheries: An Outline

This chapter outlines an adaptive approach to the management of culture-based small reservoir fisheries. The adaptive approach emphasizes that fishery management is aimed at a moving biological, economic and social target. Adaptive management entails systematic learning from management experience, and deliberate, planned experimenting with management options in order optimize stocking and harvesting regimes. The models developed in the preceding Chapters, and the qualitative guidelines obtained from them are essential ingredients of the adaptive management strategy proposed here.

5.1 PRINCIPLES OF ADAPTIVE MANAGEMENT

Adaptive management is based on the premise that the best way to optimize the exploitation of a fishery is to learn from the experience of management itself in a systematic way (Walters 1986). Basically, adaptive management consists of iterating the following steps:

(1) Construction of a model of the fishery based on current understanding and experience.
(2) Exploration of management options, and the uncertainties surrounding these options.
(3) Adoption of a stocking and harvesting regime that is likely to be beneficial and/or resolve uncertainty.

The model to be constructed in step (1) can be of any degree of complexity, ranging from a simple qualitative perception to a detailed mathematical model as developed in Chapter 4. The model must be complex enough so as to allow an exploration of available management options.

Usually, only a limited set of management options will be available for any given fishery. In a seasonal reservoir fishery with a short growth period, for example, there is no option other than a single production cycle, and the only problems are to find the right stocking density and size of seed fish (provided that different sizes are available). In a perennial reservoir fishery, on the other hand, various options are available and should be explored

The values of model parameters are usually subject to substantial uncertainty. This uncertainty must be accounted for when exploring management options. Model predictions should be obtained for a range of possible parameter values, rather than just for those values deemed "most likely" by the manager. In this way, it is possible to get an indication of the degree of uncertainty attached to potentially beneficial options.

If an option emerges as beneficial, and is subject to little uncertainty, this option may be adopted straight away, with very little risk. Conversely, if the benefit from some option is subject to substantial uncertainty, two approaches can be taken: (1) the management option in question can be adopted, if the magnitude of the possible benefits justifies the risk possibly involved; or (2) other options may allow to resolve uncertainty, while incurring a lower risk. For example, in a seasonal reservoir fishery, it may appear beneficial to operate in two production cycles. The potential benefit of this option is subject to the density-dependent growth response of the fish, i.e. the parameter values of the growth model. In this case, it may be a good idea to change the stocking density in a way that does not incur a great loss of yield, but allows to improve the estimates of model parameters. The improved model can then be used to ascertain (or reject) the potential for two production cycles, and to predict the best stocking density for the short cycles.

The risk involved in the management of culture-based fisheries is generally less than the risk involved in harvesting natural populations, because recruitment overfishing (i.e. depletion of the spawning stock) is not a concern. For the same reason, there is no inherent risk in conservative management strategies. If stocking and harvesting patterns are constant, production will also be constant except for environmental variation. However, conservative management also means that little information is gained on the dynamics of the fishery, and that potentially beneficial options remain unexplored.

5.2 MANAGEMENT OF NEW FISHERIES: DECISIONS UNDER EXTREME UNCERTAINTY

This Section deals with management in conditions of complete, or very high uncertainty. This situation is found in newly developing fisheries, as well as established fisheries for which no reliable data are available. Two situations are considered separately: stocking under complete uncertainty (i.e. first stocking), and stocking if experience from one growth period is available.

There are two main objectives in deciding on the stocking and harvesting patterns during the first two years of operation:

(1) Stocking should demonstrate the feasibility of, and the benefits from developing a culture-based fishery in the reservoir. Also, the risk of financial loss should be kept low;

(2) Stocking and catch data from the first two periods should yield a maximum of information about the dynamics of the fishery, so that the stocking and harvesting regime can be optimized.

In order to attain the second objective, stocking in the second year must be different from stocking in the first year, so that density responses can be evaluated. On the basis of modelling results (Chapter 4), the following approaches are suggested for seasonal and perennial reservoir fisheries.

