SOME MANAGEMENT ASPECTS OF PRE-RECRUITMENT ECOLOGY OF THE FRESHWATER SARDINE *LIMNOTHRISSA MIODON* IN LAKE KARIBA.

by

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Abstract

The early life history of the freshwater sardine *Limnothrissa miodon* (Boulenger, 1906) was investigated with the view of establishing the factors behind recruitment variability in the Lake Kariba sardine fishery. Environmental factors behind recruitment variability were investigated through the examination of otolith microstructure from field captured sardine larvae samples while historical length-frequency data were analysed to establish size-at-recruitment.

The larval ecology study established that food was the only possible limiting factor as far as growth and survival are concerned. Growth was described by the von Bertalanffy Growth Function while instantaneous mortality rates were obtained from catch curve analysis and both estimates were observed to fluctuate from month to month. The presence of larvae in the littoral zone through the sampling period implied continuous recruitment while fluctuation in larval catches was assumed to indicate that recruitment variability was probably established at an earlier life history stage. Response of larvae to light during capture has serious management implications to the fishery in that fishing in shallow areas would result in increased larval mortality which could be detrimental to recruitment. The occurrence of larvae in most of the shoreline sampled implies that *Limnothrissa miodon* in Lake Kariba utilizes most of the shoreline as nursery grounds.

From analysis of combined historical commercial data collected from both Zambia and Zimbabwe from 1982 to 1992, it was observed that the sardine recruited to the fishery at 41 mm in length and that based on regression analysis, the mean size of fish in the fishery has

decreased by 7% and 4% in Zambia and Zimbabwe respectively. This reduction in size however, does not pose a threat to the fishery since at the current mean size in the catch is greater than the recorded size-at-maturity. The fish therefore have a chances of spawning at least once before being harvested. It was further established that due to migration to the pelagic zone as the fish grew larger, the current minimum mesh size of 8 mm was appropriate provided fishing was restricted to areas deeper than 15 m where the adult population occurs.

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CHAPTER ONE

1.0.0 GENERAL INTRODUCTION

Recruitment variability in fish stocks has been an important issue in fishery science for many years (Anderson, 1988) because it has long been hoped that understanding it would improve management and that quantitative prediction would improve the accuracy of stock assessment. However, in spite of considerable research effort over several decades there has been no significant improvement in identifying clear causal mechanisms of recruitment variability in fish stocks. Such variability was first observed through the occurrence of strong and weak year-classes based on age from scale and otolith readings. By being able to count the annual increments in the scales and otoliths, scientists were able to discover that one year-class could dominate the fishery for years, as did the 1904 year-class of the Norwegian spring-spawning herring. This dominated the fishery until 1919 (Moksness 1992). Although recruitment regulatory processes are not yet fully understood, variable growth and mortality in the larval phase are known to influence recruitment success for most marine species with planktivorous larvae (Wehrtmann 1991). The emphasis in many studies is upon survival during the early life history stages and in particular, understanding causal mechanisms affecting this survival and subsequent recruitment. Some clear patterns have emerged from these studies: key factors for larval survival are predation, starvation or limited food resources and oceanographic conditions that may advect larvae into unfavourable environments. Moreover two determinants of early life mortality - starvation and predation - are closely linked by growth and development processes (Bailey and Houde 1989).

Much effort has been directed to studying starvation during the early stages of life, particularly in first-feeding larvae. The result was that several hypotheses have been put forward in an attempt to answer questions related to recruitment variability resulting from different extends of mortality in the early life stages of the fish. Anderson (1988) treated the major hypotheses that emerged under the following headings: mortality due to ***starvation*** (of fish larvae), mortality from ***predation*** (including cannibalism for all stages capable of it), mortality and growth resulting from ***physical dispersal*** to areas with different food, predator and physical regimes (for eggs and larvae), and mortality from ***disease*** (for adults).

1.1.0 Starvation

Four hypotheses have been advanced as causes of mortality from starvation during the early life stages in fish and these are:

1.1.1 Critical period hypothesis (Hjort 1914).

This hypothesis proposes that the transition from yolk-sac stage to active first-feeding is a critical period in the life history of the fish. The degree of success of feeding during this period determines survival and eventual year-class strength. Success will depend on the larvae encountering sufficient prey of suitable size, in the absence of this, irreversible degeneration of the digestive system occurs (Pitcher and Hart 1982; Lasker 1985). In Lake Kariba the occurrence of different densities of larvae in different substrate could be as a result of this phenomenon. Substrates which support abundant larval food of the right size at the point of yolk sac absorption will lead to better larval survival than those substrates that do not. However this factor does not act in isolation, other factors such as predation will also be at play.

1.1.2 Match-mismatch hypothesis (Cushing 1975).

This states that while annual spawning time in fishes is almost constant, the onset of the annual primary production cycle is not constant but a result of changing physical conditions. If the timing of the production cycle occurs too early or too late, then the larvae will be variably "matched" with the food abundance, resulting in varying levels of starvation and subsequent survival of a cohort. The controlling factors proposed to affect the onset of spring production range from wind strength and wind direction to irradiance and water temperature. While several variants of this hypothesis have been formulated to account for biotic and abiotic factors that influence recruitment by determining food availability (review by Anderson 1988), another hypothesis, the member/vagrant hypothesis, challenges this (Sinclair and Tremblay 1984). The member/vagrant theory advocates that the contribution of a cohort to a stock will depend on the integrity of the hydrodynamic structure that limits the cohort's initial dispersion away from the spawning ground (Sinclair and Iles 1985). Here the success of a cohort will depend on the synchronization of its development and its spatial overlap with that of suitable food concentrations (Lambert and Ware 1984). However following a study in 1985 of the spring and fall larval cohorts of herring *Clupea harangus* in the St Lawrence Estuary, Fortier and Gagne (1990) concluded that spawning times and locations may have evolved to favour the initial cohesion of larval fish cohorts by limiting dispersion. In addition, both transport and energetic processes can influence the success of a population at colonizing its range.

For the Kariba sardine where spawning seems to be a continuous process and space a limiting factor, the matching of a cohort to appropriate food levels is more of a chance event rather than the result of an explicit strategy by the parent stock. This implies that the

match/mismatch theory would be a "match" for a cohort that comes in during times of food availability while the opposite would be the "mismatch" for a cohort that comes at a time of inadequate food availability. If however the eggs are laid demersally in the shallow areas, then the member/vagrant hypothesis comes into play where the eggs are spawned in the nursery ground limiting possible dispersal to areas with poor nutritional status.

1.1.3 Food production hypothesis (Anderson 1988).

This states that the absolute magnitude of primary production varies annually depending on certain physical conditions such as temperature, wind mixing, retention zones and/or vertical stratification. When primary production is high, there is more food available for fish larvae which increases survival as a result of reduced starvation. Therefore, survival is resource limited on an annual basis due to changing carrying capacity. This can be observed in changes of annual freshwater run off from the Canadian Arctic along the Labrador coast which have been related to lagged cod catches and hence recruitment variability (Anderson 1988). The same can be said about the drop in catches of the sardine in Lake Kariba following drought years; Marshall (1982) established that the lake relies both on river inflow and run-off water for nutrient replenishment. However Mtada (1987) argues that the uneven distribution of sardine catch in Lake Kariba cannot be fully explained by river inflow alone, as weather (through the development of thermal stratification and reduced fishing effort) is another factor of equal importance. Another well-known example is the Peruvian *El Niño* event in 1972 which resulted from changes in surface currents, and caused larval deaths due to sparsity in food organisms . However the *El Niño* event of 1972 was further compounded by overfishing which resulted in the actual collapse of the fishery (Pitcher and Hart 1983, also see contributions in Pauly *et al* 1989).

1.1.4 Resource use competition hypothesis (Frank 1986).

This hypothesis states that competition for food with other planktivorous organisms will significantly affect the amount of food available for ichthyoplankton. When competition for food is high, survival of fish larvae will be low due to starvation (Smith 1985). This can relate closely to the critical period hypothesis but also to successful feeding conditions throughout the larval phase. It is possible for Kariba that reduced nutrient levels can result in there being insufficient planktonic food for the small larvae. However, possible food competitors of the Lake Kariba sardine larvae have not yet been identified.

1.2.0 Predation

Predation from planktonic or fish predators on eggs and larvae is cumulative up to age at recruitment. This results in strong or weak year-classes depending on whether predation was high or low over the pre-recruitment period. Predation is also associated with growth in that predation decreases with increasing size. Therefore, survival during the larval stage is directly related to growth. Conditions that regulate growth rate during that phase such as food availability will ultimately determine survival (Houde 1987). Predation by fish and/or cannibalism were observed to play a major role in large enclosure experiments containing larvae with and without fish predators of the same and different species (Oiestad 1985). While its magnitude in the wild is not clear it could be a contributing factor especially in times of scarce food availability.

Predation could be one of the main causes of larval mortality in the sardine *Limnothrissa miodon* in Lake Kariba. At this stage in the sardine life cycle it inhabits the littoral zone where all other species of riverine origin occur and some of them are reported to be

piscivorous (Kenmuir 1983) and the sardine is the most abundant prey in that zone. However there is no immediate evidence of this in the wild as this has not yet been studied in detail.

1.3.0 Physical dispersal

Pelagic fish eggs and early larvae are part of the plankton and drift within prevailing currents such that survival depends on being transported to places suitable for growth. Mortality will be very high if the eggs and larvae drift to unsuitable places but low if transported to areas that favour growth. Shelton and Hutchings (1982) have amply demonstrated that recruitment of the anchovy *Engraulis capensis* into the South African fishery has remained fairly constant due to the resilience of the transport mechanisms. It would appear that the anchovy is well adapted to the southern Benguela Current which would transport the larvae from the spawning ground to the west coast where widespread, extensive upwelling and consequently high levels of productivity occur which are known to be associated with the Benguela current system.

For the Lake Kariba system, this theory would apply if the sardine spawns in the open water and the eggs are transported to the shoreline by waves during incubation as has been suggested by some workers at the Lake Kariba Fisheries Research Institute (the late O. S. M. Mtada and S. Chimbuya, pers. comm.). The success of a cohort will therefore depend on whether the eggs have been transported to an area with favourable conditions or not.

1.4.0 Disease

Viral or microbial infections of eggs, larvae and juveniles can lead to high mortality rates resulting in poor year-classes. This is also another aspect that is difficult to quantify in the

wild but is assumed because of the devastation it causes on fish farms if not controlled.

It is therefore clear that the issue of what factors control fish survival prior to recruitment (which is defined as the age at which 50% or more of a year class are mature (Anderson 1988)) remains largely unresolved. In the past assumptions were made that there is a single solution, such as "larvae starve" to the complex problem of recruitment variability. A more rational approach would be to build upon existing ecological theory bearing in mind that recruitment in each species has its own special characteristics which have to be researched and analysed (Pitcher and Hart 1982).

Several workers (Gulland 1965; Cushing and Harris 1973; Cushing 1974; Ware 1975) champion the concept that size-specific growth and mortality rates interact to determine survivorship in fish populations. This concept forecasts that survival of a cohort is directly related to growth rates during the pre-recruitment period (Anderson 1988). Survival while increasing through successive life history stages, will be dependent on favourable conditions specific to each life history stage. Therefore it is important to study growth and survival for each life history stage as it is during one or more of these stages that a year-class strength is determined. These stages include: the egg; the larvae (which can be split into yolk-sac larvae or prolarvae, first feeding larvae and then later planktonic larvae or post-larvae); the first juvenile stage and finally the recruitment stage.

Houde (1987) suggests that predation is the main cause of mortality at all stages from egg to juveniles while starvation affects mainly the larval stages especially at the end of the yolk sac stage. Physical processes play a role during the egg and early larval stages when

dispersal depends on these processes while disease could take its toll during the larval and juvenile stages. He further attributes control in numbers to density-independent processes during the egg and larval phases while density-dependent processes are at play during the juvenile stage.

Therefore it goes without saying that determination of growth and mortality at each of these phases and the establishment of the causes of mortality at the respective phases are of paramount importance.

1.5.0 Objective of study

The purpose of this study therefore is to investigate the early life history and recruitment of the freshwater sardine *Limnothrissa miodon* in Lake Kariba with the aim of:

1) establishing the factors that influence recruitment variability (i.e. growth and mortality and hence survival) of *L. miodon* in Lake Kariba and
2) incorporating the knowledge gained in the study to the management strategies of the Lake Kariba sardine fishery.

So far detailed studies have been carried out on the adult population (Begg 1974; Marshall 1982, 1985, 1987; Cochrane 1978, 1984; Mudenda 1989; Chifamba 1992) where the fishery occurs. No in depth studies have been done with the early stages, especially the egg and larval stages where for most fish species cohort strength (and hence recruitment) is established (review by Anderson 1988). The fishery has so far been managed with very limited knowledge of these early life history stages. This study therefore seeks to rectify this by contributing knowledge about growth and mortality and hence survival of the early life

history stages.

1.5.1 Inference of recruitment variability

Recruitment variability in the Lake Kariba sardine fishery is inferred from yield variability as no studies have been done in the past with regard to direct observation of variability in recruitment. Unlike the example taken from Moksness (1992) of the Norwegian herring cohort of 1914 which dominated the herring fishery up to 1919 as determined by the age based on otolith and scale counts, no direct observations of variability have been done on the Lake Kariba sardine fishery. Hence the need to infer the variability from yield fluctuations.

1.5.2 Recruitment Forecasting System

Figure 1.0 shows the proposed flow diagram of the overall project, of which this study is part, which seeks to establish a Recruitment Forecasting System (RFS) for the sardine fishery on Lake Kariba.

The RFS model seeks to combine what is already known about the fish and the fishery through analysis of historical data from the commercial fishery on one hand and analysis field data gathered through field sampling and surveys. These field data are taken from both the pre-recruitment and post recruitment stages as follows:

a) Post recruitment stages, in addition to analysis of historical data from the fishery, will mainly involve analysis of abundance data collected through whole lake hydroacoustic surveys using low frequency (70 KHz) hydroacoustic equipment. These data will also include the size frequencies in the adult population as well as their spatial distribution on the lake. In

addition, seasonal patterns in both abundance and spatial distribution will also be analysed. Samples of catch from the commercial fishery will also be collected from fishing rigs during the hydroacoustic surveys to validate the size frequencies that will be provided by analysis of the hydroacoustic data.

b) Pre-recruitment stages will involve the analysis of data collected from the inshore areas through field sampling only since the fishery is not active in the inshore. These data will include abundance estimates of the larval and juvenile stages collected from inshore hydroacoustic transects using high frequency (200 KHz) hydroacoustic equipment. Seasonal and spatial patterns will also be analysed and compared to the seasonal and spatial patterns observed in the post recruitment data analysis. More data will be gathered from the larval and juvenile stages through collection of specimens from field sampling, direct ageing of specimens by the otolith increment technique, followed by the estimation of both growth and mortality rates. Information on migration from the inshore to offshore will also be gathered.

The shaded areas in the flow diagram show what is hoped would be the contribution of this study by providing growth and mortality rates and estimating abundances of the larval stages. In addition the study would contribute knowledge at the point of recruitment by establishing the size at recruitment and what effect that would have on the mean size of fish in the catch and what management implications that would have.

c) Further data on primary production and limnological aspects of Lake Kariba will be sought from other studies, especially from the University of Zimbabwe

Lake Kariba Research Station which has been carrying out research on those aspects since the formation of the lake. Information on lake levels will be obtained from the Zambezi River Authority who have monitored this aspect since lake Kariba filled up to its maximum water mark of 487 metres above sea level.

This information, i.e. from the post and pre-recruitment stages and about the physical features of the lake, would be fed into a general model describing the dynamics of the sardine *L. miodon* before and after it enters the fishery with a view for better management of the fishery. It is hoped that the trends, past and present, will be observed and form the basis of prediction of future trends once certain parameters about the future become apparent. Reference to this diagram will be made at the end of the report to describe the specific contributions of this study to this model.

1.6.0 Background information on Lake Kariba, *L. miodon* and the fishery

1.6.1 Lake Kariba

Lake Kariba, (altitude: 485 m a.s.l.; latitude: 16° 28' and 18° 04'; longitude 26° 42' and 29° 03') located on the Zambezi River which forms the boundary between Zambia in the north and Zimbabwe in the south, was formed by the impoundment of the Zambezi River between 1955 and 1959 for the purpose of hydroelectricity power generation. This resulted in a lake 281 km in length with a maximum width of 40 km and maximum surface area of 5,364 km^2 (of which 60% comprised the newly formed pelagic zone) and a shoreline length of 2,146 km. The lake is 128 metres deep at the dam wall with an average depth of 29.5 metres.

According to the classification of lakes based on thermal regimes proposed by Wetzel (1975),

Lake Kariba is a warm monomictic lake with a thermal stratification. The temperature stratification is usually at a depth of 10-15 m, with a surface temperature of 28°-30° C during the hot-wet season, December to March. During the cool-dry season, April-July, the surface temperature drops to about 22° C and there is a turnover sometime in July. Mtada (1987) found that the thermal stratification was strongest in February and March in the years 1984 and 1985 and that the general thermal stratification was similar to a chemical stratification only that the chemocline was deeper.

The lake is divided into five hydrological basins each named after a major river that feeds into it. The Zambezi River which contributes 70% of the inflow has a very large influence on Basins 1 and 2 (see Figure 2.1 below). For six months of the year (November to May), the period at which the Zambezi is at peak flow, these two basins have riverine characteristics. By July, with the recession of the floods, the influence of the river decreases with the two basins assuming lacustrine characteristics with the conventional thermocline at 12 to 15 m. Basins 3 to 5 are lacustrine throughout the year. The influence of the Zambezi River helps create a strong hydrological gradient with productivity and transparency increasing away from the mouth (Sanyanga *et al.* 1994)

Following the filling of the lake in 1963, the absence of a specialized, planktivorous, pelagic species of fish within the middle Zambezi River fish fauna now occupying the lake, became obvious (Huddart 1994). As a result, an exotic sardine *Limnothrissa miodon* was introduced in 1967/8 to fill that vacant planktivorous niche. The sardine successfully colonized that niche and propagated rapidly leading to the commencement of a commercial fishery based on the introduced sardine, on the Zimbabwean side of the lake in 1973.

1.6.2 Biology of *Limnothrissa miodon*

Since the introduction of the sardine many studies (Begg 1974; Cochrane, 1978, 1984; Kenmuir, 1983; Marshall, 1982, 1985, 1987; Mudenda, 1989; Chifamba 1990) have been undertaken to establish its biology in Lake Kariba. These studies indicate that the sardine breeds throughout the year with a peak breeding period from September to March (Kenmuir 1983) or September to February (Cochrane 1984) while Mudenda (1989) describes two annual peaks following turnover in the July/August period and from January to March following the rainy season. However up to now it is not clear where they spawn although larvae are found in the littoral zone throughout the year. These larvae then migrate to the pelagic as they grow older. Begg (1974) and Cochrane (1984) defined larvae as fish of up to 15 mm in length while between 15 and 29 mm they are juveniles. Between 30 and 40 mm the fish pass through the sub-adult stage with a lot of them maturing at that stage (Marshall 1987). At this point the fish are generally found in areas more than 20 metres deep and they recruit into the fishery. According to Mudenda (1989) they recruit into the fishery at 41 mm while Ramberg *et al* (1987) put the age at recruitment at about 3 - 4 months. The mean commercial size of 50 mm is reached at about 5 - 6 months old (Marshall 1987). In the Lake Kariba system they are estimated to have a maximum age of two years (Kenmuir 1983) but six months to one year on the average. Specimens of up to 140 mm in length regularly appear in the catch.

The pelagic zone occupied by this sardine seemed to be structurally simple with one main food chain: phytoplankton - zooplankton - *L. miodon* and finally the piscivorous tigerfish *Hydrocynus vittatus* (Marshall 1982). However, specimens of other species such as the squeaker, *Synodontis zambezensis*, the butter catfish *Eutropius depressirostris* and *Alestes*

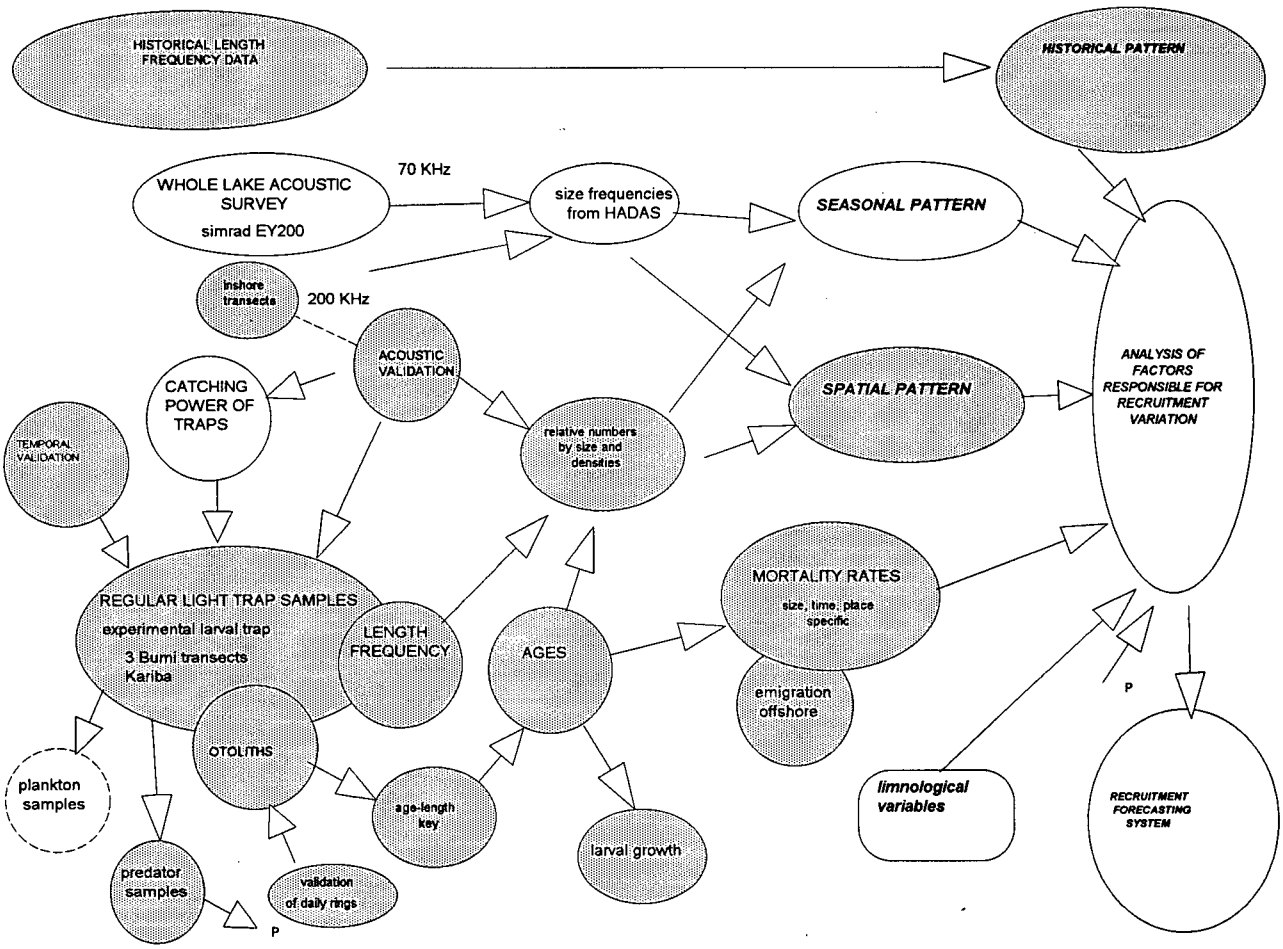
sp now regularly appear in the pelagic zone. The first two species prey on the sardine while the latter seems to compete for the same niche as the sardine.

In addition to being introduced to Lake Kariba the sardine is also found in Lake Kivu where it was introduced in the late 1950s (Bell-Cross and Minshull 1988), in the middle River Zambezi and Cabora Bassa where it invaded on its own by escaping from Lake Kariba through the turbines. It has also recently been introduced to Lake Itezhi-Tezhi on the Kafue River in Zambia where the progress of its colonizing that lake is being monitored with a lot of interest since this lake, with a mean depth of 15 m, is the most shallow location to which *L. miodon* has been introduced. As stated above, the sardine is also found in the Middle Zambezi River as well which poses the question of whether it breeds in the Zambezi River or it is just in transit to Cabora Bassa ?

1.6.3 The Lake Kariba sardine fishery

Following the successful colonization of the lake, a commercial fishery based on this sardine commenced on the Zimbabwean side of the lake. The initial catch rapidly increased from 66 tonnes in 1973 to almost 8000 tonnes in 1980 (Marshall *et al.* 1982). Following Zimbabwe's independence, a similar fishery developed on the Zambian side in the early 1980s resulting in the annual catch reaching a total of 24000 tonnes for the whole lake in 1985 (Machena and Mabaye 1987; Ramberg *et al.* 1987). Sanyanga *et al.* (1991) report of a total catch of 22 000 tonnes on the Zimbabwean side for 1990 representing an increase of 8.2 % compared to 16 % for 1989. The total catch for the entire lake is probably in the order of 30 - 33,000 tonnes.

Figure 1.0: Showing the proposed flow diagram of the project seeking to investigate factors responsible for recruitment variability on Lake Kariba with a view of setting up a Recruitment Forecasting System (RFS). Shaded areas show the major inputs of this study in the project.



While there has been an increase in annual total catch as the years progressed there occurred fluctuations within the fishery as can be observed from the Lake Kariba Fisheries Research Institute Annual Statistics. These fluctuations occurred around the years 1976/7 first, followed by another in 1982/3 and followed by yet another in 1986/7 (Figure 1.2). While the 1982/3 drop in catches could be attributed to drought during that period there is no explanation at the moment for the other two. However, the 1986/7 drop could be associated with an increase in the *Alestes* species that invaded the pelagic zone that year and appeared in the catches. A lot of fishing companies that year brought crate loads of *Alestes* species to The Lake Kariba Fisheries Research Institute that had been caught in their nets in the pelagic zone. Kenmuir (1983) reports that this species feeds on zooplankton and small aquatic insects; here it might compete with sardine depending on the species it eats. It might also prey on larval sardine. However, this has yet to be established. Balon (1974) professes that had *L. miodon* not been introduced into Lake Kariba the *Alestes* species would have colonised the pelagic zone through adaptation from shallow water to deep water conditions. Its appearance in the sardine catches during the 1986/7 period poses the question as to whether Balon's claims were valid or not.

The fishery also experiences intra-annual fluctuations with peaks in the February/March and August/September periods following the rain seasons and the lake turnover in June/July respectively. Figure 1.3 shows monthly fluctuations from 1974 when the fishery started to 1988 taken at five year intervals with repeated low catches for the months of May and November which could be attributed to depletion of nutrients in the months prior to the lake turnover and the rainy season respectively. However according to Kenmuir (1983) the catches are lowest from October to January, following plankton declines as the nutrients are

used up around August. In addition, when summer arrives, Kenmuir (1983) alleges that the fish move to the marginal areas to breed leaving the open water population depleted. The catches drop as a result of this movement to the shallow water, rising again about March when adults return to the open water. Cochrane (1978) on the other hand found a small percentage of active females in the marginal areas compared to the deep water implying that spawning might be taking place there. Mtada (1987) attributes another factor (which is often forgotten) to the drop in catches between September and December and that is the lake is usually rough during that period and fishing becomes very risky due to high winds (up to 75 km h^{-1}). Even though the fish may be abundant, the high risk of sinking among the fishing boats reduces fishing effort as the fishermen either take cover in protected bays or stay off the water altogether.

It is not clear therefore whether these fluctuations are associated with nutrient depletion or breeding behaviour or reduced fishing effort and/or a combination of all three. Figure 1.4 shows the monthly mean trends in the sardine fishery expressed as percentages of the annual catches from 1974 to 1988 based on the statistics from the Kariba area of the Zimbabwean side only. This curve indicates two peaks, i.e. one small one in April after the rain season and a high one in August after the lake turnover. By implication turnover releases more nutrients to the system than those brought in by river inflow and run-off during the rain season.

Since the commencement of the fishery the annual CPUE declined in a fluctuating fashion from 1974 to 1983 probably as a result of more people joining the fishery. From 1984 the CPUE increased slightly to a more or less stable state to this day. However the monthly

mean CPUE follows a trend almost similar to the yield curve. It has two peaks annually (Figure 1.5) one in March/April and a higher one in July/August. These could be caused by the improved catches following the rain season and turnover as effort does not increase much within the year. There is a drop in January, May and November again which could be as a result of the drop in catches during those periods.

One thing is not clear regarding the CPUE and that is the effect of light which is used to attract the fish. During times of full moon every month the fishery is temporarily closed as the light of the moon reduces the catch per night to below viable levels. There is no regulation to limit fishing during full moon, the fishermen themselves realise this drop in catches during this 4 to 5 day full moon period. Under these circumstances we can ask whether CPUE a good indicator of population density or not? We can also ask what pattern would CPUE take if commercial fishing was carried out in the absence of light?

The total fishing effort on the other hand has increased continuously as the number of licences issued increased from 3 units in 1973 to 230 in 1991 on the Zimbabwean side and to 180 between 1980 and 1991 on the Zambian side. As more and more operators turned to the use of engines, echosounders, hydraulic winches, and radios for communication the catching efficiency of each boat increased. The fishermen have also become experienced in the process and therefore more efficient as well. While effort was measured as the number of boat nights the efficiency of each boat has improved due to the reasons stated above.

Attempts are currently underway to define effort more carefully putting the recent developments into consideration. However it will be difficult to standardize effort for the

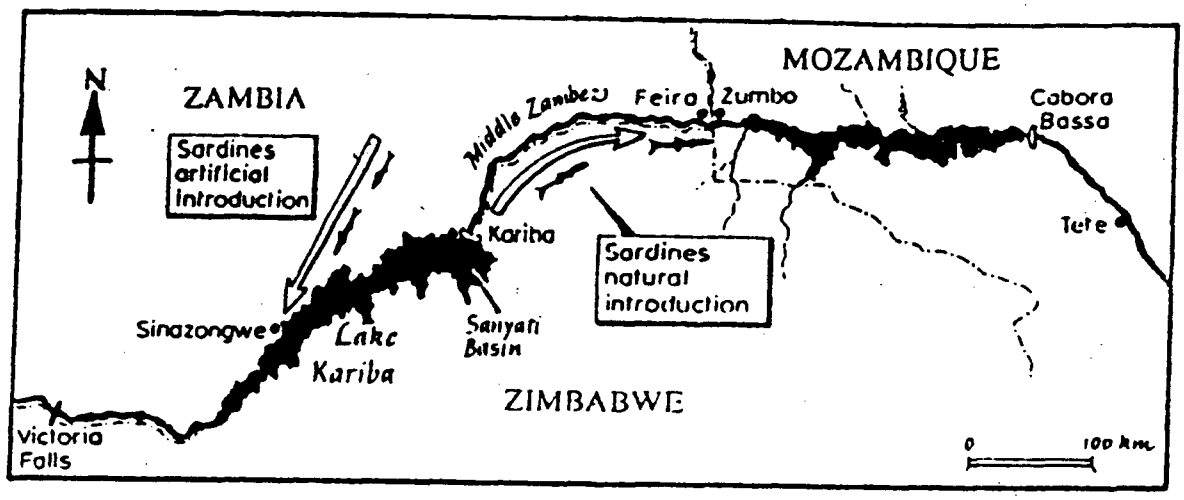


Figure 1.1: Showing Lake Kariba, (5500 km^2), where a fishery thrives on *Limnothrissa miodon*, an introduced sardine species. Also shown is Lake Cahora Bassa, another man-made ecosystem 220 km downstream, which was invaded by the sardine from Lake Kariba after escaping through the turbines on the Kariba dam wall.

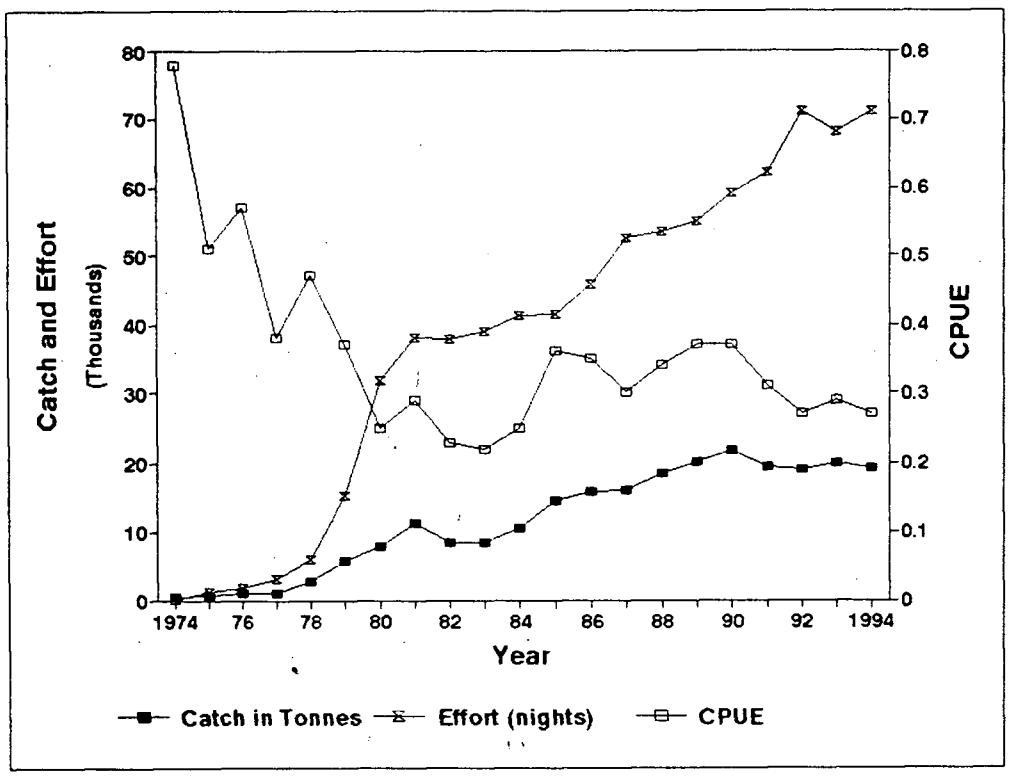


Figure 1.2: Showing the annual trends in the sardine fishery from 1974-1994 (LKFRI 1994 Fisheries Statistics).

entire lake as the efficiency of the gear on the Zambian side is not boosted by the presence of echosounders and radios as is the case in Zimbabwe. It is not certain that these instruments will be readily available for Zambian operators in the near future to allow for easy standardization of effort. As a result, some point form of system has to be made when calculating fishing effort imposed by a boat on the fishery depending on what equipment is on board.

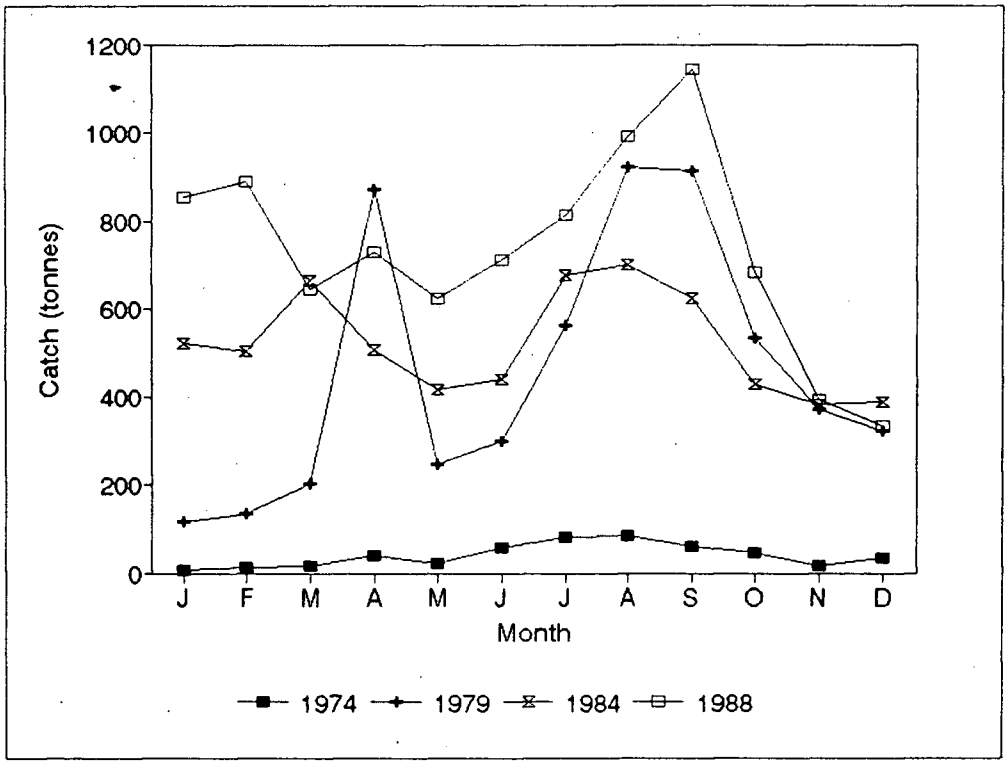


Figure 1.3: Monthly mean catches of the sardine for the years 1974, 1979, 1984 and 1988 (LKFRI 1989 Fisheries Statistics).

So far the fishery has been managed by the control of effort through the enforcement of certain regulations ranging from limitation in entry and fishing gear to closure of certain areas, mainly to protect the other species of riverine origin and the larval and juvenile stages

of the sardine. Biological knowledge on this otherwise important fish species is rather limited (Marshall 1987) and emphasis is now put on studying those aspects of the biology that can be applied to management of the fishery. Unlike the example of recruitment variability observed in the Norwegian spring spawning herring cited by Moksness (1992), no direct observations through ageing the fish by scales or otoliths were done with the Lake Kariba sardine. Recruitment variability was therefore deduced from fluctuating yields. It is hoped that with the development of ageing both larval and adult sardine by counting daily growth increments in otoliths it will be possible to directly identify by age those cohorts that dominate the fishery from year to year.

The issue of inference of recruitment variability from catch fluctuations could be further validated by the fact that with increasing effort and efficiency in effort the catch would be expected to have a steady rise while the CPUE experienced a steady decline. However this has not been the case as catch has been increasing in a fluctuating manner and CPUE has been declining as well in a fluctuating manner (Figure 1.2). Intra-annual fluctuations show peaks in those periods following the rainy season and lake turnover indicating that survival (hence recruitment) was high due to increased food availability following those events. On the other hand decline in catches is reported following periods of nutrient depletion. The sardine is known to spawn throughout the year implying that recruitment is continuous and if this was not subject to variability then there would be no fluctuations in yield. CPUE while it has been used as an indicator of density, the validity of such application on Lake Kariba is compounded by the use of lights to attract the fish during fishing. Furthermore drops in lake levels in drought years could reduce the habitat of the fish thus increasing their vulnerability to fishing gear thereby further distorting the CPUE concept. However, Karenge

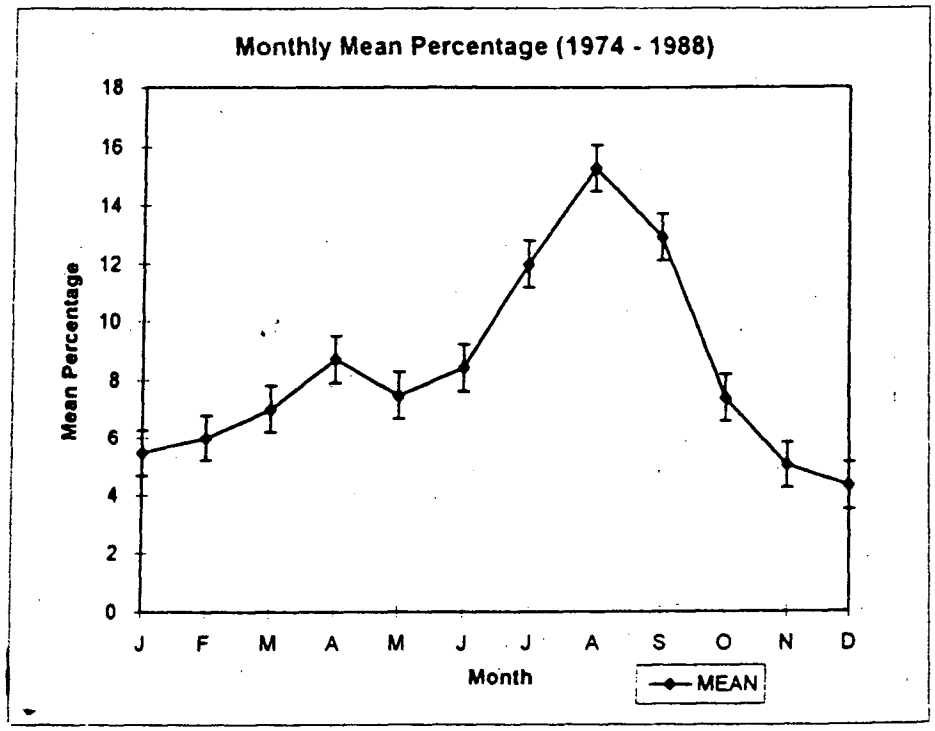


Figure 1.4: Monthly mean catches of *L. miodon* expressed as a percentage of the annual catches, 1974 to 1994 showing the 95% confidence limit.

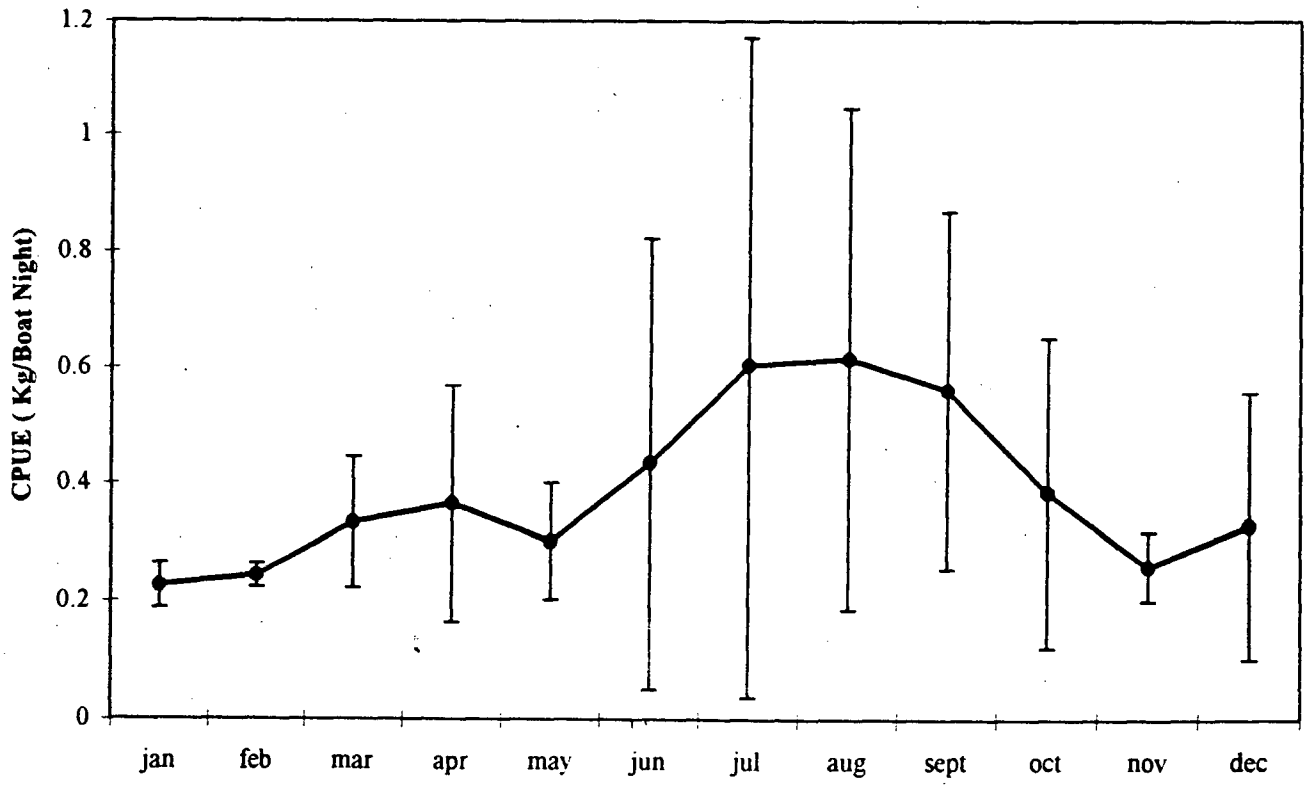


Figure 1.5: Monthly mean CPUE in the Lake Kariba sardine fishery from 1974 when the fishery commenced to 1994, showing the 95% confidence intervals.

and Kolding (1995), found no evidence to support the general notion that fluctuating lake levels (i.e. draw downs and subsequent rises) in man-made Lake Kariba have severe adverse effects on the fishery.

Lasker (1981) cites examples of decline in other clupeoid populations such as the Atlanto-Scandian herring, the Pacific sardine, the Hokkaido herring and the Japanese sardine which resulted in some cases to the collapse of the fishery. In these cases it was concluded that heavy fishing on parent stocks after the appearance of several poor year classes was sufficient to reduce the stocks's reproductive potential to a point where insufficient recruits were produced for the fishery. However what is not clear is why "several poor classes" appeared; only their effect coupled with heavy fishing is discussed.

In addition to successful colonization of Lake Kariba, *Limnothrissa miodon* also invaded Cabora Bassa, another man-made lake downstream from Lake Kariba, by passing through the turbines on the dam wall. Up until 1993 the war in Mozambique had inhibited the commencement of a fishery in Cahora Bassa based on this species. However there is no doubt that knowledge gained in this study will be of importance to such a fishery as well as the two lakes share the same hydrological regime.

1.7.0 Objectives and Organization of the Thesis

In this study I have examined the pre-recruitment ecology of *Limnothrissa miodon* in the Lake Kariba sardine fishery first through field sampling of larvae and secondly through the examination of historical data collected from the commercial fishery for a period of 10 years. My objectives were aimed at increasing our knowledge of the pre-recruitment ecology of this

otherwise very important introduced sardine on which the commercial fishery on Lake Kariba is dependent. No in-depth studies into the early life history dynamics had been carried out either on Lake Kariba or in other Lakes (i.e. Tanganyika, Kivu and Cahora Bassa) where it occurs. This is the first attempt to describe growth and mortality in the larval stages of *L. miodon.*

In Chapter Two, "Methodology", I describe in detail the field sampling I carried out and the initial processing of the specimens. Larval sardines were captured for age determination, validation of otolith ring deposition periodicity in the laboratory, and to determine spatial and temporal distribution. The results of these experiments are discussed in other chapters. I also highlight some of the problems I faced not only in the actual data collection but also those of a logistic nature, such as the late acquisition of equipment due to delays elsewhere and the breakdown of boats in a remote situation where back-up services are either non existent or difficult to come by. I also discuss attempts to validate my sampling using light attraction by hydroacoustic means which failed on technical grounds. The chapter concludes with a general discussion on the observations made and problems encountered during sampling and where possible make recommendations on how to solve some of the problems.

In Chapter Three "Estimating some early life history parameters in the freshwater sardine *Limnothrissa miodon*, from daily growth increments in otoliths" I estimated age from otolith microstructure and determined growth rates in larval *Limnothrissa miodon*. This technique has become popular for small fish in fisheries research (in both temperate and tropical climates) and it provides direct estimates of age which are very difficult to obtain in tropical situations and for those fish less than a year old in temperate systems. I attempt to explain

what factors (biotic or abiotic) are responsible for recruitment variability based on examination of otolith microstructure. I also discuss in depth the validation of daily deposition in the otoliths of larval *L. miodon* which enabled me to tentatively conclude that rings are laid on daily basis in the otolith of the Lake Kariba sardine. This validation of daily ring deposition in the otoliths is a prerequisite for using this technique to age fish (Radtke 1989).

In Chapter Four, "Larval mortality, spatial and temporal distribution and recruitment pattern of the sardine *Limnothrissa miodon* in the inshore areas of Lake Kariba.", I apply the otolith increment technique to obtain estimates of larval mortality through an age-based catch curve analysis. For this I set up age-length keys to enable me to transform length frequencies to age frequencies. Previously estimates of larval mortality in sardine have been estimated from the adult population based on the assumption that mortality is constant for all life history stages. In addition I discuss spatial and temporal distribution patterns based on field observations.

In Chapter Five "Recruitment and selection in the sardine *Limnothrissa miodon* in Lake Kariba", I examine length frequency data taken for 10 years from the commercial catches to check the pattern of recruitment. These data were collected by the Department of Fisheries in Zambia and The Lake Kariba Fisheries Research Institute in Zimbabwe. In addition I evaluated gear selectivity through my own field experiments following a suggestion from my commercial data analysis that the mean size of fish in the catch has been reducing over the years.

In Chapter Six, "General Discussion", the concluding chapter, I discuss some of the possible applications of early life history studies to fisheries management. Then I focus on the possible applications of my studies to the sardine fishery on Lake Kariba given the Recruitment Forecasting System proposed in Chapter One. These applications also include the monitoring of some of the most important aspects such as size structure, larval abundances, age-at-first capture and growth rates. I also emphasize that depth at which fishing takes place should be the main tool of management which should be monitored carefully. However because the biggest fishing fleet in Zambia operates in a shallow area, i.e. less than 15 m, I suggest an increase of the minimum mesh size from 8 mm to 10 mm. Although Zimbabwe can continue utilizing the current mesh size as long as fishing takes place in areas more than 20 metres deep it might be difficult to monitor if two different mesh sizes are recommended. Therefore a strong recommendation for increasing the mesh size from 8 mm to 10 mm is made.

CHAPTER TWO

2.0.0 METHODOLOGY

Many methods have been employed over the years to study the early life history of fish. These methods ranged in scale from the use of small traps in streams to large scale oceanic pelagic ichthyoplankton surveys (Smith and Richardson 1977). These studies have covered estimation of growth rates and survival rates or behaviour while others have provided estimates of biomass. Most growth and mortality studies have relied on the use of size frequency data or the application of otolith techniques while overall population studies have employed methods such as hydro acoustic techniques or surveys that involve the filtration of known quantities of water that provide estimates of abundances.

The purpose of this part of the report is to describe in detail the methods that were employed to capture and process specimens during the study of the early life history of *Limnothrissa miodon,* a fresh water sardine in Lake Kariba. These methods are described to cover the activities in the field and in the in the laboratory as follows:

1. In the field for the
    a) capture and initial processing of the specimens.
    b) validation of otolith increment periodicity
    c) validation of larval temporal and spatial distribution and
    d) estimation of larval abundance.

2. In the laboratory further processing of the specimens involved the

removal and preservation of the otoliths and finally the counting of the rings in the otoliths.

Subsequent sections of the report will address the different statistical analysis that were carried out to obtain estimates of growth rate, mortality rate, and abundances.

2.1.0 STUDY APPROACH

Two approaches were taken for carrying out studies aimed at understanding the recruitment dynamics of *L. miodon* namely:

a) Analysis of historical data based on the past history of recruitment as observed from length-frequency distributions of samples collected from commercial catches. The patterns of recruitment and gear selectivity were investigated from these data. It was however also necessary to obtain estimates of the latter from field experiments.

b) an ecological approach with a view to examining biotic and abiotic factors that influence growth and mortality. This part of the study involved estimating growth and mortality by examination of otolith microstructure . Attempts were also made to obtain estimates of larval abundance by hydro-acoustic methods.

2.1.1 Justification of the study approaches taken

These two approaches were chosen in conjunction, initially to throw light upon the past history of recruitment based on data from commercial catches for a period of ten years after combining data from both Zambia and Zimbabwe since these data were taken from the same basin in Lake Kariba. Secondly, through the larval ecology approach attempts are made to

investigate the dynamics of the pre-recruitment stages through the examination of otolith microstructure of field captured larvae.

So far, most growth studies on *L. miodon* have dealt with the adult population (Cochrane 1978; Marshall 1987; Mudenda 1989) and have back calculated growth of the pre-recruitment stages from data on these adult populations. It has long been recognised, and is now a general opinion, that year-class strength is established during the early life stages of fishes (Frank 1991), and seems to depend on events taking place perhaps in the first few weeks or even days after hatching (Clark and Pearson 1979). Pepin and Myers (1991) demonstrated that duration of stages in the larval phase is significantly correlated to recruitment variability which indicates that recruitment variability is linked to early life history characteristics. Thus, understanding the dynamics of early life history stages in *L. miodon* would fill that gap in our knowledge as to when the cohort strength is established for this short lived species which enters and probably leaves the fishery within the first year of life. The two approaches thus attempt to answer three important related questions:

a) what has been the recruitment pattern for the ten years that length frequency data have been collected from the commercial fishery ?

b) what have been the possible mechanisms responsible for the recruitment pattern and

c) what relevance does the recruitment pattern have to the management of the fishery?

To date, the sardine stocks have been managed without reference to any biological knowledge about the early life history stages and the monitoring of the fishery has been

based on the analysis of the catch-per-unit-effort (CPUE) and length-frequency distributions from the adult population. If it is true that recruitment variability is determined in the early life history stages, to infer events taking place in these stages from the adult population, as has been the practice, is inappropriate, hence the need to study the early life history.

2.1.2 Objectives of the study approaches

a) Analysis of historical data

Length-frequency data from commercial catches collected during the periods 1982 to 1988 on the Zambian side and from 1989 to 1992 on the Zimbabwean side were analyzed to project the nature of recruitment and gear selectivity during those periods. Selectivity was also examined by experimental fishing with a small mesh size alongside a commercial fishing rig. Length-frequency distributions from commercial catches are indicative of the range of fish that are being captured, from the smallest size that is recruiting into the fishery to the largest size susceptible to capture. This range shows what is selected by the gear in use. However, one has to make the assumption that there were no discards of smaller fish and that the samples taken indeed represented the actual catches. The specific objectives of analysing historical data are discussed below in Chapter Five.

b) The larval ecology approach

To pursue this approach, a field sampling programme was established with a view of investigating the biotic and abiotic factors that influence growth and survival. This was done with the understanding that to estimate growth and mortality rates accurately it is necessary to estimate the age of the fish accurately. For this purpose age determination based on otolith microstructure technique was chosen as the main method to study growth and

mortality. In larval fish age determination by application of the otolith microstructure technique enables cohorts to be identified and growth and mortality to be estimated (Blaxter 1989).

