THE UNIVERSITY OF MANITOBA

A STUDY ON THE ECOLOGY OF KATLE, *NEOLISSOCHILUS HEXAGONOLEPIS* (McCLELLAND), IN A NEPALESE RESERVOIR AND RIVER

BY

DEEP B. SWAR

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY
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A STUDY ON THE ECOLOGY OF KATLE, (Neolissochilus hexagonolepis) (McClelland), IN A NEPALESE RESERVOIR AND RIVER

BY

DEEP B. SWAR

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

DEDICATION

I would like to dedicate this thesis to my late parents, Veer Bahadur and Bhagirathi Swar, who could not see this end of my academic journey.

ABSTRACT

A study on feeding, age, growth and reproductive biology of katle, *Neolissochilus hexagonolepis*, was conducted in the newly created Indrasarobar Reservoir and in the Tadi River in Nepal during January, 1988, to December, 1990. The objective was to assess katle's adaptability from a riverine to a lacustrine environment.

Monthly samples of katle were collected. Volumetric gut content analysis revealed katle's euryphagous nature. Animal matter, plant matter and detritus and soil constituted 21.8, 68.8 and 9.4% respectively of the gut contents of fish from the river, and 29.0, 56.0 and 15.0% in the reservoir. One annual peak of feeding intensity was observed in both systems, as well as seasonal variation in diet composition. The contribution of plant food increased with the size of the fish. The gut length of katle was allometrically related to its total length in both habitats, more strongly in the reservoir population. This appears to be a major adaptation to the reservoir in the feeding ecology of katle.

Age determinations showed that one annulus was formed in the bony parts of katle annually. Oxytetracycline marking confirmed the validity of ages derived from pectoral fin rays. Females attained a larger size than males. The annual length increment was high for the first four years of life and declined after maturity. Growth data were fitted to the von

Bertalanffy growth model. The estimated maximum lengths L_∞ for females (73 cm for the reservoir and 45 cm. for the river) were higher than those for males (41 and 26 cm). The K values were higher in males (0.195 yr^{-1} for the river and 0.135 yr^{-1} for the reservoir) than in females (0.089 and 0.120 yr^{-1}). A positive correlation was observed between the average area of the reservoir during the warm months (April to October) and annual length increments in reservoir katle of specified age.

Radio telemetry studies of female katle revealed their upstream pre-spawning migration. Quantitative studies on the gonadal maturation cycle revealed that katle are partial spawners of low fecundity.

This study has shown that katle is a euryphagous, slow growing, long living and multiply spawning hill stream cyprinid that has adapted well to the lacustrine environment of the Indrasarobar Reservoir.

ACKNOWLEDGEMENTS

After several years in the Freshwater Institute, Department of Fisheries and Oceans (Canada), the Department of Zoology, University of Manitoba, the Fisheries Development Division, Kathmandu, and the School of Biological and Molecular Sciences, Oxford Brookes University, U. K., I have had the opportunity to meet many people who have made my tenure most enjoyable and at times, bearable. I take great pleasure at this time in thanking those people.

First and foremost, I would like to express my sincere appreciation to Dr. John F. Craig, my supervisor. Dr. Craig has always acted more as a role model than as a taskmaster, believing that motivation and inspiration must ultimately come from within. He has never demanded nor pushed but rather guided and advised. He always welcomed questions and enjoyed the ensuing discussions. Continuation of his supervision even after leaving his job in Canada is evidence of his commitment to myself and this research project. His insight and supervision in this research project were indispensable. Without his help, there is no doubt this thesis would have never been completed. He knew that I would finish the race even when I did not believe it myself. Dr. Craig, it is very difficult to find the words to thank you for all your favour.

I am also grateful to the members of my advisory committee: Drs. F.J. Ward, K.W. Stewart and T.J. Wiens of the

Department of Zoology; Dr. W. Guenter, Department of Animal Science and Dr. R. A. Bodaly, Freshwater Institute, Department of Fisheries and Oceans (Canada) for their invaluable suggestions and understanding the field problems over the course of my research. Their comments on my dissertation were very helpful to improve its quality. I would like to especially thank Drs. F.J. Ward and T.J. Wiens, who were my acting supervisors after Dr. Craig moved to the United Kingdom. I would also like to thank Dr. Wim L.T. van Denson, Wageningen Agriculture University, The Netherlands, for his helpful comments.

Dr. K. Mills and Mr. John Babaluk, Freshwater Institute, Department of Fisheries and Oceans (Canada), were very kind in assisting me in reading the cross sections of fin rays and taking the photographs of the sections. I thank them for their valuable contribution to my research.

I would like to thank the Ministry of Agriculture, His Majesty's Government of Nepal, and the International Development Research Centre, Canada (IDRC) for providing me with the opportunity of pursuing higher studies in Canada.

I would like to take this opportunity to express my appreciation to Dr. B.F. Davy and Mr. A. McNaughton of IDRC for their support toward the completion of my degree.

The Nepal Electricity Authority, Kulekhani Division, provided housing and valuable data on meteorology and water fluctuation in the Indrasarobar Reservoir.

I thank the following personnel from the Oxford Brookes University, UK: Mrs. Diana Cox for providing laboratory assistance, Mr. Derek Whiteley for assisting me in illustration and Dr. Tomek Brus for helping me in data analysis.

Dr. J. Shrestha and Mrs. A. Tamrakar, Department of Zoology, Tribhuvan University, Kathmandu, provided valuable suggestions and literature, and assisted in identifying the aquatic insects, respectively. Dr. M. Nakanishi, Centre for Ecological Research, Kyoto University, Japan, provided constant encouragement throughout the study period.

I am grateful to Messrs. M.B. Pantha, B.C. Shrestha, A.K. Rai, P.L. Joshi, K.R. Bastola, R.M. Mulmi, B. Silwal. H.N. Manandhar, B.R. Pradhan, Gagan B.N. Pradhan, Mr. D.M. Singh, T.B. Gurung, Mrs. N. Pradhan and Mrs. S. Rana, Fisheries Development Division, Kathmandu, for their support.

Mrs. Hilary Craig proofread the thesis; Dr. J.A. Mathias, Mr. L.P. Tripathy, Mrs. S. Tripathy and Ms. Martha Janzen provided support for me and my family during our stay in Winnipeg. I express my sincere appreciation for their kindness. I also benefited from the computer expertise of Mr. Bhaskar Tripathy in preparing some of the graphs.

Mr. R.B. Singh and Mrs. Sushila Singh, my parents-in-law, provided great support for pursuing this study in a variety of ways. Their kind assistance will never be forgotten.

Last but not least, I would like to express my sincere appreciation to my dear wife Bijaya, son Shikhar and daughter Smriti who are the main driving force behind my motivation and enthusiasm.

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CHAPTER I

GENERAL INTRODUCTION

The impoundment of a river can cause substantial qualitative and quantitative changes in the limnological conditions of the water body (Lewis, 1974). The aquatic environment provided by the semi-static waters of the reservoir differs markedly from that which prevailed before inundation. One immediate consequence is the conversion of a naturally lotic environment to a lentic habitat which affects several abiotic factors such as temperature, flow, substrate, dissolved and suspended substances and the chemical properties of the water. Such changes in the hydrological equilibrium have a profound influence on the aquatic environment. Generally, formation of a reservoir leads to an increase in the amount of inorganic and organic nutrients in the water derived from the catchment area. These nutrients support the development of abundant populations of phyto- and zooplankton in the new water body. The formation of the reservoir also destroys many invertebrate species that are suited to running water. This is partially due to siltation, an anoxic bottom and the pronounced drawdown that affects the littoral production. When a river environment is altered through impoundment, certain changes in the structure of the fish population have also been observed (Crisp et al., 1983; Eley et al., 1981; Motwani and Saigal, 1977; Singit et al., 1988). Those fish requiring moving water, riffle areas or holes with rock and gravel substrate will be reduced in number or lost entirely. Other fish which prefer bodies of stationary water will increase in numbers. The changes in the composition and abundance of both planktonic and benthic communities also affect the food supply to many species of fish. Besides the food resources and living conditions, the fish community in the reservoir is strongly influenced by changes in the available spawning habitats and by blockage of upstream or downstream migrations caused by dam structures across the river (Benson, 1980; Cain, 1974; Beam, 1983; Gasaway, 1970). The impact of reservoir construction on fish populations in temperate countries has been well documented and several recommendations have been put forward to mitigate the effect on the fish fauna (Craig and Bodaly, 1988; Paxton et al., 1981; Walburg, 1976, 1977; Lusk, 1981). However, only limited information is available on tropical reservoirs (Tansakul et al., 1992; Sreenivasan, 1976; Hamman, 1980; Petr, 1967). In Nepal, biological investigations on reservoirs started only ten years ago.

Nepal (26°20′-30°10′ N and 80°15-88°19′ E) has common frontiers with the Tibetan Autonomous Region of China in the north and with the Republic of India in the west, east and south. It has an area of 147,181 km^2 and is divided into three physiographic regions, from south to north: the Terai plain, the mid hills and the Himal (Central Bureau of Statistics, 1992). The Terai lies between 130 m and 500 m elevation, the lower hills up to 2,700 m, the upper hills up to 4,000 m and the greater Himalayas are located above the tree line (>4,600 m). Mountains and hills make up 83% of the area of Nepal while the Terai occupies only 17%. The Himalayas in the north strongly influence the climate of Nepal. The country may be divided into three climatic zones according to altitude: subtropical in the Terai, temperate in the hills and alpine in the mountains. The climate varies little from east to west .

The geographic and climatic range influences the diversity of the flora and fauna of Nepal. There are many suitable habitats for native fishes. A total of 172 indigenous and 10 exotic fish species has been recorded from different rivers, lakes, reservoirs and other water bodies (Edds, 1986; Rajbanshi, 1982; Shrestha, 1981, 1990a, 1992; Terashima, 1984). Rivers, lakes and reservoirs make up approximately 55% of the total water area; the rest is in the form of flood plains and irrigated rice fields. The rivers represent most of this area. Rivers and streams, numbering more than 6,000 and with a total length of about 21,000 km, flow generally from north to south (Shrestha, 1983). There are three major river systems in Nepal, each with seven main tributaries: Sapta Koshi in the east, Sapta Gandaki in the centre and Sapta Karnali in the west. In addition the Mahakali, the Babai, the Rapti, the Bagmati, the Kamala and the Mechi rivers are sizeable. These river systems drain into the River Ganges. The combined run-off from Nepalese rivers contributes a substantial percentage to the annual flow of the River Ganges.

Lakes are scattered throughout the country and have a total area of c. 5,000 ha. These lakes have different origins: glacial, tectonic and ox-bow (Sharma, 1977). Lakes located above 4,000 m (in the north) are mostly glacial in origin. These glacial lakes are the source of the country's major rivers. The majority of tectonic lakes occur in the mid hill region. Most of these lakes have been drained and used for agriculture (Malla and Shrestha, 1983). The ox-bow lakes are located in the southern flood plain of the country. They are the dead arms of rivers in the Terai region and provide suitable habitats for various species of aquatic fauna and flora.

To produce adequate electricity for its requirements, Nepal must harness its water resources. It has a long-term plan to create several multipurpose reservoirs by damming rivers at appropriate points. Pradhan (1987) has estimated that the potential area for reservoir development is c. 152,220 ha. At present, there are only nine reservoirs in Nepal with a total area of 1,500 ha. These reservoirs have been constructed mainly for hydroelectric power and irrigation (Pradhan, 1987). They include Indrasarobar (226 ha), Jagdishpur (125 ha), Trisuli (16 ha), Marsyangdi (62 ha), Panauti (50 ha), Gandak (100 ha), Sunkoshi (60 ha) and Andhikhola (90 ha).

The Indrasarobar Reservoir was formed in 1981 by the construction of a dam (height 114 m) on the Kulekhani River. This reservoir serves as a water storage basin for hydroelectric power. The filling of the reservoir started in June, 1981, but the peak water level (100.1 m) was reached only in November, 1983. Since then the annual drawdown has resulted in water level fluctuations between 17 and 46 m below the peak level.

The first documented survey of the fish species composition of the stretch of river now occupied by the reservoir was conducted in 1980 (S.B. Shrestha, personal communication). It was reported that the Cyprinidae was the most abundant family by number of species, represented by *Garra lamta* (Gray), *Neolissochilus hexagonolepis* (McClelland), *Puntius chilinoides* (Ham), *Schizothorax richardsonii* (Gray), *Puntius ticto* (Ham) and *Puntius* spp. The families Cobitidae and Channidae were represented by *Noemacheilus* spp. and *Channa gachua* (Ham) respectively. The family Sisoridae was represented by *Glyptosternum* spp. and *Coraglanis* spp. A survey of the fish fauna of the Kulekhani River upstream of the reservoir was carried out during 1984/85 by the Inland Fisheries Project assisted by the International Development Research Centre (IDRC) of Canada. It revealed that the Cyprinidae was the most abundant family (no figures given) followed in order of importance by the Sisoridae, Cobitidae and Channaidae (Pradhan, 1986). A further comprehensive investigation of the fish populations in the Indrasarobar Reservoir was made from January, 1985, to June, 1989. Monthly experimental fishing was carried out from seven stations distributed throughout the reservoir, using multipanel gill nets. The catch composition showed that the Cyprinidae was the only family which remained in the reservoir. The other families had disappeared.

Katle, *Neolissochilus hexagonolepis*, was the dominant species in the reservoir throughout the study period. The mean percentage by weight and number of katle in the total catch for the whole period of 1985 to 1989 was 69.35% and 49.9% respectively. Karange, *Puntius chilinoides*, was the second most dominant species, comprising 22.05% by weight and 44.2% by number of the total catch throughout the study period. Asala, *Schizothorax* richardsoni, the dominant species by number in the pre-impounded river, formed a very small part of gill net catches in the reservoir, never more than 2% by weight and 6% by number throughout the study period (Swar, 1992).

The construction of the Kulekhani Dam resulted in the conversion of 7 km of the river into a lake. This transformed a varied but unstable riverine environment into a relatively stable lacustrine one although subject to extensive drawdown. A profound change in the relative abundance of many species occurred within a short time of the lake's formation. This included:

a. a drastic decline in the number of asala; and

b. the disappearance of *Puntius* spp., *G. lamta*, *Noemacheilus* spp., *C. gachua*, *Glyptosternum* spp. and *Coraglanis* spp.

Katle and karange, two indigenous species, remained dominant. It is reasonable to infer that the katle and karange can adapt from conditions in a river to those in a lacustrine habitat.

The main objective of this study is to assess the adaptability of the katle by comparing food and feeding, age and growth and reproductive biology in the Indrasarobar Reservoir with that in a nearby river, the Tadi River.

Katle *Neolissochilus hexagonolepis* (McClelland)

Valid name: *Neolissochilus hexagonolepis* (McClelland 1839), Rainboth (1985). *Neolissochilus hexagonolepis,* the Nepalese "katli" or "katle", has had a very confusing nomenclature since it was first named. A short discussion on the taxonomy of katle is given in Appendix 1. The fish was originally included under the genus *Barbus* by McClelland in 1839. Weber and de Beaufort (1916) called this fish *Lissochilus*. Oshima (1919) created a new genus *Acrossocheilus*. Recently, Rainboth (1985) renamed the genus *Neolissochilus*. Similarly katle is described under different species names. McClelland (1839) was the original author to describe this fish as *Barbus hexagonolepis* from Assam. Later several authors described it under different names from different regions. Day (1878) called it *Barbus dukai*. Other authors who referred to this fish as *B. dukai* were Boulanger (1898) and Annandale (1918) from Burma, and Hora (1923) from Siam (Thailand). Duncker (1904) reported katle as *B. soroides* from Sumatra and Penang and the Malay Peninsula.

The taxonomy of katle is as follows:

Kingdom - Animal, Phylum - Chordata, Subphylum - Vertebrata, Superclass - Gnathostomata, Class - Teleostomi, Subclass - Actinopterygii, Order - Cypriniformes, Suborder - Cyprinoidei, Family - Cyprinidae, Subfamily - Cyprinini, Genus - *Neolissochilus*, Species - *hexagonolepis*.

Vernacular Names:

Katle (Nepali), Bhorkol and Buluk (Bengali), Mirpunia (Lepcha), Boka or Bokar and Boolooah (Assamese).

Main characteristics of *Neolissochilus hexagonolepis*

The fish is olive-green on the dorsal side and silvery-white on the abdomen. The body is elongated and compressed with a deep copper-coloured band above the lateral line. The snout, obtusely rounded, slightly overhangs the jaw (Fig. 1:1). The mouth is horizontal and subterminal. Eyes are more anterior towards the snout and lateral in position. The lips are thick and continuous around the angle of the mouth and the lower jaw has a sharp horny covering. There are four barbels,

Figure 1:1. A female katle from the Tadi River.


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STAINLESS STEEL

a pair each in the rostral and maxillary regions. The caudal fin is deeply forked with pointed lobes. The lateral line is complete with twenty-seven scales, and seven scales run in an oblique line from the base of the ventral fin to the ridge of the back. Males are smaller than females. The length of the head in proportion to that of the body is one to four. On the anterior part of the body the exposed surfaces of the scales represent hexagonal outlines. The fin ray counts are

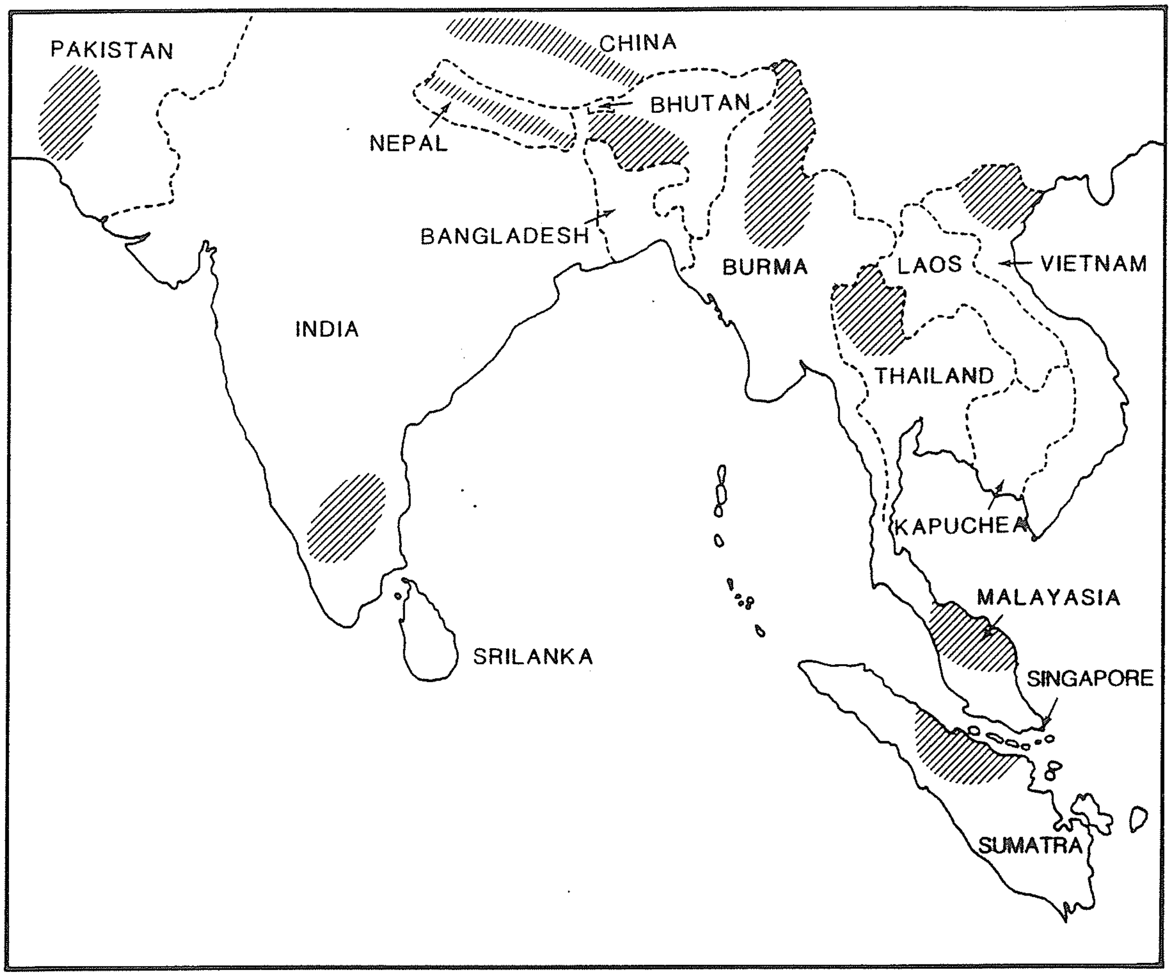
D.12: P.16: V.9: A.7: C.10/9.

In large-sized individuals, scales are blackish grey on the back, the head and the base of the fins, while the fins and the scales on the opercular plates are tipped with yellow. In young fish the fins are edged with black. This species is similar in appearance to *Tor tor* (Ham), mahseer, but can be distinguished at once by the interrupted groove behind the lower lip and it also differs in the length of its head. Head-length is shorter than the height of the body in mahseer but almost equal in katle (Hora, 1940; Hora and Misra, 1941). Shaw and Shebbeare (1937) have distinguished mahseer and katle on the basis of coloration. The katle is deep copper-coloured while mahseer is golden.

Distribution

Katle is distributed in a broad geographic and environmental range (Fig. 1:2). It has been described as a hill stream fish which is distributed in Southern Asian

Figure 1:2. Distribution of the katle in south Asia indicated by hatched areas.


PAKISTAN
CHINA
BHUTAN
NEPAL
BANGLADESH
BURMA
LAOS
VIETNAM
INDIA
THAILAND
KAPUCHEA
MALAYASIA
SRILANKA
SINGAPORE
SUMATRA

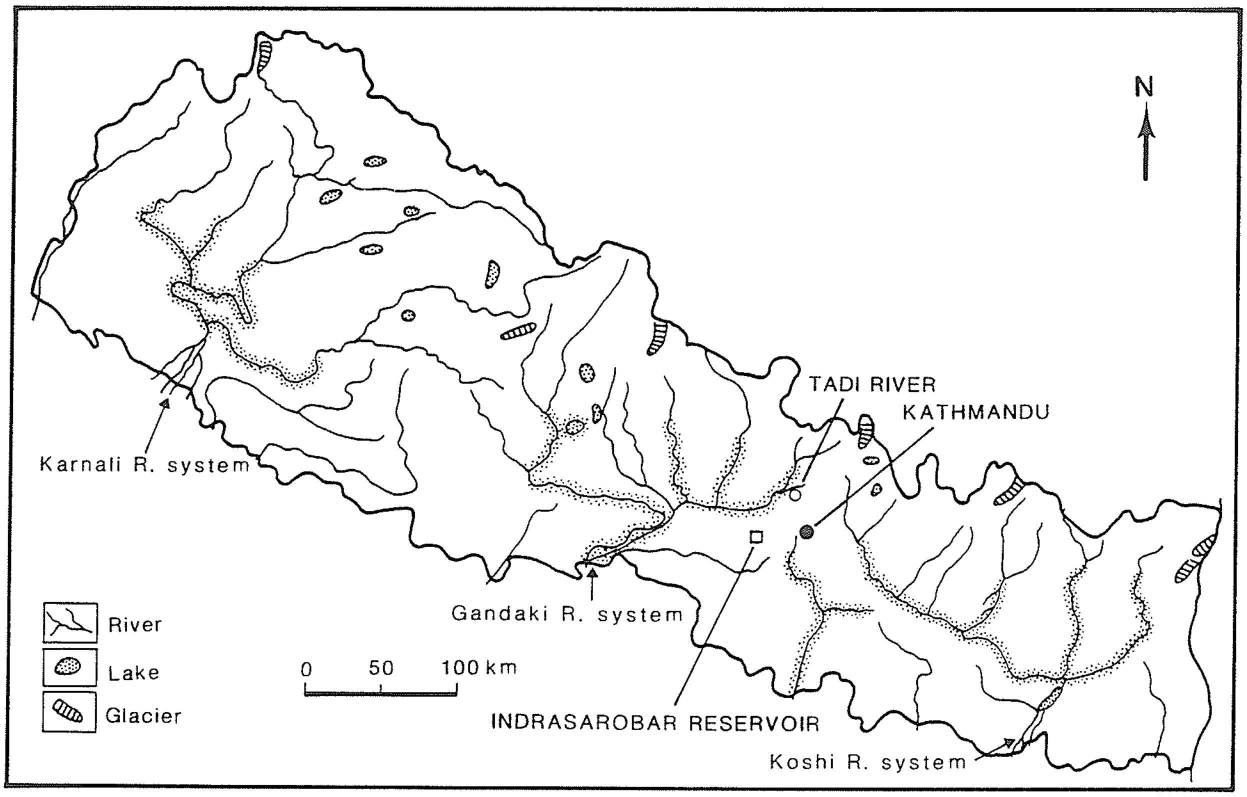
countries such as China, India (Tamil Nadu, Meghalaya, Arunachal Pradesh, Assam, East Bengal, Darjeeling, Eastern Himalayas), Nepal, Pakistan, Burma, Malaysia, Sumatra, Thailand and Vietnam (Day, 1878; Herre and Myers, 1931; Myers, 1931; Shaw and Shebbeare, 1937; Herre, 1940; Hora and Misra, 1941; Chacko *et al*., 1954; Misra, 1959; Jayaram, 1981).

Katle is abundant in most of the big rivers, lakes and reservoirs of Nepal between 250 m and 1,500 m above MSL and in a temperature range of 15-30°C (Rajbanshi, 1982; Shrestha, 1981; Ferro, 1980; Rai and Swar, 1989) (Fig. 1:3). This fish has been reported from the Koshi drainage mainly from the Sunkoshi, Indrawati, Tamor and Arun rivers up to 1,220 m (Shrestha, 1990a). It is common in several rivers like the Narayani, Tadi, Trishuli and the Kali Gandaki drainage from an elevation of 50 m, near Nepal's southern border, to 1,440 m in the mid hills (Edds, 1986). Katle has also been caught from the Bagmati and mid hill region of the Karnali river system (Shrestha, 1990a).

Biology

Katle, a large scaled cyprinid, is well known as an excellent game fish in the mountain streams of Nepal. The largest fish recorded so far is about 11 kg, from Assam, India (Shaw and Shebberae, 1937). Fish of total length >600 mm are common in the rocky, clean, hill streams and rivers of Nepal and India (Misra, 1959; Shrestha, 1992). It is a popular fish

Figure 1:3. Distribution of the katle in Nepal indicated by stippling along the river courses.


N
TADI RIVER
KATHMANDU
Karnali R. system
Gandaki R. system
INDRASAROBAR RESERVOIR
Koshi R. system
River
Lake
Glacier
0 50 100 km

for angling. This is probably the reason katle has attracted the attention of naturalists and anglers like McClelland (1839), Wood (1933) and Langdale Smith (1944), who wrote several articles on the taxonomy, distinguishing characteristics, races and colour variations of katle. However, the biology of the katle remains poorly understood. Mr. D. E. B. Manning, Divisional Forest Officer in Burma, had observed this fish in the hill streams of Burma and supplied the following notes on its habitat to Hora and Misra (1941): "The fish normally lie up in the deep still pools and only exceptionally will they be taken in rapid water. Shoals roam round the pools preferring those that are deep, black and rocky. The fish normally avoid the rocky, fast head waters but drop down to the slow, deep, rocky pools. They run up to spawn about the end of May to June and stay up till the end of September when they go down on one of the late rises. At these times they are found in the rocky swift head water streams. Throughout the year they appear to be in grand condition and appear to be very fat in comparison with the Indian mahseers."

The first authentic account of the spawning habits of katle was recorded by Langdale Smith (1944) who observed the spawning movement of katle in August in his tea estate ponds in the Darjeeling district of India. Few batches of spawners were observed by him. Katle seems to have a prolonged spawning period from April to October (Hora and Nair, 1943; Hora and Ahmad, 1946, cited in Ahmad, 1948; Ahmad, 1948; Rai, 1978;

Jhingran, 1982). According to Ahmad (1948), katle can be stripped like trout and, by providing suitable conditions, can be induced to breed in tanks like common carp. Sometimes ripe females yielded relatively few ova at a time by stripping although innumerable ova in various stages of development were found in the ovaries. It follows that all the ova in an ovary do not become mature at the same time. Ahmad (1948) incubated the fertilized ova of katle and described their embryonic development. The incubation period lasted from 103.5 to 190 hours depending on the water temperature. Dasgupta (1988a) considered the katle to be a prolific breeder though less fecund in comparison to species of mahseer. According to him, the fecundity of this fish in the Simang River (in Meghalaya, India, latitude 25°30" N, longitude 90°40" E and altitude 347 m above MSL) varied considerably from individual to individual and ranged from 533 eggs in a specimen measuring 196 mm total length and 74.4 g in weight to 11,659 in a specimen measuring 442 mm and weighing 1,000 g. The average number of eggs g^{-1} body weight and the number of eggs cm^{-1} body length were found to be 12.49 and 10.93, respectively.

The katle is omnivorous, feeding on plants, small fish, gastropods and insects (Wood, 1933; Ferro and Badagami 1980; Jhingran, 1982; Dasgupta, 1988b).

An initial study was carried out on katle from the Indrasarobar Reservoir during 1985 to 1986 (Kalkman, 1986). She briefly described their feeding, reproduction and growth, using scales to estimate age.

In recognition of the need for detailed scientific information on the biology of the katle, the present investigation was carried out under the Inland Fisheries Project of Nepal assisted by IDRC. It is hoped that the findings of this research will provide the scientific basis for the management of this fish and so increase production of katle in Nepal.

CHAPTER II

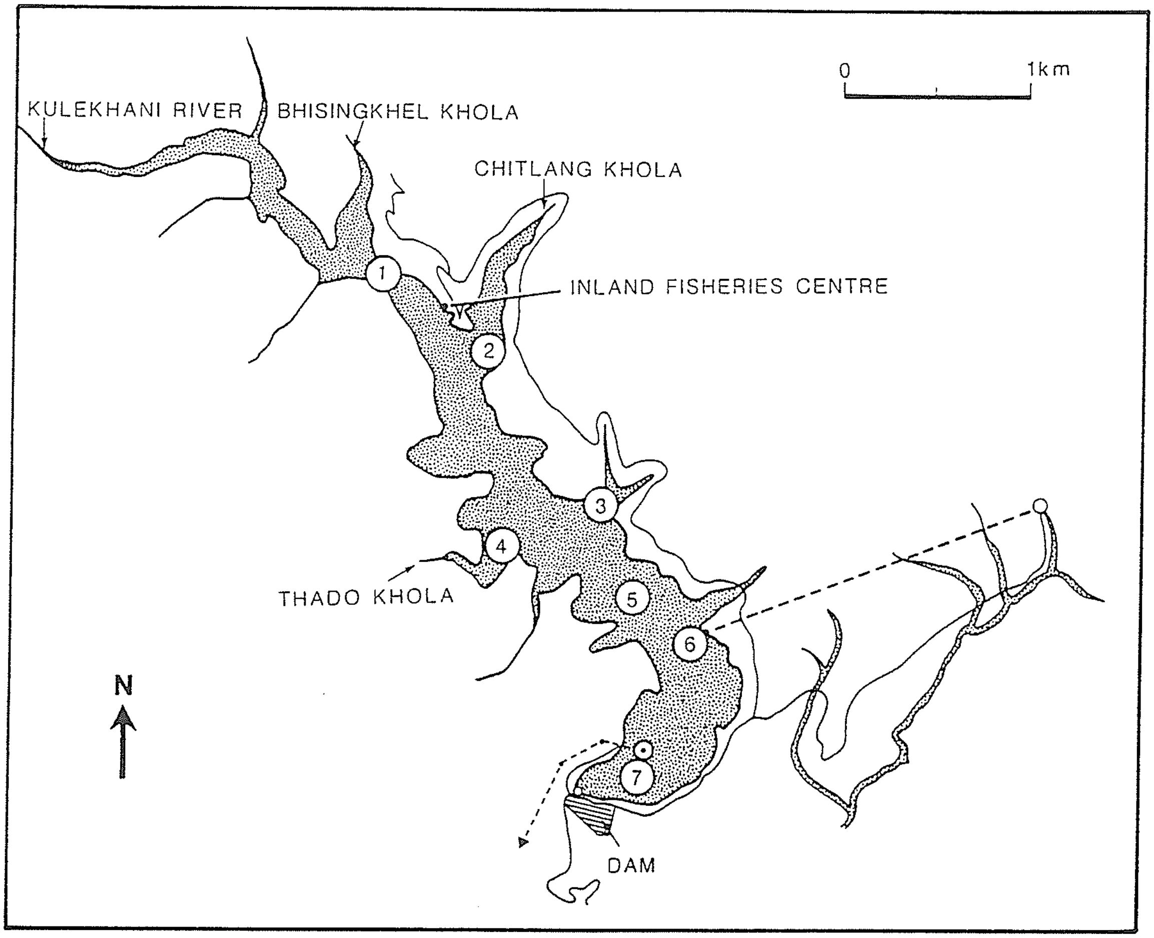
GENERAL MATERIALS AND METHODS

Description of the study area

Indrasarobar Reservoir

The Indrasarobar Reservoir at Kulekhani was formed by damming the Kulekhani River (Fig. 2:1). The reservoir is situated on the southern slopes of the Mahabharat Range at an altitude of 1,430 m above MSL and about 30 km south of the Kathmandu Valley. The catchment area of the reservoir is about 126 km^2. At full water capacity, Indrasarobar Reservoir is approximately 7 km long and 380 m wide and has a maximum depth of 105 m and a volume of 85.3×10^6 m^3. The surface area of the reservoir at full pool is about 226 ha. The valley in which the reservoir is located is steep-sided. Rapid changes in depth occur with filling and drawdown. For example, the water drawdown in June, 1986, resulted in a maximum water depth of 78 m, a volume of less than half (39×10^6 m^3) and a surface area of only 130 ha. The major rivers and streams draining into the reservoir throughout the year are the Kulekhani (Palung) River, the Chakhel River, the Thado Stream, the Chalkhu Stream and the Chitlang Stream. In addition there is the run-off water from the catchment area during the monsoon period (July-September).

Figure 2:1. Map of the Indrasarobar Reservoir showing the gill net sampling stations (1-7).


0
1km
KULEKHANI RIVER
BHISINGKHEL KHOLA
CHITLANG KHOLA
INLAND FISHERIES CENTRE
1
2
3
4
5
6
7
THADO KHOLA
N
DAM

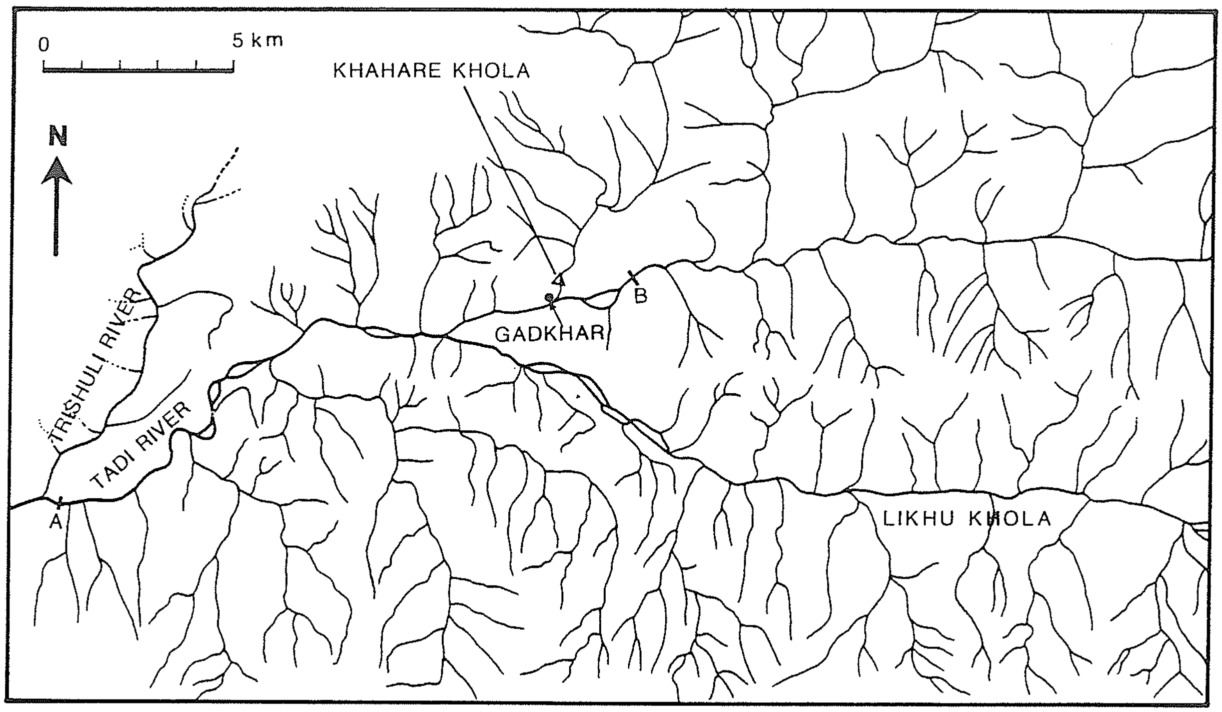
The reservoir is normally at full capacity in the winter months of November and December (Appendix 2). From December to May the discharge of the Kulekhani River is minimal, about 1.2 $m^3 s^{-1}$. Normally the rainy season begins in June and lasts until October, and the river discharge increases almost tenfold to a peak of 10-11 $m^3 s^{-1}$ in July and August.

The Indrasarobar Reservoir is almost isothermal to a depth of 60 m during the winter months of November to February. It undergoes progressive stratification during the warm months from March to June, when the water level falls. Although the reservoir continues to warm during July and August, its temperature stratification is partially broken down by the enormous volume of water entering during the July to September rains. In the short period of stratification, the thermocline is found between depths of 8-12 m. Dissolved oxygen concentration in the top 3 m of the reservoir remains >6 mg l^{-1} throughout the year except in June and July, when it is ≥4 mg l^{-1}. In contrast, oxygen concentration below 5 m depth declines to <3 mg l^{-1} from May to October. When the water temperature is >20 °C below 20 m (May to October), the oxygen concentration falls to only 1-2 mg l^{-1}. The total bicarbonate alkalinity of the reservoir water rises from 62 mg l^{-1} in December to 75 mg l^{-1} in June, and then drops during the rainy season to 36 mg l^{-1} by November. The pH in the top 2 m varies from 7.8 (December to February) to 10.0 (May to August). The annual average conductivity of the top 10 m of the reservoir is 87 mhos cm^{-2} (Pradhan and Swar, 1987).

Tadi River

This river was selected as a study site for several reasons: it is similar in physical and chemical characteristics to the Kulekhani River before damming, it is a natural habitat for katle and it is accessible by vehicles and by foot. However, it is is not in the same catchment area as the the Indrasarobar Reservoir and therefore comparisons between katle populations in the two systems are confounded by probably different gene pools. The Tadi river, which is glacier-fed, arises from "Surya Kunda", Lamtang Himal (Fig. 2:2). This is a tributary of the Gandak system. The river has an approximate length of 60 km and a catchment area of 653 km^2. It originates at about 4,609 m above MSL and joins the Trishuli River at Devighat at 463 m. The river water is clear throughout the year except during the rainy season (July to September). The river has deep pools at irregular intervals. The bottom of the river consists mainly of big rocks, boulders, gravel and sand. The average slope of the river over the first 20 km from Ghyangfedi to Bokedhunga is about 1:0.187. The slope of the river in the rest of its length is about 1:0.014. The Tadi River receives several seasonal and perennial streams. The Chake Khola, Khahare Khola and Likhu Khola (Khola = Stream) join at Bokedhunga, Chaughoda and Dhikure, respectively. From Dhikure, the Tadi runs towards

Figure 2:2. Map of the Tadi River showing the sampling area from A to B.



0
5 km
KHAHARE KHOLA
N
TRISHULI RIVER
TADI RIVER
GADKHAR
B
A
LIKHU KHOLA

Devighat through Shera Beshi, Malakot and Majhitar. Two more perennial streams named Sindure Khola and Belkot Khola join the river between Dhikure and Devighat. Average discharge for 8 years (1969-1976) was 43.16 $m^3 s^{-1}$ (Appendix 3). The maximum recorded discharge was 1,625 $m^3 s^{-1}$ on 18 July, 1973, and the minimum discharge was 1.40 $m^3 s^{-1}$ on 22 May, 1969, and 14 and 15 May, 1970 (Department of Hydrology and Meteorology, 1992). The surface water's physical and chemical characteristics vary as follows: temperature 15.5 °C - 29.1 °C; depth 39.0 - 63.0 cm; pH 6.8 to 7.2; dissolved oxygen 7.0 to 8.4 mg l^{-1}; and total alkalinity 13.9 $CaCO_3$ mg l^{-1} to 29.9 $CaCO_3$ mg l^{-1}.

Collection techniques

The Indrasarobar Reservoir was divided into seven sampling areas (Fig. 2:1). A multipanel gill net of 50 x 5 m with floats on the top and lead-lines on the bottom, having stretched mesh sizes of 25, 50, 75 and 100 mm, was set once a month at every station to catch fish over a wide range of sizes. Each panel of the 50 m long and 5 m deep net was about 12.5 m in length. The nets were usually set in the evening at 19:00 hours and lifted at about 08:00 hour in the morning, but when fish were sampled to study their food and feeding habits, nets were checked at four hour intervals to minimise both regurgitation and digestion of food in the fish's gut. Fish in the Tadi River were sampled at monthly intervals with cast nets, trammel nets, fyke nets, hook and line and other local techniques such as paso (locally made loops using horse hair) and fishing traps. Fish were collected from different sites of the Tadi River within the stretch of about 20 km from Devighat to Gadkhar (Fig. 2:2). Fish samples were also purchased from local fishermen along the Tadi River. Both reservoir and river were sampled for three years from January, 1988, to December, 1990. Katle were examined externally and internally to separate males and females by using the method described by Lagler (1978). Measurements of total length, standard length, girth and weight were recorded. Different bony structures such as scales, opercula, and pectoral and dorsal fin rays were removed for ageing the fish. Information on feeding, reproduction and growth of katle was gathered by using these monthly samples. Specific details are given in each of the following chapters.

CHAPTER III

SOME ASPECTS OF THE FEEDING BIOLOGY OF KATLE IN THE INDRASAROBAR RESERVOIR AND THE TADI RIVER.

INTRODUCTION

Feeding is one of the most important functions of a heterotrophic organism and all other activities stem from the food consumed by the organism (Nikolsky, 1963). Therefore the study of food and feeding habits forms one of the main investigations in any biological study of an animal. Investigations on the food and feeding habits of a particular fish population include detailed observation of its diet, both in quality and quantity, availability of the different food items in the environment, and the intensity or rate of feeding. These studies provide valuable information on the seasonal utilisation of natural resources by fish and how these change during their life cycle. Data of this kind are helpful to the fishery biologist in the efficient management and optimum production of fish.

Despite the use of several species of cyprinids in aquaculture and commercial fisheries, investigations on their food and feeding behaviour have not received sufficient attention in the Indian sub-continent. Most of the previous studies are limited to the examination of gut contents of commercially important cyprinids (Khan, 1934; Mookerjee *et al.*, 1947; Menon and Chacko, 1958; Chakrabarty and Singh, 1967; Bhatnagar and Karamchandani, 1970; Desai, 1970; Jyoti, 1976; Sunder and Bhagat, 1979; Sharma, 1986/1987). Some workers have contributed by determining the relationship between the type of food and the size of the alimentary canal (Das and Moitra, 1955, 1956a, 1956b, 1956c, 1963; Das and Nath, 1965; Das and Pathani, 1978; Das and Srivastava, 1979; Nath, 1982) and the change in food items with the size of the fish (Pisolkar and Karamchandani, 1981). The role of certain abiotic factors, such as temperature and turbidity, in regulating food intake as well as the nature and composition of the fish diet was described by Nautiyal and Lal (1985). Feeding habits are also frequently associated with particular body forms and functional morphologies of skull, jaws and alimentary tract (Alikuni and Rao, 1951; Barrington, 1957; Keast and Webb, 1966; Kapoor *et al.*, 1975; Hyatt, 1979). Comparative studies on food and feeding habits of several species of cyprinids co-existing in Sri Lankan waters described the relationships between their feeding habits and their morphological features (such as the shape and position of the mouth, the nature, number, size and spacing of gill rakers and teeth and mean relative length of the gut (RLG, the ratio of gut length to body length) (De Silva *et al.*, 1977, 1980).

Little is known about the feeding biology of katle. Biswas (1985) measured gut length in relation to the nature of the food items ingested at different life stages of five commercially important fish including katle. He observed that katle were carnivorous at the fry stage but the juveniles and adults ate plants as well as animals. The alimentary canal of katle is not as coiled as that of true herbivorous fish and consequently the RLG values are lower. Other studies (Jhingran, 1982; Ferro and Badagami, 1980; Dasgupta, 1988b) have indicated the change from a mainly carnivorous diet (insects) during the early fingerling stage to an omnivorous (gastropods, algae and vascular plants) diet in adult katle.

This present study investigates the feeding of katle in the Tadi River and in the Indrasarobar Reservoir and aims at assessing a) if the composition of prey items differs between the reservoir and the river, b) if there are any seasonal differences in prey, and c) if these adaptations in feeding habits affect their life histories such as growth and reproduction.

MATERIALS AND METHODS

Fish for the present study were collected from the Indrasarobar Reservoir and the Tadi River during July, 1989, to December, 1990, and treated as described in Ch. II. The mouth position and the structure of the alimentary canal were examined and recorded for each fish. Soon after collection, specimens were dissected and the alimentary tracts were removed and unravelled to facilitate measurements of their length (Al-Hussaini, 1949). Length measurements (cm) and weights (g) of the alimentary canals were taken before they were preserved in 5% formaldehyde solution.

For the analysis of gut contents, four different methods have been used in previous work: the numerical, volumetric, gravimetric and points methods (reviewed in Hynes, 1950; Pillay, 1952; Rounsefell and Everhart, 1953; Holt, 1959; Windell and Bowen, 1978 and Hyslop, 1980). The appropriateness of each method depends on the feeding habits of the fish and the objectives of the study (Beyerle and Williams, 1968; Guma'a, 1978; Crisp *et al*., 1978; Mann and Orr, 1969; Stickney, 1976; Arawomo, 1976). The volumetric and points methods were selected as best suited to the present study. To determine the composition of the gut content and its seasonal variation, the volumetric method of analysis was employed (McComish, 1966; Karlberg and Benson, 1975). The contents of the intestinal bulb were emptied into 10 ml of water and stirred. If any large organisms were present such as insects and fish fry they were removed from the rest. One ml of the remaining suspension was withdrawn and the food items contained in it were examined under a Wild Stereo M8 binocular microscope. A compound microscope (G92110, Olympus, H.S.C., Japan) was also used for detailed identification. The organisms found in the food were identified to order, family or generic levels depending on their condition. Keys used for the identification of different organisms included Pennak (1953), Ward and Whipple (1918), Malla *et al.* (1978), Swar (1979), Swar and Fernando (1979) and Nakanishi (1986). Assistance with the identification of the phytoplankton and aquatic insects was given by Dr. M. Nakanishi, Kyoto University, Kyoto, and Mrs. A. Tamrakar, Tribhuvan University, Kathmandu, respectively. After identification, each group was sorted out and its volume estimated by allowing it to settle in a graduated measuring vessel (Jude, 1971; McComish, 1966; Karlberg and Benson, 1975). Centrifugation was also employed to separate contents into distinguishable layers thereby allowing estimation of the volumes of different groups (Bonneau *et al.*, 1972). The volume of each food item found in the intestinal bulb was presented as a percentage of the total volume of the contents. The corresponding percentage for the total fish population was estimated by averaging the volume percentage of that item over all individual fish examined (Hunt and Jones, 1972). Seasonal variation in the proportions of different items in the gut contents were similarly measured by using the volumetric method.

Feeding intensity was estimated in two ways. First, the points method (Robotham, 1977) was employed to estimate seasonal feeding intensity by classifying the fullness of the alimentary canal (ranging from empty to full). Since katle have no well-defined stomach, the fullness of the whole gut was assessed. The gut of katle was divided into ten equal parts and the number of full sections estimated. The gut fullness was given a 'mark out of ten' (Robotham, 1977). All the points allocated to each section of the alimentary canal were summed and expressed as a percentage of total possible points (100). Guts scored as 0% were categorised as empty (Table 3:1).

The feeding intensity of katle was also estimated through an indirect calculation of the monthly average weight of the gut contents of a "standard" fish for each of the reservoir and the river. After estimation of the fullness of the gut of an individual fish, its contents were removed and the empty gut reweighed. The weight of the gut contents was calculated from the difference in weight of the gut with and without contents. Weights of gut content were plotted against weights and total lengths of fish for different months. A great variability was apparent among individual fish. The estimation of regression equations relating weight of food against weight or total length of fish from both locations, both on arithmetic and $\log_{10}$ scales, was attempted but these were significant only in some cases. As it was observed from the initial plots that there were no apparent differences for the same months between different years, data for each system were pooled over all years. No difference between sexes could be detected. The relationship between the total length of the

Table 3:1. Classification of gut fullness.

Gut	Description	Points(%)
Full Gut	The gut bulges considerably with food. Intestinal bulb wall transparent.	76-100
3/4 Full	The gut is almost full	51-75
1/2 Full	Food occupies about fifty percent of the gut volume.	26-50
1/4 Full	Wall of the intestinal bulb very flabby, some food remains present.	01-25
Empty Gut	No visible food in the gut when dissected.	0

fish (L) and the weight of its gut contents (G) at each of 4 different stages of gut fullness (1/4 full to full) was estimated by using the least squares method after transformation to fit the data to the equation:

$$G = aL^b; \quad \text{hence,} \quad \log G = \log a + b \log L$$

where a and b are constants.