5.2.1 Seasonal Reservoir Fisheries

First year

The first stocking of a seasonal reservoir is best done with a low density of small fingerlings. The necessary investment is low, and the maximum possible loss is also low. Small fingerlings yield a good production over a wide range of stocking densities; overstocking is almost impossible.

If small fingerlings are stocked at a low density, the fishery is probably understocked, and individual weight at harvesting is likely to be high. A catch of large fish is often interpreted as a sign of success (although actually it indicates understocking). Stocking at a high density might prevent fish from reaching a marketable size, in which case fishermen are likely to regard the fishery as unproductive.

Second year

The stocking pattern for the second year is determined on the basis of first year results. The main indicator is the average size of produce achieved in the first year. If the average size was well above the minimum marketable size, the reservoir was understocked. If the average size of produce was too small, the fishery was overstocked. In both cases, stocking density in the second year should be adjusted so as to yield produce of about the minimum marketable size. An indication of the best density can be obtained using approximate methods like the Schäperclaus-Huet formula (see Section 1.3.3). Adoption of this stocking density will improve the yield of the fishery over that from the first year, and provide much needed information for further optimization.

If, by chance, the first year stocking density turned out to be optimal (i.e. to yield produce of about the minimum marketable size), a change in density would yield information, but would also entail a loss of production or profit. Hence stocking density should be changed only if the gain in information is likely to outweigh the loss of production in the long run. This is possible if the growth period is long, so that two production cycles or staggered harvesting might increase production substantially and are worth investigating. If the growth period is short, nothing can be gained from further experimenting once the best density is found.

5.2.2 Perennial-Reservoir Fisheries

The arguments developed for seasonal reservoirs apply to perennial reservoir fisheries in a similar way. Stocking at low density during the first year should be followed by an increase in density in the second year. The optimal stocking density in a perennial reservoir depends on the fishing pattern and vice versa. Hence optimization is less straightforward than in a seasonal fishery.

Fishing mortality is likely to increase as the reservoir fishery develops, and stocking density should increase accordingly. Initially, overstocking is possible and should be avoided. Section 5.3.2 gives a more detailed account of management.

5.3 ADAPTIVE MANAGEMENT OF ESTABLISHED FISHERIES

5.3.1 Seasonal Reservoir Fisheries

If stocking of a seasonal reservoir during the first two production periods has followed the pattern suggested in Section 5.2.1. sufficient information will be available to estimate parameters of a density-dependent growth model. The empirical model developed in Section 2.1.1 can be fitted, provided that the biomass stocked differs between the first two years (which is the case if fingerlings of similar size were stocked at different numerical density). The density-dependent VBGF model has three parameters, it can only be fitted if data from at least three different stocking densities are available, or if at least one parameter is inferred from comparative studies. This possibility is discussed further in Section 5.4.

Once model parameters have been estimated, management options can be explored and the potential yield of the fishery under optimal management can be predicted. In practice, this rigorous scientific approach will be limited to a few intensively studied seasonal reservoirs.

In the management of seasonal reservoir fisheries by small cooperatives, parameter estimation and modelling are neither feasible, nor necessary. Management should be based on simple guidelines. Stocking density should be adjusted so as to produce fish slightly above the minimum marketable size. If the production period is short, there are no other management options. If the period is long, two cycles or staggered harvesting may yield a better production. A rough assessment of mortality can indicate which one of these options is likely to be better: two cycles if mortality is high, and staggered harvesting if mortality is low.

5.3.2 Perennial Reservoir Fisheries

Adaptive management of perennial reservoirs can be done in the following steps:

(1) Estimate growth and mortality parameters for the exploited population under the current stocking and fishing regime
(2) Perform a yield per recruit analysis.
(3) If necessary, change fishing patterns or stocking density.

In the short term, it is not necessary to estimate parameters for the full density-dependent growth model, though this is desirable for long term management. In the short term, it is sufficient to estimate standard VBGF parameters, and the natural and fishing mortality rates in the exploited population.

