THE ECOLOGY OF THE ZANDER

Stizostedion lucioperca L.

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SUMMARY.

The study of the ecology of the zander (*Stizostedion lucioperca* L.) followed three lines of investigation, a literature review, field studies and laboratory studies. Information on the taxonomy, behaviour, physiology, reproduction, distribution and ecological impact was reviewed. Field studies investigated the selectivity of the methods used to obtain zander from Fenland and Midland zander habitats during the period 1978 to 1981. The growth characteristics of the major zander populations were demonstrated; the methods used for age determinations were validated. The feeding habits of the zander were determined from species, size and number of prey eaten; comparisons made with the available prey fish populations indicated that zander showed a preference for relatively small prey fish, but did not show any specific selection of particular species of prey. The maximum size of prey eaten was noted and the significance of the zanders method of swallowing prey considered. Marking provided information on the zanders movement and home range; movements were sometimes rapid and over considerable distances, but home ranges were considered to exist. Data from marking provided evidence of a change of zander population number and biomass in the Great Ouse Relief Channel from 1978 to 1980. Length-weight relationships and a study of the visceral fat content, showed that there existed considerable variations in condition between populations. Sexual development and reproduction was studied and related to other percids. Laboratory studies investigated the feeding behaviour of the zander. The rate of digestion of prey fish was determined. The conversion rate and maintenance requirement of the zander at 4 temperatures was determined and hypothetical examples used to confirm existing observations of zander food requirements.

KEY WORDS: Zander, Ecology, Growth, Feeding, Movement.

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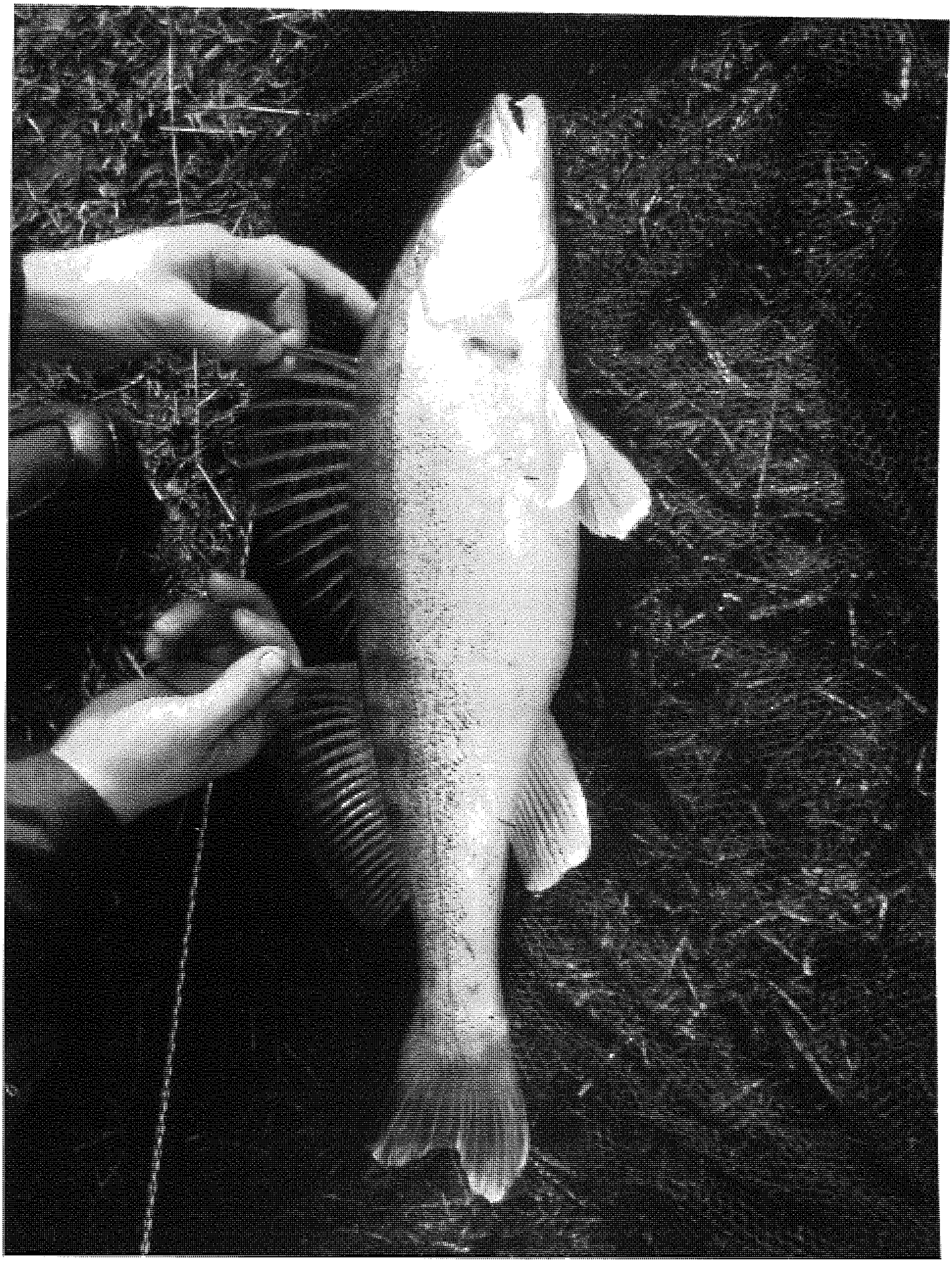