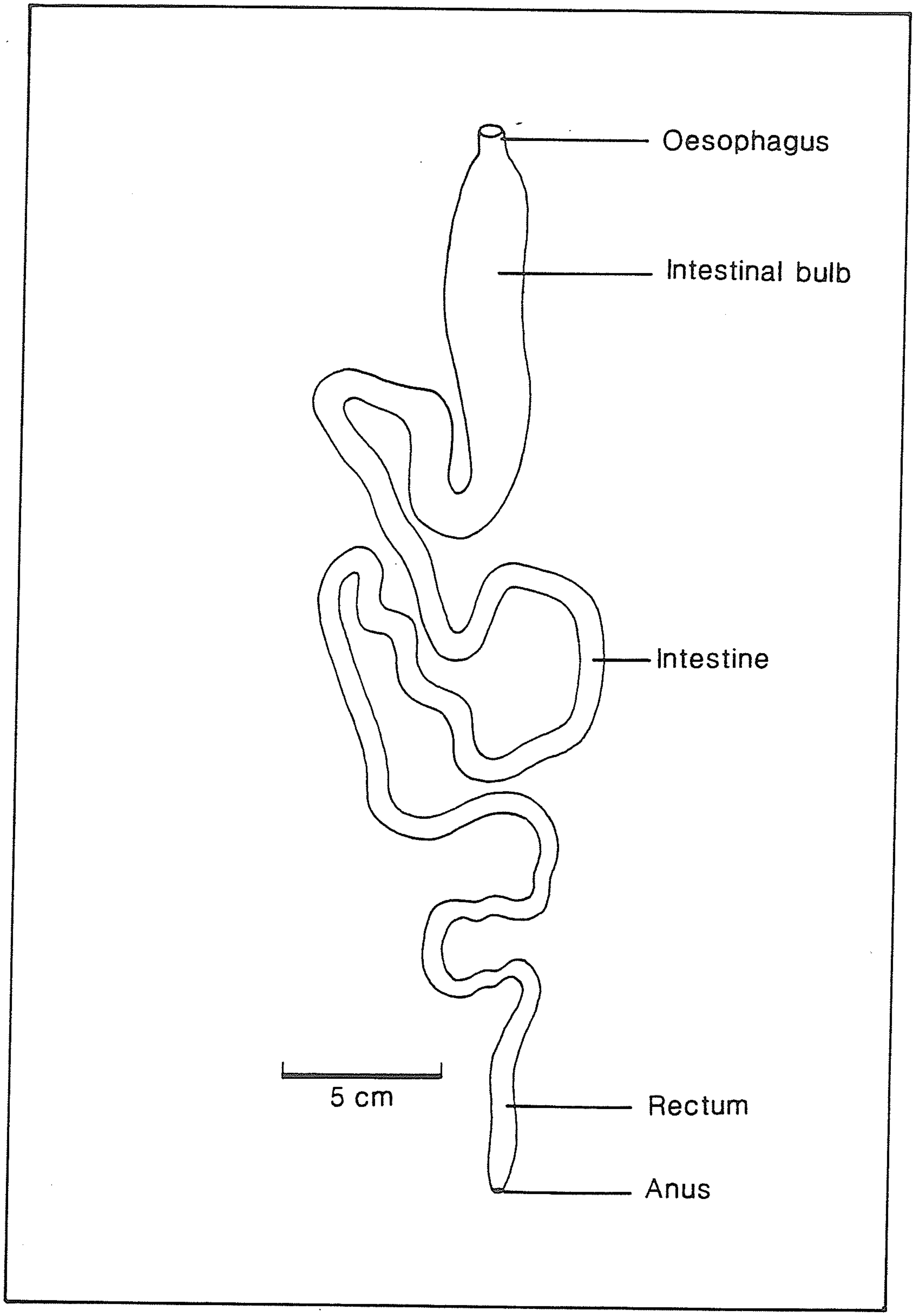
A "standard fish" was now defined for each habitat, with a total length equal to the mean of the total lengths of fish in all samples from that habitat. To estimate the monthly mean weights of the gut contents of this standard fish, the percentage of the fish in each habitat at each of the four states of fullness was calculated. For each of the four states, the weight of the gut contents corresponding to the length of the standard fish was calculated from the regression equation established for that state. These weights were then averaged using the monthly percentage of fish at that state of fullness as a weighting factor (Craig, 1978).

RESULTS

The gut

The oesophagus is the most anterior part of the alimentary canal. It is narrow, tubular, short and rather muscular. On entering the body cavity, the oesophagus expands into a thick-walled intestinal bulb (Fig. 3:1). Posteriorly the intestinal bulb curves to the left and passes into a

Figure 3:1. Alimentary canal of a female katle (total length 365 mm) from the Tadi River.


Oesophagus
Intestinal bulb
Intestine
5 cm
Rectum
Anus

coiled intestine which overlies the intestinal bulb ventrally. The wall of the coiled portion of the intestine is quite thin and of an almost uniform diameter. The intestine widens slightly at the posterior end to form the thin-walled rectum which opens ventrally at the anus.

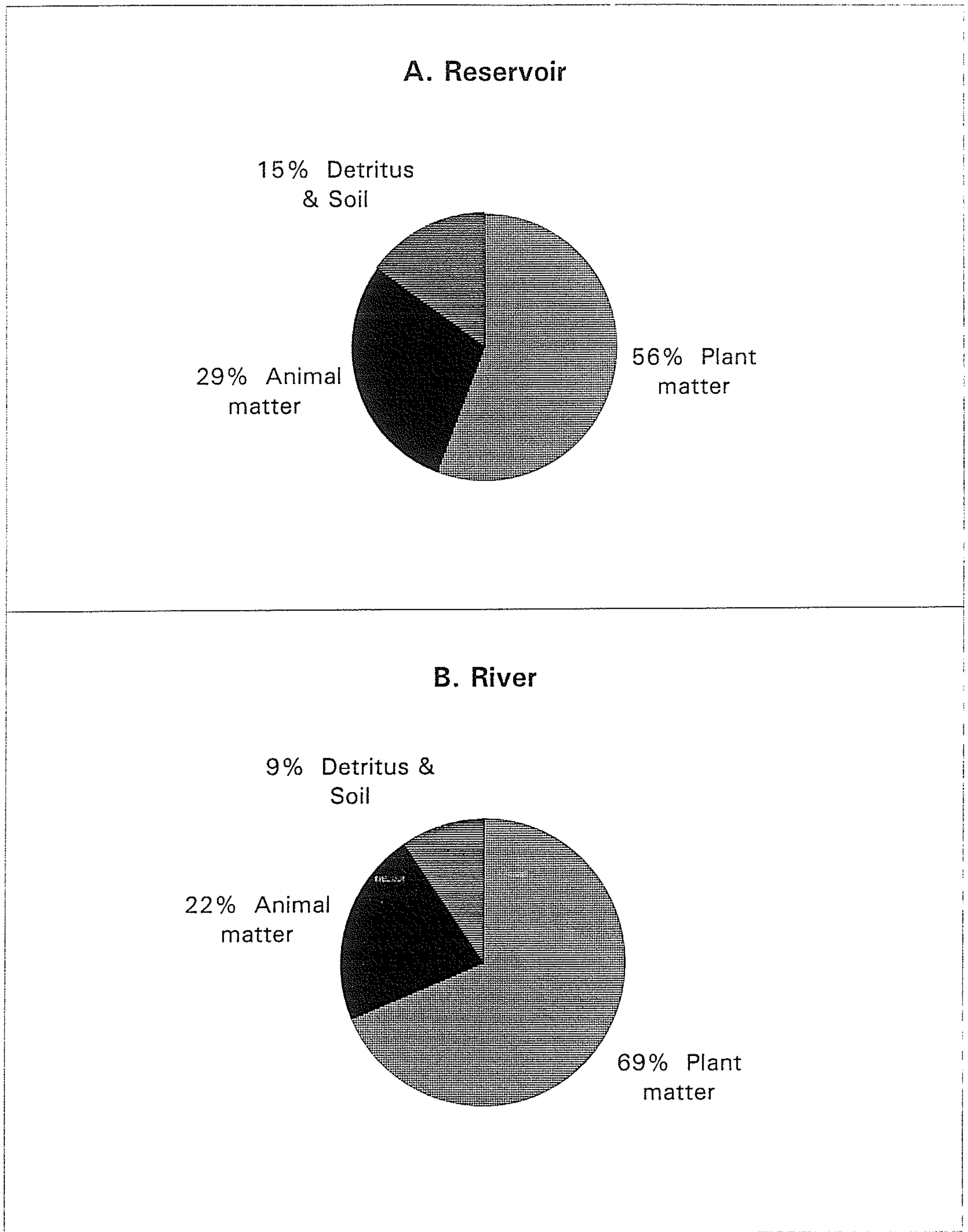
Gut content analysis

Qualitative analysis of the gut contents of katle from the Tadi River and the Indrasarobar Reservoir caught during 1989 and 1990 revealed that this fish consumes many food items and is omnivorous. The total animal food, plant food and detritus and soil were calculated to be 21.8, 68.8 and 9.4% respectively of the total volume of the gut contents of all the examined fish from the Tadi River and 29.0, 56.0 and 15.0% respectively in the Indrasarobar Reservoir katle (Fig. 3:2). The food eaten by katle can be divided into six broad groups: phytoplankton, vascular plants, zooplankton, benthic animals, detritus and sand and soil:

1. **Phytoplankton:** This group formed 39.1% and 29.3% in the gut content of katle from the river and the reservoir, respectively. It was represented by Chlorophyceae, Bacillariophyceae, Cyanophyceae and Euglenophyceae.

a. **Chlorophyceae:** The genera included were *Chlamydomonas*, *Zygenema sp.*, *Closterium*, *Oedogonium*, *Microspora*, *Hydrodictyon*, *Cosmarium*, *Pediastrum*, *Eremosphera*, *Scenedesmus*

Figure 3:2. Percentage diet composition of katle in the Indrasarobar Reservoir and the Tadi River.


A. Reservoir
15% Detritus & Soil
56% Plant matter
29% Animal matter
B. River
9% Detritus & Soil
22% Animal matter
69% Plant matter

and *Spirogyra* of which *Chlamydomonas, Spirogyra* and *Cosmarium* were the most common in the gut content of the river fish. Oedogonium and Closterium were more frequent in the diet of the reservoir fish.

b. **Bacillriophyceae:** Twelve genera were identified in the diet: *Amphora, Cymbella, Pinnulari, Pleurosigma, Cocconeis, Cocconema, Fragilaria, Navicula, Synendra, Melosira,* and *Tabellaria.* Among them *Fragilaria, Navicula, Synendra, Melosira, Cymbella, Peridinium* and *Tebellaria* were most common in the gut contents of the reservoir fish. The presence of the diatoms was not so frequent in the diet of the river fish.

c. **Euglenophyceae:** This group was represented by *Trachelomonas* and *Euglena* and was observed only in the gut of freshly killed fish.

d. **Cyanophyceae:** From this group *Oscillatoria, Anabaena* and *Ulothrix* were eaten.

2. **Vascular plants:** These were also important food items forming 32.7% and 26.4% of the gut content of katle from the river and reservoir respectively. They could be divided into

a. **Macrovegetation:** This was usually found in a masticated and semi-digested condition. It formed one of the main items of the gut contents, and was encountered more frequently in the river samples than those from the reservoir.

b. **Grass:** Occurrence and bulk of this item was particularly high during July to September, when the marginal growth of grass was submerged and uprooted grass was washed down in the reservoir and the river during monsoon floods.

c. **Twigs:** These were the small shoots of macro-vegetation ingested by the fish.

d. **Plant seeds:** This item comprised small seeds of aquatic plants. Its contribution was insignificant in the diet of katle from both systems.

3. **Zooplankton:** This made up 7.8% and 17.3% of the gut content of fish from the river and the reservoir respectively. It was represented by Rotifera, Cladocera and Copepoda. *Keratella, Polyarthra, Asplanchana and Bracchionus* were more common among the rotifers. The cladocerans were represented by *Daphnia, Bosmina, Diaphanosoma, Moina* and *Leptodora*. The copepods were represented by adults and copepodids of Cyclopoida and Calanoida. *Chaoborus* larvae were also very common in the gut contents. Zooplankton was observed only in the freshly killed fish.

4. **Benthos:** Benthic animals formed 13.9% and 11.5% of the gut content of katle from the river and the reservoir. This group was represented by aquatic insects, oligochaetes, Hirudinea, Mollusca and water mites.

a. **Aquatic insects:** This group was represented by Coleoptera, Odonata, Ephemeroptera, Plecoptera, Trichoptera, Hemiptera, Diptera and *Chironomous*.

b. **Oligochaetes:** Among the oligochaetes, Branchiura, *Limnodrilus, Branchiodrilus, Procladius, Polypedilum,* Tubificidae, Naididae, Lumbriculidae and Enchytraeidae were common.

c. **Hirudinea** was represented by Erpobdellidae.

d. **Mollusca:** Gastropods were present from the molluscs, and

e. **Water mites** were represented by Hydracarina.

Among the benthic fauna, Odonata, Trichoptera, Plecoptera, Hemiptera and Chironomidae occurred more frequently and in higher percentages in the diet of the river katle. Tubificidae, *Branchiura, Limnodrilus, Naididae, Polypedium* and *Procladius* were observed mainly in the gut contents of the reservoir population; i.e., annelids were more abundant in the reservoir and aquatic insects in the river.

5. **Detritus and Debris** (decayed organic matter): This mainly consisted of unidentifiable plant matter in a digested state. It occurred regularly in the guts of katle from the river and the reservoir throughout the year, and on an average constituted 6.9% and 13.5% by volume of the gut contents in the two habitats respectively.

6. **Soil and Sand:** This item occurred in the guts of the river katle throughout the year except in the March samples. On average, it formed 1.8% by volume. The largest quantity was

encountered in May. In the reservoir samples it was not encountered so frequently and the gut contents of the fish during January, March, May, July and October did not have any mud or sand in them. It was found during the rest of the months and formed < 2% of the gut contents by volume.

Besides the items listed above, nematodes were found in the intestinal bulb of katle from the river and the reservoir occasionally. These nematodes were not considered in the measurement of the volume of the gut contents of katle.

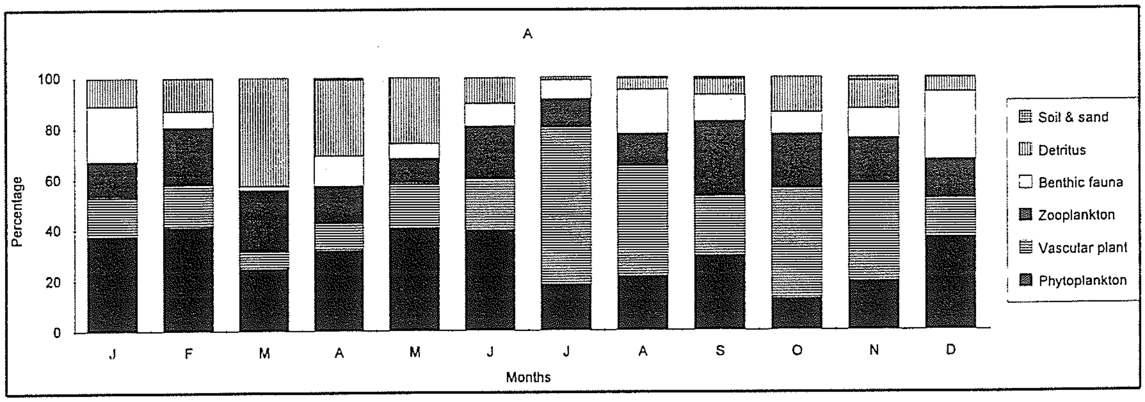
Seasonal variation in diet composition

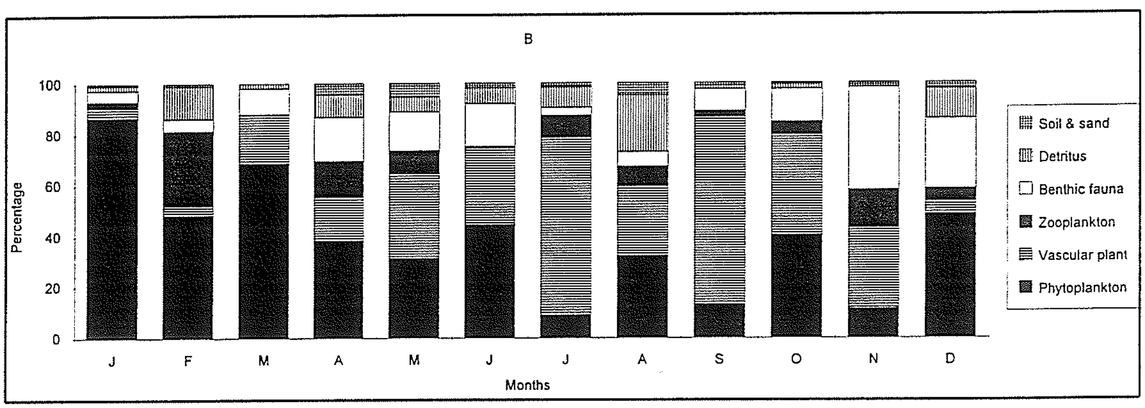
The percentages of different items in the gut contents of katle in different months are shown in Figure 3:3. It can be seen that there were considerable variations in the percentage of different items among the different months of the year and between the river and the reservoir.

The phytoplankton group formed a major source of food for katle in both the river and reservoir populations throughout the year. It constituted the highest percentage (86.4%) by volume of the gut contents of the riverine population in January and the lowest percentage (8.9%) in July. In the reservoir fish, the highest percentage (40.9%) of phytoplankton occurred in February and the lowest percentage (12.5%) in October.

The vascular vegetable matter seemed to be another major food source of katle in both systems. The quantity of vascular

Figure 3:3. Monthly variation in the percentage value of food items of katle in the Indrasarobar Reservoir (A) and the Tadi River (B).


A
100
80
60
40
20
0
Percentage
J F M A M J J A S O N D
Months
Soil & sand
Detritus
Benthic fauna
Zooplankton
Vascular plant
Phytoplankton


B
100
80
60
40
20
0
Percentage
J F M A M J J A S O N D
Months
Soil & sand
Detritus
Benthic fauna
Zooplankton
Vascular plant
Phytoplankton

plants also varied from month to month. In the gut contents of the river fish, vascular plants formed the highest percentage (74.5%) in September and the lowest quantity (5%) in December. In the reservoir fish, the highest quantity (62.5%) was observed in July and the lowest (6.8%) was recorded in March.

In the river fish, the maximum amount of zooplankton was observed in February when it constituted about 29% of the total volume of their gut content, whereas zooplankton was absent in the samples collected during March and June. In the reservoir population, zooplankton were encountered throughout the year. The maximum (29%) occurred in September and the minimum (12.8%) was encountered in August.

The benthic fauna formed significant percentages of the total diet of katle in the reservoir and the river with varying amounts in different months. Another important food item was detritus. The highest percentages were observed in fish from the reservoir during March, April and May (42.7, 29.7 and 26% respectively), whereas detritus formed a lower percentage in the river katle's diet except in August (22.32%). Soil and sand occurred in the gut of river fish in all months except March, but it constituted a very small percentage (< 2%) of the total gut content. Perhaps it was taken up by accident.

Seasonal feeding intensity

Seasonal feeding intensity was estimated first by classification of the fullness of the alimentary canal (Tables 3:2 and 3:3). In a considerable percentage of the fish examined from both systems during the study period, the gut was either empty or contained little food (< 1/2 full). The percentage of fish with empty guts during spring, summer, autumn and winter was 35.7%, 30%, 15.4% and 42.3%, respectively for the Tadi River, and 33%, 20%, 18% and 36%, respectively for the reservoir. Fish with a full gut were observed during spring, summer and autumn in the river system and during summer and autumn in the reservoir.

The feeding intensity of katle was also estimated (as described in Materials and Methods) through the indirect calculation of the monthly average weight of the gut contents of a "standard" fish for each of the reservoir and the river (no difference could be detected between sexes). Values for fitting the regression equations between the logs of gut contents and total length are shown in Table 3:4 and 3:5. All regression coefficients for the pooled data were highly significant ($P < 0.001$). The total length of the standard fish for the reservoir was calculated as 237.6 mm. From the regression equations, the estimated weight of the gut contents (with 95% confidence intervals) for this standard fish was 0.5 ± 0.85, 2.48 ± 0.33, 6.59 ± 0.18 and 13.29 ± 0.23 g with the gut 1/4 full, 1/2 full, 3/4 full and full, respectively. The

Table 3:2. Seasonal feeding intensity of katle reflected in the prevalence of different degrees of fullness of guts in the Indrasarobar Reservoir.

Season	Number of fish	Empty gut %	1/4 full %	1/2 full %	3/4 full %	Full gut %
Spring	88	33.7	35.0	25.0	7.0	0.0
Summer	91	20.0	25.0	20.0	13.0	22.0
Autumn	103	18.0	23.0	28.0	9.0	22.6
Winter	84	36.0	40.0	22.0	2.0	0.0

Table 3:3. Seasonal feeding intensity of katle reflected in the prevalence of different degrees of fullness of guts in the Tadi River.

Season	Number of fish	Empty gut %	1/4 full %	1/2 full %	3/4 full %	Full gut %
Spring	83	35.7	42.5	12.7	4.6	4.5
Summer	86	30.0	27.0	23.0	10.0	10.0
Autumn	86	15.4	27.0	27.0	8.6	22.0
Winter	77	42.3	35.3	21.4	0.0	1.0

Table 3:4. Values of the coefficients b and intercepts log a for the regressions of the weight of gut contents (G, in g) on the total length (in mm) for fish with 1/4 full, 1/2 full, 3/4 full and full gut. Also given are the number of degrees of freedom (d.f.), the S.E. for G estimates from the regression, and the estimated G (with 95 % confidence limits) for the standard reservoir katle of 237.6 mm length.

Statistic	1/4 full	1/2 full	3/4 full	Full gut
b	2.786	3.137	3.253	3.213
log a	-7.07	-7.060	-6.910	-6.510
d.f.	66	76	26	12
S.E. of G_{est}	0.436	0.166	0.088	0.105
G_{est} (standard)	0.534	2.479	6.586	13.292
± 95% CL	±0.854	±0.325	±0.180	±0.228

Table 3:5. Values of the coefficients b and intercepts log a for the regressions of the weight of gut contents (G, in g) on the total length (in mm) for fish with 1/4 full, 1/2 full, 3/4 full and full gut. Also given are the number of degrees of freedom (d.f.), the S.E. for G estimates from the regression, and the estimated G (with 95 % confidence limits) for the standard river katle of 163.9 mm length.

Statistic	1/4 full	1/2 full	3/4 full	Full gut
b	2.98	2.96	2.992	1.994
log a	-7.37	-6.63	-6.31	-3.88
d.f.	49	67	10	10
S.E. of G_{est}	0.34	0.16	0.07	0.15
G_{est} (standard)	0.169	0.932	2.070	3.434
± 95% CL	±0.683	±0.320	±0.156	±0.367

total length of the standard river fish was 163.9 mm, and the estimated weight of its gut contents was 0.17 ± 0.68, 0.93 ± 0.32, 2.07 ± 0.16 and 3.43 ± 0.37 g with the gut 1/4 full, 1/2 full, 3/4 full and full, respectively. Monthly average weights of the gut contents of the standard katle from the reservoir and river were then calculated from these values, using the monthly percentage of fish at each state of fullness as a weighting factor. It was clear that there is one annual peak in both systems. The weight of the gut content was highest in August and remained higher until November in the reservoir (Fig. 3:4), but in the river the peak was observed in September. The average weight of gut contents was relatively low during winter and spring.

Changes in food with size of fish

Analysis of the food data for the entire year from both systems indicated that both qualitative and quantitative differences existed among the various length groups (Fig. 3:5). In the river, phytoplankton was dominant in the gut content of fish from 45 to 145 mm, vascular plant tissue dominated in fish from 146 to 295 mm, and detritus was dominant in the gut of katle longer than 296 mm. In reservoir fish, phytoplankton was present in all groups but its contribution was very low in fish above 396 mm in length. Vascular plant tissue was dominant in the fish longer than 246 mm. Among the benthic animals, annelids were dominant in the

Figure 3:4. Monthly average gut content weight (g) (with ± 95 % CL) of a standard (237.6 mm) katle from the Indrasarobar Reservoir (**a**) and Tadi River (**b**).

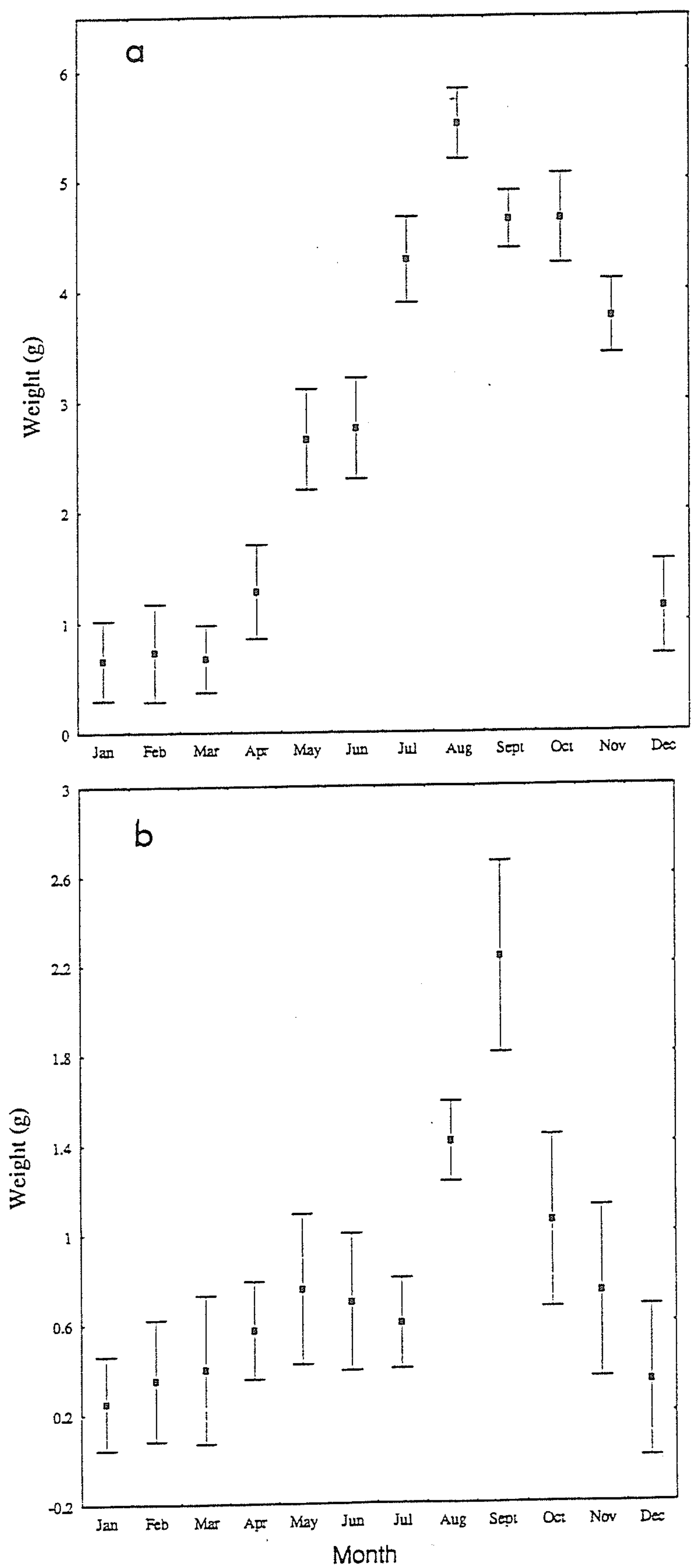
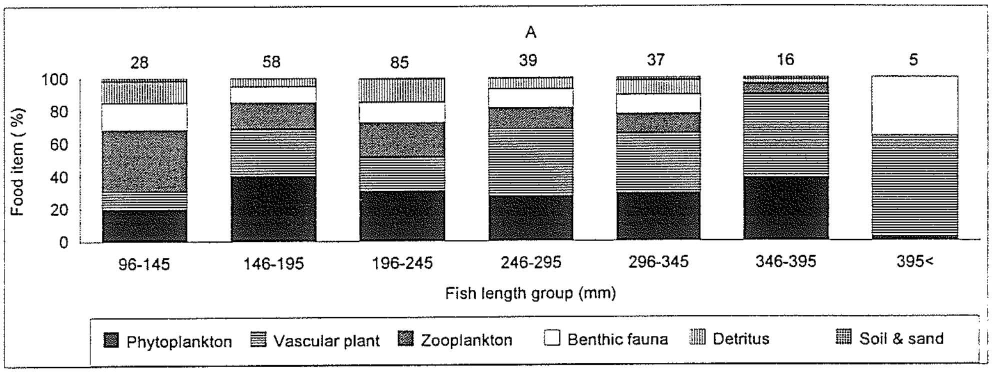
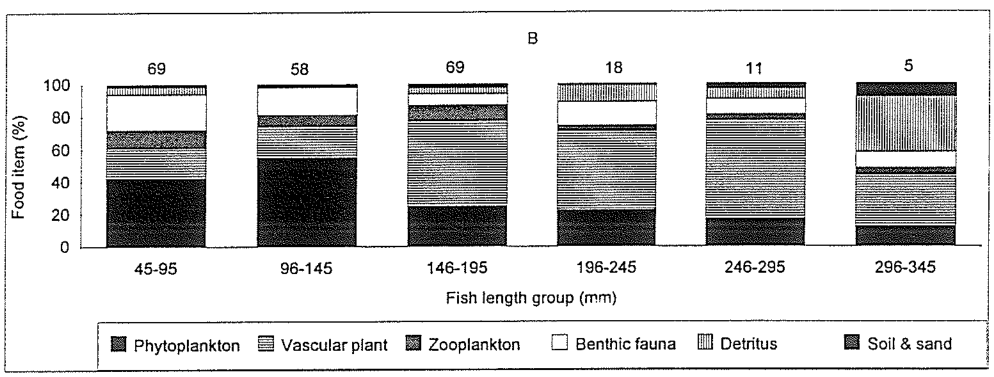

a
Weight (g)
0
1
2
3
4
5
6
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
b
Weight (g)
-0.2
0.2
0.6
1
1.4
1.8
2.2
2.6
3
Month

Figure 3:5. Food composition of various sizes of katle in the Indrasarobar Reservoir (A) and the Tadi River (B).



A
28
58
85
39
37
16
5
100
80
60
40
20
0
Food item (%)
96-145
146-195
196-245
246-295
296-345
346-395
395<
Fish length group (mm)
Phytoplankton
Vascular plant
Zooplankton
Benthic fauna
Detritus
Soil & sand



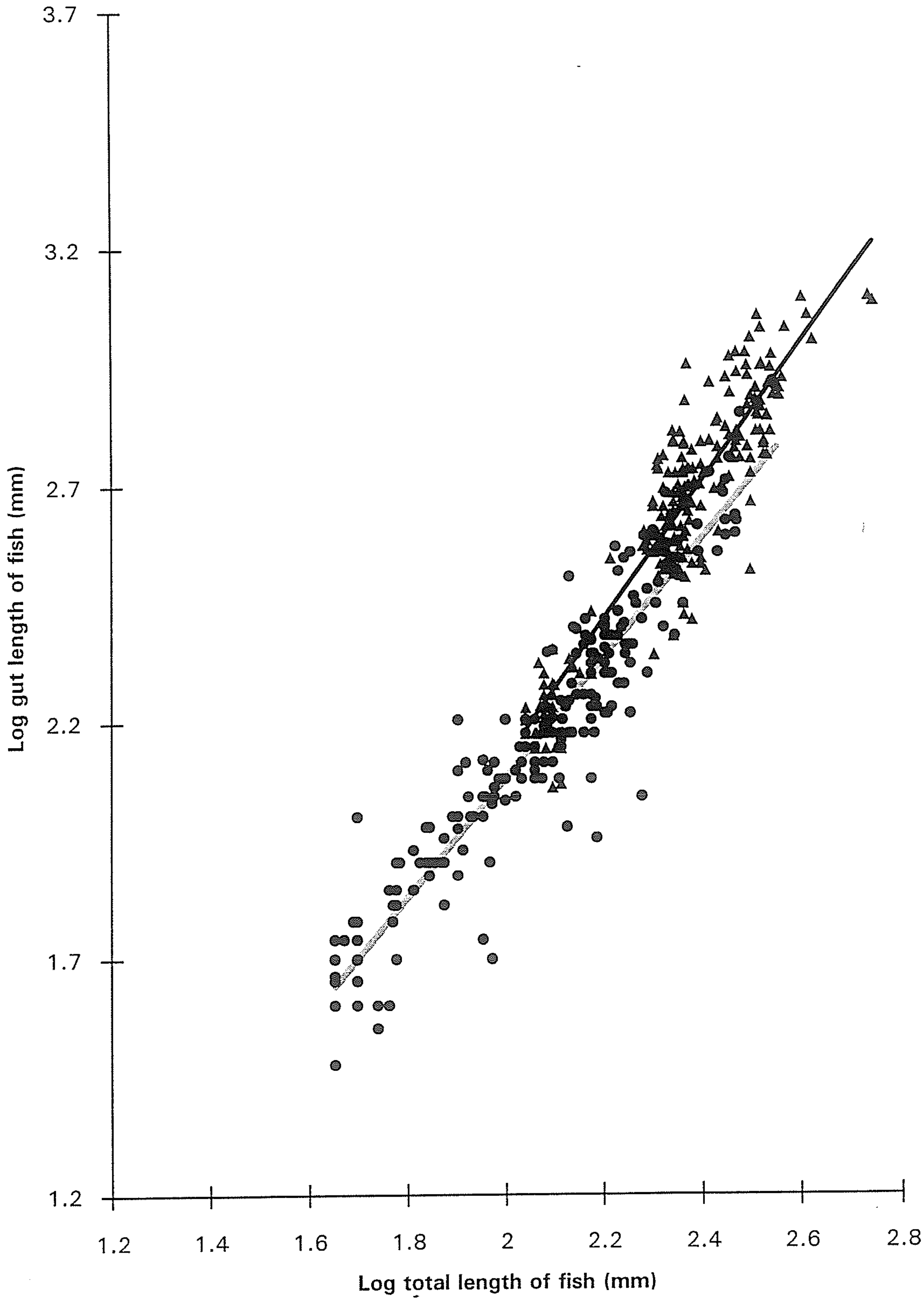
B
69
58
69
18
11
5
100
80
60
40
20
0
Food item (%)
45-95
96-145
146-195
196-245
246-295
296-345
Fish length group (mm)
Phytoplankton
Vascular plant
Zooplankton
Benthic fauna
Detritus
Soil & sand

reservoir fish while aquatic insects were quite common in the guts of river fish. No zooplankton was present in the fish longer than 396 mm. It seemed that the contribution of plant food increased with the size of the fish. In the reservoir, animal food constituted the major percentage (53.8%) of the total gut content of fish of length 95 to 145 mm, while it formed only 6.62 % of the gut content of large fish of 346 mm to 395 mm. Similarly in the river system, animal food formed 32.7% of the total gut content in smaller fish (45 - 95 mm), but only 13.33% in the gut of larger fish (296 - 345 mm).

Relative length of the gut of katle

The relationship between the gut length and the total body length was found to be allometric. The values for fitting the regression equations are given in Table 3:6 and the best fits for the relationship between $\log_{10}$ gut length and $\log_{10}$ total length of the river and the reservoir katle are shown in Figure 3:6. Both the regression coefficients were highly significant ($P < 0.001$). Student t tests carried out to test differences in b values indicated a significantly higher value ($P < 0.05$) for the reservoir population than for that of the river.

Figure 3:6. Relationship between gut length and total length of katle.
(—▲— and solid line = reservoir fish;
-●- and stippled line = river fish).



3.7
3.2
2.7
2.2
1.7
1.2
Log gut length of fish (mm)
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
Log total length of fish (mm)

Table 3:6. Values of regression coefficients b and intercepts log a for length of gut (mm) on total body length (mm) for katle from the Indrasarobar Reservoir and Tadi River.

Statistic	Reservoir	River
b	1.465	1.267
log a	-0.810	-0.453
d.f.	195	212
S.E. for $\log_{10}$(gut length)	0.099	0.099
F value	872.2	1564.2
r^2	0.817	0.881

DISCUSSION

Nikolsky (1963) recognised three main categories of food on the basis of their importance in the diets of fish. They are (a) basic food, which is normally eaten by fish and includes most of the gut contents, (b) secondary food, which is frequently found in the gut but in smaller amounts and (c) incidental food, which is found rarely in the gut. In accordance with the definition given by Nikolsky (1963), algae and vegetable matter, which formed 68.8 and 55.6 % of the gut contents in the river and the reservoir fish, can be considered as basic food. Benthic fauna, Rotifera, Crustacea and other animal matter together constituting 21.8% and 29.0% in the river and the reservoir fish, was the secondary food. Soil and sand particles which formed 2.14 and 0.47% of the gut contents in the river and the reservoir fish was an incidental item and has no food value at all.

On the basis of feeding habits, fish are broadly classified as herbivores, omnivores and carnivores. The various degrees of specialisation in food habits allow their further categorisation as monophagous (consuming just one kind of food), stenophagous (a limited range of foods), and euryphagous (mixed diet) (Nikolsky, 1963; Weatherley and Gill, 1987). It is evident that the relative gut length value, RLG, has a close relationship with the nature of the food of the fish; e.g., vegetable matter requires more time for digestion.

This is why herbivorous fish like *Labeo rohita* and *Labeo gonius* (Das and Moitra, 1956 a, b, c, 1963) have high RLG values (about 12.0 and 9.5) respectively. In omnivorous fish, the RLG values are lower (Das and Nath, 1965; Singh, 1966, 1967). Weatherley and Gill (1987) compared relative gut lengths of several species and described the gut length as a major adaptive specialisation in the feeding ecology of fish. The relative gut length of katle falls in between those of omnivores and herbivores. It is also evident from this study that katle consumes a variety of food items and can therefore be classified as an omnivorous and euryphagous fish. According to Biswas (1985), katle is carnivorous in the fry stage, but juveniles and the maturing adults subsist on both plant and animal matter. The results of the present study support this observation. This is probably why the increase in RLG value from fry to juvenile stages is not so sharp in katle as in *Labeo* and *Cirrhina* spp.

Jhingran (1975) and Dasgupta (1988b) described katle as a voracious feeder as indicated by the high values of its gastrosomatic indices (GSI) in the Indian waters. However, the present study revealed that a considerable percentage of the examined fish from both the river and the reservoir had empty or almost empty guts. The diet composition of katle in the present study agreed with the results of previous workers (Jhingran, 1975; Dasgupta, 1988b) except that the fish bones and scales encountered by Ferro and Badagami (1980) in fish from the lakes of Pokhara Valley, Nepal, were not observed. Beyond these reports, there is little previous information in the literature on the feeding biology of katle.

The food consumption of wild fish is affected by a large number of factors including the size of the fish, water temperature, activity of the fish, and availability of food organisms (Elliots, 1975; Lagardere, 1987). Water temperature affects food consumption of fish by influencing the metabolic rate of the fish and the primary production of the ecosystem (Angermeier, 1982). Surface water temperature in the Tadi River and the Indrasarobar Reservoir followed a seasonal pattern with the lowest values recorded during winter (December - February) and the highest values in summer (June - August; Figure 5:13). The pattern of gut fullness and average weight of gut content recorded in this study suggest that the intensity of feeding also followed a seasonal pattern, being relatively intense in summer and autumn and low during winter and spring. The temperature variation through the period may have affected the feeding intensity of katle in the reservoir and river. Any seasonal changes in the composition of the gut contents probably reflect the abundance and availability of each item. Besides temperature, dissolved oxygen, pH and alkalinity also fluctuated throughout the year but none of these factors appeared to be limiting (Singh and Virdi, 1983; Soemarwoto *et al.*, 1990). The rainfall was highest during the summer months: about 70% of the annual rainfall during the study period occurred then (Figs 5:15 and 5:16).

In both systems plant matter formed the highest percentage of the total volume of the gut contents, followed by animal matter and then by detritus and soil. It is evident from the study that the relative contribution of plant food increased with the size of the fish in both populations. Accompanying this switch to plant matter, an increase in the length of the gut relative to body length was observed. This increase is reflected in the fact that the b values in the logarithmic relationships between the gut length and the total length of fish were greater than 1 for both habitats (Table 3:6); further, the b value was greater in the reservoir, where plant food constituted a higher percentage of the diet, than in the river.

Besides these general similarities, some differences were observed in the food and feeding habits between river and reservoir katle. Detailed analysis of plant food revealed that the gut contents of river katle was dominated by crushed vascular tissue and filamentous algae; these items are attributed to the submerged rooted vegetation found in the marginal shallow portions of the river where the filamentous algae also remains attached to the rocks. Reservoir katle were found to be ingesting more planktonic blue-green algae and diatoms and occasionally terrestrial grass during the period of high water level. These food items are attributed to the nutrient enrichment in the reservoir from the agricultural lands in the watershed area of the reservoir and availability of grass when the water covers the marginal land during the high water levels of the summer season. The differences were also evident in the variety of animal food. In the reservoir, the percentage of zooplankton in the diet was quite high, and the benthic animals were represented mainly by annelids. In the river, zooplankton were sparse in the diet, and most of the benthic fauna were nymphs of aquatic insects. The dominance of zooplankton in the reservoir diet is probably due to the abundance of limnetic zooplankton in the water column, which is not so common in the river system. Similarly the formation of the reservoir from a fast flowing river has destroyed the habitat of aquatic insects, and their community has been replaced by different species in the reservoir (Yadav, 1989). The percentage of detritus in the gut content of reservoir katle was higher, whereas it made up only a small percentage of the total volume of the gut content of the river katle. In addition to the difference in food composition, there is an apparent difference in feeding intensity between the two populations. The reservoir population attains its peak consumption in July and maintains quite a high level until November. July is the spawning period of katle (see Chapter V). The occurrence of higher feeding intensity during the post-spawning period was also recorded by Sharma (1986/87), Malhotra (1967), Jyoti and Malhotra (1975) and Jyoti (1976) for *Tor*. The river katle attain their peak intake only in

September. This delay can probably be attributed to high turbidity due to monsoon rain during June and July. The negative influence of turbidity has also been recorded in *Tor putitora* by Nautiyal and Lal (1985a).

The average weight of gut contents (in percentage of the body weight) for different length groups in the reservoir is higher than in the river. Perhaps this is due to the higher availability of food and relatively stable conditions during the summer season in the reservoir. Similarly, as noted above, the increment in gut length with length of the fish is also greater in the reservoir. Since the percentage of animal food in the gut content of katle from the reservoir is less than the percentage of the animal food found in the gut content of fish from the river, it is probable that this increased gut length is related to a switch to mainly plant matter. Plant matter is generally higher in fibre and lower in energy. Therefore, a larger gut, permitting digestion of a larger quantity of food over a longer time period, is required in a herbivore to achieve the same rate of energy intake as a carnivore. Katle's ability to increase its relative gut length may thus be a major adaptive specialisation in its feeding ecology under reservoir conditions.

Three attempts were made to assess the effect of drawdown in the reservoir on the feeding behaviour and growth of katle. Unfortunately the experiment could not be completed due to the high mortality of fish within a week of the experiments being started.

After careful examination of the gut contents of katle from the river and reservoir and comparison of these data with those from previous work, it seems reasonable to suggest that the basic feeding behaviour of katle in both systems is similar. Apparent differences can be explained by the different environmental conditions in their respective habitats; consequently, reduced density of food may generally lead to lower fecundity and slower growth of katle in Nepalese waters. These possibilities are explored in Chs. IV and V.

CHAPTER IV

STUDIES ON THE AGE AND GROWTH OF KATLE IN THE INDRASAROBAR RESERVOIR AND THE TADI RIVER.

INTRODUCTION

Age and growth data are needed for efficient fish stock assessment and fisheries management. The evaluation of age provides a means for understanding the composition of fish populations with regard to year classes and for finding the role of particular year classes in the fluctuations of the stock. The study of the growth rate of fish leads to an effective and conclusive assessment of the sustaining power of the stock in a fishery. The von Bertalanffy growth model (von Bertalanffy, 1938) is used in the analytical methods (Beverton and Holt, 1957) employed today. The principle of age determination in fish depends on the 'annual' growth marks that are formed in certain skeletal parts such as the scales, otoliths, spines, opercula and vertebrae. The growth of fish is not normally uniform throughout the year. The fish may grow quickly during a certain part of the year and more slowly or even not at all during another part. This fluctuation of growth expresses itself on the skeletal parts of the fish as wide and narrow zones. It is important to verify that the deposition of these distinct bands or checks is annual or can be related to a distinct seasonal event such as a rainy or a dry season. Annual marks may also be related to spawning activities of the fish.

Studies on the age and growth rate of commercial fish such as cod, herring and salmon were initially developed by Norwegian scientists (Chevey, 1930). This was followed by detailed investigations on many species, especially commercial fish, in Europe and America (Menon, 1950, 1953). These studies have been confined to temperate regions which have well defined seasons. There have been a few individual attempts to determine the age and growth rate of some fish in tropical and sub-tropical waters. Mohr (1921) was one of the first biologists to examine growth checks in skeletal parts of tropical and sub-tropical fish including *Rasbora vulgaris, R. elegans, Trichopodus trichopterus, Barillus guttatus, Ambassis commersonii, Polynemus indicus* from Malaya and *R. daniconius* from Sri Lanka. He found distinct and well defined zones in the scales of the fish from both localities even though the climatic conditions between Sri Lanka and Malaya are different. Sri Lanka has rainy and dry periods whereas the climate in Malaya is fairly uniform throughout the year. Distinct growth marks on the scales and other bony structures were also observed in freshwater and marine tropical and sub-tropical fish by Whitehouse (1923), Hornell and Naidu (1924), Devanesan (1943), Nair (1949) and Chidambaram (1950). They investigated the age and rate of growth of the oil sardine, *Sardinella longiceps,* by the Peterson method which was further substantiated by scale reading. However, validation and interpretation were lacking in the above ageing studies. None of the workers addressed the problem, as outlined by Graham (1929) and von Oosten (1929), of validating the annual nature of the growth checks that they all assumed in their studies.

Several other investigators such as Hora and Nair (1940), Chacko *et al.* (1948), Chacko and Krishinamurti (1950), Chacko and Dixitulu (1951), Sunderaj (1951) and Jones and Menon (1951) examined growth marks on the scales of hilsa, *Hilsa ilisha,* and linked the formation of the radii to the physiological rhythm related to tidal periodicity. Nair (1949) used the otolith in his age studies of the oil sardine and observed growth bands as alternating translucent dark zones and opaque white ones, parallel to the margin of the otolith. He presumed that these rings were annual. Chidambaram and Krishnamurty (1951) used the otolith in studies of age and growth rate of the Indian mackerel, *Rastrelliger kanagurta.* They observed a close relationship between the number of growth rings on the otolith and the size groups of the fish. It was found to be too difficult to read the number of rings in the otolith of specimens ≥ 20 cm.

Seshappa and Bhimachar (1951) observed scales with transparent margins in Malabar sole, *Cynoglossus semifasciatus*, caught during the monsoon. The authors assumed that there was an annual interval between major growth checks.

They concluded that the rings were formed under the influence of the south-west monsoon season and referred to them as monsoon rings. They correlated the check in growth to the depletion of benthic organisms and proposed that the lack of food was the main factor in the formation of the ring. This was the first investigation in which occurrence of transparent margins in the scales of tropical fish was correlated with the depletion of food.

The studies on age and growth of cyprinids, in particular the major carp group, started in the late 1950's with the advancement of aquaculture. Several authors have studied the age and growth of *Cirrhina mrigala* from different habitats and used the von Bertalanffy growth model to describe its length at different ages (Jhingran, 1957, 1959; Kamal, 1969; Hanumantha, 1974). Natarajan and Jhingran (1963) investigated the growth of *Catla catla*. The age and growth of different species of *Labeo* have been examined in several Indian waters, for example *L. fimbriatus* in the Narbada River by Bhatnagar (1979) and in the Godawari River by Rao (1974). Chatterji *et al.* (1979) and Chatterji (1992) studied the age and growth of *L. gonius* and *L. bata* respectively in the Kali River. Das (1960) compared the growth rate of *L. rohita* and *Catla catla* in ponds. The growth of *L. rohita* has also been examined by Khan and Siddiqui (1973) in a pond and in the rivers Ganga and Yamuna. Gupta and Jhingran (1973) used scales to study the age and growth of *L. calbasu*.

Hill stream-inhabiting cyprinid species like *Tor spp* (mahseer) have also attracted the attention of several biologists. Pathani (1981a) and Tandon and Johal (1983) studied the age and growth of *Tor tor* and *Tor putitora*, and observed the highest growth in the first year of life with a steady decrease in growth thereafter. Nautiyal (1990) used the scales to study the age and growth of mahseer from two ecologically different fluvial systems, one torrential and stenothermal and the other placid and eurythermal. His results were in agreement with the findings of Pathani (1981a) and Tandon and Johal (1983).

Besides the above authors, several workers studied the growth of freshwater and marine fish from tropical and subtropical regions using their scales (Thakur, 1967; Rangaswami, 1973; Pillay, 1958; Pillay and Rao, 1962; Khumar and Siddiqui, 1990). Most of those workers examined the formation of annular bands on the scales of fish and used the von Bertalanffy growth model to explain the life history of the fish. The otolith was used in only a few studies.

Pantulu (1961, 1962 and 1963) used a different structure, the pectoral fin rays, to determine the age of three species, *Mystus gulio, Pangasius pangasius* and *Osteogeiosus militaris*. His findings were validated with results obtained by Peterson's method.

Despite the involvement of so many researchers over an extended period, the technique of direct validation of the age of fish has not been applied in the Indian subcontinent, nor have age and growth investigations apparently been attempted with katle. Little is known about this fish's age, life span and growth rate. The aims of the present investigation on Nepalese katle are: a) to work out a suitable method for age and growth determination and a technique for validation; b) to estimate length at age and annual growth rates; and c) to determine the katle's adaptability to two different habitats by comparing its growth in the reservoir to that in the river.

MATERIALS AND METHODS

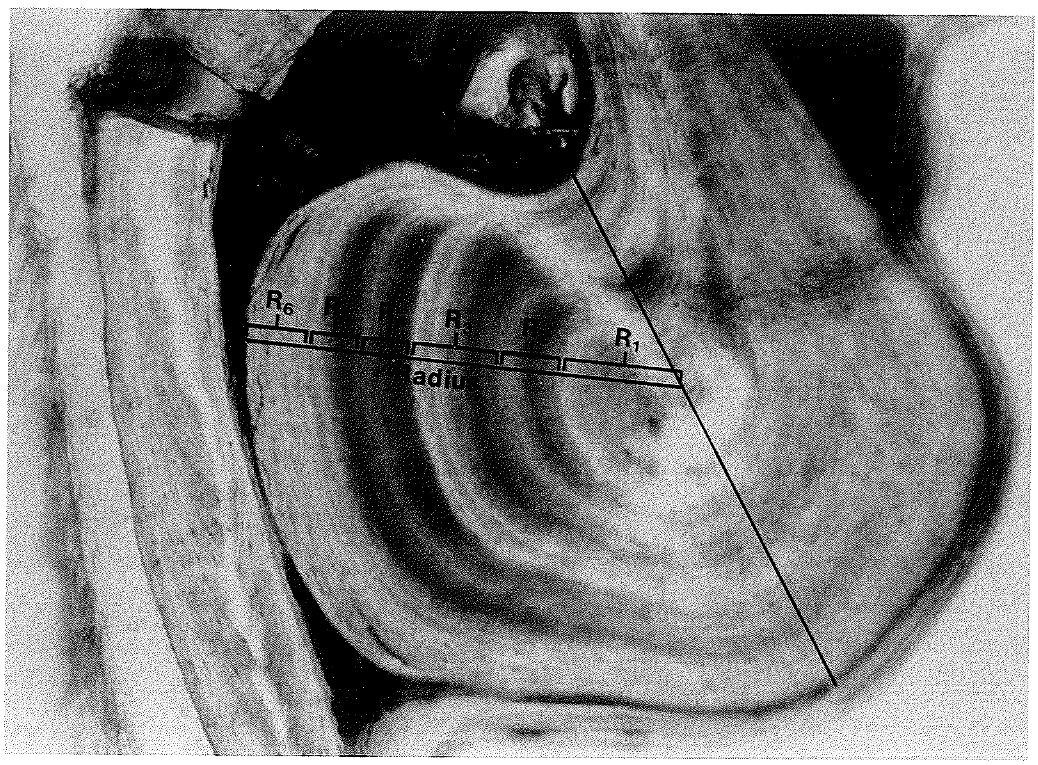
Ageing methodology

Fish samples for this study were collected from the Indrasarobar Reservoir and the Tadi River as described in Ch. II. Both the reservoir and the river were sampled for three years, from January, 1988, to December, 1990. For comparison of ageing methods, calcified structures such as scales, fin rays (pectoral, dorsal, anal) and opercula were collected from all fish sampled in 1988 as described by LeCren (1947), Pantulu (1961), Bagenal and Tesch (1978) and Casselman (1987). One hundred of each of these structures were examined to determine which best reflected the age of the fish (Campbell and Babaluk, 1979). The cross sections of pectoral fin rays were found to provide relatively easily recognisable patterns under the microscope and these were used for ageing katle in this study.