Regular marking of seed fish (fin clipping) is a good way to obtain reliable growth parameters. Length frequency analysis of the catch may be difficult given the selectivity of the gillnet or multi-gear fisheries typically operating on reservoirs.

Mortality estimates can also be obtained on the basis of marked fish. The bulk of natural mortality is likely to occur in the pre-recruit stage. The mean mortality rate in the pre-recruit stage can be estimated from the total numbers stocked and harvested. If the growth parameters and the exponent ϱ of the mortality-size relationship have been estimated, the natural mortality rate in the exploited length range of the population can be calculated approximately. The parameter ϱ is difficult to estimate, so it may be necessary to use an "educated guess". A statistically sound method for estimating mortality rates in culture-based fisheries is still to be developed.

Once parameters have been estimated, a standard yield per recruit analysis can be performed. This analysis indicates whether the growth potential of individuals is exploited optimally under the current stocking and catch pattern. If the analysis indicates growth overfishing, there are two possible remedies: a reduction of fishing mortality, or an increase in stocking density. If fishing effort is insufficient, effort must be increased or the stocking density decreased.

In a newly established reservoir fishery, fishing effort is likely to increase over time. The best stocking strategy then is to stock at a constant density, and monitor the catches. Once effort is high enough to cause growth overfishing, stocking density should be increased. This cycle of increasing effort and increasing stocking density can be repeated as long as the produce (which will become smaller and smaller on average) is marketable.

If this strategy of managing an evolving fishery is followed. data on the growth response to density accumulates automatically. No stocking experiments which might result in a deterioration of the status quo of the fishery are necessary. Once growth data are available over a range of population biomass, parameters of the density-dependent growth model can be estimated. Then, the potential yield of the fishery under optimal management can be predicted using the model.

5.4 REPLICATED SYSTEMS AND EMPIRICAL MODELS

Throughout this study, individual reservoirs have been considered as unique. However, there will often be a number of similar reservoirs in an area, and this fact can be exploited to yield valuable management information.

The reservoir fisheries introduced in Chapter 1, for example, are all representative of a group of reservoirs within an area, sharing morphometric characteristics, species composition, and overall management regime.

Replicated systems are defined here as groups of reservoirs that are qualitatively similar in terms of their morphometry, overall production ecology, species composition, and management regime. Such reservoir fisheries display similar dynamics, but the values of population parameters may differ between them.

Some population parameters are likely to be the same within the group of reservoirs, while others are likely to be unique to each reservoir. The VBGF parameter K is always constant within a small geographical area, and the competition coefficient c (or d) is expected to be constant between systems of similar population structure (e.g. seasonal reservoirs under single stocking). The degree of size-dependence of mortality ϱ is also likely to be similar if the stocked species are faced with similar predator populations (e.g. the snakehead ubiquitous in NE Thailand). This leaves only two parameters that are likely to vary strongly between populations: $W_{\infty L}$ ($L_{\infty L}$), which reflects the productivity of the individual water body, and the natural mortality rate at reference length M_r.

Obviously, knowledge gained in the investigation of a few systems can help the management of other replicates. If the values of K, c. and ϱ estimated for a subset of reservoirs show little variation, these estimates can be used in the assessment of the other systems. Estimates of $W_{\infty L}$ and M_r can be obtained after only one year of stocking. so that a comprehensive assessment of the potential yield and optimal management of an individual reservoir is possible after one year of operation

A well studied subset of replicated systems can also be used to construct empirical models, to predict population parameters from other biotic or abiotic parameters. For example. $W_{\infty L}$ can probably be predicted from nutrient levels or primary production.

If a set of replicated systems has been identified, it is probably best to concentrate adaptive management and sampling effort on a subset, in order to obtain reliable parameter estimates. If management effort is spread evenly over the whole set, the result may be a collection of very unreliable parameter estimates, and general mis-management.