An initial analysis of the otolith microstructure in juvenile *L. miodon* was presented in a short project undertaken in partial fulfilment of the requirements for an M.Sc degree. Although the technique was developed sufficiently to address some basic questions on the ecology of the early life history of the sardine, further work was required to refine the methodology and analysis of the results. During the initial study it was not possible to validate the periodicity of ring deposition or to establish the stage of initiation of that ring deposition. Neither was it possible to determine which environmental variables influence the deposition of the rings. In the initial analysis the following assumptions were made:

i) that rings in the otoliths of *Limnothrissa miodon* in Lake Kariba are deposited on a daily basis as a result of an endogenous rhythm and that, at times, sub-daily deposits occur due to environmental variables affecting the cyclicity of the rhythm as has been observed in other species (Campana and Nelson, 1985).

ii) that among the biotic and abiotic factors, feeding is more likely to lead to the formation of non-daily rings on the otoliths and that serious stress such as starvation and injury causes non-growth checks on the otoliths and

iii) that ring deposition begins after yolk-sac reabsorption to coincide with the onset of exogenous feeding, an event of biological significance in the fish's life history.

The specific aims for the sampling programme were therefore designed to test or validate, among other things, the above assumptions and can be outlined as follows:

a) to validate daily growth ring deposition in the otoliths of *L. miodon* larvae and juveniles.

b) to determine initial stage of ring deposition in the sardine

c) to obtain estimates of daily growth for larvae in the field.

d) to differentiate between daily and sub-daily rings.

e) to further investigate relationships between otolith size and fish size for the purpose of estimating, among other things, the size preferred by predators based on otoliths retrieved from stomach contents of the predators.

f) to obtain estimates of mortality for larvae in the field.

g) to identify the spawning grounds for the sardine.

h) to evaluate selectivity of the mesh size currently in use.

To fulfil some of the above aims it was necessary to keep the sardine larvae alive in aquaria for some time. At least before any technique can be applied, growth should be assumed to have gone back to normal following the stress of capture and being kept in captivity. In addition to its being very delicate as far as mark and recapture exercises were concerned (Marshall 1987), keeping the sardine alive in aquaria so far has been a major problem.

Having managed to keep the sardine alive in enclosures, the larvae were then treated with tetracycline to validate that the rings are deposited on daily basis. This was based on the assumption that tetracycline if fed or added to the environment of the fish in certain quantities is absorbed in the otoliths and can later be detected under ultraviolet light. If the

days between the date of treatment of the fish and that of sacrifice coincide with the number of rings formed on the otoliths then ring deposition is assumed to occur on daily basis.

2.1.3 Why the otolith technique was chosen rather than size frequency for ageing.

Application of the otolith increment technique was chosen in favour of size frequency based methods for estimation of growth and mortality rates because it provides the precise age of the fish. The phenomenon of daily ring formation in the bones and scales of fish is widespread, occurring in all climates and regions of the world (Campana and Nelson 1985). Although length frequency methods have been used extensively to estimate growth in larval fish, growth rates generated from these techniques may be biased by age and cohort specific changes in growth rates (Crecco *et al.* 1983). Protracted spawning periods may further complicate growth estimates from length frequency data due to difficulties associated with connecting modes in polymodal length frequency distributions (Lough *et al.* 1982). Modal progression can also only provide mean growth estimates for larval populations which are often averaged over months or years whereas the temporal scale for critical life histories may be hours or days (Fortier and Legget, 1985).

One other problem associated with length frequency analysis is that such methods assume that the samples are representative of the entire population whereas this might not be the case. Schooling fish tend to form schools of specific size groups as do migratory species. Change in habitat associated with change in size and gear selectivity can also result in bias. Wespestad and Moksness (1989) reported the development of three length modes from an essentially unimodal population of herring at hatching. They related this phenomenon to success at first feeding or to genetics because the size differences developed early. If this is

common among clupeids then this could be another source of erroneous results when growth estimates are obtained from length frequency data. One major disadvantage of applying the otolith increment technique is that, not only does it involve the killing of the animals, it is also labour intensive requiring lengthy and careful processing of each specimen. While the use of otolith daily rings for fish age and growth studies has recently become more widespread, many fishery biologists are inhibited by this labour-intensive aspect of the method (Barkman and Bengston 1987).

2.1.4 Introduction to the otolith increment technique

The use of the otolith increment technique to age fish is based upon the observation by Pannella (1971), working on temperate fish, that about 360 fine depositions occurred between annual rings and his suggestion that these were therefore deposited on daily basis. Pannella (1974) extended these findings to the otoliths of adult tropical fish to show patterns of growth that were grouped into 14-day and 28-day cycles.

2.1.5 Application of the otolith increment technique

Application of this technique to larval fish was first carried out by Brothers *et al.* (1976) who verified daily ring deposition for the northern anchovy, *Engraulus mordax* and the California grunion *Leuresthes tenuis*. Both these studies were carried out in the laboratory. Since this initial application, the technique has been used broadly to estimate larval age in different species of freshwater and marine origin and field captured larvae, though in some studies there has been inadequate validation of the rate of deposition (Jones 1986). These studies have included back-calculation of growth (Scott 1973), determination of hatch-dates and delineation of cohorts that are followed through time (Graham and Joule 1981; Barkman

1978 Yoklavich and Bailey 1990), fitting a Gompertz function to length-at-age data (Lough *et al.* 1982; Brothers *et al.* 1976; Tharrold 1988), determining daily deposition of rings (Victor 1982), comparing allometric relationships between otolith size and fish size (Taubert and Coble 1977), comparing growth in the field and laboratory (Radtke and Waiwood 1980) and comparison of growth between early and late hatched larvae (Jones 1985). Others have compared the use of length-frequency based methods with otolith techniques (Laroche *et al.* 1982), and used otolith ring deposition to compare growth rates over time (Radtke and Scherer 1982), determined length of larval life prior to recruitment (Brothers *et al.* 1983), examined otolith ring in relation to feeding, temperature and photoperiod (Campana and Neilson 1982; Campana and Hurley 1989) and described differences in microstructure of otoliths from larvae spawned in different seasons (Moksness and Fossum 1991).

2.1.6 Accuracy and precision of the otolith technique

As the otolith increment technique found broader use in fish biology and population dynamics studies, it became necessary to check the accuracy and precision with which the technique was being applied.

Accuracy is defined as the closeness of a measured value to its true value while precision is the closeness of repeated measurements of the same quantity (Sokal and Rohlf 1981). Age determination of wild, young-of-the-year fish have rarely, if ever, been reported with an associated estimate of accuracy (Campana and Moksness 1991). Indices of precision based on consistency among multiple readers or across replicated daily increment counts serve as a valuable means of reducing variance among different readers and the rejection of questionable counts. However these do not serve as proxies for tests of accuracy which

require an independent and absolute means of age determination. The accuracy of age determination by otolith deposition analysis is dependent upon a knowledge of the rate of ring deposition, thus experiments to determine precise rates of ring deposition are highly relevant to the task of assessing age. Most validation experiments are done under laboratory or artificial conditions.

The appearances of rings differ markedly between fish reared under laboratory and natural conditions and between environments that promote different growth rates (Bergstad 1984; Campana and Neilson 1985). Validation of daily ring deposition under conditions within the natural range of experience of the larvae is fundamental to accurate estimation of age in field-captured fish (Jones 1986). Furthermore, validation experiments seldom cover the entire age range characteristic of the field samples (Beamish and McFarlane 1983). Increment formation through the first one to two weeks of larval life is often taken to represent that of the entire larval and juvenile stages and this is considered to be an unjustified assumption.

Both accuracy and precision can be influenced at the sampling stage as well as by the physiological processes which control otolith growth (Anon 1991). Furthermore, otolith preparation, interpretation and instrumentation also affect accuracy and precision (Campana and Moksness 1991).

2.1.7 The hydro acoustic methods

The hydro acoustic method was preferred to other techniques for estimating abundances of Lake Kariba sardine larvae involving filtration of known amounts of water because of the presence of larval fish in the shallow waters where pilot work proved it difficult to apply the

other methods. Techniques involving the filtration of known volumes of water may be suitable for open waters in Lake Kariba but the larvae are not found in the deep areas. Most water filtration techniques involve the towing of plankton nets and this was hampered by the presence of the macrophytes that are widespread inshore so that my plankton nets were rapidly clogged. Also small traps could not be set in the weedy areas. However the occurrence of submerged trees in many parts of the lake also meant that the hydro acoustic technique would be confined to areas without submerged trees and such areas are limited as most of the shoreline has such trees. It was also assumed that *L. miodon* larvae carry out vertical migrations towards the surface at night as was observed for the adults by Lindem (1988), making it possible to detect them by sonar easily. Hydro-acoustic methods can be validated by sampling and comparing the actual size distribution of the sample to the distribution given by the echosounder.

2.2.0 STUDY AREAS

Two study areas were used in this study. Most field work was done mainly in the Sibilobilo Lagoon of the Bumi Basin of Lake Kariba (Figure 2.1). This lagoon, which is about 20 km long and between 1.5 and 5.5 km wide at the high water mark, is separated from the main water body by a chain of islands. These islands together with the mainland that surround the lagoon, support a large population and variety of wild mammals which include herds of buffalo, elephant, waterbuck, zebra, kudu, antelope and impala. These animals contribute through their droppings to the nutrient loading of the lagoon. There are also two rivers draining into it. Lake Kariba is known to rely on external sources of nutrients through run-off water during the rain season or through river inflow (Kenmuir 1983; Marshall 1987). For that reason the lagoon is richer in nutrients than the main water body making it an ideal

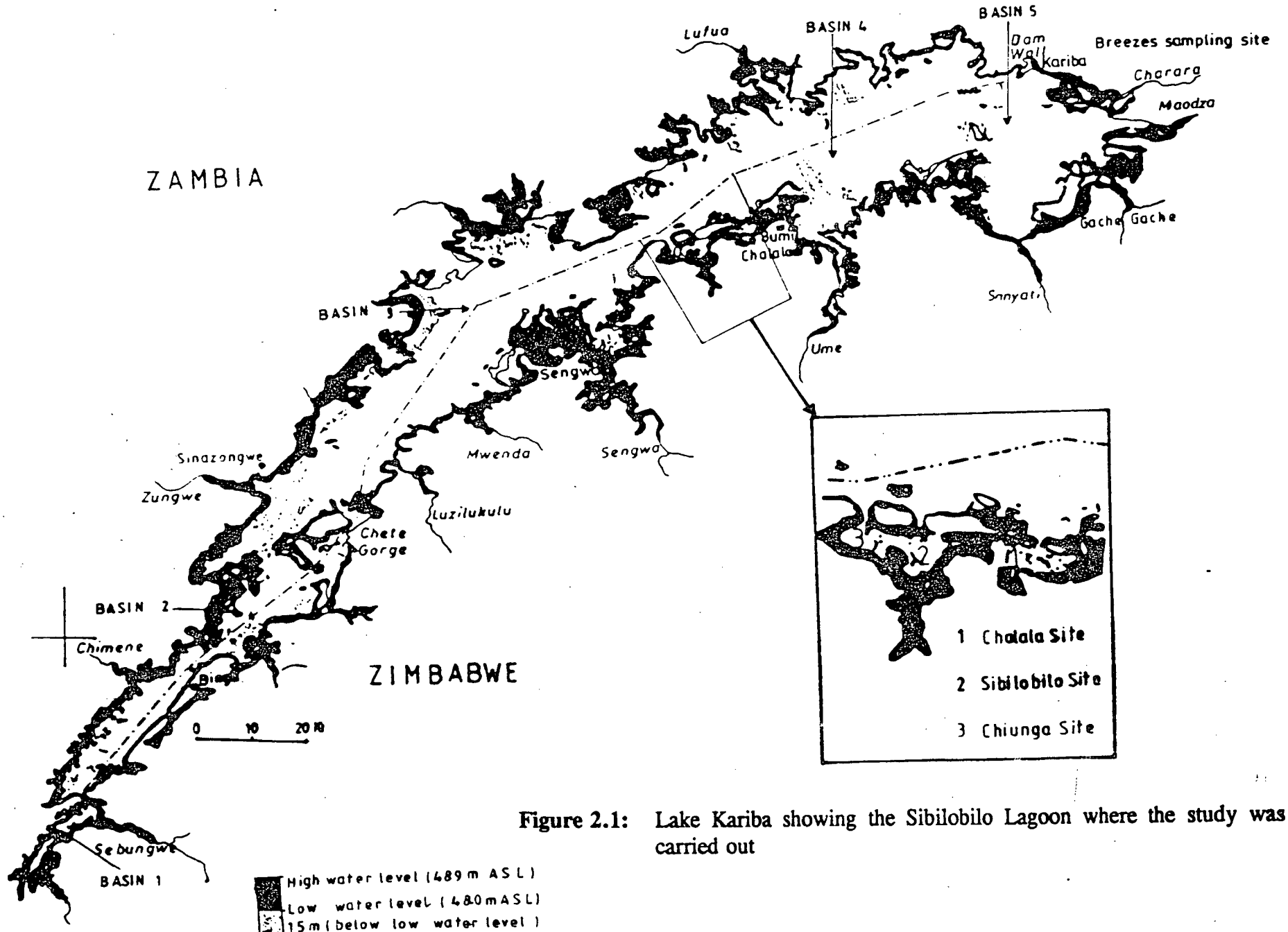


Figure 2.1: Lake Kariba showing the Sibilobilo Lagoon where the study was mainly carried out

nursery area for the sardine. Generally the lagoon is shallow (< 20 m deep) which makes it one of the closed areas as far as the sardine fishery regulations are concerned on the Zimbabwean side of the lake.

By virtue of being shallow and open, it is thoroughly mixed and on a very regular basis there is a lot of wave action which on many occasions disrupted the sampling process. Samples were taken from three sub-sites within the lagoon which are opposite the gaps from the main water body into the lagoon. The sub-sites are: Chalala Bay opposite Tiger Gap, Kayi Island opposite Sibilobilo Gap and Old Chiunga Fishing Camp opposite Chiunga Gap. These sub-sites were chosen initially on the assumption that if eggs are spawned in the main water body then they would be carried by the waves to the lagoon through these gaps. Two nights were set aside for each sub-site which are 9 kilometres from Chalala to Sibilobilo Gap and 5 kilometres from Sibilobilo Gap to Chiunga Gap.

In addition to the nursery attributes described above, due to its length, (i.e. about 20 km long) the lagoon provided an excellent opportunity to carry out the study from one continuous area compared to the other numerous small isolated bays that are found in many places along the shoreline. Different bays have different characteristics such that extrapolation of results from one bay to the next might not be appropriate. It is also not feasible logistically to study different bays at the same time for comparison purposes.

The other sampling area was in the Sanyathi Basin (see Figure 2.1) close to the Lake Kariba Fisheries Research Institute (L.K.F.R.I.). This area is characterized by a weed-free sandy bottom and sandy beach. Unlike the Sibilobilo lagoon there are no animals grazing along

the shoreline which suggests a lower level of nutrients as compared to the former. The choice of this second site was based on its proximity to L.K.F.R.I. which enabled regular sampling in validation experiments mentioned below and in the evaluation of the mesh size currently in use in the fishery (see Chapter Five).

2.3.0. SAMPLING CONSIDERATIONS

Intensive studies of fish eggs and larvae typically involve sampling during both day and night hours, and frequently require continuous or regular sampling over 24-hour periods (Snyder 1983). Most sampling programmes of this nature commence prior to the expected initiation of the spawning activity and terminate after the size group of interest is no longer present or vulnerable to the gear that is being used. During the initial planning of this study, the sampling time was set at five to six months during which period the sardine was thought to recruit to the fishery (Marshall 1987; Ramberg *et al.* 1987). Sampling was scheduled to commence in September to March which, according to Kenmuir (1983), is the peak of the breeding period. It was assumed that cohorts would be identified and followed through a period of time, with sampling taking place at regular time intervals up to the time such cohorts recruited into the fishery. Also to be investigated during this time was the distribution of eggs and larvae in the lagoon.

2.4.0 SAMPLE COLLECTION

2.4.1 Sample capture

Samples were collected from the Sibilobilo Lagoon from February 1991 to December 1992

during the last week of each month. The samples were collected using a plankton net of 250 μm mesh size, 1400 mm diameter at the mouth and 4000 mm in length. The specimens collected into a cod-end comprising a large patent closure 270 mm in length with a diameter of 150 mm on one end and 55 mm on the other. Lights were used to attract the larval fish as is done by the commercial fishermen with the adult fish. This followed several trials of sampling during the preparatory phase, towing all types and sizes of nets and at different depths, both during the day and at night but yielding nothing except in a few cases where very few larvae were captured at night in the towing nets. Damage to nets by submerged trees or floating sticks (which could not be seen and avoided at night) and the difficulties of towing nets in shallow weedy areas coupled with the failure to capture anything were the main reasons why other approaches of sampling were dropped in favour of the lift net-light attraction combination.

The net was mounted to a boom and pulley system at the stern of the research vessel R/V Pelican, a 14 metre long boat belonging to the L.K.F.R.I. The net was lowered to the required depth by simply releasing tension on the other side of the pulley system and raised by means of a hydraulic winch.

At each sub-site in the Sibilobilo lagoon (i.e. Chalala Bay, Kayi Island and Old Chiunga Fishing Camp), whenever possible, sampling was done along a transect at right angles to the shore to off shore at depth intervals of five meters as follows, 0-5 m, 5-10 m, and 10-15 metres. Earlier studies show that the Lake Kariba sardine larvae migrate from the inshore to deeper water as they grow larger (Mtsambiwa 1989, 1990). The net was lowered to the bottom and lights were switched on for 15 minutes after which the external light was

switched off leaving the bottom underwater light to attract the fish into the net as the net was being brought up. When the rim of the net reached the surface the underwater light was also switched off. Whenever practical two replicate hauls were carried out at each depth but due to unpredictable waves this was limited to one most of the time.

It was usually possible to sample once at each of three five-metre-interval depths before 2100 hours by which time weather conditions usually disrupted the sampling programme. On the other hand it only got dark enough to allow lights to be effective for sampling after 1900 hours. Thus for the reasons given above sampling was in most cases limited to two hours per night. Table 2.1 below summarises the sampling that was carried out during 1991 and 1992.

All fish captured, irrespective of whether they were sardines or not, were sorted into larvae or juveniles on board the research vessel soon after capture and preserved in a refrigerator in bottles for the very small fish and plastic bags for the juveniles. All large non sardine specimens were labelled "predators" pending further investigations. Further sorting out into species and other categories was carried out in the laboratory later.

Environmental factors such as wave action, moon phase, rainy or dry season were observed and recorded to investigate if there was any relationship between catch and environmental factors.

2.5.0 SAMPLE PROCESSING

2.5.1 Objectives

The objectives of processing the samples were:

a) to identify each specimen captured

b) to measure size of the specimens i.e. length and where possible weight

c) to remove otoliths and preserve them for use in age determination,

d) to collect stomach contents from all specimens (both sardine and others) so as to determine whether there was food competition or predation.

e) to determine time units of ring deposition in the otoliths from the live specimens after treatment with tetracycline.

2.5.2 Sardine larvae and juveniles

All specimens of the sardine larvae captured were measured for standard length under a dissecting microscope fitted with an ocular micrometer. Measurement of larvae was made to the nearest micrometer unit which is 1.5 mm. Juveniles were measured to the nearest mm on an ordinary measuring board. Initially, at random intervals, (i.e. every tenth larva) measured specimens were selected for age determination based on otolith increment counting. However measures were also taken to ensure that all length groups (especially the very small sizes) were included so as to have a truly representative sample. The larvae were placed in a drop of water on a microscope slide and the otoliths were teased out using sharp insulin needles. The larvae were then removed from the slide and the otolith were cleaned and air dried. To ensure total dehydration a drop of 98% ethanol was added to the otoliths and allowed to evaporate.

For the medium sized otoliths (i.e. from fish of 20 mm to 25 mm), although no grinding was necessary, the otoliths were etched by flooding with 0.1 M ethylenediaminetetra-acetic acid (EDTA) from an insulin needle for one minute. Following this they were flooded with water

to stop the acid etching process and then with 98 % ethanol to ensure total dehydration. After drying, each otolith was mounted on a microscope slide using nail varnish as the mounting medium as described by Moksness (1992). For the larger otoliths, preparation prior to counting was according to the method described by Mtsambiwa (1989). This method involved six procedural steps (embedding, grinding, polishing, acid-etching, washing and drying and acetate-peel replication) in preparation of an acetate peel replica of the otolith from which the counts were made. These preparations were meant to enhance the distinction between the incremental and discontinuous zones that comprise the incremental rings.

2.5.3 Otolith ring counting

Counting of the rings in the otoliths to determine the age of the specimens was conducted at three different laboratories due to the late arrival of the equipment at Lake Kariba Fisheries Research Institute, although this equipment had been ordered during the planning phase of the project. The counting was therefore done at the three laboratories as follows:

a) At the Marine Research Station at Flodevigen in Norway where a total of 99 specimens were counted in May 1992. Here otoliths were viewed for counting under a Nikon Optiphot X-A compound microscope (Figure 2.2) coupled with a RCA black and white video camera with Ultricon tube and 12" black and white RCA monitor. A Macintosh computer was connected to a 582A video coordinate digitizer through the Macintosh's modem port and the digitizer's RS232 port. The digitizer makes a vertical black line on the monitor that is controlled from the Macintosh through the mouse during the ring counting procedure. For all the otoliths the radii were measured from the centre of the primordium to the outside edge of the otolith through the

longest axis. In addition growth ring width was also measured as described by Campana and Moksness (1991) in which the vertical line on the monitor controlled from the Macintosh through the mouse is used to mark the points that define the width of the growth increment i.e. from the beginning of the incremental zone to the end of the discontinuous zone. The output from this exercise provides the age in days, the thickness of each incremental ring in micrometres, the radius of the otolith and the radius of the nucleus from the centre to the first hatch mark from where all the other measurements are made.

b) At the Lake Kariba Fisheries Research Institute where 156 were counted in May/June 1993 following the arrival and setting up of equipment similar to (a) above.

c) Finally at the Pacific Biological Station in Nanaimo on Vancouver Island, Canada, where 753 specimens were counted in October 1993. The equipment set up at this station was similar to that used in the other two places except that the equipment automatically identified and measured increment widths. It was possible to edit what the equipment had delineated as rings.

Appendix I shows the length at age data from field captured specimens of larval *L. miodon* whose age was determined by the otolith ring counting technique.

One important observation made during the sampling period is that larvae are attracted by lights as do the adults. This observation has serious implications to the management of the

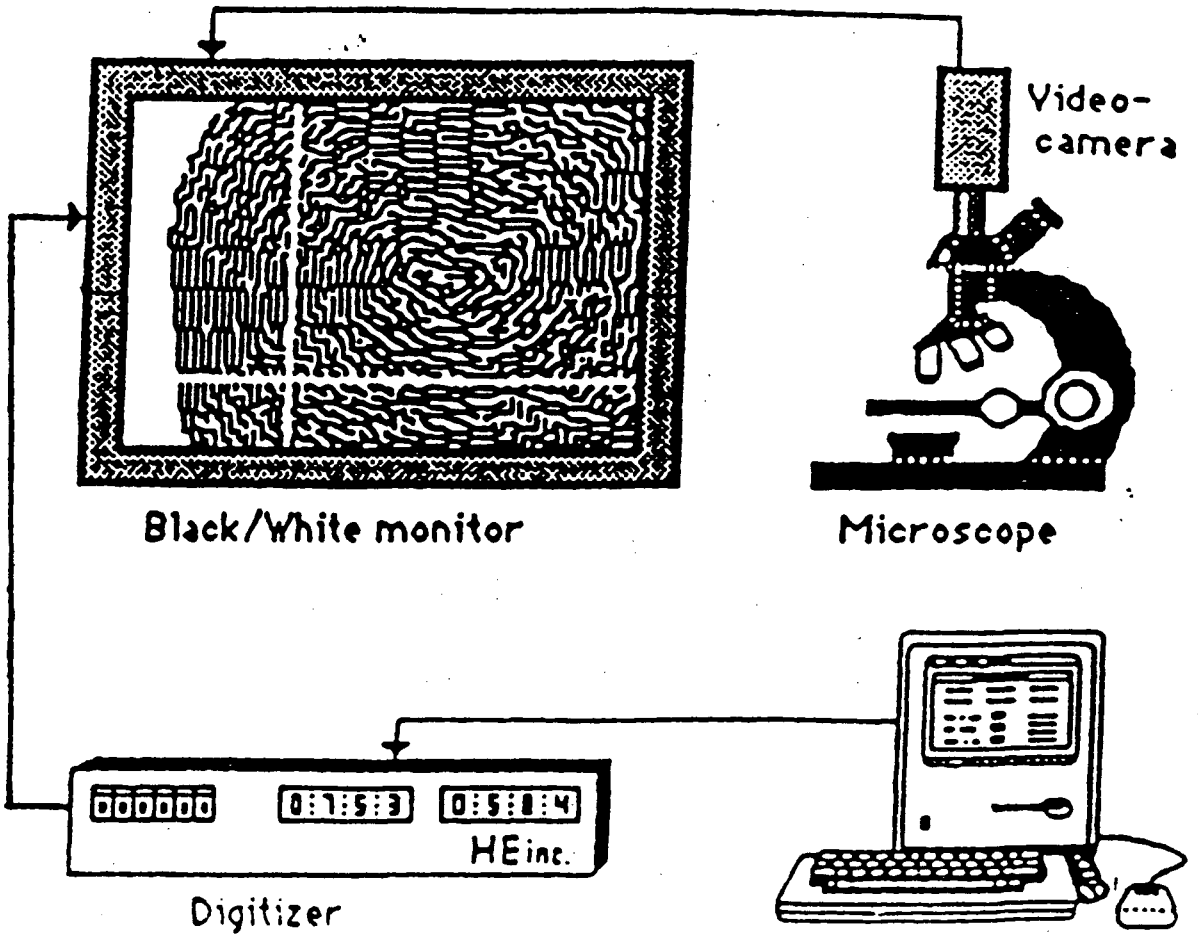


Figure 2.2: Showing the equipment set-up used for counting daily growth increments in fish otoliths.

sardine fishery which will be discussed later. Another observation made is the presence of larvae at sampling sites throughout the 24 months of sampling which seems to support the hypothesis that the sardine spawns throughout the year. This implies therefore that recruitment is continuous as well, an important factor in the choice of approach to this study and to the management of the fishery as well. Continuous recruitment has already been cited

as one weakness in using length-frequency methods for studying larval fish.

The study was also meant to investigate the distribution of eggs in the lagoon, but up to the end of the sampling period sardine eggs were not located in Lake Kariba. Two schools of thought exist as far as where *L. miodon* lays its eggs. One school believes that eggs are laid in the open waters and are transported to the shallows by waves during incubation where hatching takes place (the late O. S. M. Mtada and S. Chimbuya, pers. comm.). This theory arose from the Cochrane (1978) findings that there were more mature adults in the open waters than in the shallow areas. The other school of thought, based on Kenmuir (1983) believes that the adult sardines move to marginal areas to breed leaving the open water population depleted. Both schools of thought, which are unsubstantiated, attempt to explain the presence of larvae in the shallow waters. However while it is not clear whether sardine lays demersal or pelagic eggs, Duarte and Alcaraz (1989) cited by Houde (1994) maintain that virtually all freshwater species are dermesal spawners, producing relatively few but large eggs while marine species usually are pelagic spawners, producing many but small eggs. There is no literature on where the eggs are found in the other lakes where the sardine occurs, only that *L. miodon* larvae appear in the inshore areas (Huddart 1994). In addition, the eggs are believed to have a very rapid development rate such that they hatch quickly, in a matter of a few days rendering these eggs almost inaccessible (B. Marshall, pers. comm.).

It was also not logistically possible to sample continuously or regularly over 24-hour periods as suggested by Snyder (1983). One of the major reasons why it was not possible to sample

over 24 hour periods is that sampling could only take place at night using lights to attract the fish. In addition sudden weather changes were common on most nights, which led to the boat drifting resulting in the net collecting mud and submerged plants, as was experienced during the pilot phase of the study. In 1992, it was also not possible, due to receding water levels, as a result of drought, to follow the pattern of sampling at five metre depth intervals. As a result samples were taken from the 0-5 metre depth range only. This was the only depth range where weather conditions did not count because the boat was always tied to pegs or tree stumps and not being held in place by anchor as in other depth ranges.

Table 2.1 below shows the catch by month and the environmental outlook, i.e. moon phase, rainy, or windy conditions. Figure 2.3 shows the same catch by month which seems to follow the following trend: an increase in catch from March to July with a peak in May, a general decline in August followed by an increase in September/October and a decline in November/December. The first increase is probably linked to the rain season, with a two month time lag, when nutrients are abundant due to run-off and river inflow, while the second one is linked to the turnover following a time-lag of about two months as well.

Two t-tests to investigate the effects of environmental factors on the catchability of sardine larvae were carried out (see Table 2.2 a and b). The first test compared the effects of rain, wind and calmness while the second test compared moon phases i.e. full moon, quarter moon and no moon.

From these results of the first test based on rain, wind and calmness, there was no significant difference in catchability of the sardine larvae. The second test which compared full moon,

quarter moon and no moon suggested a significant difference between full moon and quarter moon and no significant difference between full moon and no moon. However one would have expected the opposite to be true i.e. that of a significant difference between full moon and no moon as is the case in the commercial fishery where fishermen do not fish during full moon phases. However the commercial fishery operates in the deep water where the effect of light could be different from that of the shallow water. This suggests that light attraction (in shallow water) may have distorted the effect of the full moon compared to deep water where the fishery operates. The difference in catchability between full moon and quarter moon could be attributed to factors that are not clear at this stage.

Table 2.1: Showing environmental conditions prevailing and the related catch during the sampling period from February 1991 to December 1992.

Year	1991											
Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Env. Factor	-	QMR	QMC	QMW	QMW	QMC	QMC	FMW	FMW	CLR	FMC	QMC
Catch	-	100	142	300	380	348	453	310	557	895	397	355
Year	1992											
Env. Factor	FMC	FMW	FMC	--	QMC	NMC	NMC	NMW	QMW	QMC	NMR	QMR
Catch	1200	839	499	--	849	504	338	143	528	417	367	297

QMR = QUARTER MOON/RAINY; QMC = QUARTER MOON/CALM;
QMW = QUARTER MOON/WINDY; FMW = FULL MOON/WINDY;
CLR = CLOUDY/RAINY; FMC = FULL MOON/CLOUDY;
NMR = NO MOON/RAINY; NMC = NO MOON/CALM; NMW = NO MOON/WINDY

Figure 2.3: Monthly sardine larvae catches from the Sibilobilo Lagoon for 1991 and 1992. The catches represent the actual numbers caught.

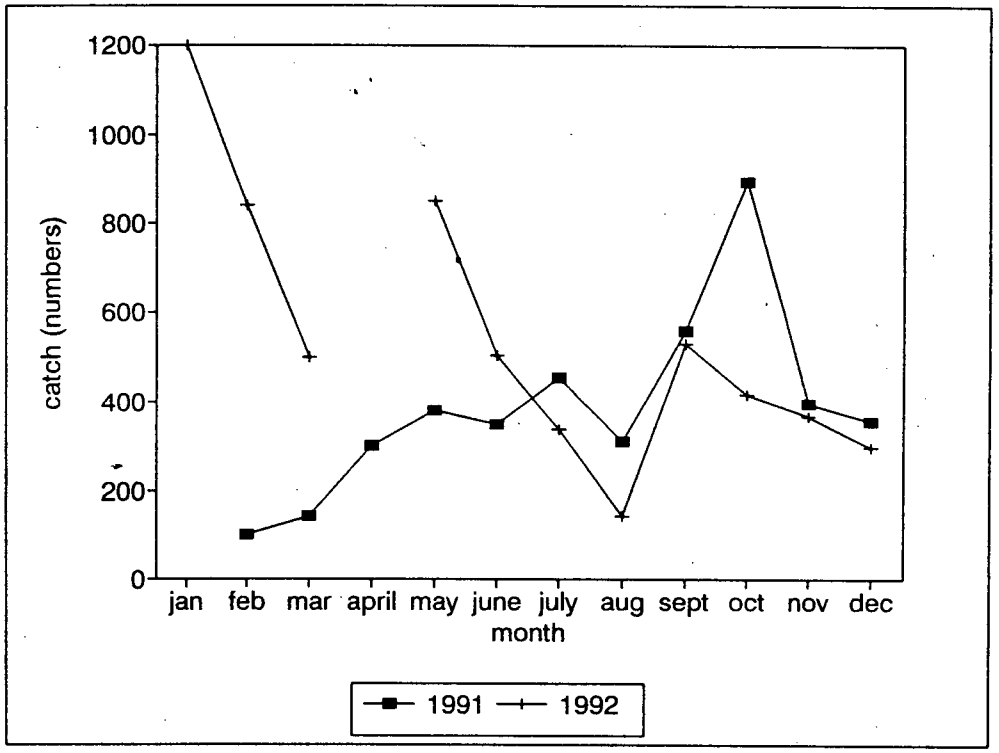


Table 2.2 a: The various environmental factors and the catchability of the sardine larvae during the years 1991 and 1992.

	Rainy	Calm	Windy
Observations	4	11	7
Minimum	100	142	143
Maximum	895	1200	839
Mean	414.75	500.18	436.71
Standard dev.	339.54	288.12	226.89
	Quarter moon	Full moon	No moon
Observations	11	6	4
Minimum	100	310	143
Maximum	849	1200	504
Mean	379	633.67	338
Standard dev.	199.63	330.96	148.80

Table 2.2 b: Probability values of T-test carried out to investigate the effects of environmental factors on the catchability of sardine larvae.

	Rainy	Calm	Windy
Rainy	-	0.639	0.904
Calm		-	0.801
Windy			-

	Quarter moon	Full moon	No moon
Quarter moon	-	0.033*	0.445
Full moon		-	0.279
No moon			-

2.5.4 Other species

a) Objectives

The objective of collecting other species captured together with the sardine larvae was to investigate the relationship between them and the larvae through the examination of stomach contents. This was meant to establish whether they preyed on the sardine larvae or not.

b) Procedure

The "other species" captured in the experimental lift nets comprised mainly *Alestes lateralis,* which were measured for length and weight. Whenever possible sex and gonad state of maturity were also determined. After that, stomach contents were collected for the purpose of determining whether these species did prey on the sardine larvae and if they did what size they had eaten based on the size of otoliths collected from these stomach contents. The stomach contents were carefully examined in water under a compound microscope searching

for small otoliths that could be compared with the ones removed from the larval specimens for age determination.

c) Results of stomach contents analysis of other species

Following a thorough search through the stomach contents from the *Alestes* species captured together with the larvae during sampling, there were no particles identified as otoliths in the contents. Moreover there were no whole or partially digested items which could be identified as larval *L. miodon* in the stomach contents. However during dissection to remove stomach contents there were certain specimens with whole larval sardines in their mouths which are thought to have ended there during hauling. This is a phenomena observed in the commercial fishery where a lot of small fish end up in the mouths of larger fish during the hauling process. It is possible that the total absence of the whole larvae or partially digested ones could be as a result of fast digestion of any of the sardine items in the stomach contents. Another possibility is that the *Alestes* spp. were not preying on sardine larvae, or that predators were present but were not susceptible to capture by the method being used. The absence of otoliths could have resulted from microscope resolution although the actual teasing and mounting of the sardine otoliths were done using the same microscope. Some of the food items observed were of insect origin.

2.5.5 Hydroacoustic surveys

a) Objective

i) To calibrate and validate the monthly samples taken using the light attraction.

ii) To estimate larval abundances in the littoral zone of Lake Kariba with a view to predicting recruitment levels.

b) Procedure

Hydroacoustic surveys were carried out in conjunction with the capture of larvae and juvenile specimens from January to December 1992. This way it was hoped that the effect of light attraction could be evaluated by comparing size distribution in captured samples and the one provided by the echosounder. Echo-sounding surveys were conducted along transects at right angles to the shore before and after capture of the sardine specimens. Hydroacoustic data were collected from R/V Pelican at an average speed of 5 to 6 knots using a 200 KHz single beam echo-sounder (Simrad EY-200), at the following settings: sound pulse duration = long, gain = 5, range = 0-100 m, pulse repetition rate = medium, TVG = 40 LogR, power = full (1/1) and attenuator = 0 . The transducer depth was 1 m and the echo analysis started 1.5 m from the transducer, i.e. 2.5 m below surface. The unit was calibrated with a -15 dB standard copper sphere on full power (1/1). The signal output was recorded on cassette tapes, starting on a new tape for every new recording, and analysed using the programme HADAS version 3.3 developed by T. Lindem (Lindem 1983).

Echo integration, fish density and target strength distribution are determined for single-fish echoes (defined as those echoes with a duration of less than twice the transmitted pulse).

Echo integration values from multiple fish echoes (i.e. echoes longer than twice the pulse duration) were converted to fish abundance using the fish density to echo integration relationship determined from the single fish echoes.

The first transect before sampling was carried out slightly before dark and the second transect was carried out after dark following the use of lights to capture the fish. This was done to investigate whether there any vertical migrations at night as was observed for the adults by Lindem (1988).

c) Results of the Hydroacoustic surveys

The hydroacoustic part of this study was unsuccessful for various reasons such that it was not possible to calibrate the monthly sampling or to estimate the larval abundances using the results obtained from the hydroacoustic surveys. Following are some of the reasons that were detected as possible explanations to the failure to obtain the expected results:

i) Following failure to digitize tapes recorded in the field at Lake Kariba Fisheries Research Institute the tapes were sent to Norway where the HADAS programme was developed and it was found that high noise levels were responsible for that failure to digitize. The source of this noise could however not be identified. While it is possible that the noise could have come from the research vessel R/V Pelican it is however not clear how that could have come about with the high frequency echosounder only as the two echosounders had been calibrated using the same vessel. For that reason the noise levels could have come from somewhere other than the boat.

ii) Five metres was also recognized as too shallow to provide reliable recordings as the

transducer is recording targets below 3 metres from the surface. According to sampling by light attraction a lot of larvae were captured in the 0-5 m depth range especially around 1.5 metres. Foote and Stefansson (1993) argue that factors such as concentration or dispersion and the degree of mixing with other species, migration and the life history of the fish have to be considered because if the fish are not accessible to acoustics, because they are in the bottom "dead zone" or near surface or shallow water, then the results must reflect this uncertainty. In this case it is most likely that the larvae appeared near the surface at night as do the adults that are observed to migrate to the surface layers at night.

iii) There was a marked difference between the size frequency distributions that were obtained from the HADAS programme from those few samples that could be digitized and the samples that were collected from the surveyed areas in an attempt to validate what was being detected by the echosounder. In addition, there was no change of pattern on the echogram when the survey was carried out into the open waters casting doubt on the results obtained using the 200 KHz SIMRAD echosounder. Larval *L. miodon* are known to migrate to the deep areas as they grow larger and yet according to the results obtained in these surveys, the larvae are evenly distributed along the inshore-offshore transect.

2.6.0 DISCUSSION

The two approaches taken in this study were the most appropriate in that one approach looks at the historical past of the fishery while the other seeks to investigate the unexploited phase which up to now had not been looked at. The role of pre-recruits to a fishery cannot be over

emphasized given the fact that it has already been established that this is an important phase which determines the amount of fish coming into a fishery.

2.6.1 Observations during sampling

The first major observation made during the sampling period was that *L. miodon* larvae are attracted by light as are the adults. This has serious management implications in that fishing in shallow areas where these larvae occur could result in high larval mortality leading to recruitment overfishing, a situation where a reduction in the proportion of fish caught would be more than compensated by the increased number of recruits to the fishery (Beddington *et al.* 1984). While the mesh size of the nets in use could allow the larvae to pass through, contact with the rough net could kill most larvae. For this reason it would be advisable to avoid fishing in such shallow areas.

The second important observation which strongly supports the study of pre-recruits by the otolith increment technique is the presence of larvae in the sampling area throughout the year. Size frequency analysis for ageing is therefore biased by the difficulty of deconvoluting the distribution mixture. Age frequency is hence a more appropriate approach. Moreover individuals of the same age might have different growth rates leading to the same-age individuals belonging to different size groups. Another possible lesson from this development is determining whether the large individuals move to deeper water earlier than the slow growers. If that is the case then estimates of natural mortality have to be corrected to account for the individuals who have migrated from the group. For management purposes the implications are not obvious, as in the case of attraction by light.

The third observation involves the preparation of the otoliths before the counting of the rings. For larval otoliths i.e. from fish less than 15 mm in length, there was no need for complicated preparations beyond mounting as the rings are clear at that stage. However for the juveniles i.e. fish between 15 to 25 mm it was necessary to etch with acid before mounting. This greatly reduced the time required for handling each individual allowing for more specimens to be processed in a short space of time.

2.6.2 Problems encountered

Several problems were encountered during sampling and processing. Notable among the problems were:

a) Unpredictable weather changes. Sudden changes in winds resulting in large waves led to the suspension of sampling as the type of gear in use requires a relative amount of calm to prevail to be effective. These changes took place in as little time as the difference between the first haul and the second one.

b) Failure by the anchor to hold ground led the boat to drift, even in soft winds, dragging the net in the mud thus leading to the collection of mud instead of the targeted fish.

c) Due to receding lake level over the year as a result of drought in the 1991/2 rain season the boat went aground in places where sampling was possible in previous months. This resulted in the abandonment of sampling in depth intervals beyond 0-5 m at the in the later part of the sampling period.

d) General boat breakdowns and difficulties in getting these sorted out at times as a result of unavailability of spares or late delivery of such spares if available also contributed tremendously to the gaps in data.

e) Otolith reading was done in three different areas due to late arrival of the equipment at Lake Kariba Fisheries Research Institute although such equipment had been ordered during the preparatory phase of the study. If the equipment had arrived in time as planned during the preparatory phase, possibly more samples would have been counted.

2.6.3 Sampling Failures

It was not possible to achieve two important aims of the sampling programme: (a) to determine the stage when the first ring is deposited and (b) to identify the spawning grounds for *L. miodon*. Failure to capture eggs or yolk sac larvae during the 24 months of sampling is mainly responsible for the failure to achieve those two goals. As a result it had to be assumed that ring deposition commences at yolk sac absorption to coincide with exogenous feeding. The period between hatching and yolk sac absorption was assumed very short in tropical areas as opposed to temperate areas.

Failure to capture eggs could imply that they are spawned demersally and my method of capture does not target them. It would be necessary to explore other methods aimed at capturing them in those areas. Failure to capture yolk sac larvae could have resulted from two factors, first that they have not yet developed response to light stimuli as the fully developed larvae have. Secondly that due to the weight of the yolk sac they could not swim towards the light and as a result could not be captured. It is however necessary to establish which of the two hypothesis is true.

CHAPTER THREE

Estimating some early life history parameters in the tropical freshwater sardine *Limnothrissa miodon* from daily growth increments in otoliths.

3.0.0 INTRODUCTION

3.1.1 Recruitment variability

Survival and recruitment of young fish depend on a combination of both biological and physical factors such as starvation, predation, larval transport, temperature and turbulence (Yoklavich and Bailey 1990). Larval size and growth are extremely important to the recruitment process because size is linked with resistance to starvation and predation (Miller *et al.* 1988), while small changes in growth rate and larval stage duration can cause significant interannual fluctuations in recruitment (Houde 1987).

The ability to age fish precisely therefore provides accurate estimates of growth and mortality, and hence facilitates assessment of larval survival and recruitment. Ageing fish larvae by the otolith increment technique is a powerful tool which in addition to refining population estimates of growth and mortality can provide individual growth (Jones 1986). Information on daily growth rates expressed in length and weight is also obtainable (Andersen and Moksness 1988) which is otherwise not possible with most of the other methods.

3.1.2 Objective of this study

In this study the otoliths increment ageing technique is applied to pre-recruitment stages of

the freshwater sardine *Limnothrissa miodon* in Lake Kariba with a view to estimating some early life history parameters.

Although the sardine is by far the most important economic species in the lake, relatively little is known about its biology (Marshall 1987). Age and growth of the population are essential for a detailed assessment of the potential and status of the fishery. Cochrane (1978) attempted but not successfully to obtain estimates of growth. Marshall (1987) estimated growth and mortality from length-frequency distributions, obtaining growth parameters from a Ford-Walford plot and mortality from a catch curve. Mtsambiwa (1989) initiated age determination of the pre-recruits of *L. miodon* based on daily ring depositions in the otoliths of the larvae and juveniles. However the study did not follow the usual procedure in studying microstructural growth patterns in the otoliths. These studies are usually preceded by validating the periodicity with which ring deposition occurs and gaining some insight into the stage of ring deposition initiation. The study also dealt with juveniles. Hardly any larvae were covered, using the definition of Kariba sardine larvae as fish that are less than 15 mm in length (Begg 1974). Of one hundred and thirteen specimens used in the analysis only five specimens were less than 15 mm in length. The major achievement of the study however was that it developed a method of preparing otoliths from the juveniles and adults to expose the bipartite zones that constitute the daily increments which are counted in age determination.

The rate of deposition of the rings in the otoliths of the freshwater sardine *L. miodon* larvae was investigated by tagging using tertracycline to confirm the daily ring deposition hypothesis.

This study is part of a broader study to understand why the sardine populations fluctuate and in the process increase our understanding of recruitment ecology. The specific aims of this present study are therefore to:

a) validate rate of ring deposition in the otoliths of larval *L. miodon*

b) investigate trend of larval abundance during the sampling period

c) obtain estimates of daily growth of larvae in the field

d) investigate relationships between fish length and otoliths radius

e) evaluate the life history parameters such as growth rates generated from the daily rings in the otoliths and from length frequency based methods.

3.2.0 MATERIALS AND METHODS

Brief descriptions of the methods used to carry out this study were introduced in Chapter Two above. Following is a more detailed description of the methods for each part of the study to achieve the above aims.

Attempts to evaluate parameters such as growth rates generated from the daily rings in the otoliths and from length frequency based methods were unsuccessful as it proved difficult to split the length frequencies into modes and therefore is not discussed further in this report.

3.2.1 Validation of daily increment deposition in otoliths

a) Objective

The objective of validating daily ring deposition in otoliths was to investigate the rate at which the rings are deposited. Initially it was assumed that ring deposition takes place on daily basis as the phenomenon is widespread in both freshwater and marine habitats

extending from polar regions to the tropics (Campana and Nelson, 1985).

b) Procedure

To validate the assumption that the rings observed in the otoliths of *L. miodon* larvae are deposited daily, some of the larvae were treated with tetracycline in 1000 ml beakers. Tetracycline is an antibiotic that is incorporated into calcium structures of fish during growth (Tharrold 1988). This can be restricted to a single day's increment on the otolith thus enabling the accurate identification of the date of treatment. Depending on the size of the fish, the treatment can either be introduced into the food fed to the fish or injected into the fish directly or introduced into the water in which the fish is living. For *L. miodon* larvae only the latter method was applicable. It appears however that choosing the right concentration of tetracycline is rather critical (Gjosaeter *et al.* 1984) as too much tetracycline could kill the larvae while little tetracycline might not be incorporated in quantities detectable under UV light. The other critical aspect is the duration of the treatment. Too short a treatment might result in tetracycline not being incorporated while lengthy periods of treatment could lead to too much stress which might result in rings not being laid down normally.

The aluminium cod-end flask attached to the plankton net used for the capture of larvae allowed some of the larvae to survive after capture. These were transferred into an aquarium on the research vessel and later to the Lake Kariba Fisheries Research Institute laboratory where the treatment was carried out. At the laboratory the larvae were kept in 100 litre tanks outside so as to expose them to the normal photoperiod and ambient temperature. The tanks were sheltered from the sun to avoid drastic temperature fluctuations which are believed to

have led to all specimens dying in earlier attempts to keep the sardine larvae alive in aquaria.

The purpose of keeping them in holding tanks under conditions close to those of their natural environment was to allow them to recover from the stress caused by capture. Recovery from capture stress also implies resumption of normal growth where deposition of increments would follow the normal daily pattern. Mtsambiwa (1989) suggests that checks (i.e. growth discontinuity) found in the otoliths of *L. miodon* juveniles had resulted from stress caused by injury or some traumatic experience which had greatly affected growth hence the formation of checks.

The first treatment trial was carried out on larvae captured on 2 January 1992 in the Sanyathi Basin of Lake Kariba close to the station. They were kept in holding tanks for eight days before three larvae were transferred into 1000 ml beakers pending treatment with tetracycline the following day. The first larva was treated with 500 mg/l tetracycline and showed a lot of stress initially almost to the extent of "jumping" out of the beaker. An hour later it was dead. Treatment of the other two killed them within two hours.

On the eleventh day, six larvae were moved to a 20 litre holding tank with an aerator for a day. Two larvae were dead by the following morning and as with all the larvae that had died in this experiment they were measured for length and otoliths removed and mounted on slides using nail varnish as the fixing agent. This was done to investigate if any checks had been formed due to stress during capture and subsequent handling. The four remaining larvae were treated with 250 mg tetracycline per litre of water in an aerated tank. These survived more than six hours but were all dead within 10 hours of the treatment. Again they were all

measured for length and otoliths were removed and mounted on slides using nail varnish as a fixing agent. These were meant for investigation as to whether the concentration of tetracycline is sufficient for being taken up by the sardine otoliths. Six hours is long enough for otoliths to absorb tetracycline but not long enough to carry out validation studies as these require fish to live at least for more than one day before they are sacrificed.

During the above two experiments, a thin oily film layer formed at the surface of the water which is thought to have resulted from a chemical reaction between the lake water and the tetracycline and could have been enhanced by aeration. It is not clear whether this contributed to the cause of mortality of the larvae or not.

Further treatment of larvae was carried out with lower concentrations of 150 mg/l and 100 mg/l and shorter durations (6 hours) before the larvae were transferred back to a larger holding tank with lake water and aerated. Of these trials only two larvae survived, one treated with 150 mg/l and the other with 100 mg/l. These survived for 8 days and 3 days respectively. They were then measured for standard length and the otoliths removed and mounted on slides as described by Moksness (1992). The mounted otoliths were then viewed under fluorescent UV and natural light with a compound microscope. Under fluorescent light an ocular marker was aligned with the fluorescent band in the otolith. The otolith was then examined under natural light and the number of rings between the marker and the otolith margin were counted.

Further treatments were carried out on fish captured on 30 January 1992. Four larvae were treated with 100 mg/l tetracycline in 1000 ml beakers for a period of six hours. All the four

larvae survived and were sacrificed on day six after treatment. The otoliths were removed and mounted on microscope slides using nail varnish as the mounting medium before examination under UV light.

3.2.2 Larval abundance trends

a) Objective

The objective of this part of the study is to investigate the trends in larval abundance so as to establish whether variability is apparent or not at this stage. Recruitment variability in fish populations is believed to be established at some early life history stage (Anderson, 1988; Houde, 1987) and this investigation aims to establish whether this is the stage or some other stage (pending further investigations) before it, that cohort strength is established in the Kariba sardine.

b) Procedure

Time series plots of monthly larval catch were plotted to see if there were any patterns or variations that might be used as an indicator of abundance of the larvae over the sampling period. The plots were based on the 0-5 m depth interval for the three sub-sites, i.e. Chalala Bay, Sibilobilo and Chiunga Gap. It was not possible to include the other depths intervals as initially planned because of the numerous gaps in data. Thus only the 0-5 m interval was the only depth used in the time series analysis to compare the monthly totals for the three sub sites. Larvae (< 15 mm) were largely found at this depth.

3.2.3 Daily growth of larvae

a) Objective

The objective of this part of the study is to describe daily growth in larval *L. miodon* using a suitable growth model. Fish growth data are usually fitted by an appropriate mathematical function to generalize the growth process, predict the growth trend and compare the growth patterns between populations or species (Chen *et al.* 1992).

b) Procedure

Daily growth in larval *L. miodon* was described by fitting the von Bertalanffy Growth Function to length-at-age data obtained by applying the otolith increment ageing technique. The VBGF was fitted in its general form as follows:

$$L_t = L_\infty\{1 - \exp[-k(t - t_o)]\} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ 1$$

where L_t is the length at time t, L_∞ represents the asymptotic length, t_o is a constant defining the "age" at which the fish would have had length zero if they had always grown according to the VBGF (Pauly 1984; Rosenberg and Beddington 1988) and K is a growth constant. The VBGF was chosen because it is one of the most ubiquitous equations in the fisheries literature which historically gained wide currency because it claimed to be developed from bioenergetic principles (Roff 1980). In addition an earlier study by Chifamba (1992) using the same otolith increment technique provided estimates of L_∞ the asymptotic length and t_o, the hypothetical age at which length is zero, which are required to fit the model to the current length-at-age data. Furthermore, Mtsambiwa (1993), in an attempt to describe growth in a limited data range fitted the Gallucci and Quinn (1979) version of the VBGF to a small sample of larval *L. miodon* length-at-age data as had been done for another tropical clupeid

larvae (*Herklotsickthys castelnaui*) by Tharrold (1988). This version substitutes the adult asymptotic length (L_∞) parameter of the original VBGF with the maximum larval size obtained. In the case of the Lake Kariba sardine this is equivalent to 15 mm (Begg 1974). However, it was necessary to fix L_∞ to the value obtained by Chifamba (1990) because failure to do so would have led the model to describe L_∞ according to the largest fish in the sample which was less than juvenile stage of the fish and therefore inappropriate. To evaluate the reliability of the different growth parameters obtained in this study they were compared to previous studies (Cochrane 1974; Marshall 1987; Chifamba 1992 and Mtsambiwa 1993) using the "phi prime test" (Munro and Pauly 1983, Pauly and Munro 1994). This test suggests that the overall growth performance is reflected by the relationship:

$$\varnothing' = \ln K + 2*\ln L_\infty \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 2$$

where $\varnothing'$ is the phi prime value.

This test is based on the fact that phi prime values are very similar within related taxa and have narrow normal distributions. Growth curves estimated for the same stock can have the same $\varnothing'$ and yet be different. If two phi primes representing alternative estimates of growth parameters for the same stock differ greatly it indicates that one or both of the estimates may be biased (Sparre and Venema 1992).