A total of 2,461 pectoral fins including the 100 used in comparison of ageing methods (2,061 from the reservoir population, 400 from the river population) were processed and examined. A complete fin was removed from close to the body of the fish using surgical bone cutters. This was necessary in order to incorporate the first year's growth. Fin rays were spread out and placed in a flattened position in envelopes. They were left to dry for 2-3 weeks. The pectoral fin rays were then embedded in epoxy resin. The blocks were then trimmed into rectangular shapes, using a pair of scissors, and the distal ends of the rays were also taken off. A low speed ISOMET circular saw with a diamond blade was used to section the blocks of pectoral fin rays. Three sections (0.6, 0.65 and 0.70 mm thick) were cut at the point of termination of the basal triangular notch. These sections were mounted on microscope slides with Diatex. The slides were left to set for 2-3 days. The prepared sections were then examined under a compound microscope (X 100 magnification). Measurements on sections of pectoral spines were made with the aid of an ocular micrometer.

An examination of the cross sections of fin rays revealed the existence of alternating opaque and transparent zones around the central medullary cavity. One opaque and one transparent zone were taken to indicate one year's growth. The border between a transparent zone and the succeeding opaque zone is referred to as a "check". All measurements of the total radius of the fin ray and of the radii up to the termination of different transparent zones in the spine section were made from the central medullary cavity along the line of maximum growth (Fig. 4:1). The line of maximum growth usually lay at about a 60° angle to a defined reference line which passes through the point of divergence of the two projections and through the central medullary cavity of the spine. The precise line along which radii were measured was selected a) to lie within the zone of maximum growth and b) to show the most clearly defined growth rings. At first, thirty pectoral fin ray sections were examined under reflected light with a binocular microscope. Ages were determined by Dr. K. Mills (Freshwater Institute, Canadian Department of Fisheries and Oceans) and by the author without reference to the fish length or weight. These sections then received a third reading from another colleague in Nepal. Independently assigned ages were compared and discrepancies were resolved by re-examination and discussion of ring characteristics. Any sections with confusing or unclear bands were excluded from the study. All of the remaining (2,431) fin ray sections of male and female katle from the river and reservoir were aged by the author by counting of the annuli. Sections from 30 fish for each age group of each sex and for the two habitats were randomly selected for further measurements of their annular radii for back-calculations of length at age. All the sections

Figure 4:1. Cross section of a pectoral fin ray of a katle showing annuli and the axis of measurement. R_1, R_2, R_3, R_4, R_5, R_6 - radii of respective annual rings; Radius - total radius of the section. A reference line passing through the central medullary cavity and the point of divergence of the two projections of the spine is also shown.


R_6
R_1

in a subgroup were measured if the number of fish was less than thirty.

Validation of ageing method

The objective of the validation procedure was to determine whether or not the increments on the pectoral fin ray sections were in fact annual increments (i.e., whether or not age determination from the pectoral fin ray was accurate). To make this determination a tetracycline compound (OTC) was injected into katle to produce marks at a specific date in bony parts of the body. Tetracycline is known to be incorporated quickly into calcifying tissues of fish during growth and to form a fluorescent band that is visible under ultraviolet light (Bevelander and Gross, 1962). Campana and Neilson (1982) recorded that injected tetracycline was incorporated into calcifying tissues within 24 hours. It is non-toxic to fish at doses required for marking (Harris, 1960) and has been used previously in fish age validation studies (Holden and Vince, 1973; Casselman, 1974; Babaluk and Campbell, 1987; McFarlane and Beamish, 1987; Babaluk and Craig, 1990).

Five hundred katle of different sizes (61 to 450 g) were collected with a cast net between 17 May and 25 June, 1989, from the Indrasarobar Reservoir. They were kept in a nylon cage for one day prior to injection and were released into the reservoir within two hours of receiving tetracycline injections administered as described below. A separate group of fifteen fish of different sizes were collected with a fyke net between 22 and 25 August, 1990, from the Tadi River. They were kept in cement tanks until 26 August, 1990, and then released after injection into an earthen pond of about 0.5 ha at Gadkhar near the Tadi River. All the fish were anaesthetized with benzocaine (25 mg l^{-1}) using the method described by Laird and Oswald (1975) and weighed to the nearest 0.5 g. They ranged in weight from 80 to 282 g. OTC was purchased under the brand name Liquamycin. Liquamycin is oxytetracycline hydrochloride dissolved in an establishing agent and supplied in volumes of 250 ml at a concentration of 100 mg ml^{-1}. Using the method outlined by Kobayashi *et al.* (1964), all 515 fish were injected intraperitoneally with a dose of 50 mg tetracycline kg^{-1} body weight, a dose used in other studies (Weber and Ridgway, 1962; Holden and Vince, 1973; Babaluk and Craig, 1990). A floy tag was attached with polyethylene filament to each injected fish. After processing, all fish were held in a recovery tank for one hour prior to release into the Indrasarobar Reservoir or into the earthen pond. Attempts were made to recapture the injected and tagged fish from the reservoir by experimental fishing and by offering a reward to the local fishermen for recaptured fish returned to the Inland Fisheries Centre. None of the tagged fish had been recaptured from the reservoir by the end of this study in 1992. Five tagged and OTC-marked katle from the earthen pond at Gadkhar near the Tadi River were recaptured on 9 October, 1991. These fish were remeasured and reweighed, and their pectoral fins were collected and sectioned as described above. Ages were estimated using a compound microscope with bright and dark field lighting. To ascertain the presence or absence of a tetracycline mark, an ultraviolet light source was used. Also, the presence or absence of a check outside any tetracycline mark was noted. Photographs were taken on Fujichrome (100 ASA) film with a 35 mm camera attachment.

Back-calculation of lengths at age

To be able to back-calculate the length of the fish from the spine sections, it was necessary to establish a relationship between the radius of the spine and total length of the fish. The total length (in cm) for each individual fish (Y axis) was plotted against each spine radius (in micrometer divisions) (X axis) to establish the relationship. The relationship between the spine radius and total length was found to be linear in all groups and could be expressed as:

$$Y = a + b X$$

where Y is the total length of fish in cm, X is the spine radius in micrometer divisions and a and b are constants. Back-calculations of lengths at ages of annulus formation could therefore be made according to the modified direct proportionality formula (Bagenal and Tesch, 1978):

$$Y_i - a = X_i/X \quad (Y-a)$$

where Y_i = length of fish in cm when annulus i was formed,

Y = total length of fish in cm at time fin ray was removed,

X_i = radius of annulus i on the fin ray in micrometer divisions (1 division = 0.0370 mm),

X = total radius of fin ray in micrometer divisions, and

a = intercept on Y axis.

Mean lengths at each age were obtained from the back-calculated lengths of individual fish, and annual length increments were calculated as the successive differences between these means. Preliminary examination of the mean length for different age groups of katle showed that there were likely to be differences between cohorts and sexes within the population. The data for these different groups were thus kept separate through the process of collection and analysis. In the final analysis of the data the mean length of young fish was first examined separately from the bulk of the data on mature adult fish.

Instantaneous or specific growth rate

The instantaneous growth rate in length G_L can be defined by the equation $dL/dT = G_L L$. This assumes that the rate of growth increases in direct proportion to present length, with G_L as the proportionality constant. G_L was calculated separately for the males and females from both habitats for each age group by using the following formula (Ricker, 1975; Ball and Jones, 1960; Bagenal and Tesch, 1978):

$$G_L = \frac{\text{Log}_e L_2 - \text{Log}_e L_1}{T_2 - T_1}$$

where L_2 and L_1 are the lengths at times T_2 and T_1 respectively. The increment of time, T_2-T_1, is usually taken as one year. Therefore, G_L is expressed as the specific rate of growth per annum, in cm cm^{-1} yr^{-1}, or % yr^{-1}.

Fitting of the von Bertalanffy growth model

The best-known growth model used in fisheries assessment is that of von Bertalanffy (1939), who based his formulation on physiological considerations. The von Bertalanffy expression for length L(t) at age t is usually written as (Dickie, 1978):

$$L(t) = L_\infty \{1-e^{[-K(t-to)]}\} \quad (1)$$

where L_∞ = the asymptotic length at t = ∞ (often referred to as final maximum length), K = the growth coefficient, and t_o = a time scaler equivalent to the (hypothetical) starting time at which the fish would have been zero-sized if they had always grown according to the equation.

The different parameters of this equation for the reservoir and the river katle were calculated in two ways. The first was a mathematical method relying on regression analysis (Ricker, 1975). To estimate L_∞, Equation (1) was rearranged in the form:

$$L(t + 1) = L_\infty [1 -e^{(-K)}] + e^{(-K)} L(t) \quad (2)$$

Then, a regression of L(t + 1) on L(t) was performed, in which the intercept (a) = L_∞ [$1-e^{(-K)}$], and

the slope (b) = $e^{(-K)}$

L_∞ could then be calculated as:

$$L_\infty = a/(1-b) \quad (3)$$

Once L_∞ had been estimated, another regression model was used to estimate K and t_o. Equation (1) was rearranged as:

$$\log_e(L_\infty - L(t)) = (\log_e L_\infty + Kt_o) - Kt \quad (4)$$

A simple regression of $\log_e(L_\infty - L(t))$ on time t was then performed, using the previously calculated value of L_∞, from which:

K = -slope, and

$(\log_e L_\infty + Kt_o)$ = intercept, so that

t_o = (intercept - log L_∞)/K.

The second method of estimating the parameters L_∞, K and t_o utilized the graphical representation developed by Ford (1933) and Walford (1946). Plots of lengths at age (t) against lengths at age (t + 1) gave a straight-line relationship for each group of fish, as Eq. 2 predicts. The line was fitted by the least squares method. The point on the x axis where this line cuts the 45° diagonal through the origin yielded L_∞ (Walford, 1946). K and t_o were then determined as in the first method, except that the slope of the graph of $\log_e(L_\infty - L(t))$ against time t was determined graphically rather than by regression analysis.

Effect of temperature and drawdown on annual growth

The effect of drawdown of the water level in the reservoir on the annual total length increment was examined for the years 1982 to 1989. The area of the reservoir, which is dependent on the annual precipitation and demand for electricity in the country, showed a great variation from 63 ha in 1982 to 172 ha during 1986. Since availability of natural food in the reservoir varies with the area of the reservoir, it was hypothesised that growth rate might be positively associated with the average area during the warm months. Detailed records were kept on the maximum depth of the reservoir throughout the study period (Appendix 2). A few paired measurements of surface area (A) and maximum reservoir depth (D) were also available. The relationship between them was found to be a linear one and could be fitted by the method of least squares as:

$$A = a + bD$$

where the values of constants a and b were - 152.63 and 3.61, respectively. This equation could then be used to calculate the area of the reservoir precisely at any depth (Swar, 1992). The average area of the reservoir during the warm months (April to October) was thus calculated for each year from 1982 to 1989.

Attempts were made to fit a regression model to explain the growth of fish as a function of both age and the water surface area available during the growing season. Several models as described by Weisberg and Frie (1987) and Maceina (1992) were considered (Appendix 5). Of these, the only significant dependence was demonstrated by a model evaluated separately for every age X:

$$\Delta L = a + b \log A$$

where ΔL = annual total length increment of the fish, and A = average area of the reservoir.

Length-weight relationship

The length-weight relationship in fish can be represented by the following equation (LeCren, 1951; Craig, 1974):

$$W = a L^b$$

or by its logarithmic form:

$$\log W = \log a + b \log L$$

where W is the weight of the fish, L is the total length of the fish and a and b are constants.

Data of total length and weight, both total and somatic (total weight - gonad weight), for both sexes, collected monthly for three years, were used to study the length-weight relationship of the katle from the Indrasarobar Reservoir and the Tadi River. Regression lines for the reservoir and river populations were calculated by the method of least squares for log of total weight and the log of somatic weight against log total length for each sex and for each month of collection. Comparisons were made between regression coefficients for each month. There were no significant differences ($p > 0.05$)

between the same months in different years for total and somatic weight regression slopes (b values). Therefore, data for the same month were pooled over all years, and b values recalculated (LeCren, 1951; Craig, 1974). The slopes for each sex were not significantly different from each other ($p > 0.05$) and were not significantly different from 3.0. Therefore, 'a' values were calculated for different months and different sexes at different stages of gonadal maturity (Ch. 5) using the b value of 3.0 throughout. The mean length of all fish of each sex at maturity stage 1 and stages ≥2, caught from both systems, were calculated. These values were taken as the standard length of a "standard" fish. Total and somatic weights for the standard male and female of stages ≥2 were calculated at each stage of maturity for twelve months, using the b value of 3.0 and calculated a values. These weights were then averaged over all stages of maturity using the monthly percentages of fish at each stage as weighting factors.

RESULTS

Evaluation of pectoral fin ray ageing method

Nature of the checks

Most of the pectoral fin ray cross sections revealed the existence of alternating opaque and transparent rings around the central medullary cavity (Fig. 4:2 and 4:3). The sequence of one opaque and one transparent zone was taken to indicate

Figure 4:2. Transverse section of the pectoral fin ray of a reservoir female katle showing eleven annuli. Annuli are marked with white dots.

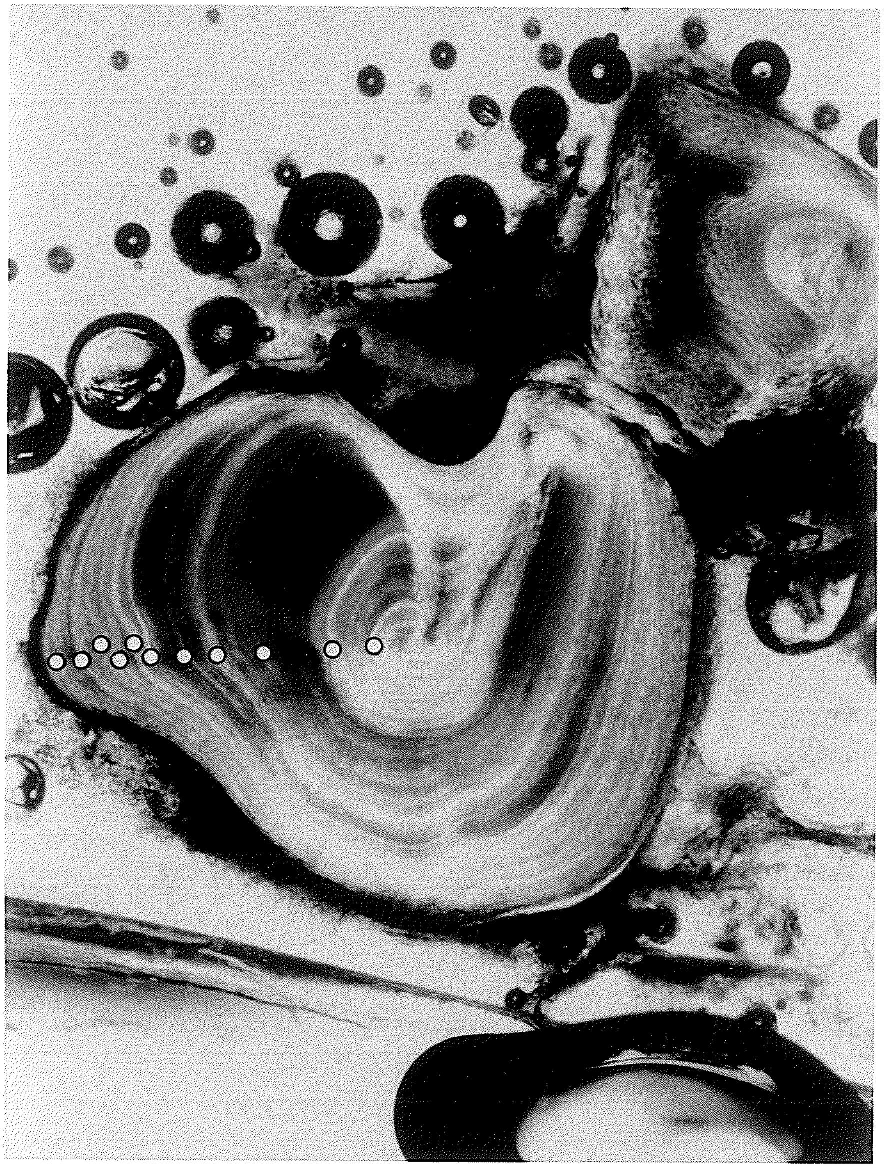
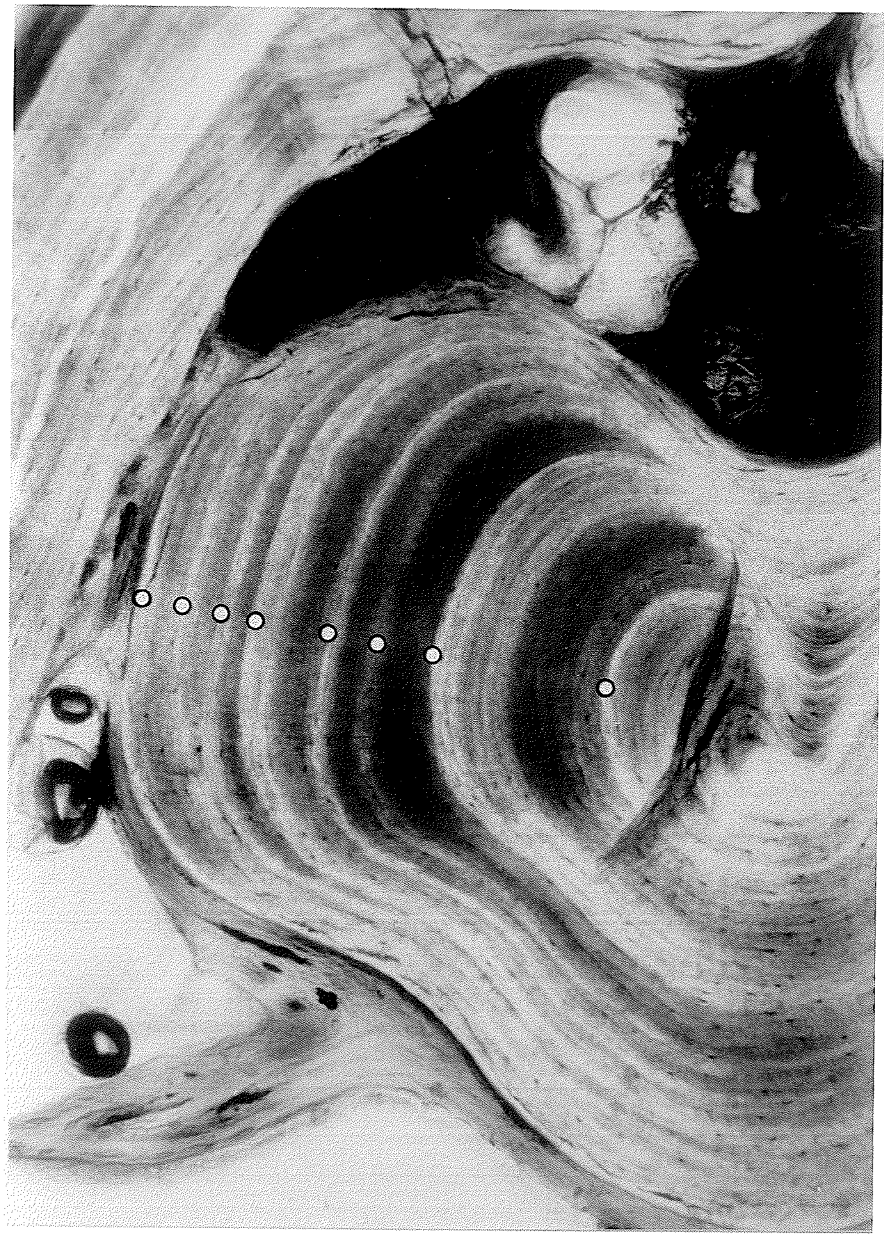


Figure 4:3. Transverse section of the pectoral fin ray of a reservoir female katle showing eight annuli. Annuli are marked with white dots.



one year's growth and was classified to be a true annulus. A few sections with patchy rings were also encountered. Rings that were patchy or broken were short, and were considered as false annuli. Further, in a true annulus which was comparatively broad, the change from transparency to opacity was gradual, whereas in a false annulus the change was abrupt. The number of false annuli was less than 5% of the total.

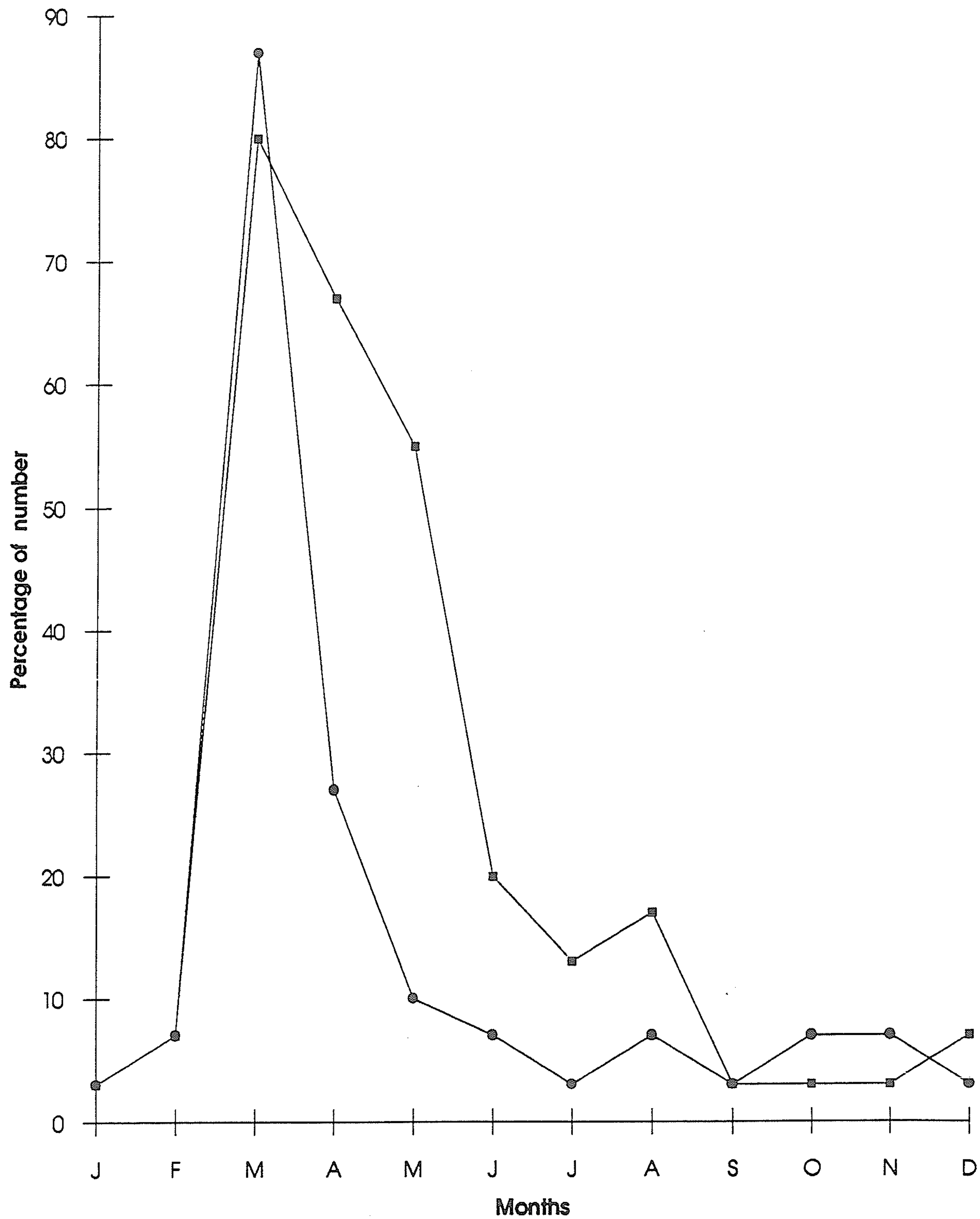
Agreement between readers

Determinations of the age of katle using the pectoral fin ray were reasonably consistent: the three readers agreed in 24 out of 30 cases. Variability of three successive pectoral fin ray age determinations of katle from the Indrasarobar Reservoir is shown in Appendix 6. Where there were disagreements, final fin ray ages were assigned by several readings and consultation between the second and third reader because the first reader was not available.

Age validation

Annual formation of transparent zones and checks: Estimation of the age of the fish depended on the assumption that an annual band was laid down in the bone. To test this assumption, a sample of thirty fin ray sections for each month was examined for a transparent zone appearing towards the edge of the section. The percentage of each month's sample having transparent bands laid down on the edge is shown in Fig. 4:4.

Figure 4:4. Percentage of katle with a transparent zone at the edge of the pectoral fin ray in each monthly sample, from January to December. —■— - reservoir katle; —●— - river katle.

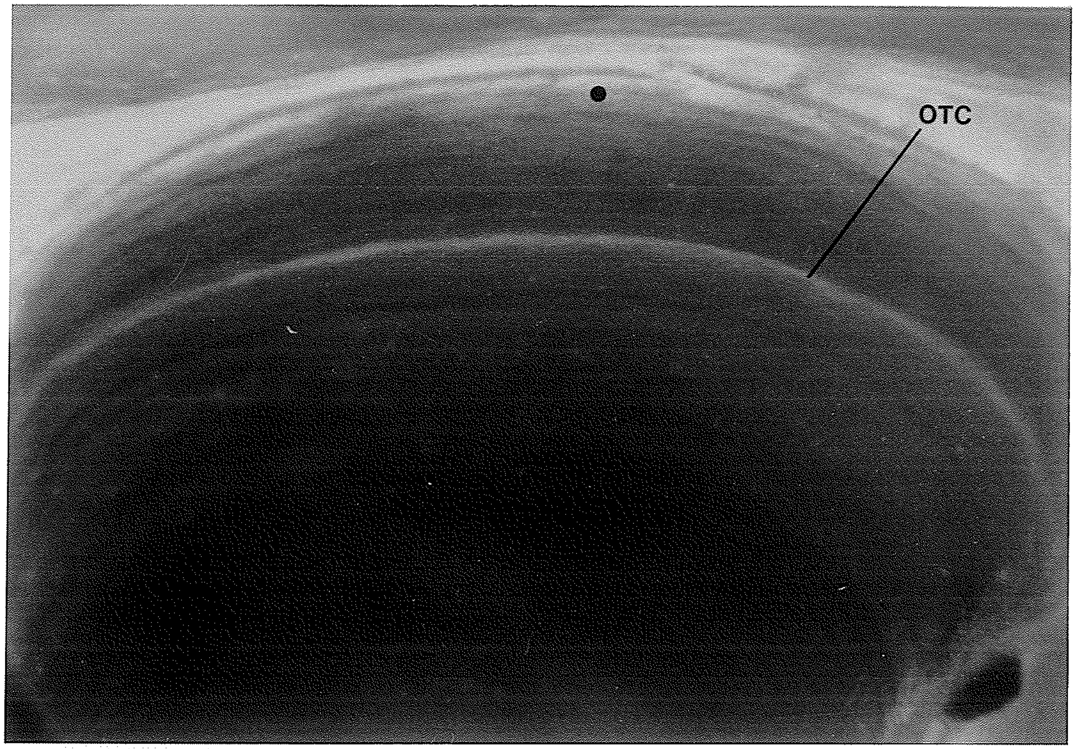

Percentage of number
90
80
70
60
50
40
30
20
10
0
J F M A M J J A S O N D
Months

It is evident from the figure that there is an opaque band at the edge of the fin ray section of katle during most months of the year. The opaque zone is presumed to represent fast growth and the transparent zone, slow growth. It should be noted that the presence of a transparent zone cannot be determined until the next opaque zone has begun to form. Thus when a band is recorded, it is an indication that growth has started again. The data presented in Figure 4:4 indicate that a pair of growth increments, one clear and one opaque, are deposited annually. Riverine fish usually laid down the opaque check in March, and in the reservoir population checks were formed during the period of March to May.

Marking with tetracycline: Examination of the cross sections of pectoral fin rays from the five recaptured fish with ultraviolet light revealed that an OTC check, indicated by fluorescence, was present in three of the fish (Fig. 4:5, top). No tetracycline marks were visible on the pectoral fin rays of two fish, probably because the OTC was not properly injected. The details of the observations on each fish are given in Table 4:1.

One annulus laid down after an OTC mark was clearly visible in the pectoral fin rays of two of the three marked fish. No check outside the tetracycline mark was found in the third fish. Since all the fish were recaptured and examined over one year (about 13 months) after the OTC injection, it is clear that only one annulus is laid down on the pectoral fin

Figure 4:5. Cross-section through an OTC-marked pectoral fin ray of a katle injected in August, 1990, and recaptured in October, 1991. Top: transmitted ultraviolet light shows the oxytetracycline mark (OTC). Bottom: transmitted white light shows the annuli (indicated by dots; not all annuli are shown).


OTC

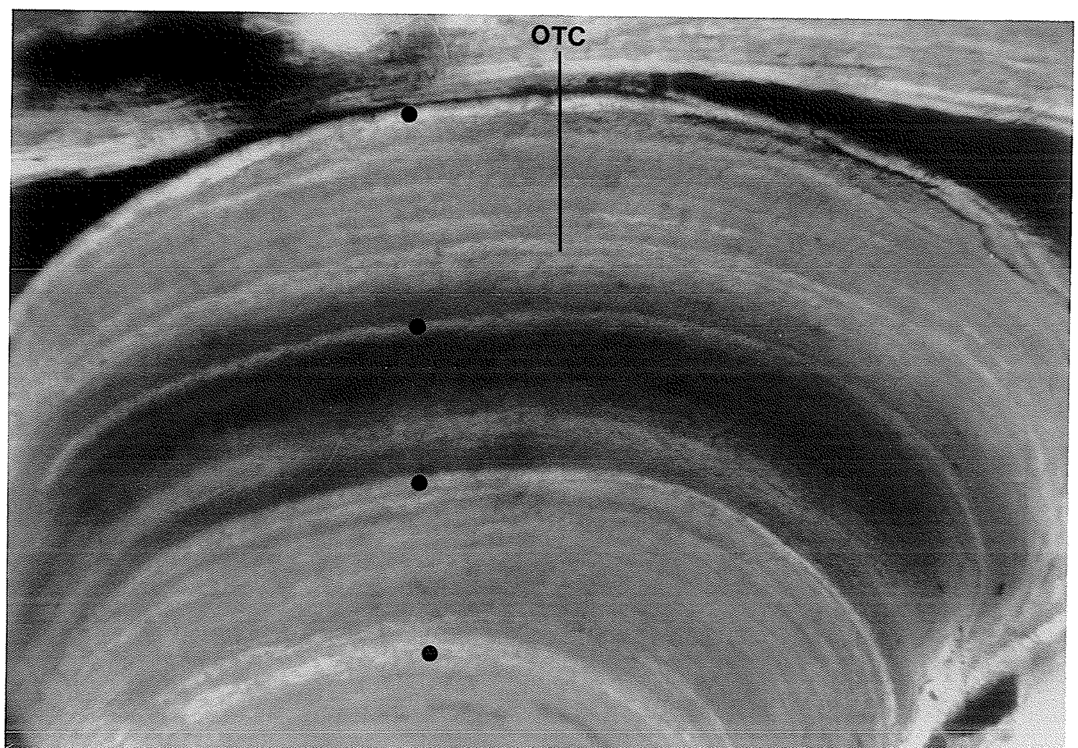

OTC

Table 4.1. Summary of completed oxytetracycline-marking experiments. Katle were injected with OTC, tagged and released into an earthen pond on 27 August, 1990; they were recaptured on 15 October, 1991 and their pectoral fin ray cross sections were examined for a fluorescent OTC mark and for growth checks outside the OTC mark.

Fish No.	Presence (strength) of OTC mark	Age (yr)	Number of checks outside OTC mark
347	Yes (strong)	5	1
348	Yes (strong)	7	1
349	No	5	-
350	No	5	-
351	Yes (weak)	6	0

rays of katle per year. This supports the conclusions drawn above from the annual formation of the transparent zones and checks. The pectoral fin ray ages of four of the five recaptured fish were one year greater than their pectoral fin ray ages at the time of marking. The recaptured fish ranged in age from 5 to 7 years. A strong check on the fin ray sections corresponding in time to the OTC injection was observed in all five fish, probably as a result of the stress of marking, tagging and handling (Fig. 4:5, bottom). It is suggested that this should be taken into consideration during age determination of previously tagged or marked fish.

In addition to these fish recovered from the earthen pond, a large number of katle over a wide size range were also marked with OTC and released into the reservoir. None of these fish were recovered by the end of this study, but since the fish are relatively long-lived, possible recapture of these katle from the reservoir in the future may allow future validation for more than one age group over a greater span of time.

Fin ray radius-total length relationship:

The relationship between fin ray radius and total length was found to be linear for all groups of katle. Scatter plots for individual fish and best fit regression lines through the points are shown in Fig. 4:6 for males in both habitats, and in Fig. 4:7 for females. Analyses of variance were carried out

Figure 4:6. Relationships between the total lengths of male katle and their pectoral fin ray radii. a. Reservoir. b. River. The fitted regression line of Table 4:3 is shown for each group.

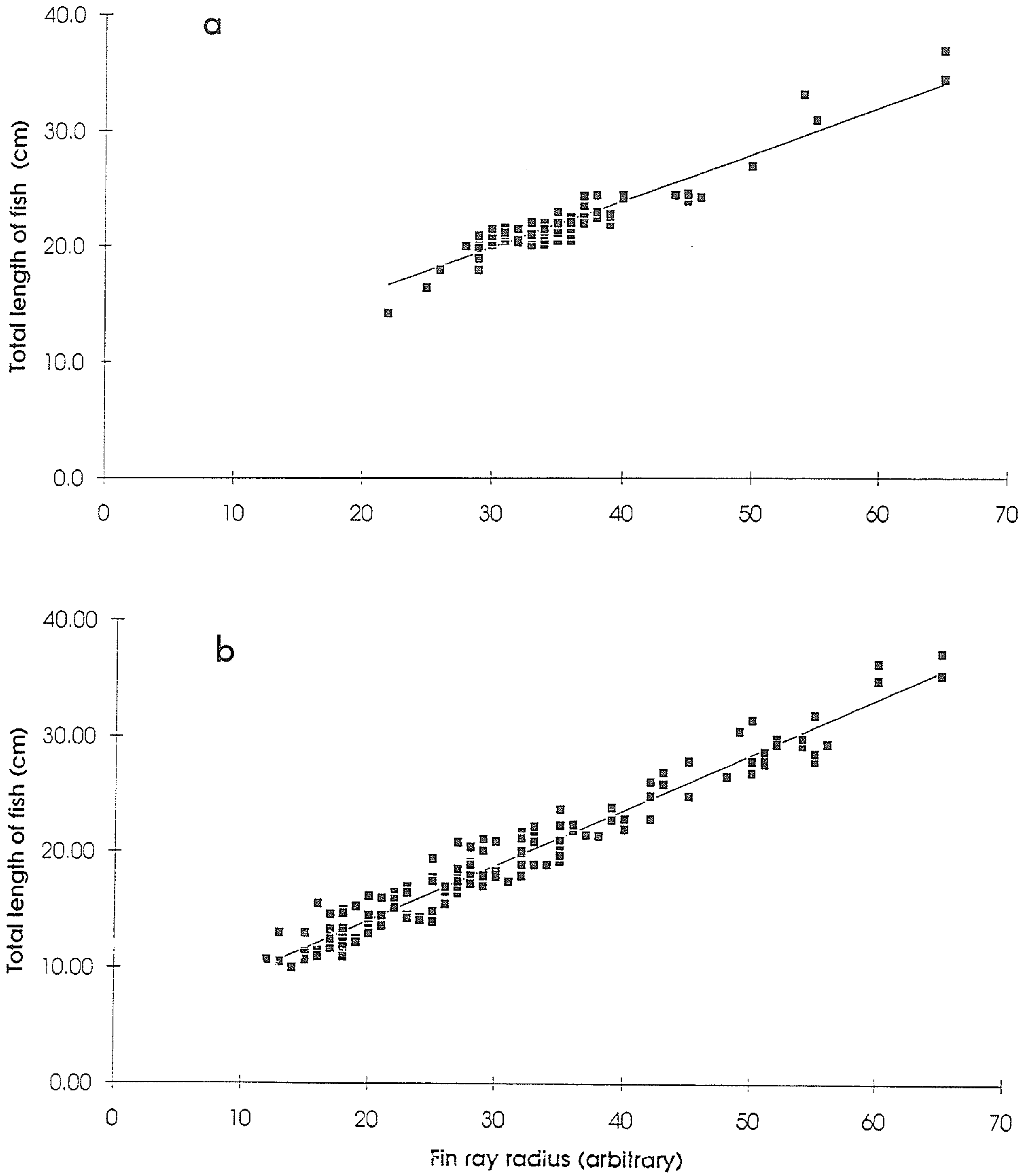
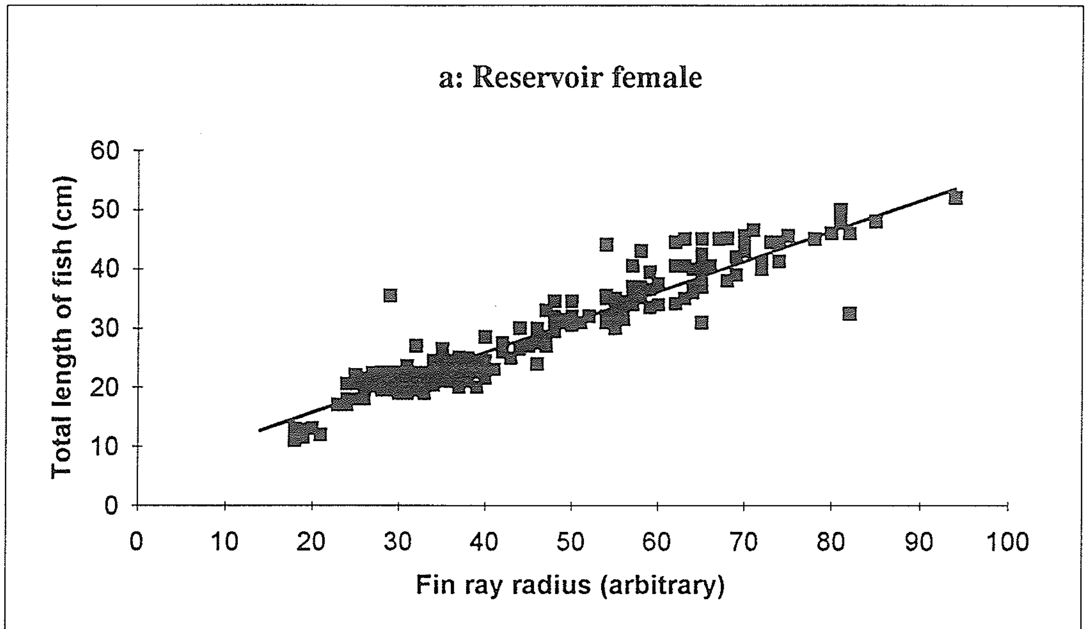
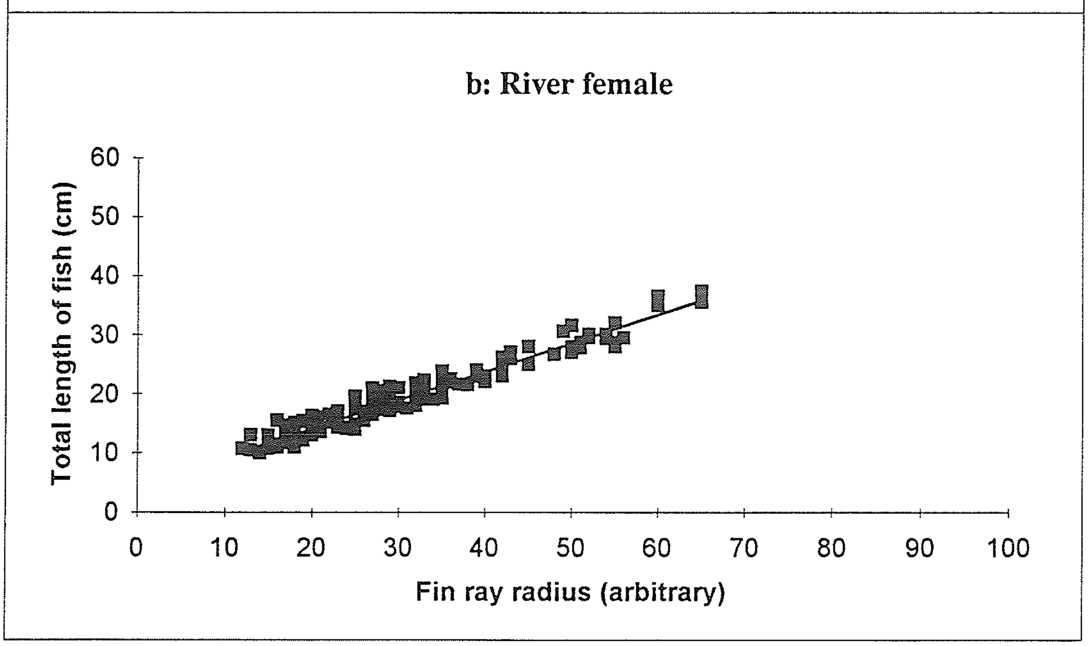

a
b
Total length of fish (cm)
Total length of fish (cm)
40.0
30.0
20.0
10.0
0.0
40.00
30.00
20.00
10.00
0.00
0
10
20
30
40
50
60
70
Fin ray radius (arbitrary)

Figure 4:7. Relationships between the total lengths of female katle and their pectoral fin ray radii. a. Reservoir. b. River. The fitted regression line of Table 4:3 is shown for each group.


a: Reservoir female
Total length of fish (cm)
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
100
Fin ray radius (arbitrary)


b: River female
Total length of fish (cm)
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
80
90
100
Fin ray radius (arbitrary)

on the b (slope) values between the various groups (Sokal and Rohlf, 1967). The significances of these analyses are shown in Table 4:2. In cases where there were two sets of data, Student's t tests were performed (Bailey, 1981). There were no significant differences in the values of b for different years, but the values of b compared between sexes and habitats were significantly different from each other. In particular, b was greater for females than for males within and between habitats. As there was no significant difference in the value of b between years, regression lines for different sexes and habitats were calculated from the pooled data for the years 1988, 1989 and 1990, and back-calculation of length was done by using 'a' (intercept) values for the respective groups (Table 4:3).

Size composition of gill net catches and effect of mesh size:

To ascertain whether the gill nets used in the reservoir captured a representative sample of the population, an analysis of the sizes of fish caught by each of the four mesh sizes was carried out (Fig. 4:8). Most of the fish were found to be caught by the 50 mm mesh size panel of the gill net, whereas the panels with 25, 75 and 100 mm mesh sizes caught relatively small numbers of fish throughout the study period (Fig. 4:8). The fish caught in the 25 mm mesh ranged from 11 cm to 15 cm in total length, with the largest number at 13 cm. No fish less than 11 cm in length (or less than three years of

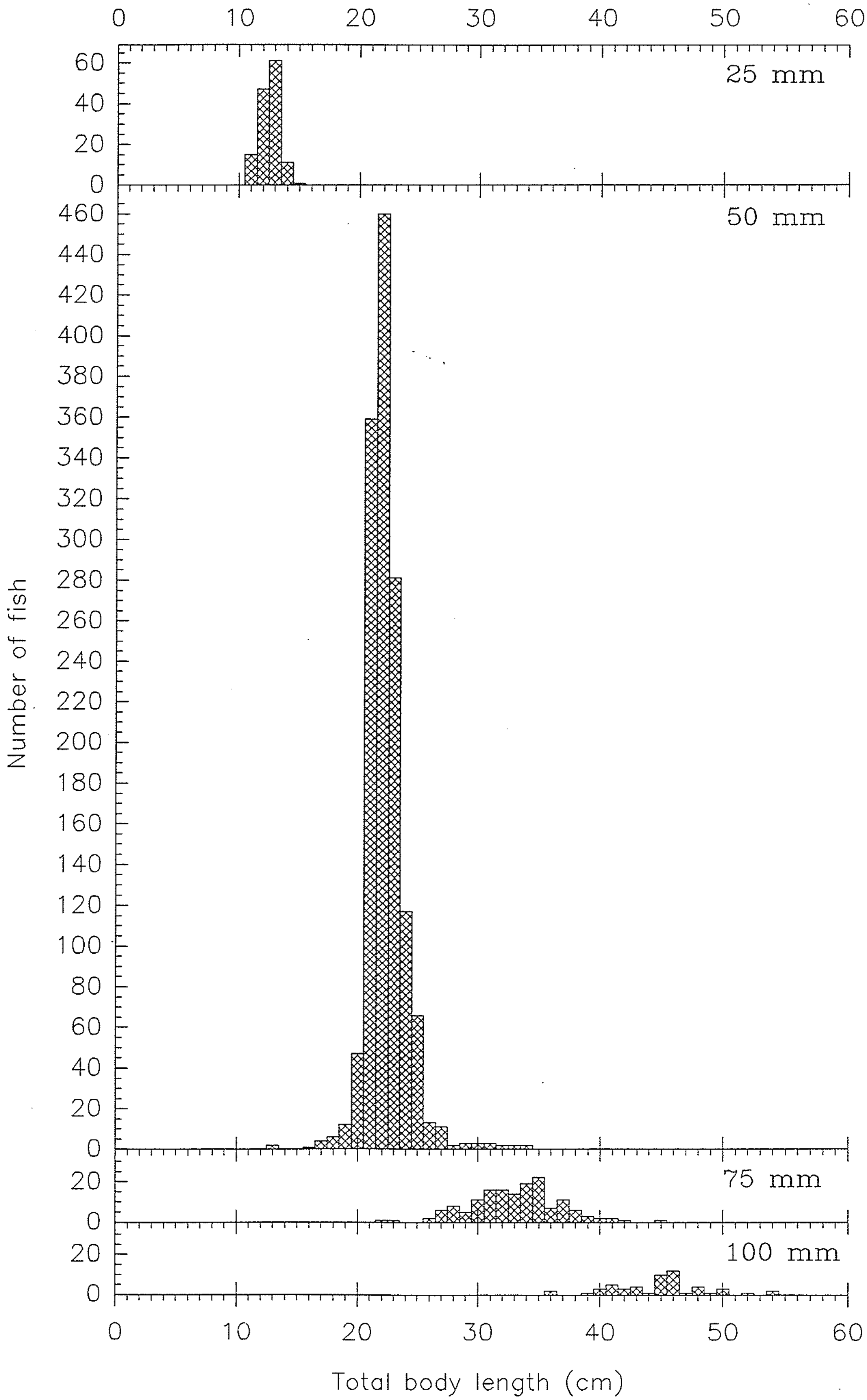
Table 4:2. Levels of significance of the differences between exponent b values for the relationships between fish length and fin ray radius (Ns = non-significant, * - $P < 0.05$, ** - $P < 0.01$).

(a)	♀	♂
Reservoir between years	Ns	Ns
River between years	Ns	Ns
1988 between habitats	**	**
1989 between habitats	**	**
1990 between habitats	**	*
Pooled years between habitats	*	*
(b)		
Pooled years river ♂ to ♀	*	
Pooled years reservoir ♂ to ♀	*	

Table 4:3. Intercept and slope values for the regressions of the total lengths of katle on their fin ray radii.

Habitat	Sex	Intercept	Slope	R^2	No.
Reservoir	♀	5.07	0.523	0.930	1461
Reservoir	♂	7.77	0.405	0.875	127
River	♀	4.45	0.482	0.948	150
River	♂	5.32	0.451	0.838	191

Figure 4:8. Size composition of katle samples caught by gill net panels of 25, 50, 75 and 100 mm mesh size. All fish caught in the Indrasarobar Reservoir during 1988 to 1990 are included.



25 mm
50 mm
75 mm
100 mm
Number of fish
Total body length (cm)

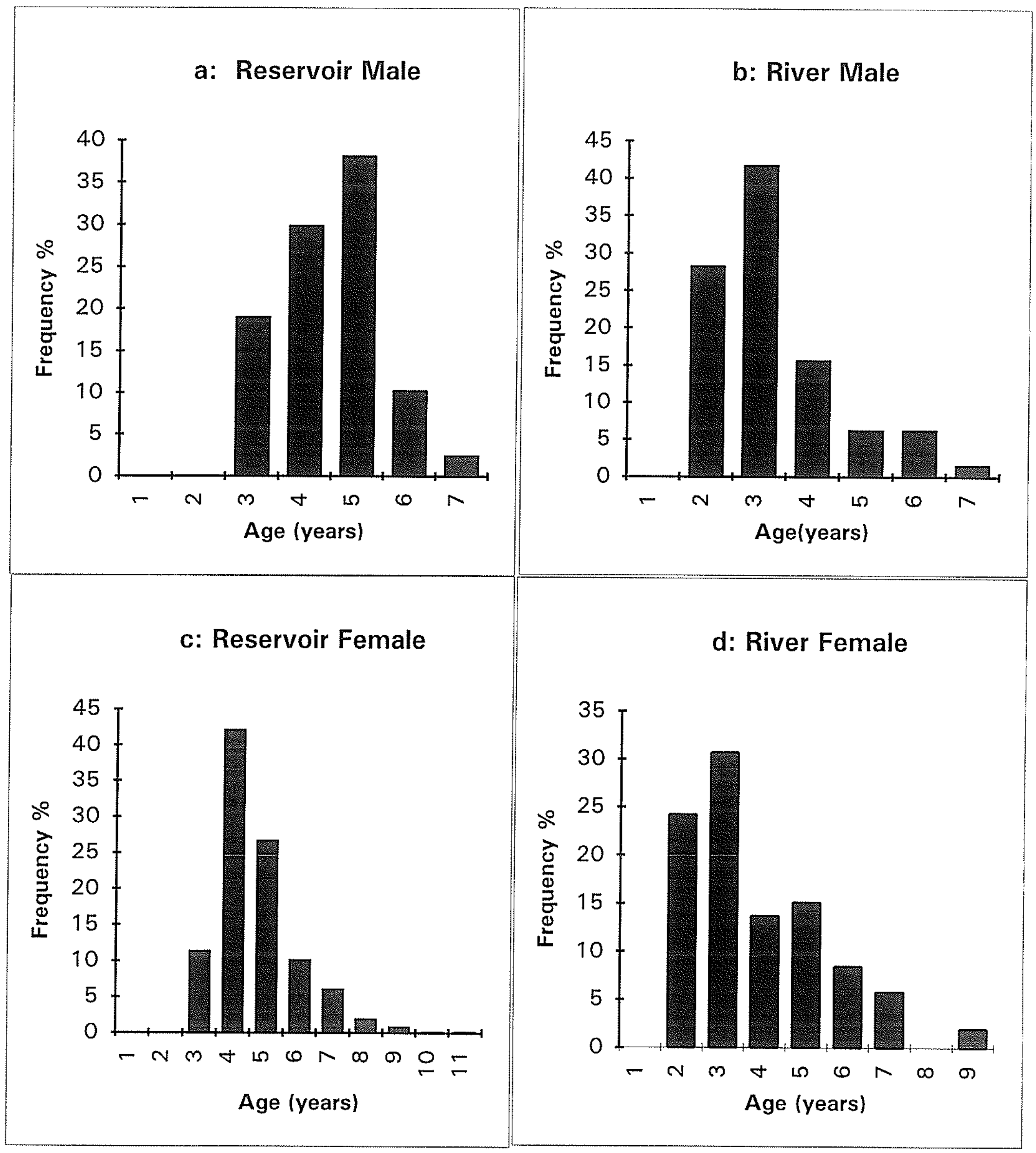
age) were caught; this represents a significant bias in the gill net samples. The 50 mm mesh caught a wide size range of katle, from 13 to 34 cm in total length, with a peak at 22 cm. The 75 mm mesh size panel of the gill net caught fish between 22 cm and 45 cm in total length. The contribution of the 100 mm mesh size panel was numerically small, the largest fish caught being 54 cm in total length and 11 years old. As these data show, the catches in the four panels overlap each other substantially in the total lengths of the fish. Thus, even though each mesh size is shown to be somewhat selective in its catch, the four mesh sizes combined would not have missed any size class completely, except for the very small fish less than 11 cm in length.