5.5 SPECIES INTERACTIONS AND ECOSYSTEM MANAGEMENT

This study has been concerned entirely with the population dynamics and management of single species. South Asian reservoirs are usually stocked with several species of cyprinids, and often tilapia. In addition, larger reservoirs may harbour natural populations of various species.

The single species approach is sufficient if the interaction between stocked species is weak. Two types of interaction can be distinguished: direct interaction due to competition or predation, and indirect interaction due to the effects of species on the ecosystem. Direct interaction between the species stocked in South Asian reservoirs is limited to competition. Indirect interactions can be strong and grass carp in particular may alter the whole energy and nutrient flow in the ecosystem by depleting macrophyte abundance. Planktivorous fish also have a strong influence on nutrient loads and overall productivity (McQueen *et al.* 1986).

The understanding of single species dynamics gained in this study should be combined with multi-species or ecosystem approaches in order to achieve optimal management of the water body as a whole.

Culture-based reservoir fisheries are in a sense large-scale, extensive polyculture systems. Hence the experience gained in polyculture systems is to a large extent relevant to reservoir fisheries. The development of robust, quantitative models for polyculture systems could advance the management of reservoir fisheries.

For the moment, it may be useful to construct simple, steady state "budget" models (e.g. within the ECOPATH framework, Polovina & Ow 1983). Such models can give a rough indication of the optimal biomass to be maintained for various species or groups of species. Individual species can then be managed using the adaptive approach developed here, to achieve the desired level of biomass in a way that maximizes economic benefits.

The adaptive approach to the management of single species entails a continuous analysis of stocking and catch data, and the adjustment of stocking and catch patterns to changes in the resource. Hence adaptive management also adjusts to the effects of species interactions. Individual species will be managed in a way that is optimal under the given overall regime. However, it is impossible on the basis of single species management to assess whether radical changes could yield a higher overall productivity.

5.6 PERSPECTIVES ON COMMUNITY-BASED AND COOPERATIVE MANAGEMENT

Small reservoir fisheries resources are often communal property, and are managed by cooperatives or village committees. How can the adaptive approach to management be implemented under such conditions?

Adaptive management seems to involve an amount of sampling, modelling, and experimenting with stocking and catch patterns that is clearly not feasible for small communal management units. However, simple rules have been devised for the management of seasonal reservoir fisheries in Section 4.4.3 and this Chapter. Adaptive management on the basis of these rules requires a minimum of sampling, and some simple calculations. Hence this approach can be used in community-based management.

The management of perennial reservoirs involves more complex tasks. However, such reservoirs tend to be larger, and support a larger number fishermen. Hence it is feasible to devote more effort to their management. Although some perennial reservoirs are managed completely by the community of users, stocking is often done by the government, while fishermen are either licensed individually, or are organized in cooperative societies. Perennial reservoirs may best be managed co-operatively by the state and fishermen's organizations. The advantage of such management is that scientific methods of fishery assessment become available, while user communities may retain control over the resource and enforce regulations (Rettig *et al.* 1989).

5.7 DISCUSSION

Management of single species

Adaptive approaches to the management of culture-based small reservoir fisheries can be developed on the basis of insights gained from the modelling results in Chapter 4. The management procedures and tools can be fairly simple; particularly in seasonal reservoir fisheries. Hence this approach is well suited for communal or co-operative (user community-state) management.

Further analysis of the models developed in this study may yield useful quantitative guidelines, for example to predict the optimal stocking density if the production period in a seasonal reservoir is split into two cycles, and the optimal density for a single cycle is known.

Another priority area is the development of robust methods for the estimation of growth and mortality parameters in perennial reservoir fisheries. Such methods are best based on the recapture of marked seed fish. Fin clipping of seed fish is common practice in Indian reservoir fisheries research

A wider perspective on management

This study is primarily concerned with the optimal management of culture-based, single species fisheries under constant external conditions. In practice, adaptive management must have a broader perspective. Some of these more general aspects are briefly outlined here.