3.2.4 Relationship between fish length and otolith radius

a) Objective

The objective of this part of the study was to investigate the relationship between the length

of the fish and the radius of the otolith so as to use this relationship for backcalculation. This allows us to backcalculate the growth pattern of the fish and can be used to provide estimates of sizes of fish preyed upon by predators based on otoliths found in predator stomach contents.

b) Procedure

Linear regressions were performed to investigate the relationships between otolith size and length of fish. Based on these relationships growth was backcalculated and somatic growth rates were inferred from otolith growth rates as defined by the width of the daily growth increments. Since it is characteristic for young fish to have variable growth rates and to undergo ontogenetic stage transitions (Hare and Cowen 1995) it was necessary in this study to check the relationship between otolith size and fish size on a monthly basis.

The regression method estimates fish length (L) at some previous age (a) through the insertion of the measured size of the otolith (O) at age (a) into a fish length-otolith radius regression derived from samples of the population as follows:

$$L_a = d + bO_a \qquad \text{.....(2)}$$

where b and d are the slope and the intercept of the regression respectively.

The procedure provides mean backcalculated lengths rather than individual values.

3.3.0 RESULTS

3.3.1 Validation of daily deposition in otoliths

As it was difficult to keep larvae alive both before and after treatment, only six sardine larvae were tested for rate of ring deposition. Otolith examination of all the larvae that had died either before or after treatment did not reveal any checks implying that whatever stress the fish suffered during capture and subsequent handling was not enough to result in the formation of checks on the otoliths. Thus capture and subsequent handling did not lead to the slow down or even stoppage of growth, a situation when checks are formed. Although some of the larvae had survived for more than six hours in the tetracycline treated water, it was difficult to detect whether the otoliths had absorbed the tetracycline in their outermost ring. As observed in this study, six hours was long enough for the otoliths to absorb tetracycline, but the outmost ring in the otolith was blurred.

For the two larvae that survived the six hour treatment in 150 mg/l and 100 mg/l and died 8 and 3 days later respectively an equivalent number of rings were counted from the day of treatment under the UV light. Further treatments were carried out with six larvae in January 1992 and Table 3.1 and Figure 3.1 summarises the results of the otolith increment deposition rate validation experiment. Based on these treatments, it was tentatively concluded that the results support the hypothesis that rings in the otoliths of larval Lake Kariba sardine are deposited on daily basis as has been observed for other species. However more data are required before it can be stated beyond doubt that rings are deposited on daily basis. Otolith ageing of larval sardine is therefore assumed to provide accurate estimates of age and hence provides the basis for the subsequent analysis of growth and mortality.

3.3.2 Larval abundance trends

Figure 3.2 shows the time series plots of catch in numbers per month for the three sub sites, Chalala, Sibilobilo and Chiunga, for 1991 and 1992 at the 0-5 m. Attempts to plot the time series at depths intervals of 5-10 m and 10-15 m depth proved futile as there were many

Table 3.1: Results of the daily increment deposition validation exercise carried for larval *Limnothrissa miodon* in Lake Kariba.

DC	Dose	NT	TT	NS	Days	Rings	STD
2/1/92	500 mg/l	1	2hrs	-	-	-	-
"	250 mg/l	1	2hrs	-	-	-	-
"	150 mg/l	4	6hrs	1	8	8	-
"	100 mg/l	3	6hrs	1	3	3	-
30/01/92	100 mg/l	6	6hrs	4	6	5	0.71

(DC = Date Captured, NT = Number Treated, TT = Treatment Time, NS = Number Survived, Days = Days Survived, Rings = Mean Number of Rings, STD = Standard Deviation).

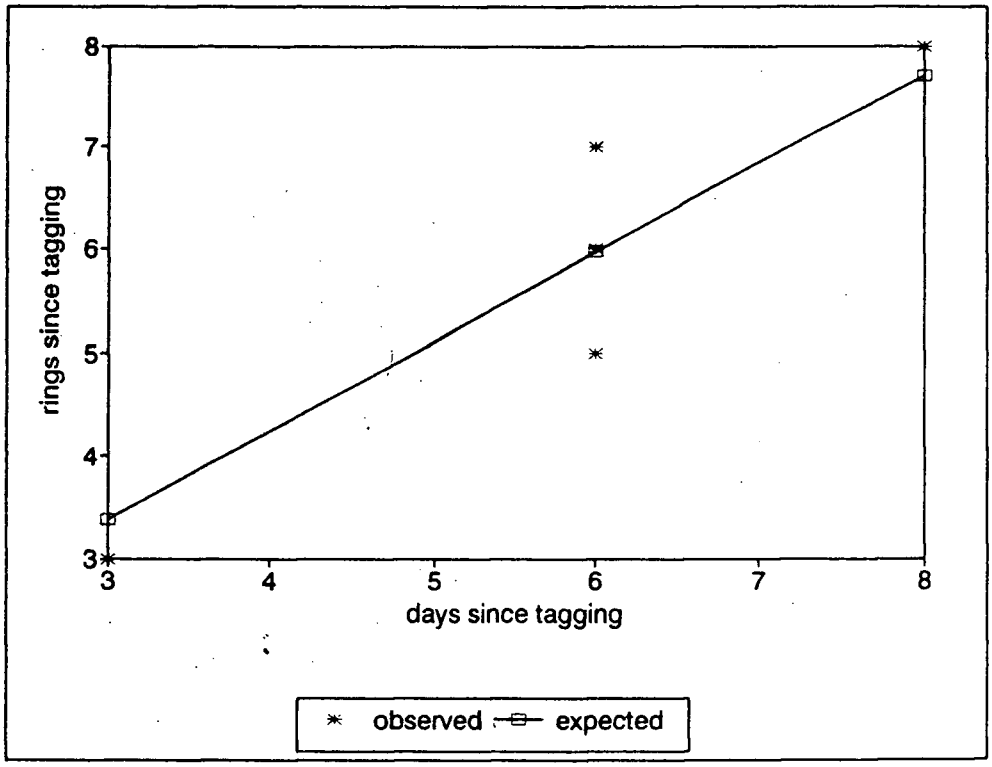


Figure 3.1: Showing the results of the otolith deposition rate validation experiment based on six individual specimens of *L. miodon* larvae that survived following treatment with tertracycline.

gaps in the data due to failure to sample continuously at those depths as initially planned. These failures resulted mainly from failure by the boat to anchor or rough weather which developed by the time it was the turn to sample there. Thus only samples from the 0-5 m depth were available consistently to allow comparison between the three sites.

The time series plots did not show any trend in the monthly larval catches but fluctuated from month to month. However more samples were captured from the Chalala subsite than the other two at Sibilobilo and Chiunga. The fact that there is a catch of larvae every month as indicated on these plots serves to confirm that spawning is spread throughout the year.

3.3.3 Daily growth of larvae

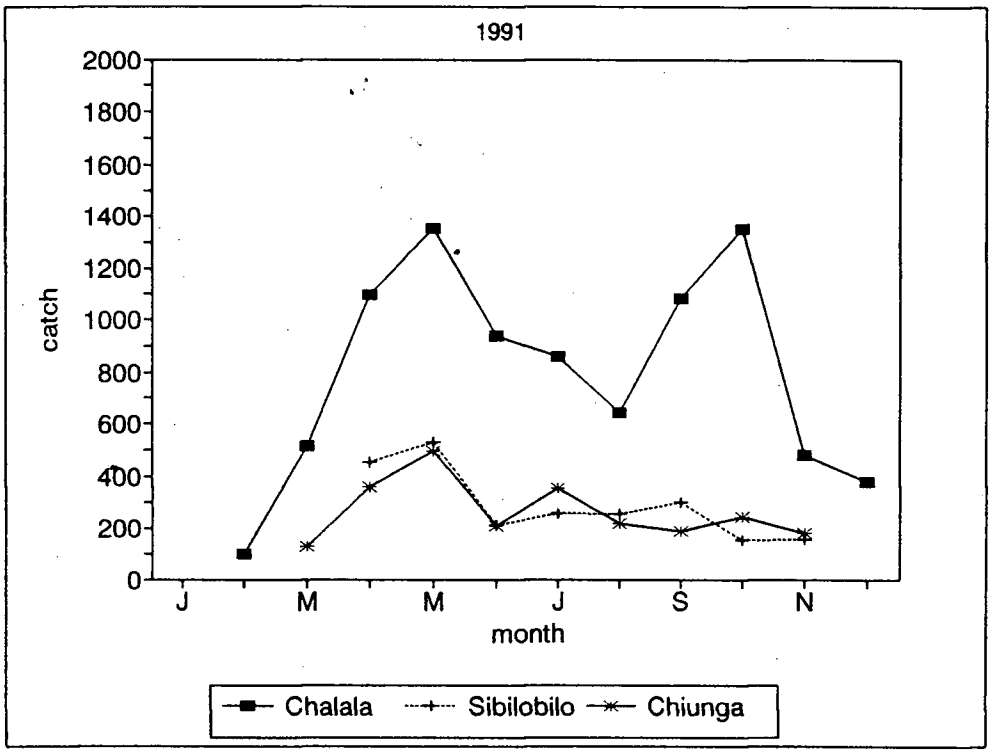
Figure 3.3 shows the von Bertalanffy growth curves that were used to fit length-at-age data for larval *L. miodon*. Based on L_∞, the asymptotic length, and t_0, the hypothetical age at which the fish has length zero, obtained by Chifamba (1992), the VBGF gave a monthly estimate of K, the growth rate, of 0.06 for 1991 and 0.053 for 1992. These rates are less than those obtained in previous studies (Cochrane, 1984; Marshall, 1987; Chifamba, 1992), that were based on the adult population when growth rate is normally lower than the early stages. Table 3.2 summarises the results of some of the previous studies. The growth rates obtained in this study are however lower than those obtained by Mtsambiwa (1993) where the Gallucci and Quinn (1979) version of the VBGF was fitted to a small sample of *L. miodon* larvae length-at-age data. In this version the L_∞ was fixed at 15 mm which represents the maximum size of the sardine larvae as defined by Begg (1974) while in this study L_∞ was fixed at 135 mm based on the Chifamba (1992) study from the adult population. This could have resulted from the use of different asymptotic lengths, i.e. one for the adults in this

study and the other for juveniles in the Mtsambiwa (1993) study. However a high K value for the early life stages when growth is fast is appropriate in comparison to the adult stages. The phi prime test shows that there is little difference in growth performance for the first three studies by Cochrane (1974), Marshall (1987) and Chifamba (1992). The low growth estimate obtained by Chifamba (1992) could be the rate at which growth approaches a much higher L_∞ compared to the other rates (Cochrane 1974 and Marshall 1987) where growth apparently approaches much lower asymptotic lengths.

The values of phi prime in the three studies however are significantly different from the Mtsambiwa 1991 and 1992 values. This could be a result of bias caused by the fact that the first three studies were performed on the adult population while the latter used age-at-length data from the larval population only and fixing L_∞ and t_o from the adult population. The Mtsambiwa (1991 and 1992) values are also significantly different from the Mtsambiwa (1993) where L_∞ is fixed at the largest larval size (according to Begg (1974)) when fitting the Gallucci and Quinn (1979) version of the VBGF. This could be an indication that in the sardine *L. miodon* it is inappropriate to fit the Gallucci and Quinn version of VBGF as the larvae grow continuously into the juvenile and adult stages without experiencing any metamorphosis as in flat fish.

Figure 3.4 shows monthly curves of the K values for 1991 and 1992. While the K values in 1992 are generally lower than the 1991 values there seems to be a seasonal growth pattern as follows: firstly an increase around the February/ March period followed by a decline around April/May; secondly an increase around June/July followed by a decline in August and thirdly an increase in September/October followed by a decline in November/December.

Figure 3.2: Showing the time series plots for 1991 and 1992 for the three sub sites, Chalala, Sibilobilo and Chiunga gaps. These catches represent numbers of fish captured per month.



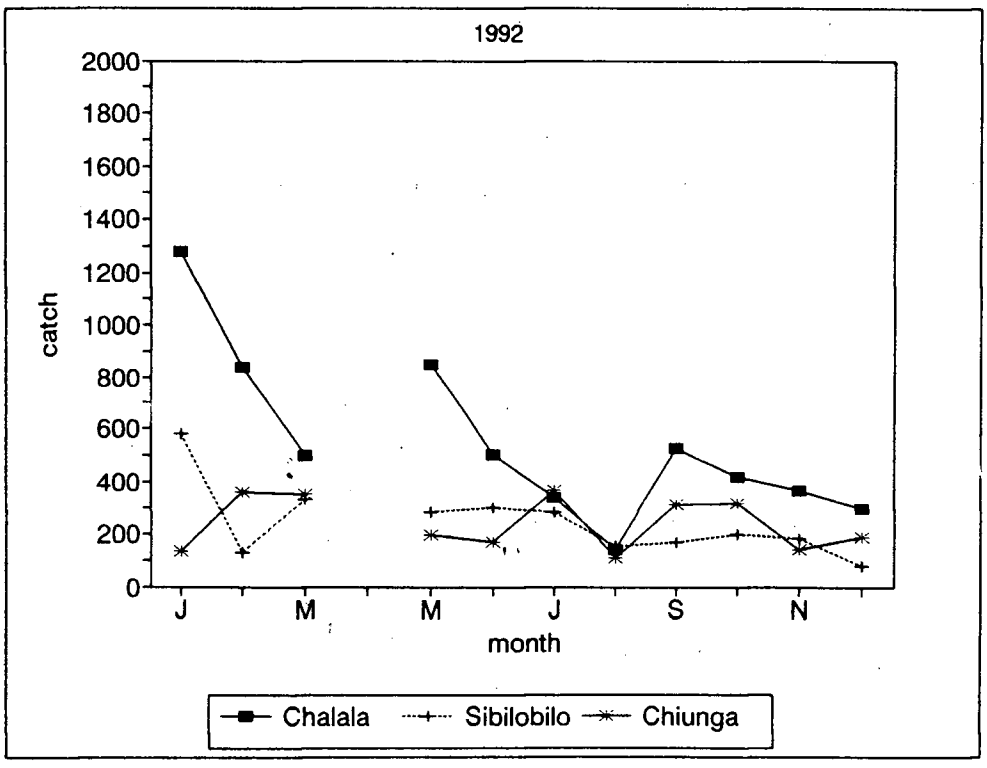
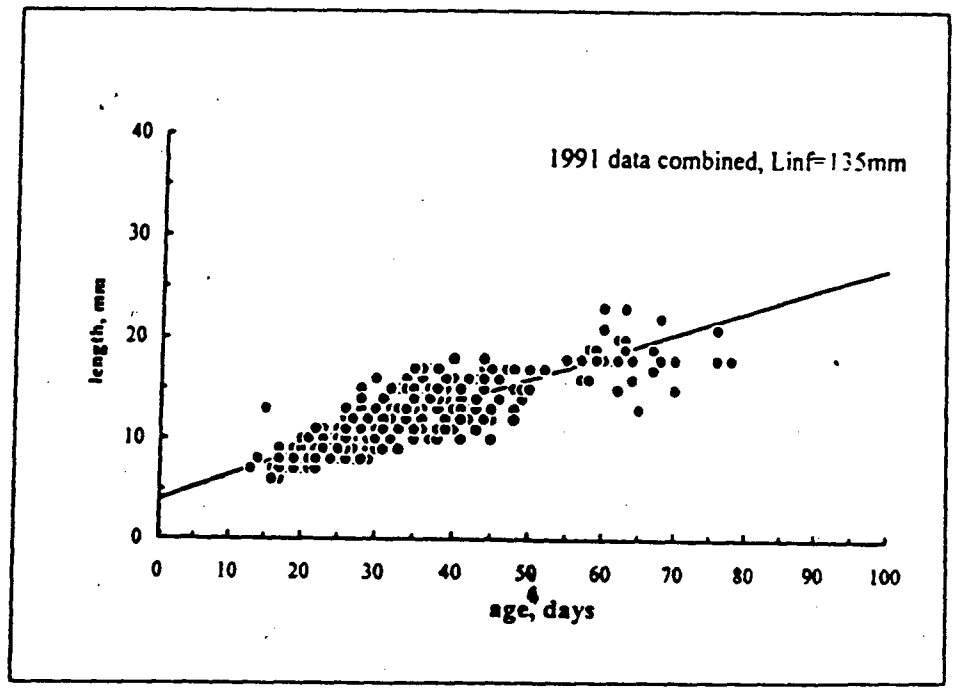


Figure 3.3: The von Bertalanffy Growth Function fitted to length-at-age data of *Limnothrissa miodon* larvae from Lake Kariba.



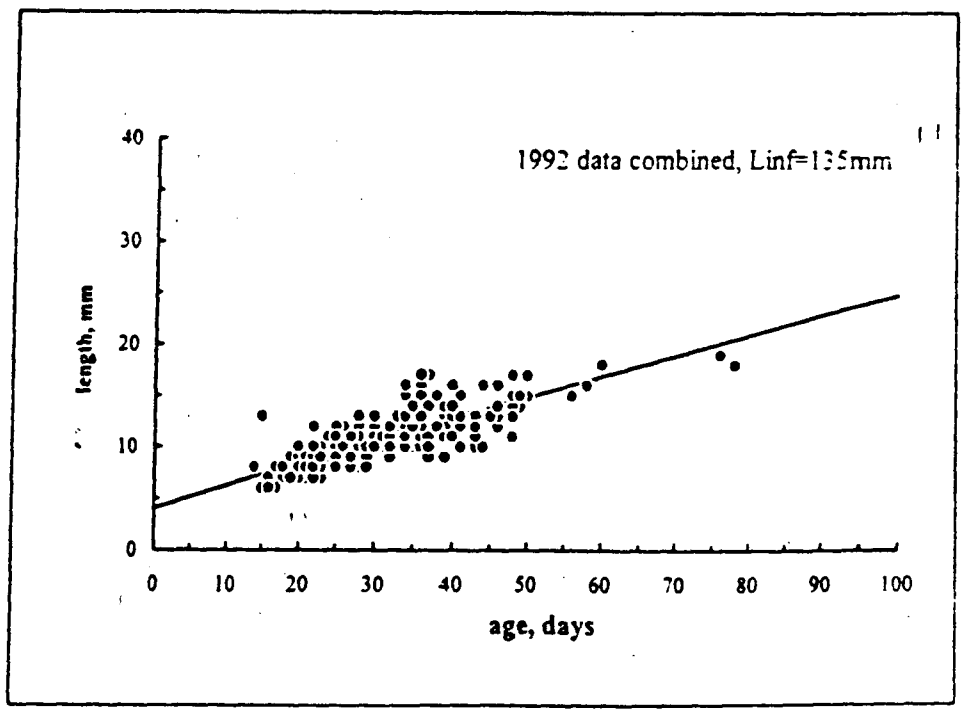
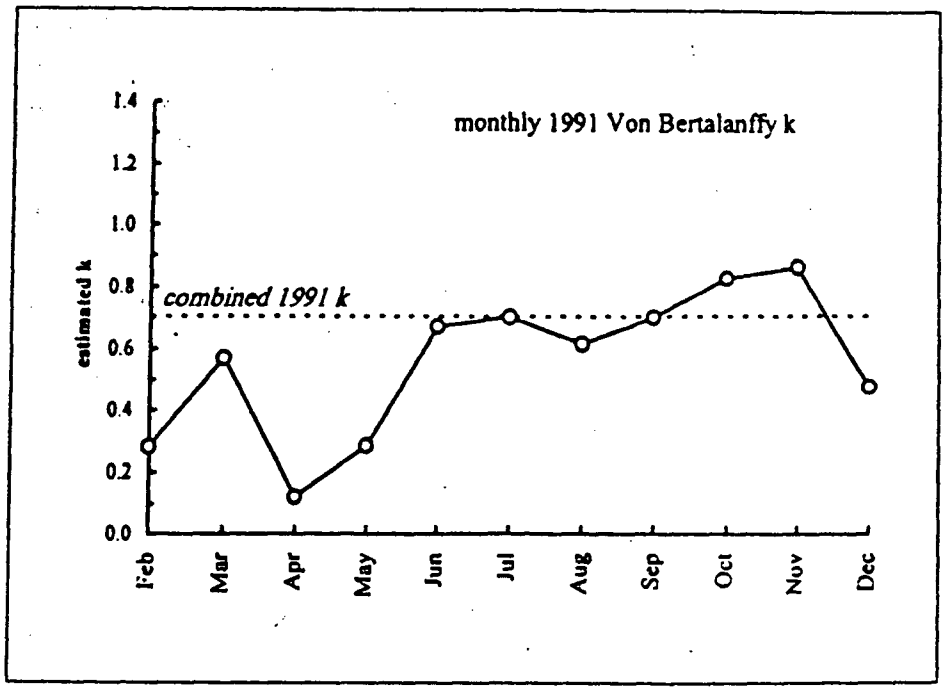


Figure 3.4: The monthly growth constant (K) of the VBGF compared to the annual estimate obtained by combining the data annually for 1991 and 1992 respectively.



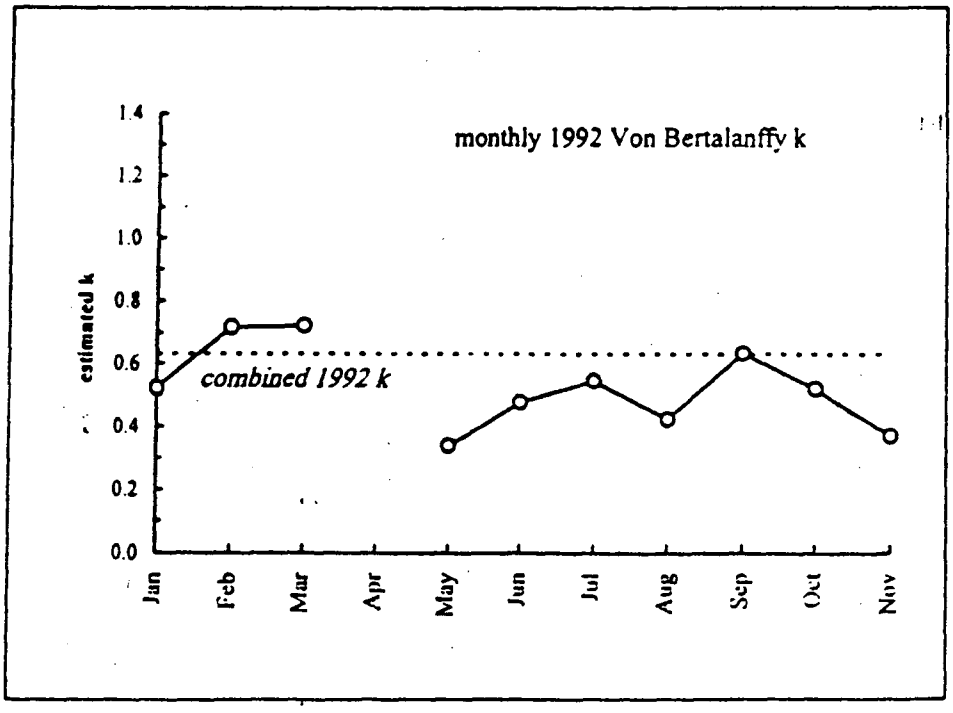


Table 3.2: Estimates of VBGF parameters L_∞ and K obtained from different studies on *L. miodon* in Lake Kariba. In this study the Chifamba (1992) value is used rather than being obtained. $\varnothing'$ is an index for comparing growth performance of fish in terms of length.

Source	L_∞(mm)	K(monthly)	$\varnothing'$
Cochrane (1974)	81.0	0.450	7.99
Marshall (1987)	74.2	0.254	7.24
Chifamba (1992)	135.8	0.079	7.28
Mtsambiwa (1993)	15.0	1.21	5.61
Mtsambiwa (this study 1991)	135.8	0.060	7.01
Mtsambiwa (this study 1992)	135.8	0.053	6.89

This pattern seems to follow the nutrient pattern closely in that the rise in February/March could be associated with the rainy season when a lot of nutrients are deposited in the lake by runoff and river flow. The rise in June/July could be resulting from lake turnover which releases nutrients trapped at the bottom of the lake. The September/October increase coincides with a windy period which could also release nutrients in the inshore areas due to wave action. Since the parameter t_0 is not a biological parameter which cannot be used to estimate values of K from values of L_∞ (Pauly, 1981) its value has not been considered in this study but is normally quoted and may bear some reflection to the hatch length which is estimated on Figure 3.3 as about 4.5 mm.

3.3.4 Relationships between fish length and otolith radius

The relationship between standard length and otolith radius was linear (Figure 3.4, Appendix IV) and was described by the regression equations shown on Table 3.3. This implies that it

is possible to use measured widths of a daily increment times series, in conjunction with the fish length-otolith radius relationship to determine both the size and the growth rate of an individual fish for each day of its life (Campana and Jones 1992). Based on data from a large sample (99 larvae) captured in Chalala, processed and counted in Flodevigen in Norway in May/June 1992 daily growth rate was observed to increase from 0.15 mm day^{-1} to 0.2 mm day^{-1} in the first five days and 0.2 - 0.25 mm day^{-1} from 5 to 28 days old. This was followed by drop from 0.2 mm day^{-1} to 0.05 mm day^{-1} from 30 to 50 days old. Maximum growth of 0.25 mm day^{-1} was experienced during the period 15 to 20 days when the fish were between 5 to 10 mm in length.

3.4.0 DISCUSSION

3.4.1 Validation of daily deposition in otoliths

The practise of otolith microstructure examination to determine age and growth in fish is based on upon two principles: firstly, that otolith growth occurs incrementally on a daily basis and secondly that there is a correspondence on the average between fish growth and otolith growth.

The tentative conclusion reported above that ring deposition in *L. miodon* larvae occurs on daily basis is assumed at this stage to meet the first principle. The other important aspect along these lines however is to determine the stage at which these daily rings initiate. This, due to failure to locate eggs and yolk-sac larvae, has not yet been determined and thus the assumption that it occurs at yolk-sac absorption to coincide with exogenous feeding is upheld. Age of *L. miodon* was estimated directly from the number of growth rings in the sagitta.

Table 3.3: Summary of the regression equations used to describe the relationship between standard length of fish and otolith radius.

Month	Sample	Regression Equation	Coefficient of Determination
February 1991	20	L = 4.85 + 0.12O	0.65
March	25	L = 2.25 + 0.26O	0.60
April	25	L = 11.23 + 0.04O	0.57
May	28	L = 8.99 + 0.06O	0.79
June	17	L = 6.91 + 0.07O	0.77
July	27	L = 5.60 + 0.09O	0.89
August	24	L = 6.42 + 0.09O	0.87
September	35	L = 5.34 + 0.11O	0.65
October	57	L = 3.91 + 0.13O	0.85
November	21	L = 5.52 + 0.09O	0.57
December	42	L = 5.29 + 0.09O	0.60
January 1992	45	L = 4.79 + 0.10O	0.70
February	65	L = 5.09 + 0.12O	0.72
March	46	L = 5.13 + 0.11O	0.84
April	-	-	-
May	26	L = 11.06 + 0.03O	0.54
June	24	L = 5.81 + 0.08O	0.65
July	21	L = 5.38 + 0.09O	0.53
August	11	L = 3.70 + 0.12O	0.55
September	38	L = 4.73 + 0.11O	0.80
October	48	L = 4.92 + 0.10O	0.82
November	23	L = 6.51 + 0.08O	0.40
December	27	L = 5.40 + 0.09O	0.56

where L = fish length and O = otolith radius

Initial growth rings have been reported to deposit prior to egg hatching, at hatching, just after hatching and at the onset of exogenous feeding (Tharrold 1988). Some temperate clupeids are known to initiate ring formation at yolk-sac absorption which often range from 3-5 days after hatching. In the tropical areas, high temperatures and hence rapid developmental rates suggest that endogenous reserves would be quickly exhausted (Houde 1974). Kariba has an annual mean water temperature of > 23°C (range 20 -33°C) which implies that the endogenous reserves are very quickly exhausted. Therefore the time between hatching and yolk-sac absorption should be extremely short allowing the assumption that the age of *L. miodon* determined from the increments in otoliths is the most accurate at the moment.

The second principle, that of a correspondence on the average between fish growth and otolith growth is discussed under section 3.4.4 below.

3.4.2 Larval abundance trends

The variable occurrence of larvae throughout the sampling period as observed from the time series plots suggests that variability in recruitment is already apparent at this stage.

This implies that recruitment variability is achieved at an earlier stage which for some technical reasons has not been included in this study. The two stages not included are the egg and yolk sac larval stages. These two stages are more vulnerable to both predation and starvation as predator avoidance and exogenous feeding are not yet fully developed. Houde (1994) however, suggests that larval-stage dynamics generally will have less influence on control or regulation of year-class strengths in freshwater fishes and that trophic interactions, competition for resources and factors such as overwinter mortality during the larval stage

maybe the predominant factors affecting their recruitment levels. The relatively large size at hatching, short stage durations and low mortality rate of freshwater fish larvae favour the probability that recruitment levels will be controlled during the juvenile stages. It is difficult at this stage to either dismiss or accept this hypothesis in the case of *L. miodon* (i.e. that the sardine juvenile stage dynamics will be relatively more important in determining recruitment levels and variability) because variability is already observed in the larval stages as depicted by the larval catches over the 24 months sampling period. Houde's hypothesis probably holds for long lived freshwater species unlike the short lived fast growing sardine. Marshall (1993) echoes the same sentiments that because of its small size, it would not be surprising to find that its population dynamics differ considerably from those of larger species.

Fluctuations in samples captured from month to month were taken as a relative index of fluctuating abundance from month to month since the sampling technique was standard in all cases. The CPUE which is used in the Lake Kariba sardine fishery as a relative index of abundance can be represented in the larval studies by the actual numbers caught if the sampling technique is taken as unity because the plankton net used, the duration of setting the net and intensity of lights used to trap the fish are the same on each sampling occasion. In the absence of abundance estimates obtained by other methods such as hydroacoustics it is difficult to quantify the actual abundances and relate these with the monthly mortality rates (see Chapter Four above) to establish the variability from month to month. The months when more larvae were caught are assumed therefore to have had higher abundance of larvae resulting from some previous favourable conditions while months with low catches are assumed to have had low abundances as a result of some unfavourable conditions. The regulation of these abundances could be related to food availability as this seems to be the

one of the major factors with potential to fluctuate. The fluctuations in nutrients were suggested to be responsible for the fluctuations in the growth factor (K) discussed above. Jenkins *et al.* (1993) echo the same sentiments citing temperature and food supply as the most important influences on growth rates which in turn influence the duration of the period of susceptibility to size-selective predation. Temperature in the tropical areas however is expected to have a major influence only in cases where food is limiting. This could be the case in Lake Kariba which is known to rely on run-off water for nutrient replenishment. In the absence of adequate food, high temperatures will have adverse effects on growth leading to mortality by starvation.

The other factor with potential to fluctuate to the extend of leading to various levels of recruitment is predation. Heavy or light predation on eggs and yolk-sac larvae can be reflected in fully developed larvae by high or low densities. However quantification of predation remains a very difficult subject.

3.4.3 Daily growth of larvae

Since the slope of the growth curves for many fish may vary between populations, the growth function that provides the best representation of growth may vary also (Chen *et al.* 1992). The result is that it is essential to assess the goodness of fit in any comparison among growth functions. Another aspect of importance in the choice of a growth function is its biological usefulness (Khon, 1986) rather than its mathematical simplicity. The choice of a function is also based on convenience and familiarity among scientists (Campana and Jones, 1993) for comparison purposes. In this study attempts were made to describe growth using polynomial curves but these could not be used beyond the third order as the growth tended

to go negative.

The advantage of describing growth using VBGF was further based on convenience in that results obtained could be compared to previous studies. The question of familiarity among scientist for the purpose of comparing with growth in other species where the curve was fitted to similar data also provided an added advantage.

The use of the Chifamba (1992) asymptotic length (L_∞) of 135 mm and not the ones obtained by Cochrane (1974) or Marshall (1987) resulted from the fact that the Chifamba study applied the otolith increment technique to age the fish as compared to length-frequency methods that were used by the other workers. As stated above, the otolith increment technique was the method used to age the larval fish in this study. It was also not possible to use size frequency distributions to generate growth rates so as to compare with those generated by the otolith increment which was one of the objectives of this study.

3.4.4 Relationship between fish length and otolith radius

The otolith is an information storage structure in which the daily growth ring is used not only for ageing but also for recording some aspects of the growth history of the fish. The changing width of the daily growth rings in the otolith is an indication of changes in daily growth rates in the fish and these are linked to the growth history of the fish. The width of the daily growth rings changed with time, they were narrow in the first five days indicating a period of slow growth followed by wider rings between five to twenty-eight days indicating a period of fast growth followed by another drop in ring width from thirty to fifty days. The first narrow rings follow yolk-sac absorption implying that the feeding activity of the fish is

limited. This can result from the absence of the prey of the right size or from the inability of the fish to swim fast enough to capture prey or from the inability of the fish to have a mouth gap large enough to catch the prey. An increase in the growth ring width implies an improvement on any of the above resulting in intense feeding hence fast growth. The third phase of a drop in ring width could be linked to growth becoming asymptotic as the fish enters a new growth stanza during juvenile life. This pattern of growth generally agrees with Houde's (1987) suggestion that starvation is the main agent of mortality in the larval stages especially at the end of the yolk-sac stage. Fast growth means remaining for a limited period in the stage of high mortality through predation. The final stage of a slow down in growth to mark the entrance into a new growth stanza could also be linked to the early development of gonads but this needs to be confirmed through further observations of age and gonadal development.

Relationships between otolith size and fish size have been used in several studies to extrapolate information gathered from the otolith size to infer respective information to fish size. In most cases this results from some statistical analysis to determine the degree of closeness of the relationship. In this study the relationship is linear following natural logarithm transformation which means otolith size has a bearing on the fish size. Thus otolith growth ring width whether wide or narrow and used to describe fast or slow otolith growth rate can also be used to describe fast or slow growth rate in fish length . This is further confirmed by a strong relationship between otolith size and age of fish established in the Mtsambiwa (1989) study. The ideal situation would have been to check on the relationship between the number of rings in the otolith and known age of fish. In this instance this is not possible because the stage of growth ring initiation remains largely unknown as the eggs and

or yolk-sac larvae have not yet been captured to determine whether initiation begins before or after hatching. Thus in the absence of this information the relationship between otolith size and age (as determined from the number of rings on the otolith) serves to confirm that otolith size does represent fish size as described by the regression equation above. However this cannot be used to describe growth of fish from different locations or spawned in different seasons as can be seen from Mosegaard *et al.* (1988)'s assumed decoupling of otolith growth from fish growth as an effect of differences in temperature response. This factor alone tends to discredit the idea of setting up standard age-length keys for the Kariba sardine if decoupling occurs there too due to some other reason other than temperature, as temperature is fairly above the basal metabolic rate. The other factors include different growth rates on monthly basis as well as in different areas of the lake such that samples would have to be collected from all these places to set up these keys. This might not be feasible due to the costs involved.

Hare and Cohen (1995) provide evidence that the basic assumption of proportional back-calculation maybe violated in the early life history stages of fish. Ontogenetic changes in the relationship between otolith size and fish size imply that there are ontogenetic changes in the relationship between otolith growth and somatic growth. In addition, if individual growth rates change relative to population growth rates, then as a result of growth rate effects, the proportionality between otolith growth and somatic growth must necessarily change (Campana 1990). For that reason it was deemed necessary to investigate the relationship of otolith growth to somatic growth on monthly basis rather than use one equation for the two years as growth rates were observed to fluctuate from month to month.

CHAPTER FOUR

Larval mortality, spatial and temporal distribution and recruitment pattern of the sardine *Limnothrissa miodon* in the inshore areas of Lake Kariba.

4.0.0 INTRODUCTION

With the exception of simple surplus production models, all mathematical models of fish stock dynamics include as a parameter the instantaneous rate of natural mortality (M) (Vetter 1988). But because natural mortality has proved extremely difficult to measure directly, M is assumed almost universally to be some constant specific to whatever stock is being modeled. Decreases in natural mortality with increasing age during the egg and post larval stages are so dramatic compared to post recruitment stages such that variations in M during these later (post recruitment) ages are often assumed negligible. Vetter (1988) concludes that natural mortality is far from constant for many fish stocks and that this variability is extensive enough that it should not be ignored.

The application of the otolith increment technique to estimate larval mortality has seldom been used (Essig and Cole 1986) and is still being developed. In order to understand the causes of variations in larval fish survival and subsequent recruitment, it is necessary to determine which individual pre-recruits die at different stages in early life (Pepin 1989). In line with the view that daily mortality rates decrease with increasing size, slow growing individuals are more likely to die at some critical stage than are faster-growing individuals. By implication it is important to consider variability in growth rates so as to predict survivorship. Analysis of otolith microstructure allows estimation of growth rates of the survivors through back-calculation.

Houde (1987) argues that changes in population characteristics due to external selective factors should be reflected in otoliths of a representative group of the population. Thus by contrasting the distribution of growth rates we can determine which proportion of the population survived and hence estimate mortality rates. If the susceptibility of larval fish to different environmental factors is known, then it is possible to infer factors responsible for observed changes in distribution at different stages. The essential data to isolate the factors that affect recruitment of a year class or cohort can be collected through the use of the newest technological tools available in fisheries research which include determination of birthdates, growth rates and ages of fish larvae and recruits using counts of daily rings of the otoliths (Lasker 1985). Pepin (1989) shows that the distribution (i.e. mean(μ) and variance(s^2)) of growth rates of fish within a cohort must be considered in order to estimate mortality rates and uncover the causes of variations in survival during early life.

However to estimate growth rates of individuals using otolith microstructure analysis two important conditions have to be met; (1) that an empirical relationship exists between the age of an individual and the number of the increments on the otoliths, and in this case, that otolith microzonation has a daily periodicity; and (2) that there exists an empirical relationship between the length of fish and the size of the otoliths. However Secor *et al.* (1989) discuss several confounding characteristics of otolith growth which can limit comparisons between somatic growth and otolith microstructure. These include (a) measures of an individual's daily and weekly somatic growth rates, correlate poorly to increment widths for corresponding time periods, (b) otolith growth continues during periods of starvation and negative somatic growth, (c) there can be a maximum asymptotic limit to daily otolith growth in fast growing fish, (d) temperature affects the relationship between somatic

and otolith growth and (e) intraspecific variation in the manner in which otoliths scale to body size is influenced by somatic growth rate where slower growing fish have relatively larger otoliths than fast growing fish of the same somatic size. These factors are indicative of the complex manner in which otolith growth is related to fish growth. Lo *et al.* (1989) found the estimated mortality rate to be biased high when the larval growth rate was overestimated and biased downward when the growth rate was underestimated. Beyer (1989) points out an inverse relationship between growth and mortality, that is the cornerstone of the growth-mortality hypothesis which is finding broader use in larval ecology today.

The three major hypotheses suggested as mechanisms that control survival of larval fishes are starvation, predation and advection to unfavourable environments. Morse (1989) views advection as a special case which differs little from predation in its effects on larval population and may be viewed as an abiotic "predator". This way the predator-prey interactions in the pelagic ecosystem may then be partitioned, in terms of mortality, into starvation and predation. However it is often not clear whether larvae actually die from lack of adequate food supplies or become more vulnerable to predation as a result of starvation. Crecco *et al.* (1983) presuppose that lack of food would enhance larval mortality indirectly by reducing larval growth and stamina, thus rendering the larvae vulnerable to predation for prolonged periods. This again implies that larval predation is a complex process whose interaction with biotic and abiotic factors is difficult to measure in field surveys. Lasker (1985) points out that the difficulty has been and continues to be the quantification of predation.

Another important factor to complicate the estimation of larval mortality in the field is the

behaviour of the fish themselves. For example, the sardine *Limnothrissa miodon* in Lake Kariba is known to migrate from the inshore to the offshore as it grows both in size and age, such that fast growing individuals migrate to deeper water faster than slow growing individuals of the same cohort as evidenced in Mtsambiwa (1989)'s age and length data from different depths. Thus when estimates of mortality are obtained this consideration should not be left out.

4.1.0 Objectives of study

The purpose of this study is:

1) to obtain estimates of mortality in the sardine *Limnothrissa miodon* larvae in Lake Kariba.
2) to validate spatial distribution of the sardine larvae in Lake Kariba
3) to validate temporal distribution of the sardine larvae in Lake Kariba
4) to examine recruitment patterns of *L miodon* larvae in the inshore areas

The first three of the above exercises will be reported as separate self-contained sub-units, each with its own (i) objectives, (ii) procedures and (iii) results and there will be a general discussion. Recruitment patterns will be discussed in light of the spatial and temporal distribution and general observations from the entire sampling programme.

4.1.1 Larval mortality estimation

Of the two conditions discussed above regarding the use of growth increments in otoliths to infer somatic growth the first condition of otolith microzonation having a daily periodicity was partially fulfilled through a study discussed in Chapter Three above, which tentatively

validated daily deposition of increments by tagging with tetracycline. The second condition, of a close relationship between otolith growth and somatic growth, is based on a regression analysis of standard length of fish on radius of otolith. The problems outlined above regarding possible decoupling of otolith growth from somatic growth are considered and the effects of these factors on the inferred estimates of larval mortality are addressed. Mosegaard *et al.* (1988) discusses decoupling between somatic and otolith growth resulting from differences in temperature response in Arctic char (*Salvelinus alpinus*) as a possibility. However given the tropical nature of Lake Kariba the possibility of temperature differences leading to decoupling between otolith and somatic growth is questionable. The climate of Kariba is characterised by consistently high temperatures (monthly mean 20 - 30 °C with a seasonal variation. October and November are the hottest months (33 - 38 °C)ndropping to about 23°C in June/July. This suggests that somatic growth rate cannot differ so much to lead to the decoupling as a result of temperature differences.

Starvation could be the other possible contributor to this decoupling but Houde (1989) suggests that temperate larvae take a long time to die of starvation due to reduced metabolic rates such that there is a possibility of the decoupling. Tropical larvae take a shorter time to die of starvation and this might happen before decoupling takes place. The suggestion here is that decoupling takes place after some time and the time duration required for it to occur is not enough for tropical fish while it is possible for temperate fish species. Houde (1989, 1990) echoes the same sentiments by the suggestion that the larvae of species that inhabit cold environments should be more susceptible to environmental fluctuations than species that inhabit warmer waters as a result of longer development time. The same argument is put forward when the issue of the duration of yolk sac absorption is considered. Due to

differences in metabolic rates again related to the temperature differences in the two ecosystems yolk-sac absorption takes longer in temperate than in tropical clupeids, as observed by Tharrold (1988). Given the type of temperatures in Lake Kariba this yolk-sac absorption should take a very short time. This is probably why the yolk-sac larvae of *L miodon* are hardly found (B. Marshall; pers. comm. 1996).

Pepin (1991) advocates size as the other factor that is important as far as survival in the early life history of fish is concerned. The size of an organism determines the size and average abundance of prey and predators with which it will interact. Miller *et al.* (1988) concluded that the survival of species with small offspring should be more variable than the survival of species with larger offspring because of increased vulnerability to starvation and predation with decreasing size. Size could be a very important aspect as far as larval sardine survival is concerned. As this study has shown larval sardines are found in the littoral zone throughout the year where they interact with all the other species on the lake. It recruits to the pelagic zone after the juvenile stages and during all that time it is exposed to predation by the other species of riverine origin and possibly cannibalism. Therefore the duration of its early life history plays an important role in so far as determining the level of predation suffered during that time. Another artifact linked to size is food availability. Survival will depend as well on whether prey particles of the right size are available for larval fish (Pitcher and Hart 1982). Swimming speed necessary for escapement from predators on one hand and for capture of prey on the other hand is another limiting factor which again is linked to size.

However given all these doubts which are otherwise difficult to quantify for field captured larvae it is appropriate therefore to consider the use of a distribution (mean (μ) and

variance(s^2)) in growth rates rather than individual growth rates when estimating mortality as suggested by Pepin (1989). The direct effects of environmental factors (biotic or abiotic) can hardly be made through direct observations, except under laboratory conditions which are different from the natural conditions experienced by the fish. Therefore under these conditions the best approach is by inferences from otolith microstructure which as observed in Chapter Three above, is a powerful tool for the estimation of growth rates in larval fish. However certain assumptions have to be made when applying this technique to larval fish mortality and these include:

a) mortality is constant with age

b) larval cohorts initially recruit to the same gear at the same size and

c) all age groups analyzed are equally vulnerable to the sampling gear.

These assumptions are no different from those inherent in the traditional catch curve studies. Based on the results of the regression analysis carried out in Chapter Three above to investigate the relationship between otolith size and fish size as well as between otolith size and age of fish (obtained in Mtsambiwa 1989) estimates of larval mortality were then calculated. This was achieved by first converting length frequencies to age frequencies by the use of age-length keys, then performing catch curve analysis and finally deducting the offshore migration factor. This offshore migration factor was obtained using the Mtsambiwa (1989) data and the few data points taken in this study from the 1991 sampling programme when it was possible to sample and age a limited number of specimens from other depth ranges.

a) Age-length keys

The initial step involved the preparation of age-length keys based on a smaller sample for

which age and length were known from each month. This was done in line with the important assumption underlying the appropriate use of age-length keys that they are drawn from the same population, at the same time and place as the larger length-frequency samples. Sub-sample sizes within each length category were proportional to the number of fish in that length category as proposed by Kimura (1977). The range of length categories in the key span the same range as that observed in the length sample as outlined by Campana and Jones (1992). Length-frequency distributions representing total fish captured each month from February 1991 to January 1992 were converted to age-frequency distribution using the age-length keys.

b) Catch curve analysis

Mortality estimates were obtained from catch curve analysis on the assumption that abundances of fish decreased exponentially with age. Catch curve analysis generally consists of determining the best-fit straight line through the decreasing portion of logged frequency distributions of ages, because if the decrease in abundance is truly exponential, the slope of the line through the log-transformed data is the instantaneous rate of decrease in abundance (Ricker 1975). Abundances with age were converted to log abundances and a regression line was fitted using only the data with descending abundances. Converting the abundances to their logarithmic values often results in a relatively linear decrease during most captured ages (or sizes) after some initial increase in vulnerability. Hence the ascending data points were ignored when fitting the regression. The absolute value of the slope of the fitted regression was the estimate of the natural mortality. The monthly data were also pooled for both 1991 and 1992 years and catch-curve analysis of the pooled data was carried out to produce a

single average mortality estimate.

c) Offshore migration rate

Offshore migration of the larvae as they grow in size and age was considered as one of the factors that could bias the instantaneous mortality rate results upward. Because it was not possible in this study to consistently sample the other depth ranges (either due to bad weather or drought) estimates of the migration rate were obtained by the use of the limited data points from 1991 and from an earlier study by Mtsambiwa (1989) where sampling was performed at four different depths. To obtain the rate of migration the following steps were taken:

i) a regression analysis of mean age on depth was performed to provided an estimate of the rate at which fish moved from one depth range to another. This rate of movement from one depth range to another was represented by the slope of the regression analysis.

ii) to estimate time taken to move through a depth range covered by the light attraction a radius of 6 metres ($\pm$ 3 metres) was assumed to be the radius under the influence of light during sampling. The time (T) taken by the fish to grow through this distance was obtained as follows:

$$T = D/R \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 1$$

where D is the time distance affected by light attraction which assumed to be 6 metres ($\pm$ 3 metres) in this study and R is rate of movement offshore, expressed as metres of depth increase per day.

iii) The loss rate (L) from the population was then calculated by:

$$L = 1/T \qquad \text{.....2}$$

where T is the time taken for the fish to grow through the 6 metres distance. which was considered to be equivalent to the instantaneous rate of mortality due to migration which was then deducted from the instantaneous rates of mortality obtained by catch curve analysis above. While working out this correction factor, i.e. the instantaneous loss rate of fish from one depth range to the next, consideration was also made of the effect of light attraction on those individuals that might have left or in the process of leaving the depth range but were attracted back by light.

4.1.2 Results

a) Age-length keys

Figure 4.1 shows the resultant histograms for the age frequency distributions that were obtained from converting length frequency distributions to age frequency using age length keys. Data were pooled for 1991 and 1992 respectively.

b) Catch curve analysis

Table 4.1 summarises the daily rates of instantaneous mortality on monthly basis obtained from catch curve analysis. Figure 4.2 (see Appendix VI) shows the regression lines fitted to the logged abundances. From the above results, daily instantaneous mortality rates varied from month to month ranging from 0.02 day^{-1} to 0.16 day^{-1} . The least mortality rates were obtained during the September 1991 at 0.003 day^{-1} implying that whatever conditions

prevailed were favourable, however the r^2 was very low making the fit questionable. An instantaneous loss rate of fish from one depth range to another of - 0.043 was estimated and used as the instantaneous mortality rate correction factor. The last column of Table 4.1.0 shows instantaneous rates of mortality after deducting the instantaneous rate of loss of fish estimated from the few data points when it was possible to sample other depth ranges in 1991. Some of the months had negative instantaneous mortality rates following the deduction of the correction factor. This could be explained in part from the fact that the actual rate of loss of fish for the period being analysed could be lower than the one obtained from the few 1991 data points. The 1989 data provided a higher correction factor and therefore was not used.

c) Off-shore migration rate

From Mtsambiwa (1989) the rate of movement offshore per metre of depth increase per day was estimated at 0.269 m day^{-1} and that from the 1991 data was estimated at 0.256 m day^{-1}, the latter, being the lower of the two was used in subsequent calculations. The time taken by the fish to grow through the distance affected by light attraction (assumed to be 6 metres) was obtained as follows:

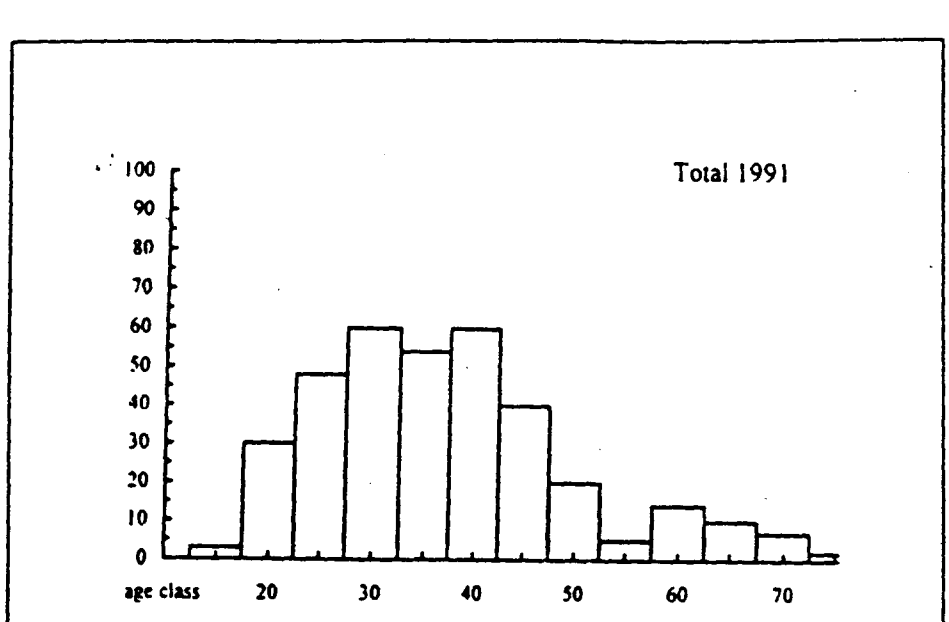
$$6/0.258 = 23.31 \text{ days}$$

This gave a loss rate of fish from the population in the depth range of:

$$1/23.31 = 0.043$$

This rate was deducted from the instantaneous rate of mortality obtained by catch curve analysis to give a corrected rate of instantaneous mortality given in the last column of Table 4.1 above.

Figure 4.1: Age-frequency distributions that were obtained following conversion of length-frequency distributions to age-frequency using age-length keys.



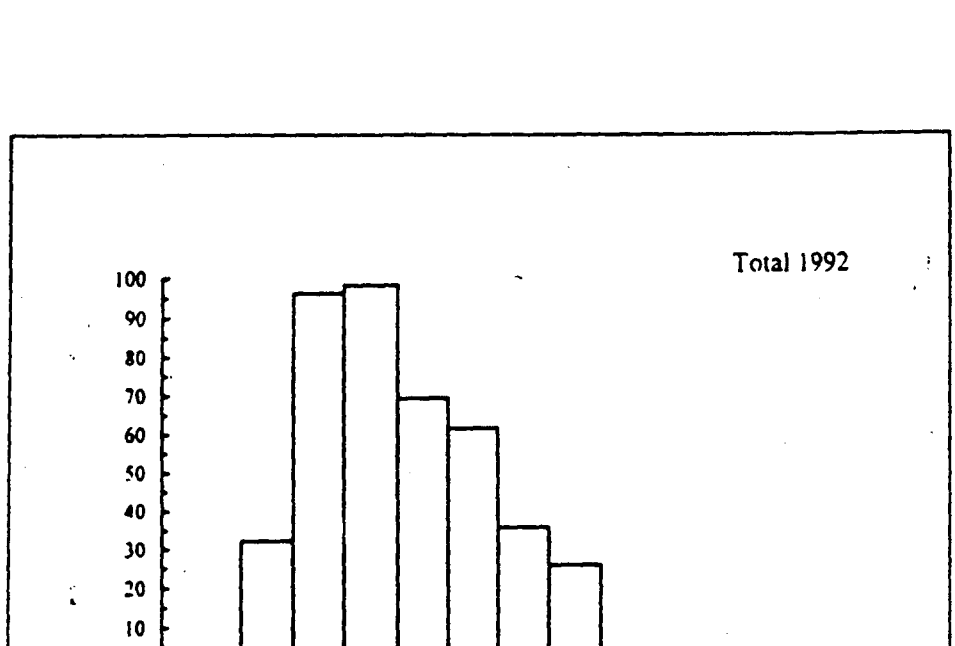


Table 4.1: Summary of the monthly instantaneous mortality rates in larval *L. miodon* in Lake Kariba as represented by the slope of the regression curve in catch curve analysis.