PART 1: INTRODUCTION

1.0. GENERAL INTRODUCTION

The natural freshwater fish fauna of the British Isles is extremely impoverished when compared with the variety found on the mainland of Europe (Maitland 1977). Much of this can be attributed to the last ice age, some 10,000 years ago. On the retreat of ice cover the fish fauna of Great Britain consisted partly of cold tolerant forms which were able to survive in the lakes and rivers associated with the ice cap, partly of marine fishes, and partly of fishes living in Southern Europe beyond the limit of the ice cap. With the rising of the sea level and the severing of the land bridge with mainland Europe, the opportunity for natural re-invasion with fish of the varied European fauna was removed.

The result of this was a very limited British freshwater fish fauna, becoming less diverse towards the North and West of the British Isles. It was not until recent times that man in his extensive travels started to add to our native fish species. Of the 215 freshwater fish species (Maitland 1977) listed for Europe, only 38 are indigenous to this country.

The fish associations left after the ice age could be considered as somewhat atypical of those of coldwater or temperature regions. This lack of diversity may have had repercussions on the stability of fish populations. The subsequent introductions of fish from the mainland of Europe, Asia and North America, in an indiscriminate manner would appear to be fraught with possible dramatic changes in the ecology of our native fish populations.

Fortunately the majority of introductions have been of fish species which are either outside of their natural range or at the limit of their natural tolerance. Therefore, only a few introduced fish species have been successful. One notable exception is the subject of this study, the zander or pike-perch (*Stizostedion lucioperca* L.).

1.1. THE ZANDER

1.1.1. TAXONOMY

Phylum Vertebrata.

Subphylum Craniata.

Superclass Gnathostomata.

Series Pisces.

Class Teleostomi.

Subclass Actinopterygii.

Order Perciformes.

Suborder Percoidei.

Family Percidae.

Sub Family Luciopercinae.

Tribe Luciopercini. (Jordan and Everman 1896).

Genus Stizostedion. (Rafinesque 1820).

Species Stizostedion lucioperca. (Linnaeus 1758).