Age composition of the reservoir and river populations:

The samples collected in this study gave an approximate age composition of the male and female populations in the two systems (Fig. 4:9), even though the youngest age group is inadequately represented, as shown in the preceding section.

In the reservoir male population, the five-year-old group formed the highest percentage (38.2%) and older groups formed only small percentages of the total catch (Fig. 4:9a). In the sample of the reservoir females, four-year-old fish formed 42.2% of the total, and the contribution of the older fish declined successively (Fig. 4:9c). In river males, the catch was dominated by three-year-old fish, which constituted 41.9%

Figure 4:9. Age composition of katle populations by sex and habitat, as sampled in this study.
a. Reservoir males (n = 127).
b. River males (n = 150).
c. Reservoir females (n = 1461).
d. River females (n = 191).


a: Reservoir Male
Frequency %
Age (years)
b: River Male
Frequency %
Age(years)
c: Reservoir Female
Frequency %
Age (years)
d: River Female
Frequency %
Age (years)

of the total catch (Fig. 4:9b); older fish formed a relatively small percentage of the total fish catch. For river females, two- and three-year-old fish formed 24.2% and 30.7% of the total catch (Fig. 4:9d), and the contribution of older fish again decreased successively. No river female was caught at the age of eight, while nine-year-old fish formed 2% of the total catch of female katle.

Growth of katle in the first three years of life:

The data for the back-calculated mean lengths at the end of the first year of life showed no consistent differences between sexes and locations. The average lengths at age one year were 7.68 and 8.17 cm for the females from the reservoir and the river respectively. The one-year-old males from the reservoir and the river were 8.33 and 8.03 cm long on average (Tables 4:4 and 4:6). The slight average length difference between males in the two habitats was not significant. In the second year, the annual length increment in river females was slightly higher than that of their reservoir counterparts. In the third year, however, the reservoir females' length increment exceeded that of the river females (Tables 4:5 and 4:7). In the case of males the length increment during the first three years was almost identical in both populations.

Table 4:4. Mean total lengths (cm) of Indrasarobar Reservoir male katle grouped by age (yr) at capture (Age at Capt): ***E (bold italics) - mean length observed at capture;*** BC (light) - mean length back-calculated to year n of life. $\overline{BC}$ - mean value of BC at year n for all fish; I - annual length increment for all fish ($\overline{BC}_n$ - $\overline{BC}_{n-1}$).

Age at Capt	No. of Fish	Age at fin ray annulus formation (yr)						
		1	2	3	4	5	6	7
1+								
2+								
3+	30	8.55	13.34	***15.67***				
4+	47	8.32	13.00	15.97	***20.38***			
5+	60	8.27	12.56	15.59	19.32	***21.72***		
6+	16	8.66	12.98	15.96	19.45	21.52	***23.74***	
7+	04	7.90	11.81	16.30	21.25	24.82	28.75	***33.93***
$\overline{BC}$		8.33	12.75	15.80	19.44	22.18	28.75	
I			4.43	3.05	3.64	2.74	6.57	
SD of BC		0.80	1.11	0.97	0.94	1.58	2.29	
SD of E				***1.29***	***1.42***	***0.87***	***1.37***	***2.51***

Table 4:5. Mean total lengths (cm) of Indrasarobar Reservoir female katle grouped by age (yr) at capture (Age at Capt):
E (bold italics) - mean length observed at capture;
BC (light) - mean length back-calculated to year n of life.
$\overline{BC}$ - mean value of BC at year n for all fish;
I - annual length increment for all fish ($\overline{BC}_n$ - $\overline{BC}_{n-1}$).

Age at Capt	No. of Fish	Age at fin ray annulus formation (yr)										
		1	2	3	4	5	6	7	8	9	10	11
1+												
2+												
3+	30	7.69	11.75	***16.85***								
4+	89	8.06	11.79	18.70	***20.88***							
5+	90	7.81	11.44	16.83	21.92	***24.75***						
6+	90	7.53	11.12	17.50	24.35	24.86	***29.90***					
7+	89	7.47	11.48	16.23	21.22	28.00	29.99	***33.81***				
8+	29	7.15	11.69	16.75	22.33	28.16	32.44	34.04	***37.87***			
9+	14	7.76	11.98	16.95	22.99	27.89	32.47	34.00	36.61	***47.31***		
10+	2	7.76	12.31	17.63	22.53	26.85	32.77	34.11	35.97	41.69	***51.00***	
11+	3	8.37	11.83	16.90	23.31	28.36	32.95	34.15	36.39	44.61	47.95	***53.40***
$\overline{BC}$		7.68	11.50	17.26	22.51	26.76	30.87	34.04	36.51	43.44	47.95	
I			3.82	5.76	5.26	4.25	4.11	3.17	2.47	6.94	4.51	
SD of BC		0.67	0.85	7.19	10.92	13.52	2.43	1.01	1.13	3.59	2.70	
SD of E				***3.5***	***1.21***	***1.34***	***3.16***	***3.87***	***2.29***	***1.58***	***1.41***	***0.1***

Table 4:6. Mean total lengths (cm) of Tadi River male katle grouped by age (yr) at capture (Age at Capt): ***E (bold italics) - mean length observed at capture;*** BC (light) - mean length back-calculated to year n of life. $\overline{BC}$ - mean value of BC at year n for all fish; I - annual length increment for all fish ($\overline{BC}_n$ - $\overline{BC}_{n-1}$).

Age at Capt	No. of Fish	Age at fin ray annulus formation (yr)						
		1	2	3	4	5	6	7
1+								
2+	30	7.59	***10.97***					
3+	30	8.08	11.00	***13.31***				
4+	30	8.35	11.39	13.97	***16.18***			
5+	12	8.09	10.63	13.24	15.39	***18.42***		
6+	12	8.12	11.36	15.17	16.57	17.92	***22.01***	
7+	3	8.09	11.47	14.56	16.84	17.92	20.70	***23.90***
$\overline{BC}$		8.03	11.15	14.10	16.07	17.92	20.70	
I			3.12	2.95	1.97	1.84	2.78	
SD of BC		0.52	0.46	0.36	0.33	0.33	0.15	
SD of E			***1.08***	***1.21***	***1.41***	***1.48***	***1.38***	***0.36***

Table 4:7. Mean total lengths (cm) of Tadi River female katle grouped by age (yr) at capture (Age at Capt):
E (bold italics) - mean length observed at capture;
<u>BC</u> (light) - mean length back-calculated to year n of life.
$\overline{BC}$ - mean value of BC at year n for all fish;
I - annual length increment for all fish ($\overline{BC}_n$ - $\overline{BC}_{n-1}$).

Age at Capt	No. of Fish	Age at fin ray annulus formation (yr)								
		1	2	3	4	5	6	7	8	9
1+										
2+	30	8.32	***13.00***							
3+	30	8.14	12.53	***15.25***						
4+	21	8.09	12.58	16.04	***18.75***					
5+	19	8.01	12.58	15.42	18.32	***21.77***				
6+	11	8.04	12.71	16.71	19.57	22.22	***26.96***			
7+	9	8.49	12.53	16.03	20.21	22.03	24.60	***29.63***		
8+	0	-	-	-	-	-	-	-	-	
9+	3	7.98	12.84	16.87	21.04	22.90	25.92	28.77	30.94	***36.46***
$\overline{BC}$		8.17	12.60	16.01	19.25	22.23	24.93	28.77	30.94	
I			4.43	3.41	3.23	2.98	2.69	3.84	2.16	
SD of BC		0.56	0.83	1.18	1.67	0.84	1.17	1.13	0.62	
SD of E			***1.72***	***1.39***	***1.43***	***2.13***	***1.09***	***1.55***	-	***0.95***

Adult growth in katle

The reservoir population: In nearly every case the mean length at the end of the third and subsequent years was smaller for males (Fig. 4:10a) than for females of the same age (Fig. 4:11a). This difference was also obvious in annual increments. The annual increments in adult males were 3.05 cm between the ages of 3 and 4, 3.64 cm between 4 and 5 and 2.74 cm between 5 and 6 years (Table 4:4). These were lower than those in females, which were 5.75, 5.26 and 4.25 cm over the same periods of life (Table 4:5). Male katle above the age of seven were not observed throughout the study period. Average total lengths at age determined by back-calculation were in agreement with those observed at capture in most cases, but for the four-year-old age group the back-calculated average length was significantly higher than the length at capture in both sexes. A similar discrepancy was found for six-year-old males, but the back-calculated average length for this group was based only on a small sample (4).

The river population: Similar trends of mean length and annual increments were found in river fish as had been seen in the reservoir population. The length increments in males in years 3, 4, and 5 were 2.95, 1.97 and 1.84 cm respectively (Table 4:6). The length increments in those years for females were 3.41, 3.23 and 2.98 cm respectively (Table 4:7). The length increments in the fish (male and female) above six years of age seem quite high, but these means were based on

Figure 4:10. Average total lengths of male katle from the reservoir (a) and the river (b) at age. Lengths observed at capture - ▲; back-calculated lengths - ■. ± 95 % confidence limits are shown.

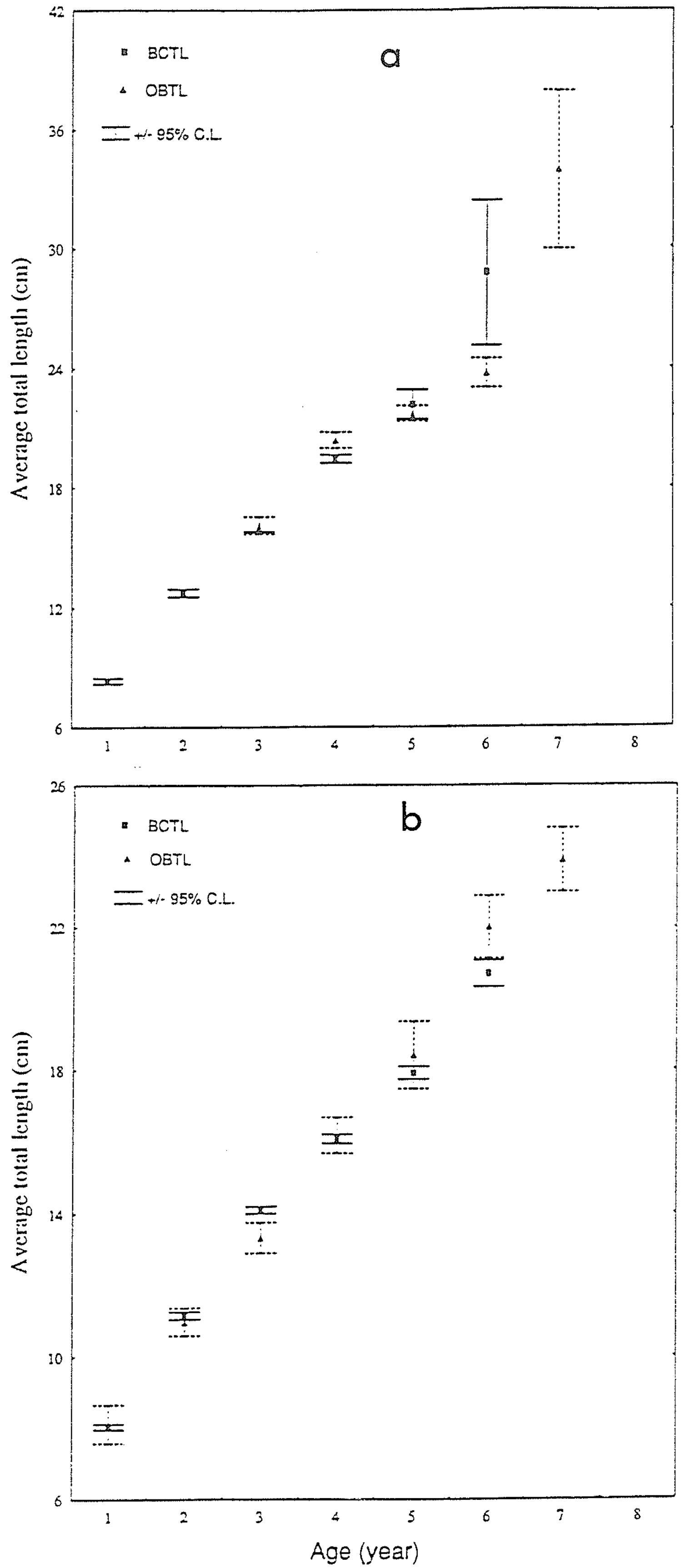
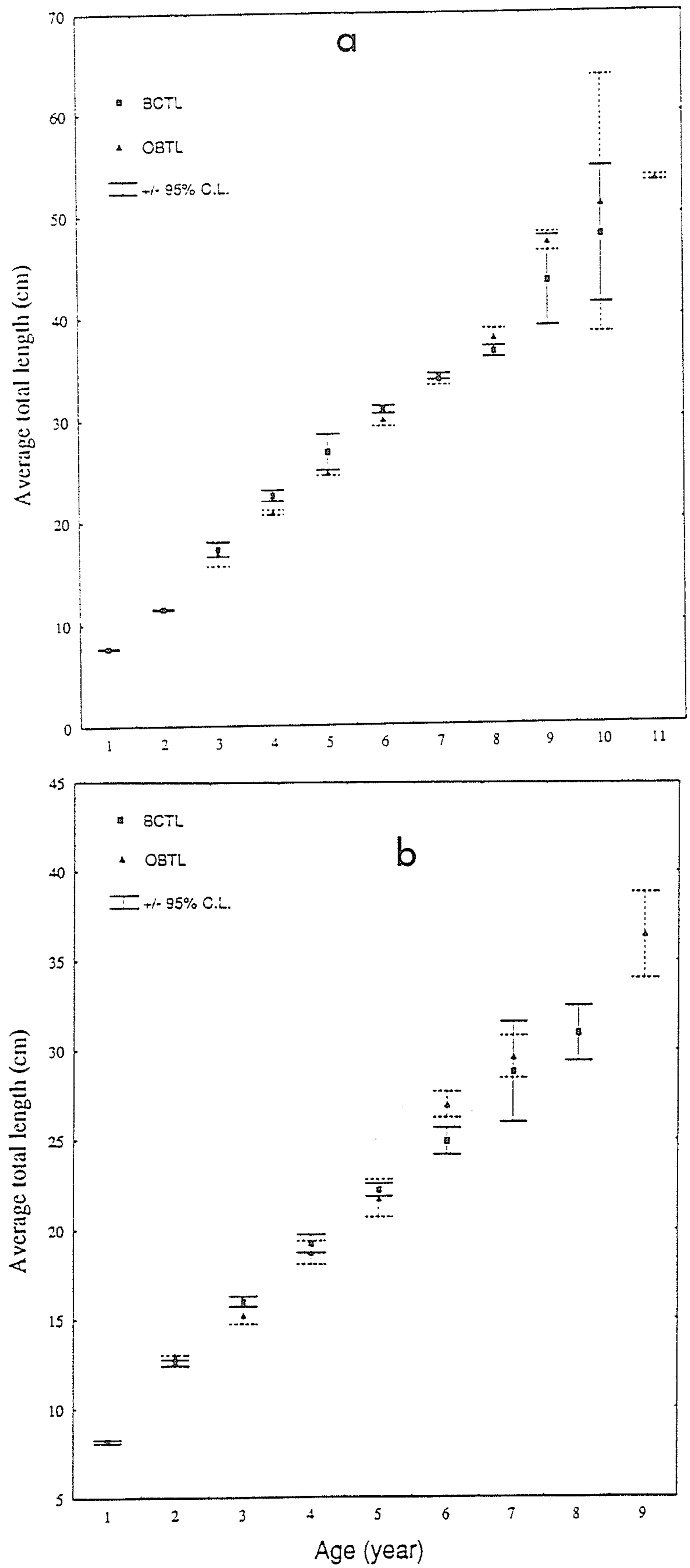

a
BCTL
OBTL
+/- 95% C.L.
Average total length (cm)
42
36
30
24
18
12
6
1
2
3
4
5
6
7
8
b
BCTL
OBTL
+/- 95% C.L.
Average total length (cm)
26
22
18
14
10
6
1
2
3
4
5
6
7
8
Age (year)

Figure 4:11. Average total lengths of female katle from the reservoir (a) and the river (b) at age. Lengths observed at capture - ▲; back-calculated lengths - ■. ± 95 % confidence limits are shown.


a
BCTL
OBTL
+/- 95% C.L.
Average total length (cm)
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
b
BCTL
OBTL
+/- 95% C.L.
Average total length (cm)
45
40
35
30
25
20
15
10
5
1
2
3
4
5
6
7
8
9
Age (year)

only three fish of each sex so these data were not taken into account in the estimation of asymptotic growth and other parameters of the von Bertalanffy equation. As in the reservoir population, average total lengths at age observed at capture agreed with the back-calculated values in most cases. In males, the back-calculated length was significantly higher in the three-year-old age group and lower in the six-year-old age group (Fig. 4:10b). In females, the observed average total length was found to be significantly higher than the back-calculated one for the six-year-old age group (Fig. 4:11b).

Comparison of average total lengths back-calculated to a particular age from fish of different ages at capture were in good agreement for all groups. Specifically, there was no consistent decrease in back-calculated length with increasing age at capture, a tendency frequently noted in other studies and known as Lee's phenomenon (Ricker, 1969; Bagenal and Tesch, 1978).

Differences between the populations

Mean lengths of male katle at the end of their first year were not significantly different between habitats. The reservoir males grew faster than the river males from the second year on. The oldest males encountered in the catches from both the reservoir and the river were 7 years old. There was a significant difference of 10 cm between their average total lengths, the 7-year-old reservoir males being larger

(33.93 cm) than the river ones (23.90 cm). Again, these average lengths are derived from small sample sizes (3 fish from the river and 4 fish from the reservoir).

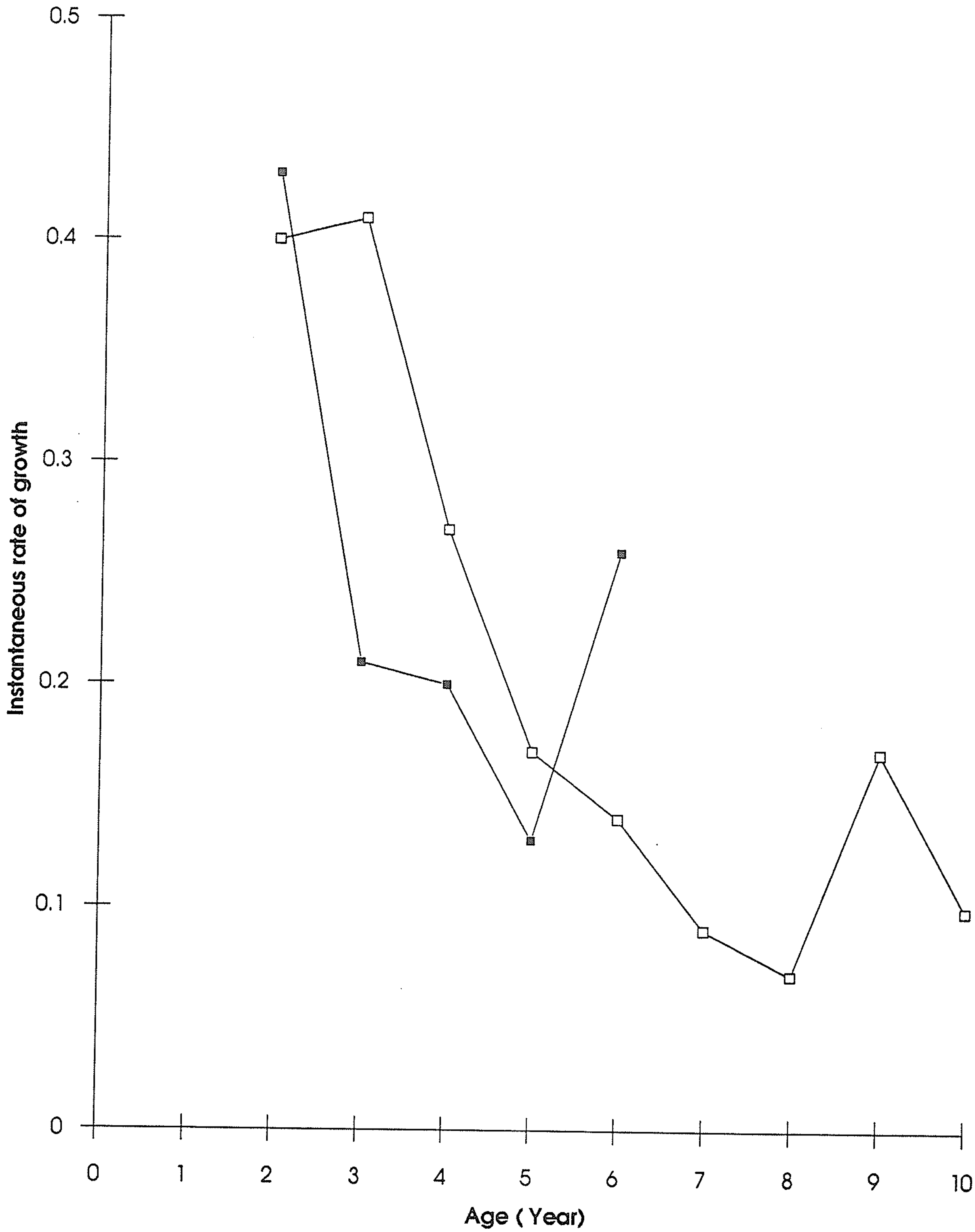
The mean lengths of the reservoir females at the end of the first and second years were lower than those of the river females at the same age. However, the average total lengths (and the annual increments) in female fish older than 4 years were significantly higher in the reservoir population than in the river. The oldest females in the river were nine years old while three 11-year-old fish were encountered in the reservoir samples.

Instantaneous rate of growth

In the reservoir population, the instantaneous rates of growth per annum (G_L) between the ages of 1 and 2 years were 0.40 and 0.43 cm cm^{-1} yr^{-1} respectively in males and females (Fig. 4:12). In the next year the growth rate remained more or less the same (0.41 cm cm^{-1} yr^{-1}) in females but dropped to 0.21 cm cm^{-1} yr^{-1} in males. The growth rate continued to decrease with increasing age in both sexes and ultimately it was only 0.07 cm cm^{-1} yr^{-1} between the ages of 7 and 8 years in females and 0.13 cm cm^{-1} yr^{-1} between the ages of 4 and 5 years in males. The growth rate between ages 8 and 9 years in females and 5 and 6 in males showed some apparent increase, but the sample sizes were small.

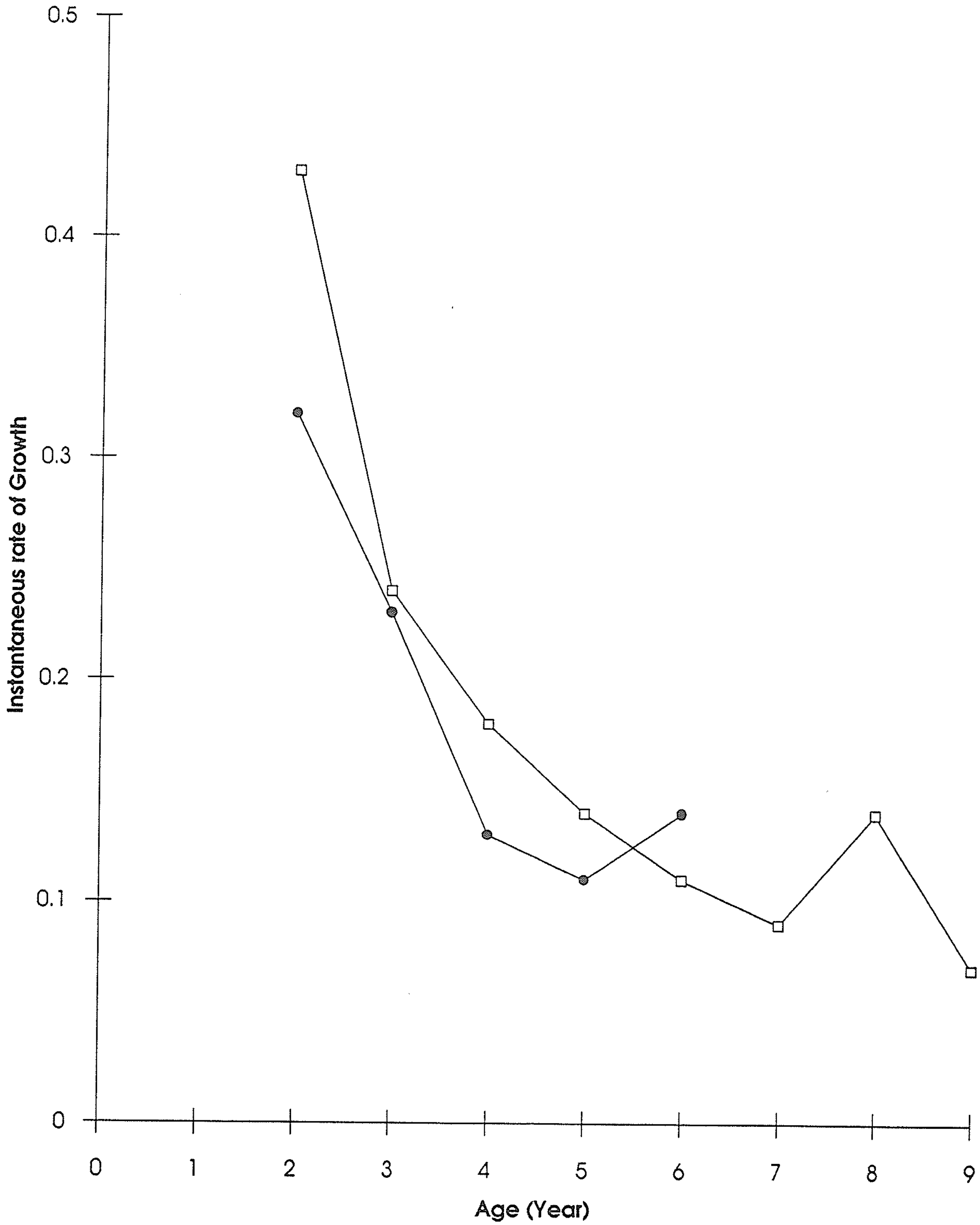
The instantaneous growth rates in the river population

Figure 4:12. Instantaneous rate of growth (cm cm^{-1} yr^{-1}) of katle in the reservoir for male (—■—) and female (—□—) fish of various ages.



0.5
0.4
0.3
0.2
0.1
0
Instantaneous rate of growth
0
1
2
3
4
5
6
7
8
9
10
Age (Year)

Figure 4:13. Instantaneous rate of growth (cm cm^{-1} yr^{-1}) of katle in the river for male (—●—) and female (—□—) fish of various ages.



0.5
0.4
0.3
0.2
0.1
0
Instantaneous rate of Growth
0
1
2
3
4
5
6
7
8
9
Age (Year)

showed a similar decline with age. The highest values, 0.43 cm cm^{-1} yr^{-1} in females and 0.33 cm cm^{-1} yr-1 in males, occurred between the ages of 1 and 2 (Fig. 4:13). The rate dropped to 0.24 cm cm^{-1} yr^{-1} in females and 0.23 cm cm^{-1} yr^{-1} in males in the next year and ultimately to 0.07 cm cm^{-1} yr^{-1} in females and 0.14 cm cm^{-1} yr^{-1} in males between the ages of 8 and 9 and 5 and 6 years respectively.

A simple linear regression model was fitted to the data for instantaneous growth rate against log age:

$$G_L = (\text{slope}) \log \text{age} + \text{intercept}.$$

The slopes and intercepts (Table 4:8) were compared between sexes within the same location and for the same sex between the locations. In the case of male versus female in the reservoir, the slope and the intercept of the male model differed from those for the female by approximately 0.6 and 0.9 standard errors respectively. The decline in growth rate with age was not significantly different between the two sexes in the reservoir. The slopes and intercepts for males and females in the river differed by approximately 1.1 and 1.5 standard errors and were also not significantly different at the 5% level. In the case of the females compared between the two habitats, the slopes and intercepts differed by about 2 and 3 standard errors. The difference between the slopes was not statistically significant while the intercepts (representing the G_L value at 1 year of age) were significantly different ($p > 0.05$). The differences between

Table 4:8. Intercept and slope values for regressions of instantaneous growth rates on log age.

Habitat	Sex	Intercept(SE)		Slope	(SE)	r^2
Reservoir	♀	0.586	(0.064)	-0.217	(0.037)	0.83
Reservoir	♂	0.483	(0.141)	-0.179	(0.102)	0.50
River	♀	0.383	(0.032)	-0.155	(0.022)	0.89
River	♂	0.443	(0.065)	-0.193	(0.047)	0.84

the slopes and intercepts were not significant between males from the river and reservoir. It appears that the regression models were all within a distance from each other that could be explained by random variation. Only one comparison, the intercepts between females from the river and reservoir, showed significance. Overall, the data suggested that the habitat and sex factors do not influence the decline in the instantaneous growth rate of katle with age.

The von Bertalanffy growth curve

The mathematical and graphical methods for estimating L_∞, K and t_0 yielded very similar values within each group of fish, although they differed between groups. The values of L_∞ for male and female katle from the reservoir and river indicate their predicted maximum size in both habitats. The predicted maximum sizes for males in the reservoir and the river were calculated to be 41 and 26 cm respectively. Similarly, the predicted maximum sizes for the females in the reservoir and the river were 73 and 45 cm respectively (Table 4:9). The highest K value (the growth coefficient) was calculated for the males from the river (0.196) and the lowest was for the reservoir females (0.087). The values for the von Bertalanffy growth parameters indicated that males grew faster than the females but to a smaller maximum size.

Table 4:9. Values for von Bertalanffy growth parameters estimated by the graphic method for fitting growth curves for katle from the Indrasarobar Reservoir and Tadi River. Also shown are the maximum ages of fish captured.

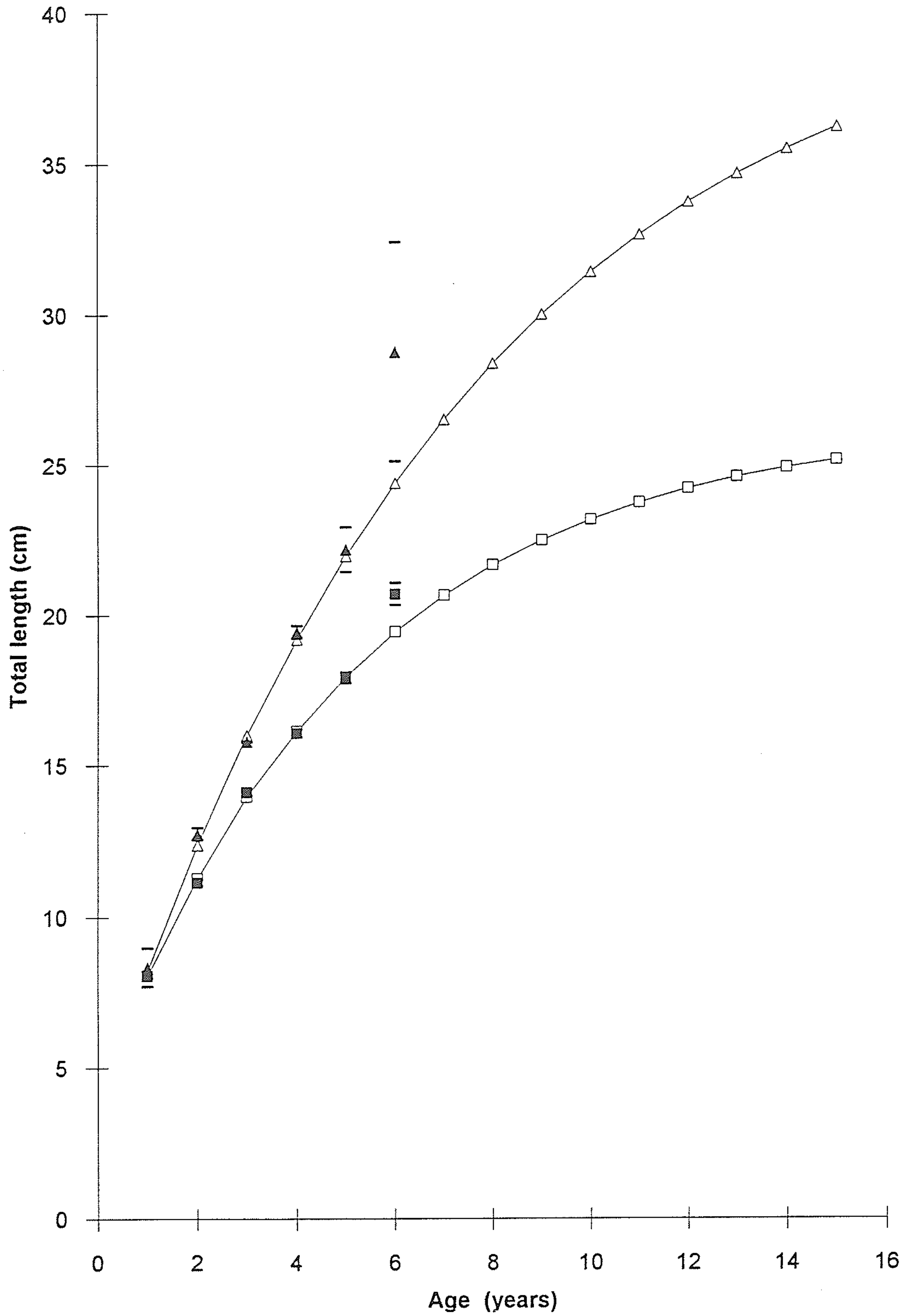
Habitat	Sex	Maximum Age (yr^+)	$\underline{L_\infty}$ (cm)	$\underline{K}$ (yr^{-1})	$\underline{t_0}$ (yr)
Reservoir	♀	11	73	0.089	-0.117
Reservoir	♂	7	41	0.135	-0.650
River	♀	9	45	0.120	-0.682
River	♂	7	26	0.195	-0.875

The observed growth curves for male and female katle from both systems (back-calculated length against age) are shown in Fig. 4:14 and 4:15, along with the mathematically fitted von Bertalanffy growth curves in each case. The mathematical curves can be seen to fit the data quite well, passing within the 95% confidence limits of almost all data points. The few exceptions were mostly for the larger, older fish with small sample sizes.

Variation in growth in different years and its correlation with abiotic factors

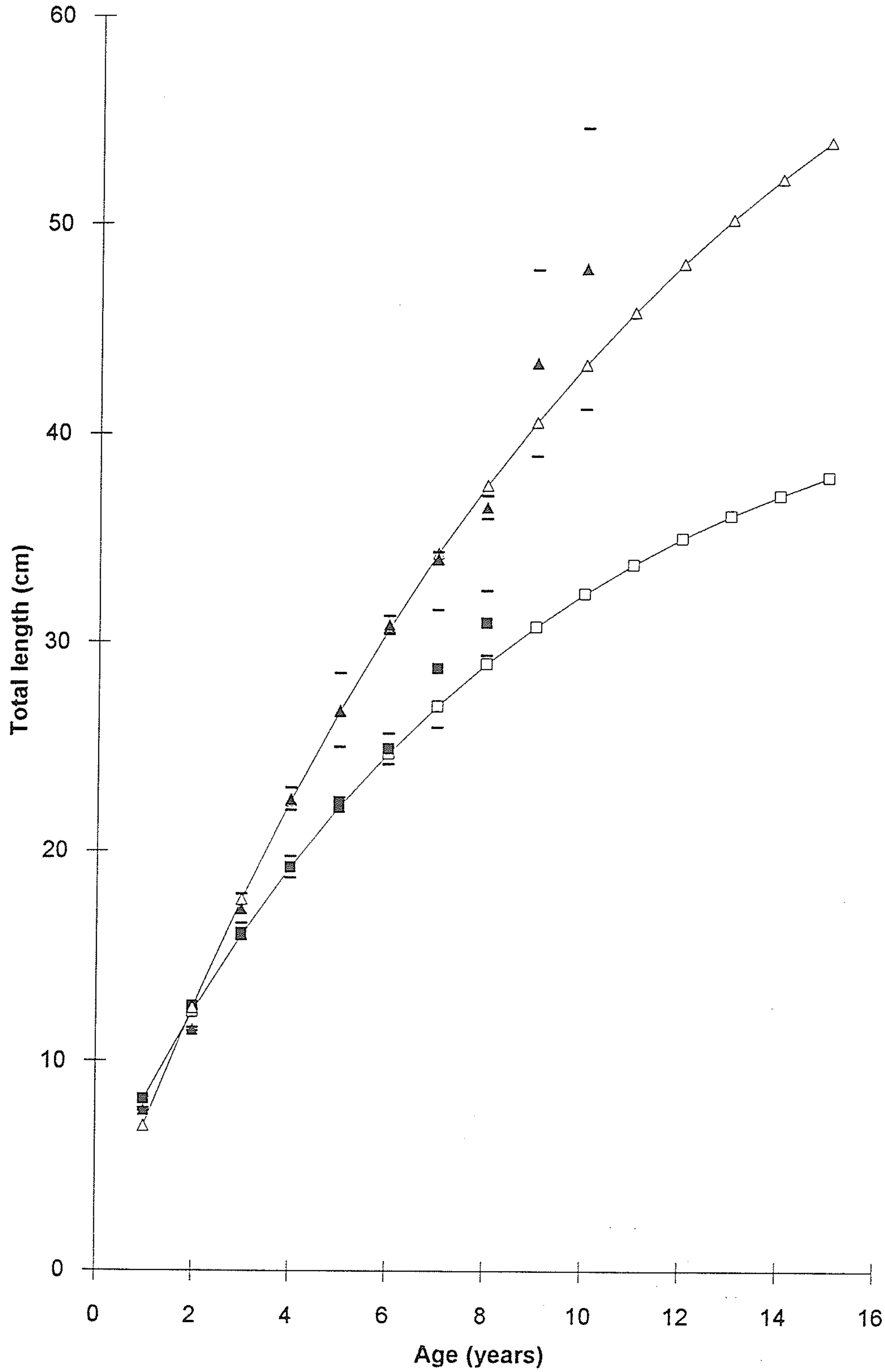
Effect of temperature variation between years: Preliminary examination of the growth of the reservoir katle showed quite clearly that there was a year-to-year variation in the annual total length increment within the same age groups. As it was observed that most of the transparent zones in the fin ray cross-sections (indicating slow growth) were laid down during winter or early spring (Fig. 4:4), it appears that new growth of the fish in the reservoir starts about in April. Most of the annual growth was achieved between April and October, the warmer months. Katle are known to live in a wide temperature range from 15 to 30°C (Rajbanshi, 1982) and breed naturally in temperatures between 20 - 23°C (Rai, 1978) or between 21 to 26.7°C (Ahmad, 1948). It was thus hypothesised that temperature above 20°C might be optimal for its growth.

Figure 4:14. Growth curves for male katle from the Indrasarobar Reservoir (△) and the Tadi River (□). Solid symbols show average back-calculated lengths for each age with 95% confidence limits (dashes). Curves and hollow symbols show predicted lengths at each age calculated from the von Bertalanffy growth equations fitted to the data.



Total length (cm)
40
35
30
25
20
15
10
5
0
0
2
4
6
8
10
12
14
16
Age (years)

Figure 4:15. Growth curves for female katle from the Indrasarobar Reservoir (△) and the Tadi River (□). Solid symbols show average back-calculated lengths for each age with 95% confidence limits (dashes). Curves and hollow symbols show predicted lengths at each age calculated from the von Bertalanffy growth equations fitted to the data.



Total length (cm)
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
16
Age (years)

Therefore, an attempt was made to examine the effect of temperature variation between different years on the annual growth of katle in the reservoir. Surface water temperature was taken at 10:00 h each day beginning in 1982 by personnel from the Indrasarobar Hydroelectricity Sub-station, and after 1985 by personnel from the Inland Fisheries Centre. These temperature data were used to calculate the number of degree days above 20°C (the sum over all days of the difference between the daily temperature and 20°C) for the period of April to October from 1982 to 1989. It was found that the number of degree days above 20°C between 1982 and 1989 ranged between 595.7 in 1984 and 611.2 in 1985. This small variation, by only 15.5 degree days or less than 3% of the total, seems unlikely to have influenced the growth rate of katle.

Effect of variation in surface area due to drawdown: The regression described in the Materials and Methods:

$$\Delta L = a + b \log A$$

where ΔL = annual total length increment of the fish, and A = average area of the reservoir, was evaluated separately for every age X, to determine whether growth varied with drawdown and, if so, whether the dependence of growth on area differs from one age to another. The results demonstrated a distinct positive linear relationship between total length increments and average reservoir area for all ages (Table 4:10), but it is difficult to see any pattern from one age group to the next as slopes differed significantly among them.

Table 4:10. Age-specific regressions of katle's average annual length increment ΔL on log_{10} of the average surface area A of the Indrasarobar Reservoir for years from 1982-1989.

Age	Regression equation	r^2	P value	No.
Age 1	$\Delta L = +26.8 + 11.0 \log A$	0.78	0.006	35
Age 2	$\Delta L = -38.9 + 15.2 \log A$	0.85	0.001	45
Age 3	$\Delta L = -55.9 + 21.5 \log A$	0.79	0.003	30
Age 4	$\Delta L = -36.0 + 17.1 \log A$	0.55	0.034	30
Age 5	$\Delta L = -99.6 + 28.1 \log A$	0.71	0.015	30
Age 6	$\Delta L = -86.7 + 26.2 \log A$	0.95	0.001	30
Age 7	$\Delta L = -57.3 + 20.6 \log A$	0.65	0.098	30
Age 8	$\Delta L = -30.9 + 10.8 \log A$	0.79	0.107	30

Length-weight relationship:

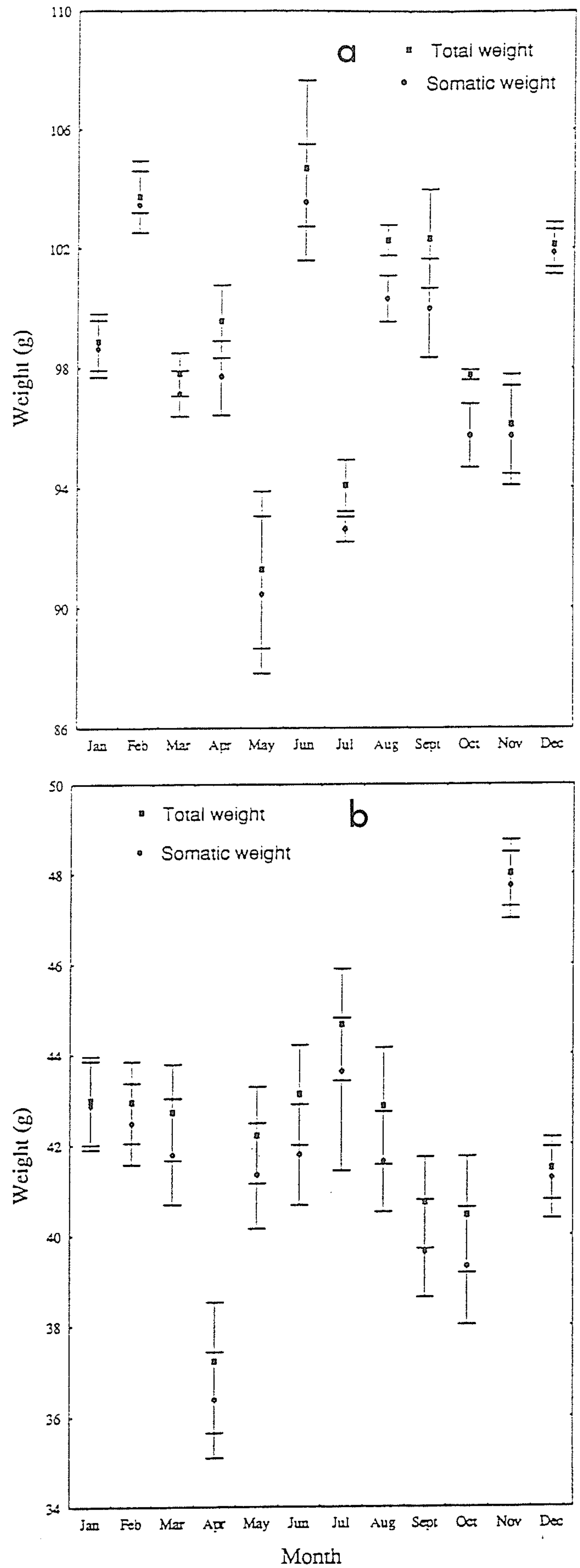
As described in the Materials and Methods, the length-weight relationship was applied in its logarithmic form:

$$\log W = \log a + b \log L$$

where W and L are the weight and the total length of the fish. The constant b did not differ significantly from 3.0 for any group, so this value of b was used to calculate values of log a from the regression equations for reservoir and river populations (Appendices 7 and 8). The mean lengths of all fish caught from the reservoir were: 19.0 cm for males at stage 1 of gonadal maturity (see Ch. 5); 22.1 cm for males at stages ≥2; 19.3 cm for females at stage 1; and 24.5 cm for females of stages ≥2. Similarly the mean lengths of all the fish caught from the river were 11.6 cm for males at stage 1, 16.9 cm for males at stages ≥2, 12.9 cm for females at stage 1 and 20.8 cm for females at stage ≥2. These values have been taken as "standard" lengths of standard fish in further analyses.

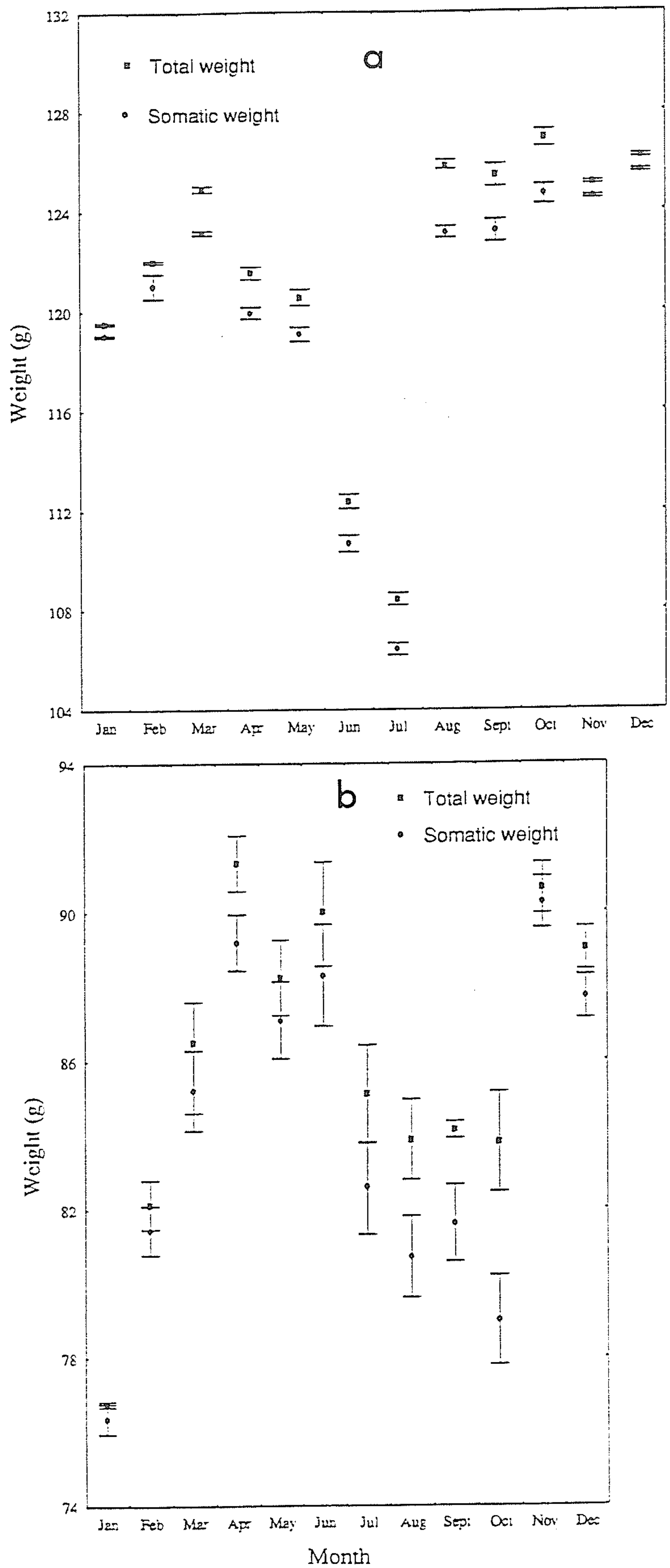
Monthly total and somatic weights (± 95 % CL) of standard males and females from both locations at their different stages of gonadal maturity through a year were calculated from monthly regression equations. These are presented in Appendices 9, 10, 11, 12 and illustrated in Fig. 4:16 and 4:17. In the reservoir standard male the total weight ranged between 94.08 ± 0.86 g in July and 104.68 ± 2.96 g in June (Fig. 4:16a). The average total weight of the reservoir standard female ranged between 108.42 ± 0.24 g in July and

Figure 4:16. Monthly average total weight and somatic weight (g) of the standard (22.1 cm) male katle from the reservoir (a) and of the standard (16.9 cm) male from the river (b), ± 95% confidence limits.



a
Total weight
Somatic weight
Weight (g)
110
106
102
98
94
90
86
Jan Feb Mar Apr May Jun Jul Aug Sept Oct Nov Dec
b
Total weight
Somatic weight
Weight (g)
50
48
46
44
42
40
38
36
34
Jan Feb Mar Apr May Jun Jul Aug Sept Oct Nov Dec
Month

Figure 4:17. Monthly average total weight and somatic weight (g) of the standard (24.5 cm) female katle from the reservoir (a) and of the standard (20.8 cm) female from the river (b), ± 95% confidence limits.



a
Total weight
Somatic weight
Weight (g)
132
128
124
120
116
112
108
104
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
b
Total weight
Somatic weight
Weight (g)
94
90
86
82
78
74
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sept
Oct
Nov
Dec
Month

126.15 ± 0.15 g in December (Fig. 4:17a). The fact that the reservoir fish experienced their lowest weight in July was probably due to the effect of reproductive activities, despite relatively higher feeding intensity in reservoir fish during July (Ch. 3). The minimum value of average total weight in the river males was observed in October (40.45 ± 1.38 g), and was immediately followed by the highest value (48.01 ± 0.75 g) in November (Fig. 4:16b). In the case of the river females the values of average total weight ranged between 76.76 ± 0.08 g in January and 91.33 ± 0.75 g April (Fig. 4:17b). No definite trend was observed in the variation of total weight of the fish between the locations and sexes.