Month	Regression Equation	Coefficient of Determination	Corrected Rate
February 1991	Y = 4.69 - 0.05X	0.99	0.007
March	Y = 2.28 - 0.03X	0.75	-0.013
April	Y = 9.30 - 0.16X	0.37	0.117
May	Y = 6.13 - 0.06X	0.56	0.017
June	Y = 2.64 - 0.04X	0.67	-0.003
July	Y = 2.45 - 0.02X	0.65	-0.023
August	Y = 4.27 - 0.04X	0.43	-0.003
September	Y = 4.21 - 0.003X	0.003	-0.04
October	Y = 6.17 - 0.06X	0.66	-0.017
November	Y = 6.12 - 0.10X	0.40	0.057
December	Y = 6.10 - 0.06X	0.75	-0.017
January 1992	Y = 7.64 - 0.07X	0.50	0.027
February	Y = 7.37 - 0.08X	0.90	0.037
March	Y = 7.96 - 0.14X	0.60	0.097
April	-	-	-
May	Y = 8.38 - 0.12X	0.87	0.077
June	Y = 5.08 - 0.04X	0.32	-0.003
July	Y = 7.97 - 0.14X	0.99	0.097
August	Y = 5.11 - 0.02X	0.48	-0.023
September	Y = 6.09 - 0.05X	0.63	0.007
October	Y = 2.30 - 0.04X	0.55	-0.003
November	Y = 7.21 - 0.08X	0.64	0.037
December	Y = 7.73 - 0.11X	0.39	0.067

Where Y is the Abundance and X represents the Age of the fish.

Figure 4.3: Estimates of daily instantaneous mortality rates showing 95% confidence limits.

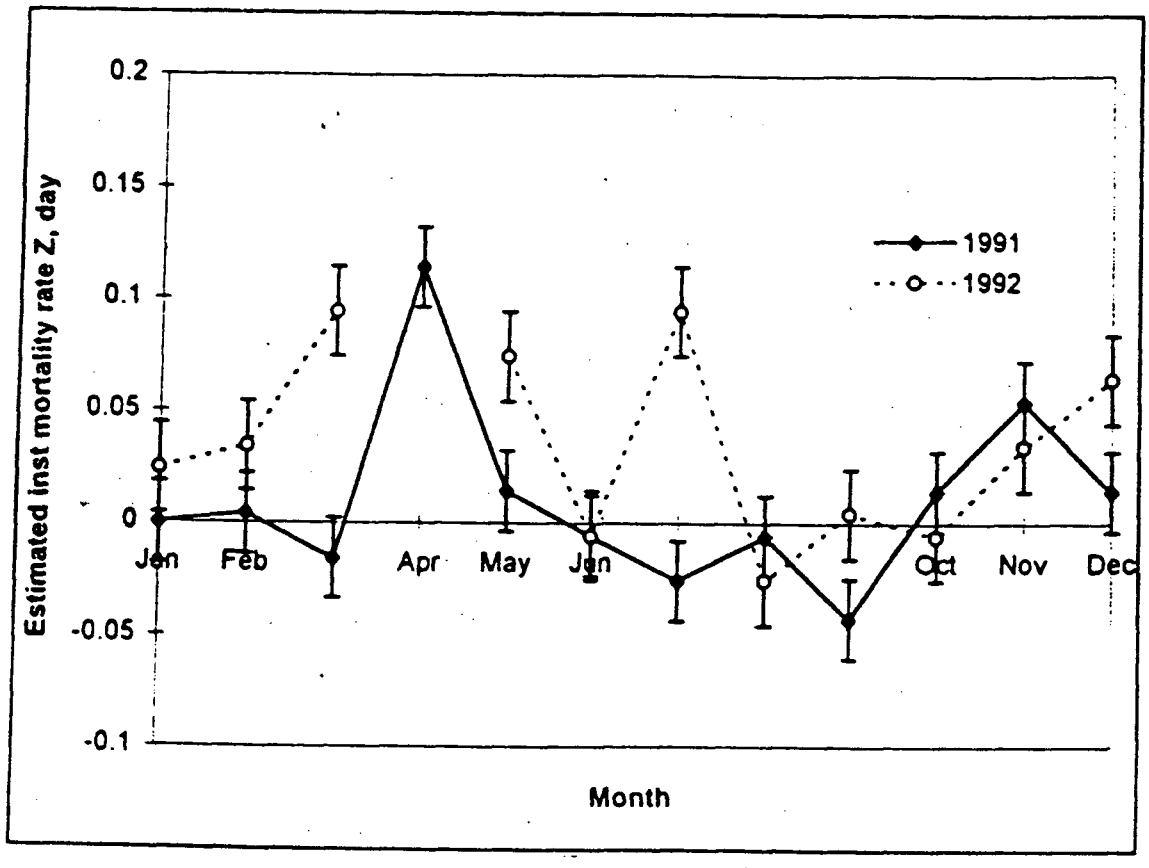
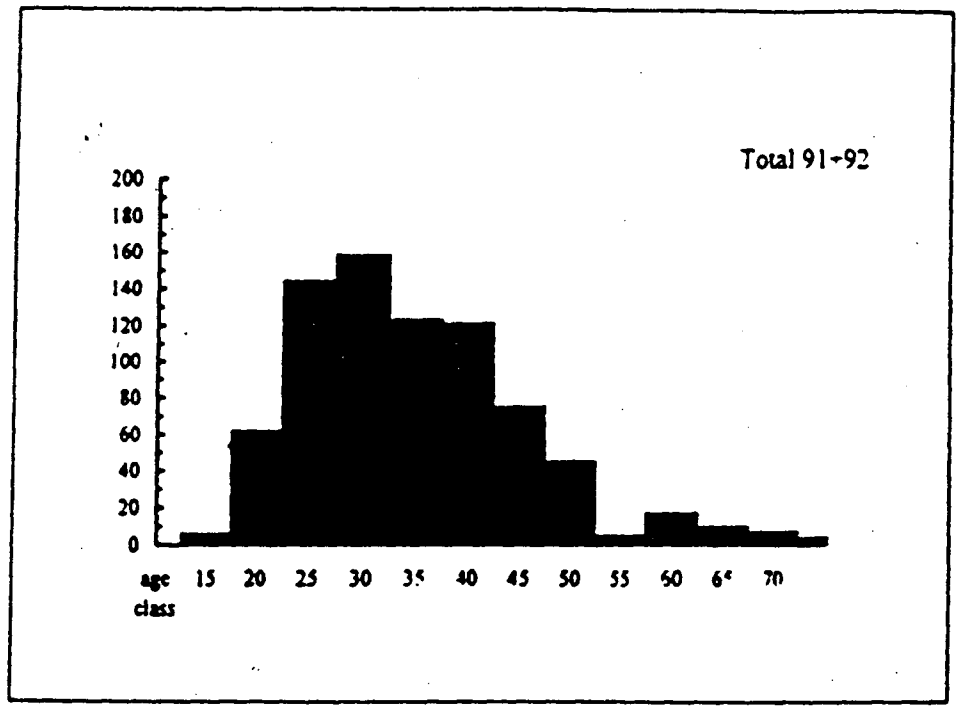
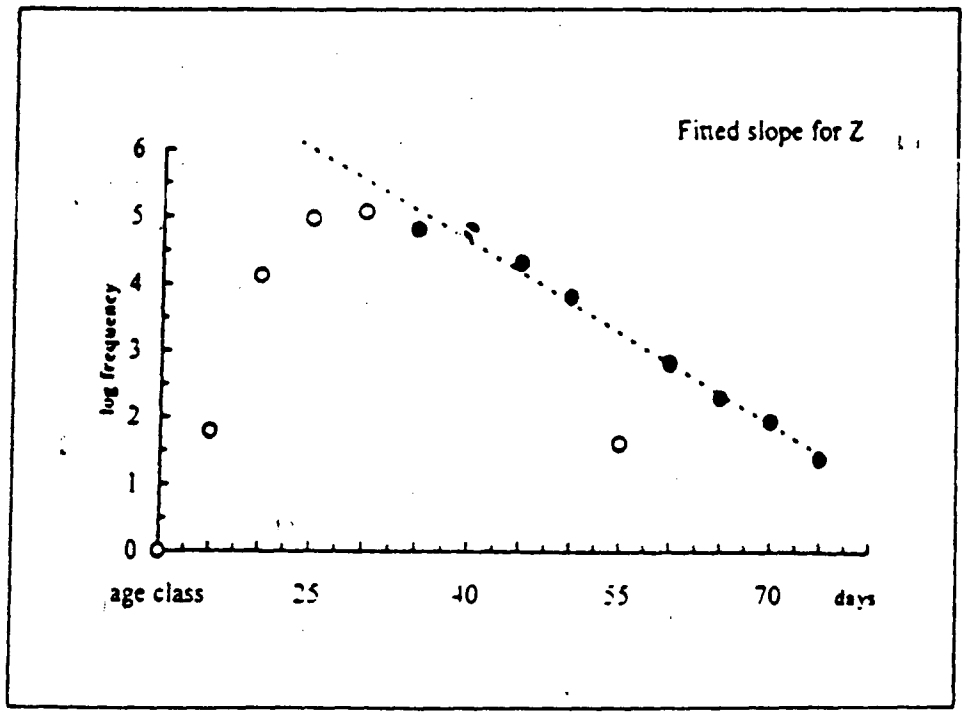


Figure 4.3 above shows high mortality rates for the months of April and November 1991 while in 1992 the rates are high from March to May, then in July increasing again from November to December. Thus in the two years it would seem the periods around April and around November have high mortality rates. These could be linked to high predation as the nutrient status is improved during that those times. Figure 4.4 shows the pooled data for 1991 and 1992 which were used to obtain the annual rates.

Figure 4.4: Showing age-frequency distribution for the 1991 and 1992 data pooled togather and the subsequent catch curve analysis of the same data the gave estimates of Z the total mortality.





4.2.0 Validation of spatial distribution of larvae

4.2.1 Objective

The objective of the validation of spatial distribution of larvae was to investigate the extent to which the shoreline of lake Kariba acts as a nursery ground for the sardine larvae.

4.2.2 Procedure

To achieve the above objective, sampling during a whole lake cruise was carried out at points randomly selected along the shoreline from Sanyathi Basin to the Mlibizi Basin, a distance of about 300 km. Two criteria determined the random selection of the sampling points:

i) any area of the shoreline that was reached by the research vessel at sundown during the cruise and

ii) any site within that area where there were limited submerged trees to allow easy sampling. Considerations were also made for the type of physical features to avoid sampling in identical places only.

Samples were captured using the standard light-trapping method applied throughout the whole study (see Chapter Two). At each sampling site physical features of the area such as substrate (rocky, sandy or weedy) and the steepness of the slope were also recorded. The number of fish samples captured were described as large if on counting they exceeded 50 and as small for anything less than 50 larvae. No further processing of the larvae was carried out as the purpose of this exercise was first just to establish whether larvae were present in an area or not and secondly to check if they occurred in large or small numbers.

Six such sampling cruises were carried out during the two years of sampling.

4.2.3 Results of validation of spatial distribution of larvae

Table 4.2 shows the larval catches captured at the randomly selected areas for six cruises. Larvae were caught at all the sites sampled showing that the entire shoreline could be a nursery ground for larval Lake Kariba sardine.

The type of substrate also seemed to matter with small samples being caught in rocky areas while large samples were caught in weedy areas in general. This can be probably explained by the fact that weedy areas provide cover against predators compared to other substrate types. In addition weedy areas could have secondary production that made food particles of the right size abundant. According to a simple G-test carried out there was interaction between substrate and slope in determining the density levels ($P=0.5$).

The presence of larvae above all types of substrate sampled is a demonstration that *L. miodon* has the capacity to utilize varied environments as nursery grounds, although some environments are more preferable than others. However nothing at the moment can be said about those areas with submerged trees which could not be sampled by the type of gear in use. Larvae were also found in abundance in the Andora Harbour which is heavily congested with boats and now believed to be polluted more than any other place in the lake (Prof. C. Magadza, University of Zimbabwe, pers. comm. 1992). It is possible therefore that at the time of sampling this pollution did not seem to have an adverse effect on the larval sardine.

Table 4.2: Summary of the results of the validation of spatial distribution of larval sardine in some of the littoral areas of Lake Kariba.

Date	Cruise Number	Location	Features	Quantities
4/91	1	Kasese Harbour	Weedy/shallow	Large
4/91	1	Nyaodza River	Rocky/shallow	Small
4/91	1	Fothergill Island	Weedy/shallow	Large
4/91	1	King's Camp	Muddy/shallow	Large
4/9	1	Paradise Island	Sandy/shallow	Small
4/91	1	Sinamwenda	Rocky/shallow	Small
6/91	2	Andora Entrance	Sandy/shallow	Large
6/91	2	Dandawa	Muddy/shallow	Small
6/91	2	Chalala Harbour	Muddy/shallow	Large
6/91	2	Lokola Lagoon	Rocky/shallow	Small
6/91	2	Mlibizi Harbour	Weedy/shallow	Small
11/91	3	Andora Harbour	Weedy/shallow	Large
11/91	3	Msampakaruma Island	Rocky/shallow	Small
11/91	3	Msampa Camp	Weedy/shallow	Large
11/91	3	Katete Bay	Weedy/shallow	Large
2/92	4	Charara Point	Sandy/shallow	Large
2/92	4	Dandawa	Weedy/shallow	Large
2/92	4	Ume River	Rocky/shallow	Small
2/92	4	Xmas Island	Rocky/steep	Large
2/92	4	Binga	Muddy/shallow	Small
2/92	4	Mlibizi	Weedy/shallow	Small
7/92	5	Redcliff Island	Rocky/steep	Large
7/92	5	Gache Gache	Weedy/shallow	Large
7/92	5	Hydro Bay	Sandy/shallow	Small
7/92	5	Chibuyu	Rocky/shallow	Small
10/92	6	Andora Harbour	Weedy/shallow	Large
10/92	6	Long Island	Sandy/shallow	Small
10/92	6	Starvation Island	Sandy/shallow	Small
10/92	6	Photo Corner	Sandy/shallow	Small
10/92	6	Chete Area	Rocky/steep	Small

4.3.0 Validation of temporal distribution of larvae

4.3.1 Objective

The objective of the validation of temporal distribution of larvae was to confirm the presence of larvae at particular sampling sites during a lunar cycle. In the main study, larvae had been collected from the same site at the end of each month, making it desirable to check if they were present throughout the month as well.

4.3.2 Procedure

To achieve the above objective it was necessary to sample at a specific site at regular short time intervals. By virtue of its proximity to the Lake Kariba Fisheries Research Institute the sampling site in the Leisure Bay, was chosen for this exercise. Samples were captured using the standard larval sampling method (see Chapter Two). Samples were collected at two-day intervals during the last two weeks of February 1994 and the first two weeks of March 1994. Although desirable, it was not possible to sample at two-day intervals in the month of February only due to boat problems during the first half of that month, hence the period stated above.

Samples were collected from the 0-5 metre depth interval only, as logistics could not permit sampling every other night at all subsequent depth intervals as was done in part of the main study. All specimens captured were measured in length to the nearest millimetre to investigate whether the same size of larvae were present at the same site throughout.

4.3.3 Results of validation of temporal distribution of larvae

Table 4.3 shows the larval numbers caught during the periods stated. While the time in question is short compared to the entire sampling period of the study it indicates that larvae were present in the sampling site throughout the period sampled. It also implies that horizontal migrations could be limited as larvae were present every time sampling was carried out.

During the sampling period no environmental factors were recorded as the initial aim of this exercise was just to check the temporal distribution of larvae. The variability in catches between different days necessitated the need to investigate the cause of this variation. Auto-correlations were calculated and it was observed that there was a shift from positive to negative autocorrelation with a mean lag of 4 days (range 3-6 days) which could not be explained. Moon phases were then noted from the February 1994 and March 1994 calendars and Table 4.4 summarises the results. The shift in autocorrelations from positive to negative could not be explained by moon phases. Some other environmental factors such as cloud cover and wind could have been responsible for the observed autocorrelations. Further work needs to be done to establish this.

4.4.0 DISCUSSION

Before the development of the daily increment ageing method, mortality was estimated by enclosure experiments or field observations of the decline in abundance of progressively larger size classes (Campana and Jones 1992). The difficult with this length-based approach is that sources of mortality are often time-specific and cannot be discerned with length-based

Table 4.3: Showing catches taken from one site on every other day from mid February 1994 to mid March 1994 to check if larvae are present on the site all the time.

MONTH: February, 1994

DATE	13	15	17	19	21	23	25	27
DAY	1	3	5	7	9	11	13	15
CATCH	36	120	14	20	11	73	44	19

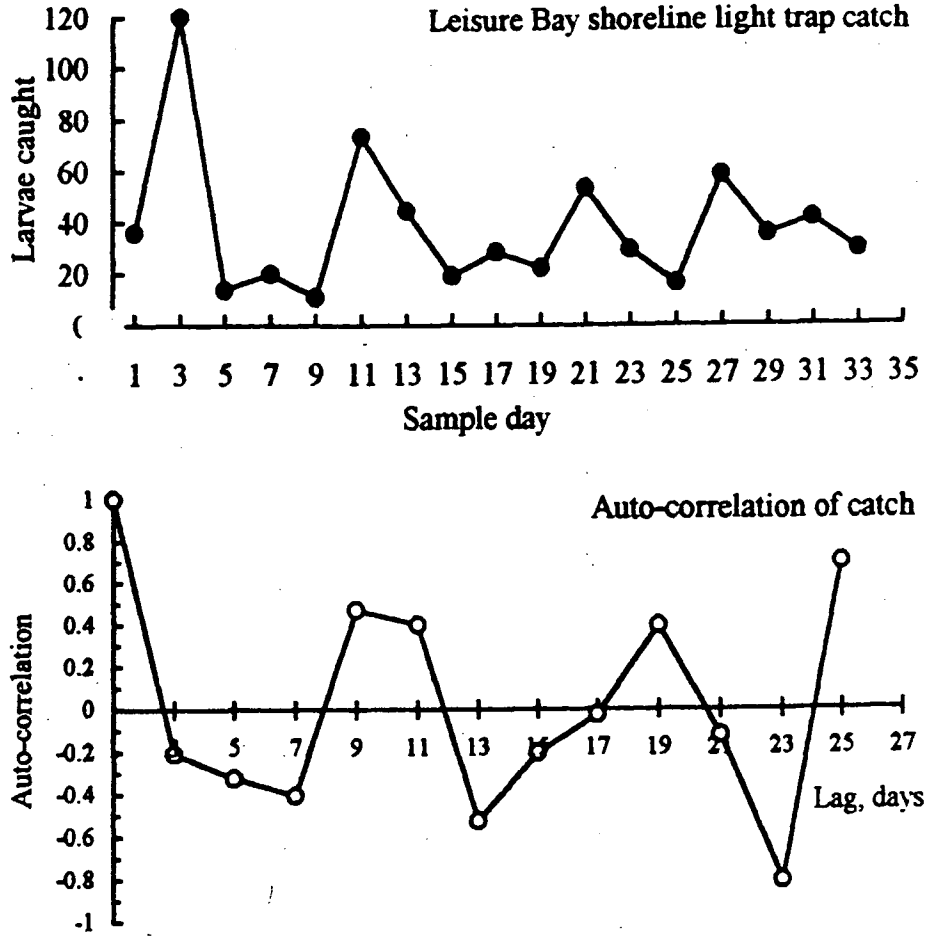
MONTH: March, 1994

DATE	1	3	5	7	9	11	13	15	17
DAY	17	19	21	23	25	27	29	31	33
CATCH	28	22	53	29	16	58	35	41	29

Table 4.4: Autocorrelations of catches of *L miodon* larvae and the respective moon phases during the temporal validation exercise in February/March 1994.

Lag	**Days**	**Autocorrelation**	**Moon phase**
0-2	3	positive	new moon
3-7	5	negative	first quarter
8-11	4	positive	half moon
12-17	6	negative	full moon
18-20	3	positive	last quarter
21-23	3	negative	no moon
24-27	4	positive	new moon

Figure 4.5: Larval catches and autocorrelation of the catch of *L. miodon* larvae taken every other day at the Breezes sampling station to investigate temporal distribution in February and March 1994



measures. Because size in general is not a particularly good indicator of age, length-based methods do not track well-defined cohorts and therefore yield results which are often too crude to be useful. One other added advantage when using the otolith increment technique to obtain estimates of mortality is that there is no requirement as in growth studies to determine the stage when ring deposition is initiated.

In general natural mortality is extremely high during egg and larval stages decreasing quickly during the juvenile period becoming relatively stable during adulthood and may increase again in senescence (Vetter 1988). The estimation of mortality in larval fishes is based, almost exclusively, on catch curve analysis, even though the methods section of papers may not explicitly state this (Campana and Jones 1992). Catch curves plot the frequency of fish grouped by either size or age but because size is often a poor indicator of cohort membership, age estimated from daily increment ageing technique is preferred. Abundance-at-age as stated above usually decreases exponentially making the slope, Z (expressed as a positive number by convention) the time specific rate of mortality. This value can either be estimated by non linear regression of untransformed data or by converting abundance to log of abundance which results in a more or less straight line with a negative slope which can then be fit through ordinary least squares regression. Due to incomplete capture by the sampling gear often the abundance in the youngest age category will be less than the peak abundance resulting in an ascending left limb which is ignored when fitting the regression.

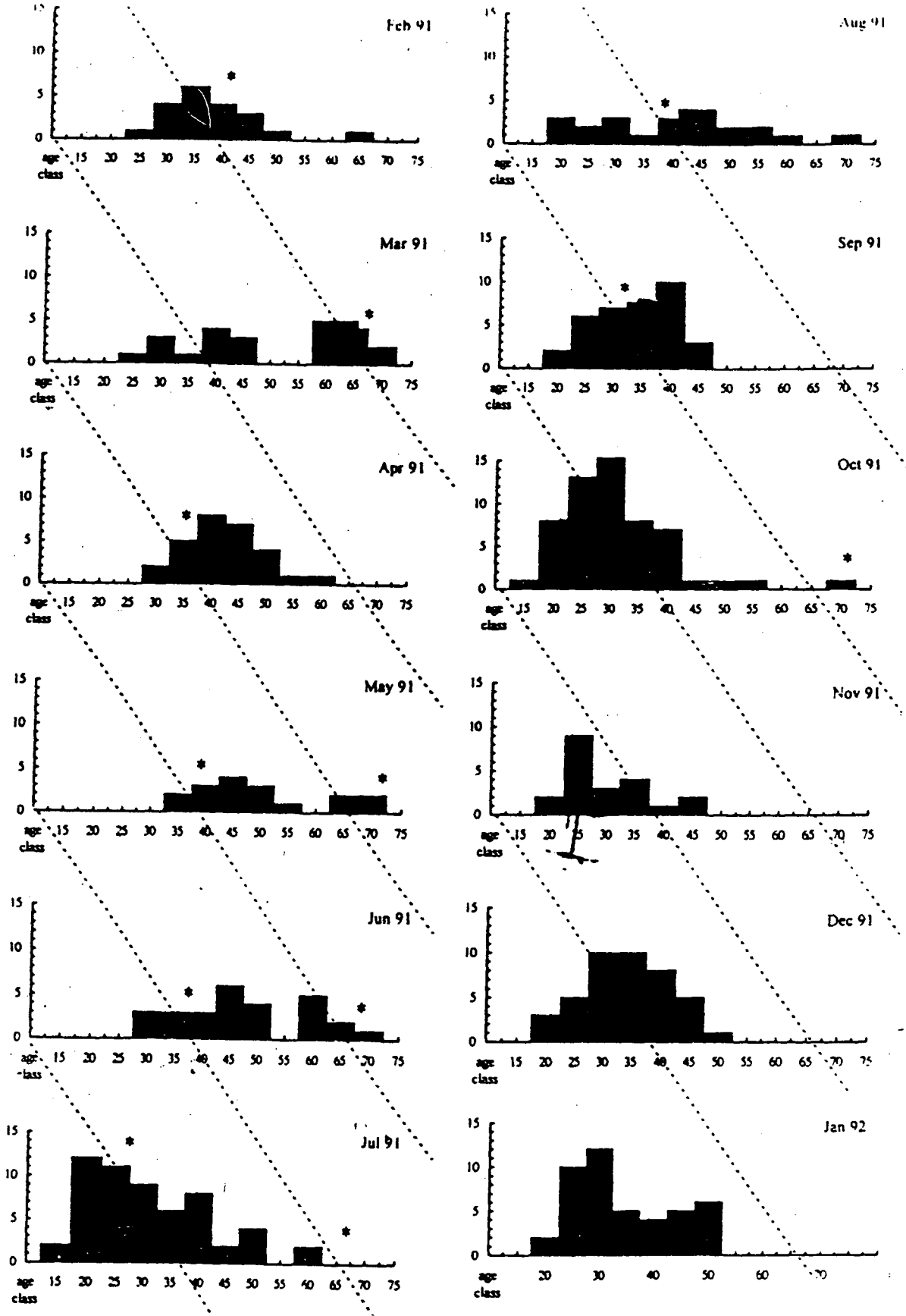
The estimates of instantaneous natural mortality obtained for *L. miodon* in this study were obtained with full recognition of the above outlined attributes. This is the first attempt to obtain estimates of sardine larval mortality making it impossible to compare with other results. Other estimates of sardine mortality are given by Marshall (1987) and Mudenda (1989) for the adult population based on size frequency distributions. They obtained natural mortality estimates of about 0.06 $month^{-1}$ from commercial catch as compared to 2.2 - 4.4 $month^{-1}$ for larval fish obtained in this study. This agrees very well with the notion that instantaneous mortality rate is often very high initially decreasing over time (Campana and Jones 1992). However there are reservations about the accuracy of the adult natural mortality

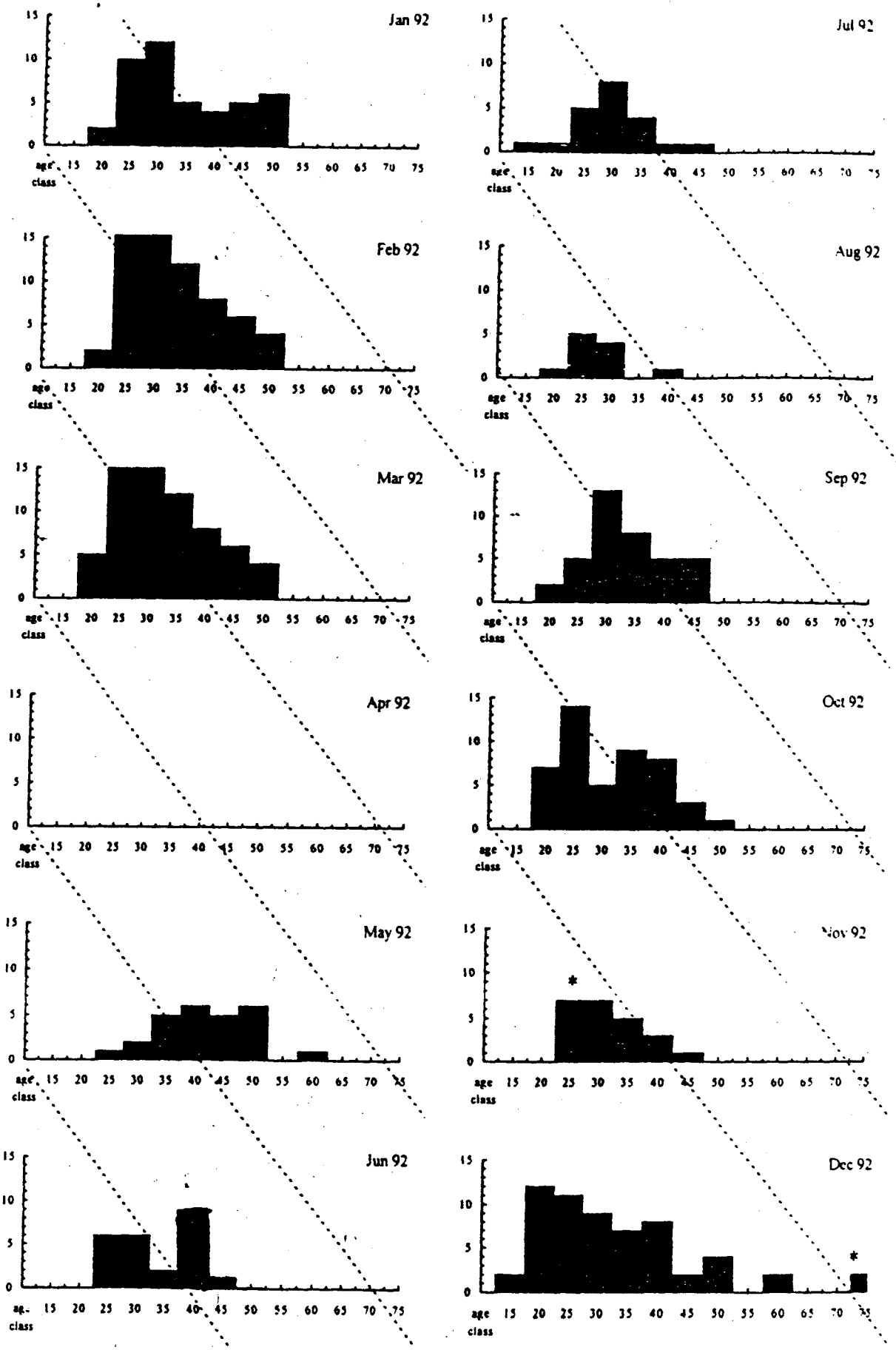
estimates in that doubt has generally been expressed on the use of size frequency distributions as size is not a good indicator of membership to a cohort.

Larval *L. miodon* have been reported to migrate from shallow to deep water as they grow larger (Mtsambiwa 1989, 1990). However the effect of this migration and the use of lights to capture the fish have not yet been properly quantified making it difficult to adjust the estimates accordingly. While it would have been considered adequate for the purpose of the study to assume that emigration balances immigration, in this particular study it would be inappropriate as the depth range being studied is the littoral zone. This implies that all offshore migration commences in this depth range where the smallest fish are found. The effect of light can perhaps be ignored as light has been used in all sampling. However any attempt to obtain estimates of rate of migration offshore cannot ignore the effect of light when sampling as it is bound, depending on the radius of its effects, to attract certain individuals back to the stage they had already gone past hence its use when estimating the correction factor above.

Another factor that could possibly affect the accuracy of the estimates of mortality rates obtained in many studies is net avoidance by some of the larvae during sampling. This is also difficult to quantify in field studies but can be observed in part by the sudden change in the larval size distribution with the sudden disappearance of the oldest larvae as this is what is probably happening in the July 1991 and October 1992 mortality curves. Switching off the underwater light before the ream of the net touched the water surface during sampling possibly allowed some of the oldest and fastest swimming larvae to escape.

Figure 4.6: Showing the monthly age distribution of *L. miodon* larvae caught in the Sibilobilo Lagoon from February 1991 to December 1992. Fish of 30 days of age appear in each sample.




Jan 92
Feb 92
Mar 92
Apr 92
May 92
Jun 92
Jul 92
Aug 92
Sep 92
Oct 92
Nov 92
Dec 92
15
10
5
0
age 15 20 25 30 35 40 45 50 55 60 65 70 75
class

The monthly variations in instantaneous rates of mortality, are a clear indication that the forces at play in either increasing or reducing larval mortality have different intensities. These could be related to a lot of other factors such as the abundance of predators, unfavourable conditions and inadequate food.

The presence of larvae in the littoral zone throughout the period sampled and in all station sampled is an indication of continuous recruitment. However a more intensive study is needed to establish the sufficient basis for recruitment prediction for the fishery. It was also observed from the results that fish of around 30 days old (fully recruited to the gear and sample zone) are always present in the samples (Figure 4.6) and that it was possible to follow certain cohorts from one month to the next. Other cohorts completely disappeared from the age range sampled. The disappearance of some of the cohorts within a month is either a result of fast growth and hence migration to deeper water for the cohort in question or gear avoidance by fish that have disappeared. Future work should attempt to test this hypothesis.

CHAPTER FIVE

Recruitment and selection in the sardine *Limnothrissa miodon* on Lake Kariba.

5.0.0 INTRODUCTION

Recruitment and selection are usually conveniently distinguished when examining how fishing mortality varies with the age of the fish. Recruitment is a characteristic of the fish themselves and is a process whereby the young fish previously inaccessible to the ordinary fishing gear become, as a result of growth, change in behaviour or movement into fishing grounds, potentially vulnerable to fishing. Selection on the other hand is a characteristic of the fishing gear and the way it is operated (Gulland 1983). The process of recruitment and the separation of a species into two groups i.e. the pre-recruits and the post recruits is conceptually important and useful for fisheries management purposes. Most fisheries biology studies have concentrated on the exploited phase of the population because sampling can easily be done from commercial catches whereas the sampling of early life stages necessitates experimental and usually expensive surveys for any data collection. As both processes, recruitment and selection, are largely determined by the size of the fish they are likely to be best studied by length-based methods (Gulland and Rosenberg 1992).

In addition to physical selection, there are other factors that influence fishing mortality increases among fish. For example, the way fishermen use the gear, especially the times and places they fish, can have considerable influence on fishing mortality. Biological aspects of recruitment e.g. migrations into the fishing grounds, schooling in fish of the same size or changes in behaviour can also have an influence or bearing on selection. Thus an estimation

of the combined effects of recruitment and selection can be obtained just by examining the length distributions of the catches. The rising left hand limb of a length-frequency curve provides a good first estimate of the pattern of entry into the fishery. When recruitment is periodic, mean length of samples is smallest in the month of recruitment and largest in the month just before recruitment, but this is unlikely where recruitment is continuous as in the sardines.

5.0.1 Length-at-fist capture concept

The mean size at which fish are first exploited (L_c) greatly influences the yield obtained from a population, and control of the size of first capture is important in the management of many fisheries (Beverton and Holt,1957). This size-at-first capture is determined by the relationship:

$$L_c = S*D$$

where S is the selectivity specific to a species and D the related mesh size (Jones 1976). The values of selectivity S are determined experimentally or estimated from empirically determined relationships between S and fish length/depth ratio or fish length/girth ratio. In single species fisheries the optimal L_c and hence mesh size can be determined from the Beverton and Holt (1956) yield-per-recruit analysis. However this usually requires estimates of instantaneous natural mortality rate (M) and parameters of the von Bertalanffy growth equation (W_∞, the asymptotic weight and K, the growth constant) to calculate the yield obtainable from an arbitrary number of recruits as a function of fishing mortality (F) and size-at-first capture. The mean size-at-first capture resulting in the greatest yield-per-recruit

can then be selected for any value of F which allows the greatest yield to be harvested from whatever number of recruits enter the population. The application or enforcement of a minimum mesh size regulation in a fishery is therefore a measure to maintain the size-at-first capture at a given size.

5.0.2 Selectivity concept

The simplest type of selectivity to estimate is obtained from the bag-type of gear i.e. trawls, seines and lift nets where it is usually assumed that the size composition of the fish entering the mouth of the net is the same as that in the immediate vicinity of the gear (Gulland 1969). Selectivity in such gears therefore becomes a question of escape through the meshes of the fish that have entered the net. The selection curve may extend over a range of sizes of fish implying that as young fish begin to grow into the selection range, they first suffer only a low fishing mortality. Their chances of escaping through the meshes reduce as they grow in size and eventually are too large to escape at all; only then are they exposed to the full fishing mortality rate. In practice, however, it is usual to represent the selection process by a single mean selection length (L_c) and assume that all fish of length less than L_c can escape and that those with a length greater than L_c would be retained by the gear and are thus subject to the full fishing mortality. For selection curves that are symmetrical, or nearly so, the mean selection length L_c will be the length at the midpoint of the curve i.e. the 50% length at which half the fish entering the net escape and half are retained. However if the curve is not symmetrical L_c can be calculated by equating the two areas between the selection curve on the Y-axis and the line $L=L_c$ (Gulland 1983). Fishing mortality is therefore related to the selection curve (ogive) in such a way that when selectivity is zero the fishing mortality must be zero and when selectivity is 1.0 fishing mortality is at its highest level.

Thus fishing mortality, as a function of length, has the same shape as selectivity but it has a different level (Sparre *et al.* 1989).

Selection can be affected by the condition of the fish, the towing speed of the gear or the material and construction of the meshes (light flexible materials (e.g. nylon) give higher selection factors than thicker materials (e.g. manila) (Gulland 1983). Selection may also vary with the size and nature of the catch. In trawl catches fish may find it difficult to escape from a large catch or one with a lot of rubbish, weed etc thus giving a lower selection factor. In this study, selection is used in its broader sense to include the effects of all factors (not just gear selection) which could result in the length-composition of the catches not being identical with that of the population. In this situation, of the sample being different from the population, the total mortality (Z) is clearly not constant over the entire size range in the population. Natural mortality is considered to be higher among the smaller fish and lower among adults while fishing mortality is lower among the smaller fish and higher among the bigger fish.

For *L. miodon*, where recruitment seems continuous, the mean length of fish would be expected to be small in those months of high recruitment and high in months of low recruitment. Depth at which fishing takes place will also be important in determining the mean size of the fish caught. The sardine is known to migrate to the deep water as it grows larger implying that a high mean length will be found in the deep end compared to the shallow end.

5.0.3 Resultant curve concept

Selection can also occur with other processes such as recruitment and a curve similar to the selection curve is obtained when the fish are recruiting to the fished area. This is called the "recruitment curve" (Sparre *et al.* 1989). In practice a curve which combines the effect of both recruitment and selectivity referred to as the "resultant curve" is obtained. Thus the probability that a fish is retained by the gear (trawl, lift-net or seine net) is the product of two probabilities:

a) the probability that the fish is present on the fishing ground i.e. that it has recruited to the fishing ground.

b) the probability that the fish is retained by the meshes once it has entered the net.

However in instances when the meshes are so large that there is no overlap of the recruitment curve with the selection curve, the recruitment element can be ignored so that the "resultant curve" is determined by selection only.

5.1.0 THE LAKE KARIBA SARDINE FISHERY MANAGEMENT

5.1.1 Fishing regulations

Management when the fishery commenced on the Zimbabwean side in 1973 included the enforcement of the following regulations:

a) limitation on entry through licensing. Each licence contains the number of fishing units which are equivalent to the number of lift nets of a specific size, with each lift net being operated from one fishing rig.

b) limitation of fishing gear through the application of a minimum mesh size of

8 mm.

c) limitation of fishing to areas more than 20 m deep.

The limitation on entry is important in control of fishing effort while limitation on both mesh size and fishing areas have a bearing on the biology of the fish. Minimum mesh size is intended to reduce the likelihood of both recruitment and growth overfishing.

Limiting fishing to areas more than 20 metres deep initially was done more to protect the species of riverine origin which inhabit those parts of the lake. Any depth beyond that was also defined at that time as open waters or pelagic. It was later discovered that the sardine spent the early part of its life cycle in these shallow areas, recruiting to the open waters as they grew larger. Fishing was also prohibited within a 2 km radius of all river mouths, again to protect the species that were known to conduct spawning runs up the rivers. A third restriction to fishing areas on the Zimbabwean side resulted from the conflict with tourism. No fishing is allowed within 3 km of a tourist resort area because of the excessive noise made by generators on the fishing boats at night.

While the limitation of entry and fishing gear is common to both the Zambian and Zimbabwean sides of the lake there are variations in their application. The official minimum mesh size in both countries is 8 mm but adherence to this regulation is doubtful due to limited enforcement capacity of the regulation by the authorities. The regulation regarding exclusion from specific areas and depth zones is not yet in force on the Zambian side though they are currently under consideration. As relatively few rigs carry echo sounders it is also difficult to determine whether the regulation which restricts fishing to areas greater than

twenty meters deep is and will be adhered to.

5.1.2 Objectives of study

The purpose of this study therefore is to:

a) investigate recruitment and selection patterns from length frequency distributions

b) investigate the effect of recruits on the mean size of fish in the catches and

c) investigate whether there has been a reduction in mean size over a period of time

d) estimate gear selectivity in the L. Kariba sardine fishery

e) recommend the most effective minimum mesh size depending on whether there has been a decline in mean size due to current exploitation practices in the fishery.

These objectives therefore have a significant practical relevance to the management of the fishery in that the results obtained should enable the current mesh size regulations to be evaluated in terms of their impact upon recruitment to the fishery.

5.2.0 MATERIALS AND METHODS

For the purposes of evaluating the minimum mesh size, samples were collected from the Leisure Bay in the Sanyathi Basin in January 1994 using two fishing vessels. One was a commercial rig belonging to Mafanzou Fisheries mounted with a lift net of 8 mm mesh size while the other was the research vessel R/V Pelican, belonging to the Lake Kariba Fisheries

Research Institute, fitted with a lift net of similar mesh size but with a mosquito gauze inside. The two boats were juxtapositioned with the nets within the same light radius. The two nets were then lowered to the required depth and lights were switched on for one hour before the nets were raised by hydraulic winches on either vessel. Sampling was done along a transect from the inshore to offshore at four sampling stations of 5 m, 10 m, 15 m and 20 m in depth respectively.

Length frequency distributions of samples from both vessels were used to calculate the proportion of the size intervals that was retained by the commercial net. A regression analysis of the proportions on the length intervals was performed to obtain the constants S_1 and S_2 (i.e. the intercept and the slope of the regression respectively) used in subsequent analysis.

5.3.0 DATA ANALYSIS

Since the length frequency data used in this study from the two countries were collected at different times (1982-1988 in Zambia and 1989-1992 in Zimbabwe) and under different management practices or regulation enforcement practices, they were analyzed separately. Although the samples were taken from the same basin (i.e. Sanyathi basin) this separation allowed for comparison. The recruitment and selection processes were also treated separately in the analysis. Any difference in the results would indicate the need to standardize the regulations in the fishery as well as the enforcement of such regulations.

5.3.1 Recruitment

a) To identify the recruitment from length frequency distributions, size intervals/groups

in the samples were converted to catch percentages and plotted on cumulative ogives. These ogives represented the proportions of fish in catch on a cumulative basis expressed as percentages between 0 and 1 with the latter representing 100%. Based on inspection of these ogives, the minimum size fully represented in the samples throughout the years was identified and plotted on histograms of the monthly percentage. These were plotted to investigate the monthly patterns of these minimum sardine size as they entered the fishery. Residuals were also plotted to assess the pattern of scatter around the mean abundance of the incoming recruits.

b) To investigate the influence of the incoming recruits on the mean size of the fish in the catches on a monthly basis, monthly means were plotted for each year and the patterns were compared to the recruitment curves.

c) To assess whether there has been a reduction in mean size over the period, monthly mean lengths from January 1982 to December 1988 for Zambia and from January 1989 to December 1992 for Zimbabwe were calculated from the monthly length-frequency data. Based on these monthly means, annual means were then determined. A regression analysis of the annual mean was performed to estimate the slope that was used to determine whether there had been an increase or decrease in mean length over the period.

5.3.2 Selectivity

The gear selection ogive was described by the mathematical expression which produces the logistic curve as follows:

$$S_L = 1/(1 + \exp(S_1 - S_2 * L)) \quad \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where S_L equals the number of fish of length L in the cod-end, divided by the number of fish of the same length in the cod end and cover in the case of trawl experiments. In this case the number of fish in the "cod-end" came from the commercial rig while those in the "cod-end and cover" came from the experimental rig with a smaller mesh size. S_1 and S_2 are constants from a regression analysis which was done over a length range between zero (0) and full (1) retention excluding those length intervals with no or full retention. S_1 and S_2 represent the intercept and slope respectively while L represents the mid-length.

The selection range was described by the length range from $L_{25\%}$ to $L_{75\%}$ which were symmetrical around the $L_{50\%}$ which are lengths at which 25%, 50% and 75% of the fish are retained in the cod-end. This selection range defines the sharpness of a selection curve i.e. whether selection occurs over a small or wide range. Beverton and Holt (1957) describe "knife-edge" selection curve with a selection range of zero. Sparre *et al.* (1989) contest that knife-edge selection should be considered a hypothetical model which would never describe a real situation. However, knife-edge selection is often used as an approximation to the selection ogive. The $L_{25\%}$, $L_{50\%}$ and $L_{75\%}$ were obtained as follows:

$$L_{25\%} = (S_1 - \ln 3)/S_2 \quad \text{.....(2)}$$

$$L_{50\%} = S_1/S_2 \quad \text{.....(3)}$$

$$L_{75\%} = (S_1 + \ln 3)/S_2 \quad \text{.....(4)}$$

The selection range was then obtained by the relationship:

$$L_{75\%} - L_{25\%} = 2 * \ln 3/S_2 \text{ or}$$

$$L_{75\%} - L_{50\%} = \ln 3/S_2 = L_{50\%} - L_{25\%} \text{ .....(5)}$$

The ultimate aim of these calculations is to obtain the mean selection factor which is the ratio of the length $L_{50\%}$ to the mesh size and is defined as follows:

$$L_{50\%} = \text{S.F.} * \text{(mesh size)}$$

and based on the above relationship, the $L_{50\%}$ of different mesh sizes can be obtained which is a useful way of determining the minimum mesh size appropriate for a fishery.

5.4.0 RESULTS

5.4.1 Recruitment

Figure 5.1 (see Appendix II) shows the monthly cumulative frequency distributions from January 1982 to December 1992. Based on inspection of these ogives it was observed that fish of 41 mm in length constituted the size that consistently seemed to be recruiting into the fishery in both countries. These constituted about 70% of fish in catch which were ≤41 mm and were represented in 90% of the monthly samples. In addition fish of this size constituted up to 45% of the catch during some years of high recruitment (notably from 1986 to 1988). During these years there were high percentages of fish of ≤41 mm in commercial catches for most of the years. For the rest of the period under study, fish of ≤41 mm in length

constituted less than 20% of the fish in the catch. Figure 5.2 (see Appendix III) shows the histograms of the monthly percentage and the residual plots at the 41 mm size. These do not show any particular pattern such as specific peaks in specific months of the year. This is an indication of variable recruitment on monthly basis.

Table 5.1 summarizes the monthly mean lengths of *L miodon* in the commercial catch from January 1982 to December 1992. Figure 5.3 shows the mean monthly sizes of fish in commercial catches for each year which were also observed to fluctuate from month to month. However when these monthly mean lengths were pooled together for the years 1982 to 1992 two peaks with large mean lengths were observed in February and in September (Figure 5.5). This would imply that recruitment is reduced during those months on annual basis.

The monthly means were then superimposed on the recruitment curves to investigate the influence of the recruits on the mean size of fish shown on Figure 5.4 (see Appendix IV). As would be expected, the mean monthly size of fish fluctuated in an opposite direction to the recruitment patterns. Those months that had a high percentage of recruits were marked by a reduction in mean size of fish in the fishery while those months with low recruitment were characterized by an increase in mean size.

Figure 5.6 shows the slopes defined by the regression equation based on year on annual mean. The slopes indicate that there was a 7% decline in mean size from 55 mm to 51 from 1982 to 1988 on the Zambian side and 4% from 57 mm to 55 mm from 1989 to 1992 on the Zimbabwean side. However in the absence of the regression fits (both of which are not

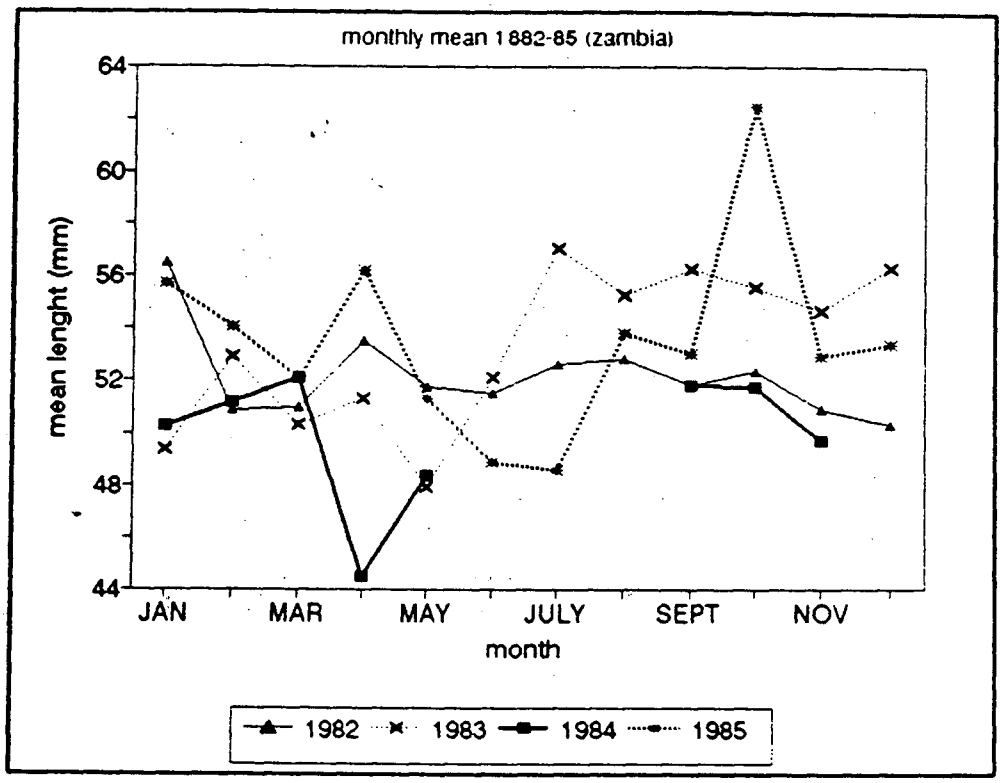
significant with correlation co-efficients r^2 = 0.21 and 0.12 for Zambia and Zimbabwe respectively) it is difficult to reach this conclusion as the annual means also fluctuate from year to year depending on what size groups are dominant in the catches.

Table 5.1: Summarising monthly mean length in millimetres from January 1982 to December 1988 for Zambia and January 1989 to December 1992 for Zimbabwe.

	JAN	FEB	MAR	APRIL	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
1982	56.5	50.87	50.99	53.52	51.79	51.51	52.59	52.79	51.83	52.35	50.89	50.32
1983	49.38	52.88	50.33	51.32	47.91	52.13	57.08	55.28	56.26	55.55	54.65	56.24
1984	50.28	51.16	52.13	44.51	48.4				51.83	51.76	49.75	
1985	55.71	54.07	52.06	56.17	51.34	48.87	48.54	53.82	53.01	62.45	52.94	53.35
1986	48.77	50.44	59.97	50.61	50.99	52.69	51.67	54.7		51.32		
1987			49.48	44.44	44.96	44.46	51.48	46.46	54.14	45.09	45.86	47.76
1988	47.63		46.45	45.64	45.76	49.75	60.59	60.84	61.79	61.32		60.97
1989	55.68	57.4	55.62	55.31	55.12	58.33		62.23	61.22	62.52	64.52	56.9
1990	55.93	63.15	49.93	54.51	62.62	52.36	49.37	52.78		58.23	63.57	
1991		52.16	57.42	51.42	51.92	50.36	53.11	49.52			53.13	54.99
1992		53.51				54.13	58.32	62.75	62.46			53.75
$\bar{x}$	52.49	53.96	52.44	50.75	51.08	51.46	53.64	55.12	56.57	55.62	54.41	54.29
s	3.54	3.81	3.86	4.21	4.84	3.42	3.89	5.10	4.29	5.66	6.10	3.79
UL	56.03	57.77	56.30	54.96	55.92	54.88	57.53	60.22	60.86	61.28	60.51	58.08
LL	48.94	50.15	48.57	46.53	46.25	48.04	49.75	50.01	52.28	49.96	48.32	50.49

UL = Upper limit; LL = Lower limit

Figure 5.3: Showing the monthly mean lengths of fish from January 1982 to December 1988 for Zambia and January 1989 to December 1992 for Zimbabwe.



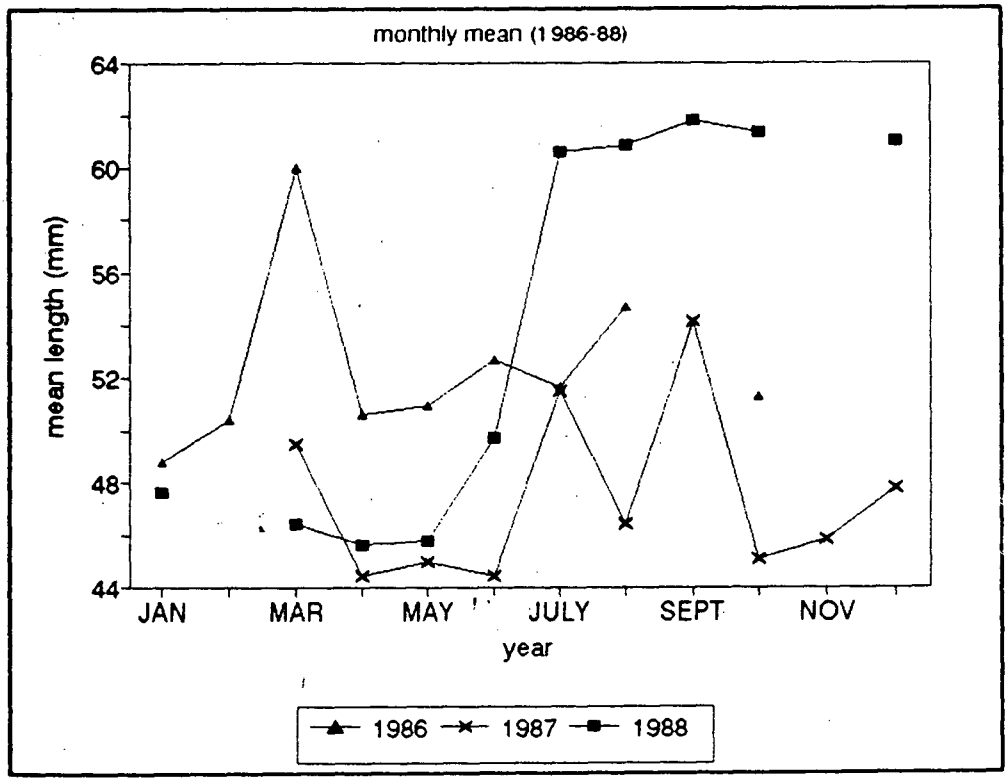


Figure 5.3: continued.