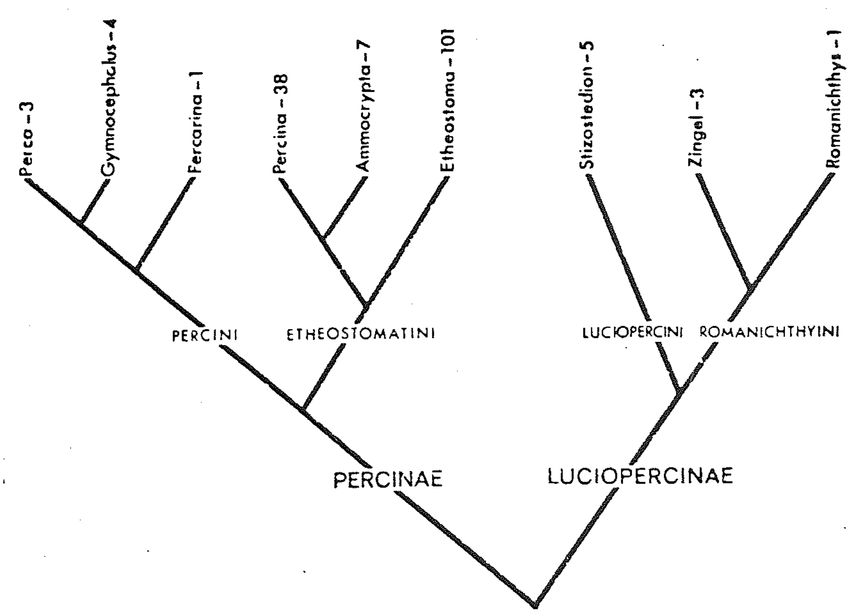


FIG. 1. Relationships of the subfamilies, tribes, and genera of the Percidae. Number of species indicated for each genus.

1.1.2. GENERAL DESCRIPTION OF THE FISH

The zander is the largest European member of the family Percidae, a family which comprises 163 known species (Sterba, 1962; Berg, 1949). A large benthic predator, the zander has a characteristic appearance and cannot be confused with any extant fish species found in Great Britain. (Plate 1).

The body is elongate and moderately compressed. The jaws have a wide gape and are powerful. In the adult, the upper jaw extends behind the vertical from the mid-eye. Canine teeth are usually present on the jaws and palatines, these fitting into sockets in the opposite member. The pre-opercular bone is posteriorly serrated, with spines directed forward and below. The operculum terminates in a small, posteriorly directed spine.

The brachiostegal rays number 7-8. The gill rakers are stubby tooth bearing nodules. The two dorsal fins are set close together, but do not touch. The first has spiney rays while the second has one to three spines, the rest being soft. The scales are numerous, small and ctenoid with a characteristic spine structure (Gunther 1859; Linfield and Rickards 1979).

The eye is large with a tapetum lucidium, (Wunder 1930, Moore 1944, Ali and Anctil 1968) consisting of a layer of light reflecting pigment. The effective area of the tapetum is somewhat less in the zander compared to the walleye, (*Stizostedion vitreum vitreum* Mitchill). This may be partly responsible for the two species differing behaviour. The lateral line is continued onto the caudal fin, with accessory lateral lines on the upper and lower caudal lobes.

Colour is variable, the back ranging from olive green, brown, grey or nearly black. Over this, on the back above the lateral line, thick bars of a diffuse transverse nature overlay the basic colour. These bars tend to be more apparent in younger fish. The flanks are silver or gold, merging with white on the underside. The first dorsal fin is greyish in colour with hints of yellow. This is overlaid by rows of black spots. The second dorsal is grey with black spots and the tail is grey with a white lower lobe. The remaining fins are an off white colour.

During the spawning season, (February to June depending on latitude) males are said to have a blueish colouration on the underside. The profile of the male's head is also said to be slightly concave, the female being more robust and the head less pointed.

1.1.3. REPRODUCTION AND GROWTH

The age at which zander reproduce for the first time depends on growth rate. Alm (1959) states that rapid growth leads to maturity 1-2 years earlier than in the case of slow growth. Maturity is reached earlier in areas such as Turkey (Aksiray 1961), Poland (Filuk 1962), and the Netherlands (Havinga 1945), all areas characterised by good zander growth. According to Tanasiychuk (1974) zander mature at 2-3 years in the Caspian Sea and 6-9 years in the Karelian lakes.

Spawning occurs between 8 and 15 degrees C^{o} and according to Deedler and Willemsen (1964) the female zander lays all her eggs simultaneously. Table 1 gives the fecundity of zander from various

Russian Rivers (Berg 1949).