Species interactions and ecosystem management have already been mentioned, and this is certainly a key problem. Apart from biological interactions between species, there is also the interaction between fisheries aimed at different species. Small "trash fish" species may be exploited using fine mesh nets, while the optimal exploitation of stocked species may call for larger minimum mesh sizes. Small "trash fish" are often exploited by the poorest sections of the user group, and these may loose out if gear restrictions are enforced to protect the culture-based fishery.

Depending mainly on economic and socio-economic factors, it may be feasible to develop small reservoirs for more intensive fish culture, as either pond or cage-culture systems. The relative benefits of culture-based fisheries and more intensive modes of production are likely to change as economic development proceeds.

Summary

South Asian small reservoirs are man-made water bodies, which do not support self-perpetuating populations of valuable food fish species. Such reservoirs can be developed as culture-based fisheries, i.e. fisheries based on the regular stocking of farm-produced seed fish.

The aim of this study is to investigate the dynamics of culture-based reservoir fisheries, and to develop methods to assess such fisheries, and estimate their potential yield under optimal management. The study is organized in several parts. First, mathematical models for key population processes in a culture-based fishery are developed and tested. Second, some economic aspects directly relevant to the stocking and harvesting of small reservoir fisheries are considered briefly. Third, a general population model for culture-based fisheries is developed, which incorporates the process models developed earlier. The general model is used to explore the dynamics of culture-based fisheries, and to derive qualitative management guidelines. Finally, an adaptive approach to the management of small reservoir fisheries is outlined.

Density-dependent growth and size-dependent mortality are identified as the key population processes in a culture-based fishery. Density-dependent growth can be described by an extension of the von Bertalanffy growth function (VBGF). The density-dependent VBGF provides an excellent description of carp growth experiments in ponds. Size-dependent mortality is well described by a power function of individual size, both in natural populations and in pond culture. The interaction of density-dependent growth with size-dependent mortality results in density-dependent mortality.

Economically, the price-size relationships of seed fish and produce are directly relevant to the optimal stocking and harvesting regimes of culture-based fisheries. Hence the cost-size relationship for seed fish, and the revenue-size relationship for produce are investigated in an example.

A length-structured matrix model for culture-based fisheries is developed and analyzed. The model incorporates the growth and mortality sub-models developed in this study. The following paragraphs summarize model results on the dynamics of culture-based fisheries.

It is generally optimal to produce fish at or slightly larger than the minimum marketable size. If large fish can be sold for a higher price than small fish, the optimal size of produce is slightly, but never much higher than the minimum marketable size

In seasonal reservoirs fisheries, the stocking density must be adjusted so that fish of the desired size are produced. During long growth periods, production can be improved by operating two production cycles if mortality is high, or by staggered harvesting if mortality is low.

A wide range of sizes of seed fish can yield approximately the same production or profit. Small seed fish must be stocked at a higher density than large ones, but not in inverse proportion to their individual-weight. The optimal biomass to be stocked increases with the size of seed fish.

Perennial reservoirs are best utilized as continuous culture systems. The temporal pattern of stocking has little influence on total production, provided that a sufficient population biomass is maintained throughout the year.

The highest production in perennial reservoirs is reached at a high stocking density and high fishing effort, producing fish of the minimum marketable size. Growth overfishing may occur at low stocking density, and can be prevented by a decrease in fishing effort, an increase in gear selection length, or an increase in stocking density. If fishing effort is low, care must be taken not to overstock the reservoir.

Adaptive management strategies for seasonal and perennial reservoir fisheries are outlined. Such strategies are well suited to optimize stocking and harvesting regimes under communal or co-operative management.