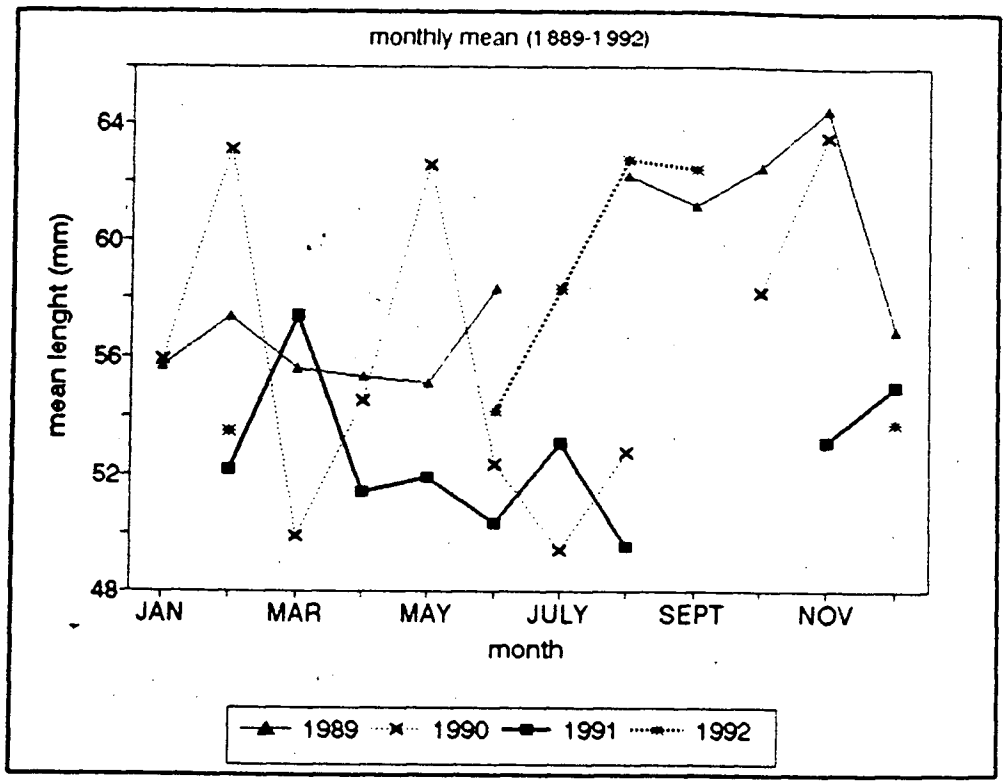


Figure 5.4: Annual monthly mean lengths of *L. miodon* pooled together to show seasonal patterns in recruitment based on mean lengths of fish from 1982 to 1992 when samples were collected from the commercial catch.

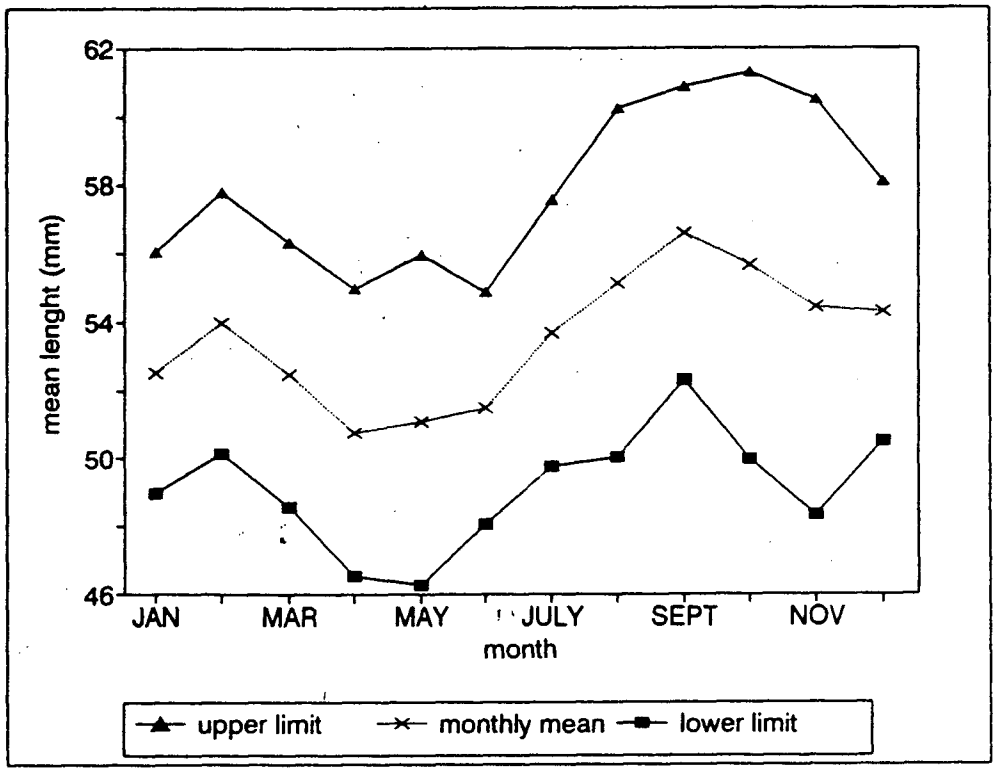
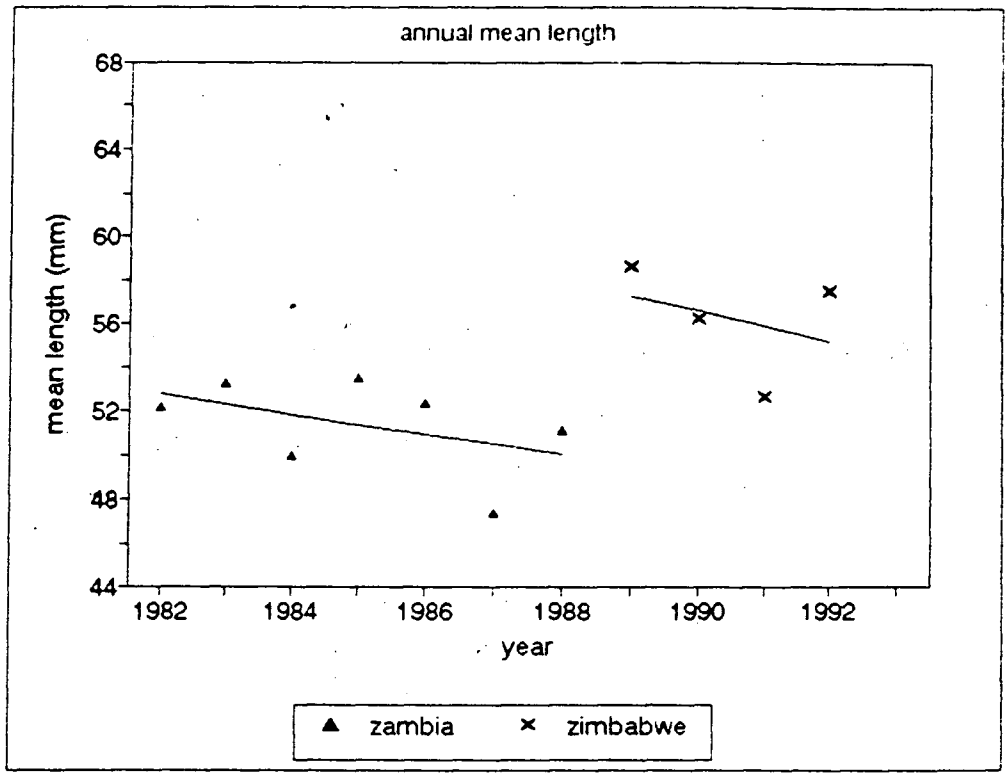


Figure 5.6: Showing the regression slopes that were used to define the degree of reduction of mean size of fish in the commercial catch over the years.



5.4.2: Selectivity

Table 5.2 shows the samples collected fishing at 15 metres from an experimental rig mounted mosquito net fishing next to a commercial rig in the Leisure Bay. Based on these samples the selectivity of the lift net was worked out.

Figure 5.7 shows the selectivity curve that was estimated from the equation:

$$S_L = 1/(1 + \exp(13.7 - 0.63*L)$$

where the figures 13.7 and 0.61 represent S_1 and S_2 which are the intercept and slope of the regression analysis done over the length range between zero (0) and (1) full retention

excluding those length intervals where no or full retention was obtained. The points used in this experiment lie between the length intervals 17-20 mm and 29-32 mm in Table 5.2 below The other intervals between 09-12 mm and 13-16 mm where there was no full retention and between 29-32 mm and 37-40 mm where there was full retention were not used in the regression analysis.

Table 5.4: Summary of size frequencies taken at 15 metres from an experimental rig fishing next to a commercial rig in the Leisure Bay.

Length	Commercial rig	Experimental rig	Total
09-12	0	10	10
13-16	0	26	26
17-20	22	155	177
21-24	170	120	290
25-28	220	11	231
29-32	178	0	178
33-36	60	0	60
37-40	24	0	24

The following results were obtained:

$L_{25\%}$ = (13.7 - ln3/0.63) = 20.0 mm

$L_{50\%}$ = 13.7/0.63 = 21.7 mm

$L_{75\%}$ = (13.7 + ln3/0.63) = 23.5 mm

Selection Range = 2 * ln3/0.63 = 3.5 mm

Selection Factor = 21.7/8 = 2.71

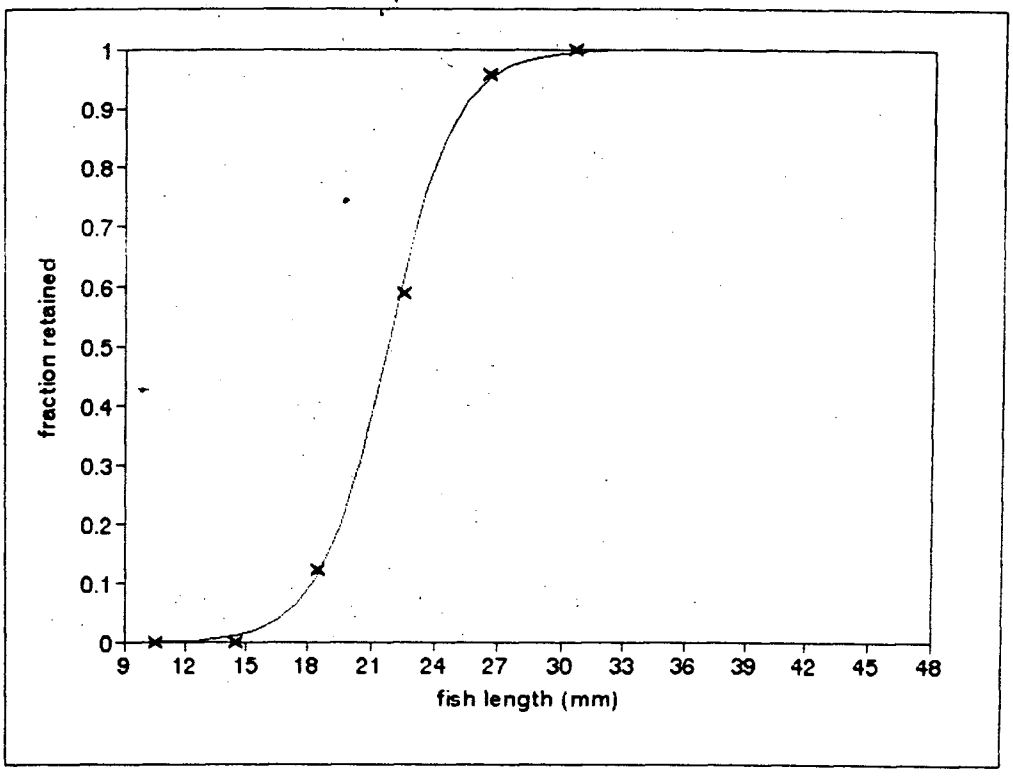


Figure 5.7: Selectivity curve for *L. miodon* estimated from a depth of 15 m by fishing with an experimental net mounted with mosquito net next to a commercial rig with a mesh size of 8 mm.

This implies that when the fish of about 22 mm in length come into contact with the gear 50% will be retained. How does this compare with the 41 mm length at first capture worked out under recruitment above? It means to continue using the same gear other considerations have to be made and these are discussed below.

5.5.0 DISCUSSION

5.5.1 Recruitment

The recruitment pattern, as shown by the results of this analysis, fluctuates from month to month every year without any obvious sequence that could lead to a definition of an annual recruitment pattern. However, in most years around the months of January, May and September (this includes periods immediately before or after these months if the occurrence did not take place during those months themselves), there are pulses of high percentages of recruits. Kenmuir (1983) reports a peak breeding period from September through to March every year which would contribute to the high recruitment around January and probably also for the increased recruitment around May reported in this study. Mudenda (1989) describes two annual breeding peaks following lake turnover in the July/August period and from January to March following the rainy season. The July/August could contribute to the high recruitment around the September period.

The fluctuating percentages of small fish in the catches from month to month are indicative of recruitment variability even on such short time scales. Thus, while spawning seems to take place throughout the year it is difficult to establish from just the length frequency analysis what factors are responsible for the variation in recruitment. Suffice to say that the presence of the incoming recruits throughout the year serves as a basis for assuming continuous spawning albeit at varying levels of intensity. The presence of high percentage of recruits in catches during the 1986 to 1988 period is indicative of a phase of continuous recruitment success during that period as compared to the other years which in the study period are characterized by low average recruitment with only a few months of high recruitment.

The fluctuating mean size in catches is indicative of a changing size structure within the population. As noted above these changes result from a fluctuating recruitment pattern which influences the mean size of fish in the catches. In most years, the month of May is characterized by a low mean size compared to other months of the year.

However when the data were pooled for the ten years, high mean lengths were observed for the months of February and September which would mean that recruitment is reduced during those periods. The mean length is small from April through to June which could be a result of favourable conditions following the rain season with a time lag of about three to four months after the peak of the rainy season in December. The period after that starting from July through to September is characterized by increase in mean size which also implies reduction in recruitment followed by a decrease in mean length from October to December. This latter development could be a result of the lake turnover which released more nutrients in the system three to four months earlier in June/July.

The gradual decline in annual mean size going by the results of the regression above could have resulted from an increase in fishing over the years. Kenmuir (1983) reports of a similar drop in the breeding size from 48 mm in 1973/74 to 40 mm in 1975/76. The fishery had commenced on the Zimbabwean side in 1973. While the fishery commenced much later on the Zambian side, the mean size of fish from 1982 to 1988 is already, on average, lower than the mean size of fish in the catches on the Zimbabwean side from 1989 to 1992. The implications are that the Zambian fishery has targeted a smaller size of fish from the very beginning. Given that, officially, the regulation of a minimum mesh size of 8 mm is operative in both countries and assuming that this is adhered to by the fishermen, the resultant difference in mean size of fish might be a result of fishing at different depths. As

noted above, *L. miodon* migrate to deeper waters as they grow larger, thus if Zambian fishing rigs operate in shallower water than their Zimbabwean counterparts, they would catch a higher proportion of smaller fish which would reduce the mean length of captured fish. This view is further substantiated by the fact that there are virtually no echo sounders on the Zambian side leaving the fishermen to guess the depth at which they operate their rigs. Another factor which may contribute to the tendency of Zambian operators to fish in shallow water is lack of mobility on most of the fishing fleets in Zambia. As a result Zambian operators tend not to tow their vessels far out into the open waters as is the case in Zimbabwe where fishing vessels may travel for several hours to the fishing grounds.

5.5.2 Selectivity

The gear in use has a narrow selection range as can be seen from the sharpness of the selection curve (Figure 5.7). The $L_{50\%}$ of about 22 mm defines the length-at-first capture applicable using a lift net of 8 mm mesh size. Pauly (1982) obtained a length-at-first capture of 20-30 mm generated by a net of 8 mm mesh size for anchovy in the San Miguel Bay, Philippines. While the two nets used are different, (i.e. lift net for Kariba and a trawl net for San Miguel Bay) the lengths at first capture are comparable since body shape of the two clupeids are similar and Gulland (1983) classifies these "bag" type of gear as giving the same type of selectivity.

Another important determinant of the selectivity of the gear is the depth at which the fish were captured. As noted, the sardine migrate from the inshore to the pelagic zone as it grows larger and Mtsambiwa (1989) reports mean sizes of 15, 20, 23 and 32 mm at depths of 1.0, 3.0, 10.0 and 15 metres respectively. Experimental fishing in this study was

conducted in water at 15 metres deep. The influence of light during fishing could have brought together a wide range of sizes within the population at that depth although the extent to which light attracts the fish has not been established. Schooling behaviour of the sardine could be responsible for fish of about the same size occurring together but again attraction by lights could include the smaller sizes depending on the depth radius between their preferred depth and the one being fished. The regulation on depth which stipulates no fishing in areas less than 20 m is appropriate in that it excludes the larval (i.e. fish of 15 mm and less) and most juveniles (i.e. fish of between 16 to 25 mm) from capture by commercial nets.

In summary the study has revealed that *L. miodon* seems to recruit into the fishery at 41 mm as observed from the length frequency samples taken from the commercial catch. According to Kenmuir (1983) the minimum breeding size of fish was 40 mm in 1975/76 and Marshall (1993) puts the size at which the sardine attains maturity in Lake Kariba at 35 mm in length at about 3 months old. The mean size in the catch in this study was 51 mm and 55 mm on the Zambian and Zimbabwean sides respectively which means that by the time they are fully exploited most of the fish would have had the chance to spawn at least once thereby contributing to the future catch. Thus the mesh size in use is inappropriate if it was the only factor controlling the length caught but since the fishery operates in water 20 m deep care should be taken to ensure that the fishery does not move to inshore areas. If the net is allowed to fish in depths less than 20 m where the experiment was carried out a lot of fish of the size about 22 mm will be caught which would lead to recruitment overfishing. To avoid this it would be necessary to increase the mesh size to allow the small fish to escape.

CHAPTER SIX

GENERAL DISCUSSION

6.0.0 INTRODUCTION

Historically, the need to understand the origin of variation in the adult population size of exploited fish species has led to an interest in various aspects of their early life history. This interest in larval fishes and the factors responsible for recruitment variation has increased rapidly in recent years. The initial focus, which was dominated by examination of stock-recruitment relationships, has shifted to understanding the mechanisms underlying recruitment variability, and whether they are driven by environmental variations or biotic interactions.

Gulland (1989) discusses an often-stated justification for research on the early life history of fish, namely, that such work provides short-term forecasts of recruitment, thereby allowing managers to adjust fishing regulations in response to changes in stock size. This utilization of short-term (i.e. annual) predictors of recruitment in the management of fish stocks has recently been challenged by Walters and Collie (1988) and Walters (1989). Bradford (1992) contends that, even if studies of the early stages of marine fish reveal insights into their ecology, the high degree of ecological variation means that it is unclear whether sufficiently accurate forecasts of recruitment will ever be possible from such studies. He suggests that the assertion that year-class strength is fixed in the early larval stages may not be general and, furthermore, under field conditions it is extremely difficult to quantitatively test such a hypothesis. Walters and Collie (1988) contend that, if for no other reason than pure scientific curiosity, fisheries scientists should be concerned with understanding the

physiological, behavioral and ecological linkages through which environmental factors influence recruitment rates and distribution patterns. Research on environmental effects on fish populations is however often justified by its potential economic value for fisheries management if improved predictions of recruitment do actually ensue.

Walters and Collie (1988) review alternative management strategies for dealing with recruitment variability, and suggest what predictions are needed under each strategy and how to obtain these predictions most cheaply and reliably. They also comment on whether existing research approaches are likely to provide the predictive models that are required. To stimulate further debate on these topics they take a deliberately provocative viewpoint, arguing that (i) better prediction is much less important today than better monitoring and feedback strategies and that (ii) even where prediction is needed, existing research approaches are incapable, even in principle, of meeting that need. Laurence (1988) echoes the same sentiments by describing recruitment in fisheries science as a difficult concept which is simultaneously a conundrum, a paradox and an ambiguous term, used on three definitional levels by fisheries scientists. The simplest and most pragmatic use is as a quantitative index of the level of an incoming year class while the second, higher order, usage involves variation in size and timing associated with year-class formation. This second order usage thus refers to a discrete time period when there is a transfer of biomass from the unexploited to the exploited segment of a fishery. All things become relevant to this event and it serves as a focal point for population dynamics. The most complex definition Laurence goes on to say, is that recruitment is a synergism of variable processes which include interactions between fecundity, spawning, growth, mortality/survival, trophic level interchange, and effects of the physical environment which in short is a very complicated

situation. All attempts this far by fishery researchers to understand the mechanistic and functional aspects of recruitment in a general sense have been unsuccessful.

Recruitment variability is therefore seen as some form of response by a population to some variable environmental factors which are very difficult to predict or quantify. The unpredictable nature of recruitment is innate and given the complexities of associated synergisms between the environment and organisms, it seems inconceivable that there could be a common, unifying, or consistent pattern or operational mode on a continuous annual basis. Fisheries science is considered to be a branch of applied ecology such that fisheries sciences are logically included as parts of ecosystems. However ecosystem theory is particularly weak with regard to predicting changes in its components which, of course, is the major goal of fisheries science and a justification for studying recruitment. Laurence (1988) goes on to elaborate that the reason for this weakness is that primary phenomena controlling future species abundance within ecosystems are mainly random and, thus, theoretically unpredictable except within very broad limits. These primary factors which effect recruitment maybe defined as, physical forcing and biological response. Physical forcing is unpredictable as it is influenced to a large extent by climatological-meterological factors. Forecasting of weather patterns is notoriously unreliable and predictions extending beyond 48 hours have little validity. There is no theory or methodology available to predict the weather on any scale more than 24-48 hours in advance. Biological response interact in the short-term as competitive species interaction, or lethal or sublethal physiological response. Ecological systems have not been able to forecast species abundance. Man's influence, which can dominate fisheries systems, is also highly unpredictable due to the range of human responses associated with social, economic, and political factors which defy even

general description, let alone prediction.

Biological response to unpredictable events can only be quantified through measurement of growth and mortality rates, which are virtually synonymous with fish population dynamics. They are the only two major parameters that can be measured, albeit with difficulty, during all life stages and are important in that they represent the degree or expression of population success. They are the end result of the synergy of all the regulatory factors. Growth rates during the first year of life are extremely high , as much as 10-20 % a day for weight and a total periodic change of as much as 5 orders of magnitude during larval stages. Mortality rates are also extremely high during the early life history stages. In addition these rates are also extremely variable among individuals as well as between populations.

6.1.0 Use of early life history (ELH) studies

Moksness (1992) discusses in depth the use of early life history studies, especially based on analysis of otolith microstructure, as a useful tool in recruitment studies to estimate mortality rates, verify or discard hypotheses (such as those put forward by Hjort 1914, Cushing 1972 and Lasker 1975), identify cohorts of larvae and identify which part of the hatching period the recruits originate from and trace their growth history. Such studies can have management implications in that they can provide an insight into the understanding of the spawning stock-recruitment relationships. Moksness (1992) used this technique to separate spring-spawned and autumn-spawned Norwegian herring and to identify from which spawning area autumn spawned recruits originate. Using otolith microstructure Moksness showed that significant differences in the growth rate of herring from different areas in the North Sea which are related to spatial differences in primary and secondary production.

6.2.0 Applicability of ELH studies to L. Kariba sardine fishery

The purpose of this part of the report is to examine the results of recruitment, selection, growth and mortality obtained in this study, and to consider their application to the management of the sardine fishery in Lake Kariba. A primary function of fisheries management is the regulation of the harvest in order to ensure that stocks are not over fished. Walters and Collie (1988) suggest that the best policy involves the use of some feedback relationship between harvest rate and stock size, such that catches are regulated up and down in response to the to natural variability in stock size, to maintain a fairly stable escapement (stock remaining after harvest) each year. While this might be possible with fisheries which operate a Total Allowable Catch (TAC) approach to management it might not be applicable in the case of the sardine fishery on Lake Kariba where the fishing effort (in terms of number of licensed fishing rigs) rather than catch is controlled. Given this situation of not regulating the catch the following approaches are suggested as the possible application of the early life history studies to the management of the sardine fishery on Lake Kariba:

a) the setting up of certain monitoring programmes which would provide some kind of feedback as to how the fish are responding to fishing pressure.

b) setting up programmes that lead to the prediction of recruitment through the use of the Recruitment Forecasting System proposed in Chapter One.

6.3.0 Monitoring Programmes

Since management in the sardine fishery on Lake Kariba implies regulating effort rather than catch as was discussed above, the following monitoring programmes, based mostly on the outcome of this study, are suggested.

6.3.1 Monitoring of the size structure

Monitoring the population through observation of the size frequency distributions of the catch is an important tool which should indicate the response of the fish biologically to the pressure exerted upon it by fishing effort maintained in the fishery. If the reduction in mean size of fish in catch from 1982 to 1992 reported in this study is an indication that sardine stocks in Lake Kariba are under a certain degree of stress due to exploitation then monitoring the size distribution of fish will serve as a means of quantifying the impact of fishing. According to Mudenda (1989) and confirmed in this study, the sardine recruits into the fishery at 41 mm in length while the mean lengths in the catch in Zambia and Zimbabwe stand at 51 mm and 55 mm respectively. As according to Kenmuir (1983) and Marshall (1993) the sardine come into breeding condition at 40 mm and 35 mm respectively, the mean size of captured specimens is well above the minimum breeding size, thus there is no imminent danger of destroying the brood stock at the moment.

6.3.2 Monitoring the depth where fishing takes place.

In this study the selection curve was calculated from a depth of 15 metres which is not very far from the shore for most of the lake. Here the fish population was representative of a wide range of sizes. Any depth less than that (usually close to the shoreline) was dominated mainly by juvenile fish while in areas deeper than 20 metres the population was dominated by adult fish which had fully recruited to the gear because the mean size in the commercial rig was the same as that of my experimental rig, implying a full retention by the gear. Thus a close observance of the no fishing in areas less than 20 metres deep regulation should be maintained. However most fishing grounds on the Zambian side, especially around the Sinazongwe area where Zambia's largest fishing fleet is found, are generally less than 20

metres deep. Enforcement of no fishing in waters less than 20 metres would therefore reduce the fishing ground in Zambian waters tremendously. Consideration based on mean size of fish caught between 15 to 20 metres should be given to allow the Zambians to fish in waters more than 15 metres deep.

In addition to the banning of fishing in shallow water a minimum mesh size of 8 mm should be maintained for all sardine nets. A recent visit to the fishing grounds on the Zambian side of Lake Kariba revealed that mesh sizes as little as 6 mm were sometimes in use. According to the selection curve worked out in this study (see Chapter Five), a minimum mesh size of 6 mm would generate a length at first capture of only 16 mm which represents the late larval/early juvenile stages. This will result in exploitation of the sardine before the size at breeding of 40 mm or 35 mm referred to above.

In order to monitor the mean size in catch throughout the lake a revised system of length frequency data collection has to be put in place to involve the commercial sector. These data can be readily collected from the fishing community along the entire shoreline if efficient collection points can be set up. At present, for logistic purposes, data are being collected from a limited number of sites. By involving fishing companies themselves in the data collection exercise a far more comprehensive and extensive data set can be accumulated which will enable length frequency variation (and also sample collection) over the whole lake to be monitored.

6.3.3 Monitoring increment width in otoliths

Increment width in the otoliths can be monitored as an indicator of cohort strength i.e. a

larval population that generally has wide rings indicates fast growth (Barkman and Bengtson 1987) which in turn implies high survival rates. Examination of otolith microstructure can also be used to identify the important nursery areas. As noted by Moksness (1992) this can be achieved by observing the differences in growth rate from different areas through the examination of otolith microstructure from those respective areas. Also growth rates in Lake Kariba can be compared this way to other lakes in the region, e.g. Cahora Bassa where the sardine invaded by passing through the turbines from Lake Kariba (Kenmuir 1983). Another important use of analysis of otolith microstructure will be to generate estimates of growth and mortality rates at different times for use in simulation models. This information can be useful in advising the operators what to expect during a forthcoming period i.e. whether its expected to be good or bad thereby preparing them for whatever management options to be taken.

6.3.4 Monitoring age-at-recruitment and age-at-first capture

Another important aspect is to monitor the age-at-recruitment and age-at-first capture to ensure that these two moments in the life of the fish are interspaced by an age-at-first spawning so that fish are given a chance to spawn before exposure to full capture by the gear. These three important moments (i.e. age-at-recruitment, age-at-maturity and age-at-first capture) can be easily monitored by examination of otolith microstructure and since the sardine is a short lived species it is possible to age even the adult population by the same technique. However rigorous preparations to enhance the incremental zones are necessary before counting the rings in the adults.

6.3.5 Monitoring larval abundance in the littoral zone

In this study larvae were captured in all areas sampled in the littoral zone leading to the assumption that the entire littoral zone could be one continuous nursery ground for larval sardine. If this conclusion is correct then generally high or low catches of larvae in the littoral zone should indicate whether there is going to be a strong or weak cohort. However this has to be supported by other factors such as wide rings in the otolith which as discussed above is an indicator of fast growth which in turn results in high survival rates.

6.4.0 RECRUITMENT FORECASTING SYSTEM

The shaded areas on Figure 1.0 (Chapter One), the proposed flow diagram of the project seeking to investigate factors responsible for recruitment variability of the sardine in Lake Kariba, were hoped to be the major inputs of the early life history studies to the proposed setting up of a Recruitment Forecasting System. Three major paths to provide the inputs from the early life history studies were as follows:

a) analysis of historical data to investigate recruitment and selection,

b) the use of hydroacoustics to estimate abundances and to validate the light trap sampling programme and

c) the application of the otolith increment technique to estimate growth and mortality rates.

6.4.1 Historical data analysis

Following historical data analysis it was noted that the sardine recruits into the fishery at 41 mm in length while the average size in the fishery stood between 51 mm and 57 mm. Analysis of the size frequency data by Hydro Acoustic Data Acquisition System (HADAS)

following hydroacoustic surveys using the 70 kHz SIMRAD EY-M echosounder at will show abundances of fish $\geq$ 41 mm which would be an indicator of the exploitable stock from which levels of yield canbe established. It should be noted here that according to Kenmuir (1983) and Marshall (1987) the fish mature at about 35-40 mm such that whatever levels of exploitation are chosen, room should be given for a part of the population to still escape for breeding purposes.

6.4.2 Estimation of larval abundances

The use of hydroacoustic methods to estimate larval abundances failed for the reasons given above (see Chapter Two) and therefore a lot more work needs to be done to establish how larval abundances canbe estimated. Three sources of failure were observed and these are:

a) unexplained excessive noise levels which could not have come from the research R/V Pelican as calibration of both the 70 kHz and 200 kHz had been done on the R/V Pelican before the hydroacoustic surveys. The suggestion here is that the source of noise could be linked to the depth at which the surveys were conducted. The calibration was done at Peter's Point close to the dam wall which is the deepest part of the lake but surveys were carried out in the shallow areas. It is possible that the 200 kHz echosounder is suitable for sampling the pelagic zone as the 70 kHz which has produced sound results.

b) the composition of planktonic organisms recorded were difficult to separate into their respective categories. The size distribution from hydroacoustic data acquisition system were different from those of captured larvae using a planktonic net implying that more than just fish had been recorded.

c) surveys undertaken beyond the depth range being studied had similar echogram picture implying that small fish were also found in the deep areas which is not correct as the fish are known to migrate to the deep areas as they grow larger. Thus to get around this problem and that described under (b) above, it would be necessary to establish the composition of the organisms that are being recorded as it is clear that more than just fish are being recorded.

6.4.3 Otolith increment technique

The application of the otolith increment technique to estimate larval growth and mortality rates and the field surveys to validate both spatial and temporal distribution, provided useful results that could be refined and used to describe larval population dynamics in the Recruitment Forecasting System. One of the major areas that need to be refined is the acquisition of the rate of migration from the inshore to offshore. This is crucial to obtain proper estimates of mortality as some fish are lost from a depth range through this ontogenetic migration and yet wrongly classified as having been lost through natural mortality. Another area that needs close examination is to establish what preys on larval *L. miodon*. It was not possible in this study to establish the relationship between the sardine larvae and the other fish species caught together. The idea was that otoliths would be retrieved from stomach contends of the other species if the relationship was predator-prey one. The size of the otolith would also reveal what size of fish were being taken by the predators. However, since no otoliths were recovered from the stomach contends it is still important to establish the predators of the sardine larvae. The other area that would need refining is the daily increment deposition hypothesis. This study only tentatively accepted the

hypothesis based on a very small sample and more samples would be necessary to conclude beyond any shadow of doubt that rings are laid on a daily basis.

6.5.0 CONCLUSIONS

In conclusion this study has in part answered some of the important aspects related to the management of the Lake Kariba sardine fishery. However a lot more work needs to be done to address the numerous questions that have been raised by the study. For example the question of why recruitment variability occurs has not been answered. It has only been suggested that it occurs at some stage before or during the larval phase as there were fluctuations in the catches at those stages. In addition a submission is made that due to unpredictable nature of environmental factors, it is not possible to predict recruitment with certainty. Instead it is further suggested that only inferences from otolith microstructure could provide useful insights into the relationship between the organism and its environment.

The study also elucidates that depth at which fishing takes place rather than the mesh size is more important in the management of the fishery. The larval stages as the adult population, are attracted by light but are effectively separated by habitat preferences which are defined by depth in this instance. The fishery should therefore capitalise on this behavioural pattern and exploit the sardine only in the deep areas where the adults are. This way the fishery can continue to be sustainable. However the mean size has to be monitored closely so that should it fall towards the size-at-first spawning it might be necessary the to increase the mesh size.

Future work should attempt to answer some of the issues which were not answered in this study. Notable among these are:

a) Investigations into the dynamics of eggs and yolk sac larvae to establish if cohort strength is established during these stages. There will also be need to establish from yolk sac larvae when ring deposition starts in the otoliths. Since one of the reasons why these were not captured is associated with the gear used, it would be necessary to investigate what type of gear canbe used for sampling eggs and yolk sac larvae.

b) Investigations into larval densities in littoral zone areas with submerged trees. The gear used for sampling in cleared areas or those areas without submerged trees were inappropriate for studying density levels in areas with submerged trees where a lot more larvae could be found because of the added security provided by this habitat.

c) Continue validation of daily increment deposition rate to unequivocally prove that rings are laid on a daily basis. Because of the difficulties associated with the whole process of capturing and keeping larvae alive and then treating with OTC only a few samples were done in this study so further work building on what was achieved in this study will add validity to the hypothesis that rings are laid on daily basis.

d) Carry out chemical analysis of the otolith to infer the timing of day-to-day environmental changes or changes of physical habitat as suggested by Jones (1992).

e) Investigate the possible ways of rectifying the problems encountered with the hydroacoustic techniques so as to obtain reliable results from that technique.

f) Investigate the rate of migration from the inshore to offshore so as to have a correct value to separate loss of fish from a depth range due to migration vis-a-vis natural mortality.

g) Future studies can also test the hypothesis such as that fast growth results in high

survival. The methods used to keep the Lake Kariba sardine larvae alive in tanks developed in this study could be the starting point of such studies.

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APPENDIX I

Table 1: Length-at-age data from field captured larval specimens of *Limnothrissa miodon* in Lake Kariba. The length is in mm while the age is in days. Age was determined by counting daily growth rings in the otoliths of larval specimens. The terms OTORAD and HATRAD represent the otolith radius and the hatch ring radius respectively. OTORAD was used in the study to establish the relationship between fish length and otolith radius for backcalculation purposes. HATRAD was not used in this study but can be used for cohort identification.

YEAR	MONTH	CODE	LENGTH	AGE	OTORAD	HATRAD
1991	FEBRUARY	1	9	27	46.38	6.78
		2	9	23	40.35	3.56
		3	9	26	45.65	3.92
		4	11	31	57.7	3.91
		5	12	31	56.88	7.46
		6	13	36	52.29	4.62
		7	12	35	57.99	4.27
		8	13	34	67.05	6.41
		9	12	44	65.31	6.4
		10	12	28	52.99	5.79
		11	13	33	70.9	4.89
		12	13	42	76.31	5.71
		13	13	44	76.7	5.33
		14	14	37	61.65	5.69
		15	14	39	72.43	6.77
		16	13	65	73.29	4.98
		17	14	38	62.81	4.99
		18	14	49	75.58	6.06
		19	14	31	76.71	6.06
		20	13	30	64.83	6.77
1991	MARCH	1	10	22	41.28	5.7
		2	11	29	51.09	5
		3	13	34	56.98	6.31
		4	12	26	57.37	5.34
		5	14	37	74.33	4.99
		6	13	45	74.95	6.41
		7	14	28	76.86	7.11
		8	15	41	77.22	6.42
		9	15	70	82.32	7.21
		10	15	62	74.7	9.5
		11	16	64	80.98	7.98
		12	15	39	76.88	7.41
		13	16	42	75	6.97
		14	16	40	75.21	7.11
		15	17	38	76.15	6.38
		16	18	58	77.93	7.61
		18	20	62	80	6.99
		19	21	60	83.11	7.32
		20	20	63	87	7.55
		21	18	60	82	7.34
		22	21	76	84.21	7.63
		23	23	60	81.24	7.35

		24	22	68	82.14	7.13
		25	23	63	84.21	6.97
1991	APRIL	1	12	45	74.68	9.62
		2	14	38	62.81	4.99
		3	13	43	73.09	5.34
		4	14	43	76.38	6.42
		5	14	37	76.86	7.1
		6	13	30	53.91	6.4
		7	13	32	64.81	6.16
		8	15	49	104.28	7.46
		9	15	38	125.11	6.98
		10	15	50	110.15	6.75
		11	15	48	99.13	5.69
		12	15	39	87.33	5.69
		13	16	34	90.98	6.01
		14	16	43	146.21	7.11
		15	16	44	130.63	6.97
		16	16	39	122.31	6.75
		17	16	30	90.77	6.56
		18	16	58	128.54	7.07
		19	16	40	13.79	7.03
		20	16	44	138.54	8.01
		21	16	40	132.07	7.32
		22	16	42	133.55	7.19
		23	15	33	91.52	6.48
		24	15	32	90.88	6.73
		25	17	38	101.34	7.02
		26	17	35	99.75	6.93
		27	17	48	128.52	7.15
		28	17	52	130.11	7.28
1991	MAY	1	13	45	72.77	6.41
		2	14	40	89.38	5.9
		3	15	44	93.13	6.75
		4	15	34	90.66	6.83
		5	15	35	90.31	6.77
		6	16	42	115.17	7.01
		7	16	40	116.51	6.97
		8	17	50	100.21	7.03
		9	17	47	103.11	6.9
		10	17	48	106.87	7.02
		11	18	44	132.21	7.32
		12	18	40	125.26	7.14

		13	18	68	145.33	7.36
		14	18	55	132.87	6.95
		15	18	61	122.13	7.22
		16	18	70	146.66	7.26
		17	18	64	132.76	7.12
1991	JUNE	1	8	29	39.69	5.31
		2	9	29	45.53	6.05
		3	10	41	65.74	7.1
		4	11	35	69.66	7.12
		5	11	36	68.45	6.05
		6	12	35	56.58	5.34
		7	12	44	71.76	6.41
		8	14	46	76.4	5.69
		9	15	44	78.11	6.33
		10	16	43	76.62	5.99
		11	16	36	70	6.65
		12	15	34	74.82	6.55
		13	16	30	77.11	7.1
		14	16	42	98.44	7.41
		15	16	57	133.86	7.09
		16	15	36	73.11	6.79
		17	17	47	98.75	7.01
		18	17	50	112.45	7.03
		19	17	48	117.12	7.03
		20	17	44	121.01	6.99
		21	18	60	135.77	7.13
		22	19	67	142.02	7.09
		23	19	59	136.07	7.17
		24	19	63	139.22	8.03
		25	18	57	133.56	7.13
		26	18	62	138.43	7.32
		27	19	59	139.02	7.08
1991	JULY	1	8	29	38.58	3.55
		2	8	29	33.28	3.56
		3	8	29	46.03	3.92
		4	8	27	40.54	5.33
		5	7	25	24.15	4.28
		6	7	20	22.39	5.08
		7	8	16	27.07	4.27
		8	8	22	25.08	4.98
		9	8	20	29.75	4.98
		10	8	22	36.35	4.25
		11	8	23	34.7	4.51

12	8	20	27.76	4.98
13	8	20	20.65	4.62
14	8	14	33.95	4.97
15	7	21	29.32	4.98
16	8	18	35.9	5.33
17	8	25	38.7	6.4
18	8	22	23.36	5.7
19	7	17	27.25	5.34
20	6	19	27.45	6.75
21	8	17	29.32	4.66
22	6	18	35.9	5.92
23	9	23	41.86	4.98
24	10	23	46.53	5.34
25	10	22	48.28	6.4
26	10	22	40.48	6.04
27	10	30	33.67	6.04
28	10	20	43.34	5.69
29	10	26	66	7.48
30	9	32	46.03	6.04
31	11	27	60.07	4.98
32	11	27	48.08	5.7
33	12	25	74.8	7.12
34	13	32	76.78	6.04
35	13	35	28.14	4.62
36	13	15	65.86	6.06
37	13	33	65.8	7.13
39	13	41	71.44	6.04
40	13	30	57.25	6.05
41	13	36	69.15	5.69
42	13	48	76.74	4.98
43	14	39	74.22	6.42
44	14	46	76.4	5.69
45	14	35	71.03	6.41
46	14	40	89.38	5.9
47	15	49	105.19	7.46
48	15	38	123.68	6.75
49	16	34	116.89	6.73
50	16	46	125.13	7.15
51	16	44	119.97	6.93
52	17	37	131.11	7.21
53	18	78	153.13	7.57
54	17	36	115.81	6.98
55	17	36	118	6.77

		56	16	58	121.01	7.23
		57	16	40	111.13	6.93
		58	18	60	138.23	7.54
1991	AUGUST	1	7	19	29.93	4.99
		2	8	25	35.88	4.62
		3	8	20	32.78	5.33
		4	9	19	29.17	5.07
		5	10	24	45.22	5.69
		6	11	31	55.79	5.33
		7	11	29	49.9	5.16
		8	11	28	52.93	5.34
		9	12	28	45.37	5.7
		10	12	36	62.86	6.4
		11	13	48	77.3	6.42
		12	14	38	72.43	6.77
		13	14	41	76.96	6.05
		14	15	50	90.99	6.75
		15	15	44	75.13	6.44
		16	16	36	70.32	6.37
		17	17	67	138.33	7.21
		18	17	52	121.42	6.99
		19	17	45	123.37	7.27
		20	17	36	90.31	6.89
		21	18	55	126.11	6.97
		22	18	44	123.33	6.95
		23	18	59	124.79	7.12
		24	18	76	143.12	7.43
1991	SEPTEMBER	1	8	28	46.9	6.4
		2	8	231	32.78	6.04
		3	8	19	31.85	5.34
		4	8	26	41.47	6.4
		5	9	20	40.38	6.04
		6	10	37	63.67	6.41
		7	10	23	47.94	6.77
		8	10	38	65.81	6.05
		9	9	22	38.31	5.69
		10	10	27	48.28	7.46
		11	10	35	55.11	6.05
		12	11	39	75.02	7.14
		13	11	26	54.43	5.35
		14	11	23	44.53	5.69
		15	11	23	36.55	5.33
		16	11	25	45.81	5.69

		17	12	30	55.68	5.69
		18	12	42	74.79	6.06
		19	13	30	71.85	6.42
		20	13	35	72.24	6.12
		21	13	38	75.93	5.69
		22	14	35	77.14	6.58
		23	14	39	74.22	6.42
		24	14	35	71.03	6.41
		25	14	38	62.81	4.99
		26	14	37	61.65	5.69
		27	15	44	101.01	6.78
		28	15	35	75.33	6.71
		29	15	37	83.24	6.68
		30	15	28	70.02	5.99
		31	15	34	76.67	6.03
		32	15	38	80.99	6.79
		33	15	44	113.13	6.98
		34	15	39	93.27	6.79
		35	15	32	66.66	6.63
		36	15	35	73.79	6.73
1991	OCTOBER	1	9	24	37.71	4.98
		2	9	17	28.86	4.63
		3	8	18	28.03	5.07
		4	10	28	46.62	7.12
		5	9	31	46.09	4.63
		6	10	30	49.7	5.33
		7	10	28	47.49	3.2
		8	10	37	76.47	7.11
		9	10	23	41.83	4.99
		10	10	29	46.98	5.68
		11	10	25	44.3	6.04
		12	10	27	39.44	4.64
		13	10	27	43.04	4.63
		14	10	20	43.85	5.71
		15	10	26	52.41	5.69
		16	11	27	53.71	5.33
		17	11	33	57.16	6.04
		18	11	32	53.66	5.69
		19	11	29	52.71	4.98
		20	11	30	48.73	4.56
		21	12	29	52.85	4.96
		22	13	34	56.98	6.31
		23	12	26	57.37	5.43

	24	13	35	60.78	7.82
	25	13	26	76.88	5.69
	26	13	40	76.71	6.77
	27	12	39	76.05	6.04
	28	13	40	76.42	6.76
	29	14	37	76.86	7.1
	30	14	35	71.03	6.41
	31	15	35	76.88	6.79
	32	16	44	83.11	7.01
	33	16	39	82.87	6.99
	34	17	35	80.01	6.85
	35	17	38	83.22	7.03
	36	18	55	101.25	6.99
	37	17	48	94.03	6.77
	38	18	68	120.36	7.14
1991 NOVEMBER	1	7	22	29.72	4.62
	2	7	21	25.18	3.91
	3	8	22	35.71	6.4
	4	8	24	33.87	4.64
	5	8	24	37.07	4.98
	6	8	19	25.63	4.63
	7	8	20	29.91	4.27
	8	9	22	37.22	5.34
	9	10	21	35.71	4.27
	10	9	23	37.82	4.62
	11	9	23	37.81	5.69
	12	11	31	56.34	5.69
	13	12	41	62.8	5.69
	14	12	32	63.78	6.05
	15	11	27	51.27	5.34
	16	12	31	63.75	6.41
	17	12	27	59.28	5.69
	18	13	41	75.91	5.38
	19	13	34	75.64	6.4
	20	13	30	72.71	6.77
	21	15	38	123.68	6.75
1991 DECEMBER	1	6	16	35.93	5.92
	2	7	22	30.21	5.33
	3	8	21	29.05	4.99
	4	8	19	31.02	4.98
	5	8	28	38.41	6.4
	6	8	17	22.51	4.62
	7	8	22	27.25	5.69

		8	9	27	37.42	6.04
		9	10	37	71.51	6.77
		10	10	38	76.6	6.77
		11	9	26	44.56	4.86
		12	9	30	46.93	5.78
		13	10	45	66.73	6.78
		14	10	26	42.05	6.16
		15	9	31	51.06	5.57
		16	10	30	51.94	6.05
		17	10	32	47.19	6.75
		18	9	33	46.18	5.69
		19	9	25	38.21	4.98
		20	11	36	69.52	7.31
		21	11	35	62.77	6.4
		22	11	28	62.17	5.34
		23	11	38	68.6	6.23
		24	11	33	77.55	6.76
		25	11	26	56.02	6.76
		26	11	22	53.01	5.69
		27	11	43	70.77	6.41
		28	11	36	63.41	7.12
		29	11	40	68.75	6.4
		30	11	35	60.46	6.41
		31	11	31	47.15	5.69
		32	11	39	74.41	5.7
		33	12	27	45.44	5.7
		34	12	34	57.95	6.06
		35	13	34	5154	6.04
		36	13	45	76.76	6.18
		37	12	41	76.8	5.71
		38	12	48	74.49	5.34
		39	14	28	76.19	6.4
		40	14	35	75.02	6.4
		41	15	38	76.33	5.69
		42	15	41	77.22	6.49
1992	JANUARY	1	6	17	27.45	6.67
		2	6	16	35.59	5.99
		3	7	18	29.99	4.98
		4	7	22	30.21	5.33
		5	8	23	30.61	4.96
		6	8	26	43.36	5.33
		7	9	24	35.35	5.33
		8	9	27	42.95	4.79

	9	9	24	39.59	5.69
	10	9	25	39.49	5.33
	11	9	39	63.84	5.89
	12	9	32	50.07	6.06
	13	8	29	50.45	6.4
	14	8	29	37.91	5.33
	15	8	24	38.5	5.33
	16	10	43	76.6	6.41
	17	10	27	49.46	5.33
	18	10	29	41.88	6.06
	19	10	32	51.44	6.04
	20	10	25	49.86	5.93
	21	10	28	43.74	4.77
	22	10	25	47.17	4.98
	23	10	28	40.68	5.54
	24	10	25	38.31	4.27
	25	10	30	49.66	5.33
	26	10	27	43.05	4.62
	27	10	32	48.28	5
	28	10	31	50.45	5.33
	29	10	25	41.37	4.98
	30	10	29	50.6	5.34
	31	10	29	47.49	4.98
	32	10	35	59.83	5.69
	33	11	38	56.14	5.35
	34	11	48	74.44	5.34
	35	11	43	73.78	5.7
	36	11	48	76.9	5.69
	37	12	41	76.64	4.28
	38	12	46	75.86	5.34
	39	12	38	59.36	5.84
	40	12	39	71.91	6.76
	41	12	43	68.15	5.7
	42	13	46	70.02	5.69
	43	13	44	76.49	6.39
	44	14	46	76.4	5.69
	45	15	50	90.99	6.75
1992 FEBRUARY	1	7	22	29.72	4.62
	2	7	20	24.15	4.28
	3	7	16	22.39	5.09
	4	8	25	40.54	5.33
	5	9	25	35.3	5.34
	6	9	24	40.84	5.33

7	9	26	46.49	5.34
8	9	25	40.67	6.05
9	9	23	39.2	4.98
10	10	28	39.08	4.98
11	10	25	39.83	4.62
12	10	21	33.17	5.69
13	10	30	45.02	5.33
14	9	23	36.83	4.62
15	9	21	33.19	5.33
16	10	31	41.28	6.41
17	10	25	44.72	4.27
18	10	25	47.16	4.62
19	10	25	45.43	5.33
20	10	28	37.65	4.99
21	10	25	41.23	4.98
22	10	30	50.23	4.98
23	10	26	45.18	5.33
24	10	29	40.53	4.98
25	10	24	44.89	5.35
26	10	25	42.02	5.44
27	11	26	43.67	5.33
28	11	35	57.95	5.33
29	11	31	46.52	4.63
30	11	35	52.63	4.99
31	11	43	71.7	4.28
32	11	28	44.21	4.99
33	11	29	50.35	6.04
34	11	27	46.49	5.67
35	11	28	46.8	5.71
36	11	29	53.4	6.76
37	11	27	38.4	5.69
38	11	31	48.27	6.04
39	11	29	53.69	5.4
40	12	34	62.04	4.98
41	12	28	53.55	6.05
42	12	41	47.51	4.63
43	12	34	66.2	6.41
44	12	35	73.47	6.77
45	12	27	66.03	6.41
46	12	34	75.6	6.4
47	13	46	75.02	5.69
48	13	45	76.76	6.18
49	13	39	76.7	7.11

		50	13	42	76.26	7.12
		51	13	39	64.11	6.4
		52	13	43	64.42	5.7
		53	13	41	67.58	6.4
		54	13	36	61.01	7.11
		55	14	40	89.38	5.9
		56	14	38	62.81	4.99
		57	14	49	75.58	6.06
		58	14	37	62.65	5.69
		59	15	35	63.11	5.09
		60	15	34	62.63	5.76
		61	15	34	62.12	6.01
		62	16	36	66.22	5.98
		63	17	36	66.94	6.08
		64	17	48	100	7.01
		65	17	50	103.62	7.12
1992	MARCH	1	7	16	22.39	5.08
		2	7	19	29.93	4.99
		3	7	17	21.54	4.28
		4	8	22	30.82	4.98
		5	9	22	36.93	4.27
		6	9	25	36.99	4.99
		7	9	26	39.72	5.34
		8	9	25	37.81	5.33
		9	9	24	37.41	4.99
		10	9	24	36.48	4.27
		11	9	25	42.98	4.62
		12	9	19	25.87	5.69
		13	8	25	35.9	5.33
		14	9	20	30.5	4.62
		15	9	21	33.19	5.33
		16	10	31	41.28	6.41
		17	10	25	44.72	4.27
		18	10	25	47.16	4.62
		19	10	25	45.43	5.33
		20	10	28	37.65	4.99
		21	10	25	41.23	4.98
		22	10	30	50.23	4.98
		23	10	26	45.18	5.33
		24	10	29	40.53	4.98
		25	10	24	44.89	5.35
		26	10	25	42.02	5.44
		27	11	26	43.67	5.33

	28	11	35	57.95	5.33
	29	11	31	46.52	4.63
	30	11	35	52.63	4.99
	31	11	43	71.7	4.28
	32	11	28	44.21	4.99
	33	11	29	50.35	6.04
	34	11	27	46.49	5.67
	35	11	28	46.8	5.71
	36	11	29	53.4	6.76
	37	11	27	38.4	5.69
	38	11	31	48.27	6.04
	39	11	29	53.69	5.4
	40	12	34	62.04	4.98
	41	12	28	53.55	6.05
	42	12	41	47.51	4.63
	43	12	34	66.2	6.41
	44	12	35	73.47	6.77
	45	12	27	66.03	6.41
	46	12	34	75.6	6.4
	47	13	46	75.02	5.69
	48	13	45	76.76	6.18
	49	13	39	76.7	7.11
	50	13	42	76.26	7.12
	51	13	39	64.11	6.4
	52	13	43	64.42	5.7
	53	13	41	67.58	6.4
	54	13	36	61.01	7.11
	55	14	40	89.38	5.9
	56	14	38	62.81	4.99
	57	14	49	75.58	6.06
	58	14	37	62.65	5.69
	59	15	35	63.11	5.09
	60	15	34	62.63	5.76
	61	15	34	62.12	6.01
	62	16	36	66.22	5.98
	63	17	36	66.94	6.08
	64	17	48	100	6.76
	65	17	50	103.62	6.04
1992 MAY	1	10	30	56.98	6.06
	2	11	36	74.63	6.6
	3	12	31	56.88	7.46
	4	12	22	69.35	9.96
	5	12	30	48.73	4.56