TABLE 1: Fecundity of the Zander

Fecundity (eggs per kg fish)	Author
150,000*	Berg (1949)
230,000**	" "
107,000***	" "

* Data for S. lucioperca from the Don.

** Data for S. lucioperca from the delta of the Kuban.

*** Data for S. marina.

Reproduction therefore occurs only once per fish per season. Spawning occurs in couples in water at least three feet in depth, with a fairly hard sand or gravel bed. The male digs a nest of about its own length, the eggs being laid on aquatic roots laid bare by the nest building activities of the male (Huet 1970). Fertilization is external and Botsjarnikowa (1952) describes a spawning ritual during which the male initially circles the female for 20-25 minutes before both fish join together to swim around energetically making the water turbid. During this period of 10-15 minutes the eggs are laid. When the water becomes clear again the female has gone leaving the male to guard the eggs (Negonovskaya 1972).

In stillwaters spawning may occur at depths of up to 17 metres (Belyi 1962) though usually much shallower water is used. In rivers spawning is usually carried out in shallow sections (0.5 to 1.0 metres) near the banks with a current velocity of 0.1 to 0.2 metres per second. (Berg et al 1949, Botsjamikowa 1952, Belyi 1962).

Percentage fertilization is said to be high; 91 to 100%. The eggs are 1.0 to 1.5 mm in diameter, pale yellow in colouration and sticky, so that they adhere to the roots of the plants on which they are laid.

The incubation period of eggs depends on temperature and can be calculated as degree days. Woynarovich (1968) states that 110 degree days are necessary before hatching occurs. At a temperature of 10^{o}C, hatching takes place in 10-12 days. Although at a higher temperature they hatch at an earlier date, the larvae produced are smaller.

Havinga (1945) gave the relation of egg number to body size and age (Table 2), and concluded that relative fecundity (number of eggs per gram of body weight) increases with length. However Chugunova (1931) states that the relative fecundity of zander at 800 mm amounts to less than half of the younger females.

TABLE 2: Relation of egg number to body length and age (Havinga, 1945, quoted in paper by Deedler and Willemsen, 1964).

Age	Length mm	Weight gm	Egg No X 1000	Egg No per gm of zander
3	420	615	52	85
4	510	1150	200	174
5	560	1600	320	200
6	580	1770	400	226

Exogenous feeding of the larvae begins when the yolk sac and oil globule are used up. This occurs when the young zander are about 5-6 mm in length. The first food of the fry consists of eggs, larvae and juveniles of Copepoda or Rotifera, later the adult

Copepoda and Cladocera. After having reached 15 mm the fry also eat insect larvae, plankton, Chironomids and Ephemera (Huet 1972). If suitable prey fish are available the young zander will become piscivorous at 25-30 mm (Szalay 1973), or 40 mm (Huet 1972).

Poltavsuk (1969) notes that on an invertebrate diet only, young zander reach 60-70 mm and a weight of 4-13 gms during the first summer. Piscivorous feeding sees considerably faster growth with lengths of 140-210 mm and weights of 40-150 gms attained by the first autumn. The feeding requirements of the fry are only satisfied up to a certain size by invertebrates and above this, they must feed on small fish.

Woynarovich (1960) states that clear water is unsuitable for the survival of young zander although the reason for this is not specified. However the experiences of Tesch and Willemsen suggest that even in crystal clear water with plenty of food for the larvae, survival of the young can be high. This contradictory result could be explained in terms of a negative phototactic reaction of the larvae to strong (i.e. harmful) light, which means that the larvae stay in the shade of water plants in clear water. Presumably this is because of the light sensitive nature of the zander eye (Wunder 1936, Ali and Anctil 1968).