Appendix

A. Glossary of Symbols

Symbol	First occurrence	Definition
a	2.1.2	Coefficient of the weight-length relationship
b	2.1.2	Exponent of the weight-length relationship
B_0	2.1.1	Initial biomass density
B_t	2.1.2	Biomass density at time t
B_∞	2.1.1	Carrying capacity
c	2.1.2	Competition coefficient for weight growth (d.d. VBGF)
c_0	3.2.2	Parameter of the cost-length relationship for seed fish
c_1	3.2.2	Parameter of the cost-length relationship for seed fish
c_L	3.2.2	Cost of individual seed fish at length L
c_t	4.1.1	Catch vector
d	2.1.2	Competition coefficient for length growth (d.d. VBGF)
dL	2.1.2	Length differential
dt	2.1.2	Time differential
dW	2.1.2	Weight differential
F	4.1.2	Fishing mortality rate
g_{ij}	4.1.1	Element of the growth projection matrix
G_t	4.1.1	Growth projection matrix
GP	4.2.2	Gross profit (revenue minus seed cost)
h_{ii}	4.1.2	Element of the diagonal harvesting matrix
H_t	4.1.1	Harvesting matrix
K	2.1.2	VBGF parameter
L	2.1.2	Length
L_i	4.1.1	Lower length bound of length group i
L_i'	4.1.2	Back-calculated length of L_i at time t-dt
L_r	2.2.1	Reference length for size-dependent mortality
L_t	2.1.2	Length at time t

Symbol	First occurrence	Definition
L_∞	2.1.2	VBGF parameter
$L_{\infty L}$	2.1.2	Limiting L_∞ (density-dependent VBGF)
$L_{\infty B}$	2.1.2	L_∞ at biomass B (density-dependent VBGF)
M_j	4.1.2	Natural mortality in length group j
M_L	4.1.2	Natural mortality at length L
M_r	2.2.1	Natural mortality at reference length
M_W	2.2.1	Natural mortality at weight W
$M_{1,2}$	2.2.1	Mean mortality during time interval $[t_1, t_2]$
N_t	2.1.2	Population density in numbers at time t
n_t	4.1.1	Population density vector
P	2.1.2	Index of growth performance
p_0	3.2.1	Parameter of the price-length relationship
p_1	3.2.1	Parameter of the price-length relationship
p_L	3.2.1	Price of produce (individual) at length L
Pr	4.2.2	Production per unit area
s_{jj}	4.1.1	Element of the diagonal survival matrix
S_t	4.1.1	Survival matrix
TC	3.2	Total costs
TP	3.2	Total profit
TR	3.2	Total revenue
u_t	4.1.1	Stocking density vector
v_j	4.1.2	Gear selectivity for length group j
W	2.1.2	Weight
W_r	2.2.1	Reference weight for size-dependent mortality
W_t	2.1.2	Weight at time t
W_∞	2.1.2	VBGF parameter
$W_{\infty L}$	2.1.2	Limiting W_∞ (density-dependent VBGF)
$W_{\infty B}$	2.1.2	W_∞ at biomass B (density-dependent VBGF)
W^{-}	2.2.1	Weight at mean length
WC_t^{*}	4.2.2	Mean weight in the catch at time t
r^2	2.1.1	Coefficient of determination
α	2.1.1	Constant of the empirical model for density-dependent growth
β	2.1.1	Coefficient of the empirical model for density-dependent growth
ΔL	2.1.1	Length increment
Δt	2.1.1	Time period
ϱ	2.2.1	Exponent of the mortality-size relationship

B. Estimation of Parameters of the Density-Dependent VBGF

The development of numbers and average weight in a cohort under constant mortality and density-dependent growth is described by the following system of differential equations:

$$\frac{dN}{dt} = -M\ N \qquad (B.1)$$

$$\frac{dW}{dt} = -3\ K\ W\ (1 - \frac{W_{\infty L}^{1/3} - c\ N\ W}{W^{1/3}}) \qquad (B.2)$$

To predict the average weight at harvesting, the system of equations is solved subject to the initial conditions:

N_0=Stocking density

W_0=Average weight of seed fish

The equations are solved using a fourth-order Runge-Kutta algorithm (Press *et al.* 1986).