		6	12	32	50.64	5.34
		7	13	36	52.29	4.62
		8	13	34	67.05	6.4
		9	13	33	70.9	4.89
		10	13	42	76.31	5.71
		11	14	38	62.81	4.99
		12	14	49	75.58	6.06
		13	13	41	68.19	5.34
		14	13	44	76.7	5.33
		15	13	43	73.09	5.34
		16	14	37	61.65	5.69
		17	13	45	73.29	4.98
		18	14	47	74.33	4.99
		19	14	48	76.86	7.11
		20	13	35	60.78	7.82
		21	15	36	70.28	5.76
		22	15	56	96.44	6.85
		23	15	49	97.89	7.12
		24	15	50	102	7.31
		25	15	48	93.99	6.44
		26	15	38	76.33	5.69
1992	JUNE	1	8	28	38.41	6.4
		2	8	28	46.9	6.4
		3	8	26	41.47	6.4
		4	9	25	42.65	6.75
		5	10	24	44.53	6.75
		6	10	23	44.23	4.98
		7	9	23	36.83	4.98
		8	10	26	41.97	4.9
		9	10	25	47.29	4.98
		10	11	40	76.49	6.4
		11	11	24	49.27	6.4
		12	11	38	72.71	5.33
		13	11	38	74.16	6.4
		14	11	34	71.18	6.4
		15	11	34	76.8	6.46
		16	11	38	77	5.7
		17	12	28	58.34	6.41
		18	12	30	67.38	6.41
		19	12	42	76.86	5.7
		20	12	39	76.05	6.04
		21	12	39	74.41	6.41
		22	13	39	76.71	6.77

	23	13	40	76.42	6.76
	24	14	40	76.86	7.1
1992 JULY	1	6	17	28	6.75
	2	6	15	26.99	6.47
	3	8	22	35.71	6.41
	4	8	26	39.38	5.44
	5	9	32	55.5	4.63
	6	9	37	65.12	5.7
	7	10	26	38.43	6.41
	8	10	28	42.84	6.4
	9	10	27	46.35	4.98
	10	10	22	44.83	6.75
	11	10	25	42.02	5.44
	12	10	22	41.8	5.7
	13	10	25	46.13	5.33
	14	11	32	54.79	4.62
	15	11	26	42.38	5.34
	16	11	27	54.09	4.98
	17	12	33	76.09	7.47
	18	12	42	78.69	4.84
	19	12	33	71.59	6.76
	20	12	26	45	6.04
	21	13	28	65.86	6.06
1992 AUGUST	1	7	19	27.25	5.34
	2	7	22	32.21	5.33
	3	8	29	39.69	5.31
	4	8	26	43.36	5.33
	5	8	23	30.61	4.96
	6	9	24	35.35	5.33
	7	9	27	42.95	4.79
	8	9	24	39.59	5.69
	9	10	37	52.63	6.06
	10	10	25	40.18	5.33
	11	11	26	46.01	5.69
1992 SEPTEMBER	1	7	19	23.99	4.27
	2	7	20	25.08	4.17
	3	8	22	29.73	4.62
	4	9	24	32.48	4.27
	5	9	25	33.24	4.98
	6	9	26	38.5	4.98
	7	9	23	36.63	3.55
	8	8	29	39.58	3.55
	9	9	27	46.38	6.78

		10	8	29	33.28	3.56
		11	10	41	64.34	6.06
		12	10	36	58.99	5.7
		13	10	34	52.4	3.92
		14	10	28	49.1	4.98
		15	10	34	43.38	4.27
		16	10	37	47.73	4.56
		17	10	28	46.62	7.12
		18	10	30	46.95	5.35
		19	11	30	48.73	4.56
		20	11	30	54.06	5.69
		21	11	28	51.26	6.76
		22	11	26	44.85	5.34
		23	11	34	62.9	5.5
		24	12	33	71.59	6.76
		25	12	26	45	6.04
		26	12	43	72.27	5.35
		27	12	39	74.41	6.41
		28	12	41	74.23	6.76
		29	11	35	64.03	5.69
		30	12	41	70.48	7.13
		31	12	25	52.61	6.42
		32	12	32	75.77	4.84
		33	13	30	72.71	6.77
		34	13	34	75.64	6.4
		35	14	38	76.85	7.1
		36	14	35	77.14	6.58
		37	14	39	74.2	6.42
		38	15	41	77.22	6.42
1992	OCTOBER	1	7	21	25.18	3.91
		2	7	21	31.9	4.63
		3	7	22	29.72	4.62
		4	7	20	24.15	4.28
		5	7	16	22.39	5.08
		6	7	19	29.93	4.99
		7	7	17	21.54	4.28
		8	7	18	29.32	4.98
		9	9	21	37.67	5.7
		10	9	22	38.5	5.7
		11	9	24	39.1	5.33
		12	9	22	37	6.06
		13	8	22	38.7	6.4
		14	8	17	23.36	5.7

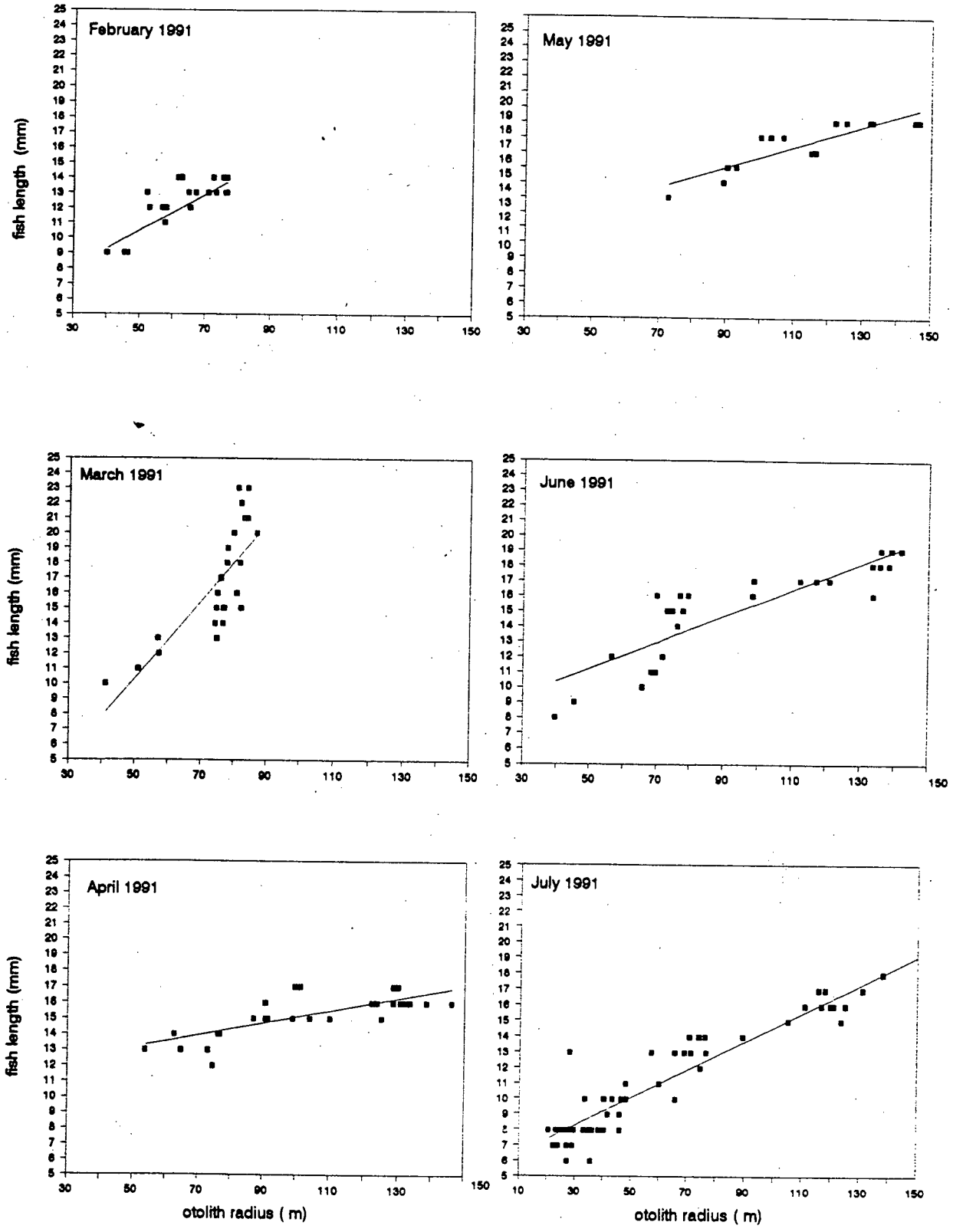
	15	8	18	29.32	4.66
	16	8	18	29.03	5.07
	17	8	21	29.05	4.99
	18	9	23	41.86	4.98
	19	9	22	40.38	5.69
	20	9	27	54.23	6.07
	21	9	29	51.37	5.69
	22	10	44	70.15	5.29
	23	10	33	55.94	6.41
	24	10	32	47.79	4.99
	25	10	31	56.97	7.11
	26	11	37	66.93	7.12
	27	11	25	52.69	6.06
	28	11	36	72.44	6.5
	29	11	40	72.58	6.05
	30	11	37	68.15	6.41
	31	11	30	51.21	5.69
	32	11	43	69.05	6.77
	33	11	39	72.79	6.16
	34	11	25	41.01	4.99
	35	11	48	52.33	6.04
	36	11	31	59.11	6.37
	37	11	31	56.62	6.31
	38	12	34	69.45	5.69
	39	12	35	73.34	6.78
	40	12	32	75.77	4.84
	41	12	25	52.61	6.42
	42	12	41	70.48	7.13
	43	12	36	62.98	7.13
	44	12	38	77.2	5.69
	45	13	34	75.64	6.4
	46	14	37	76.86	7.1
	47	15	30	72.71	6.77
1992 NOVEMBER	1	8	22	27.25	5.69
	2	8	29	39.69	5.31
	3	8	23	30.61	4.96
	4	10	37	52.63	6.06
	5	10	25	40.18	5.33
	6	10	34	67.9	6.36
	7	10	22	45.81	5.33
	8	10	29	42.05	4.9
	9	9	24	35.35	5.33
	10	9	27	42.95	4.79

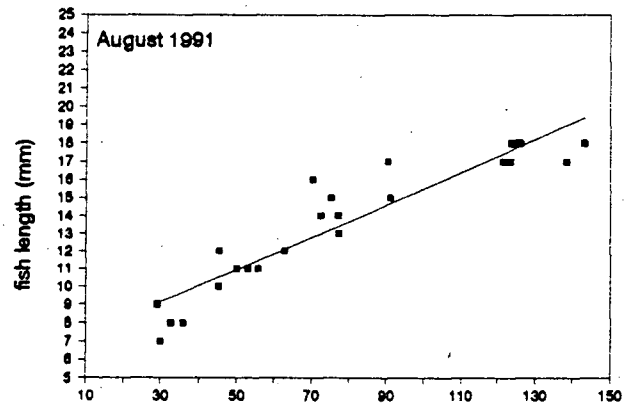
	11	9	24	39.59	5.69
	12	10	29	43.44	5.33
	13	9	25	39.49	5.33
	14	9	39	63.84	5.89
	15	11	34	50.35	6.4
	16	11	32	52.13	5.69
	17	11	40	71.25	7.46
	18	12	43	73.26	6.33
	19	12	35	56.58	5.43
	20	12	28	61.21	6.04
	21	13	34	51.54	6.04
	22	13	30	57.25	6.05
	23	11	28	42.35	6.04
1992 DECEMBER	1	8	29	38.58	3.55
	2	8	29	33.28	3.56
	3	8	27	46.03	3.92
	4	8	25	40.54	5.33
	5	7	20	24.15	4.28
	6	7	16	22.39	5.08
	7	8	22	27.07	4.27
	8	8	20	25.08	4.98
	9	8	22	29.75	4.98
	10	8	23	36.35	4.25
	11	8	20	34.7	4.51
	12	8	20	27.76	4.98
	13	8	14	20.65	4.62
	14	8	21	33.95	4.97
	15	7	18	29.32	4.98
	16	8	25	35.9	5.33
	17	8	22	38.7	6.4
	18	8	17	23.36	5.7
	19	7	19	27.25	5.34
	20	6	17	27.45	6.75
	21	8	18	29.32	4.66
	22	6	16	35.9	5.92
	23	9	23	41.86	4.98
	24	10	22	46.53	5.34
	25	10	22	48.28	6.4
	26	10	30	40.48	6.04
	27	10	20	33.67	6.04
	28	10	26	43.34	5.69
	29	10	32	66	7.48
	30	9	27	46.03	6.04

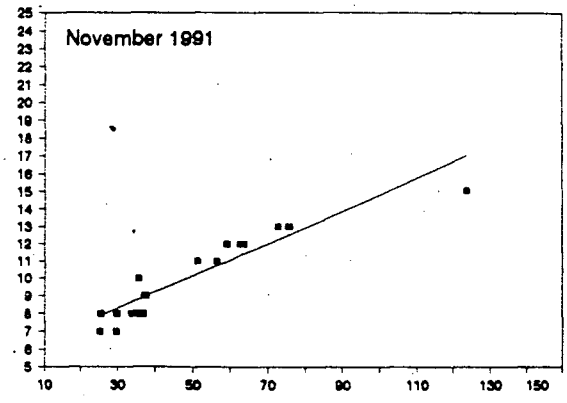
31	11	27	60.07	4.98
32	11	25	48.08	5.7
33	12	32	74.8	7.12
34	13	35	76.78	6.04
35	13	15	28.14	4.62
36	13	28	65.86	6.06
37	13	33	65.8	7.13
38	13	34	64.9	6.9
39	13	41	71.44	6.04
40	13	30	57.25	6.05
41	13	36	69.15	5.69
42	13	48	76.74	4.98
43	14	39	74.22	6.42
44	14	46	76.4	5.69
45	14	35	71.03	6.41
46	14	40	89.38	5.9
47	15	49	105.19	7.46
48	15	38	123.68	6.75
49	16	34	116.89	6.73
50	16	46	125.13	7.15
51	16	44	119.97	6.93
52	17	37	131.11	7.21
53	18	78	153.13	7.57
54	17	36	115.81	6.98
55	17	36	118	6.77
56	16	58	121.01	7.23
57	16	40	111.13	6.93
58	18	60	138.23	7.54
59	19	76	159.01	7.45

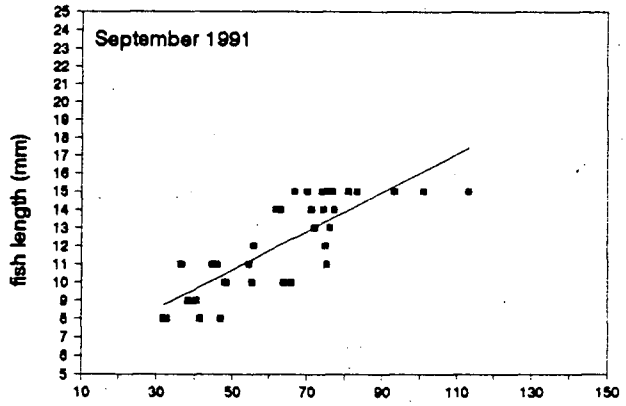
APPENDIX II

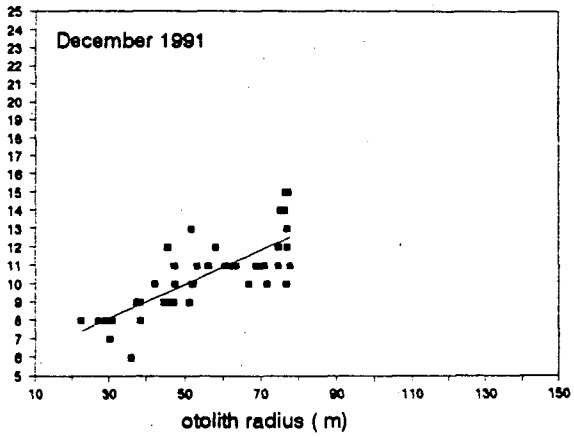
Figure 3.4: Relationship between standard length of fish in mm and the radius of otolith in μm. This relationship is used in the study to backcalculate and to infer growth rates of fish from the width of a ring in the otolith. Thick rings imply fast growth while thin ones mean slow growth.

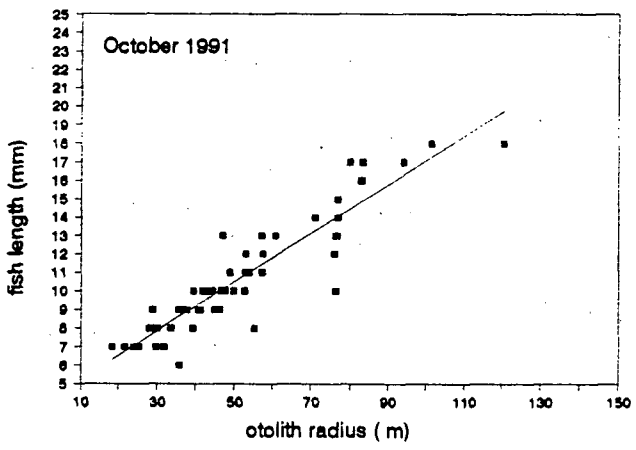

February 1991
May 1991
March 1991
June 1991
April 1991
July 1991
fish length (mm)
otolith radius (m)

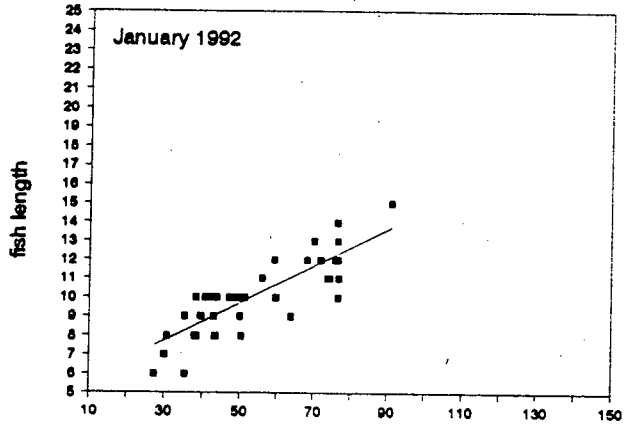

August 1991
fish length (mm)

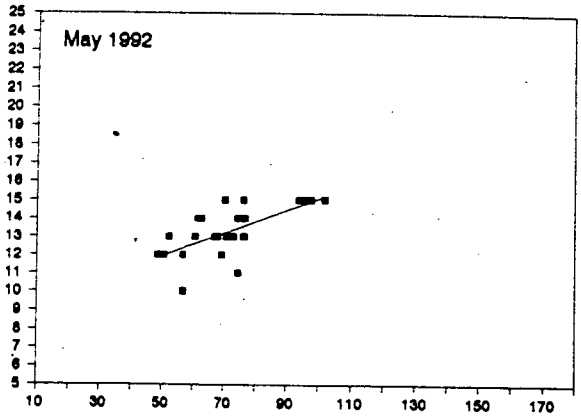

November 1991

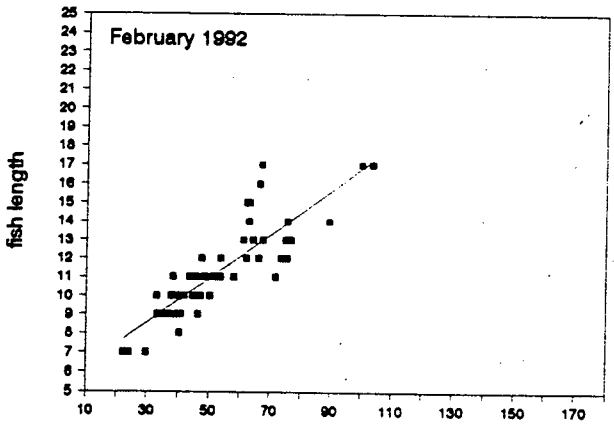

September 1991
fish length (mm)

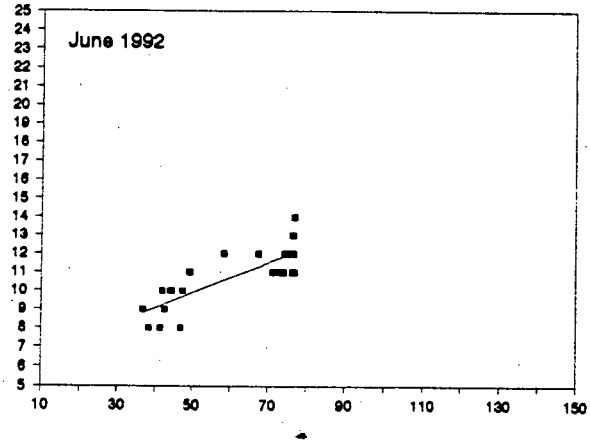

December 1991
otolith radius (m)

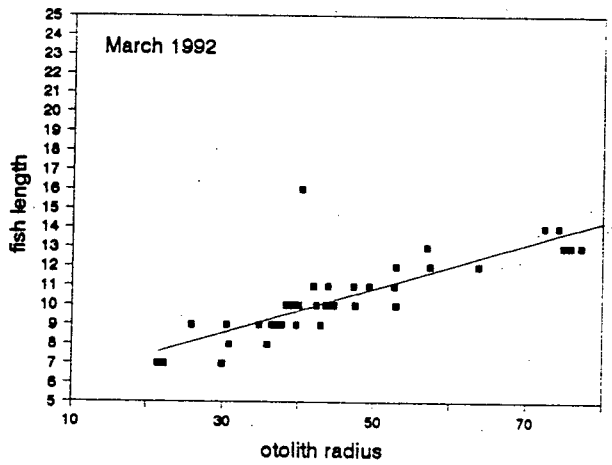

October 1991
fish length (mm)
otolith radius (m)

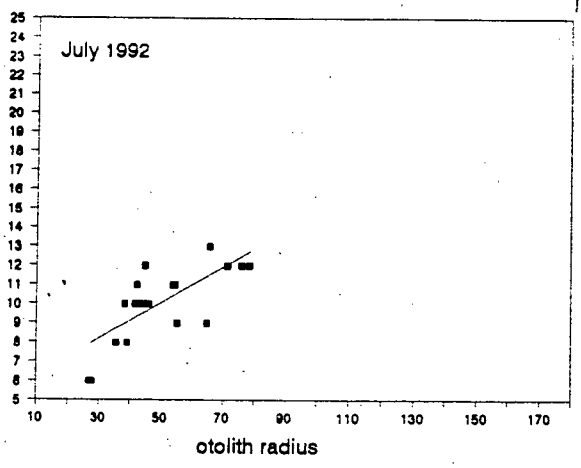

January 1992
fish length

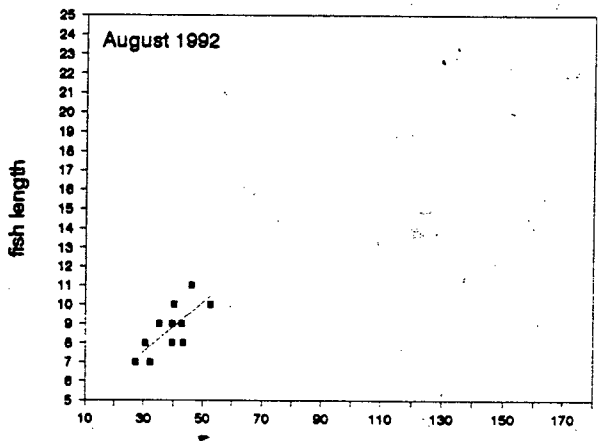

May 1992

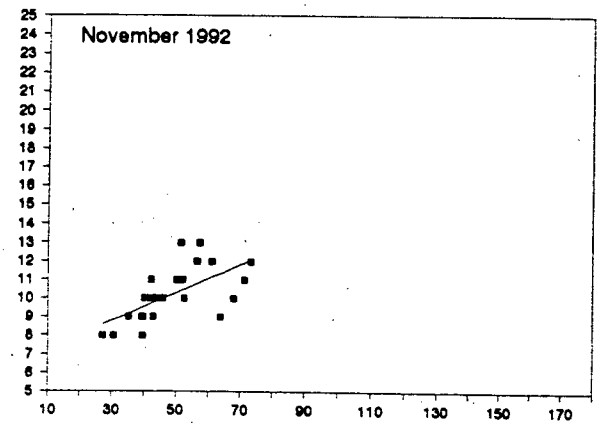

February 1992
fish length

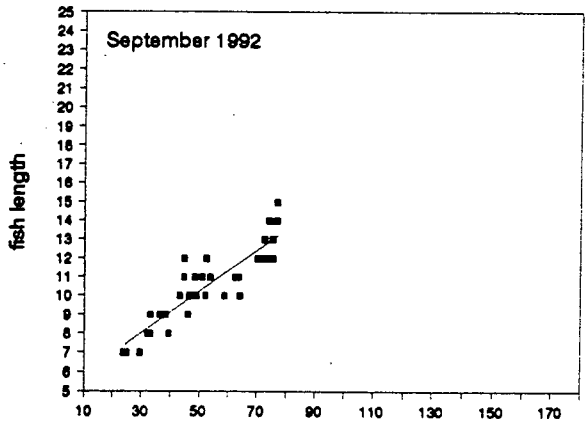

June 1992

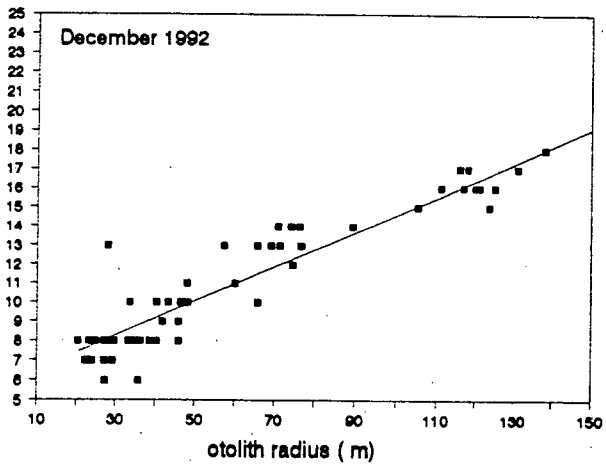

March 1992
fish length
otolith radius

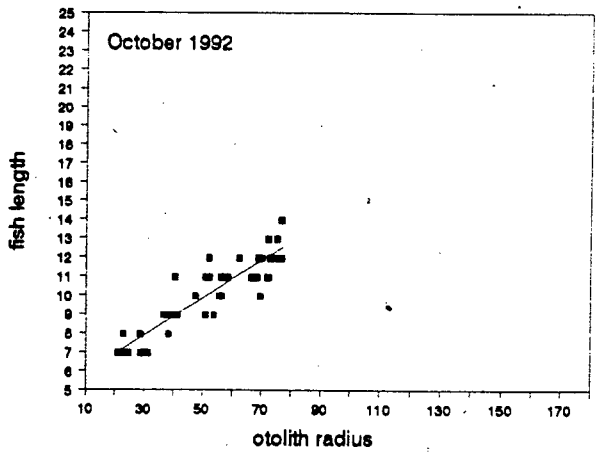

July 1992
otolith radius


August 1992
fish length


November 1992

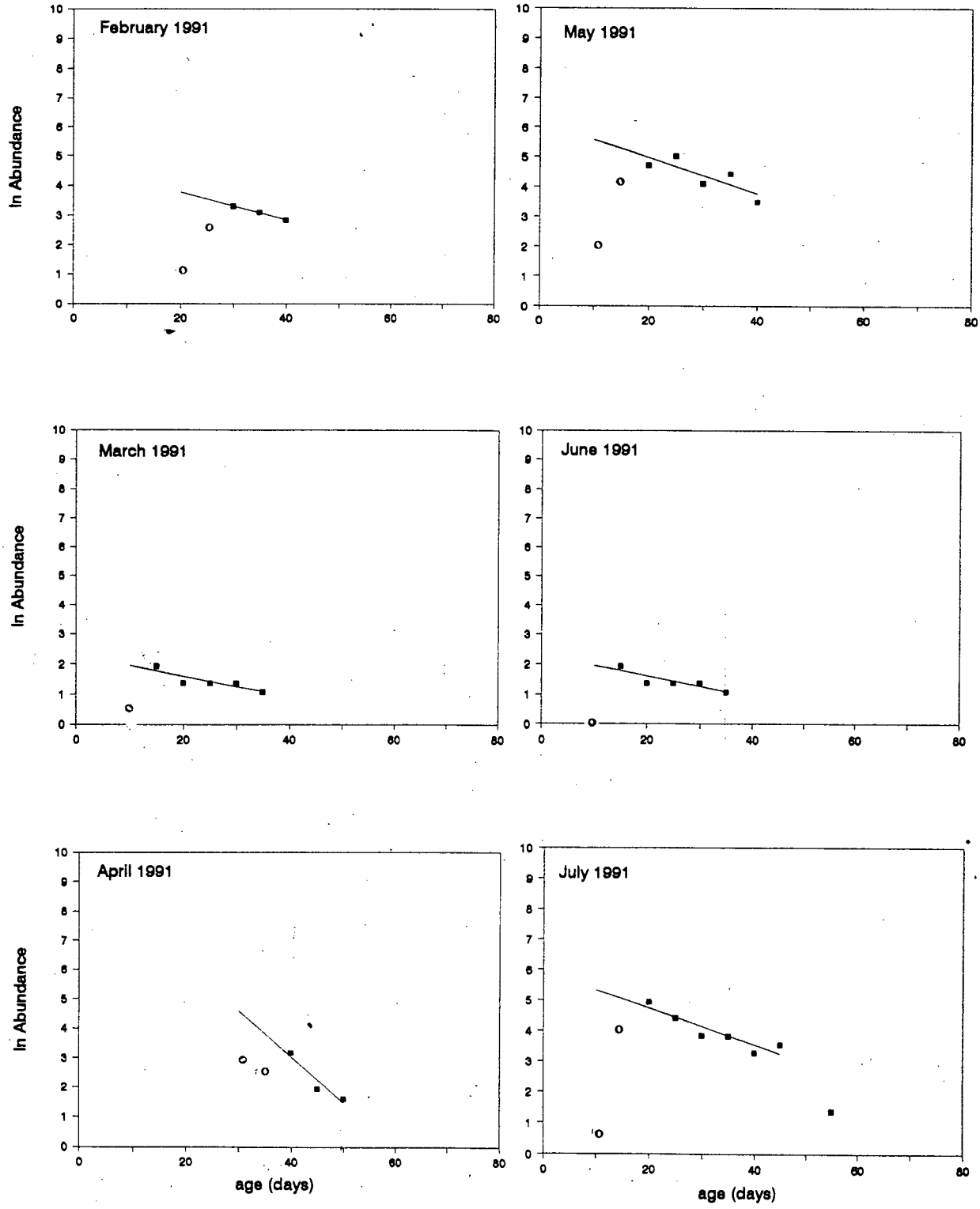

September 1992
fish length

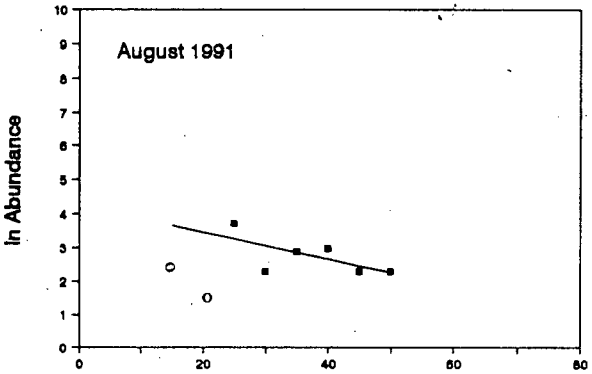

December 1992
otolith radius (m)

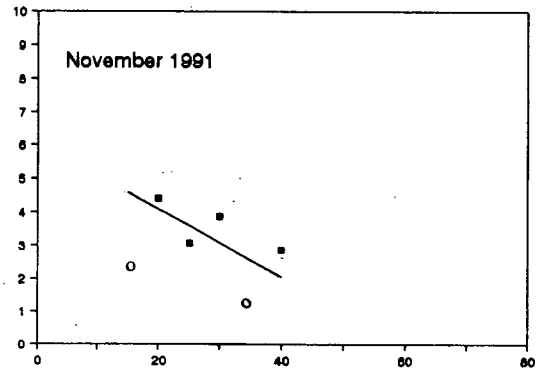

October 1992
fish length
otolith radius

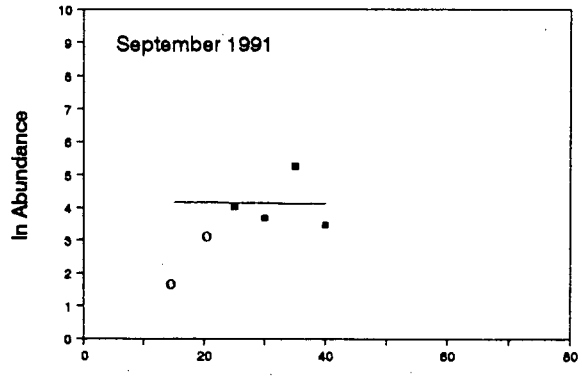
APPENDIX III

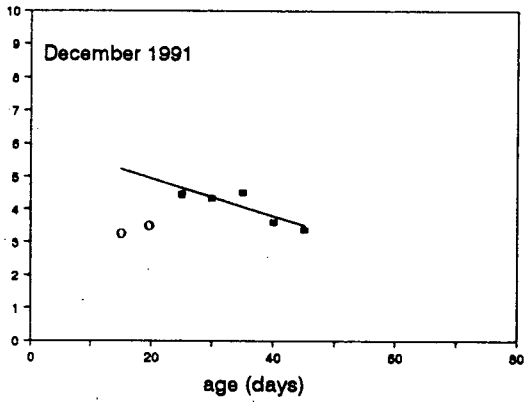
Figure 4.2: Daily instanteneous mortality rates of larval *Limnothrissa miodon* based on catch curve analysis. Age length keys were used to convert length frequency distributions. The effect of migration has not been deducted from these values. The points represented by (o) were not used in the regressions (see text for explanation).

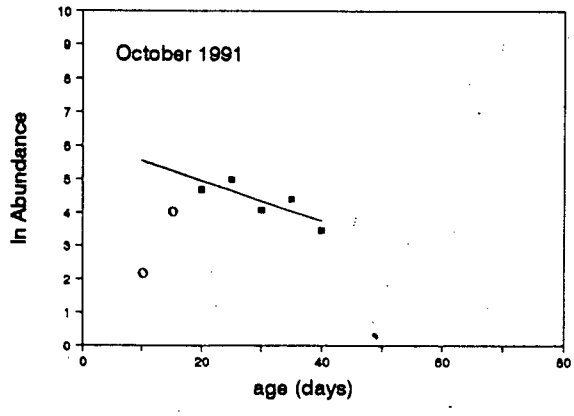

February 1991
May 1991
March 1991
June 1991
April 1991
July 1991
ln Abundance
age (days)

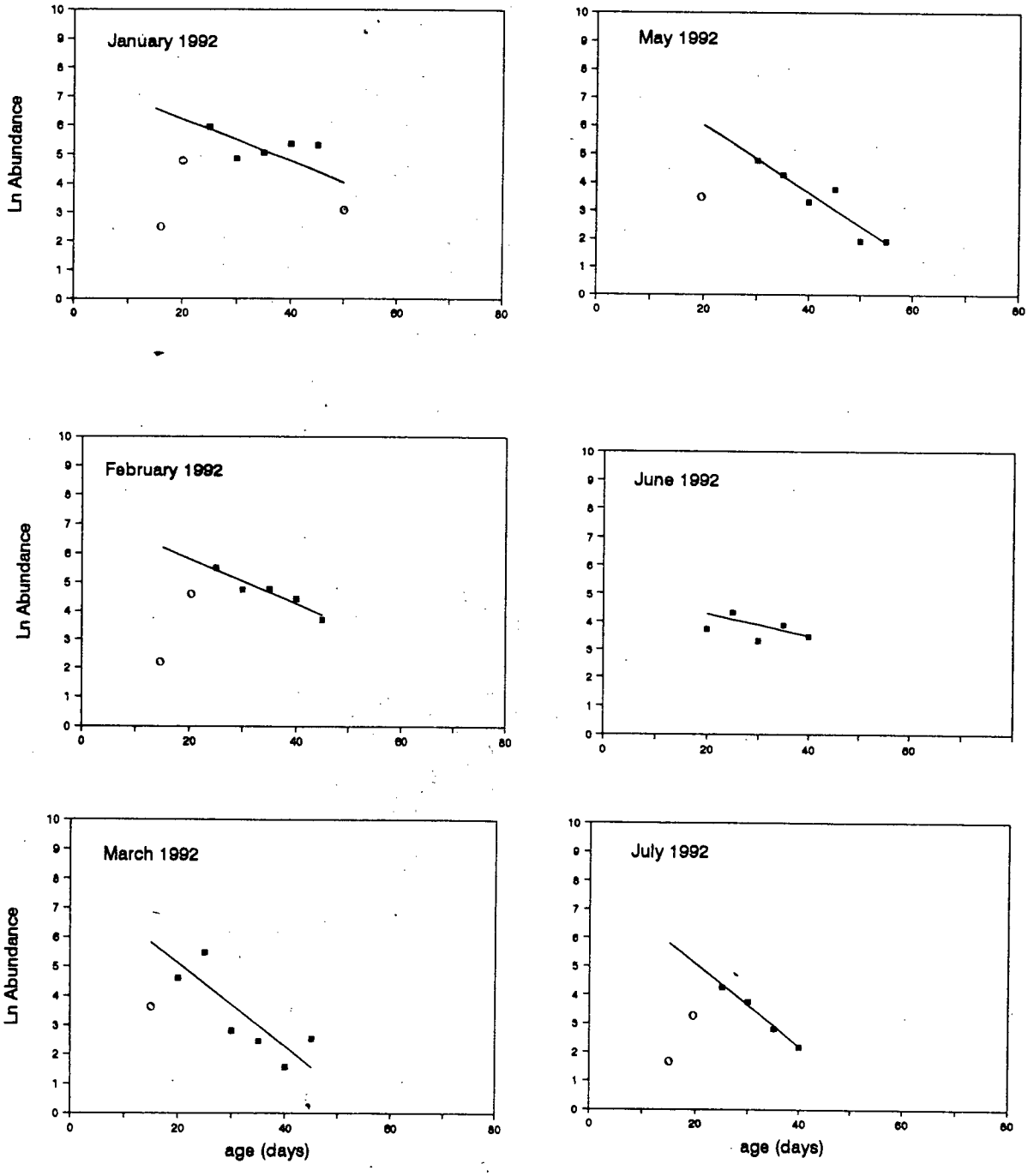

August 1991
ln Abundance

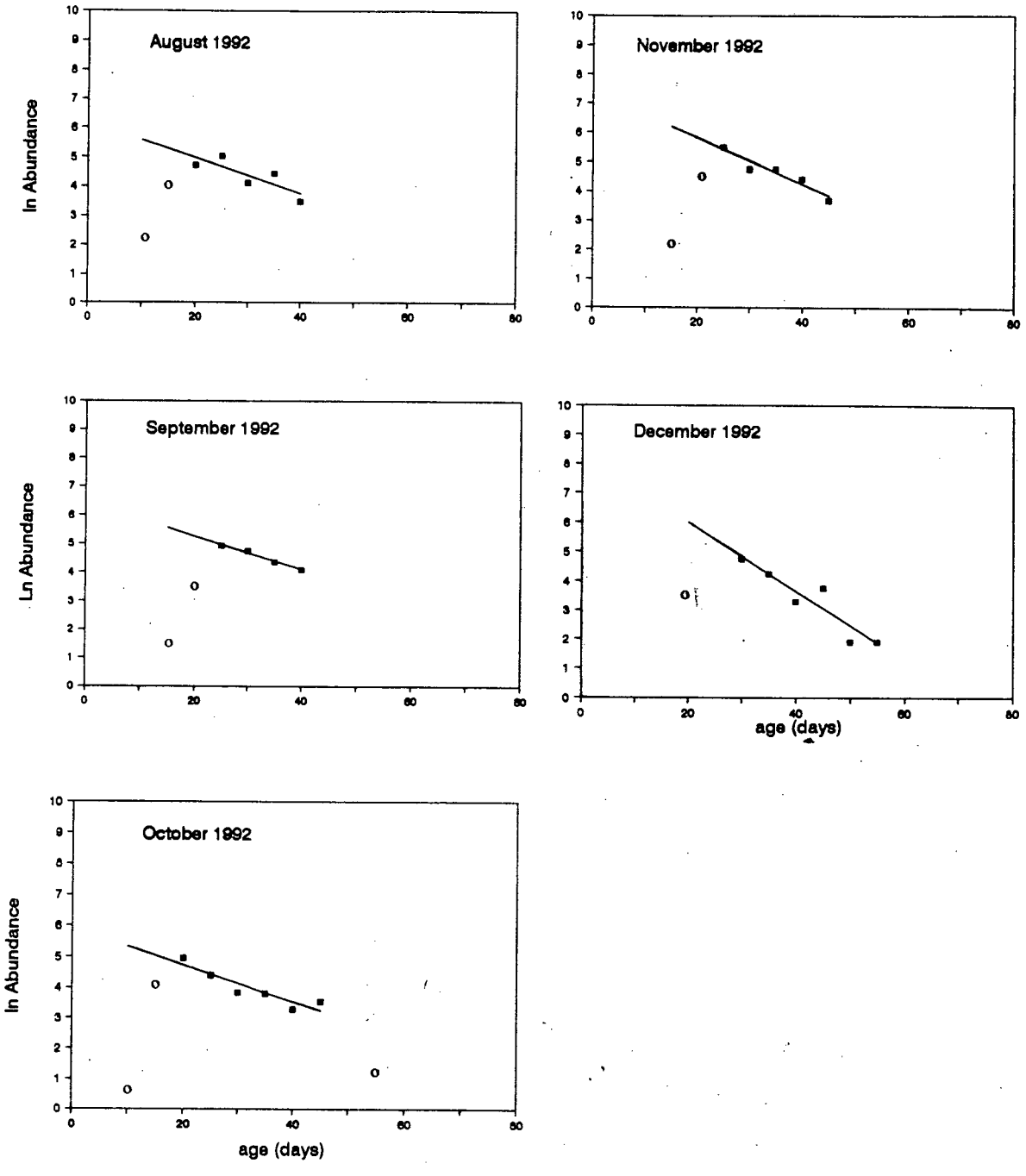

November 1991


September 1991
ln Abundance


December 1991
age (days)

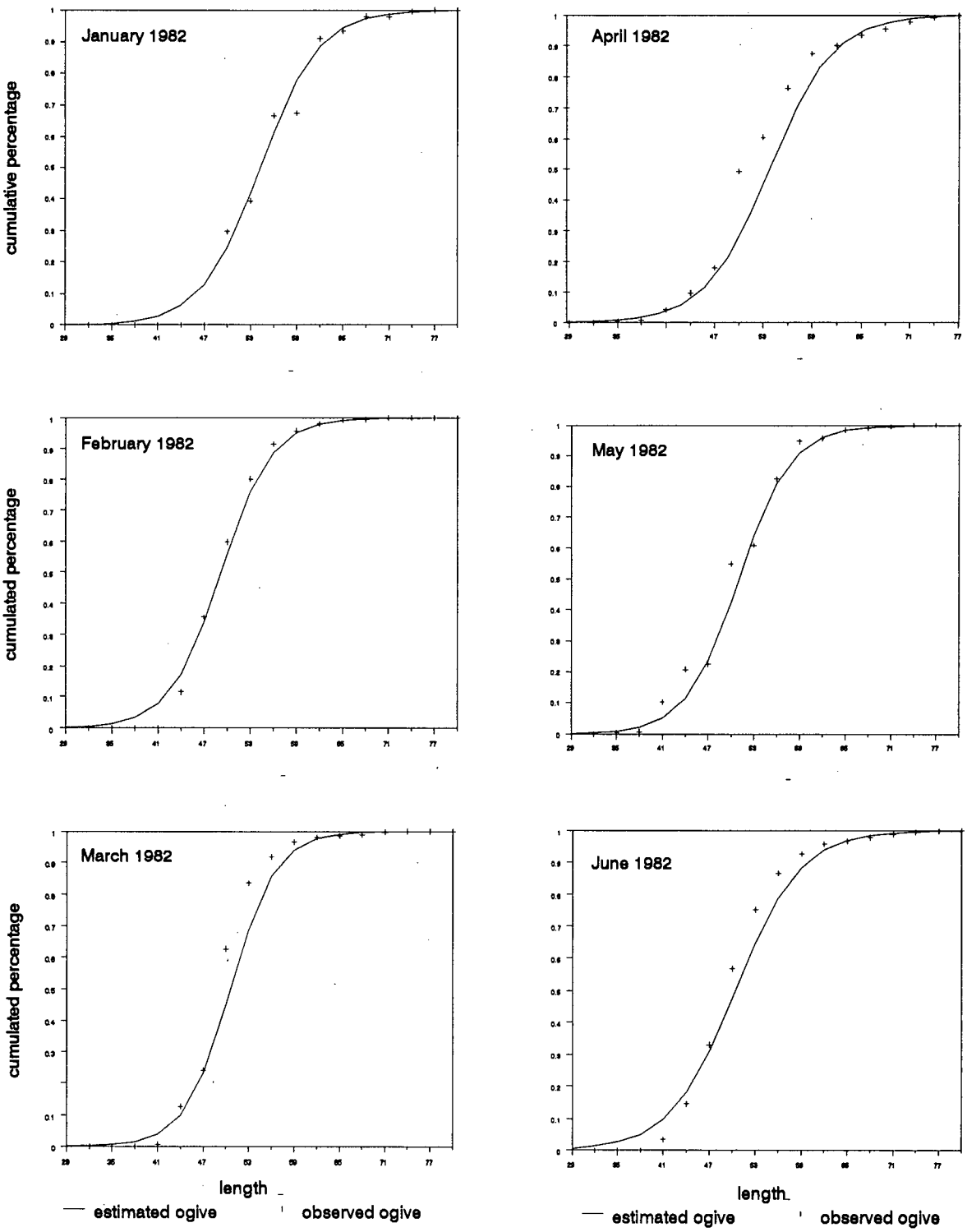

October 1991
ln Abundance
age (days)

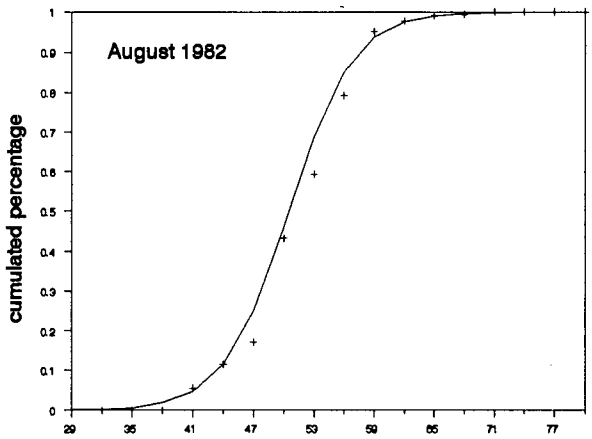

January 1992
May 1992
February 1992
June 1992
March 1992
July 1992
Ln Abundance
age (days)

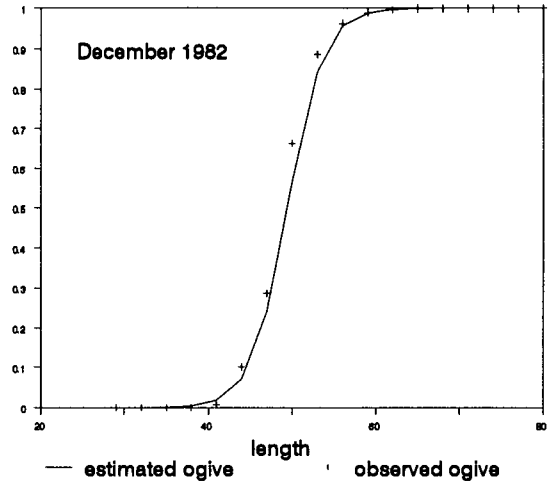

August 1992
November 1992
September 1992
December 1992
October 1992
ln Abundance
Ln Abundance
age (days)

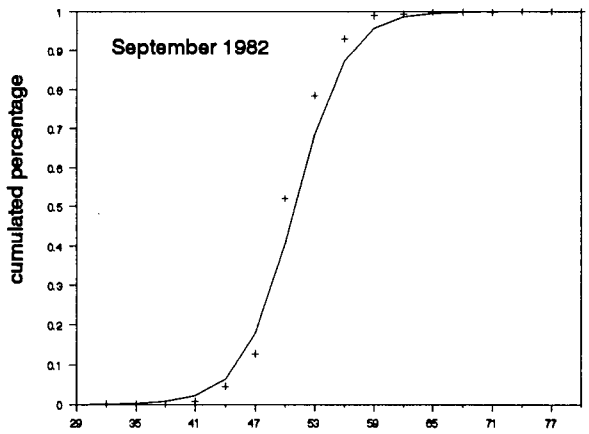
APPENDIX IV

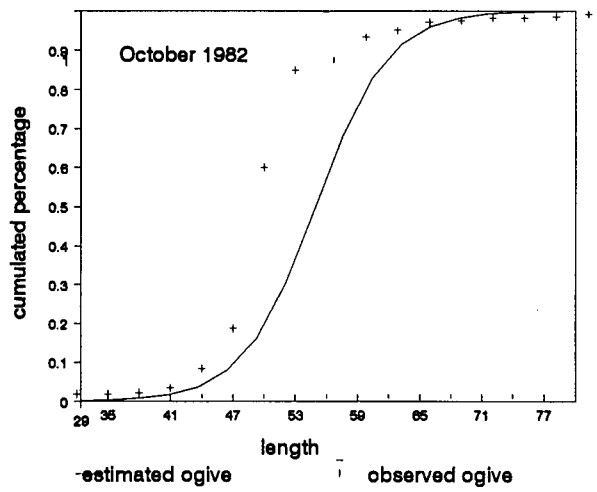
Figure 5.1 Monthly cumulative frequency distributions from January 1982 to December 1992. Based on inspection of these ogives, it was observed that fish of 41 mm in length constituted the size that seemed to recruiting into the fishery.