It was also obvious from Fig. 4:16 and 4:17 that the total and somatic weights of katle did not differ significantly during the winter months (November to February). Significant differences between total and somatic weight, reflecting the weight of the gonad, were observed from March to October in both systems, but the differences were not very large. The low gonadal weight that this implies is probably due to the fact that katle are partial spawners.

DISCUSSION

The formation of marks on bony structures such as scales, fin rays, otoliths and opercula is well documented for fish from temperate waters. Such annulus production is usually the result of periods of slow winter and fast summer growth during the course of a year. The present study has established for the first time the occurrence of growth checks in katle similar to those found previously in both temperate and tropical fish (see Introduction). This study has furthermore provided validating evidence that the observed annuli are indeed annual growth rings. Careful examination of the transparent margins of fin ray sections revealed that the highest percentages of well defined rings or annuli were laid down during March and April. It seems that the new growth begins at that time and that the preceding transparent bands are laid down in the previous months (January to March). This interpretation is supported by the results of oxytetracycline marking: only one growth check was found to be laid down during the 15 months between the time of administration of the OTC (indicated by a sharp fluorescent ring in the fin ray cross-section) and the recapture of the fish. These results therefore provide evidence that age can be determined reliably from the pectoral fin rays of katle. This is not unexpected: being situated above 26 ° 20′ N, Nepal exhibits four distinct seasons in a year with temperature variation of about 14°C.

The average surface water temperature in the Indrasarobar Reservoir and the Tadi River ranges from 13.5°C in February to 27°C in July (Fig 5:16). The formation of checks in both habitats in the spring would then arise from an acceleration of growth due directly or indirectly to rising temperature or other seasonal effects, and slower growth would be expected in the cooler winter season.

Growth is generally defined as a change in the length of fish over time. Several general features were observed for the growth of katle in both the river and the reservoir populations. Females attain a larger size than the males. Comparison of the von Bertalanffy equations for each sex from the reservoir and the river revealed that L_∞ for females is greater than that for males and that K values are higher for males than for females, even though the differences are not significant in all cases (Appendix 4). The males tend to mature when a year or more younger than the females, and faster-growing individuals mature earlier than slow growers. A comparison of growth rate in various age groups of katle from the river and the reservoir shows that the growth in length was rapid during the first three or four years. Thereafter the growth rate declines and, during old age, growth in length practically ceases.

A complicating factor in these results is that a wide range of sizes is observed among fish of the same age or age classes. As suggested by Frost and Kipling (1967), this may be because spawning of all the individuals of the population does not take place at one time. In katle the spawning season lasts for about seven months (April to October). The fish that hatch earlier than the others may have an advantage in getting plenty of food and having comparatively less competition. Katle populations in the Indrasarobar Reservoir and the Tadi River face heavy mortality due to intensive fishing and poor environmental conditions. Most of the fish are either fished out or die as a result of heavy monsoon floods, siltation from soil erosion in the river, heavy drawdown in the reservoir, or other unfavourable conditions. This may be the reason for meagre samples in the larger size groups from both locations. A related complication is that the samples from both habitats do not represent those populations with complete accuracy. The scarcity of one- and two-year-old fish from the Indrasarobar Reservoir may be because of the selective action of the multi-panel gill net whose meshes were too large to catch the smaller katle (Fig. 4:8). Biological segregation according to maturity (Hile and Frank, 1941) also may have contributed to the scarcity of katle of the younger age groups from both habitats. Similarly, the catch of juveniles (one-year-old katle) from the river will also have been affected by the use of selective gear.

Craig (1987) has described the physiological process of growth, the various stages that intervene between feeding and eventual tissue deposition, and the effects of abiotic factors such as temperature and light on growth of temperate-zone fish. The growth pattern observed is the result of an interaction between a potential for growth defined by the genotype of the fish and the environmental conditions experienced by the fish (Wootton, 1992). Three main reasons have been advanced in this study for the arresting of growth during several months of the year:

1. Reproduction,
2. Temperature, and
3. Effects associated with drawdown.

Fish use a certain portion of the energy gained through food consumption for gonad development; as the gonads increase in size with increasing age, maturation of the gonads requires an increasing amount of energy at the expense of somatic growth (Craig, 1977). However, the proportion of the energy diverted to the gonad depends on the spawning pattern of the fish. The majority of the cyprinids that are single spawners spend a considerable amount of energy in gonadal development. During the spawning season of these species, the gonads enlarge and most of the growth potential is directed towards this development (Biswas *et al*., 1982). The space for the gut is also reduced through enlargement of the gonads, and this results in low feeding and slower growth. The elaboration of gonadal production during the fasting periods probably accelerates the depletion of fat reserves and exaggerates the low physical condition which is reflected in the bony structures of the fish (Das and Fotedar, 1965; Jhingran, 1971; Payne, 1976). It is doubtful whether gonadal investment is the prime reason for growth checks, as maturation is frequently preceded by a long period of negligible feeding in many species (Welcomme, 1985). Many cyprinids including katle are partial spawners and have an extended spawning period (April-October); these species do not seem to put a large fraction of their energy into gonad development at this time. Katle produce only a few eggs at one time and the average weight of the mature gonad is < 10 % of the total body weight. However, it is very likely that activities related to reproduction such as moving away from feeding grounds, involvement in spawning rather than in feeding, and diversion of energy to migrations and gonadal development would reduce the annual growth rate of katle.

The most important external factor in influencing fish growth is temperature (LeCren, 1955, 1958; Craig, 1980). The formation of annual checks in the bony structures of katle demonstrated in the present investigation suggests that temperature is also of great importance in the growth of all ages of katle. It is most likely that reduced temperature influences the growth of katle in two ways. First, it may slow down metabolic activities, including feeding. Even though katle is reported to survive in a wide temperature range between 15 and 30°C (Rajbanshi, 1982), the fact that it has only been observed to breed at temperatures above 20°C suggests that the optimum for growth is probably also above 20°C. Secondly, it may also be possible that lower temperatures along with other physical factors have a negative effect on the whole biota and thus on the food supply of the fish, which will eventually lead to the scarcity of food.

Besides the influence of temperature reflected in the annual growth cycle of katle, an attempt was made to examine the effect of temperature on the year-to-year variation in growth (LeCren 1958; Mann, 1976) between 1982 and 1989. There did not appear to be enough variation in the number of degree days above 20°C in the Indrasarobar Reservoir during these years to influence the interannual variation in growth of katle.

Nonetheless, studies of the growth of katle in the reservoir show that there are considerable year-to-year variations in growth. This study has shown that the intensity and the duration of drawdown can account for much of this variation. Analysis of age data and annual drawdown on growth of katle revealed a distinct inverse effect of drawdown of water level in the reservoir on the total length increment of katle. A negative impact of water drawdown on the growth of two species of *Hydrocynus*, *H. brevis* and *H. forskahlii,* has also been observed in the Neiger River (Dansoko, 1975; Dansoko *et al.*, 1976). These workers studied the growth of these two species during 1971 and 1972 when there was an extensive drawdown in the river and found that growth, particularly of the young of the year in both species, was poor during these two years. Such year-to-year variation in growth within the same species has also been observed for some cichlid species in the Kafue River in central Africa. Here, Dudley (1974) and Kapetsky (1974) found significant correlations between some physical variables and the main growth increment. The intensity and duration of flooding in combination with low temperature in the dry season accounted for the year-to-year variation in the growth of year class 1 and 2 of *Tilapia rendalli, Oreochromis andersoni* and *O. macrochir*. In most situations, drawdown is also responsible for creating crowded conditions for the fish population, reducing the amount of food per individual and eventually reducing the growth rate of the fish. However, there is not enough information to determine the effects of population density on the growth of katle in this study.

This study did reveal a strong effect of riverine versus lacustrine habitat on growth patterns over the lifetime of katle. Comparison of the von Bertalanffy equations showed that L_∞ is larger for reservoir katle than for river katle, and that K values are greater for river katle of both sexes. The higher values of L_∞ in the reservoir can probably be attributed to higher feeding intensity observed there throughout the greater part of the year (Ch. 3). Fish with higher K and lower L_∞ values approach their ultimate size faster than those with lower K and higher L_∞. Therefore, the reservoir female would need to live longer than the river female to achieve its ultimate size.

According to Beverton (1987), the level of feeding has a powerful influence on the ultimate size L_∞, whereas K is much more strongly influenced by genetics (unless the shape of the growth curve is distorted by marked changes in the availability of food during life). In the present study, there is not enough information to distinguish between genotypic and phenotypic effects between these two populations, derived from different gene pools. Beverton (1987) considers that there is good evidence in several species for growth and longevity being phenotypic responses to the environment. This is supported by differences in the correlations of longevity with growth in cohorts of a single perch population (Craig *et al.*, 1979; Craig, 1982) and by intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.) stocks (Jennings and Beverton, 1991). It is most likely that the observed differences in growth between the reservoir and the river populations of katle are largely a response to environmental factors. Effects of regulation of the River Tees upon growth and reproduction of bullhead (*Cottus gobio* L.) were observed by Crisp *et al.* (1983), who studied the population before and after impoundment. Investigations on the fish population in the Indrasarobar Reservoir area before as well as after its formation would have provided valuable information to help isolate the genotypic and phenotypic influences on differential growth of katle in the river and reservoir populations.

CHAPTER V

ASPECTS OF THE REPRODUCTIVE BIOLOGY OF KATLE IN THE INDRASAROBAR RESERVOIR AND THE TADI RIVER.

INTRODUCTION

Studies on the reproduction of cyprinids in the Indian subcontinent have concentrated mainly on two groups. The first group is that of the Indian major carp, which comprise *Labeo* spp., *Cirrhina* spp. and *Catla catla*. The second group is hill stream fish which include *Tor* spp., *Neolissochilus hexagonolepis* and *Schizothorax* spp. *Tor* spp. and *Neolissochilus hexagonolepis* are commonly called the large-scaled barbels or the mahseers, and *Schizothorax* spp. is called by the popular name of snow-trout. These studies have been stimulated by the desire to understand and control the reproductive processes in these species which are used extensively in aquaculture and sport fishing.

Scientific observations on the reproduction of Indian cyprinids started in the 1940's (Hora, 1945). On the basis of their spawning frequencies, Indian cyprinids are divided into two broad categories (Sathyanesan, 1961, 1962; Prabhu, 1956; Qasim and Qayyum, 1962, 1963; Parameswaran *et al*., 1970):

a) Single spawners: those which possess a well marked size group of oocytes and have a short breeding season which lasts for 2 to 4 months. All the Indian major carp fall into this category.

b) Multiple spawners: those which contain oocytes of various sizes with no well marked batches. Gravid individuals occur over the greater part of the year. It seems that if conditions for spawning are favourable, the cycle can occur at any time of the year. Spawning in each individual is not synchronous with those of other individuals of the population. The mahseers belong to this category.

The spawning behaviour of the cyprinids in natural and controlled conditions has been investigated by several workers and the roles of different abiotic factors have been described. Intensive floods, caused either by rainfall or artificially, which inundate shallow areas are essential to induce spawning in many carp (Hora, 1945). Floodwater has been considered to assist the fish in migrating to their shallow spawning grounds (Ganapati and Alikuni, 1950; Alikuni and Rao, 1951; Ganapati *et al.*, 1951; David, 1955).

Shaha *et al.* (1957) investigated the spawning behaviour of carp in controlled conditions and found that floodwater played a role in lowering the pH of the water to a favourable level to induce spawning. Dubey and Tuli (1961) observed the breeding of all three major carp species, *Labeo rohita* (rohu), *Catla catla* (catla), and *Cirrhina mrigala* (mrigal), in Madhya Pradesh, India. They found that rohu and mrigal breed in flooded areas with a depth range of 0.46 m to 0.91 m, while the catla requires a spawning ground with a water depth greater than 1.24 m. All fish spawn within a pH range of 7.2 to 8.2 and a temperature range from 26 to 33°C.

Similarly the reproductive biology of different species of hill stream fishes has been studied by many workers and the role of water temperature has been emphasized. The optimum temperature for the mahseers was found to be from 20 to 28°C with ≥6 $mg.l^{-1}$ dissolved oxygen content (David, 1953; Desai, 1973; Pathani, 1978, 1981b, 1982; Sunder and Joshi, 1977; Chaturvedi, 1976; Kulkarni, 1970; Kulkarni and Ogale, 1978), whereas the snow-trouts (*Schizothorax longipinnis* Heckel, *Schizothorax essocinus* Heckel, *Schizothorax richardsoni* Grap and Hard and *Schizothorax niger* Heckel) were described as spring spawners at a temperature range of 14-17°C (Sunder, 1984, 1986; Raina, 1977; Qadri *et al.*, 1983; Jyoti and Malhotra, 1972; Malhotra, 1970).

Among the Indian cyprinids, carp have the highest relative fecundity (Chonder, 1970; Hanumantharao, 1971; Sinha, 1975; Singh and Shrivastava, 1982). The snow-trouts have lower fecundity than that of the carp species (Jyoti and Malhotra; 1972, Raina, 1977), while the mahseers are the least fecund of the three groups (Desai, 1973; Dasgupta, 1988b; Nautiyal, 1984; Nautiyal and Lal, 1985).

All these studies on cyprinids have been performed in Indian waters. Similar studies in Nepal were started only in the late 1970's. Masuda (1985) bred *Tor putitora* by collecting mature fish from the Tadi River in the month of August, 1979. Similar work was carried out by Shrestha (1986) in the Tadi River during the mid-1980's. In addition to breeding *Tor putitora*, Shrestha (1990) investigated the spawning period and location of this species in the Tadi River and its feeder streams. Shrestha *et al.* (1990) successfully conducted the induced breeding of *Tor tor,* using hormonal injection. The fish were initially caught from Lake Phewa and held in floating net cages for two years. The females were injected with an extract of the pituitary glands of common carp in 5% sodium chloride solution (6 mg kg^{-1} per dose) three times at 0, 6, and 18 h intervals. The males were given only one injection (3 mg kg^{-1}). These workers were able to strip about 4,500 eggs from a female of 2 kg weight. Hatching occurred in 64 hours with a 97% survival rate.

Despite the interest of several workers in economically important cyprinids, the reproductive biology of katle is poorly known. One of the earliest and most important documented observations on the reproductive ecology of katle was carried out by Langdale Smith (1944). He observed the spawning movements of katle in his tea estate pond at Darjeeling during early autumn and collected some eggs from the pond. Ahmad (1948) collected and incubated the fertilized eggs of katle and studied their embryonic development. Rai (1978) collected mature katle from Trishuli River in central Nepal and stripped eggs from them. The eggs were fertilized and incubated at temperatures of 18 to 21°C. Dasgupta (1988a) collected 24 female katle from the Simsang River, Meghalaya, India, and estimated their fecundity. He considered the katle as a prolific breeder but less fecund than other species of mahseers. No further information is available about the reproductive biology of katle in Nepalese rivers and reservoirs. The present study is an attempt: a) to investigate the reproductive adaptability of katle by comparing its reproductive season, spawning behaviour and movements, and fecundity in the Tadi River with fish in the Indrasarobar Reservoir; and b) to assess the influence of abiotic factors such as temperature, daylight length and annual precipitation on reproductive biology of katle.

MATERIALS AND METHODS

Two thousand two hundred and seventy three (2,273) katle ranging from 80 mm to 553 mm were collected from the Indrasarobar Reservoir (1,572) and The Tadi River (701) from January, 1988 to December, 1990 as described in Ch. II. Katle from both sites were examined externally and internally to separate males from females. Measurements of total length, standard length, girth and weight were recorded. The gonads were removed and weighed. Ovaries were stored in Gilson's fluid for fecundity estimates. Information on gonad development was noted. The gonads were classified according to their stage of development as suggested by Laevastu (1965).

Radio tagging

Radio tags were used to investigate the spawning migration and locate the breeding sites of reservoir female katle. Radio telemetry equipment was obtained from Austec Electronics Ltd., Alberta, Canada. Low frequency (49 MHZ) radio transmitters were used in the study. Each tag had a unique frequency in the 49.1 to 49.9 MHZ range. The specific requirements for the tags included:

- 140 days' life span;
- lithium battery power for reliability;
- tag weight (14 g in air) suitable for adult fish;
- external type with whip antenna.

Out of 6 radio tags received two were defective. An ATS "Challenger 200" model radio receiver was used to detect and locate tagged fish.

Initially, the radio tags were tested on three common carp *(Cyprinus carpio)* in a pond of area 0.5 ha at Godawary Fishery Development Centre near Kathmandu during August 7-15, 1990. That experiment provided the following key information on equipment performance:

a. The range of reception of a transmitter submerged 1 m in a pond varied between 200 m and 1 km.

b. The carp were recaptured after a week and it was found that the transmitters were still securely in place.

c. Experience was gained in using the receiver and antenna. The katle for the experiment were captured during August 26 and 27, 1990, with gill nets set in the area of station number 1 (Fig. 2:1). Sexually mature, spawning females were selected by external examination for radio tagging. Tagged fish were 360-520 mm in total length and 450-1400 g in weight. The fish were anaesthetized with benzocaine (25 mg l^{-1}) using the method described by Laird and Oswald (1975). Anaesthesia usually took 1-2 minutes. Transmitters were placed beside the dorsal fin following the sub-dorsal fin mount procedure described by Winters (1978). After the Teflon-coated wire was threaded through the tissue under the dorsal fin with the aid of a 16 gauge hypodermic needle, the transmitter was secured to the fish with a neoprene disc followed by a plastic disk on the opposite side of the fish. Both disks were 1 cm in diameter. The fish were usually out of the water for about one minute for the attachment of the transmitter. When the fish were placed in a tub of fresh water, they recovered in 5-10 minutes. They were then placed in the reservoir. The fish were hand-held until they could break away and swim off. The tag signal output was continually monitored during tagging and after release. All the 4 fish were released at station number 2 (see Table 5:1). Tracking of the fish was done either from land, walking along the shore of the reservoir and upstream, or from a boat. Forty-five tracking trips were made between August 26 and September 15, 1990.

Table 5:1. Data on transmitters and katle tagged in the Indrasarobar Reservoir, August-September, 1990.

Fish No	Tag Channel No	Release Date	Release Location	Total Length (mm)	Weight (g)
1	8	Aug. 26	Station 2	360	450
2	1	Aug. 26	Station 2	470	470
3	6	Aug. 27	Station 2	520	1400
4	9	Aug. 27	Station 2	380	550

Observation of spawning movements

Besides following ripe female fish by radio tracking in the reservoir, an attempt was made to observe the spawning behaviour of katle in the Tadi River in August, 1991. Preliminary information on the spawning location and behaviour of katle was provided by technicians of The Trishuli Fishery Research Centre and local fishermen. The Khahare Khola was identified as one of the spawning sites of katle. The Khahare Khola is one of the feeder streams of the Tadi River. A field station of the Trishuli Fishery Research Centre is located at the confluence of the Tadi River and the Khahare Khola (Fig. 2:2). According to the local people and information from the literature, the second half of August was considered as an appropriate period for observation. Intensive observation was conducted from 15 August, 1991, until 7 September, 1991. The movement of fish in the Khahare Khola from the Tadi River was watched continuously. Four fishermen (from the Fishery Research Centre) were employed to do this. Diurnal movements of the fish were observed by men sitting beside the stream. Fyke nets were set at the Khahare Khola near its confluence with the Tadi River every evening at about 19:00 hours to measure the nocturnal upstream and downstream movements of the fish. The nets were checked at intervals of 4 hours until 06.00 hours. Physical features of the water such as temperature, pH, turbidity and dissolved oxygen were measured during the period of observation. The shallow areas with gravel bottoms were surveyed for fish eggs once a day using a long-handled dip net. This net was thought to cause minimum disturbance.

Ova diameter measurement

The ova diameters were measured for two purposes. The first was to determine the size of ova at different stages of maturity. For this, 200 preserved eggs were randomly selected from both the anterior and posterior parts of the ovary of fish in the second, third, and fourth stages of maturity from both the reservoir and river. The eggs were spread out evenly on a slide and their diameters were measured using an ocular micrometer in a G92110 monocular microscope, Olympus, H.S.C., Japan. The scale of the micrometer at the magnification used was 1 minor division = 0.037037 mm.

The second purpose of ova diameter measurements was to examine the size range of ova in mature ovaries. One hundred eggs from each fraction were measured giving a total of 300 eggs from each fish. The ova from each fraction were spread out evenly on the slide and diameters were taken from randomly selected eggs.

Fecundity assessment

Bagenal (1971) reviewed the major methods available for the estimation of absolute fecundity in fish. He defined fecundity as the number of ripening eggs in the female prior to the next spawning. These methods and this definition are not, however, readily applicable to many tropical species. As pointed out by Bagenal (1971), such fish are frequently multiple spawners and, as a result, a gonad may contain a wide range of egg sizes and maturity stages. This complicates both the assessment of total egg numbers and the recognition of "mature" egg sizes. To partly avoid these problems, the following method described by Blake (1977) was used in this study.

The ovary was removed and weighed. The outer ovarian wall was removed and the gonads split longitudinally and preserved in Gilson's fluid (Bagenal, 1971). The jars containing the eggs and fluid were agitated at regular intervals to facilitate egg separation. Microscopic investigations revealed the presence of many very small eggs, and the decanting of the supernatant fluid during washing required great care. It was, therefore, inevitable that some ovarian tissue debris remained in the sample, but egg separation in general was satisfactory and counting was not impeded.

After one month in Gilson's fluid the eggs were sufficiently hardened to allow handling and the estimation of numbers and sizes. At least three size ranges were present, in two of which the eggs were yellow and yolky, and in the third, small and white. Eggs in the first and second groups were considered to be developing ova and those in the third were considered to be oocytes. As sub-sampling was necessary it was desirable to separate the eggs into the three fractions according to diameter. The entire sample was poured into a sieve of 10 cm diameter and with 1700 μm apertures. The eggs were copiously washed and the residue retained. The filtrate eggs were then washed through a similar diameter sieve with apertures 1000 μm and the filtrate and residue retained separately. For each fraction, four subsamples of one thousand eggs each were taken and placed in separate petri dishes. The remainder of the eggs were spread on a large pan. All these five containers were air-dried for 48 hours. All four subsamples of one thousand eggs and the remainder were weighed to the nearest 0.0001 g. Total numbers of eggs were calculated by the weight of known numbers of eggs (average weight of 1000 eggs) and the weight of the remainder. The number of eggs in the gonad, absolute fecundity, was estimated by the formula:

$$Eg = \frac{1000}{\Sigma\ (Ws)/N} \times Wg$$

where Eg = total number of eggs in the ovaries, Ws = weight of sample mean, Wg = weight of the total eggs, and N = number of sub-samples. ($Wg = Wr + \Sigma(Ws)/N$, where Wr = weight of remainder.)

The total number of eggs was counted if the number was less than 4000. The fecundity was determined from 84 ripe females from the Indrasarobar reservoir and 35 from the Tadi River during 1990 and 1991. They ranged in total length from 155 to 535 mm. Generally the egg number (absolute fecundity) was related to the fish length by the expression (Bagenal, 1967):

$$F = a\ L^b$$

where F = absolute fecundity (no of eggs), L = fish length (mm) and a and b are constants. In the logarithmic form this expression becomes:

$$\log F = \log a + b \log L$$

In order to make a comparative study of fecundity of the katle in the river and the reservoir, the number of eggs g^{-1} of fish (relative fecundity) was estimated (Das, 1964).

Collection of abiotic data

Surface water temperatures of the reservoir and the river were measured once every day during the study period. The readings were taken at 09:00 with a Yellow Springs Instrument (YSI) Model 54 temperature probe. The YSI 54 instrument was regularly calibrated using a standard glass thermometer. The reservoir temperature was measured at station 5 (Fig. 2:1) and the temperature of the river was measured near the field station of the Trishuli Fishery Research Centre (Fig. 2:2). Daily data on precipitation at both locations and length of daylight in Kathmandu were obtained from the Department of Hydrology and Meteorology, Ministry of Water Resources, His Majesty's Government of Nepal. The mean monthly temperature and length of daylight and total monthly precipitation were calculated from the daily data for the respective parameter.

RESULTS

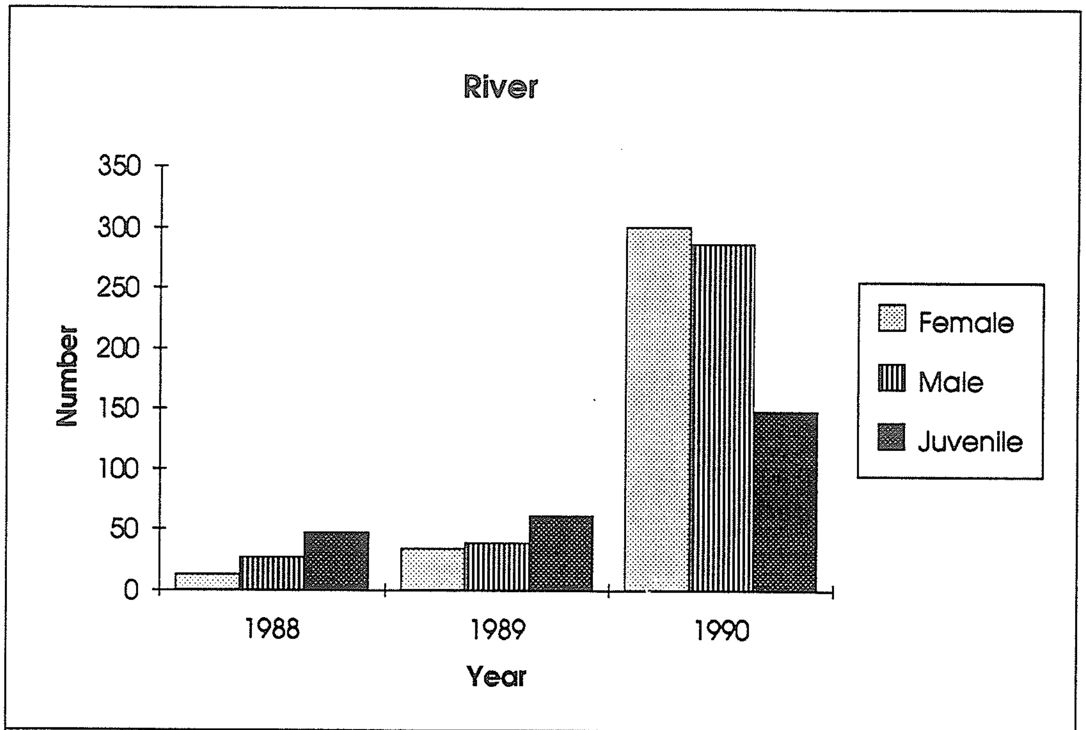
Sex ratio

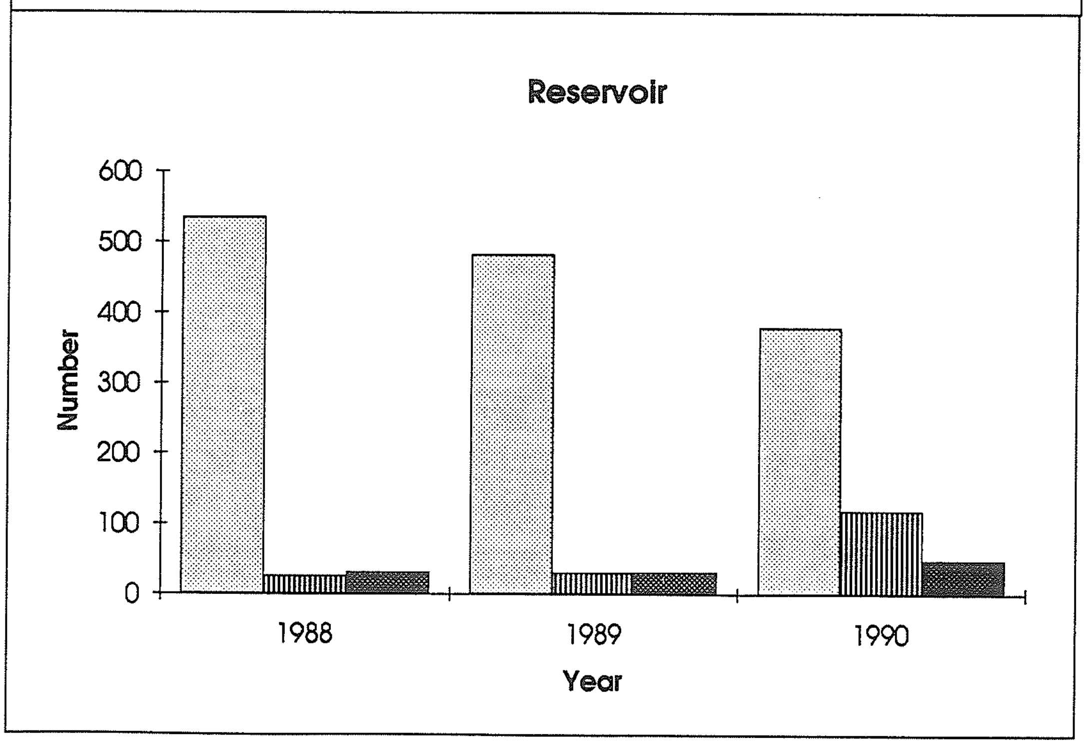
The sex ratios between females and males are summarised in Table 5:2. In the reservoir the female to male ratios during 1988 to 1990 were 1:0.05, 1:0.06 and 1:0.31 respectively. In contrast the ratios in the river were 1:2.08, 1:1.15 and 1:0.95 during the same years. It was observed that during the whole study period the reservoir population was dominated by females, and that males were more abundant in the river. The sampling areas in both the habitats were extended during the second half of 1989 and in 1990. The upper area of the Indrasarobar Reservoir was sampled with different fishing gears and the sampling area in the Tadi River was extended by 2 km to the north and south beyond the usual 10 km sampling area of the river. As the sex ratios show, the abundance of the males in the reservoir increased slightly during 1989/90, and the proportion of females increased in catches from the river during 1989/90 (Fig. 5:1). However, overall, the reservoir fish population was dominated by females while males made up more than half of the total adult fish specimens from the river. A statistical test of proportion indicated that the proportion of females was significantly higher than that of males ($p < 0.05$) in the samples collected from the reservoir throughout the study period. Males were significantly dominant in the river samples of the year 1988. However, the proportion

Table 5:2. The sex ratio of katle in the two habitats.

YEAR	HABITAT	NUMBER OF FEMALES	NUMBER OF MALES	♀ : ♂
1988	Reservoir	535	26	1:0.05
1988	River	13	27	1:2.08
1989	Reservoir	482	32	1:0.06
1989	River	34	39	1:1.15
1990	Reservoir	379	118	1:0.31
1990	River	301	287	1:0.95

Figure 5:1. Number of male, female and juvenile katle in the river and the reservoir.


River
Number
350
300
250
200
150
100
50
0
1988
1989
1990
Year
Female
Male
Juvenile


Reservoir
Number
600
500
400
300
200
100
0
1988
1989
1990
Year

of males and females was not significantly different ($p < 0.05$) in the river samples of 1989 and 1990.

Maturity stages

The ovary was observed at seven different stages of development in female katle from the reservoir and river (Fig. 5:2). At the first and second stages of maturation, the ovary was like two small pieces of compact tissue under the air bladder, and the oocytes were not visible to the naked eye. The oocytes became visible at stage three. The ovaries gradually increased in size and the oocytes became more distinct and translucent at the successive stages (Table 5:3). Seven different stages of testes were also observed in male katle from both systems (Fig. 5:3). At stage 1, the testes were very thin thread-like paired organs under the vertebral column. They gradually increased in size and ultimately occupied about two thirds of the ventral cavity (Table 5:4). The margin became wavy with transverse grooves. At stages 5 and 6, testes were pinkish white and turgid, and milt ran with slight pressure. The 'partly spent' stage of gonads expected to be found in a partial spawner like katle was not encountered in the present study.

Cycle of maturation

Since the annual maturation cycle of the katle in both habitats was similar in each year of the study period, all the monthly samples from 1988 to 1990 for each sex and each

Figure 5:2. Diagrammatic drawings of the ovaries at different stages of maturation: 1. virgin; 2. recovering spent; 3. developing; 4. developed; 5. gravid; 6. spawning.

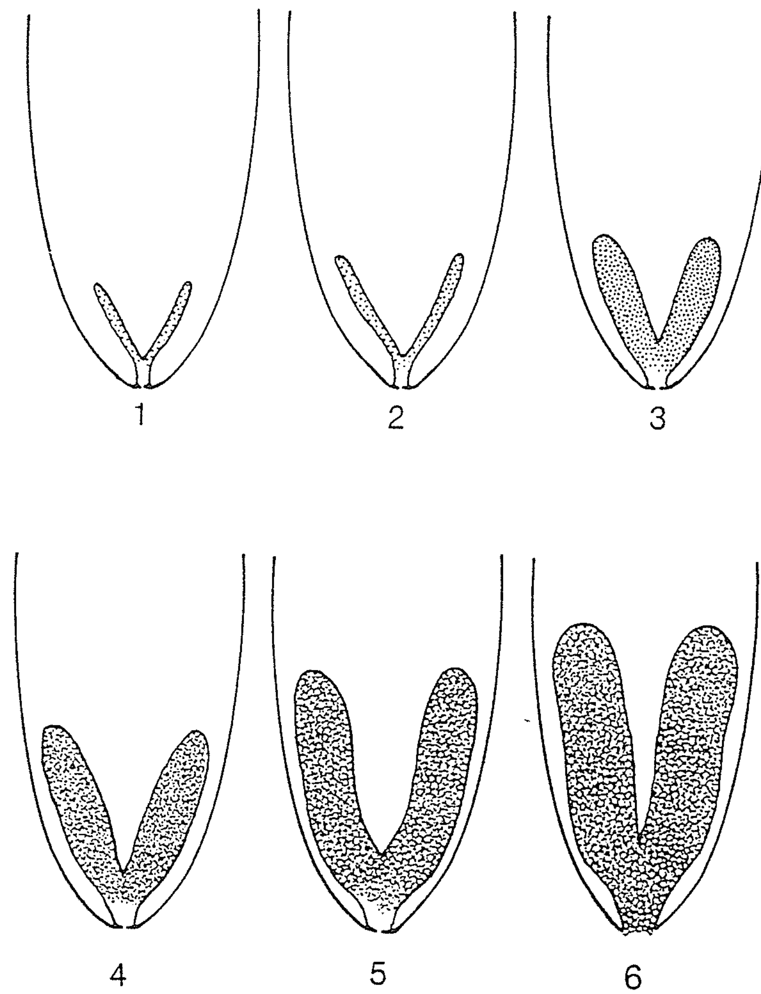
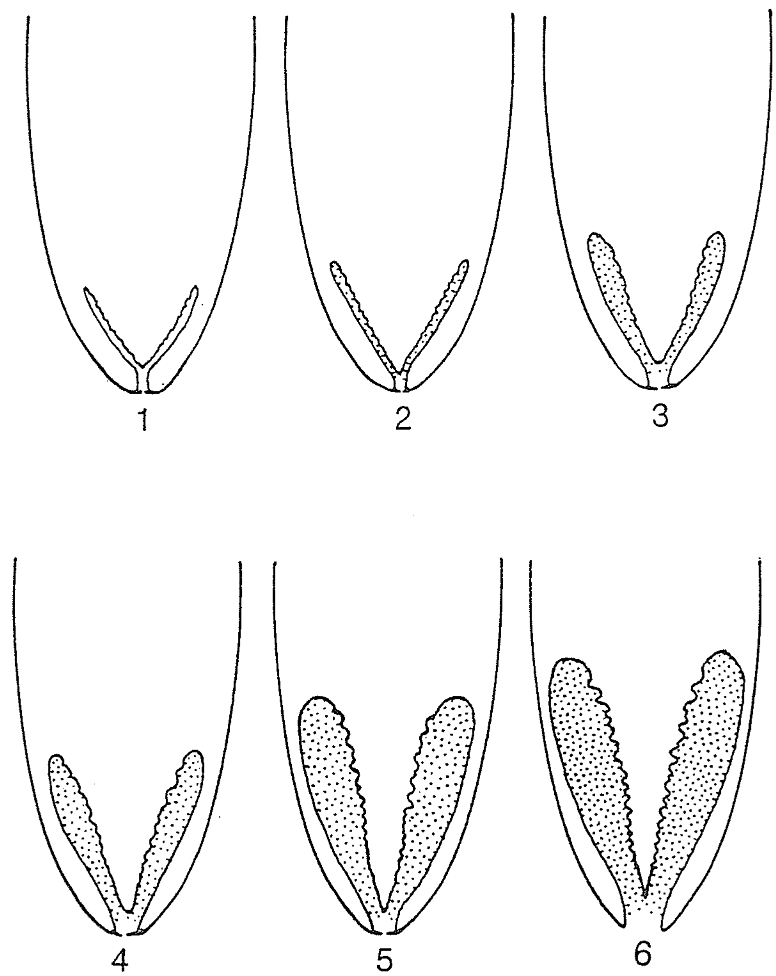

1
2
3
4
5
6

Figure 5:3. Diagrammatic drawings of testes at different stages of maturation: 1. virgin; 2. recovering spent; 3. developing; 4. developed; 5. gravid; 6. spawning.



1
2
3
4
5
6

Table 5:3. Distinctive features of the ovaries of katle at different stages of gonadal maturation.

1.	Virgin	Thin, small, two pieces of compact tissue underneath the air bladder. Grey in colour, oocytes not visible to naked eye, 30 to 60 μm in diameter.
2.	Maturing virgin and recovering spent	Ovaries with compact lobes, creamy to pale yellow in colour, ova spherical, particularly laden with yolk, egg visible with magnifying glass.Oocytes 50-160 μm in diameter.
3.	Developing	Ovaries light yellow in colour with distinct blood capillaries, eggs completely opaque under microscope. Visible to naked eye, whitish and granular. Oocytes 200-300 μm in diameter.
4.	Developed	Ovaries large, bright yellow in colour with conspicuous blood capillaries and with distinct oval shaped oocytes, 300-2000 μm in diameter.
5.	Gravid	Ovaries enlarged and fill ventral cavity, yellow eggs completely round and semi-transparent. Primary oocytes as in stage 1 and 2 present. Eggs 300 to 2800 μm in diameter.
6.	Spawning	Ovaries much distended, yellowish white, jelly-like, eggs run with slight pressure, most eggs translucent.
7.	Spent	Ovary empty, shrunken, bag-like, a few residual oocytes may be visible.

Table 5:4. Distinctive features of the testes of katle at different stages of gonadal maturation.

1.	Virgin	Very small paired organs, close under the vertebral column, connected to air bladder, transparent.
2.	Maturing virgin and recovering spent	Slightly larger than stage 1, length about half of the ventral cavity, transparent, reddish grey in colour.
3.	Developing	Opaque and reddish with blood capillaries. They occupy about half of the length of the ventral cavity.
4.	Developed	Reddish white with wavy margin and distinct blood capillaries. They occupy about two thirds of the ventral cavity.
5.	Gravid	White, wavy margin with transverse grooves and occupy the length of the ventral cavity. Drops of milt exuded on pressure.
6.	Spawning	The testes occupy the length of the ventral cavity. They are pinkish white, turgid and milt runs with slight pressure.
7.	Spent	Flaccid, grey in colour with blood capillaries, without milt.

habitat were pooled to describe the cycle of maturation. Reservoir females in stages 1 and 2 were found throughout the year (Fig. 5:4). From March, stages 3 and 4 began to develop and all stages, 1 to 6, were observed in the samples from April to October. More than 60% of the total catch were at stage 2 except in March. Females at stage 3 were next in frequency, the percentage varying from 9.6% in May to 37.8% in March. Females of stage 4 were found in the monthly reservoir samples from March to October. Their percentage was lowest in May (4.8%) and highest in September (12.2%). Gravid females were caught from April to October but formed a small percentage of the total catch. No running or spent females were caught throughout the study period.

The number of males caught was very low in the reservoir samples (n = 176). Stage 2 development was dominant among the reservoir males caught throughout the study period (Fig. 5:5). Stage 3 was observed every month from March to October except during May. Males at stage 4 were present in the reservoir samples in April, July and August. Males of stage 5 were found only in July and August. No males of stages 6 and 7 were ever observed in the samples from the reservoir. No males above stage 2 of maturity were caught from November to February.

The general cycle of gonadal maturation of the katle in the Tadi river was similar to that in the Indrasarobar Reservoir except that stage 1 constituted the highest percentage of the total monthly catch in both sexes except in

Figure 5:4. Monthly change in the reservoir catch frequency (as percentages of the total female catch) of female katle at different stages of maturity (1 to 7).

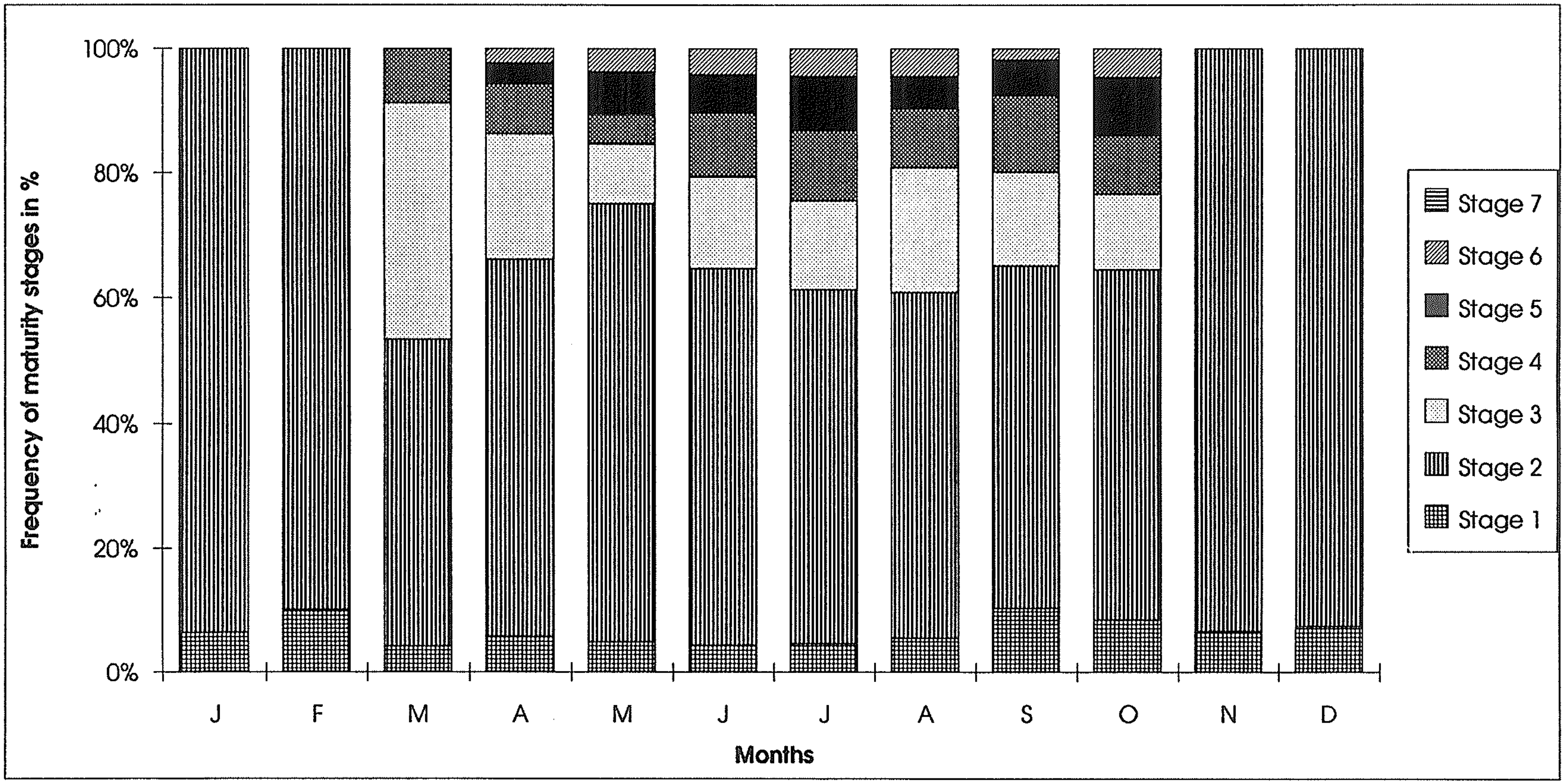
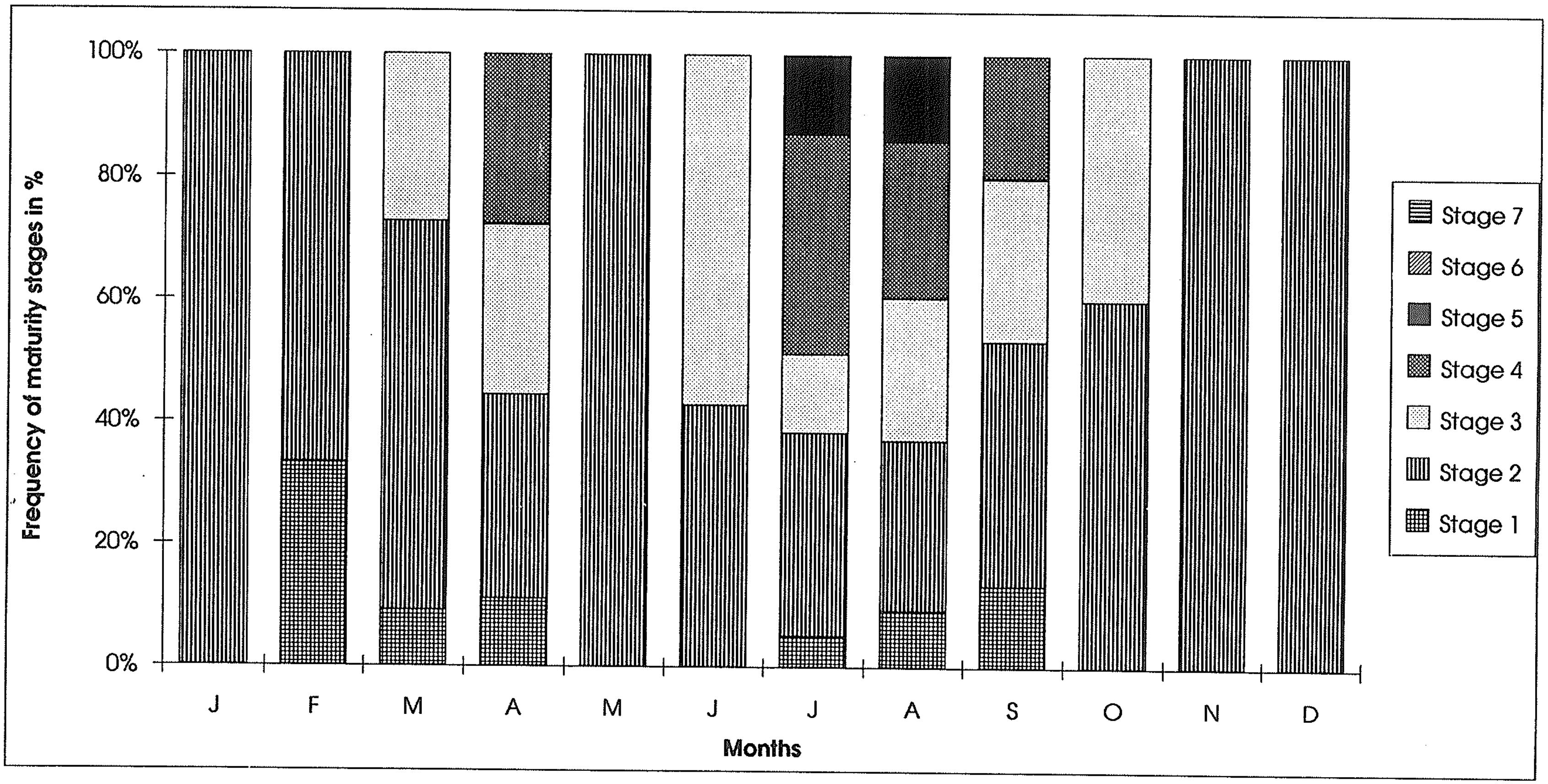

Frequency of maturity stages in %
100%
80%
60%
40%
20%
0%
J
F
M
A
M
J
J
A
S
O
N
D
Months
Stage 7
Stage 6
Stage 5
Stage 4
Stage 3
Stage 2
Stage 1

Figure 5:5. Monthly change in the reservoir catch frequency (as percentages of the total male catch) of male katle at different stages of maturity (1 to 7).



Frequency of maturity stages in %
100%
80%
60%
40%
20%
0%
J
F
M
A
M
J
J
A
S
O
N
D
Months
Stage 7
Stage 6
Stage 5
Stage 4
Stage 3
Stage 2
Stage 1

September. Females at stage 2 were found throughout, ranging from 77.3% in December to 31.2% in September. Females at stage 3 appeared in the catch in March and were frequently caught until October (Fig. 5:6). Their proportion varied from 12.5% in July to 25% in May. Stage 5 was observed only in the samples from July to October, the highest percentage being observed in September (20.3%) and the lowest in October (7.7%). Stage 6 was observed in September and October, while spent females were encountered only in the month of October.

Males at stage 2 frequently occurred throughout the study period. Their percentage occurrence varied from 18.9% in June to 63.6% in December. Stages 3, 4 and 5 appeared in March and were observed until October (Fig. 5:7). Stage 6 fish were found from June to October. Spent males were observed only in the month of September.

The occurrence of different stages over a greater part of the year (March-October) indicated the extended spawning season of the katle in both systems.

Age at first maturity

Among the cyprinids, males are frequently smaller than females, and females become sexually mature 1 year later than males (Mann, 1991). Katle are no exception to this general rule. More than 50% of the river males caught during their second year were mature (in the sense of having maturing gonads), and more than 90% had reached maturity by their third

Figure 5:6. Monthly change in the river catch frequency (as percentages of the total female catch) of female katle at different stages of maturity (1 to 7).