Growth parameters are estimated by minimizing the sum of squared differences between the log transformed observed and expected weights. Minimization is performed using the AMOEBA routine of Numerical Recipes (Press *et al.* 1986). This routine uses the downhill simplex method, which does not require derivatives of the objective function.

C. Estimation of ϱ

This Section deals with the problem of estimating the parameter ϱ of the mortality-weight relationship (Equation 2.13) from cohort stocking data. Such data is often available from pond culture or seasonal reservoirs.

If mean mortality and weight at stocking and harvesting (W_i and W_h, respectively) are available for at least two cohorts stocked or harvested at different weight, ϱ can be estimated.

The aim here is to find an estimator of ϱ that does no require explicit knowledge of, and is insensitive to the growth pattern. The approach taken here is that of a linear regression of log transformed mortality against log transformed weight, using different measures of weight:

Initial weight	W_i
Mean weight	$W_m=(W_i+W_h)/2$
Weight at mean length	$W^*=((W_i^{1/3}+W_h^{1/3})/2)^3$

The sensitivity of the estimators based on different measures of weight to the growth pattern is assessed using simulation modelling. Simulations comprise the following steps:

(1) The value of ϱ is fixed (at 0.2, 0.4, 0.6, 0.8, and 1.0).

(2) For each value of ϱ, 100 sets of density-dependent VBGF growth parameters and mortality at reference length are selected at random from the following intervals:

K	$[0.2\ y^{-1}, 1.0\ y^{-1}]$
$W_{\infty L}$	$[10\ \mathrm{kg\ ha}_{-1}, 40\ \mathrm{kg\ ha}_{-1}]$
c	$[0.005\ \mathrm{ha\ kg}_{-2/3}, 0.015\ \mathrm{ha\ kg}_{-2/3}]$
M_r	$[0.1\ y_{-1}, 1.0\ y_{-1}]$

(3) For each set of parameters, two cohorts are "stocked", and "harvested" after 6 months. Their initial weight W_i and initial density N_i are selected at random from the intervals:

W_i	[0.01 kg, 0.30 kg]
N_i	$[10\ \mathrm{ha}_{-1}, 400\ \mathrm{ha}_{-1}]$

The corresponding weight and population density at harvesting are calculated using the cohort model (see Appendix B). Mean mortality, mean weight and weight at mean length are calculated

(4) Estimates ϱ' are obtained by two-point linear regression of the log of mean mortality against the log of initial weight, mean weight and weight at mean length of both cohorts.

The performance of the three estimators is assessed on 100 simulated data sets for each true value of ϱ, using the criteria:

Coefficient of variation	$CV(\varrho')=STD(\varrho')/\varrho$
Relative bias	$RB(\varrho')=(MEAN(\varrho')-\varrho)/\varrho$

Here STD denotes the standard deviation, MEAN denotes the arithmetic mean, ϱ' is an estimate, and ϱ is the true value. The coefficient of variation is a measure of how sensitive an estimator is to the growth pattern. The relative bias indicates whether estimates are consistently too high or too low. The results of the simulation are shown in Tab. C.1.

Tab. C.1. Coefficient of variation and relative bias of the estimators for ϱ using initial weight, mean weight, or weight at mean length.

True ϱ	Coefficient of variation (%)			Relative bias (%)		
	Initial weight	Mean weight	Weight at mean length	Initial weight	Mean weight	Weight at mean length
0.2	137	73	9	-6	34	-10
0.4	91	84	9	-6	49	-8
0.6	25	112	8	-29	64	-8
0.8	32	110	8	-24	64	-5
1.0	18	66	7	-28	57	-3

Weight at mean length is by far the best estimator for ϱ by both criteria. It is insensitive to the growth pattern, and the estimates are only slightly biased. The use of initial weight or mean weight yields estimates of ϱ that are highly sensitive to the growth pattern, and are strongly biased.

The purpose of this simulation is solely to investigate the sensitivity of the estimators to the growth pattern. Further investigations are necessary of the statistical properties of the estimators.

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