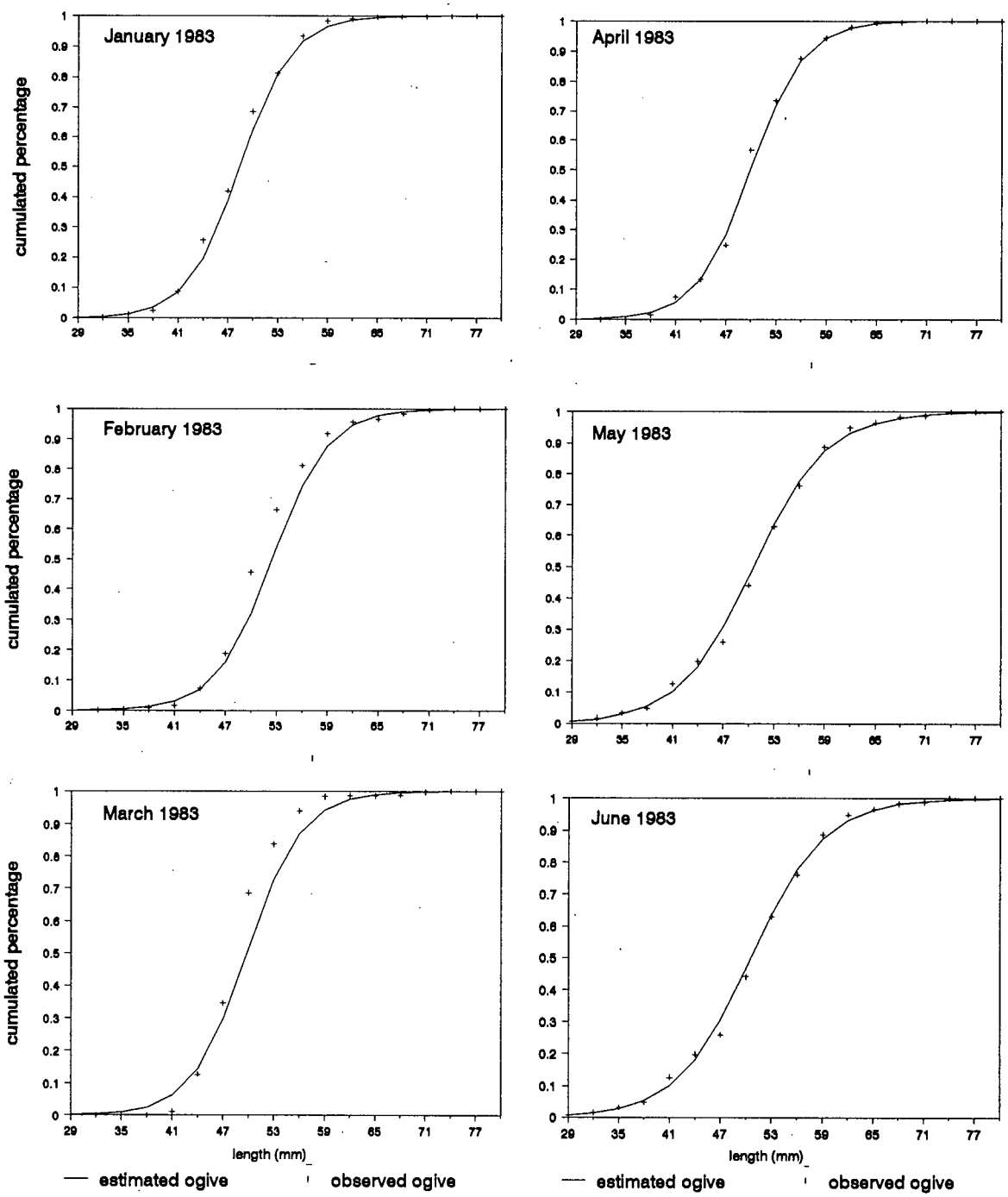

January 1982
April 1982
February 1982
May 1982
March 1982
June 1982
cumulative percentage
cumulated percentage
cumulated percentage
length
length
estimated ogive
observed ogive
estimated ogive
observed ogive

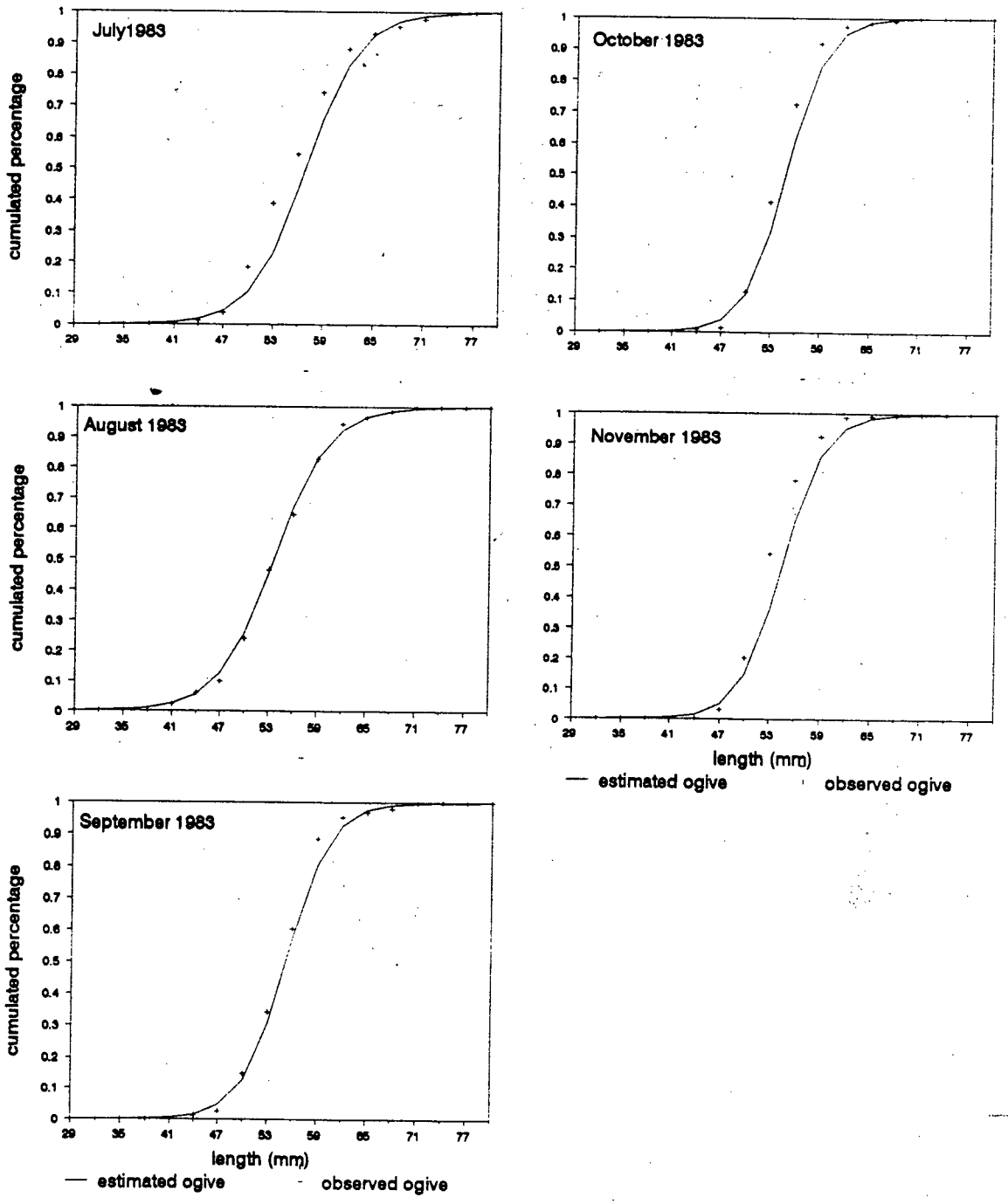

August 1982
cumulated percentage
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
29
35
41
47
53
59
65
71
77

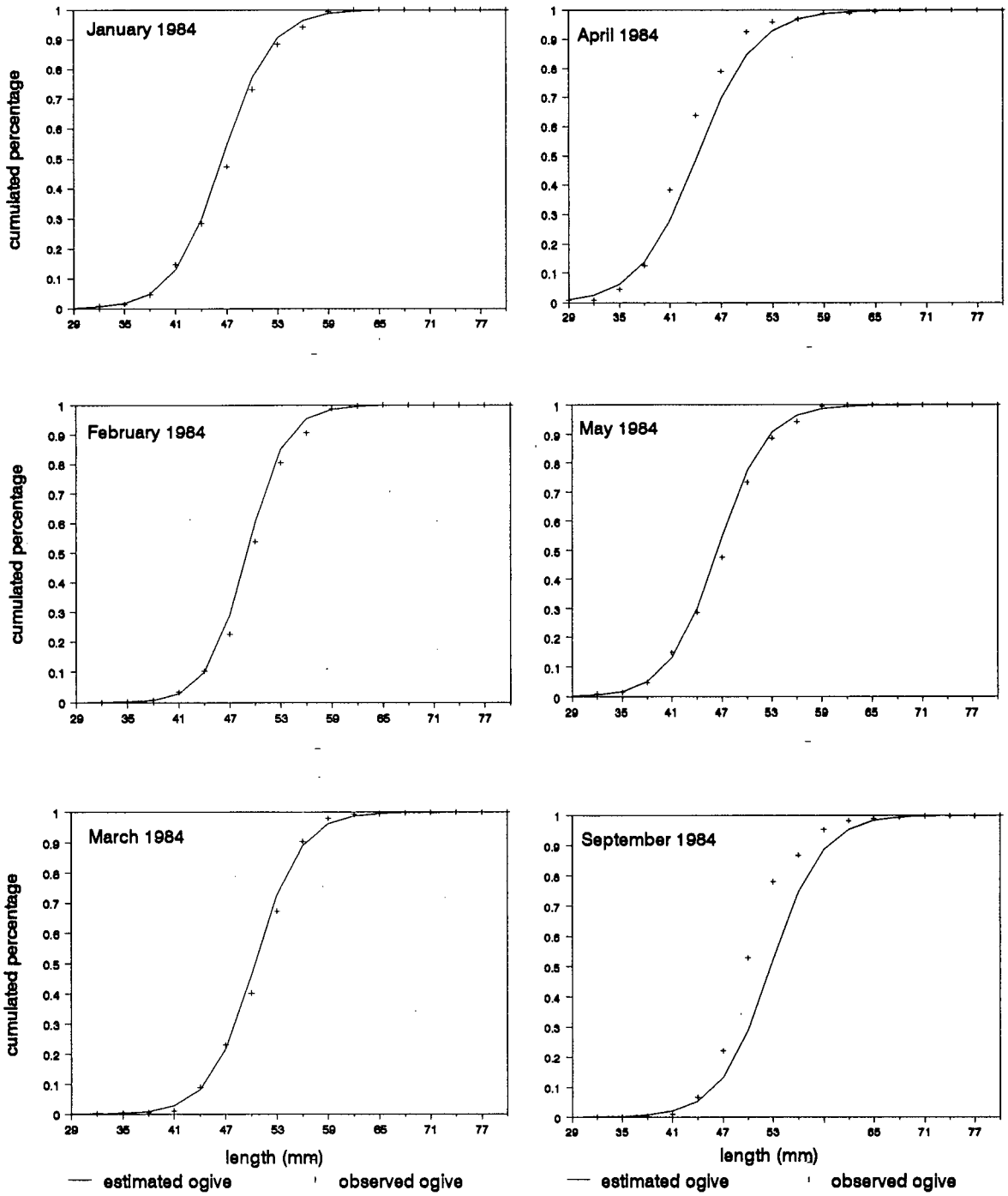

December 1982
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
20
40
60
80
length
estimated ogive
observed ogive

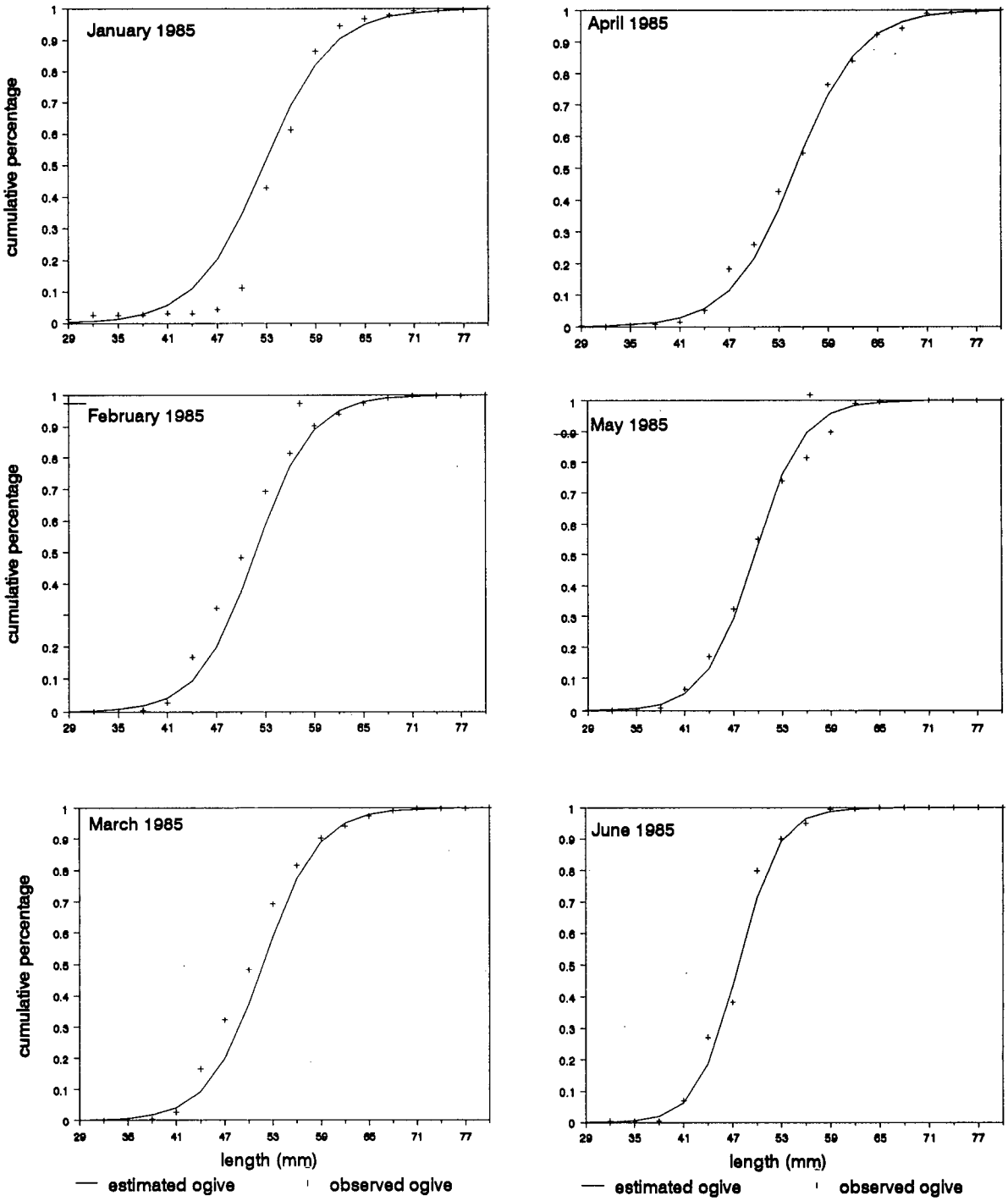

September 1982
cumulated percentage
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
29
35
41
47
53
59
65
71
77

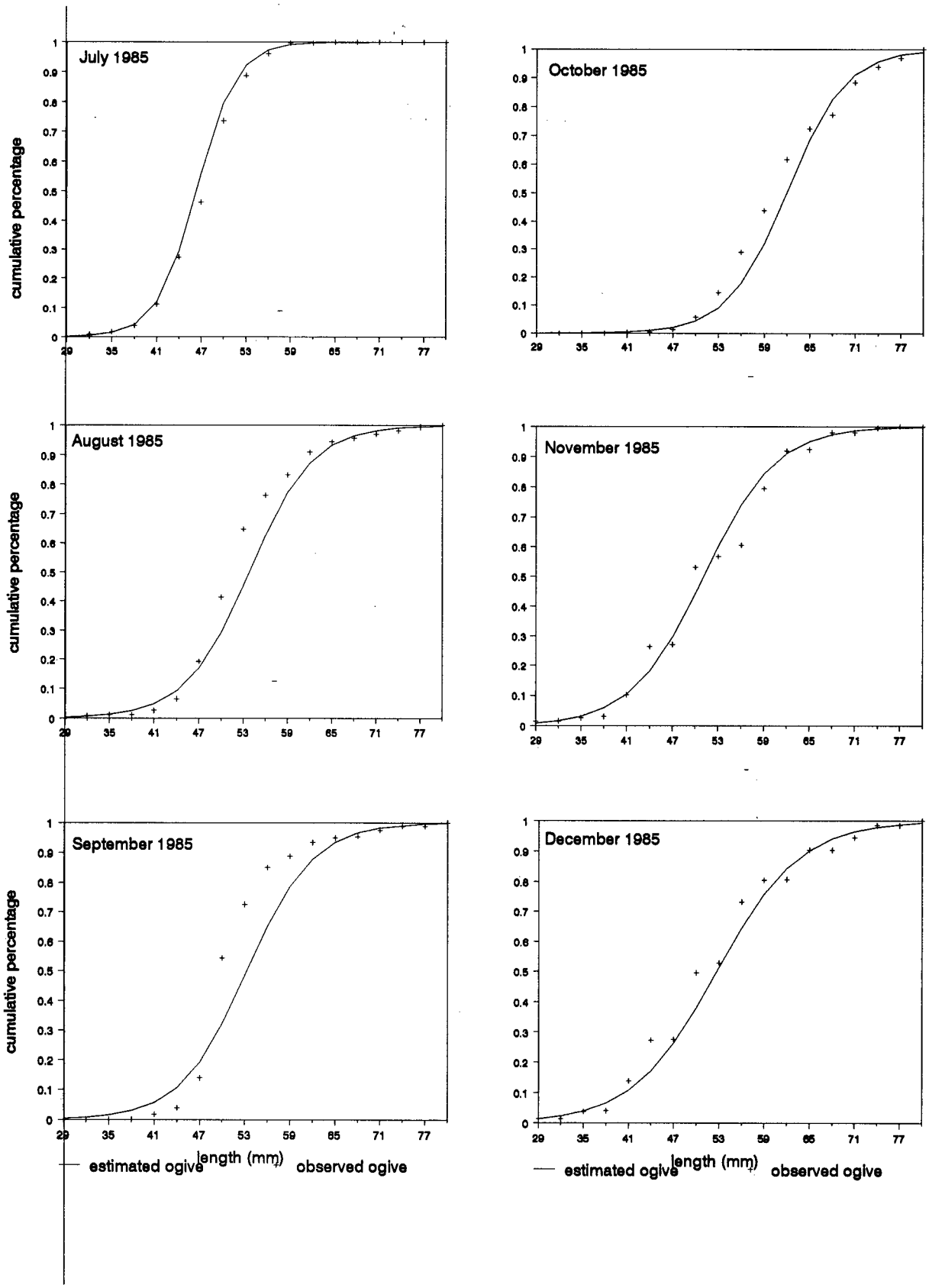

October 1982
cumulated percentage
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
29
35
41
47
53
59
65
71
77
length
estimated ogive
observed ogive

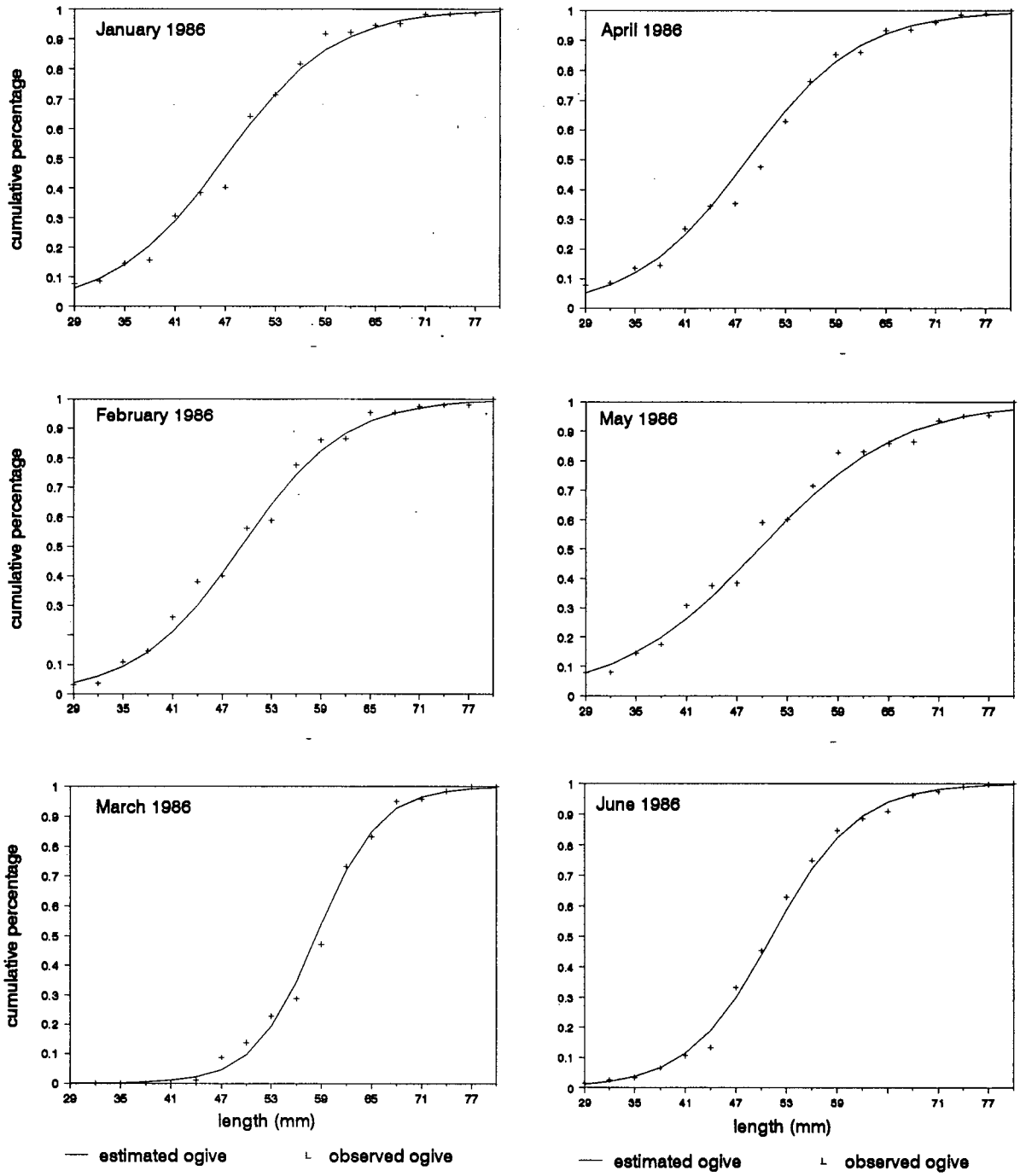

January 1983
April 1983
February 1983
May 1983
March 1983
June 1983
cumulated percentage
length (mm)
estimated ogive
observed ogive

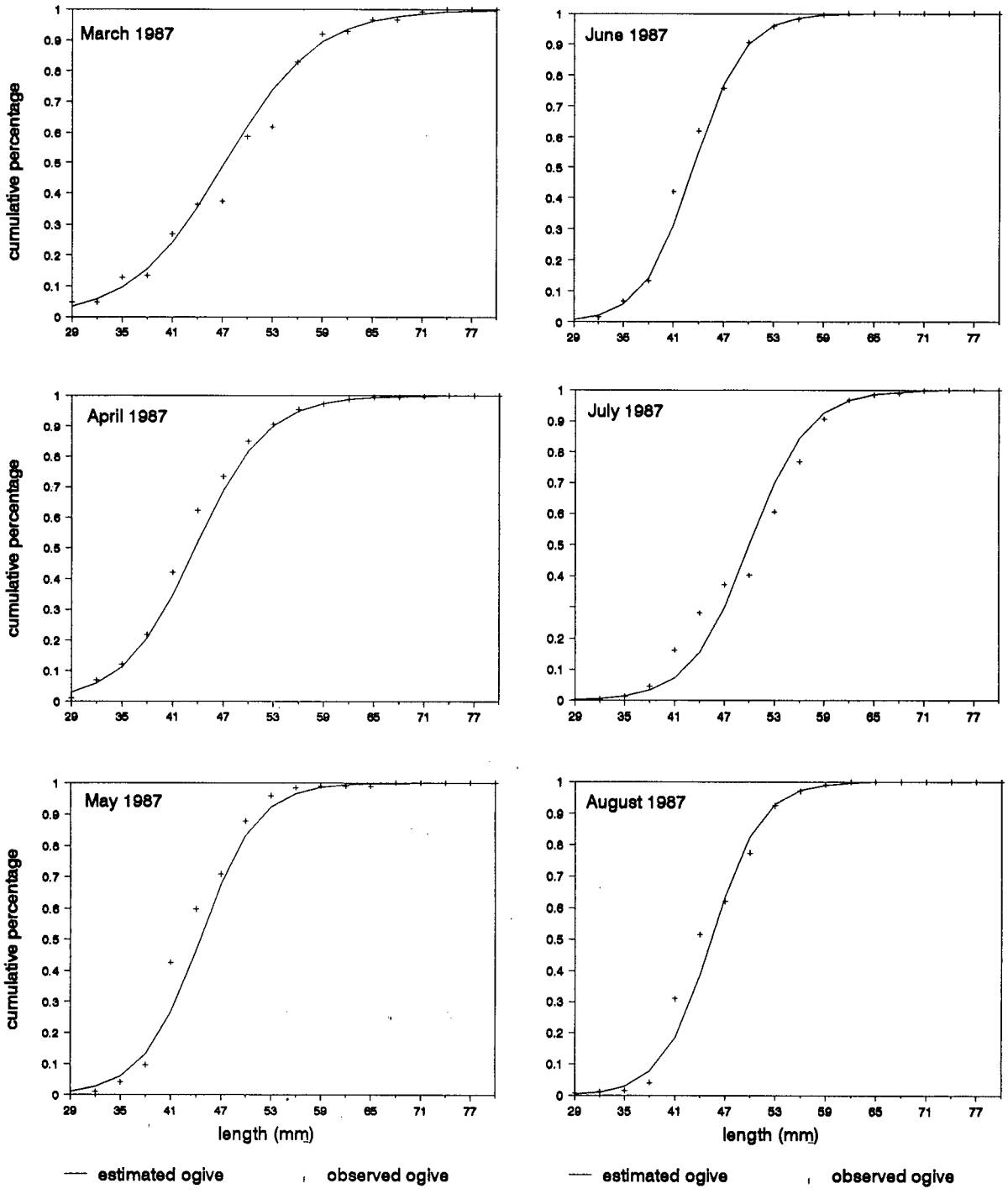

July1983
October 1983
August 1983
November 1983
September 1983
cumulated percentage
length (mm)
estimated ogive
observed ogive

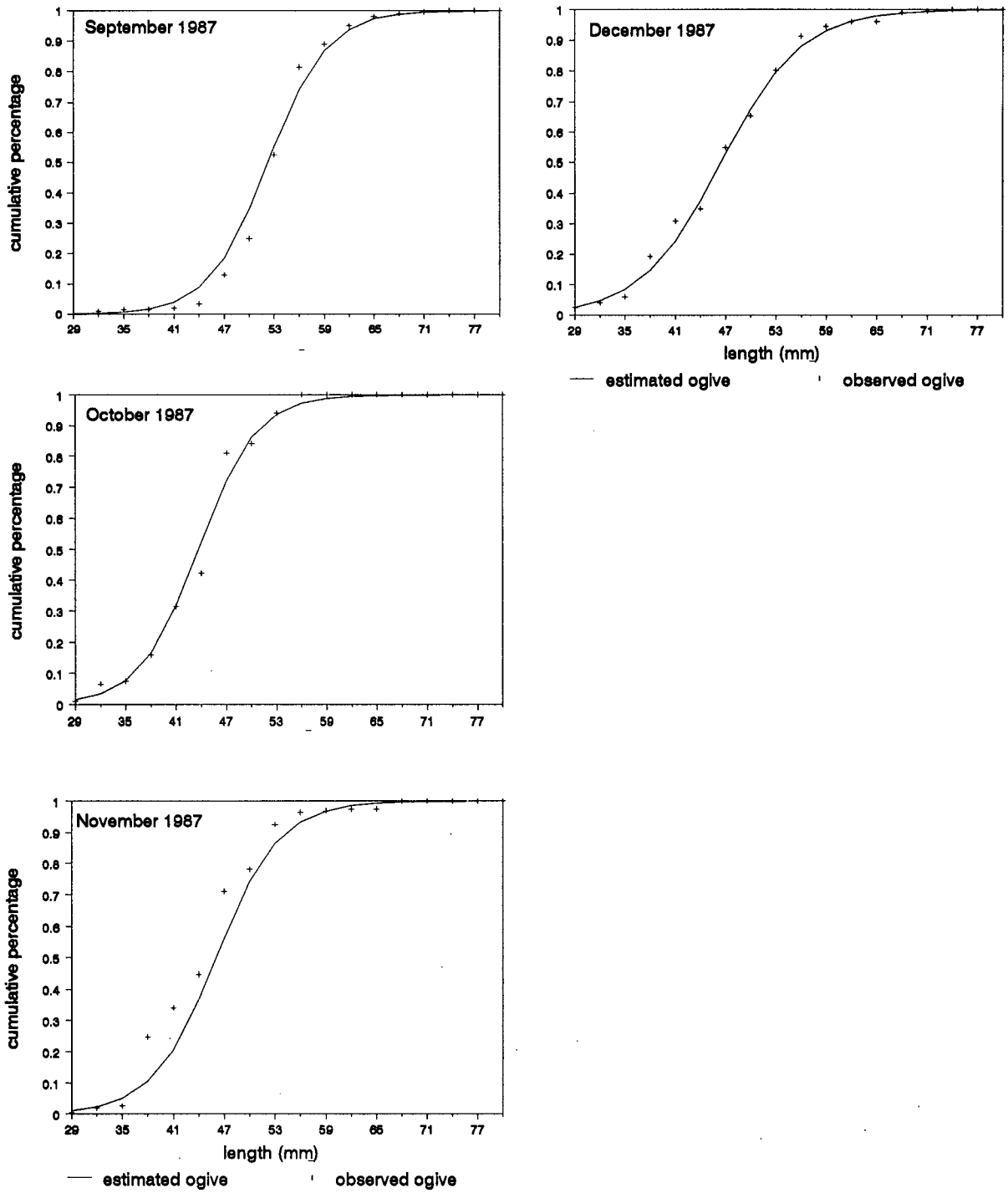

January 1984
April 1984
February 1984
May 1984
March 1984
September 1984
cumulated percentage
length (mm)
estimated ogive
observed ogive

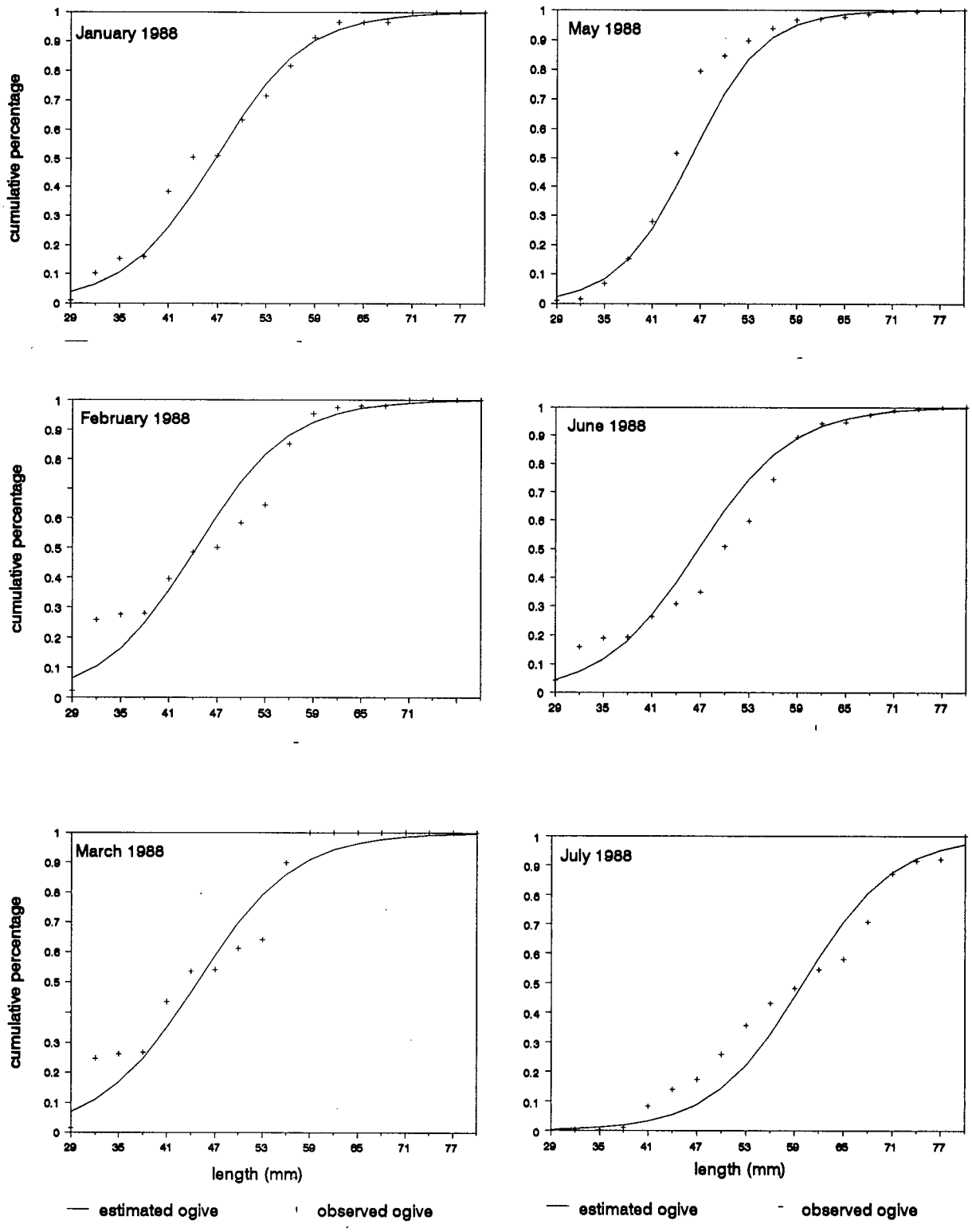

January 1985
February 1985
March 1985
April 1985
May 1985
June 1985
cumulative percentage
length (mm)
estimated ogive
observed ogive

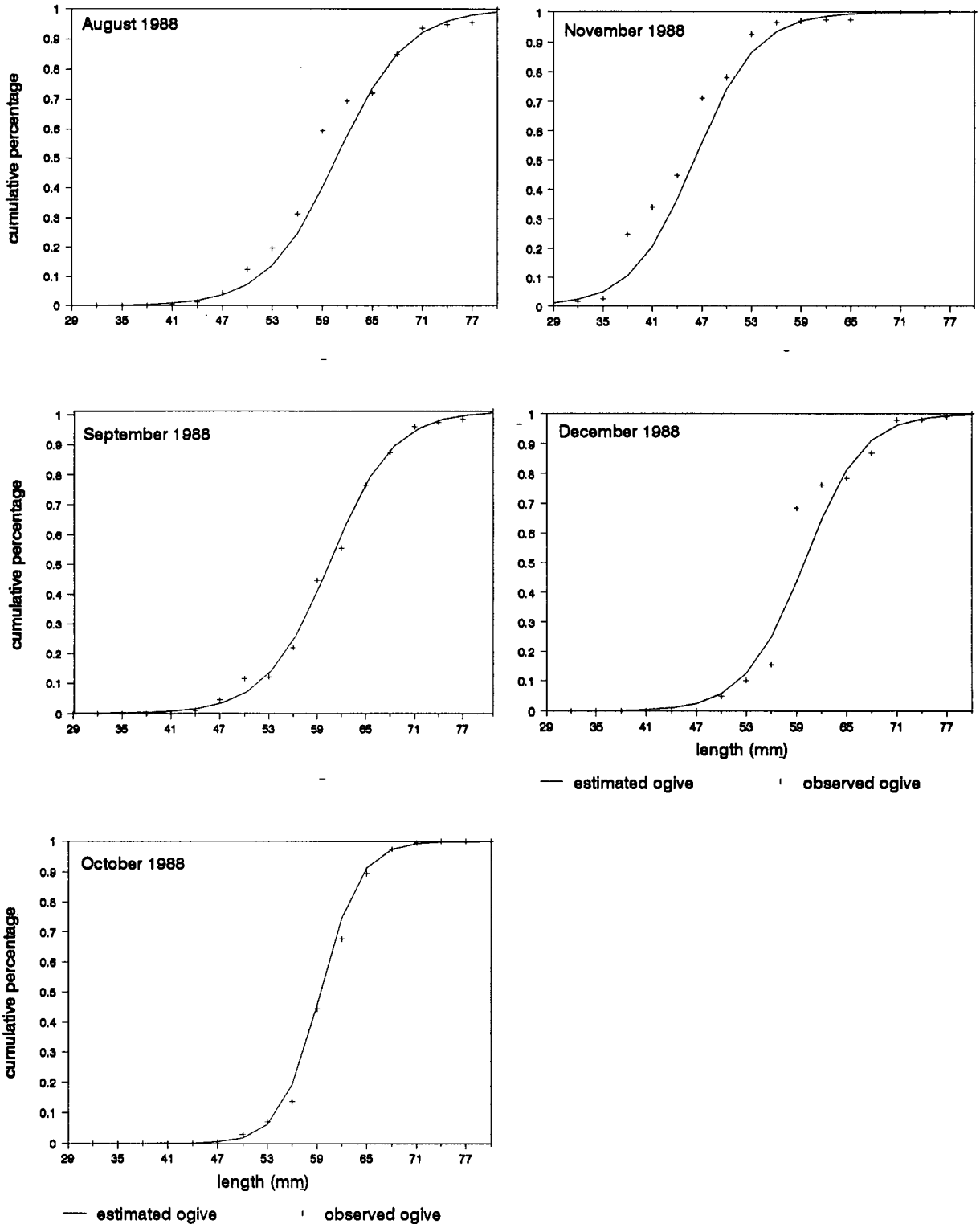

July 1985
October 1985
August 1985
November 1985
September 1985
December 1985
cumulative percentage
length (mm)
estimated ogive
observed ogive

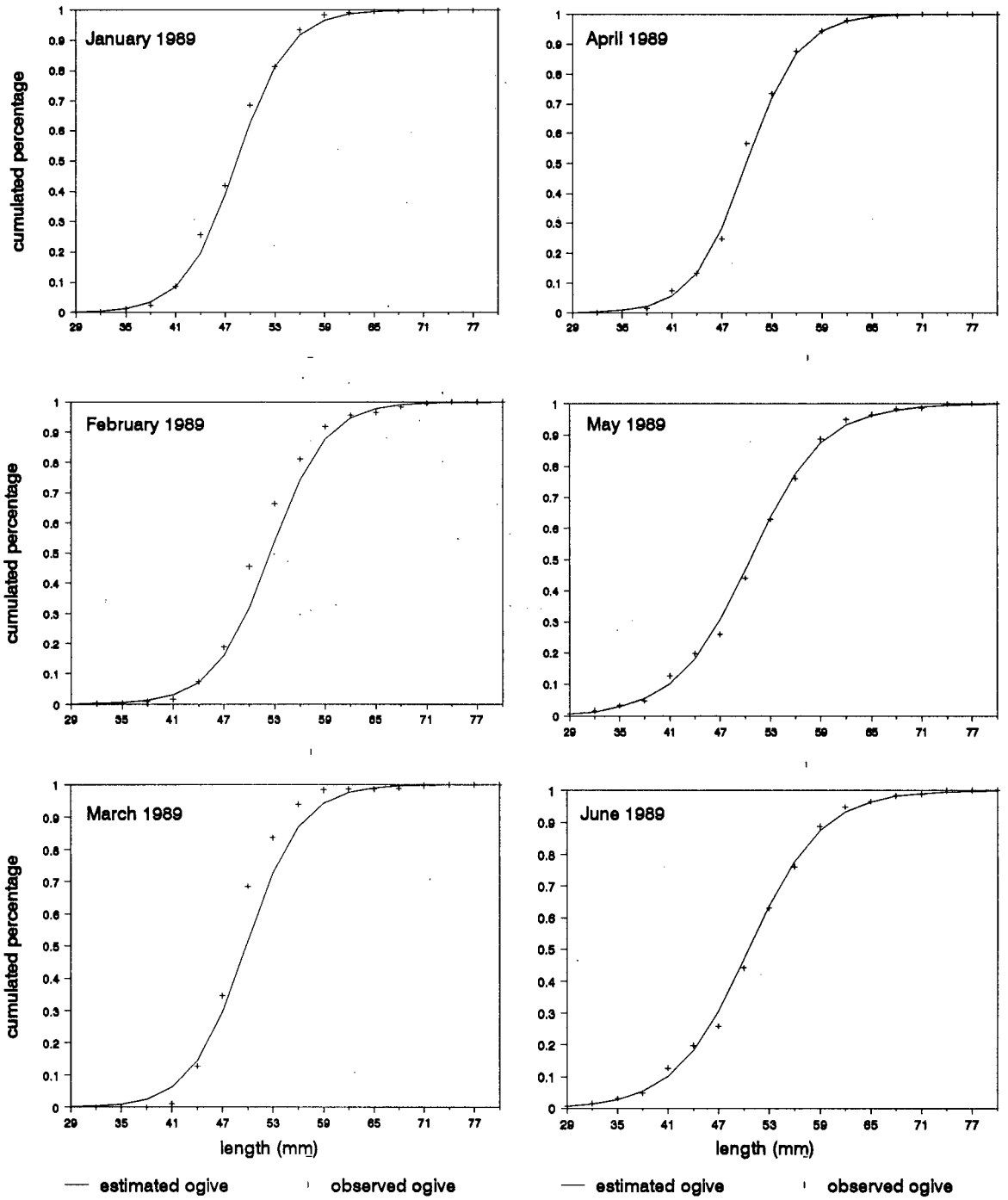

January 1986
April 1986
February 1986
May 1986
March 1986
June 1986
cumulative percentage
length (mm)
estimated ogive
observed ogive

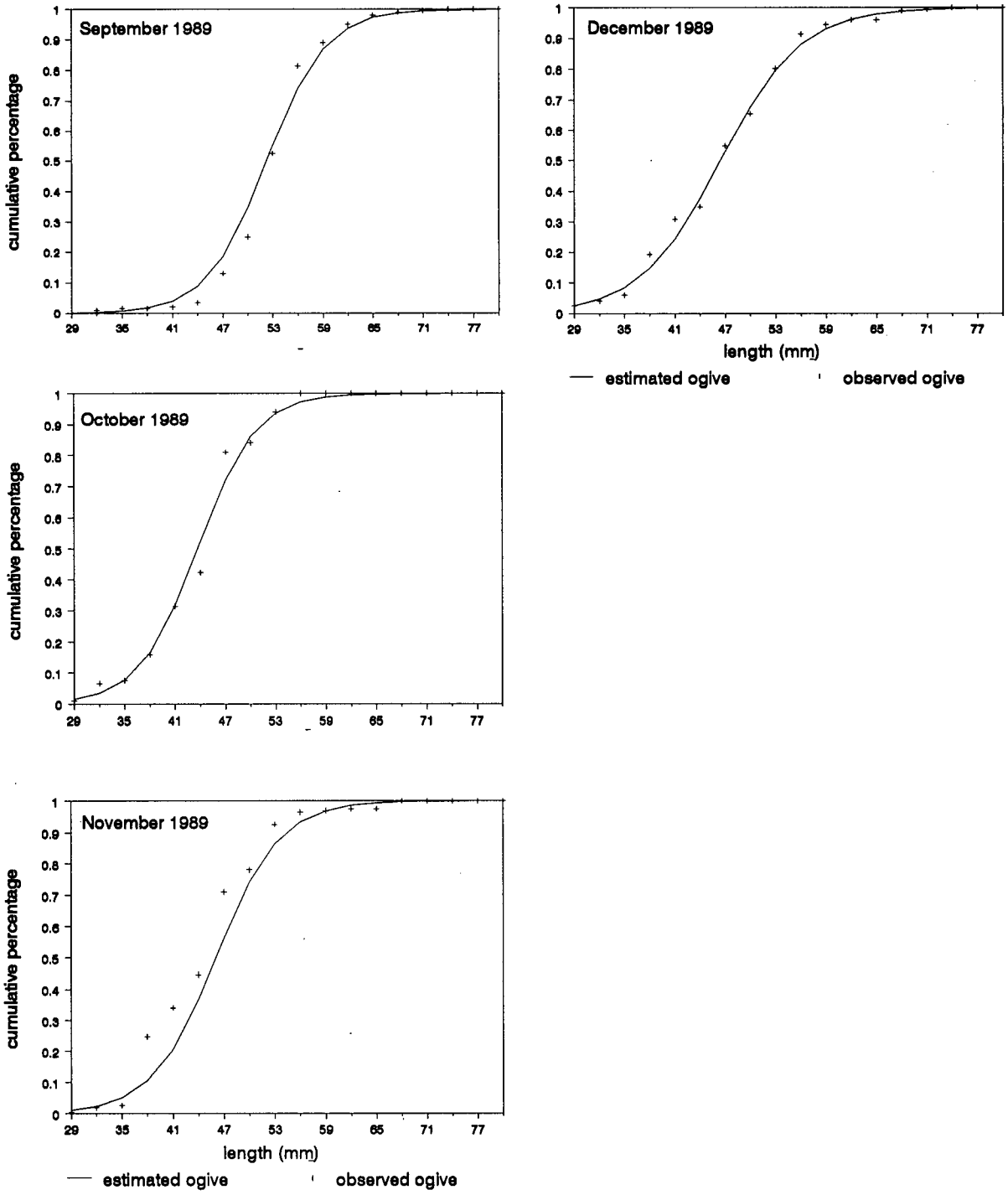

March 1987
June 1987
April 1987
July 1987
May 1987
August 1987
cumulative percentage
length (mm)
estimated ogive
observed ogive

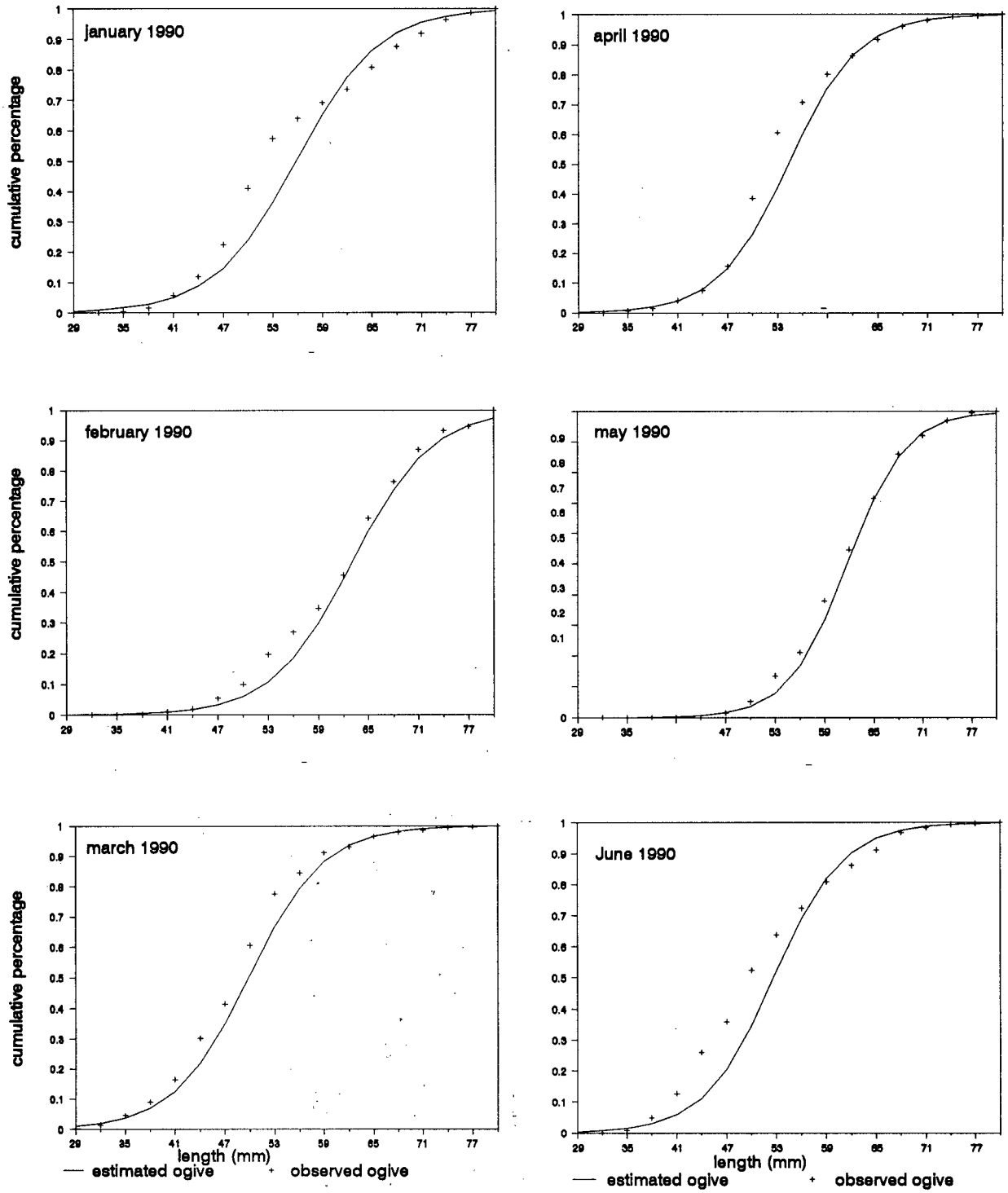

September 1987
October 1987
November 1987
December 1987
cumulative percentage
length (mm)
estimated ogive
observed ogive

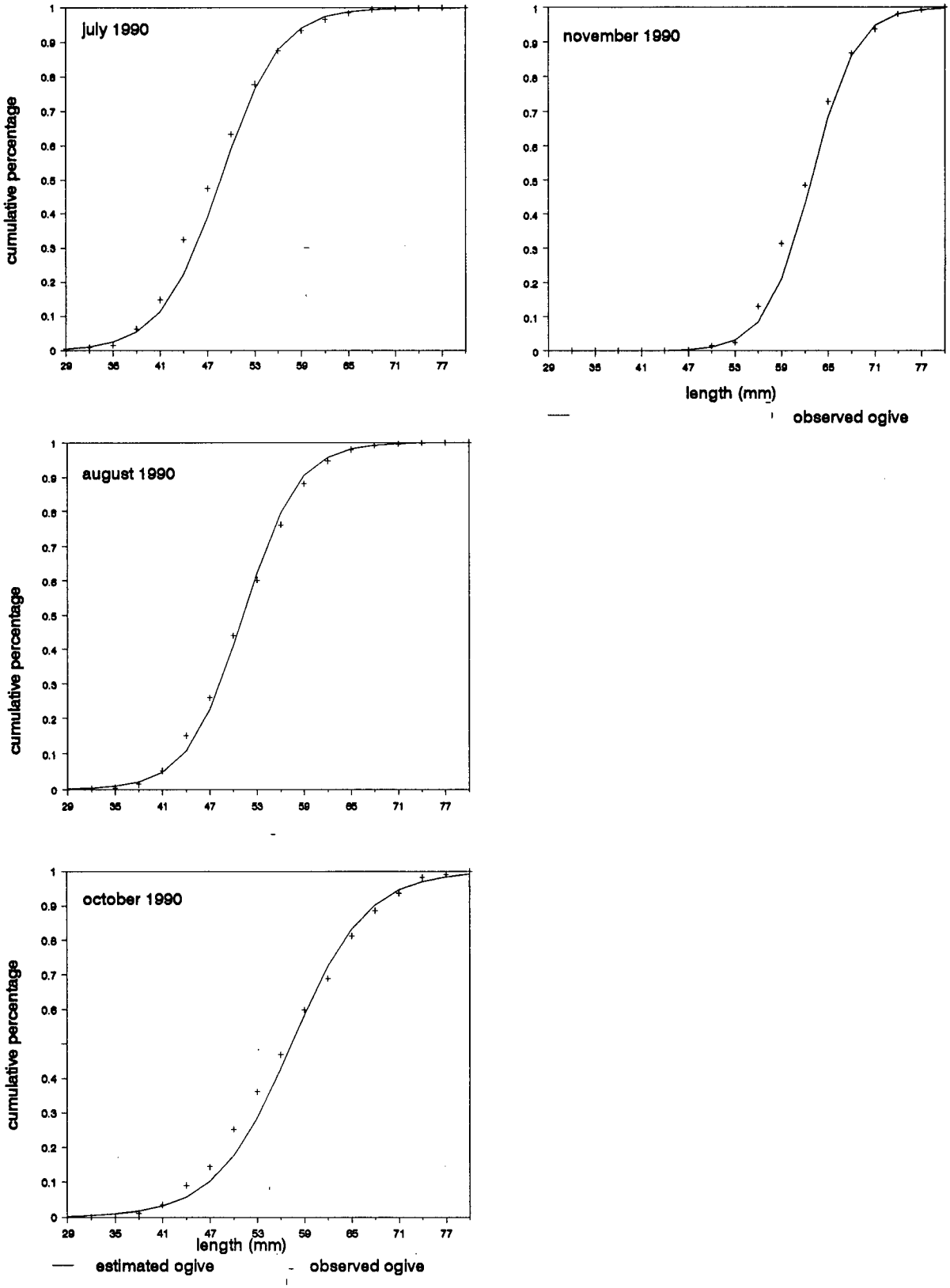

January 1988
May 1988
February 1988
June 1988
March 1988
July 1988
cumulative percentage
length (mm)
estimated ogive
observed ogive

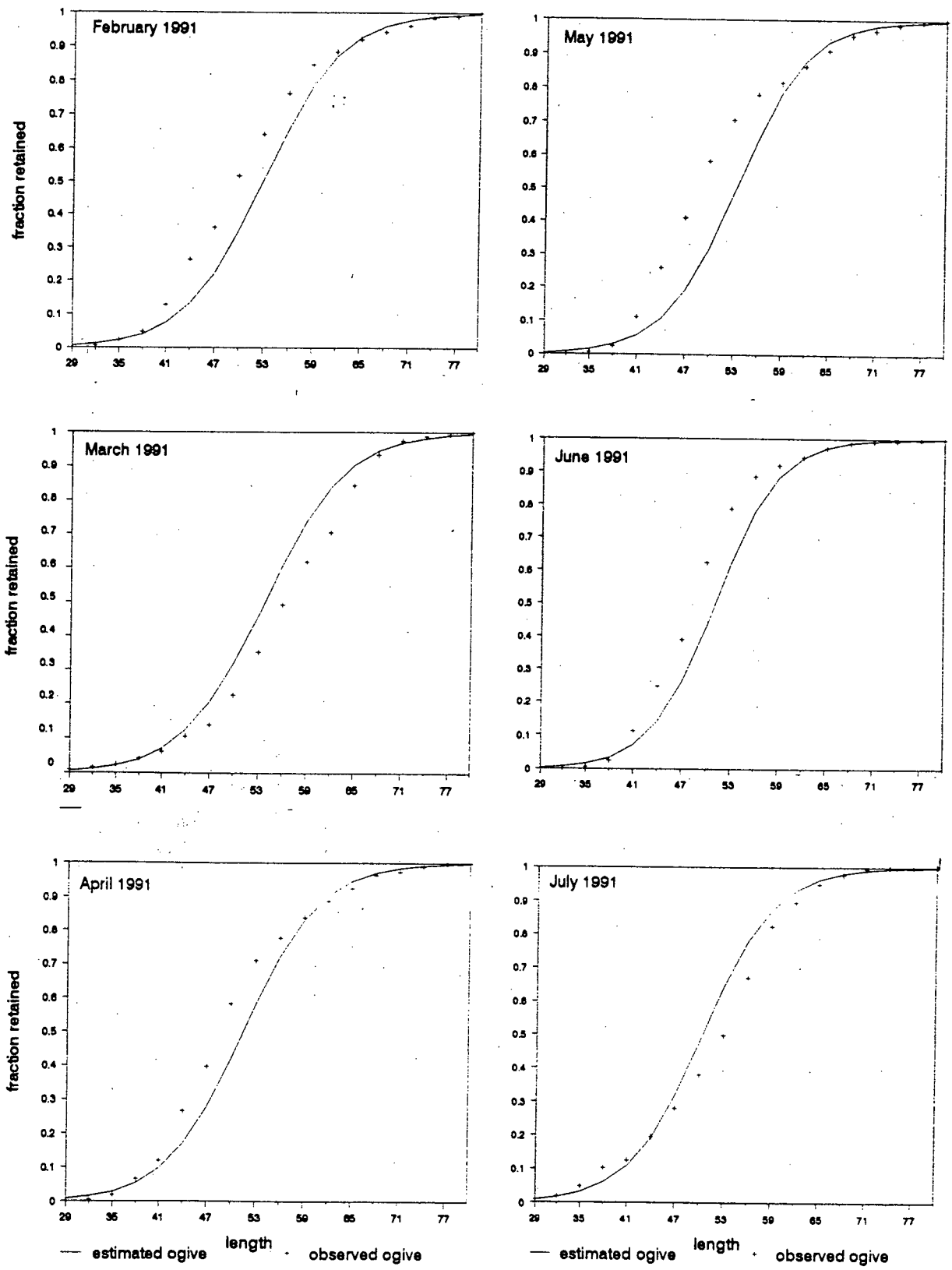

August 1988
November 1988
September 1988
December 1988
October 1988
cumulative percentage
length (mm)
estimated ogive
observed ogive