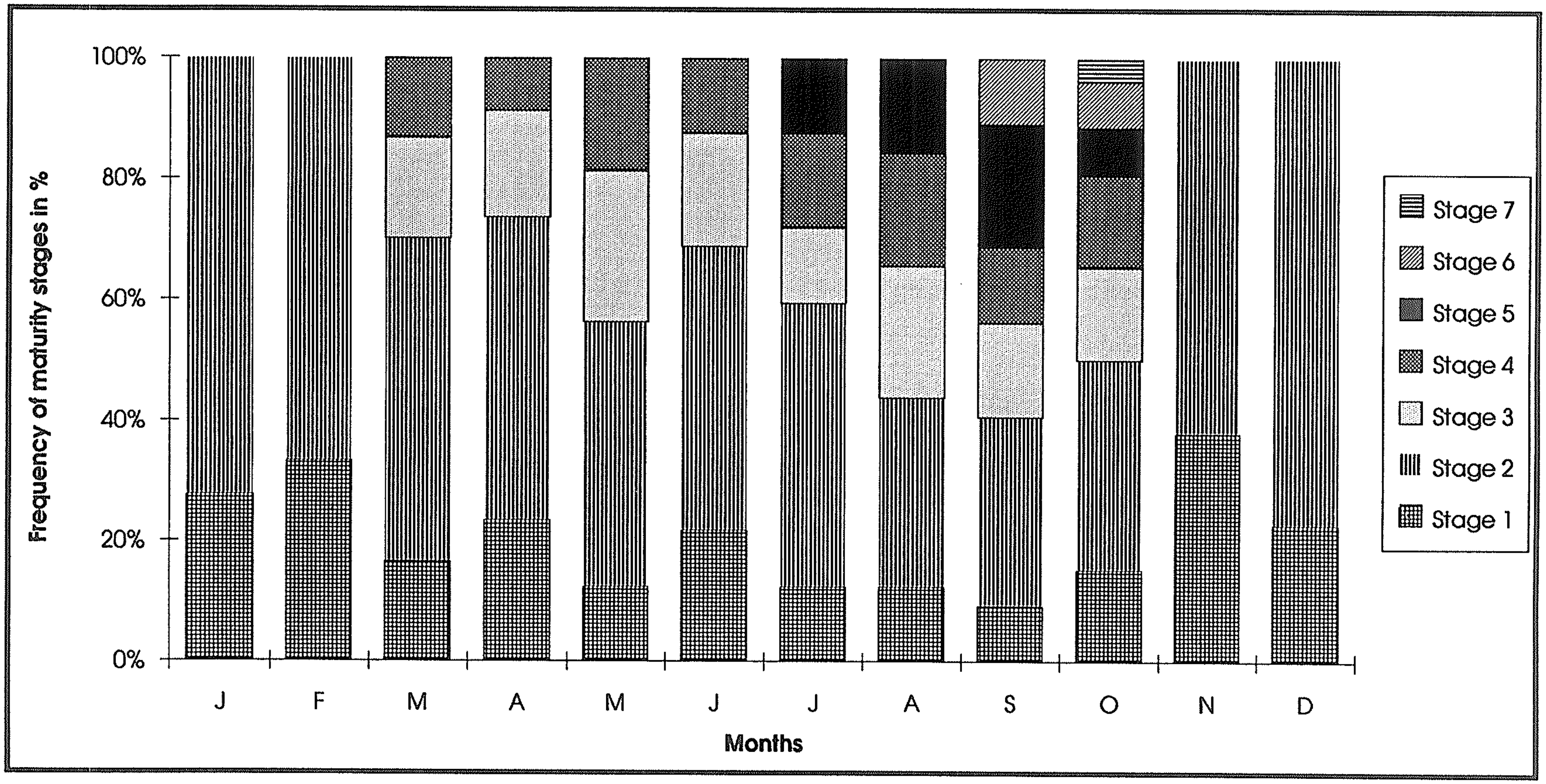
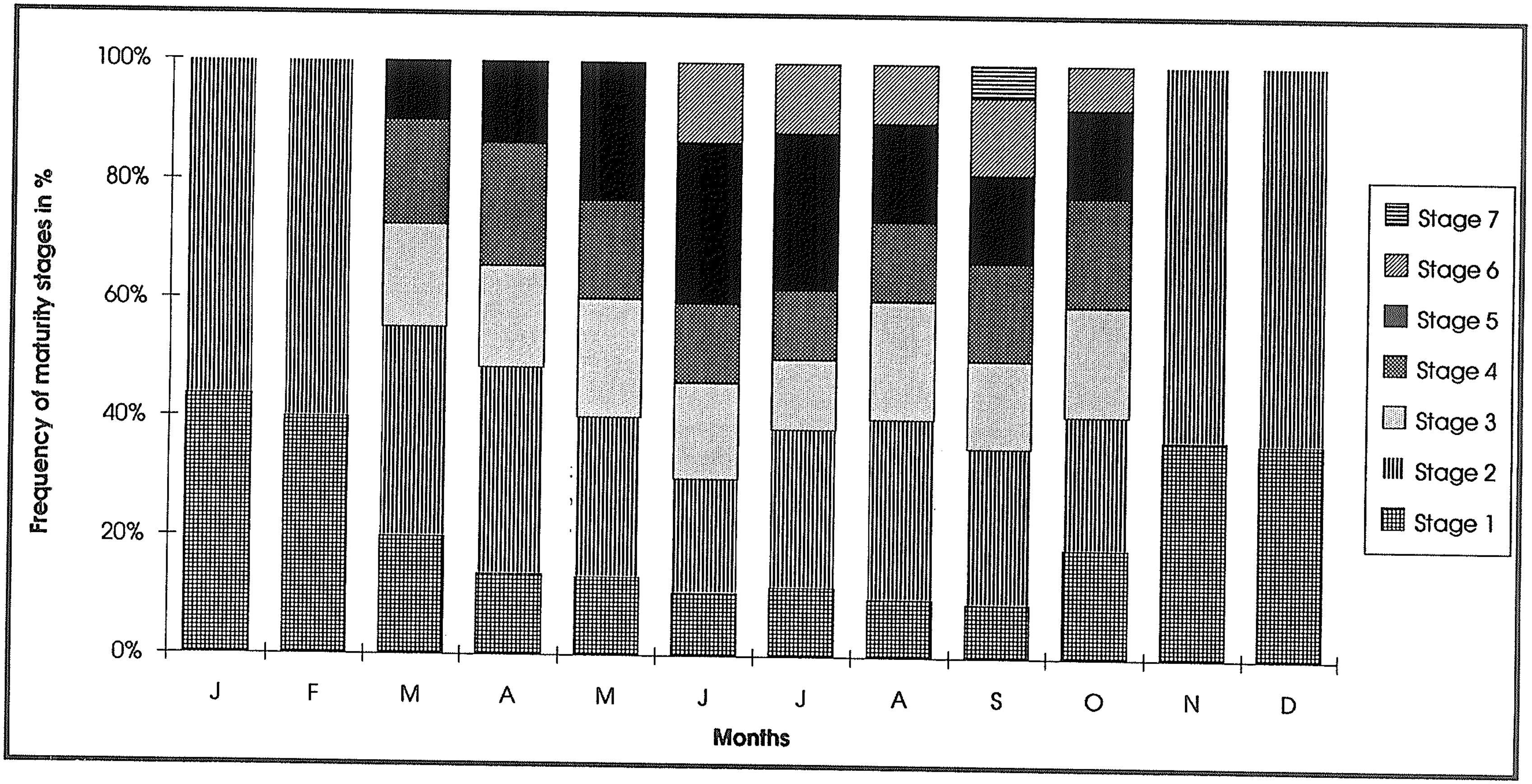

Frequency of maturity stages in %
100%
80%
60%
40%
20%
0%
J
F
M
A
M
J
J
A
S
O
N
D
Months
Stage 7
Stage 6
Stage 5
Stage 4
Stage 3
Stage 2
Stage 1

Figure 5:7. Monthly change in the river catch frequency (as percentages of the total male catch) of male katle at different stages of maturity (1 to 7).


100%
80%
60%
40%
20%
0%
Frequency of maturity stages in %
J
F
M
A
M
J
J
A
S
O
N
D
Months
Stage 7
Stage 6
Stage 5
Stage 4
Stage 3
Stage 2
Stage 1

year of life. Only 5% of river females were mature at the age of 2 years but almost all of them were mature at the age of three years.

Most of the three-year-old reservoir males were mature. No fish less then 3 years old was caught from the reservoir, mainly because of the use of relatively large-meshed gill nets (25-100 mm mesh). In the reservoir about 50% of the three-year-old females were mature, and almost all fish in their fourth year of life had maturing gonads. The immature fish were significantly smaller than the mature ones of the same age in both sexes in both reservoir and the river populations. Maturation appears to be correlated with both size and age but the analysis of the relative importance of the two factors is complicated because, while size and growth rate can vary continuously, the method of assessment allows age to vary only in units of a whole year. It was therefore considered beyond the scope of this study to distinguish the effects of age and size more precisely than has been described.

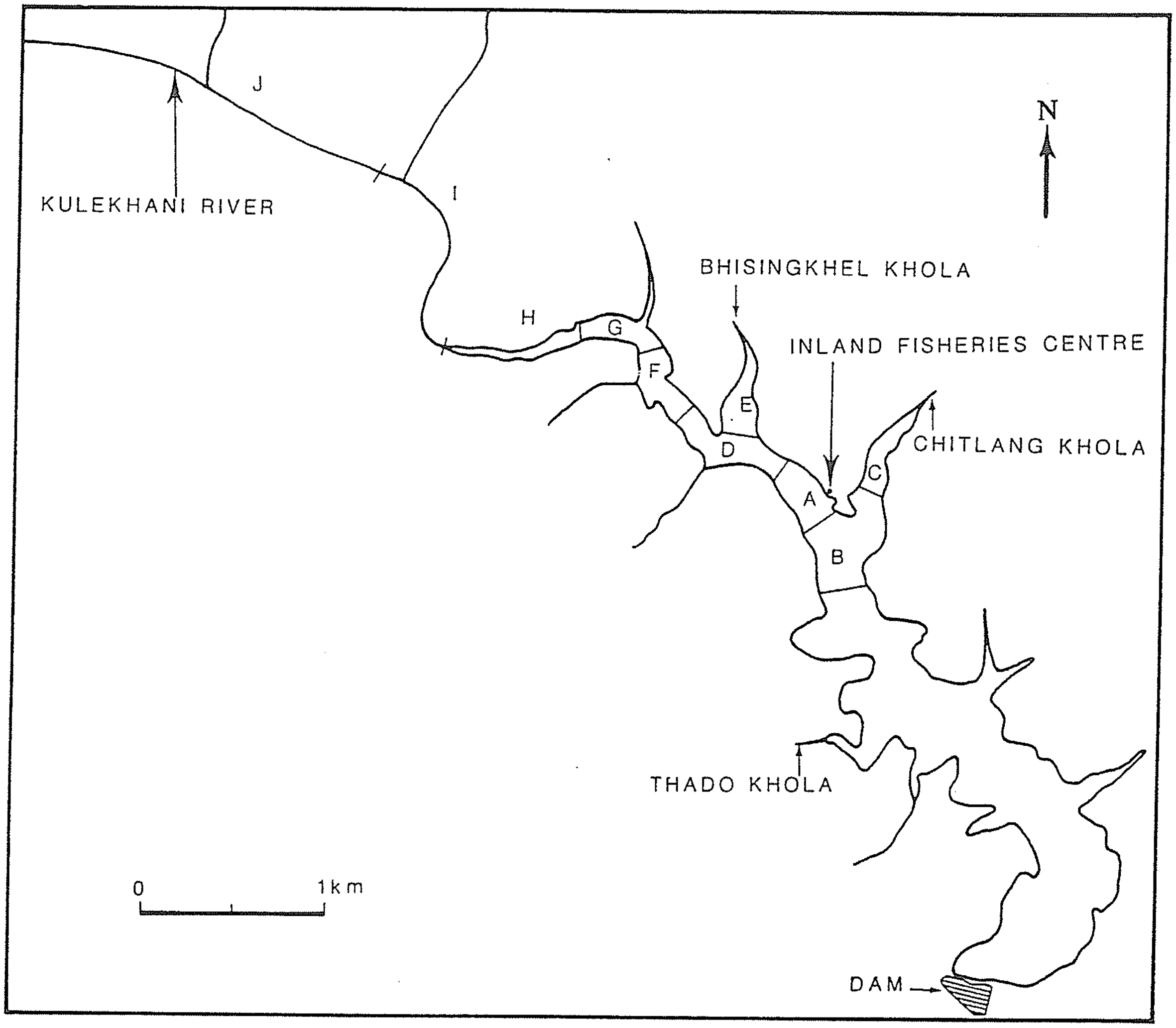
Fish movement

Four mature female fish fitted with radio tags, released at Markhu (A) on 26 and 27 August, 1990, remained near the release site (A) for two days (Fig. 5:8 and Table 5:5). Fish number 1 moved towards site B on the third day (28 August) and was located around site B on 29 August. It moved towards site C on 30 August where the Chitlang Khola joins the reservoir.

Figure 5:8. Map of the Indrasarobar Reservoir showing the locations of tagged fish.

Table 5:5. Summary of the movement of katle as determined by radio tagging in Indrasarobar Reservoir, 26 August to 15 September, 1990 (- = not located).

Date	Location of fish 1	Location of fish 2	Location of fish 3	Location of fish 4
26 Aug.	A (release)	A (release)	-	-
27 Aug.	B	A	A (release)	A(release)
28 Aug.	B	C	A	A
29 Aug.	B	C	D	A
30 Aug.	C	-	D	D
31 Aug.	-	A	C	C
01 Sept.	-	A	C	C
02 Sept.	D	D	-	G
03 Sept.	D	E	-	G
04 Sept.	D	E	D	H
05 Sept.	A	F	E	H
06 Sept.	C	F	F	I
07 Sept.	C	I	G	I
08 Sept.	C	I	H	I
09 Sept.	C	-	H	I
10 Sept.	C	-	I	J
11 Sept.	C	-	I	J
12 Sept.	C	-	J	J
13 Sept.	C	-	-	-
14 Sept.	-	-	-	-
15 Sept.	-	-	-	-



N
J
I
H
G
F
E
D
A
B
C
KULEKHANI RIVER
BHISINGKHEL KHOLA
INLAND FISHERIES CENTRE
CHITLANG KHOLA
THADO KHOLA
0
1km
DAM

This fish could not be located on 31 August and 1 September but the radio receiver indicated its presence near site D on the morning of 2 September. It was located in that vicinity from 2 September to 4 September. The fish returned to the area A on 5 September and again moved to site C on 6 September. The presence of the fish at location C was observed and recorded twice a day from the 7th to the 13th of September. When it was realised that the fish was not moving from the area, gill nets and cast nets were used to try and capture the fish. However, neither the tag nor the fish were recovered.

Fish number 2 moved towards site C on 28 August and remained in that area until 29 August. The fish could not be located on 30 August but the radio receiver indicated its presence near site A on 31 August and 1 September. On 2 September the fish moved towards site D and then it migrated to site E. After being located in that area for one more day it moved to site F on the 5 September. It remained in that location on 6 September and then travelled to area I on 7 September. The fish remained in area I until 8 September and thereafter could no longer be located.

Fish number 3 moved towards site D on 29 August and remained there on 30 August. It travelled towards site C on 31 August. It was located in the same area on 1 September but was not found during 2-3 September. It was relocated at site D on 4 September and in area E on 5 September. The fish reached site F on 6 September and site G on 7 September. It moved towards site H on 8 September and passed into the Kulekhani River area I on 10 September and remained at that site on 11 September. The presence of fish number 3 in area J was recorded on 11 September but it could not be traced after this date.

Fish number 4 was recorded near area A until 29 August. Then it moved towards area D on 30 September and to C on 31 September. It travelled from areas C to G on 2 September. From area G the fish travelled towards H on 4 September, continued its upstream journey and passed into the Kulekhani River on 6 September. It spent three days in area I and then it moved towards site J on 10 September and was recorded in that area until 12 September. The location of fish number 4 could not be traced after that date.

About a 15 km stretch of the Kulekhani River was regularly surveyed from area A to Palung until 15 September, 1990, but no signals were received. All the mature females, after being tagged, migrated upstream. Three spawners moved towards the Kulekhani River and the fourth towards Chitlang Khola. It seems likely that all the ripe fish migrated upstream in search of appropriate breeding grounds. However, none of them were recaptured. There are six full-time and twenty part-time fishermen engaged in fishing in the reservoir and in the upstream river (personal observation). Since fishing pressure in the Indrasarobar and Kulekhani River was quite high, the fish numbered 2, 3 and 4 may have been caught by local fishermen who may then have thrown the radio tags away. It was surprising to receive a strong signal from fish number 1 in area C without any sign of movement of the fish. It is possible that either the fish had been captured by a fisherman and the tag was thrown away in that area or the fish had died at that location and the tag remained on the bottom.

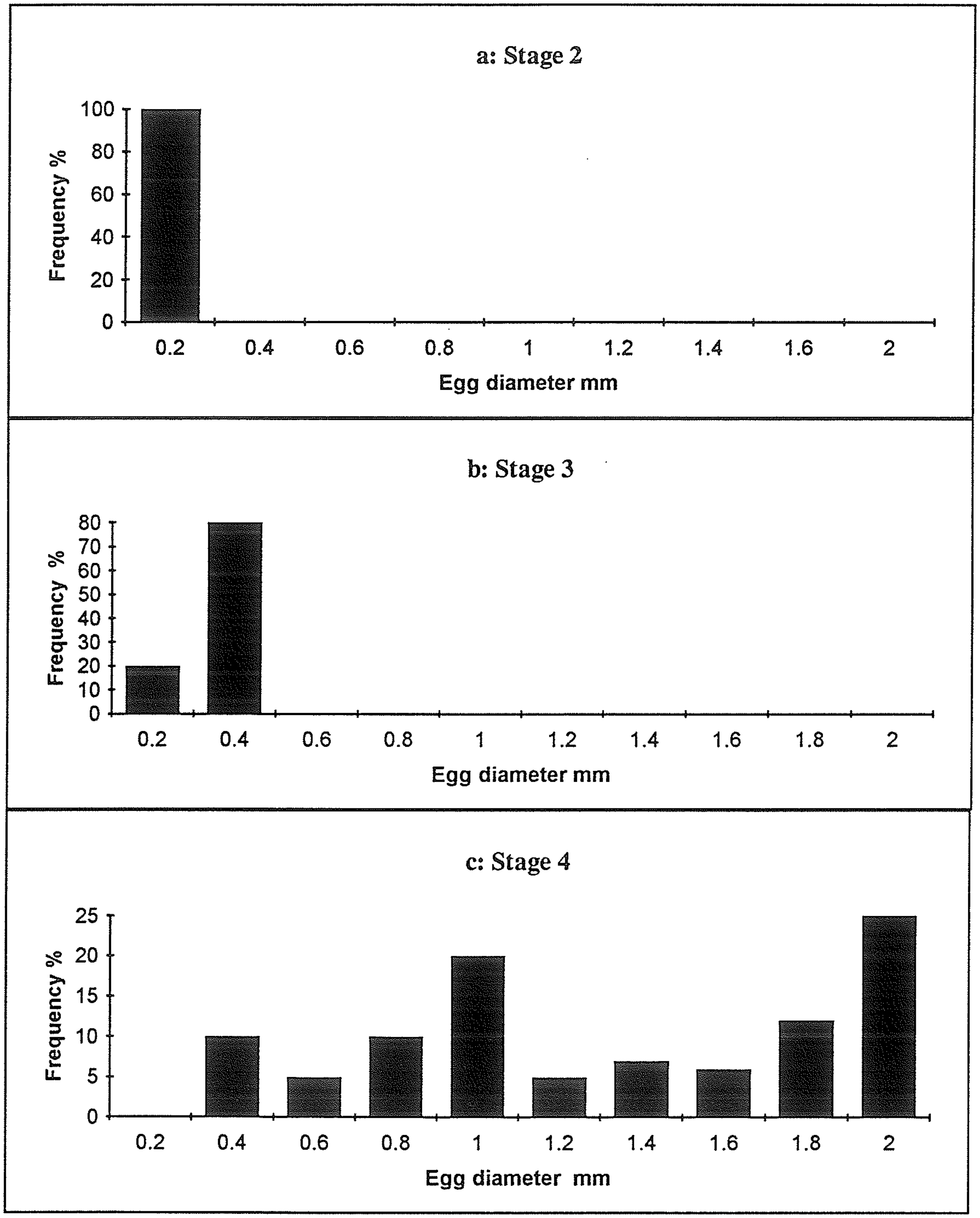
Visual observations of spawning of katle

Upstream movement of 3 fish to the Khahare Khola stream from the Tadi River was observed on 20 August at about 16:00. The fish were followed. They appeared to move rapidly for the first 300 m. They slowed down after they reached the shallow and slow moving part of the stream. The largest fish, probably female, was leading and two smaller fish, presumably males, followed her. As soon as they found a wide, shallow pool with a gravel bottom, they stopped. They then started to swim in a non-directional manner, over and around the spawning substrate. Some movements were circular (anti-clockwise and clockwise), whereas others were spiral and upward. Both the males were seen to be equally active and swimming alongside the female. Unfortunately further under-water movement was not visible from the bank of the stream partly due to darkness and partly due to the turbidity of the water. A torch was used but with little success. After half an hour the same fish were noticed entering the Khahare Khola. A fyke net, facing towards the stream, was set near the confluence of the river and stream. The net was watched from the shore. Two spent fish (one female and one male) were caught in the net at about 01:00. Both fish were examined externally and internally. Their length, weight and gonadal condition were measured and recorded. The total length of the female was 365 mm and its weight was 600 g. The male was 320 mm in total length and 300 g in weight. The spawning site was observed the next morning and eggs were found on the gravel bottom of the stream, which confirmed the lithophilic spawning behaviour of the katle. One thousand fertilized ova were collected with the help of a long-handled dip net. The ova were transferred to the Fishery Research Station, Trishuli, and incubated at the hatchery. The water temperature at the spawning ground ranged from 20-22°C; the average values of the dissolved oxygen content and pH at 08:00 during the observation period (15-25 September, 1991) were 6.98±0.098 mg l^{-1} and 6.73±0.113 (± 95% CL), respectively.

Ova diameter

Ova measurements compared between individuals from the river and reservoir, at the same stage of maturity (2-4), show no significant difference in their frequency distributions between habitats. Eggs were taken from the various parts of the ovaries of fish at stages 2, 3 and 4 of maturity. Measurements were made to the nearest 0.01 mm. These were grouped in intervals of 0.20 mm and their percentage frequencies are presented in Figure 5:9.

Figure 5:9. Egg size (mm) distribution in the ovaries of katle at stages 2 to 4 of maturation, combined for river and reservoir fish (Egg size groups: 0.2 = 0.01-0.2; 0.4 =0.21-0.4; 0.6 = 0.41-0.6; 0.8 = 0.61-0.80; 1.0 = 0.81- 1.0; 1.2 = 1.01-1.20; 1.4 = 1.21-1.4; 1.6 = 1.41-1.60; 1.8 = 1.61-1.80; 2.0 = 1.81-2.0 mm).



a: Stage 2
Frequency %
100
80
60
40
20
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
2
Egg diameter mm
b: Stage 3
Frequency %
80
70
60
50
40
30
20
10
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Egg diameter mm
c: Stage 4
Frequency %
25
20
15
10
5
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Egg diameter mm

At stage 2, which represented immature fish, the majority of oocytes were in the size range of 0.05 to 0.16 mm (Fig. 5:9a). As maturation progressed, the oocytes gradually increased in size with the formation of yolk around the nucleus. At stage 3, the size of ova ranged from 0.16 to 0.30 mm in diameter and two distinct batches of oocytes were seen (Fig. 5:9b).

At stage 4, the size of oocytes further increased and varied from 0.30 to 1.60 mm in diameter. Three distinct types of oocytes (immature, maturing and mature) were present in the ovary. Three peaks were clearly visible (Figure 5:9c).

At stage 5, the mature eggs increased in size and their diameter was ≥1.60 mm. The second batch shows a peak at 0.80 mm and the third batch of eggs shows its peak at 0.30 mm (Fig. 5:10). At stage 6, all three batches of ova further increased in size. Data on the diameters of mature eggs of katle of stage 5 from the reservoir and river over four different months (July to October) were analysed using two-way analysis of variance. As can be seen in Table 5:6, the location on its own does not appear to have much influence on the size of the eggs, but the time of maturing (month) definitely does. The estimated means of the egg diameter for the different locations and months suggest that the sizes of the eggs maturing in different months are significantly different (Fig. 5:11). The largest eggs were produced in September and the smallest were produced in October. Production of the largest

Figure 5:10. Egg size (mm) distribution in the mature ovaries (stage 5) of the katle: **a**. Reservoir; **b**. River (Egg size groups: 0.2 = 0.01-0.2; 0.4 = 0.21-0.4; 0.6 = 0.41-0.6; 0.8 = 0.61-0.80; 1.0 = 0.81-1.0; 1.2 = 1.01-1.20; 1.4 = 1.21-1.4; 1.6 = 1.41-1.60; 1.8 = 1.61-1.80; 2.0 = 1.81-2.0; 2.2 = 2.01-2.2; 2.4 = 2.21-2.4; 2.6 = 2.41-2.6 mm).

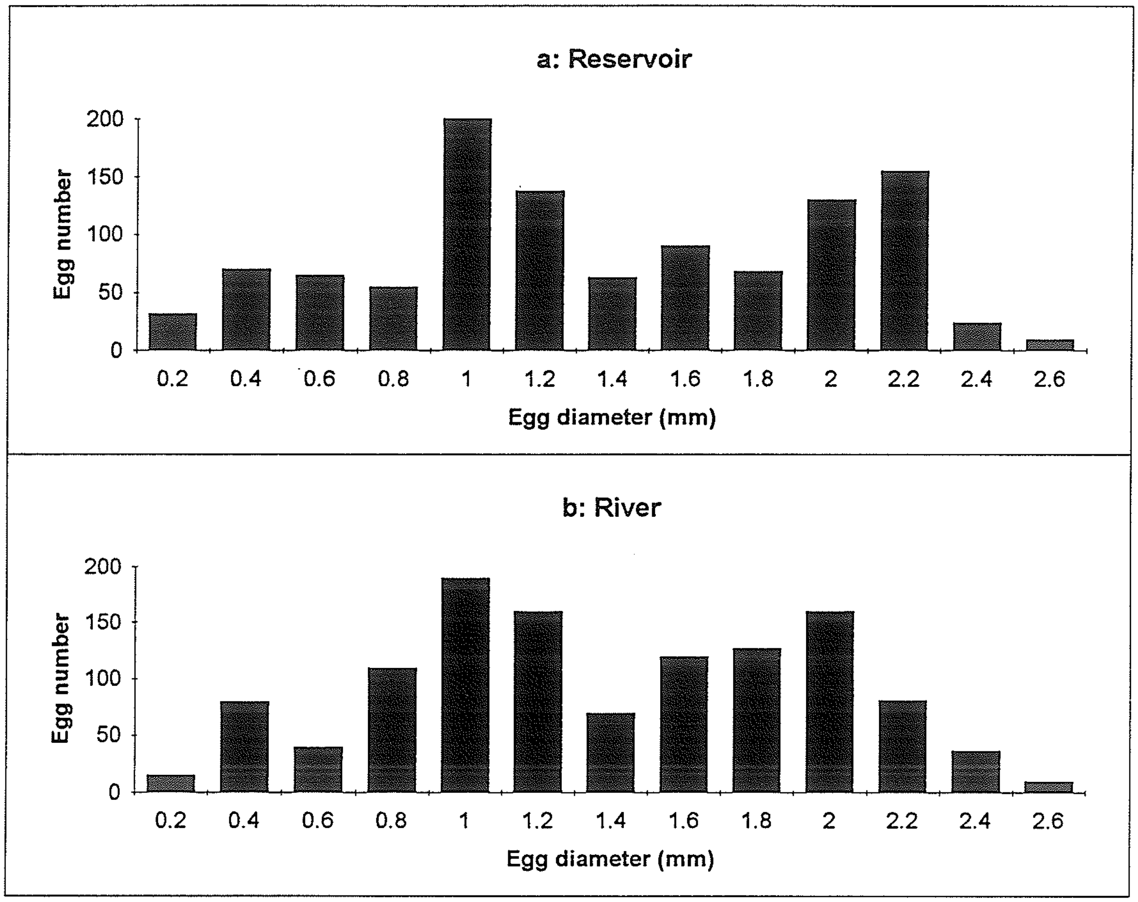

a: Reservoir
Egg number
200
150
100
50
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
Egg diameter (mm)
b: River
Egg number
200
150
100
50
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
Egg diameter (mm)

Figure 5:11. Variation of mean egg diameter (with 95% confidence limits) in mature katle from the reservoir and river during July to October. (Location: 0 = reservoir; 1 = river) (Months: 1 = July; 2 = August; 3 = September; 4 = October)

```
                               Individual 95% CI
Location          Mean         ---------+---------+---------+---------+--
       0          1.944                      (-------------*-------------)
       1          1.903        (-------------*--------------)
                               ---------+---------+---------+---------+--
                                      1.890     1.920     1.950     1.980

                              Individual 95% CI
  Month           Mean        -+---------+---------+---------+---------+
      1          1.825                (---*---)
      2          2.005                           (---*---)
      3          2.165                                     (---*---)
      4          1.701        (---*---)
                              -+---------+---------+---------+---------+
                            1.650     1.800     1.950     2.100     2.250
                                           (mm)
```

Table 5:6. Results of analysis of variance on egg diameters of katle.

Source	DF	SS	MS	F	Results (5% level)
Location	1	0.1005	0.1005	1.821	Non-significant
Month	3	7.4375	2.4792	44.91	Significant
Interaction	3	0.8260	0.2753	4.987	Significant
Error	232	12.797	0.0552		
Total	239	21.161			

eggs in September probably indicates that this is the main breeding period of katle.

Fecundity

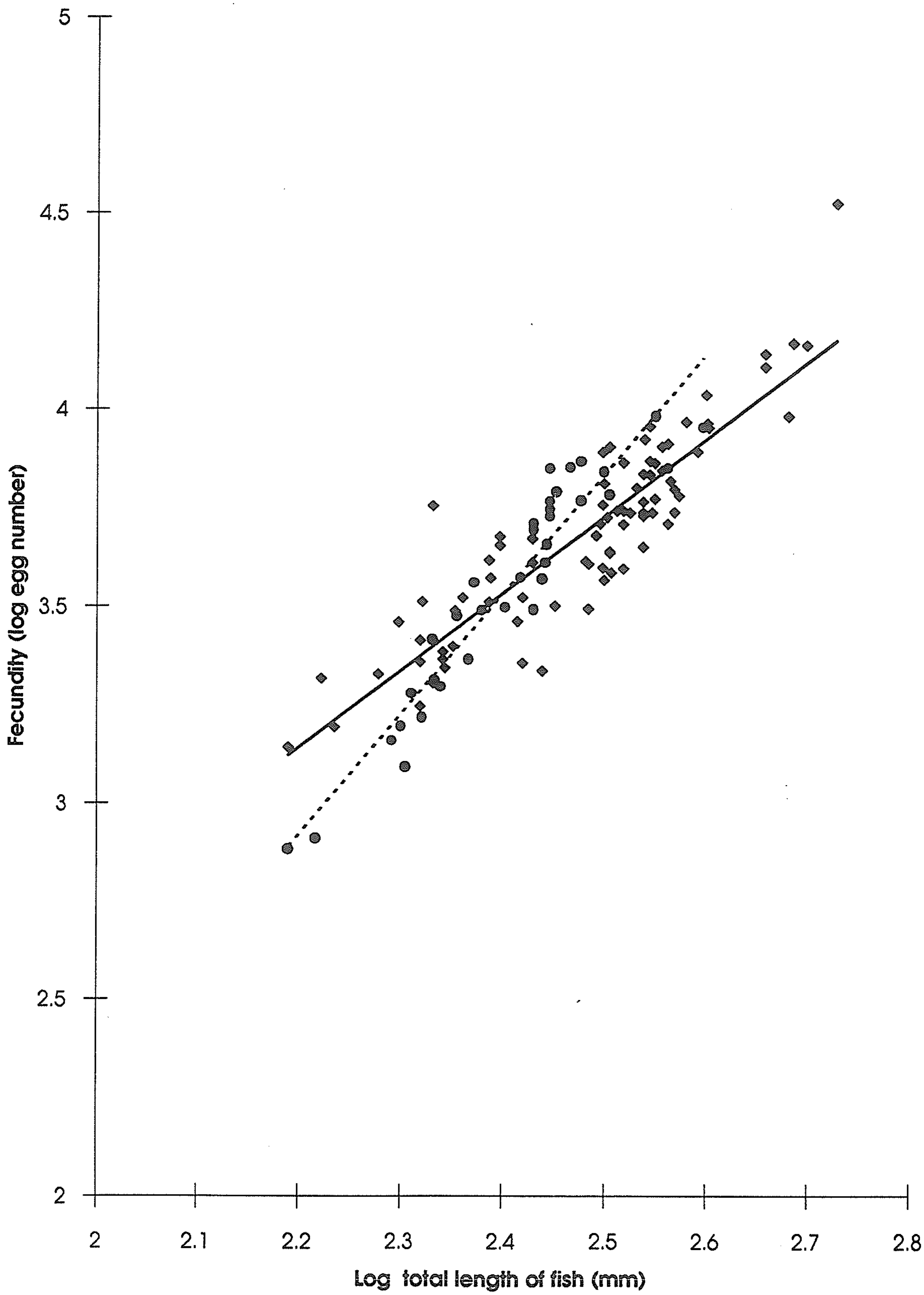
Absolute fecundity of katle in both the river and reservoir varied considerably from individual to individual. It ranged from 1,387 eggs (in a specimen of 160 mm and 53.8 g) to 33,270 eggs (535 mm and 1750 g) in the reservoir population, and from 760 (155 mm and 40 g) to 8,951 (395 mm and 500 g) in the river population. These data were plotted (Fig. 5:12) and the line of best fit determined by the method of least squares. Slopes (b coefficients) of the 1990 and 1991 fecundity regression lines for riverine and reservoir populations were tested for homogeneity and then compared. The b coefficients were not significantly different between years within habitat ($p < 0.05$). Therefore, data for two years were combined to provide the following relationship:

Reservoir: $\log F = -0.9846 + 1.8848 \log L$ ($r^2 = 0.77$, $n = 84$)

River: $\log F = -4.3014 + 3.2996 \log L$ ($r^2 = 0.85$, $n = 35$)

Analysis of variance showed that the slopes were significantly different between reservoir and river fish ($p > 0.01$). Katle from the river were less fecund than the reservoir katle at the smaller size; however, absolute fecundity seemed to increase with size more rapidly in the river fish, and they

Figure 5:12. Relationship between fecundity and fish length (mm) in katle
(—■— - reservoir; ...●... - river).



5
4.5
4
3.5
3
2.5
2
Fecundity (log egg number)
2
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
Log total length of fish (mm)

were more fecund than the reservoir fish at the higher total length (Fig. 5:12). The average relative fecundity in the reservoir population was 19.13 ± 1.56 eggs g^{-1} compared to 22.57 ± 1.41 eggs g^{-1} for the riverine population. A Student t test showed that the relative fecundities of the reservoir and riverine populations were significantly different ($p < 0.01$).

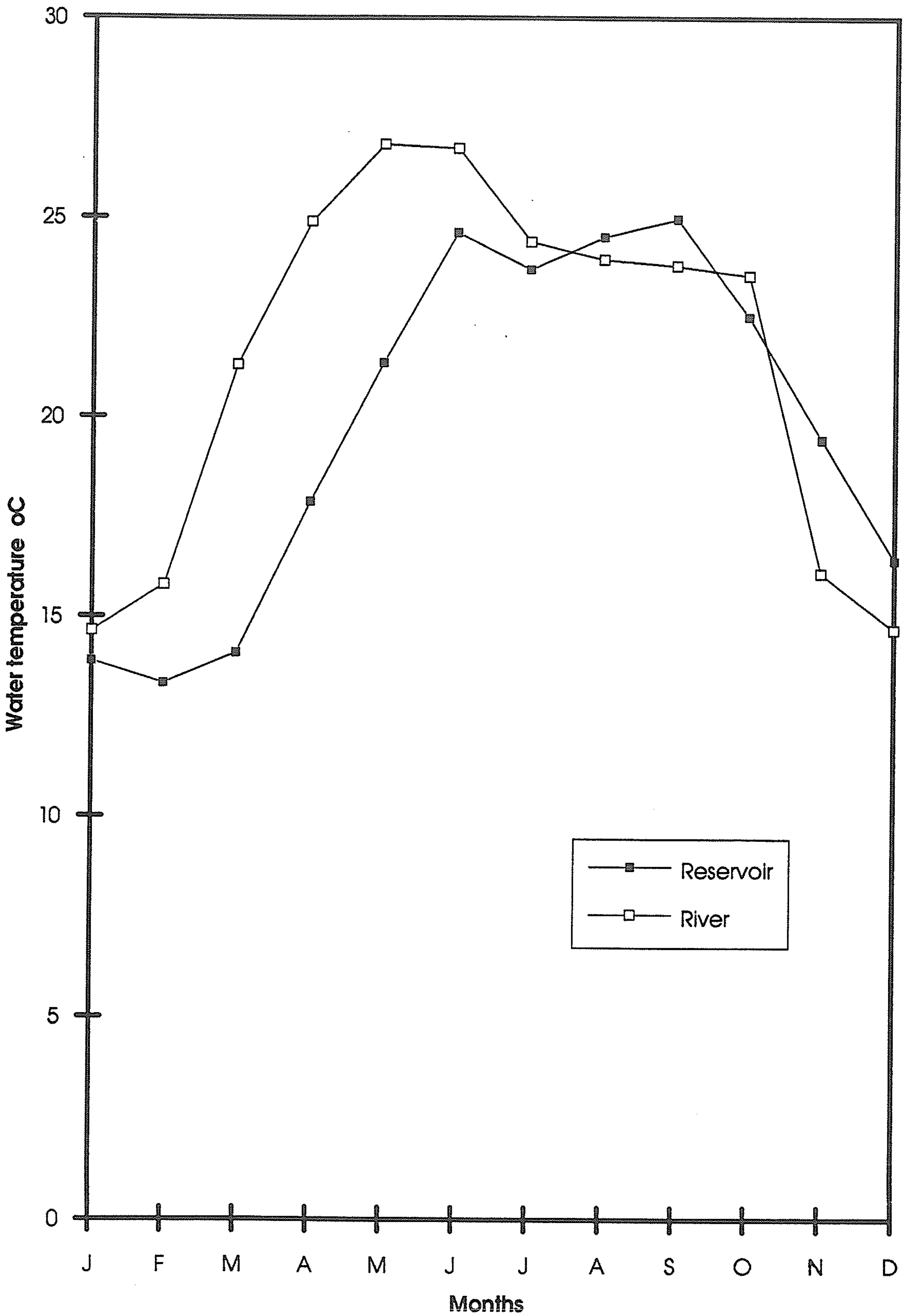
Seasonal variation in abiotic factors

a. Water temperature: The average surface water temperature in the reservoir was about 14°C during January and February. It started to rise from March and remained above 20°C between May and October (Fig. 5:13). There are significant seasonal differences in surface water temperature between the river and the reservoir. The average surface water temperature of the river was higher than that of the reservoir during March and July and lower during November and December (Fig. 5:13).

b. Day length: The average day length in Kathmandu Valley varies from 625 minutes in December to 831 minutes in June. It remains relatively long between April and September and relatively short from November to March (Fig. 5:14).

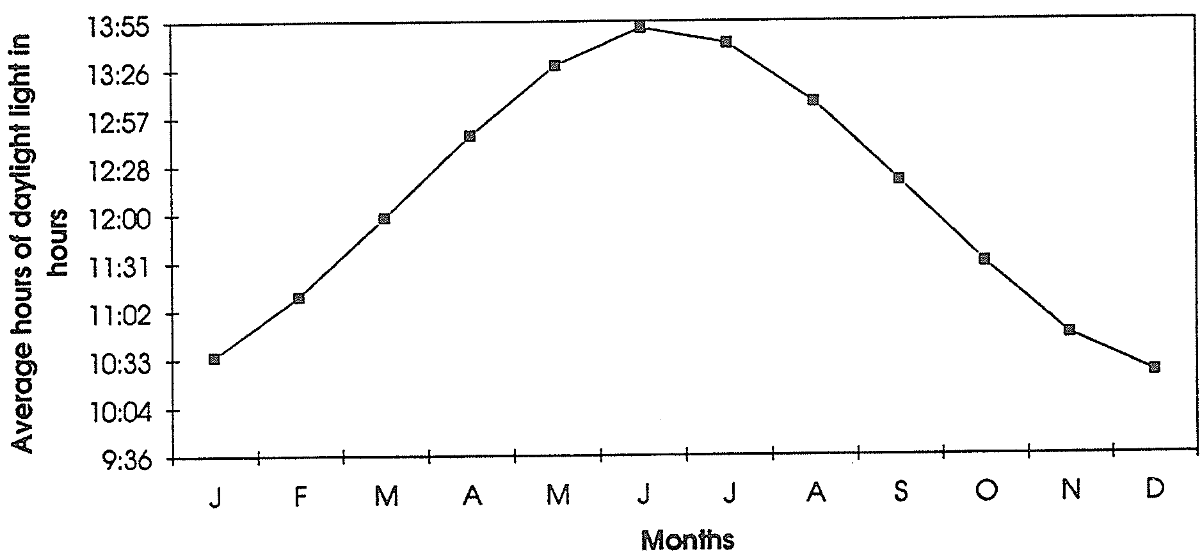
c. Annual precipitation: There are distinct dry and wet seasons in Nepal. Usually the monsoon starts in June and lasts until September. Most of the rainfall occurs during this period reaching a peak in July and August. The river's

Figure 5:13. Seasonal variation in surface water temperature (°C) in the Indrasarobar Reservoir and the Tadi River.



30
25
20
15
10
5
0
Water temperature oC
J
F
M
A
M
J
J
A
S
O
N
D
Months
Reservoir
River

Figure 5:14. Length of daylight hours in the study area during the year.



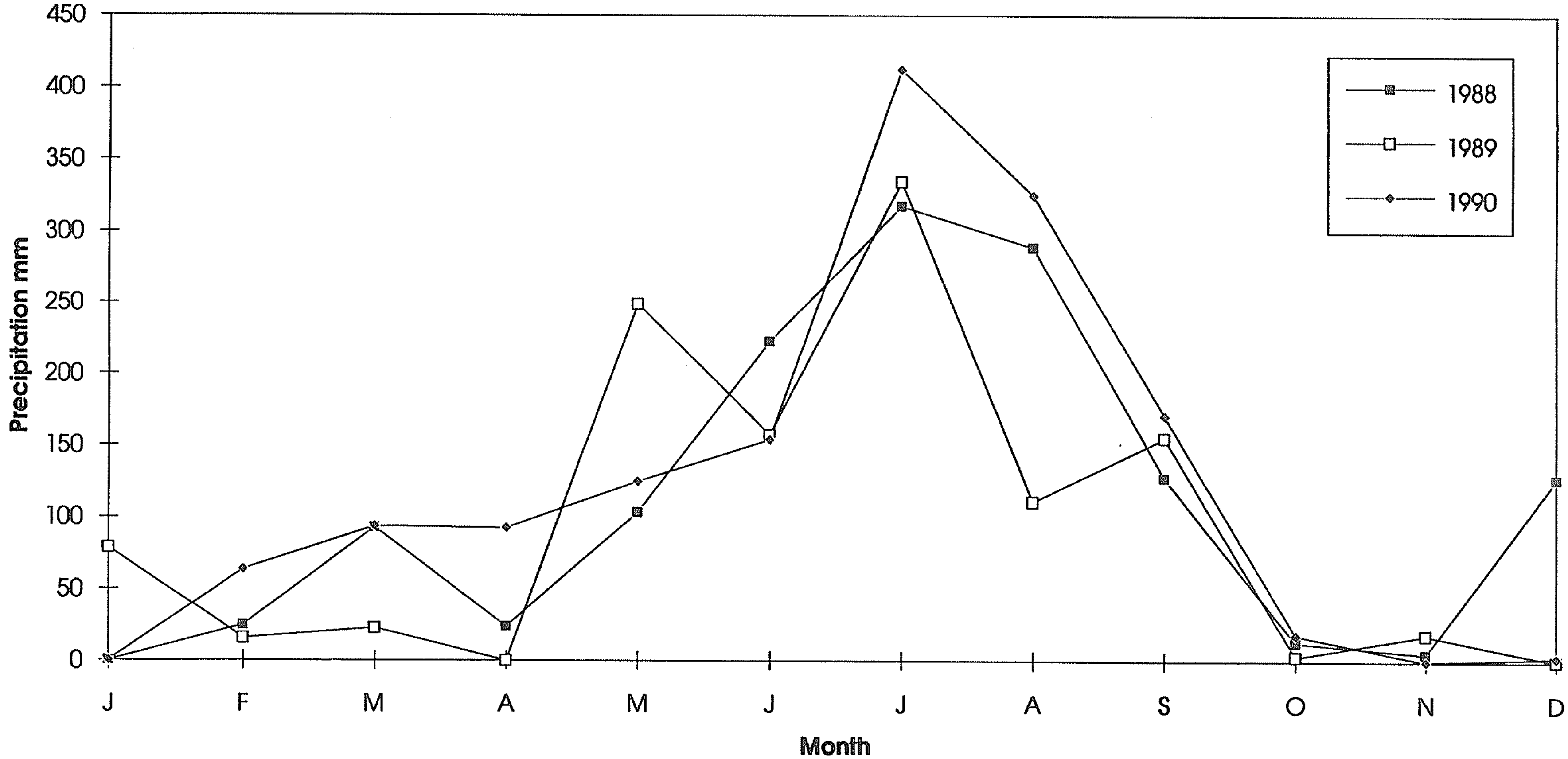
Average hours of daylight light in hours
13:55
13:26
12:57
12:28
12:00
11:31
11:02
10:33
10:04
9:36
J
F
M
A
M
J
J
A
S
O
N
D
Months

watershed area receives higher precipitation annually than that of the reservoir (Figs. 5:15, 5:16).

DISCUSSION

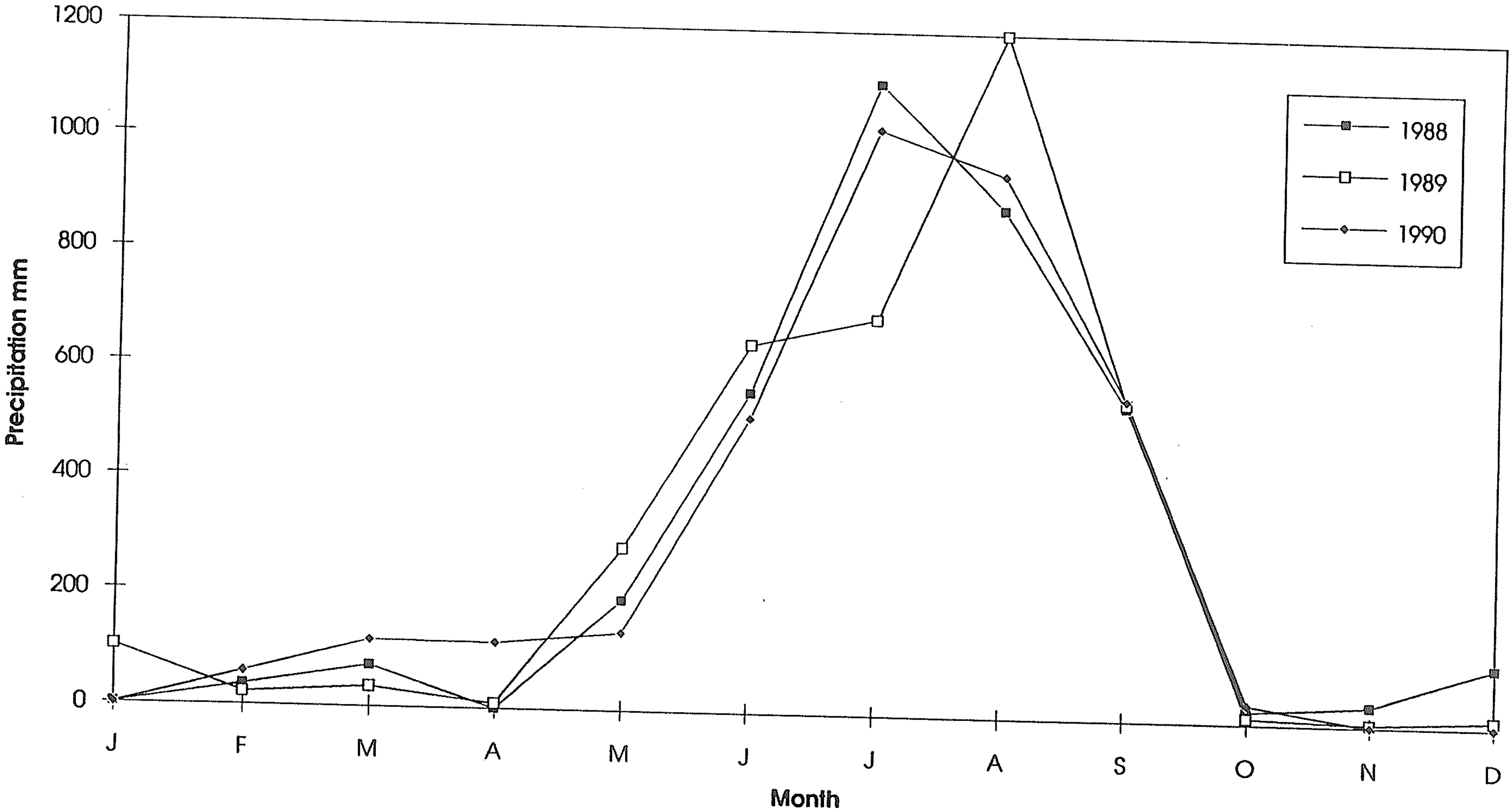
A significant departure of the sex ratios from 1:1 was found in the reservoir: females were dominant throughout the study period. The number of males was higher in the river catches during 1988 and 1989 but the number of females was slightly higher in the catch of 1990. Higher numbers of males than females have been reported in other species of cyprinids, sampled mainly in streams (Siddique *et al*., 1976; Mann, 1980; and Cooper, 1983). These workers suggested that this imbalance was related to a number of factors including differences in age composition due to higher mortality in the males and asynchronous spawning migrations. Since the females had a prolonged breeding season, they may have remained upstream for a longer period than the males. Al-kholy (1972) and El-Absy (1977) have reported shoreward migrations of *Puntius barberinus* to safer spawning grounds and that females stayed longer in the spawning areas than males. This significantly reduced the proportion of females in the main populations. Similarly in this study, katle were found to have a prolonged breeding season from April to October and most of the mature females migrated to suitable breeding grounds, possibly remaining there for longer periods than the males. It seems

Figure 5:15. Monthly precipitation (mm) in the Indrasarobar Reservoir area throughout the study period (1988-1990).



450
400
350
300
250
200
150
100
50
0
Precipitation mm
J
F
M
A
M
J
J
A
S
O
N
D
Month
1988
1989
1990

Figure 5:16. Monthly precipitation (mm) in the Tadi River area throughout the study period.



1200
1000
800
600
400
200
0
Precipitation mm
J
F
M
A
M
J
J
A
S
O
N
D
Month
1988
1989
1990

that the higher ratio of males to females during the year 1988 was the result of the spawning migration of the females upstream in the Tadi River beyond the sampling area. This was confirmed by the increased proportion of females during the second half of 1989 and the year 1990 when the sampling areas were extended by 2 km upstream in the river.

The extremely low number of male fish in the reservoir is difficult to explain. There is no evidence of sex reversal in this species, as is found for some teleosts (Reinboth, 1970; Chan, 1970). One of the possible reasons for the lower numbers of males in the reservoir may have been their preference for living in the riverine environment (in the Kulekhani River). They may participate in spawning activities when the mature females migrate upstream in search of suitable breeding grounds. Another reason may have been that males have a higher mortality rate so there are fewer older males. No males larger than 350 mm in length were caught from the reservoir throughout the study period. The use of different sampling gears may have been a reason for recorded differences in the proportion of males at the two sites. The reservoir was sampled using multi-panel gill nets and the smallest fish caught were 130 mm in total length. The smallest males caught in the river were 80 mm and they were observed at a different stage of maturity. Therefore, it seems possible that males between the sizes of 80 mm and 130 mm constituted a significant percentage of the katle population in the reservoir and that these were not caught by the gill nets employed.

Another distinct difference observed between the sexes in this study was that the males matured at least one year earlier than the females. Precocious male sexual maturation has likewise been described in other species of fish, including salmonids (Burgner, 1991; Salo, 1991). There also seems to be a tendency for larger individuals in both habitats to mature earlier than smaller ones, and for river fish to mature earlier than those in the reservoir.

The reproductive cycle can be divided into two main phases, gametogenesis and spawning. During gametogenesis, specialized gametes (oocytes and spermatozoa) are formed from simple germ cells (oogonia and spermatogonia). Spawning involves a complex sequence of events which is more variable in duration than gametogenesis. This involves the liberation of gametes, meiosis resumption, oocyte maturation, ovulation and oviposition in females, and spermiation and sperm release in males (Craig, 1987). Various factors, both intrinsic and extrinsic, have been shown to regulate gametogenesis and spawning in fish (Bullough, 1939; Ang, 1971). The intrinsic factor is the internal gonadal rhythm (hormonal), while the extrinsic factors are environmental conditions which determine the actual time of breeding. Temperature and photoperiod are apparently the most important external factors that regulate breeding in fish while other factors have a secondary effect

(Vlaming, 1974). Sexual development and spawning in cyprinids are modulated both by temperature and photoperiod, although temperature is the predominant influence in most species (Bye, 1984). The common carp exhibits an interesting evidence of the influence of temperature on its reproductive cycle. Though in temperate conditions it spawns a single batch per year, spawning may be spread over several days by drawing on portions of a single batch of matured eggs (Horvath, 1985). This repeat spawning within days is quite distinct from fractional spawning, as the carp requires some 3-3.5 months at 20-22°C between two ovulations. In temperate climates any possible second spawning is suppressed until the following year due to low temperature. However, in a tropical climate the common carp is a true fractional spawner, producing two or even three batches of eggs each year. Reproductive effort may be relatively low, with the female gonads forming around 10% of body weight at maturity (Horvath, 1986). Although in cyprinids several warm days induce a rapid rise in plasma gonadotropin, this does not inevitably lead to ovulation if the environmental conditions are not appropriate. Temperature and photoperiod interact with the endogenous reproductive cycle to ensure that gonads are mature at the appropriate season. The timing of the endogenous reproduction cycle is synchronised by these environmental stimuli. The external information is transmitted to the brain via the nervous system which in turn regulates the anterior pituitary gland. This gland controls gonadal development via the endocrine system (Mills, 1991).

From the inspection of gonadal patterns in this study it appeared that the katle went into a quiescent phase in their reproductive cycle between the months of November and February. In this period both males and females had small gonads and no brooding females were caught. The gonads started to develop in March and entered into a reproductive phase from March to October.

An attempt was made to relate the effects of several environmental factors such as day length, temperature and precipitation to the reproductive behaviour of the katle. The average surface water temperature in the reservoir and the river remained low during winter (January, February), started to rise in March, remained higher during the months of April to October and decreased from November, reaching its lowest level in January and February. Gonadal developmental in the katle seemed to coincide with the rise of temperature in both the river and reservoir. Similarly average day length varied from 625 minutes in December to 831 minutes in June. It remained longer during summer and early autumn and shorter during winter. There are distinct dry and wet seasons in Nepal. Usually the monsoon starts in May and lasts until September. From March to October the periods of longer day length and higher temperature coincided with the initiation of reproductive activities in katle. This is consistent with suggestions of several workers (Pickford and Atz, 1957; Aronson, 1957; Abidin, 1986; Hyder, 1970) that high temperature and intense sunlight are environmental factors that trigger reproductive activity in cyprinids.

The role of floodwaters in the spawning of freshwater fish has been studied by many workers (Hora, 1945; Alikunhi and Rao, 1951). Since the katle has a prolonged spawning season, pre-monsoon to post-monsoon, flooding does not seem to be an essential factor in its spawning. Still, the katle may be taking advantage of floodwater to reach the shallow breeding grounds. Similar upward migration of *Tor tor* during monsoon flood in the river Narmada was been recorded by Desai (1973). The spawning movements of ripe females in the reservoir and the river suggested that the katle were very selective in finding a suitable place to lay eggs. It appears that they preferred to lay eggs upstream on a gravel bed free of mud and algae. Their pre-spawning migration seems to be associated with the search for a suitable spawning ground with a freshly inundated gravel bottom. A similar situation was observed in *Mirogrex terraesancte*, a cyprinid in Lake Kinneret, by Gafny *et al.* (1992). The fish selected the near shore and spawned on algae-free rocky beds when these were available. This resulted in increased egg survival.

Ahmad (1948) reported that katle breeds from April to October with a peak period in August and September whereas Jhingran (1982) reported its breeding from May to September.

In the present study mature katle were observed from March to October. However running and spent katle were not recorded in the reservoir. It seemed that the majority of mature fish migrated from the reservoir after reaching maturity stage 4 and 5. This was further supported by the activities of the mature females whose movements were tracked by radio telemetry.

The presence of different sizes (batches) of oocytes indicates that the katle is a serial spawner. In several studies of the fecundity of serial spawners, attempts have been made to estimate batch size and number of batches (Macer 1974; Mackay and Mann 1969). Batch size can be defined as the number of oocytes which will be released together as a group. The least mature batch comprised the smallest ova, which were transparent and white. The second category contained eggs that were intermediate in size and yellow in colour. The most mature batch of ova were the largest, being yellow-orange, translucent and heavily yolked. The presence of several sizes of ova in a mature ovary is an indication of multiple spawning (Behmer, 1967; Johnson, 1971). It may be assumed that the largest ova are spawned first, the intermediate ova then mature to be spawned, a third batch may then develop, and so on. This sequence of events would probably continue as long as the temperature, photoperiod and food supply remained adequate and the fish was in a physiologically responsive state. In serial spawners, fecundity would appear to be very flexible, since the process of synchronous oocyte development and oocyte resorption makes it possible to control the egg number during the current spawning season. More eggs may therefore be released in a favourable season than in an unfavourable one. The term favourable might relate, for example, to the abundance of food, since there is evidence that the latter can affect fecundity (Bagenal, 1969).

Nikolsky (1969) stated that multiple spawning was only possible when there was a long period of adequate food supply for the larvae. However, he warned that it would be wrong to regard this life history strategy as an adaptation to food supply alone because it could also be an adaptation to unstable spawning conditions. Burt *et al.* (1988) have extended Taylor and Williams (1983) optimal life-history model and suggested that continuous reproduction was a conceptual standard condition. They believed that multiple spawning within a season resulted from seasonality constraining reproduction to a particular time of the year, whereas single spawning resulted from more severe environmental constraints. They suggested that multiple spawning within a season was associated with: (1) less seasonal change in the environment; (2) small body sizes; and (3) smaller relative ovary sizes. Although these three claims probably have substance for fish in general, they do not seem to be applicable to katle, which is found in seasonal waters and whose body size is relatively large. In this long-lived low fecundity species perhaps multiple spawning may have developed as an adaptation to spawning under labile conditions for egg survival (Nikolsky, 1969) and to high recruitment variability.

There are several advantages conferred upon fish that are multiple or serial spawners:

(1) Increased fecundity: Just prior to ovulation, oocytes hydrate and increase greatly in size. If all the oocytes hydrate at the same time, the restriction of space within the ovary limits fecundity. However, if small batches of the eggs hydrate and are spawned at intervals, more eggs can be accommodated in the ovary over time (Miller, 1984; Burt *et al.*, 1988).

(2) The risk of predation of eggs and larvae is spread over a longer period (Lambert and Ware, 1984).

(3) The impact of larvae on their prey species is spread over time.

(4) The risk of spawning at a time of unfavourable climatic, hydrographic or feeding conditions is spread out.

Dasgupta (1988a) has described katle as a prolific breeder but not very fecund. Low fecundity was also observed in the present study. The relative fecundity and recorded age of katle was compared with some other Indian cyprinids observed by several workers (Table 5:7). Katle had the lowest number of eggs g^{-1} body weight among them. It seems that the multiple spawning behaviour of the katle with low fecundity is an adaptation to the high mortality of juveniles in the hill

Table 5:7. Relative fecundity and recorded age of some cyprinids.

SN.	Species	R-Fecundity No Egg g^{-1}	Age (yr)	Source
1	*Rasbora daniconius*	630.00	-	Nagendra et al, 1981
2.	*Labeo dero*	397.12	6	Bhatanagar, 1964; Biswas *et al.*, 1982.
3.	*Labeo bata*	393.04	7	Chetterjii et al,1979.
4.	*Labeo calbasu*	217.77	8	Rao & Rao, 1972; Gupta & Jhingran,1973.
5.	*Labeo rohita*	62	10	Singh & Srivastava, 1982; Khan & Siddique, 1973.
6.	*Labeo fimbriatus*	171	6	Rao, 1974.
7.	*Catla catla*	232.02	-	Singh & Srivastava, 1982.
7.	*Cirrhina mrigala*	214.74	7	Hanumantharao, 1971.
8.	*Cyprinus carpio*	110.80	6	Das, 1964; Das & Fotedar, 1965.
9.	*Schizothorax niger*	29.04		Jyoti & Malhotra, 1972.
10.	*Tor Putitora*	25.00	17	Tandon & Johal, 1983.
11.	*Tor tor*	06.13	-	Nautiyal & Lal,1985
12.	*Neolissochilus hexagonolepis*	16.00	-	Dasgupta, 1988a
13.	"	20.50	11	Present study

streams due to high monsoon flooding.

The reproductive strategy of a species is a summation of a suite of adaptive traits that enables individual fish to leave the maximum number of offspring (Mills, 1991). Though there have been few conclusive experimental demonstrations of the cost of reproduction (Reznick, 1985), it is likely that the earlier and greater the degree to which energy resources are diverted from maintenance of somatic growth to reproductive output, the lower will be the parents' survival to future spawning. It has been argued that this trade-off will be conditioned by the balance between pre-and post-maturity rates of mortality and that selection will favour lower fecundity and greater longevity with increased variation in spawning success (Mann and Mills, 1979).

The data collected on age, growth and reproduction of the katle revealed that it is a long-lived, slowly growing and multiply spawning species of low fecundity. Extreme environmental conditions, such as high flooding in the fast flowing rivers caused by monsoon rain and the substantial annual drawdown in the reservoir, probably cause high mortality among juveniles. Surviving adults exhibit slow growth, long life and a modest investment of energy in gonadal development. It seems reasonable to suggest that the multiple spawning and low fecundity of the katle is a reproductive strategy, an adaptation to the unfavourable hydrographic conditions of hill streams and fluctuating natural reservoirs.

CHAPTER VI

GENERAL SUMMARY AND DISCUSSION

This study has revealed interesting similarities and differences between a reservoir and a river population of katle, *Neolissochilus hexagonolepis* (McClelland), and also between katle and other groups of fish. The overall feeding patterns of katle in the Indrasarobar Reservoir and the Tadi River were found to be basically similar. In both groups, plant matter formed the highest percentage of the total volume of the gut contents, followed by animal matter and then by detritus and mud. It was evident from the study that the contribution of plant food increased with the size of the fish in both habitats. Associated with this dietary shift was an increase in the relative length of the gut with increasing total length of the fish in both populations (see below).

Along with these general similarities, some differences were observed in feeding habits between the river and reservoir katle. The gut contents of the river katle were dominated by vascular plant tissue and filamentous algae, while terrestrial grass and planktonic blue-green algae were more common in the diet of the reservoir population. Differences were also evident in the variety of animal food. In the reservoir, zooplankton constituted a higher percentage of the total gut contents, and annelids were the most common benthic animals in the diet. In the river, on the other hand, zooplankton were very scarce in the diet, and the predominant benthic dietary items were the nymphs of aquatic insects. These differences probably reflect the differential availability of the respective prey species in the two habitats: zooplankton thrive in the reservoir's water column and annelids are abundant on the reservoir floor, whereas insects favour the flowing water conditions of the river bottom to reproduce (Yadav, 1989).

The percentage of detritus in the gut contents of the reservoir katle was considerably higher than in the gut contents of the river katle. There is also an apparent difference in feeding intensity between populations. The reservoir population attains its peak consumption in July and maintains quite a high rate until November. The river katle attain their peak intake only in September. These differences are probably also environmentally induced: the reservoir achieves its peak surface area (conducive to food generation) only in July and then maintains a high area until the winter, whereas the river katle's food suuply is diminished by the flushing effect of monsoon floods through July and August (Fig. 5:16; Appendix 3).

The average weights of gut contents (in percentage of the body weight) for different length groups in the reservoir are higher than those in the river. Relative gut length was also influenced by habitat: while the length of the gut was similar between the reservoir and river for intermediate-sized fish (total length approximately 150 mm), the rate of increase in relative gut length during further growth of the fish was greater in the reservoir.

It seems apparent that the increase in relative gut length is related to the observed shift from carnivorous to herbivorous feeding during the growth of katle (Biswas, 1985). The guts of the smallest katle caught in this study contained 32% to 53% animal matter, while the animal content in the larger fish's guts was only 6% to 13%. Herbivorous cyprinids in general have relatively longer guts than carnivorous ones (Das and Moitra, 1956a,b,c, 1963; Weatherley and Gill, 1987), presumably because vegetable matter is digested more slowly. It is interesting to note that when katle are presented with the environmental opportunity to benefit from increased herbivory (in the reservoir), they can respond by increasing their relative gut length. This capacity may be a major adaptive specialisation in the feeding ecology of katle in the reservoir.

Overall, after careful examination of the feeding behaviour of katle from the river and reservoir and comparison of these data with those of previous workers, it seems reasonable to suggest that the feeding differences observed between katle in the two systems can be explained by differing environmental conditions and the fish's adaptability.

The growth of katle also showed both similarities and differences between the two systems. It seems to be a feature of katle from both populations that females attain a larger size than males. Males, however, mature about a year earlier than females, between the ages of two and three years. This male reproductive precocity is a feature shared with other groups of fish, including salmonids (Burgner, 1991; Salo, 1991). Faster growing individuals were observed to mature earlier than slow growers.

Comparison of specific growth rates in various age groups of katle from the reservoir and river shows that the relative growth in length is rapid during the first three or four years in both habitats. All the fish have reached maturity by the age of four years and the growth rate in length declines after maturity. In the reservoir population, the instantaneous rate of growth was 40% yr^{-1} in both females and males between the ages of 1 and 2 years. In the next year the growth rate remained more or less the same in females but dropped to about 21% yr^{-1} in males. The growth rate continued to decrease with increasing age in both sexes. The trend for the instantaneous growth rate in the river population to decline with age was similar. The growth rates of 43% yr^{-1} in females and 33% yr^{-1} in males between the ages of 1 and 2 decreased in each successive year in both sexes.

Estimation of the ultimate size L_∞ and the growth coefficient K of the von Bertalanffy growth model for each sex from both habitats revealed that L_∞ is greater for females (73 and 45 cm in the reservoir and river respectively) than for males (41 and 26 cm), and that K values are higher for males (0.195 yr^{-1} in the reservoir and 0.135 yr^{-1} in the river) than for females (0.089 and 0.120 yr^{-1}). L_∞ is clearly greater for the reservoir katle than for the river katle, while K values are greater in the river population than in the reservoir.

Comparison of reproductive biology between the reservoir and river populations did not reveal any strong differences such as might have been expected on the basis of the observed differences in feeding and growth. One apparent difference was in the sex ratio: the reservoir catches were dominated by females while males were more abundant in the river catches during the whole study period. The use of the different sampling gears may have been a reason for recorded differences in the proportion of males in the two habitats. The reservoir was sampled using multi-panel gill nets and only a few fish under 130 mm in total length were caught. In the river, sampled with a variety of gear, the smallest males caught were 80 mm in total length and they were observed to be at different stages of maturity. Therefore, it is likely that males between the sizes of 80 mm and 130 mm constitute a significant percentage of the katle population in the reservoir and that they were not caught by the fishing gear employed.

The inspection of gonadal cycles revealed that katle in both habitats went into a quiescent phase between the months of November and February. In this period, both males and females had small gonads and no brooding females were caught. The gonads started to develop in March and remained in their reproductive phase until October. The spawning movements of ripe females in the reservoir and river suggested that katle are very selective in finding a suitable place to lay eggs. They apparently prefer to lay eggs in fast flowing streams on a gravel bed free of mud and algae. The pre-spawning migration in both systems seemed to be associated with the search for a suitable spawning ground with freshly inundated gravel bottoms. The presence of batches of oocytes of different sizes indicated that the katle is a serial spawner. The average relative fecundity was found to be somewhat lower in the reservoir than in the river (about 19 vs. 23 eggs gm^{-1}). The absolute fecundity increased with the size of the fish in both populations. At smaller sizes, reservoir fish were more fecund than river fish, while larger fish were significantly more fecund in the river than in the reservoir.

The data collected on food and feeding, age, growth and reproduction revealed that katle is a) a highly plastic omnivorous cyprinid which has evolved to live successfully under a variety of conditions, b) a multiple spawner with a pre-spawning migration and low fecundity, and c) a long-lived, slowly growing hill stream fish with large ultimate size. Its feeding intensity, seasonal growth and reproductive cycle are probably mainly governed by the seasonal variations in water temperature and length of daylight, and ultimately by abundance of natural food resources. Extreme environmental conditions such as high flood in the fast flowing rivers due to monsoon rain and substantial annual drawdown in the reservoir probably cause high mortality among juveniles, but surviving adults exhibit slow growth, long life and probably modest investment of energy in gonadal development.

Its omnivorous feeding habits enable this fish to maximize its utilization of available food in the ecosystem. Katle provide a herbivore link with the first trophic level in the food chain in freshwater rivers and reservoirs. Further, the large ultimate size of katle makes it valuable and attractive for food and sport. Its long spawning period also helps it to continue recruitment during the larger part of the year (April to October). Considering these characteristics, it is reasonable to suggest that katle has relatively high potential for development as a food and sport fish in Nepalese reservoirs.

Although the above-mentioned are positive features, low fecundity and slow growth may be two limitations of katle as a species for commercial fisheries. However, fecundity is variable in serial spawners, since the number of eggs produced can be controlled through the processes of synchronous oocyte development and oocyte resorption. More eggs may therefore be released in a favourable environment than in an unfavourable one. Similarly, the annual length increment of katle is higher in the reservoir than in the river. Therefore, it can be assumed that the growth rate of katle could be further improved by providing an optimal environment.

Besides the above (genotypic or phenotypic) characteristics of katle, certain abiotic factors including natural calamities, man-made barriers and weather conditions play important roles in the survival, growth and propagation of katle in Nepalese rivers and reservoirs. For instance, the extent of water drawdown, which determines the area of the reservoir, was found to be inversely related to annual length increments of katle at different ages. Low feeding intensity of the river katle due to high turbidity during monsoon months (June and July) can be cited as another example of a negative impact of abiotic factors on the life history of katle. The survival of katle is also severely hampered by heavy fishing and indiscriminate blasting of winter pools with explosives when the water level has gone down and the fish are resting at the bottom.

The experience gained with the Indrasarobar Reservoir has yielded important lessons. Katle grow to a large size in this lacustrine environment, feeding well on the reservoir's flora and fauna. Their success here can be related to their preference for larger pools in their natural stream habitat; in contrast, fish specialized for the fast flowing parts of streams, such as asla, have not survived in the reservoir. However, the stability of the lacustrine environment that favours katle's success is routinely disrupted by the annual drawdown of the reservoir, serving its primary purpose of power generation. As described, drawdown has a negative impact on the annual length increment. This probably represents a major obstacle to a viable katle fishery in hydroelectric reservoirs. While the effect of drawdown requires further study, it seems clear that drawdown should be carefully limited to minimize negative impact on fish. Unfortunately, in practice, drawdown is governed by the economic consideration of demand for electricity, and the requirements of the fishery have not received equal attention. Even with the adverse effects of these fluctuations, however, the reservoir is presently supporting a commercial fishery that provides needed income to local residents. This creates yet another problem that this fishery shares with many others around the world, namely overfishing. Excessive fishing pressure appears to be limiting the bulk of the katle stock to low size and age classes at which many of the fish are not yet sexually mature. A conclusion that can be drawn is that, while katle is a successful fish in the reservoir, government regulation of both the reservoir's drawdown and of fishing pressure is definitely needed to sustain a katle fishery in the future.

Recommendations

Katle is well known as an excellent food and game fish in the mountain streams of Nepal. It has adapted to the Indrasarobar Reservoir and plays an important role in the reservoir fisheries. For rational exploitation of katle in the existing and future reservoirs, the following measures are suggested.

1. Restoration of natural habitat: Natural vegetative cover of stream and reservoir margins needs to be restored to provide suitable feeding and breeding grounds for katle as well as other indigenous fish fauna. Removal of stones from the river bed and shore should not be allowed. The spawning grounds of fish have to be legally and strictly protected.

2. Mitigation of the effects of man-made barriers: Dams, especially those that have been raised in the mid-region of the migratory route, are obstructions to spawning migrations. Suitable fish passes are required around these barriers for the spawning movements of the fish. Certain minimum water levels must be established and maintained during the growing season of fish.

3. Fishing regulations: Age composition of katle in both systems revealed that the populations were dominated by fish

of 3 to 4 years, not all of which were yet mature. Older fish were scarce in both systems. This is an indication of high fishing pressure which might eventually eradicate the fish in the reservoir and the rivers. Fishing pressure can be reduced by increasing the mesh size of fishing gear (≥ 75 mm). Fishing should also be prohibited on spawning grounds during the prime breeding season of the fish.

4. The existing Aquatic Life Protection Act of Nepal (1960) needs to be updated to the present context and implemented. This would prohibit blasting and poisoning of fish in rivers and streams, among other abuses.

5. Reservoir management: The needs of the fishery should be considered in determining how much the reservoir is drawn down during the dry season. Limits on drawdown should be established and respected to protect fish populations.

6. Farming of katle: Domestication and artificial breeding of katle at Trishuli Fisheries Research Centre, Nepal (P. L. Joshi, personal communication) should be continued to ensure the survival of this species in the face of increased destruction of their natural habitat and increased fishing pressure.

In addition to the above listed suggestions, the following areas are important for future research on katle:

a. A pre-impoundment study on the biology of commercially important fish like katle should be carried out before the construction of any dam in the future. This will provide valuable information on the existing status of these fish. Involvement of a fishery biologist from the early planning phase of any new reservoir is required.

b. The effect of drawdown on the growth and production of fish is a very important aspect of the reservoir fishery which could not be investigated fully in the present study. This investigation should be attempted in the future.

c. Comparisons of mitochondrial DNA of the river and reservoir populations may be helpful in determining whether the apparent differences between the two populations are genotypic or phenotypic.

d. Studies to locate the precise breeding grounds of the reservoir katle will be worthwhile for the management of the reservoir fishery.

e. In-depth studies on hatchery management, nursing, rearing and brood maintenance should be carried out. Studies on physico-chemical requirements (including water exchange rate, optimum temperature and food supply at different stages) will be very helpful in cultivation of katle under controlled conditions.

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Appendix 1

A short discussion on the taxonomy of katle

Nomenclature:

Valid name: *Neolissochilus hexagonolepis* (McClelland 1839), Rainboth (1985)

Neolissochilus hexagonolepis, the Nepalese 'katli' or 'katle', has a very confusing taxonomic history from its initial identification in 1839 to the present. The fish was first included in the genus *Barbus* with four other large-scaled barbels by McClelland (1839). Later Weber and de Beaufort (1916) placed this fish in the genus *Lissochilus,* and Oshima (1919) created a new genus *Acrossocheilus*. Recently, Rainboth (1985) proposed and described the genus *Neolissochilus*.

Katle has been described under several different species names. McClelland (1839) was the first taxonomist to deal with the large-scaled barbels of India and described five species of *Barbus: B. hexastichus*, *B. progeneius, B. macrocephalus, B. hexagonolepis* and *B. megalepis*. The first four species were described from Assam while the last species was obtained in the River Koshi, Bihar (the northern state of India). The main characteristics of *Barbus hexagonolepis* described by McClelland (1839) are as follows:

Length of the head to that of the body (total length minus head length) is in the ratio of one to four; there are twenty-seven scales along the lateral line and seven in an oblique line from the ventral fin to the ridge of the back. On the anterior part of the body the exposed surfaces of the scales represent hexagonal outlines. The dorsal fin originates midway between the tip of the snout and the base of the caudal fin. The rays of the ventral and pectoral fins are small. The fin ray formula is:

D.12: P.16: V.9: A.7: C.10/9.

The head is small and slightly compressed, the snout smooth and slightly rounded, and the postorbital plates less expanded in this than in any of the other *Barbus* species. It has a smooth dorsal spine and large scales. In large-sized individuals, scales are blackish grey on the back, head and the base of the fins, while fins and scales on the opercular plates are tipped with yellow.

After a detailed investigation on a series of specimens of the species from Assam described by McClelland (River Brahamaputra and some tributary streams), Hora (1940) found that McClelland's descriptions were brief and inadequate and his illustrations were inaccurate. Therefore, Hora (1940) revised their taxonomy and placed them in the following order (Table 1).

Day (1876/78) considered *B. hexagonolepis* as a valid species and described its characters as follows: Length of head 5 to 5.5% of the total length, dorsal and abdominal profiles equally and slightly convex, interorbital space rather convex, upper jaw longer than the lower, lower labial fold interrupted, opercle higher than wide, pores on the

Table 1. The identity of McClelland's five species and their position provided by Hora (1940):

McClelland	Assamese name	Hora
1. *Barbus hexastiches*	Loburo	*Barbus (Tor) tor* (Ham.)
2. *B. Progenius*	Jungha	*Barbus (Tor) progeneious* McClelland
3. *B. Macrocephales*	Burapetea	*Barbus (Tor) putitora* (Ham.)
4. *B. hexagonolepis*	Bokar	*Barbus (Lissochilus) hexagonolepis* (McClelland)
5. *B. megalepis*	--	*Barbus (Tor) mosal* (Ham.)

cheeks sometimes present, lateral line scales 28-31. He also stated that this species can be distinguished at once from *B. hexastichus* (*Tor tor*) by the interrupted groove behind the lower lip.

On the basis of the presence of pores on the snout, Day (1876/78) separated a few young specimens from the Tista River below Darjeeling, India, and placed them in a different species, *Barbus dukai*. *B. dukai* has also been recorded from Siam (Hora 1923) and the Indo-Australian Archipelago (Weber and Beaufort, 1916). Other authors who have identified katle as *B. dukai* include Boulanger (1898) and Annandale (1918) from Burma, and Hora (1923) from Siam. Duncker (1904) recorded this katle as *B. soroides* from Sumatra and the Penang Malay Peninsula.

In 1925 Nichols described a species under the genus *Barbus* as *B. caldwelli* from Fukien, China. The fish was characterised by 24 scales along the lateral line and the left side of the snout with only a band of small crowded, warty points above the maxillary. Later in 1928 he included this species in the sub-genus *Spinibarbus* Oshima, but Lin (1933) after a thorough study placed it in the genus *Lissochilus*. Hora and Misra (1941) redescribed the species, found that it was more allied to *L. hexagonolepis*, and put *L. caldwelli* as a synonymy, with a query. Weber and de Beaufort (1916) studied the fish grouped under *Barbus* and divided them into several new genera. They proposed the genus *Lissochilus* for *B. dukai*, and a new species *L. dukai* from Sumatra. The most characteristic features of the genus *Lissochilus* according to Weber and de Beaufort (1916) are as follows:

1. The post labial groove, though continuous round the corners of the mouth, is interrupted in the middle.
2. The lower lip is conspicuously separated from the jaw, which is provided with a horny covering and
3. The snout is provided with horny tubercles or a series of open pores.

A group of Chinese Barbus-like forms have also been assigned to the genus *Lissochilus* by various authors, and their systematic position has been studied by Herre and Myers (1931), Myers (1931) and Lin (1933). The nine identified

Chinese species are as follows:

1. *L. labiatus* (Regan)
2. *L. monticola* (Gunther)
3. *L. hemispinus* (Nichols)
4. *L. barbodon* (Nichols and Pope)
5. *L. kreyenbergii* (Regan)
6. *L. formosanus* (Regan)
7. *L. invergatus* (Oshima)
8. *L. fasciatus* (Steindachner)
9. *L. paradoxus* (Gunther)

The Chinese *Lissochilus* species are small in size and the number of scales along the lateral line is generally 40 or more. Most of the species are characterised by the possession of short vertical bars across the body. They are mostly confined to southern China. Other species of *Lissochilus* of the *hexagonolepis* type are not only large-scaled but also grow to large size and are mostly confined to the Brahamaputra and Chindwin drainages in India and various rivers in Burma, Siam, the Malay Peninsula and the Malayan Archipelago. Hora and Misra (1941) agreed with the statement of Herre and Myers (1931) that a difference of 10 scales in the count along the lateral line is not a valid generic character but suggested that this difference coupled with the geographical position of the two groups merits some sort of distinction. Hora (1940) also proposed to assign them to a separate subgeneric rank.

Several species have since been described in the genus

Lissochilus although according to Hora (1940) their systematic position is somewhat doubtful. These species are:

L. dukai (Weber and de Beaufort, 1916).

L. sumatranus (Weber and de Beafort, 1916)

L. caldwelli (Lin, 1933),

L. dukai (Fowler, 1934),

L. hutchinsoni (Fowler, 1934),

L. dukai (Suvatti, 1936),

L. hutchinsoni (Suvatti, 1936),

L. sumatranus (Suvatti 1936),

L. tweedie (Herre and Myers 1937),

L. dukai (Fowler, 1937),

L. dukai (Fowler, 1938),

L. hendersoni (Herre, 1940).

The first non-Indian record of *Lissochilus hexagonolepis* equivalent to *Barbus dukai* Day was by Boulenger (1898), from Burma. The lateral line scales in that fish varied from 26 to 28. The species was next recorded by Duncker (1904) from the Malay Peninsula and from Sumatra as *Barbus soroides*. The number of lateral line scales varied from 26 to 29 and the pre-dorsal scales were 9 in number. Weber and de Beaufort (1916) studied this fish and Day's *B. dukai* and found them identical. They also described another new species of *Lissochilus* (*L. sumatranus*) from Sumatra, which was based on a single specimen of 148 mm in length. *L. sumatranus* differs from *L. dukai* by having fewer scales along the lateral line

(24-25 in *L. sumatranus* compared to 26-29 in *L. dukai*). But as Hora (1940) mentioned, the Indian specimen of *Barbus hexagonolepis* has the lateral line scales varying in number from 22 to 32. According to Hora and Misra (1941) no reliance can be placed on small variations in this character.

Lissochilus sumatranus was recorded from Siam by Suvatti (1936). The black colour of both lobes of the caudal fin in the specimens described by Weber and de Beaufort (1916) is similar to that of specimens from Siam. Therefore, according to Hora and Misra (1941) these specimens and the Indian specimens of *Lissochilus (L. hexagonolepis*) are synonymous.

Fowler (1934) described *L. hutchinsoni* from Nakon Sritamarat, Siam. His description was based on a 148 mm long fish with 23 lateral line scales and 7 pre-dorsal scales. Fowler stated that this fish was closely related to *L. sumatranus* Weber and de Beaufort, but the coloration of the caudal lobes and the dorsal and anal fins differed from *L. sumatranus*. According to Hora and Misra (1941) there was no dark blotch on the anal fin as described by Fowler (1934). Therefore, they regarded *L. hutchinsoni* as a synonym of *L. hexagonolepis*.

Herre and Myers (1937) described *L. tweediei* from the River Yum, China. Their description was based on four very young specimens of 62 to 92 mm in total length. This species had 26 lateral line scales, 8 pre-dorsal scales and a broad sharp, horny edge to the lower jaw. According to Hora and

Misra (1941) these characters were similar to those of *L. hexagonolepis*.

In 1940 Herre described another species of *Lissochilus* (*L. hendersoni*) from Malaya (Penang Island). His description was based on 28 specimens ranging from 59 to 70 mm in length. The lateral line scales were 23 and the pre-dorsal scales were 5-6 in number. Hora and Misra (1941) examined the para type of this species and found 23-24 scales along the lateral line, and 6-7 pre dorsal scales. They came to the conclusion that this species cannot be separated from the young of *L. hexagonolepis*. Realizing the great range of variation exhibited by Indian *L. hexagonolepis,* they concluded that the Malayan *Lissochilus* species should be regarded as synonyms of *L. hexagonolepis*. The list of non-Indian *Lissochilus* and their main characters are given in Table 2.

Oshima (1919) described a new genus *Acrossocheilus* with a type species *Gymnostomus formosonus* Oshima. The diagnostic characters of *Acrossocheilus* are: body elongate, not very deep and the compressed abdomen rounded. Head short, broad, with several rows of horny tubercles on the sides in front of and below the eyes; these may be absent in some examples, and they may be represented by pores when tubercles have fallen off. Snout obtusely rounded, slightly overhanging jaw. Mouth moderate, horizontal subterminal. Eyes moderate, lateral in position, not visible from below ventral surface. Lips thick, continuous round the angle of mouth. Labial fold interrupted in the middle. Lower jaw covered by sharp horny covering. Four barbels, a pair each of rostral and maxillary. Caudal fin

Table 2. Non Indian *Lissochilus* and their main characters:

Name	No of Scales along lateral line	Place	Source
B. dukai	26-28	Burma	Boulenger, 1898
B. soroides	26-29	Malaya	Duncker, 1904
L. sumatranus	24-25	Sumatra	Weber and de Beaufort, 1916.
L. sumatranus	24-25	Siam	Suvatti, 1936
L. sumatranus	24-25	Burma	Annandale, 1918
L. dukai	-	Siam	Hora, 1923
L. caldwelli	24	China	Nichols, 1925
L. hitchinsoni	23	Siam	Fowler, 1934
L. tweedie	26	River Yun	Herre and Myers, 1937
L. hendersoni	23	Malaya	Herre, 1940

deeply forked with pointed lobes. Scales large. Lateral line complete with 22-32 scales. A scaly appendage is present before each pelvic fin.

The Nepalese katli or katle is reported by Misra (1959) as *Acrossocheilus hexagonolepis*. According to him the fish attains 609 mm (2 ft) or more in length and is an important game fish. In the description he has mentioned that the sides of the snout and suborbital region have horny tubercles. The lateral line scales number 22-32 and the pre-dorsal scales, 8-10.

Jayaram (1981) has given the diagnostic characters of *Acrossocheilus* Oshima and figured *Acrossocheilus hexagonolepis* after Misra (1962). Shrestha (1981) has reported *Acrossocheilus hexagonolepis* from different river systems, lakes and reservoirs of Nepal. The lateral line scales are 28 and the pre-dorsal scales are 10 in number.

Recently Rainboth (1985) comprehensively studied the southern and southeastern Asian species of *Acrossocheilus* including katle and created a new genus *Neolissochilus*. His description for the new genus is as follows:

Dorsal fin IV/9 (rarely IV/8), with large unbranched and unserrated rays. Pectoral fin i/ 13-17, the first ray longest. Pelvic fin i/8 (rarely i/7); anal fin iii/5, caudal fin VII-X, 10/9, vi-ix, deeply forked with convex distal margin of each lobe. Body deep anteriorly, trunk and peduncle smoothly tapered from rather broad head to strongly compressed peduncle. Trunk slightly arched pre-dorsally, ventral profile straight or convex. Lateral line scales 20 to 29. Pre-dorsal scales large, uncrowded, 6 to 10. Transverse scales 4 or 5/4 with pelvic fin on third row below lateral line.

Head broad, snout blunt, with mouth placement varying from oblique and near-terminal, horizontal and inferior. Species with horizontal mouth often with rostral cap overhanging on the upper lip. Mouth smoothly rounded. Lower lip with incomplete post-labial groove. Lips thick, intermandibular space usually broader than mandibles. Long maxillary and rostral pairs of barbels always present. Cheeks with numerous tubercles, occasionally a few tubercles immediately anterior to 'rostral' barbel, but even across the tip of the snout.

Gill rakers long, slender, medially directed branches, 2 to 6 rakers on epibranchial and 7 to 12 rakers on hypobranchial segment. Pharyngeal bones stout, with three rows of hooked teeth. Grinding surfaces of each in outer row widest on uppermost teeth, width progressively decreasing along row ventrally. Uppermost teeth in outer row with three or four ridges across face of grinding surface.

Living individuals are dark green on dorsal side of head and body and may have a lighter area between the dorsal and the lateral line with a wide bluish lateral stripe running from eye to the base of caudal fin. The belly is silvery white. Fins vary from yellowish to reddish brown, and through various shades of grey, usually slate-grey.

Katle is now included under this new genus and named as *Neolissochilus hexagonolepis* (McClelland, 1839).

Objective Synonymy:

1839. *Barbus hexagonolepis* McClelland, Asiat. Res. 19 pp. 270-336, pl. 41, Fig-3.

1878. *Barbus hexagonolepis* Day, Fish. India, p. 564, pl. CXXXVII, Fig. 4 (pores on snout not shown present in the specimens).

1878. *Barbus dukai*, Day, Fish. India, P. 564, pl. CXLIII, Fig. 3.

1889. *Barbus hexagonolepis*, Day, Fauna Brit. Ind. Fish. 1, p. 305.

1889. *Barbus dukai*, Day, Fauna Brit. Ind. Fish., I, p. 306.

1994. *Barbus soroides*, Duncker, Milt. Naturhist. Mus. Hamgurg, XXI, p. 178, pl. I, Fig. 7. (Sumatra and Pahang, Malay Peninsula).

1898. *Barbus dukai*, Boulenger, Ann. Mag. Nat. Hist., (6) XII, p. 201. (S. Shan States, Burma).

1913. *Barbus hexagonolepis*, Chaudhuri, Rec. Ind. Mus., VIII, p. 249.

1913. *Barbus hexastichus*, Chaudhuri (nec McClelland), Rec. Ind. Mus., VIII p. 249.

1916. *Lissochilus dukai*, Weber & Beaufort, Fish. Indo-Austral. Archipel., III, p. 168 (Sumatra).

1916. *Lissochilus sumatranus*, Weber & de Beaufort, Idid., p. 169, Figs. 68-69. (Sumatra).

1918. *Barbus dukai*, Annandale, Rec. Ind. Mus. XIV, p. 35, (S-Shan States Burma).

1921. *Barbus hexastichus*, Hora (nec McClelland), Rec. Ind. Mus., XXII, p. 186.

1923. *Barbus (Lissochilus) dukai*, Hora, Journ. Nat. Hist. Soc., Siam, VI, p. 155. (Siam).

1924. *Barbus hexastichus*, Hora (nec McClelland), Rec. Ind. Mus., XXVI, p. 27.

1929. *Barbus hexastichus*, Prasad and Mukerji, Rec. Ind. Mus., XXXI, p. 200, text-fig. 7. (Indawgyi Lake, Burma).

1934. *Lissochilus hutchinsoni*, Fowler, ibid., p. 120, Figs. 76, 77 (Siam).

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1935. *Barbus hexagonolepis*, Hora and Mukerji, Rec. Ind. Mus. XXXVII, p. 389.

1936. *Barbus hexagonolepis*, Hora, Rec. Ind. Mus., XXXVIII, p. 330.

1936. *Lissochilus dukai*, Suvatti, Index Fish. Siam, p. 55. (Siam).

1936. *Lissochilus hutchinsoni*, Suvatti, ibid., p.55. (Siam).

1937. *Lissochilus tweediei*, Herre and Myers, Bull. Raffles, Mus. Singapore, No. 13, p. 61, pl. V. (Perak, F. M. S.).

1937. *Lissochilus dukai*, Fowler, Proc. Acad. Nat. Sci. Philadelphia, LXXXIX, p. 188. (Siam).

1937. *Barbus hexagonolepis*, Hora, Rec. Ind. Mus., XXXIX, p. 334.

1937. *Barbus* (*Lissochilus*) dukai, Shaw and Shebbeare, Journ. Roy. Asiat, Soc. Bengal, Science, III, p. 37. pl. V, Fig. 6,text-fig. 33.

1938. *Lissochilus dukai*, Fowler, Fisheries Bull., No. 1, p. 66. (Malaya Peninsula).

1940. *Lissochilus hendersoni*, Herre, Bull. Raffles, Mus. Singapore, No. 16, p. 10, pl. IV.

1959. *Acrossocheilus hexagonolepis*, Misra, Rec. Indian Mus. Vol. 57, pp. 148-149.

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Appendix 2

Mean monthly maximum depth of the Indrasarobar Reservoir from June 1981 to December 1989.

Month	1981	1982	1983	1984	1985	1986	1987	1988	1989
Jan	-	86.84	75.53	96.63	92.63	96.84	103.00	90.10	78.55
Feb	-	81.31	72.89	94.74	90.63	98.00	98.00	84.04	72.96
Mar	-	79.47	67.89	92.11	88.42	86.84	93.00	78.19	66.22
Apr	-	68.95	61.05	89.47	85.79	86.00	86.00	71.14	59.28
May	-	47.36	62.11	80.00	83.95	76.32	82.00	63.53	53.38
Jun	19.47	40.79	54.21	75.26	84.21	73.16	78.00	60.69	50.84
Jul	41.58	48.95	66.31	80.00	87.89	94.00	67.00	65.50	59.58
Aug	58.95	60.00	81.05	88.95	90.00	96.00	86.00	74.00	72.66
Sep	77.37	74.21	91.05	94.74	98.42	103.00	93.66	84.00	73.94
Oct	87.63	82.10	97.89	95.26	99.75	105.00	96.89	89.00	75.97
Nov	88.42	82.63	100.00	96.31	100.00	105.00	98.33	84.00	72.25
Dec	88.42	82.10	100.00	96.31	100.00	105.00	95.24	82.15	71.50

Appendix 3

Mean monthly discharge of the Tadi River in $m^3\ sec^{-1}$ (1970-1986).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1970	6.08	4.68	3.95	3.15	4.66	31.0	114.0	161.0	84.5	47.9	27.9	15.9
1971	10.10	7.43	6.63	11.60	13.10	90.9	117.0	140.0	82.7	56.9	27.5	14.2
1972	9.43	8.57	7.34	6.70	6.10	20.5	111.0	118.0	120.0	45.6	30.7	14.2
1973	10.30	6.95	6.78	5.22	12.20	78.10	90.1	129.0	127.0	65.4	29.3	13.6
1974	8.75	5.31	3.57	3.81	5.68	24.90	93.8	163.0	139.0	61.6	30.5	18.8
1975	13.70	11.0	5.55	5.73	6.79	35.10	120.0	118.0	151.0	56.8	23.7	14.5
1976	10.90	8.43	5.17	6.16	17.30	46.40	77.2	113.0	103.0	47.1	24.7	12.5
1977	8.49	6.74	4.82	7.97	9.73	20.60	104.0	151.0	66.7	32.3	16.7	10.2
1978	7.41	5.57	5.37	5.77	11.40	59.30	171.0	200.0	90.7	53.8	22.0	12.5
1979	8.35	7.32	4.11	4.72	4.00	14.20	78.0	130.0	67.1	28.6	18.7	14.8
1980	10.50	8.26	7.34	6.10	7.65	38.30	120.0	157.0	66.5	27.5	15.2	9.86
1981	7.78	6.03	4.21	6.81	9.01	20.80	89.7	116.0	63.7	21.6	14.9	9.87
1982	7.45	7.10	5.54	5.49	4.67	16.00	71.0	88.6	57.1	21.4	15.6	10.3
1983	7.93	6.15	5.18	5.74	9.67	11.30	80.8	94.6	57.1	21.4	15.6	10.3
1984	12.1	8.53	5.51	6.09	12.30	30.90	104.0	103.0	98.1	27.6	17.1	11.6
1985	9.07	7.18	4.56	4.38	6.24	21.40	104.0	152.0	142.0	55.6	23.9	13.2
1986	9.20	6.52	4.04	5.32	7.16	40.00	99.3	83.0	-	55.6	23.9	13.2

Appendix 4

Fitting of the von Bertalanffy growth model

Mathematical estimation of growth parameters. As described in Ch. 4, a mathematical regression analysis was used to fit the von Bertalanffy growth curve to the observed growth data for the four separate groups of fish. The results of this analysis are summarised in Tables 1 and 2. Table 1 gives values of a, b and L_∞, and their errors. Since ultimate size L_∞ is obtained from a and b through a nonlinear equation (Eq. 3 in Ch. 4), it is difficult to estimate the errors in L_∞ from the errors in a and b. Therefore, 95 % confidence intervals for L_∞ have been constructed in a non-standard way. The following method has been used.

Let $\min L_\infty = [a - S.E.(a)]/\{1-[b - S.E.(b)]\}$

$\max L_\infty = [a + S.E.(a)]/\{1-[b + S.E.(b)]\}$

Intuitively, min L_∞ is the smallest value L_∞ can obtain when a and b deviate by 1 standard error. Max L_∞ is defined analogously. The intervals listed in Table 10 are of the form [minL_∞, maxL_∞].

Table 1. Results of regression analysis between L(t+1) and L(t).

Population	Sample size	Parameter (with S.E)	Estimate of L_∞ (with 95 % CL)
River male	4	a = 4.660 (0.5168)	L_∞ = 26.32
		b = 0.823 (0.0407)	[19.03, 37.98]
River female	5	a = 5.150 (0.3314)	L_∞ = 44.78
		b = 0.885 (0.0202)	[35.64, 57.82]
Reservoir male	4	a = 5.270 (0.9409)	L_∞ = 41.17
		b = 0.872 (0.0642)	[22.52, 97.35]
Reservoir female	8	a = 5.840 (0.8636)	L_∞ = 73.00
		b = 0.920 (0.0370)	[42.53, 155.90]

Table 2 shows the values of K and t_0 calculated from these values of L_∞ and the regressions of Eq. 4 (Ch. 4).

Table 2. Results of regression analysis between $\log_e(L_\infty - L(t))$ and t.

Population	Parameters (with S.E.'s)	Estimate of K (with S.E.'s)	Estimate of t_o
River ♂	intercept= 3.10(0.52)	0.195(0.04)	0.8749
	slope = -0.195(0.040)		
River ♀	intercept= 3.72(0.004)	0.12(0.001)	0.6818
	slope = -0.12(0.001)		
Reservoir ♂	intercept 3.63(0.014)	0.135(0.005)	0.6500
	slope -0.13(0.005)		
Reservoir ♀	intercept 4.28 (0.008)	0.089(0.001)	0.1174
	slope 0.089(0.001)		

The regression lines, $\log_e(L_\infty - L(t))$ on t, for all four populations were compared by looking at estimates of their intercepts, and differences between K and t_o values among the populations were assessed. The results are given in Table 3. It is clear from Tables 2 and 3 that the reservoir females appear to grow to a larger final size at a slower rate, and

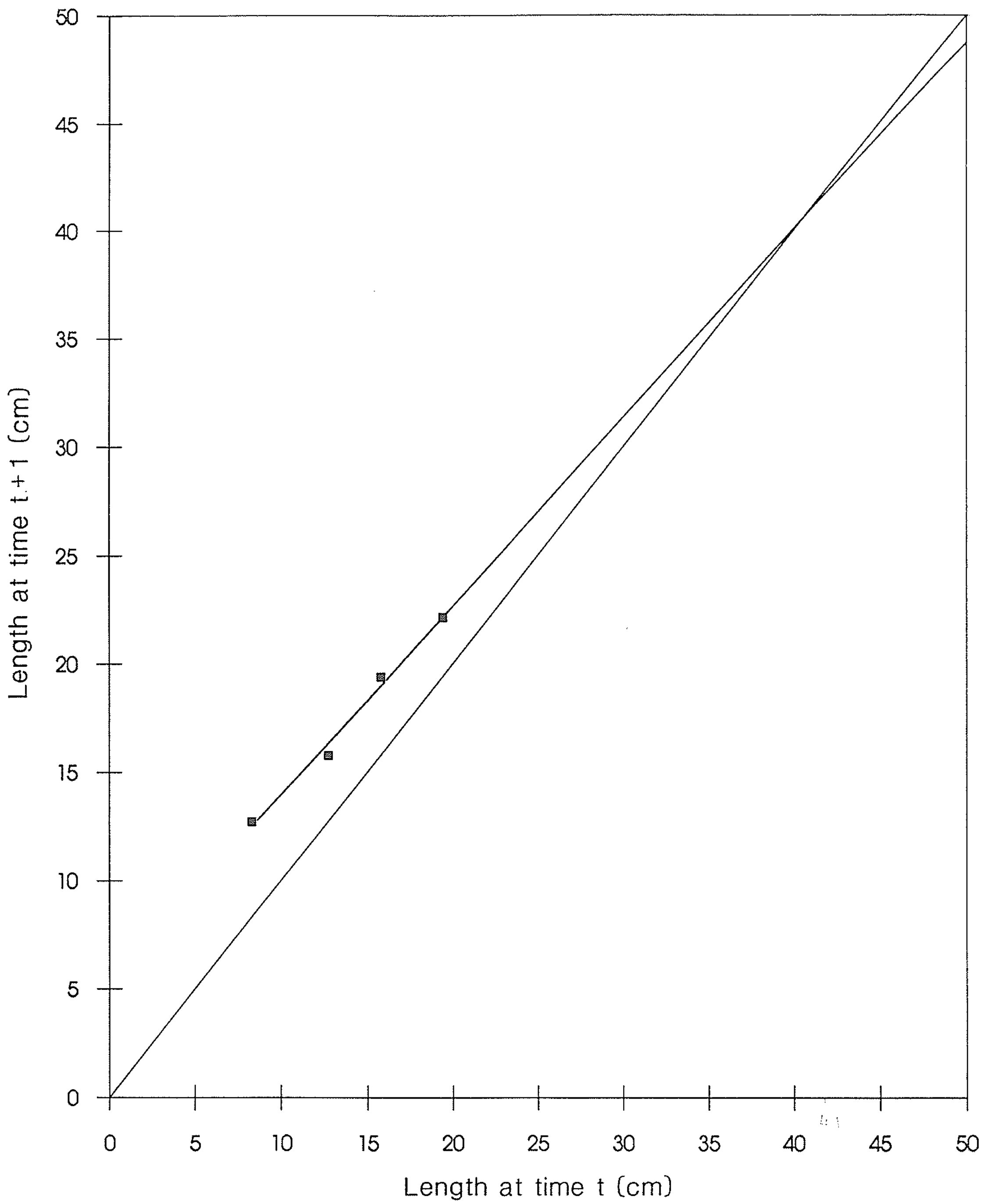
Table 3. Level of significance on the differences in intercepts and slopes of regression lines for von Bertalanffy growth model between sexes and populations. (Ns = non-significant and * = P < 0.05).

Pair of populations	Parameter	S.E. for difference	t statics	Conclusion
River ♂ vs ♀	intercept	0.516	1.199	Ns
	slope	0.040	1.841	Ns
Res. ♂ vs ♀	intercept	0.017	37.985	*
	slope	0.005	7.989	*
River ♂ vs	intercept	0.517	1.025	Ns
Res. ♂	slope	0.041	1.461	Ns
River ♀ vs	intercept	0.009	56.598	*
Res. ♀	slope	0.002	12.829	*

L_∞ and K values for this group are significantly different from the others ($p < 0.05$). The difference may be attributed to the availability of more food and space in the reservoir. The L_∞ and K values in all other groups did not differ significantly among themselves ($p > 0.05$).