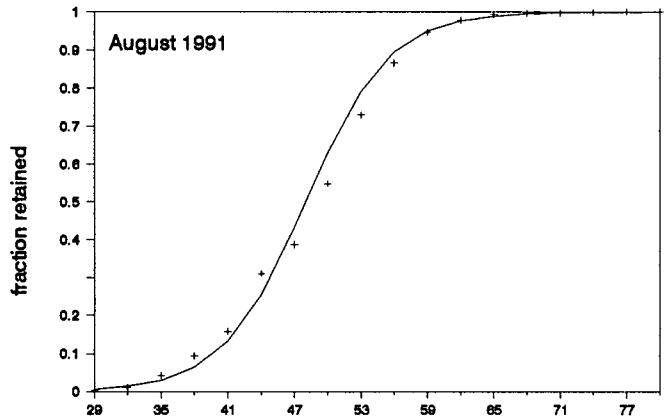

January 1989
April 1989
February 1989
May 1989
March 1989
June 1989
cumulated percentage
length (mm)
estimated ogive
observed ogive

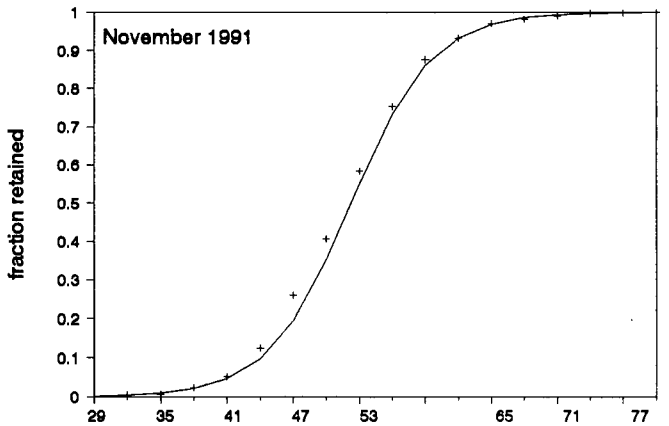

September 1989
December 1989
October 1989
November 1989
cumulative percentage
length (mm)
estimated ogive
observed ogive

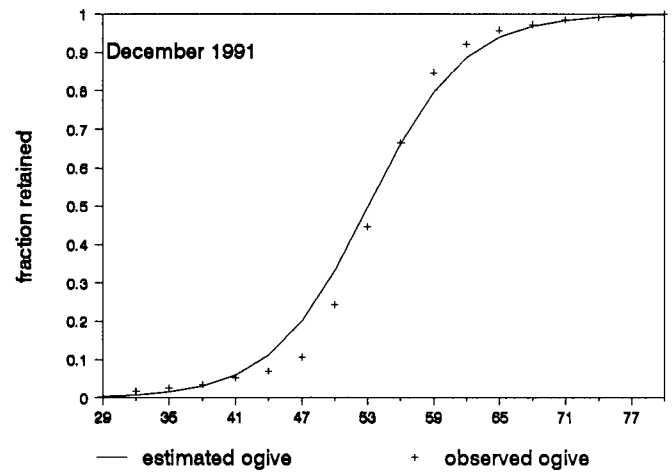

january 1990
april 1990
february 1990
may 1990
march 1990
June 1990
cumulative percentage
length (mm)
estimated ogive
observed ogive

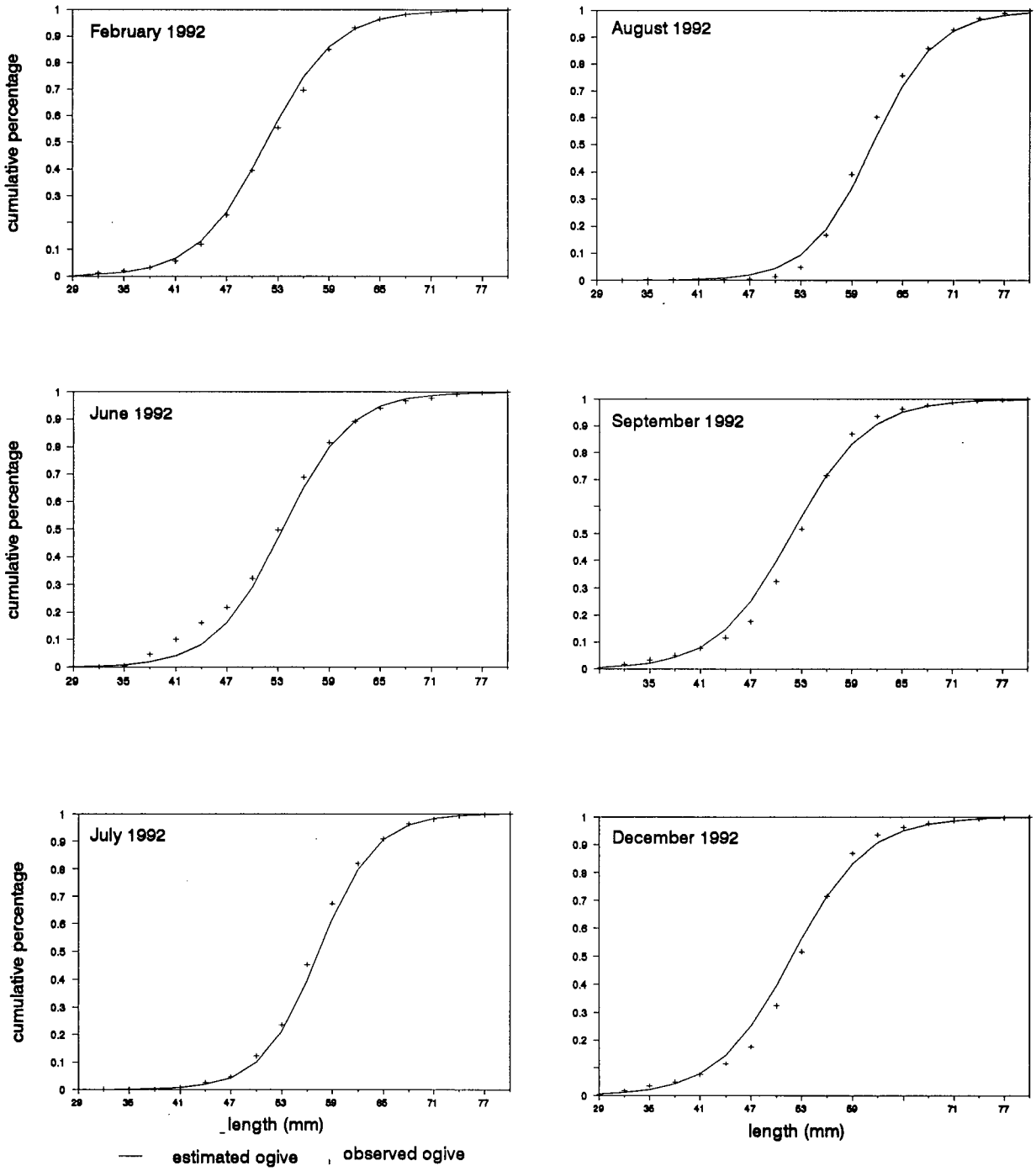

july 1990
november 1990
august 1990
october 1990
cumulative percentage
length (mm)
estimated ogive
observed ogive


February 1991
May 1991
March 1991
June 1991
April 1991
July 1991
fraction retained
length
estimated ogive
observed ogive


August 1991
fraction retained
1
0.9
0.8
0.7
0.6
0.5
0.4
0.2
0.1
0
29
35
41
47
53
59
65
71
77

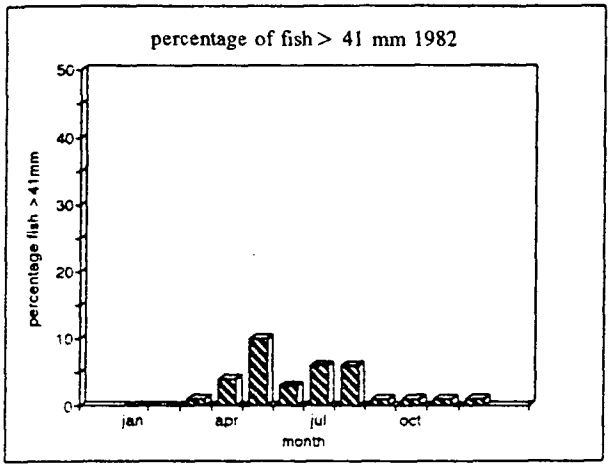

November 1991
fraction retained
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
29
35
41
47
53
65
71
77

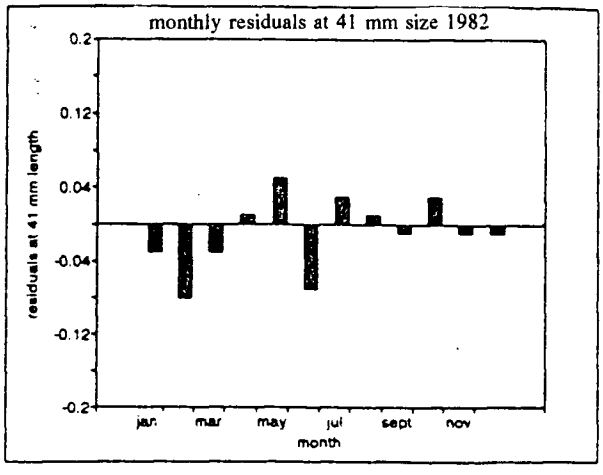

December 1991
fraction retained
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
29
35
41
47
53
59
65
71
77
estimated ogive
observed ogive

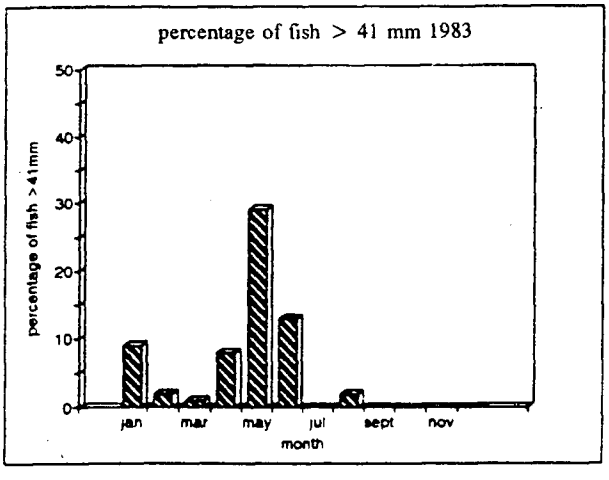

February 1992
August 1992
June 1992
September 1992
July 1992
December 1992
cumulative percentage
length (mm)
estimated ogive
observed ogive

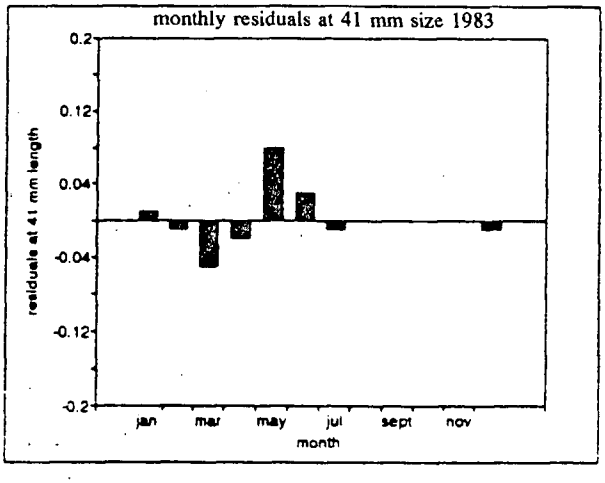
APPENDIX V

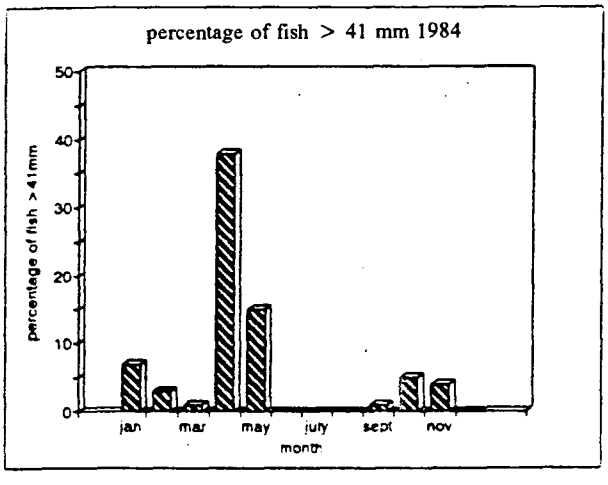
Figure 5.2: Histograms of the monthly percentages and their respective residual plots at 41 mm length. For each month, the percentage of fish that are ≤ 41 mm in length provide an stimate of the part of the population that has recently recruited into the fishery. Months with higher percentages imply higher recruitment. Residuals are calculated from the annual monthly mean for each year from January 1982 to December 1992.

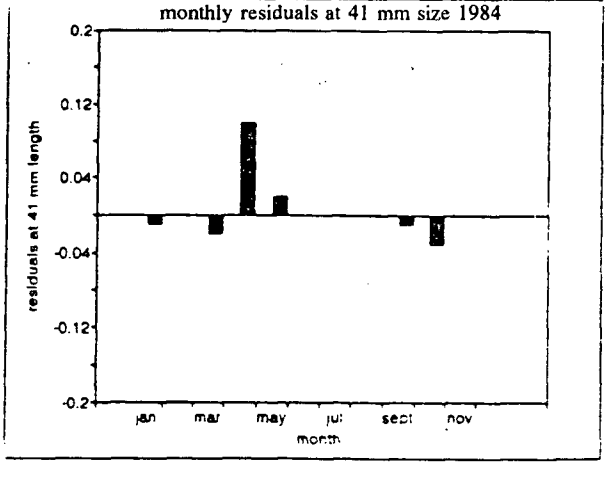

percentage of fish > 41 mm 1982
percentage fish >41mm
50
40
30
20
10
0
jan
apr
jul
oct
month

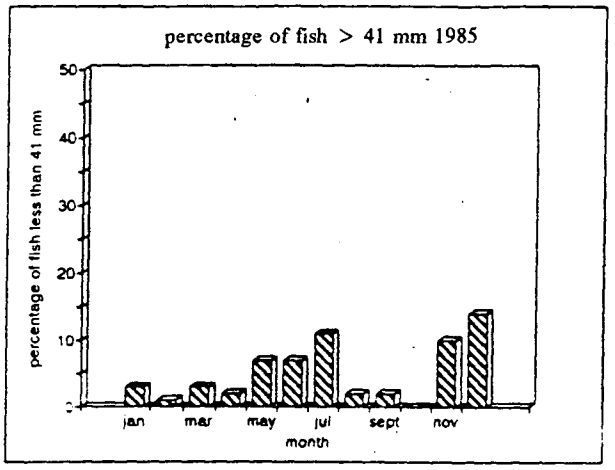

monthly residuals at 41 mm size 1982
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

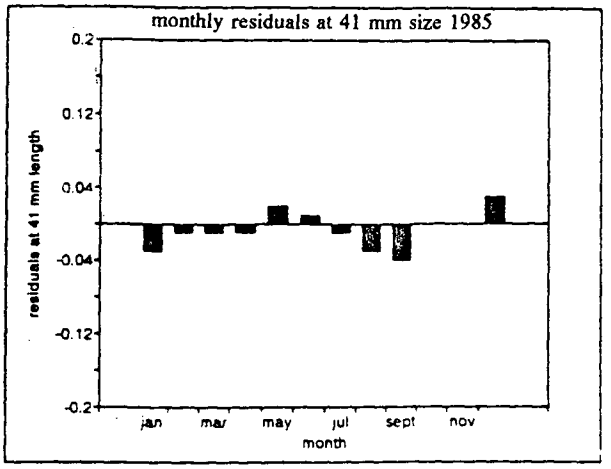

percentage of fish > 41 mm 1983
percentage of fish >41mm
50
40
30
20
10
0
jan
mar
may
jul
sept
nov
month

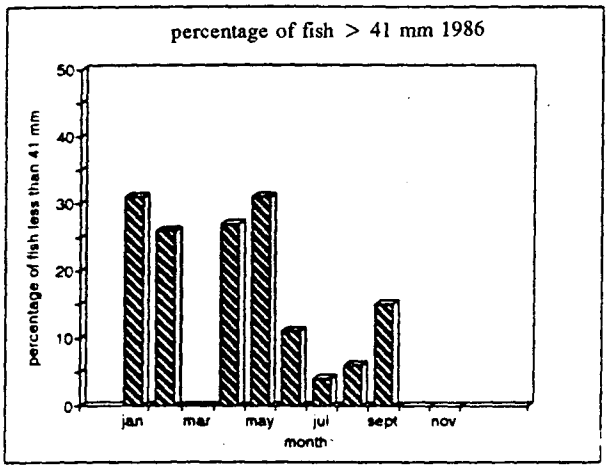

monthly residuals at 41 mm size 1983
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

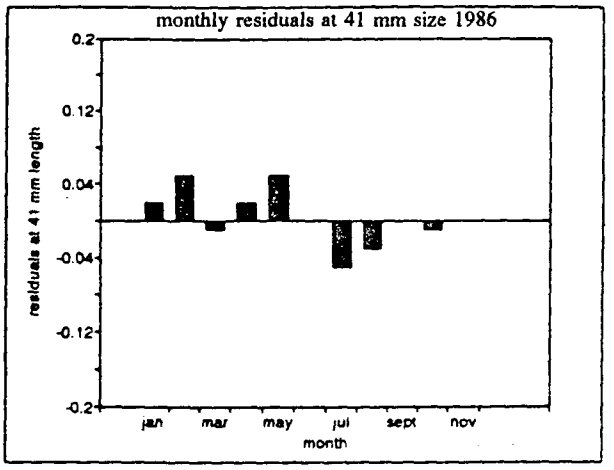

percentage of fish > 41 mm 1984
percentage of fish >41mm
50
40
30
20
10
0
jan
mar
may
july
sept
nov
month

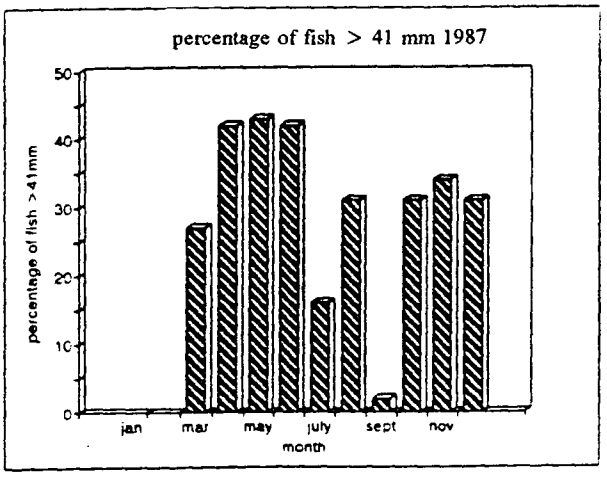

monthly residuals at 41 mm size 1984
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

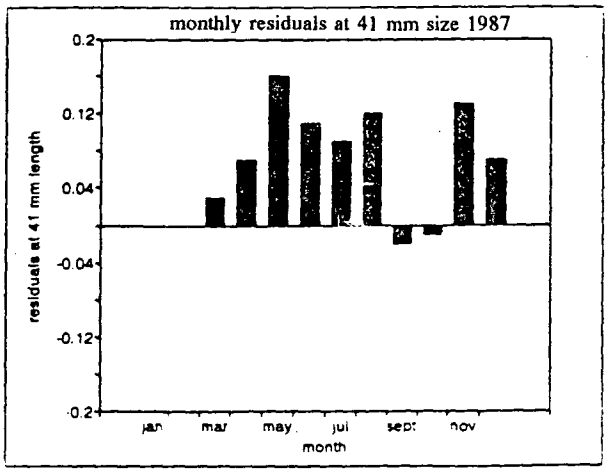

percentage of fish > 41 mm 1985
percentage of fish less than 41 mm
0
10
20
30
40
50
jan
mar
may
jul
sept
nov
month

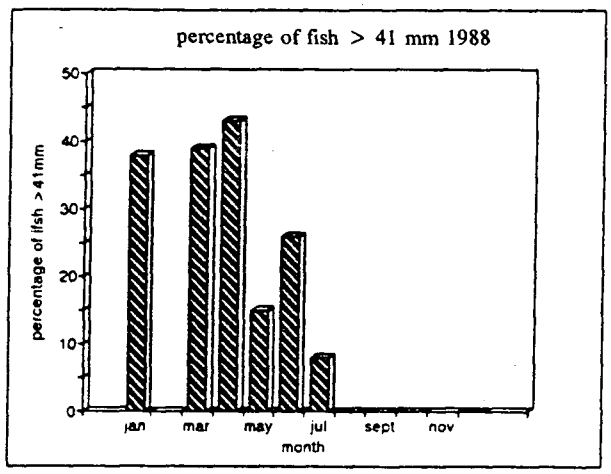

monthly residuals at 41 mm size 1985
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

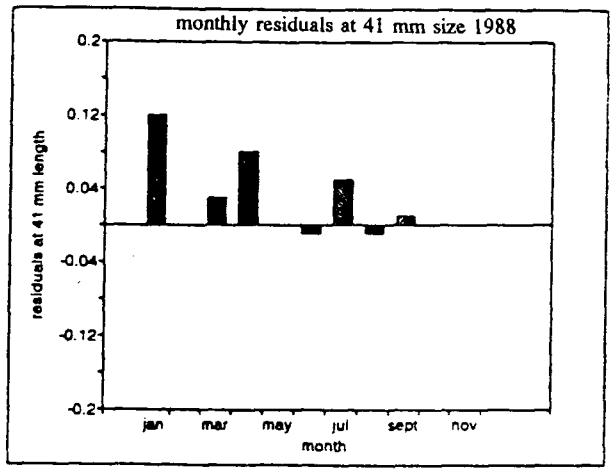

percentage of fish > 41 mm 1986
percentage of fish less than 41 mm
0
10
20
30
40
50
jan
mar
may
jul
sept
nov
month

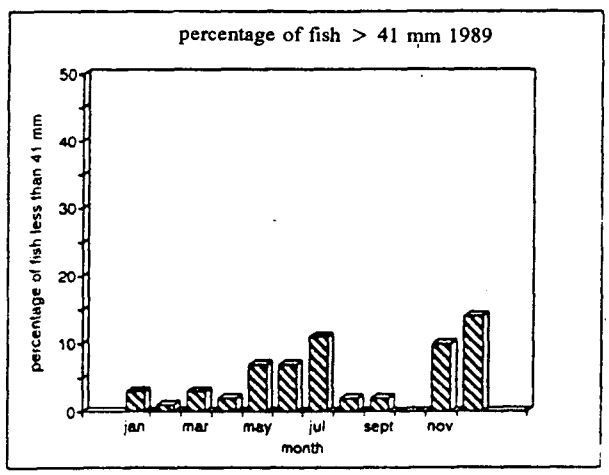

monthly residuals at 41 mm size 1986
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

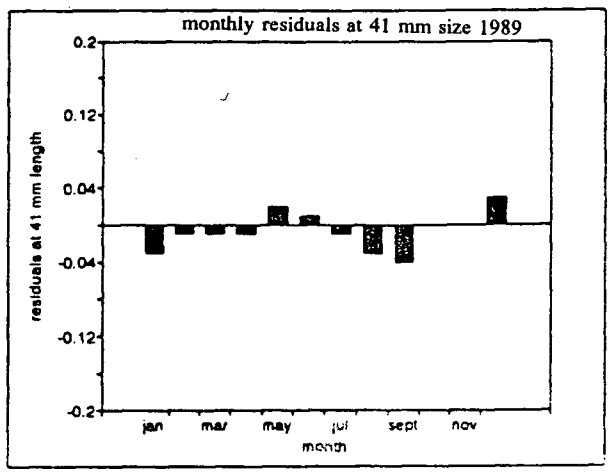

percentage of fish > 41 mm 1987
percentage of fish >41mm
0
10
20
30
40
50
jan
mar
may
july
sept
nov
month

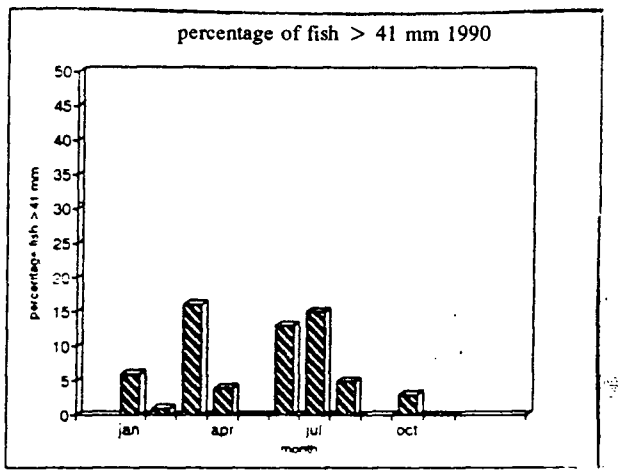

monthly residuals at 41 mm size 1987
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

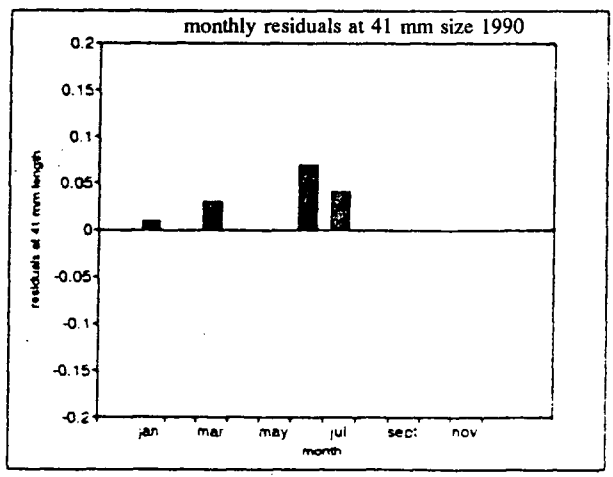

percentage of fish > 41 mm 1988
percentage of ifsh > 41mm
50
40
30
20
10
0
jan
mar
may
jul
sept
nov
month

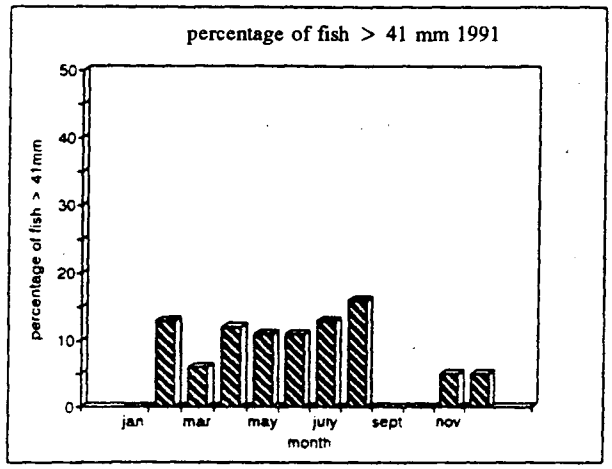

monthly residuals at 41 mm size 1988
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

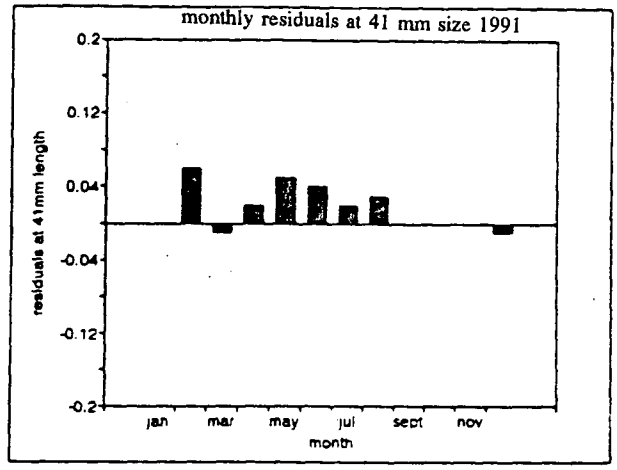

percentage of fish > 41 mm 1989
percentage of fish less than 41 mm
50
40
30
20
10
0
jan
mar
may
jul
sept
nov
month

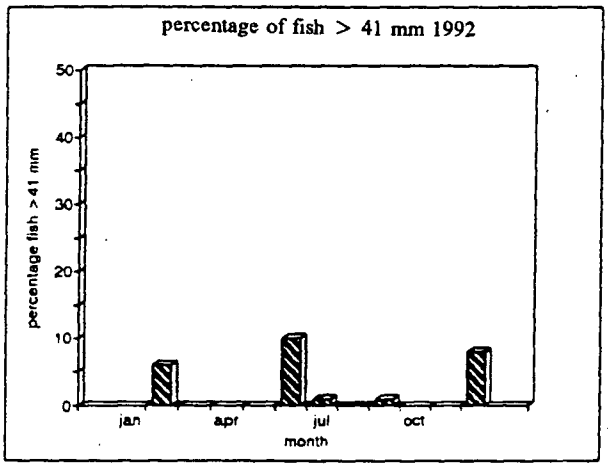

monthly residuals at 41 mm size 1989
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

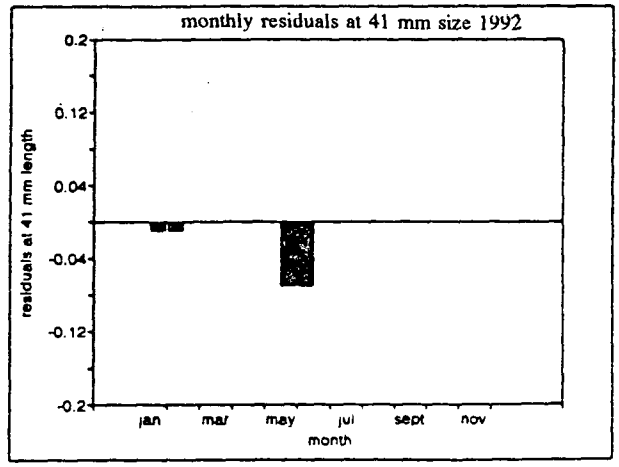

percentage of fish > 41 mm 1990
50
45
40
35
30
25
15
10
5
0
jan
apr
jul
oct


monthly residuals at 41 mm size 1990
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.15
-0.2
jan
mar
may
jul
sept
nov


percentage of fish > 41 mm 1991
percentage of fish > 41mm
50
40
30
20
10
0
jan
mar
may
july
sept
nov
month

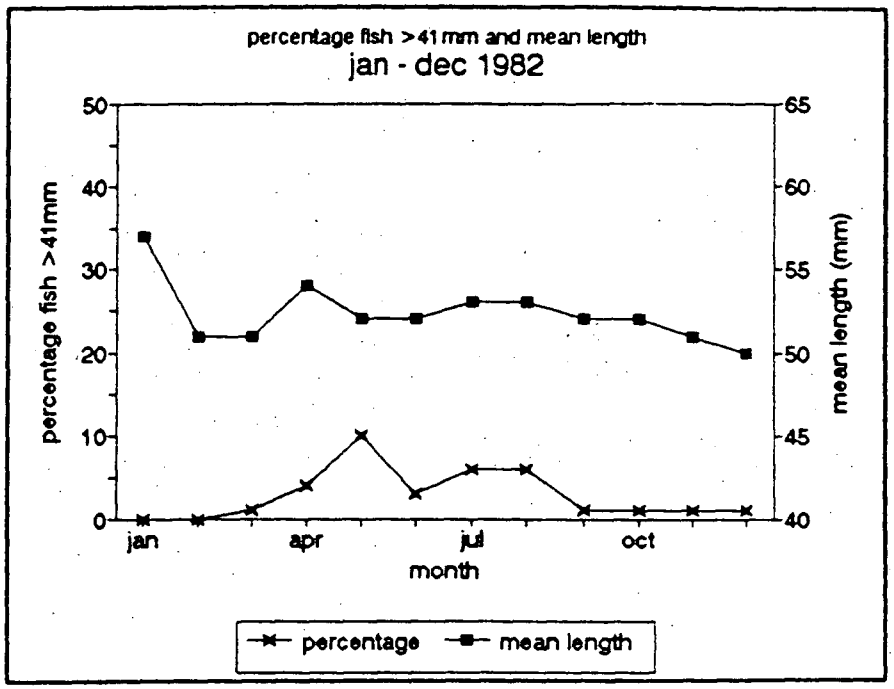

monthly residuals at 41 mm size 1991
residuals at 41mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

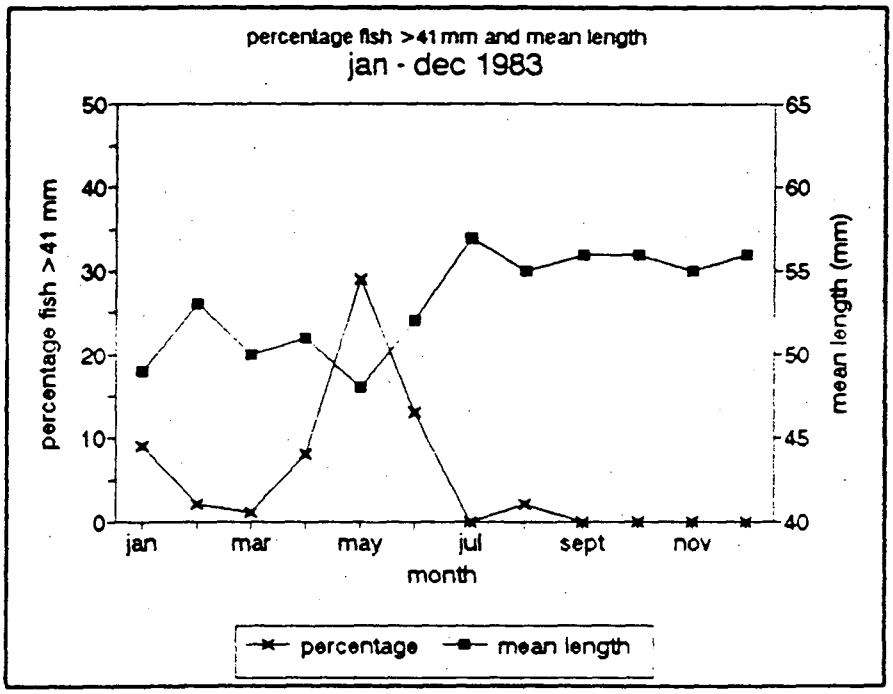

percentage of fish > 41 mm 1992
percentage fish > 41 mm
50
40
30
20
10
0
jan
apr
jul
oct
month

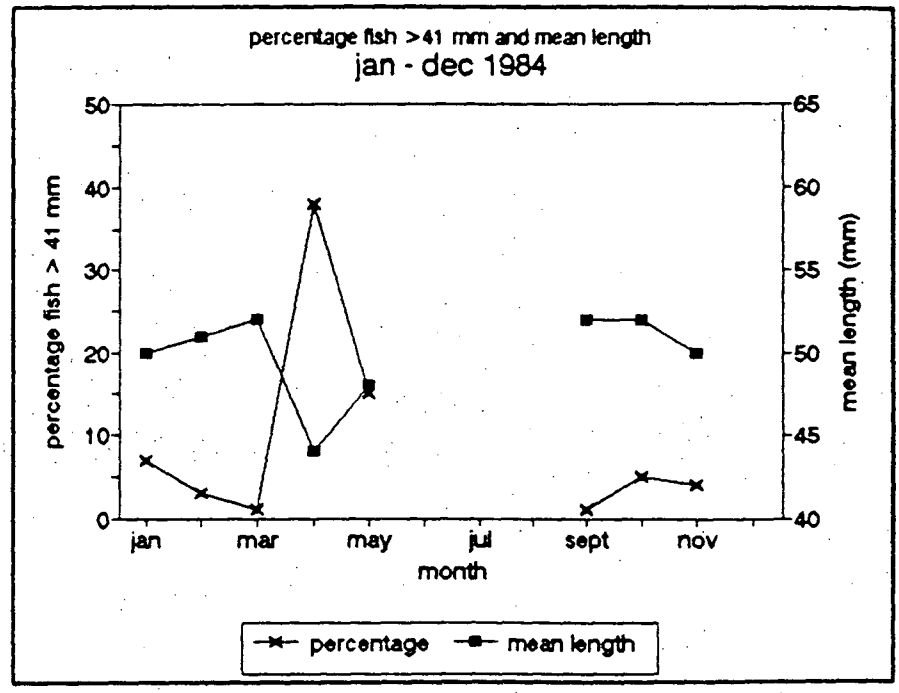

monthly residuals at 41 mm size 1992
residuals at 41 mm length
0.2
0.12
0.04
-0.04
-0.12
-0.2
jan
mar
may
jul
sept
nov
month

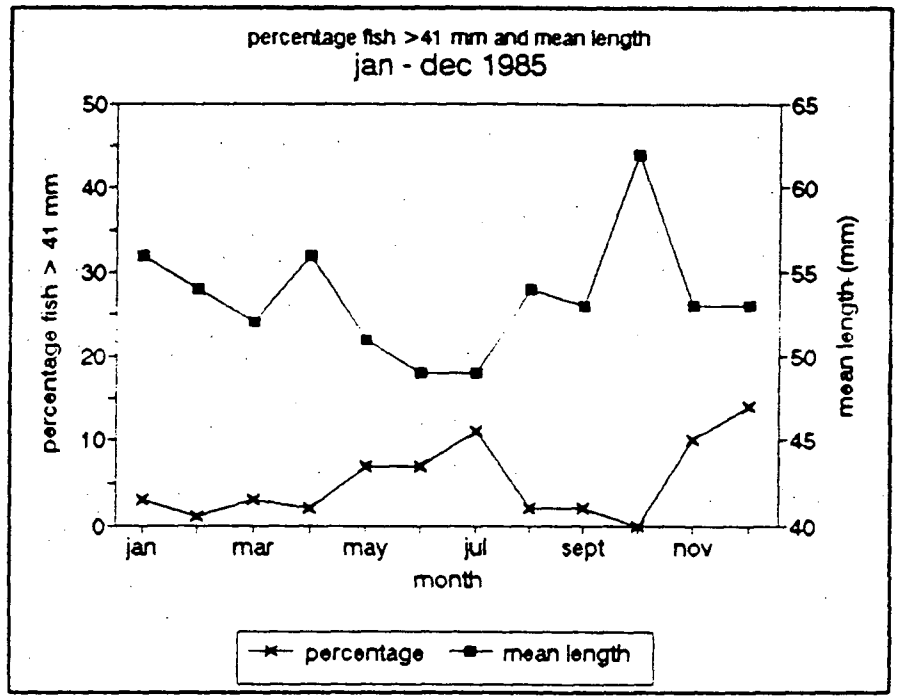
APPENDIX VI

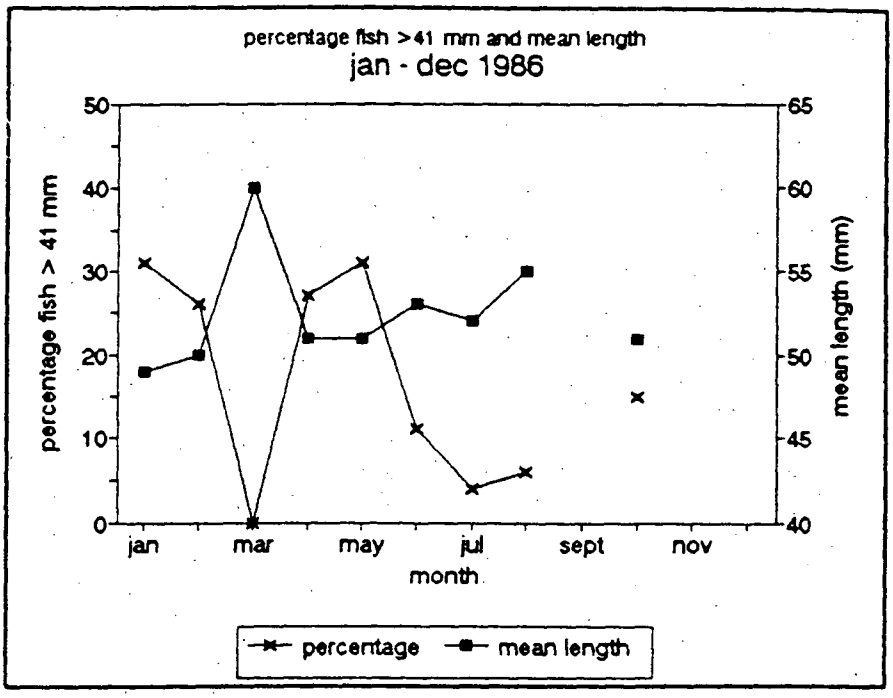
Figure 5.4: Monthly mean sizes of fish in the fishery superimposed on the recruitment curves to investigate the influence of recruits on the mean size of fish in the catch. Months of high recruitment are identified by a small mean size in catch and vise versa.

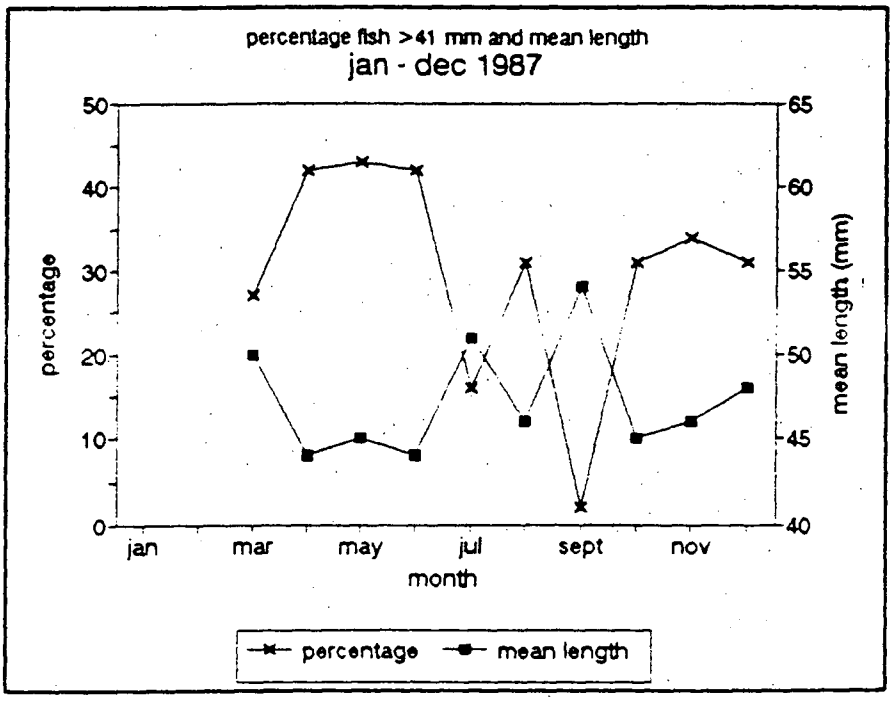

percentage fish >41mm and mean length
jan - dec 1982
percentage fish >41mm
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
apr
jul
oct
month
percentage
mean length

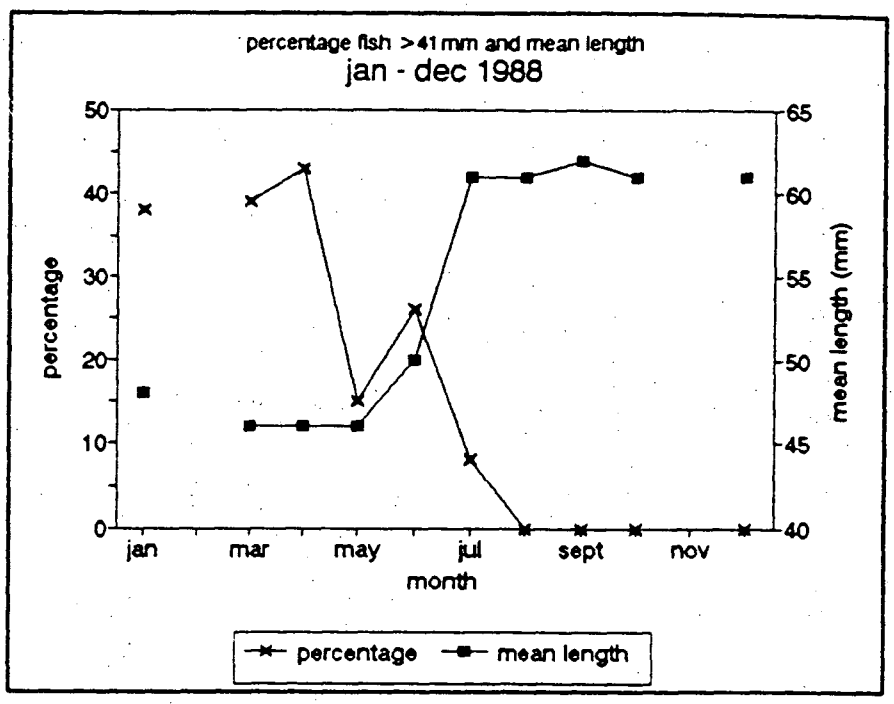

percentage fish >41 mm and mean length
jan - dec 1983
percentage fish >41 mm
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
mar
may
jul
sept
nov
month
percentage
mean length

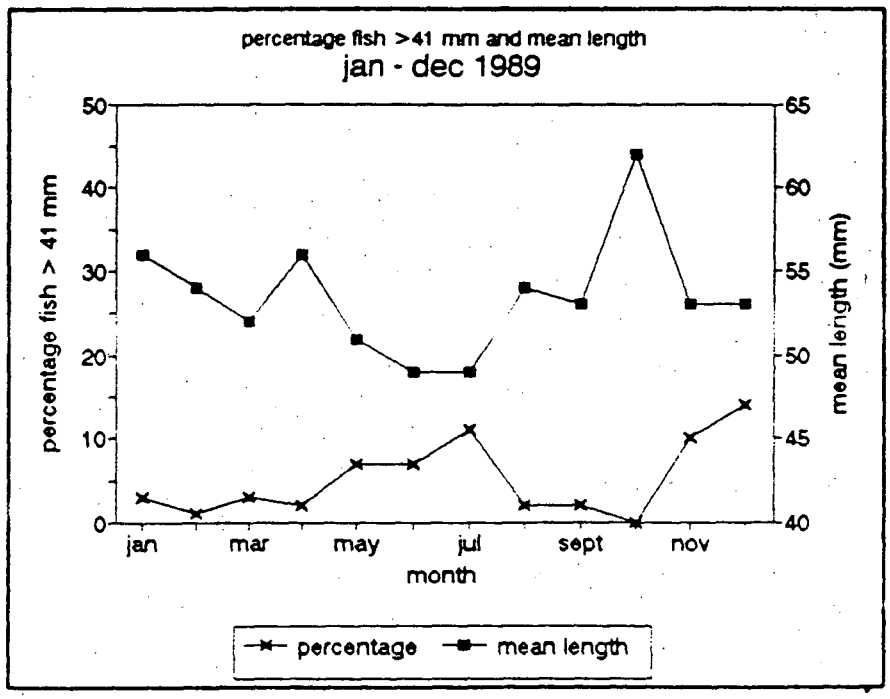

percentage fish >41 mm and mean length
jan - dec 1984
percentage fish > 41 mm
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
mar
may
jul
sept
nov
month
percentage
mean length

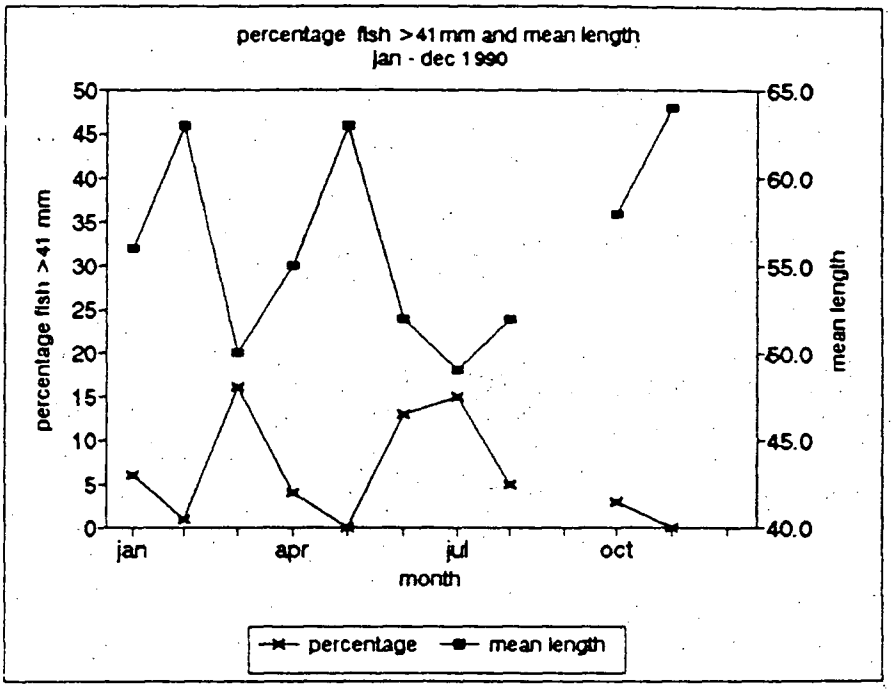

percentage fish >41 mm and mean length
jan - dec 1985
percentage fish > 41 mm
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
mar
may
jul
sept
nov
month
percentage
mean length

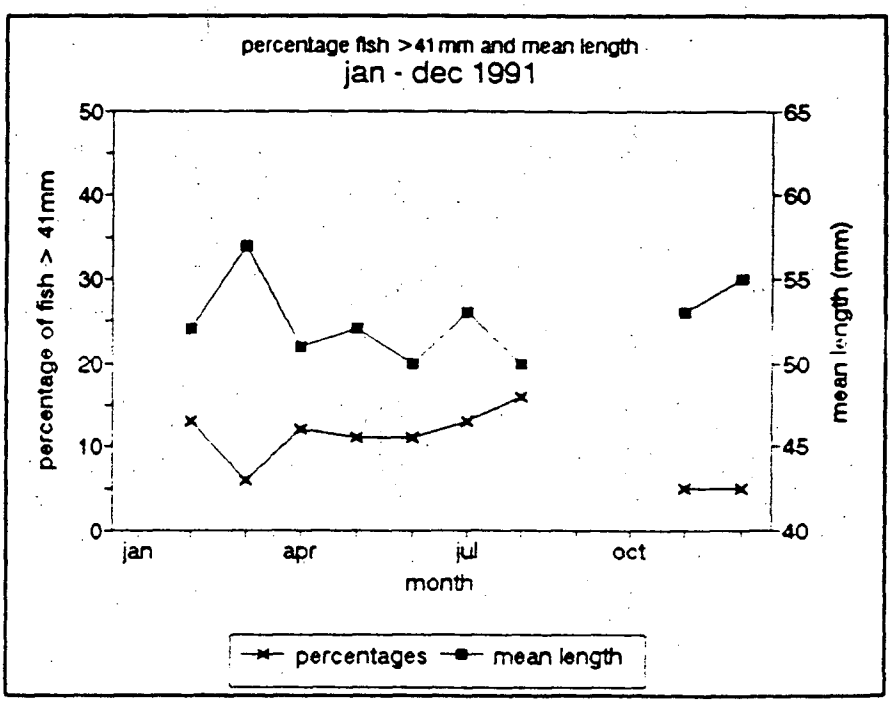

percentage fish >41 mm and mean length
jan - dec 1986
percentage fish > 41 mm
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
mar
may
jul
sept
nov
month
percentage
mean length

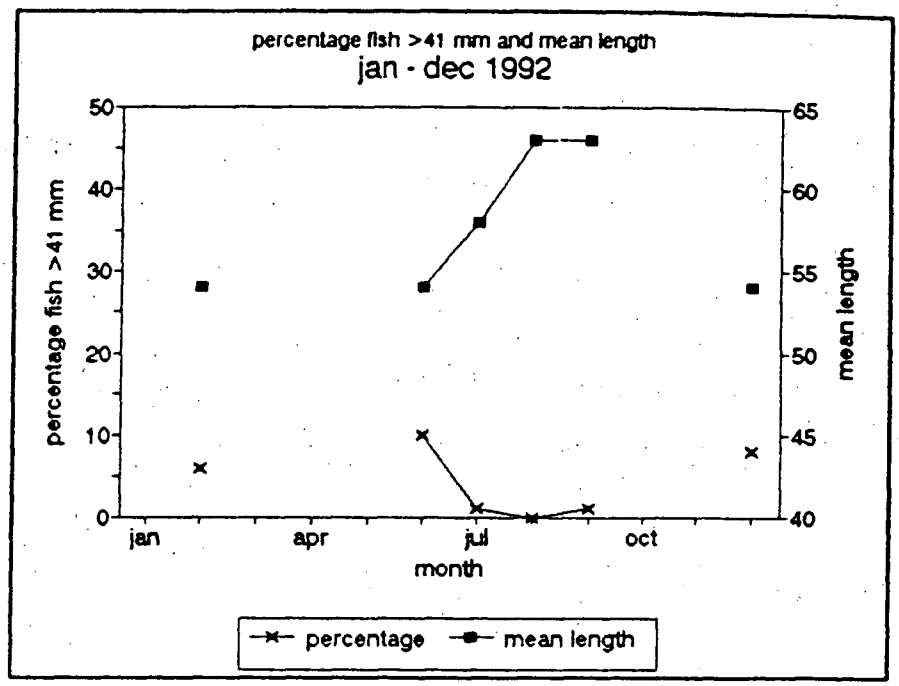

percentage fish >41 mm and mean length
jan - dec 1987
percentage
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
mar
may
jul
sept
nov
month
percentage
mean length


percentage fish >41 mm and mean length
jan - dec 1988
percentage
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
mar
may
jul
sept
nov
month
percentage
mean length


percentage fish >41 mm and mean length
jan - dec 1989
percentage fish > 41 mm
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
mar
may
jul
sept
nov
month
percentage
mean length


percentage fish >41 mm and mean length
jan - dec 1990
percentage fish >41 mm
mean length
50
45
40
35
30
25
20
15
10
5
0
65.0
60.0
55.0
50.0
45.0
40.0
jan
apr
jul
oct
month
percentage
mean length


percentage fish >41 mm and mean length
jan - dec 1991
percentage of fish > 41mm
mean length (mm)
50
40
30
20
10
0
65
60
55
50
45
40
jan
apr
jul
oct
month
percentages
mean length


percentage fish >41 mm and mean length
jan - dec 1992
percentage fish >41 mm
mean length
month
jan
apr
jul
oct
0
10
20
30
40
50
40
45
50
55
60
65
percentage
mean length