Graphical estimation of growth parameters. The parameters of the von Bertalanffy growth curve were also estimated by using a geometrical interpretation of the pattern of growth in length developed by Ford (1933) and Walford (1945). The formula on which the graphic method of Ford and Walford was based assumed that the successive increments added to length yearly decrease in magnitude in geometric progression until a limiting value of total length (ultimate length) is approached. Ford-Walford plots of lengths at age (t) against lengths at age (t + 1) for female and male katle from the reservoir and the river gave straight-line relationships (Fig. A:1, A:3, A:5 and A:7). The lines were fitted by the least squares method. The point on the x axis where this line cuts the 45° diagonal from the origin yielded L_∞. The values of K and t_0 were then estimated by plotting $\log_e (L_\infty - L(t))$ against age t (Fig. A:2, A:4, A:6 and A:8). This plot yielded a straight line with slope of -K and intercept a on the ordinate, equal to $(\log L_\infty + Kt_0)$, so $t_0 = (a - \log L_\infty)/ K$. Thus the various parameters of the von Bertalanffy equation for katle from the reservoir and the river were calculated. The values of L_∞, K and t_0 obtained by the graphic method are given in Table 4:9 (Ch. 4).

Figure A:1. Ford-Walford plot of L(t) against L(t+1) for male katle from the Indrasarobar Reservoir.



50
45
40
35
30
25
20
15
10
5
0
Length at time t+1 (cm)
0
5
10
15
20
25
30
35
40
45
50
Length at time t (cm)

Figure A:2. Log_e (L_∞ - L(t)) plotted against t to determine t_0 and K for male katle from the Indrasarobar Reservoir.

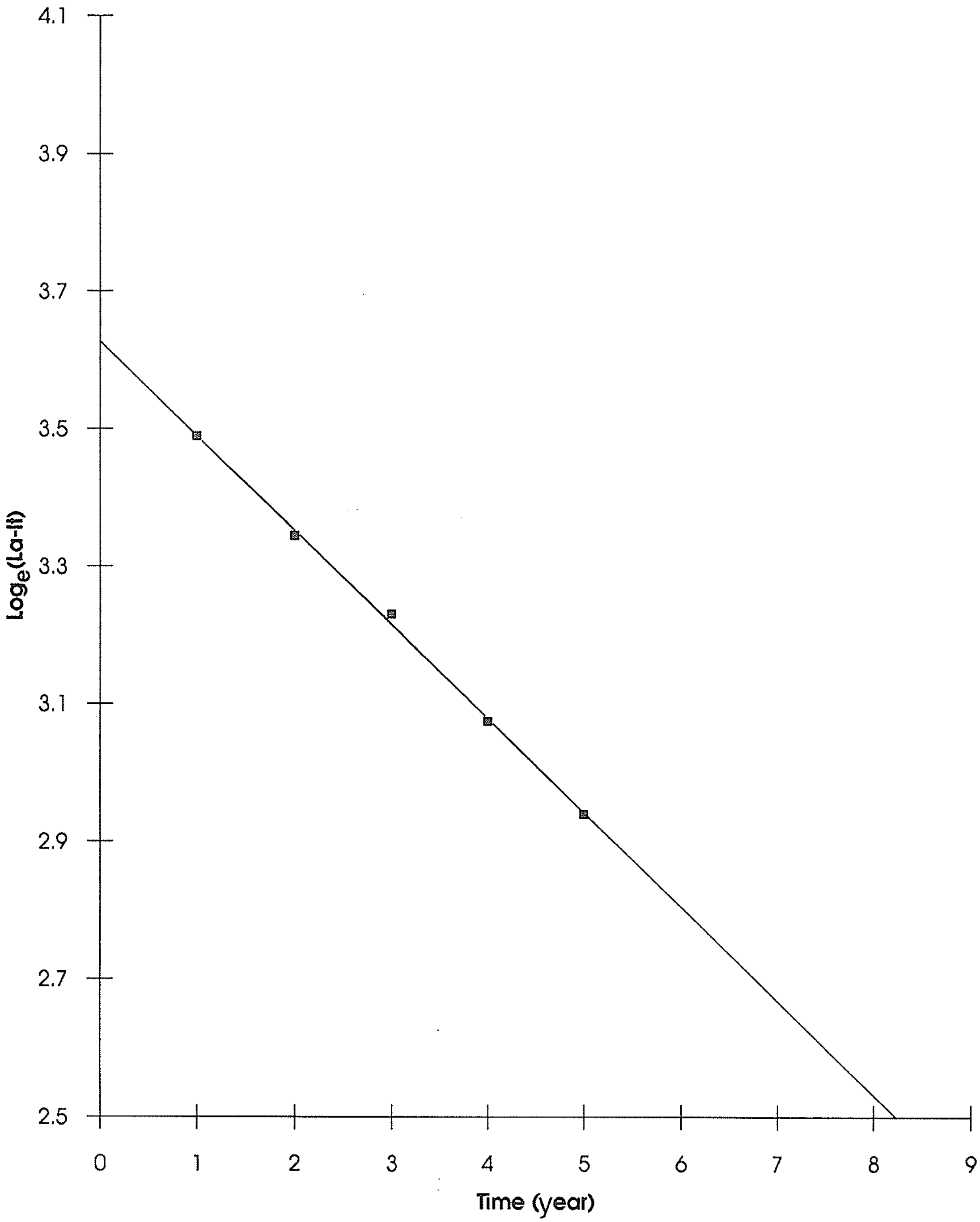
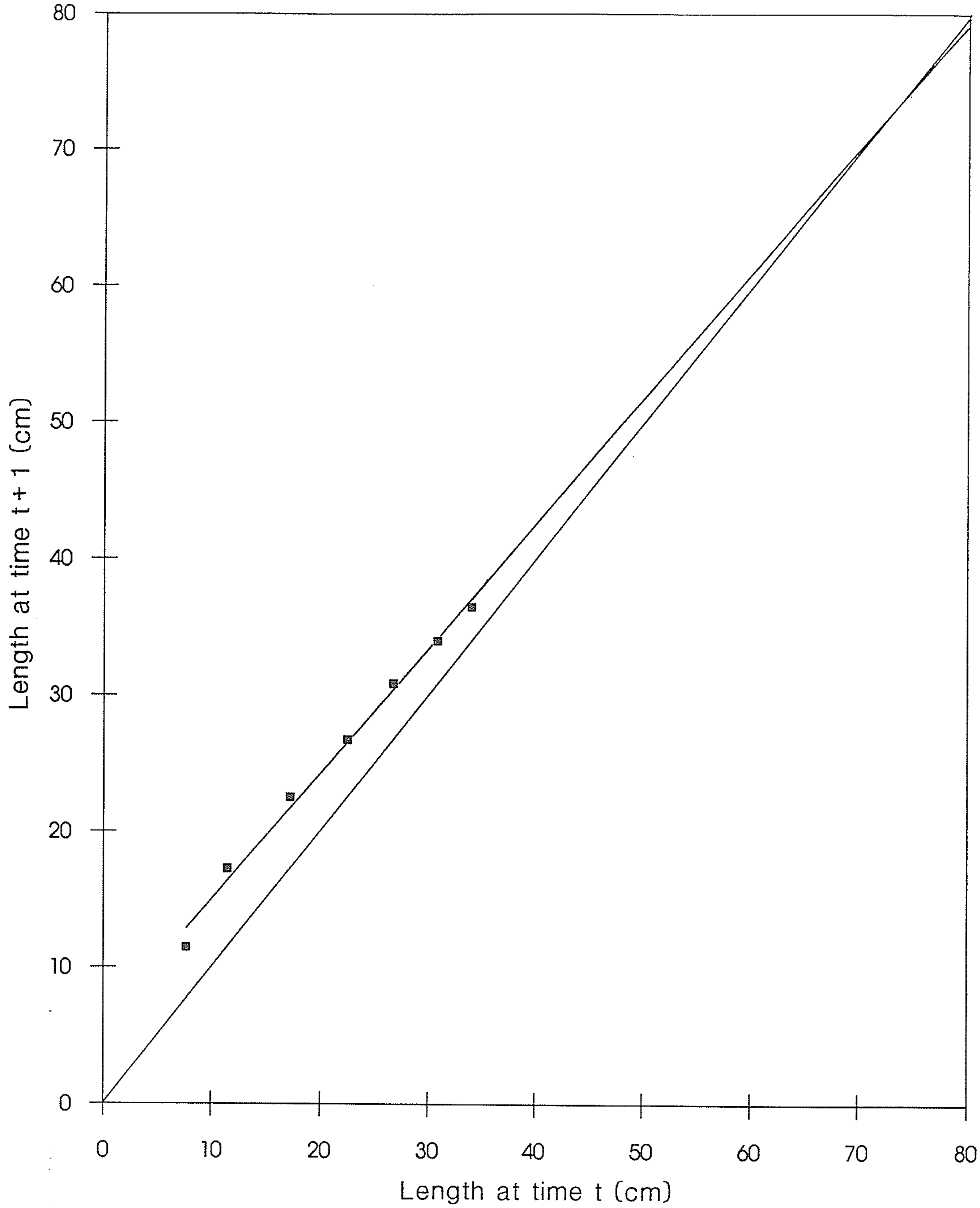
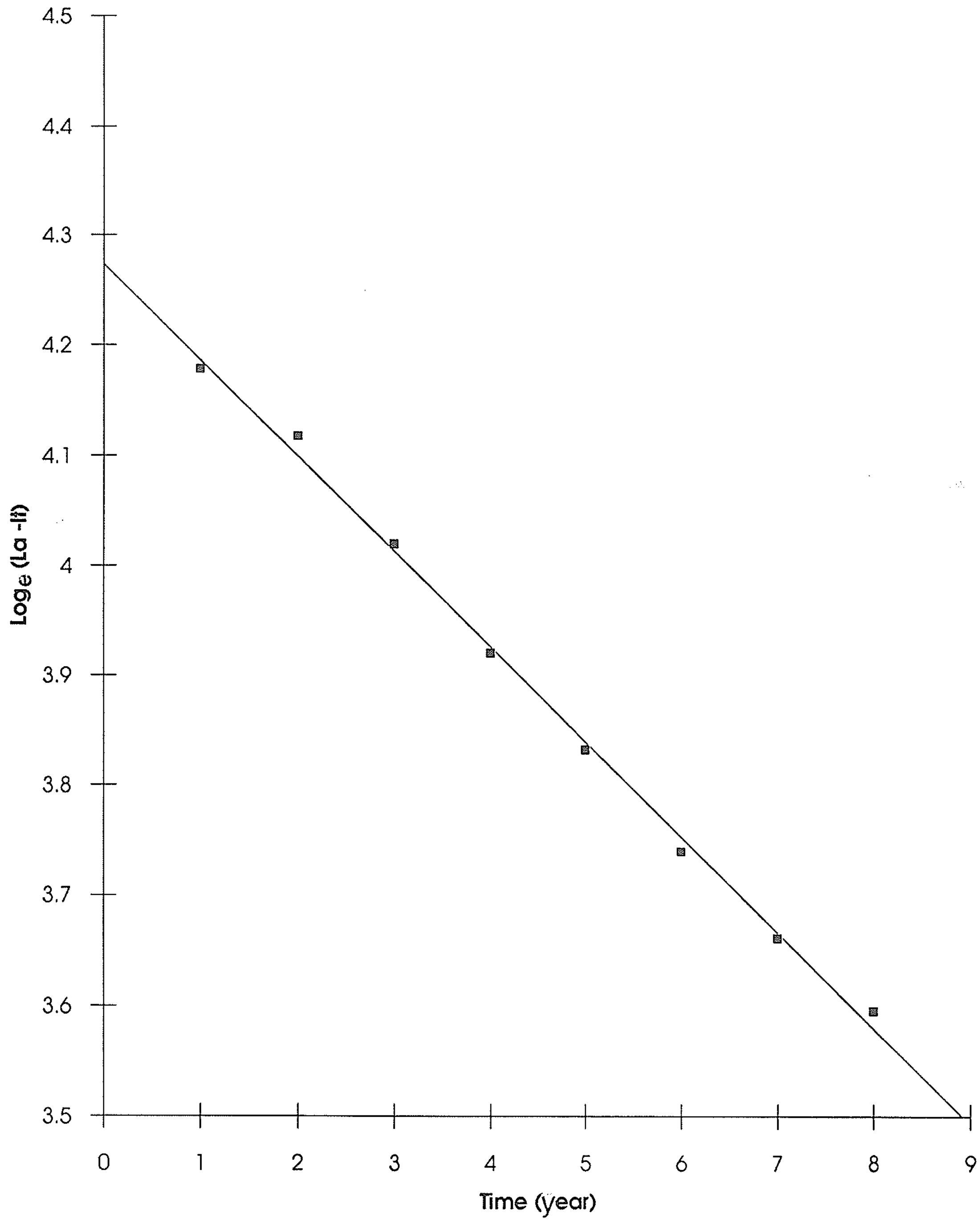

4.1
3.9
3.7
3.5
3.3
3.1
2.9
2.7
2.5
Log$_e$(La-lt)
0
1
2
3
4
5
6
7
8
9
Time (year)

Figure A:3. Ford-Walford plot of L(t) against L(t+1) for female katle from the Indrasarobar Reservoir.



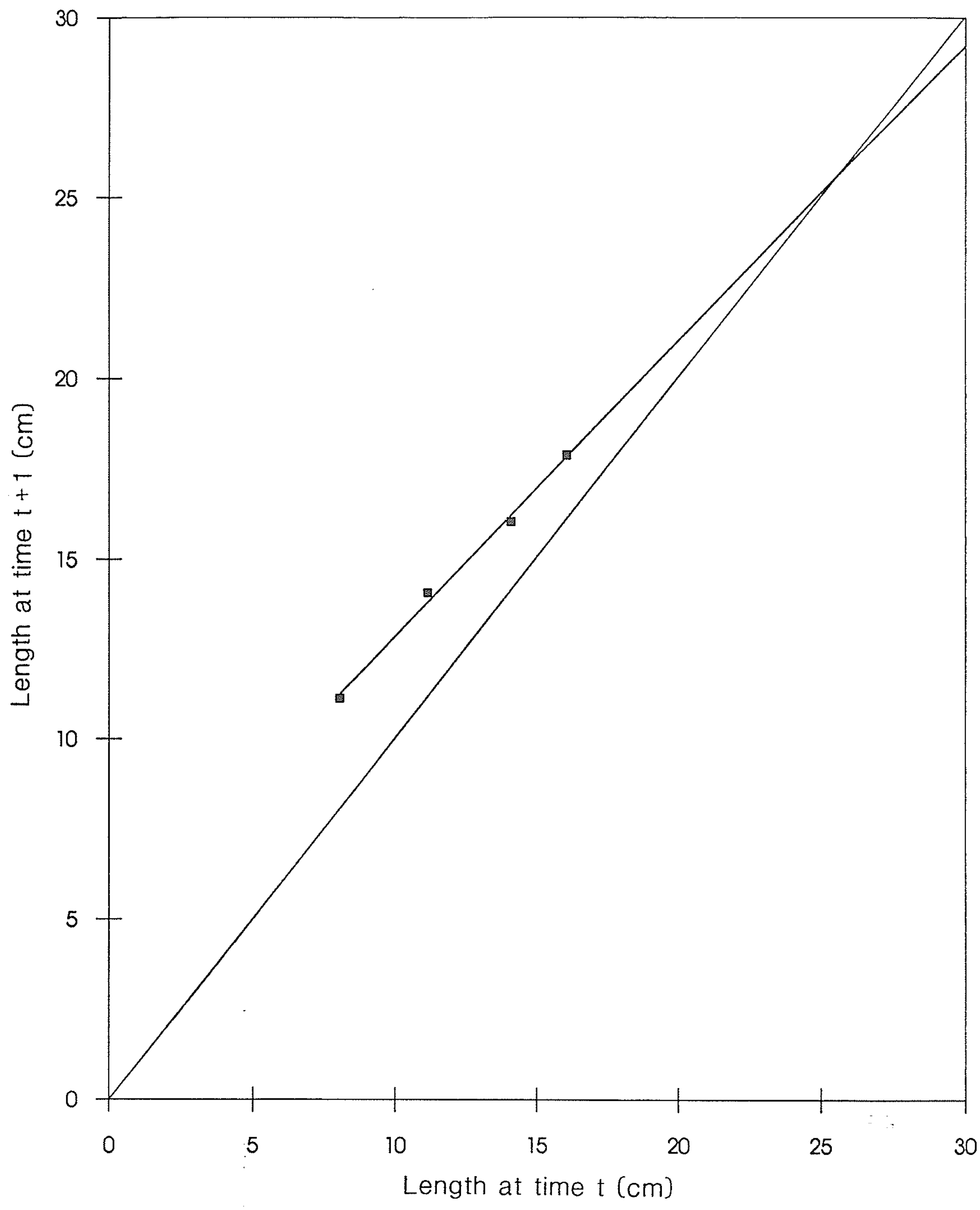
Length at time t + 1 (cm)
0
10
20
30
40
50
60
70
80
0
10
20
30
40
50
60
70
80
Length at time t (cm)

Figure A:4. Log_e $(L_\infty - L(t))$ plotted against t to determine t_o and K for female katle from the Indrasarobar reservoir.



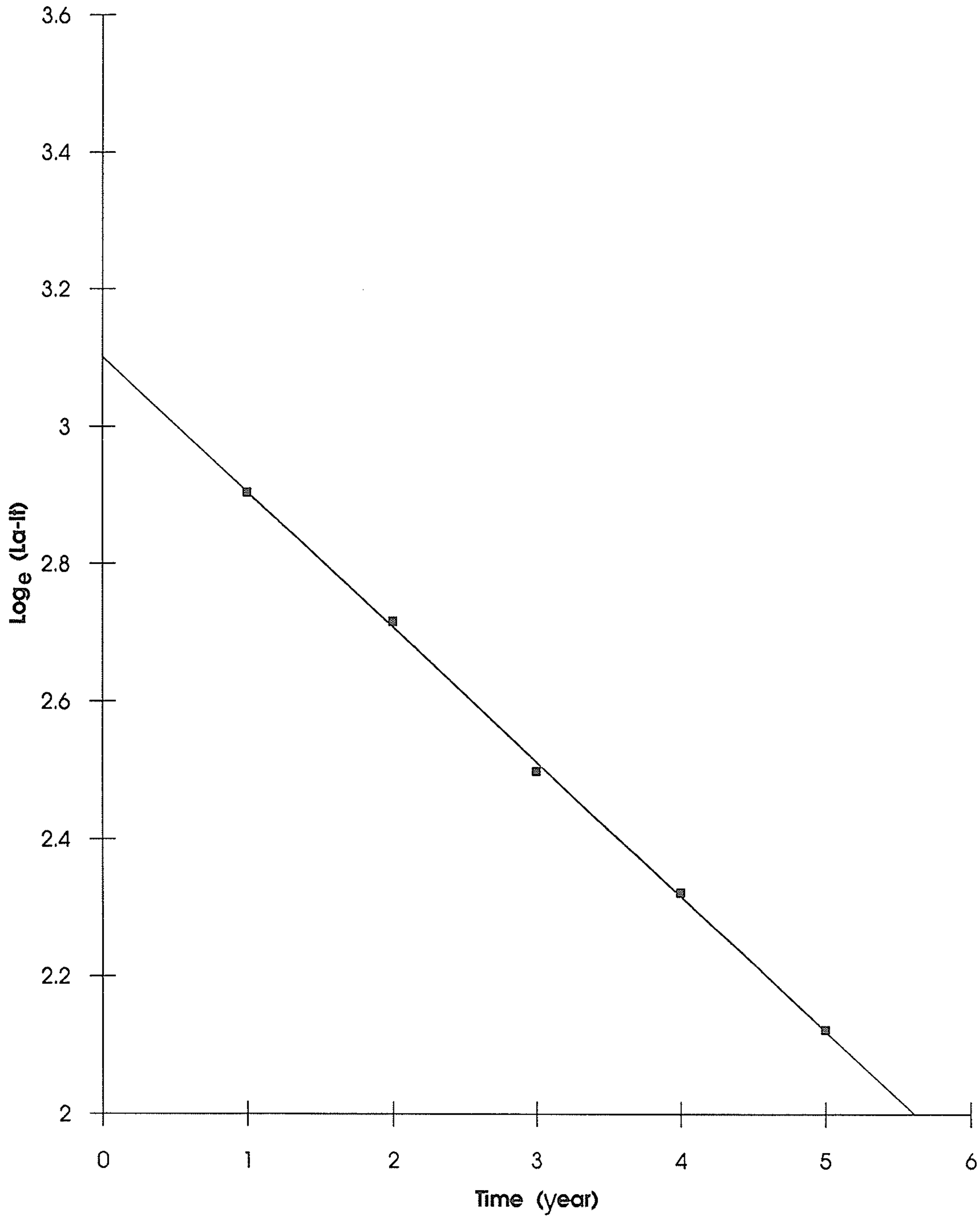
4.5
4.4
4.3
4.2
4.1
4
3.9
3.8
3.7
3.6
3.5
Loge (La -lt)
0
1
2
3
4
5
6
7
8
9
Time (year)

Figure A:5. Ford-Walford plot of L(t) against L(t+1) for male katle from the Tadi River.



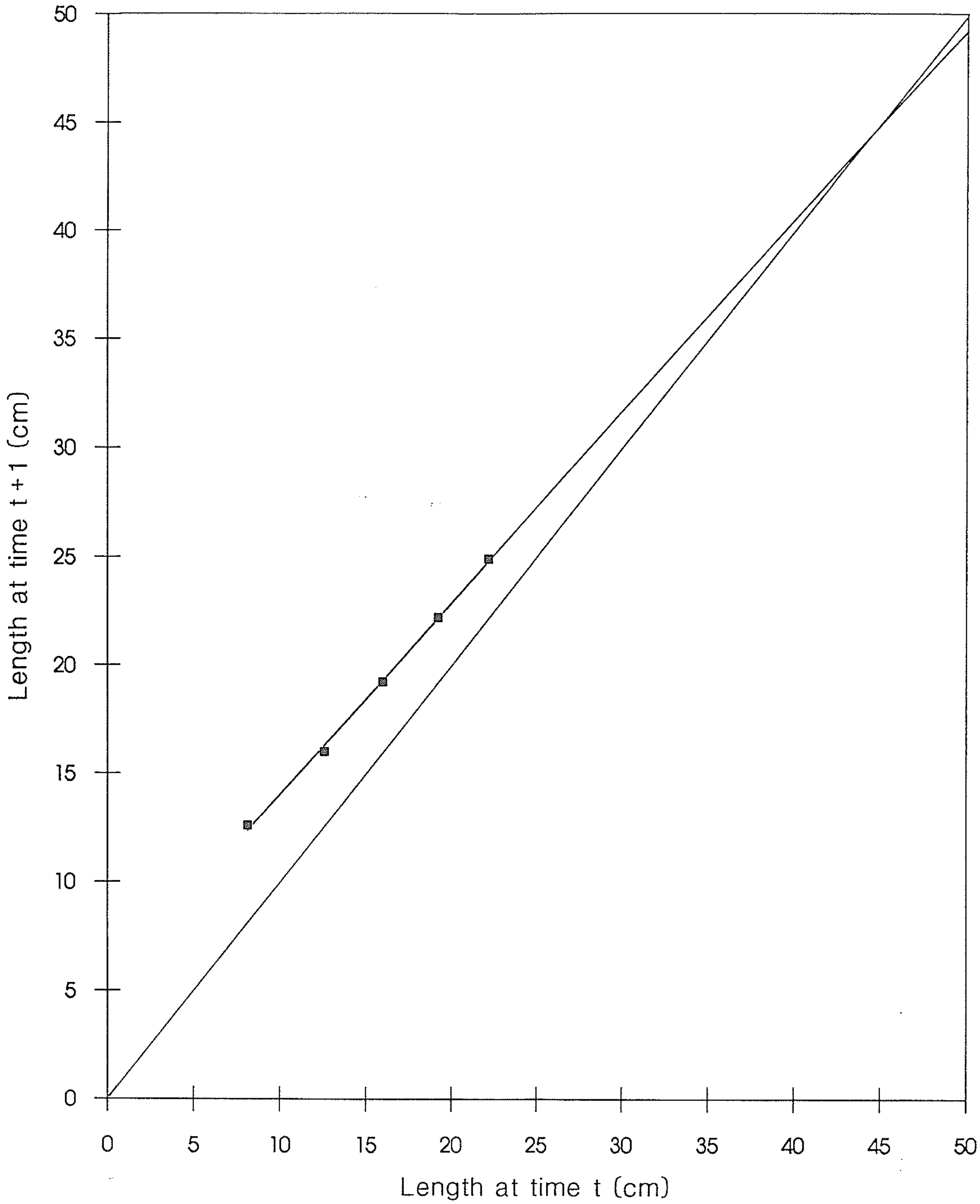
30
25
20
15
10
5
0
Length at time t+1 (cm)
0
5
10
15
20
25
30
Length at time t (cm)

Figure A:6. $\mathrm{Log}_e\ (L_\infty - L(t))$ plotted against t to determine t_o and K for male katle from the Tadi River.



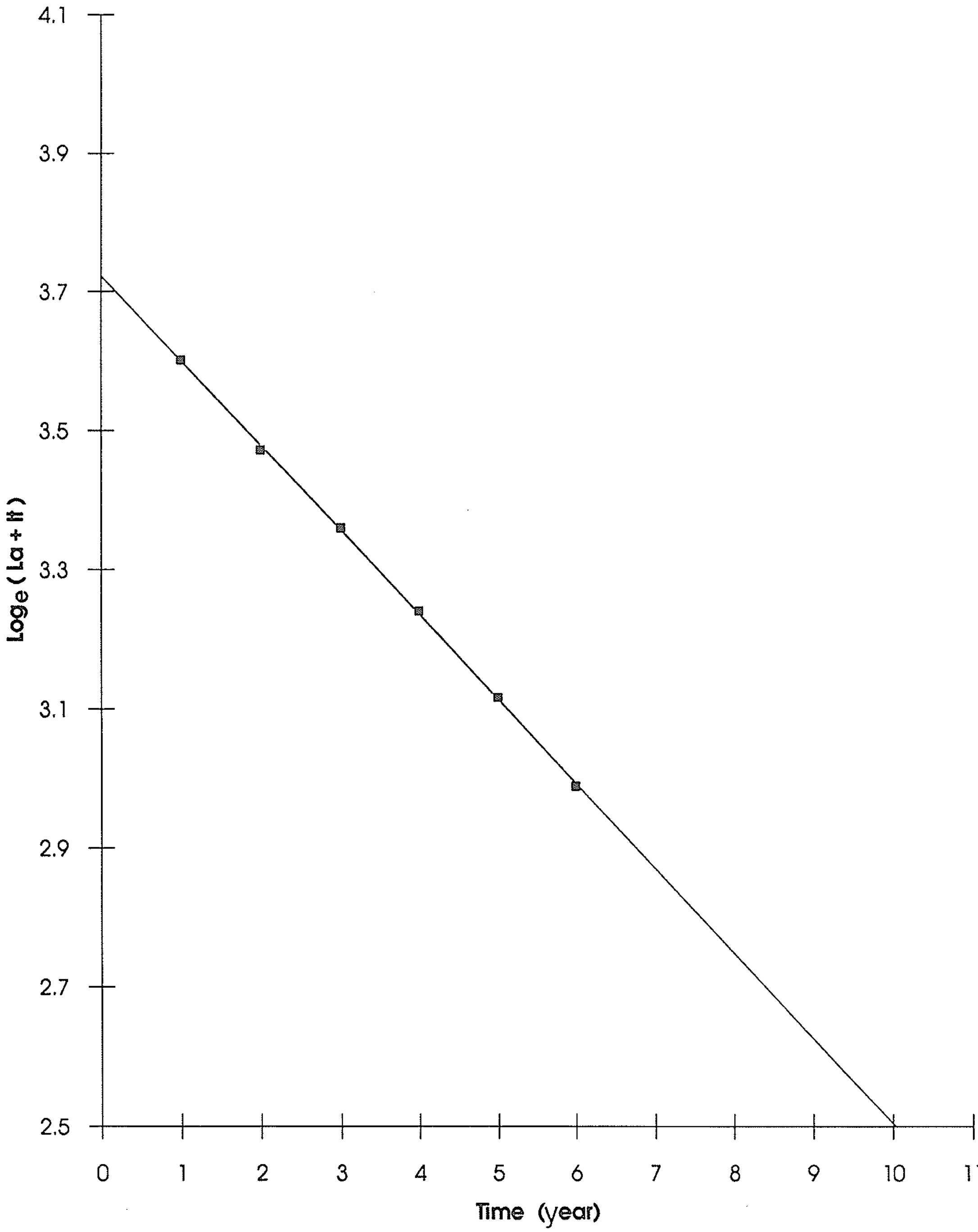
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
2
Log_e (La-li)
0
1
2
3
4
5
6
Time (year)

Figure A:7. Ford-Walford plot of L(t) against L(t+1) for female katle from the Tadi River.



Length at time t+1 (cm)
Length at time t (cm)
0
5
10
15
20
25
30
35
40
45
50

Figure A:8. $\log_e (L_\infty - L(t))$ plotted against t to determine t_o and K for female katle from the Tadi River.


4.1
3.9
3.7
3.5
3.3
3.1
2.9
2.7
2.5
Loge (La + lt)
0
1
2
3
4
5
6
7
8
9
10
11
Time (year)

Appendix 5

Effect of variation of surface area on annual length increment

Attempts were made to fit a regression model to explain the growth of fish as a function of both age and the surface area available during the growing season. Besides $\Delta L = a + b \log A$, the following models were looked at:

1. $$\Delta L = a + b \log X$$

where ΔL = annual total length increment of the fish, X = age of the fish and a and b are constants. It was evident from Tables 4:4 to 4:7 that length increment appeared to decline with age. Therefore, it was assumed that the logarithmic transformation of age would improve the fit. Even then, length increments did not describe the fit between these two variables to any great extent. The coefficient of determination did not show much improvement (Table 1).

2. $$\Delta L = a + b \log (A/X)$$

Here ΔL, X, a and b were defined as before, but A = average area of the reservoir. This model improved the relationship but seemed inadequate to explain the influence of age and average area of the reservoir on length increments of katle (Table 1).

3. $$\Delta L = a + b \log X + c \log (A/X)$$

Here ΔL, X, A, a and b were defined as before whereas c was an additional constant to be estimated. The extra explanatory variable (A/X) added to model (1) slightly improved the

Table 1. Summary of the regression analysis to assess the katle's growth dependence on age and the average area of the Indrasarobar Reservoir.

Model	Regression equation	r^2	P value	No.
1	$Y = 68.0 - 18.1 \log X$	0.43	0.000	53
2.	$Y = -23.5 + 19.15 \log(D/X)$	0.57	0.000	53
3	$Y = -34.6 + 2.66 \log X + 21.3 \log(D/X)$	0.58	0.000	53

relationship but not adequately to explain the influence of fish age and average area of the reservoir on length increments of katle. However, when the data were examined at separate ages (Table 4:10), it became clear that the combined data of model 3 hid considerable structure that existed at each age (Table 4:10) when considered separately. In Table 4:10, the age was controlled to see if there was any linear structure in the data. In fact Table 4:10 demonstrated a linear relationship between the total annual length increment and the average area of the reservoir in any given year. However, it was difficult to see any pattern from one age group to the next, and it was also difficult to determine what exactly was happening at each age. For instance fish at the ages of 7 and 8 displayed a strange tendency of growth acceleration for large values of average area. Perhaps this can be attributed to the high mortality of katle before they reach the age of 7 or more. Therefore, the few remaining fish might have the opportunity to grow quickly.

Appendix 6

Variability of three successive pectoral fin ray age determinations of katle from Indrasarobar.

First reader	Second reader	Third reader	Final Fin ray age
6	6	6	6
3	3	3	3
7	7	7	7
3	3	4	**3**
4	4	4	4
2	2	2	2
1	2	2	**2**
3	3	3	3
5	5	5	5
3	3	3	3
3	3	3	3
5	5	5	5
3	3	3	3
2	2	2	2
4	4	4	4
3	-	-	**rejected**
6	6	6	6
5	5	5	5
7	7	7	7
6	6	6	6
5	5	6	**5**
6	6	6	6
2	2	2	2
4	4	4	4
6	6	6	6
4	5	4	4
3	3	2	**3**
4	4	4	4
11	11	11	11
9	8	9	**9**

Note: bold and underlined data indicate assigned fin ray ages, which were agreed upon by two readers.

Appendix 7

Estimated values of log a for length-weight relationships of the reservoir katle at different stages of maturity throughout the year.

Month	Maturity stage	Total weight ♀	Total weight ♂	Somatic weight ♀	Somatic weight ♂
January	1	−2.03	-	−2.04	-
January	2	−2.06	−2.04	−2.04	−2.04
February	1	−2.04	−2.02	−2.04	−2.02
February	2	−2.04	−2.00	−2.52	−2.02
March	1	−2.01	−2.03	−2.02	−2.03
March	2	−2.02	−2.05	−2.06	−2.05
March	3	−2.03	−2.03	−2.04	−2.04
March	4	−2.01	-	−2.02	-
April	1	−2.05	−2.19	−2.06	−2.20
April	2	−2.05	−2.03	−2.06	−2.04
April	3	−2.07	−2.03	−2.07	−2.03
April	4	−2.02	−2.04	−2.03	−2.06
April	5	−1.93	-	−1.95	-
April	6	−2.07	-	−2.10	-
May	1	−2.02	-	−2.02	-
May	2	−2.06	−2.07	−2.06	−2.07
May	3	−2.05	-	−2.07	-
May	4	−2.06	-	−2.08	-
May	5	−2.05	-	−2.07	-
May	6	−2.00	-	−2.02	-
June	1	−2.10	-	−2.11	-
June	2	−2.09	−2.00	−2.11	−2.01
June	3	−2.09	−2.02	−2.11	−2.04
June	4	−2.08	-	−2.10	-
June	5	−2.04	-	−2.08	-
June	6	−2.04	-	−2.06	-
July	1	−2.07	−1.97	−2.08	−1.98
July	2	−2.09	−2.07	−2.09	−2.08
July	3	−2.17	−2.04	−2.18	−2.06
July	4	−2.12	−2.04	−2.14	−2.06
July	5	−2.08	-	−2.01	-
July	6	−1.99	-	−2.06	-
August	1	−2.00	−2.01	−2.01	−2.02
August	2	−2.03	−2.03	−2.04	−2.03
August	3	−2.03	−2.01	−2.04	−2.03
August	4	−2.04	−2.02	−2.06	−2.04
August	5	−2.03	−2.02	−2.55	−2.04
August	6	−2.04	-	−2.06	-
September	1	−1.98	−1.98	−1.98	−1.99
September	2	−2.04	−2.02	−2.04	−2.03
September	3	−2.04	−2.01	−2.05	−2.03

September	4	−2.03	−2.04	−2.05	−2.06
September	5	−2.03	−	−2.05	−
September	6	−2.01	−	−2.03	−
October	1	−2.01	−	−2.01	−
October	2	−2.03	−2.04	−2.03	−2.05
October	3	−2.03	−	−2.03	−
October	4	−2.04	−2.01	−2.05	−2.03
October	5	−2.06	−	−2.08	−
November	1	−2.03	−	−2.03	−
November	2	−2.04	−2.05	−2.03	−2.05
December	1	−2.03	−	−2.03	−
December	2	−2.04	−2.02	−2.04	−2.03

Appendix 8

Estimated values of log a for length-weight relationships of the riverine katle at different stages of maturity throughout the year.

Month	Maturity stage	Total weight ♀	Total weight ♂	Somatic weight ♀	Somatic weight ♂
January	1	−2.00	−1.95	−2.00	−1.96
January	2	−2.07	−2.00	−2.07	−2.00
February	1	−1.98	−1.99	−1.99	−2.00
February	2	−2.04	−	−2.04	−
March	1	−2.04	−2.03	−2.04	−2.04
March	2	−2.00	−2.10	−2.00	−2.10
March	3	−2.05	−2.03	−2.06	−2.04
March	4	−2.04	−2.05	−2.05	−2.07
March	5	−	−2.02	−	−2.04
April	1	−2.05	−2.09	−2.05	−2.94
April	2	−1.99	−2.09	−2.00	−2.09
April	3	−1.98	−2.07	−2.00	−2.08
April	4	−2.00	−2.15	−2.29	−2.17
April	5	−	−2.14	−	−2.16
May	1	−2.09	−2.05	−2.12	−2.05
May	2	−1.98	−2.08		
May	3	−2.02	−2.05	−2.03	−2.06
May	4	−2.03	−2.07	−2.06	−2.09
May	5	−	−2.01	−	−2.02
June	1	−1.99	−1.95	−1.99	−1.96
June	2	−1.99	−2.05	−1.99	−2.06
June	3	−1.98	−2.05	−1.99	−2.06
June	4	−1.92	−2.01	−1.94	−2.03
June	5	−	−2.05	−	−2.07
June	6	−	−2.05	−	−2.07
July	1	−2.10	−2.05	−2.11	−2.06
July	2	−2.04	−2.02	−2.06	−2.02
July	3	−2.08	−2.01	−2.08	−2.02
July	4	−1.99	−2.06	−2.01	−2.08
July	5	−1.96	−2.03	−2.00	−2.05
July	6	−	−2.06		−2.07
August	1	−2.08	−2.08	−2.07	−2.09
August	2	−2.05	−2.04	−2.05	−2.04
August	3	−2.01	−2.04	−2.02	−2.05
August	4	−2.03	−2.06	−2.05	−2.08
August	5	−2.02	−2.07	−2.05	−2.09
august	6	−	−2.06	−	−2.07
September	1	−2.09	−2.05	−2.09	−2.05
September	2	−2.02	−2.01	−2.02	−2.01
September	3	−2.03	−2.06	−2.03	−2.07
September	4	−2.01	−2.05	−2.02	−2.06
September	5	−2.01	−2.05	−2.07	−2.06
September	6	−2.04	−2.13	−2.06	−2.15

September 7	-	−2.02	-	−2.02
October 1	−2.04	−2.07	−2.04	−2.08
October 2	−2.01	−2.06	−2.01	−2.07
October 3	−2.00	−2.08	−2.01	−2.09
October 4	−2.07	−2.07	−2.01	−2.09
October 5	−1.96	−2.05	−1.99	−2.15
October 6	−2.09	−2.13	−2.12	-
October 7	−1.88	-	−1.88	-
November 1	−2.04	−1.99	−2.04	−1.99
November 2	−1.99	−2.00	−1.99	−2.00
December 1	−2.09	−2.05	−2.11	−2.05
December 2	−2.04	−2.06	−2.04	−2.06

Appendix 9

Total and somatic weight (± 95% CL) of the standard reservoir males at different stages of maturity (January -December)

Month	Stage	No.	Total weight g	Somatic weight g
January	2	8	98.87 ± 0.94	98.65 ± 0.94
February	1	3	66.09 ± 2.58	65.74 ± 2.59
February	2	6	103.73 ± 1.21	103.45 ± 1.15
March	1	2	64.55	64.21
March	2	14	96.36 ± 0.61	95.84 ± 0.61
March	3	6	101.26 ± 1.12	100.22 ± 1.12
April	1	2	65.14	64.55
April	2	6	99.92 ± 1.09	99.32 ± 1.10
April	3	5	100.92 ± 1.31	100.03 ± 1.31
April	4	5	97.75 ± 1.28	93.45 ± 1.18
May	2	4	91.28 ± 2.61	90.45 ± 2.61
June	2	3	107.00 ± 2.58	106.26 ± 2.57
June	3	4	102.95 ± 1.48	101.49 ± 1.48
July	1	2	72.72	72.45
July	2	13	90.04 ± 0.66	89.61 ± 0.66
July	3	5	97.82 ± 1.35	96.04 ± 1.35
July	4	14	97.96 ± 0.65	94.02 ± 0.65
July	5	5	90.09 ± 1.35	86.95 ± 1.35
August	1	4	66.60 ± 1.72	64.28 ± 1.75
August	2	12	101.26 ± 0.68	100.78 ± 0.68
August	3	10	105.14 ± 0.76	102.33 ± 0.76
August	4	11	102.23 ± 0.72	98.40 ± 0.72
August	5	6	102.85 ± 1.11	99.49 ± 1.11
September	1	2	70.88	70.38
September	2	6	102.09 ± 1.15	101.44 ± 1.15
September	3	4	105.13 ± 1.70	101.78 ± 1.70
September	4	3	99.04 ± 2.63	94.71 ± 2.62
October	2	6	97.54 ± 0.17	96.97 ± 1.67
October	4	4	98.09 ± 0.17	93.89 ± 0.17
November	2	4	96.12 ± 1.67	95.74 ± 1.67
December	2	10	102.12 ± 0.75	101.87 ± 0.75

Appendix 10

Total and somatic weight (± 95% CL) of the standard reservoir females at different stages of maturity (January - December).

Month	Stage	No	Total weight g	Somatic weight g
January	1	8	65.89 ± 1.00	65.59 ± 1.00
January	2	120	119.52 ± 0.20	119.02 ± 0.20
February	1	9	65.29 ± 0.88	65.28 ± 0.87
February	2	89	121.97 ± 0.23	121.97 ± 0.23
March	1	6	68.89 ± 1.14	68.57 ± 1.14
March	2	73	120.45 ± 0.25	119.68 ± 0.25
March	3	56	128.39 ± 0.30	126.10 ± 0.30
March	4	13	135.15 ± 0.67	129.81 ± 0.31
April	1	7	63.47 ± 0.99	62.88 ± 0.99
April	2	75	121.78 ± 0.26	121.04 ± 0.23
April	3	25	117.21 ± 0.48	115.48 ± 0.48
April	4	10	130.68 ± 0.76	126.65 ± 0.76
April	5	4	159.85 ± 2.29	150.36 ± 0.28
April	6	3	116.79 ± 2.67	108.88 ± 2.66
May	1	5	68.54 ± 1.40	68.13 ± 1.40
May	2	73	119.17 ± 0.26	118.37 ± 0.26
May	3	10	121.69 ± 0.81	120.24 ± 0.81
May	4	5	119.96 ± 1.39	118.30 ± 1.39
May	5	7	125.31 ± 1.05	118.88 ± 0.56
May	6	4	135.51 ± 1.88	130.07 ± 1.91
June	1	5	56.57 ± 1.41	56.30 ± 1.41
June	2	70	111.64 ± 0.26	110.82 ± 0.26
June	3	17	109.70 ± 0.61	108.36 ± 0.61
June	4	12	112.62 ± 0.71	109.57 ± 0.71
June	5	7	117.26 ± 1.01	10.82 ± 1.02
June	6	5	124.42 ± 1.45	118.65 ± 1.45
July	1	8	60.25 ± 1.02	59.82 ± 1.02
July	2	100	110.98 ± 0.25	110.24 ± 0.25
July	3	25	89.37 ± 0.57	87.50 ± 0.57
July	4	20	102.82 ± 0.63	99.56 ± 0.63
July	5	15	114.21 ± 0.71	108.43 ± 0.71
July	6	8	139.17 ± 0.92	131.12 ± 0.92
August	1	12	70.90 ± 0.68	70.20 ± 0.68
August	2	122	126.07 ± 0.20	124.22 ± 0.20
August	3	44	126.94 ± 0.32	124.22 ± 0.32
August	4	21	122.83 ± 0.49	118.30 ± 0.49
August	5	11	127.06 ± 0.73	120.64 ± 2.03
August	6	10	124.19 ± 0.86	118.23 ± 0.85
Sept.	1	11	74.50 ± 0.73	74.22 ± 0.73
Sept	2	58	124.98 ± 0.29	124.23 ± 0.29

Sept	3	16	123.69 ± 0.58	121.05 ± 0.57
Sept	4	13	126.47 ± 0.64	121.23 ± 0.64
Sept	5	6	129.69 ± 1.14	122.10 ± 1.14
Sept	6	2	133.17 ± 9.24	126.78 ± 9.23
October	1	9	69.60 ± 0.83	68.99 ± 0.84
October	2	60	128.24 ± 0.27	127.56 ± 0.27
October	3	13	129.22 ± 0.67	125.95 ± 0.67
October	4	10	125.20 ± 0.85	120.44 ± 1.35
October	5	10	118.27 ± 0.87	111.91 ± 0.87
October	6	5	125.81 ± 1.35	120.44 ± 1.35
November	1	5	66.52 ± 1.33	66.28 ± 1.33
November	2	71	125.11 ± 0.26	124.52 ± 0.26
December	1	6	67.64 ± 1.10	67.77 ± 1.10
December	2	75	126.15 ± 0.25	125.57 ± 0.25

Appendix 11

Total and somatic weight (± 95% CL) of the standard river males at different stages of maturity (January -December).

Month (g)	Stage	No	Total weight (g)	Somatic weight
January	1	7	14.46 ± 1.07	14.40 ± 1.07
January	2	9	42.99 ± 0.97	42.88 ± 0.97
February	1	6	15.48 ± 1.09	15.38 ± 1.09
February	2	9	42.95 ± 0.90	42.47 ± 0.90
March	1	8	14.34 ± 0.93	12.65 ± 0.92
March	2	14	38.12 ± 0.76	37.85 ± 0.76
March	3	7	44.84 ± 1.04	43.77 ± 1.04
March	4	7	42.04 ± 1.08	40.41 ± 1.08
March	5	4	45.44 ± 1.74	43.96 ± 1.73
April	1	4	12.69 ± 1.88	12.64 ± 1.88
April	2	10	38.75 ± 0.93	38.44 ± 0.93
April	3	5	40.72 ± 1.43	39.76 ± 1.43
April	4	6	33.61 ± 1.51	32.12 ± 1.50
April	5	4	34.52 ± 1.73	33.34 ± 1.74
May	1	4	13.98 ± 2.10	13.93 ± 2.10
May	2	8	39.24 ± 0.99	38.82 ± 0.99
May	3	6	42.89 ± 1.22	41.53 ± 1.23
May	4	5	40.70 ± 1.31	38.94 ± 1.30
May	5	7	47.29 ± 1.14	45.73 ± 1.15
June	1	4	17.36 ± 1.80	17.28 ± 1.89
June	2	7	42.36 ± 1.03	42.07 ± 1.03
June	3	6	42.91 ± 1.18	41.78 ± 1.18
June	4	5	46.62 ± 1.42	44.47 ± 1.42
June	5	10	42.40 ± 0.83	40.70 ± 0.83
June	6	5	42.33 ± 1.38	40.84 ± 1.38
July	1	4	13.80 ± 1.69	13.51 ± 1.67
July	2	9	45.85 ± 0.87	45.61 ± 0.87
July	3	4	47.41 ± 1.85	46.56 ± 1.85
July	4	4	42.06 ± 1.73	40.22 ± 1.72
July	5	7	44.75 ± 1.04	43.33 ± 1.04
July	6	6	41.63 ± 1.26	40.40 ± 1.26
August	1	3	12.85 ± 2.59	12.75 ± 2.58
August	2	9	44.07 ± 0.82	43.54 ± 0.82
August	3	6	43.59 ± 1.46	42.25 ± 1.46
August	4	4	41.21 ± 1.74	39.27 ± 1.74
August	5	5	40.73 ± 1.46	39.01 ± 1.46
August	6	3	41.93 ± 2.68	40.35 ± 2.69
September	1	5	13.77 ± 1.34	13.04 ± 1.48
September	2	14	41.21 ± 1.30	40.64 ± 1.30
September	3	7	35.59 ± 1.17	33.92 ± 1.17
September	4	8	41.23 ± 0.90	39.36 ± 0.90
September	5	8	42.58 ± 0.97	41.09 ± 0.97
September	6	9	42.36 ± 0.85	41.88 ± 0.85
September	7	3	45.99 ± 2.90	45.74 ± 2.90

October	1	5	13.16 ± 1.48	13.04 ± 1.48
October	2	6	41.21 ± 1.30	40.64 ± 1.30
October	3	5	39.75 ± 1.36	38.77 ± 1.36
October	4	5	40.92 ± 1.42	39.71 ± 1.42
October	5	4	42.12 ± 1.63	40.41 ± 1.65
October	6	2	35.46 ± 0.00	33.44 ± 0.00
November	1	7	16.07 ± 1.02	15.99 ± 1.02
November	2	12	48.01 ± 0.74	47.74 ± 0.74
December	1	8	13.89 ± 0.94	13.82 ± 0.94
December	2	14	41.47 ± 0.69	41.25 ± 0.69

Appendix 12

Total and somatic weight (± 95% CL) of the standard length river females at different stages of maturity (January - December)

Month	Stage	No	Total weight g	Somatic weight g
January	1	5	21.44 ± 1.31	21.34 ± 1.31
January	2	13	76.76 ± 0.71	76.35 ± 0.71
February	1	7	22.59 ± 1.08	22.45 ± 1.08
February	2	14	82.13 ± 0.66	81.44 ± 0.66
March	1	5	19.53 ± 1.38	19.42 ± 1.38
March	2	16	89.50 ± 0.58	88.95 ± 0.58
March	3	5	80.06 ± 1.33	78.09 ± 1.33
March	4	4	82.63 ± 1.71	79.14 ± 1.70
April	1	8	19.01 ± 0.99	18.89 ± 1.99
April	2	17	91.05 ± 0.73	89.84 ± 0.73
April	3	6	92.81 ± 1.17	89.78 ± 1.17
April	4	3	89.87 ± 3.07	84.27 ± 3.05
May	1	2	17.04 ± 9.38	16.96 ± 9.39
May	2	7	94.27 ± 0.99	93.27 ± 0.99
May	3	4	85.05 ± 1.85	83.07 ± 1.85
May	4	3	83.10 ± 2.70	78.07 ± 2.73
June	1	7	21.91 ± 1.00	21.72 ± 0.99
June	2	15	90.63 ± 0.66	90.25 ± 0.66
June	3	6	93.10 ± 1.09	90.31 ± 1.10
June	4	4	83.10 ± 2.70	78.07 ± 2.73
July	1	4	16.83 ± 1.96	16.68 ± 1.95
July	2	15	82.58 ± 0.61	81.72 ± 0.61
July	3	4	75.36 ± 1.78	73.65 ± 1.78
July	4	5	91.05 ± 1.39	87.06 ± 1.42
July	5	4	97.08 ± 1.78	89.39 ± 1.79
August	1	4	18.21 ± 1.78	18.03 ± 1.78
August	2	10	79.67 ± 0.81	78.99 ± 0.81
August	3	7	87.98 ± 0.99	84.88 ± 0.99
August	4	6	84.70 ± 1.11	80.16 ± 1.11
August	5	5	85.59 ± 1.37	79.08 ± 1.37
September	1	6	17.18 ± 1.12	17.07 ± 1.12
September	2	20	86.34 ± 0.52	85.69 ± 0.52
Sepetmber	3	10	84.14 ± 3.14	82.61 ± 3.14
September	4	8	87.95 ± 0.92	85.00 ± 0.92
September	5	13	79.95 ± 0.68	74.88 ± 0.68
September	6	7	81.34 ± 1.00	77.37 ± 1.00
October	1	4	19.29 ± 1.41	19.29 ± 1.41
October	2	9	87.41 ± 0.82	83.94 ± 0.82
October	3	4	90.14 ± 1.75	85.18 ± 1.75
October	4	4	75.11 ± 1.84	68.97 ± 1.82
October	5	5	85.20 ± 1.40	76.40 ± 1.42
October	6	2	73.02 ± 00	66.67 ± 00
October	7	1	117.44 ± 00	113.81 ± 00
November	1	8	19.23 ± 0.90	19.12 ± 0.90

November	2	13	90.64 ± 0.69	90.25 ± 0.69
December	1	5	17.27 ± 1.49	17.16 ± 1.49
December	2	17	89.02 ± 0.58	87.71 ± 0.58