Biro (1977) noted on Lake Balaton that, during the 1st year, growth in length almost stopped after September, and virtually did not change from autumn to the following spring. Bodyweight during winter usually decreases. Environmental factors do not always favour the fry; underfeeding, high ~~colloid~~ suspended solid content of waters (presumably affecting respiration) and sudden temperature changes have a considerable influence. Kelso (1973) found that the energy content of walleye dropped from autumn to spring, increasing again in the summer. The warmer the summer the larger the size attained by the young zander and the better the chance of surviving to the next spring.

The development of scales has been studied by Biro (1970). Scales were first formed on the caudal peduncle at 20mm. The lateral key scales were formed at 40 mm (body length), 45 mm (total length). Priegal (1964) noted a similar manner of scale development for the walleye.

Opinions vary as to the longevity of the zander. Berg et al concerning Russian zander, (1949) states 15-16 years, while Boiko (1963) also working on Russian zander, and using cuts of anal fin rays, found zander to be as old as 17 years. Biro (1977) quotes the maximum age of zander from Lake Balaton to be 15 plus years. Tanasiychuk (1974) noted that the lifespan of the zander in the north was greater than in the south. This was connected with the retarded growth rate and late maturation. Thus the zander reaches an age of 24 years, a length of 1150 mm and a weight of 7 kg in Syamozero (Balagurova 1963), but an age of 8-9 years in the Volga-Caspian region (Kuz'min 1952). Chugunova (1931) records a 17 year old weighing 16 kg from the Ural Delta.

Popova and Sytina (1977) note that: "The growth rate of the zander is greater from the north to the south, and therefore southern populations are typified, relative to northern populations, by accelerated growth and maturation, and higher fecundity. However, these biological characteristics are not stable even within the same water and may alter in different years, depending on changing environmental conditions". The comparative growth rates of zander at different latitudes are summarised in Table 3, based on the results of Novokshonov, (1974).

TABLE 3: Comparative growth of zander at different lattitudes
Modified from Novokshonov (1974)

Northern Lat. 60N			Mid Lat. 50-60N		Southern Lat. 50N below	
Age	Len	Wt	Len	Wt	Len	Wt
1	120	38	120	31	180	73
2	160	99	240	231	310	392
3	220	176	320	488	390	754
4	260	260	410	864	450	1236
5	320	429	470	1401	510	2534
6	360	621	520	1832	570	2534
7	400	882	580	2472	640	3805
8	440	1204	620	3242		
9	480	1555	670	4386		
10	510	1916				
11	530	2024				
12	560	2500				
13	580	3488				
14	580	2720				

Male zander generally grow slower than females. Svardson and Molin (1968) note that in Lake Hjalmaren, males are shorter than females in four age groups out of five. Rizanov (1970) notes that in Lake Ladoga males grow initially faster than females up to 4 years, then the situation is reversed. Males would also appear to be less long lived than females. In Kremenchug reservoir during the years

1969-1977, the following percentage of males in spawning stock was noted.

TABLE 4: (Rizanov 1970)

	Age											
	3	4	5	6	7	8	9	10	11	12	13	No
Percentage of males	67	48	38	35	34	42	25	28	0	0	0	1169

Woynarovich (1959, 1968) states that the rate of growth is a function of the available quantity of food. He notes that zander do not develop well in muddy, shallow water (as is the case in Lake Balaton), because its natural habitat is deep water above a gravel and sand bottom.

Steffens (1960) gave some density relations for young fish. At 20,000 per hectare the average length was 77 mm, whereas at 1,800 per hectare the average length was 127 mm. He also noted that the development of zander fry halts if they do not start predatory life in the first summer. Specimens of similar age, but of different modes of food consumption may differ by as much as 100 mm in length. Neuhaus (1934) noted that in the Bay of Vistula, zander developed very well in those years when the principle food item, the smelt (Osmerus eperlanus L.), was numerous.

1.1.4. FEEDING

Popova and Sytina (1977) summarised the zander's predatory behaviour with the following statement: "The zander is an ambush pursuit predator that feeds at low light intensities or at night. It is always found with a complex of other species and becomes a fish predator within a few months of hatching. When zander become predatory, the main food is mature and young schooling fishes up to 200 mm long, which inhabit open water. Zander often eat large numbers of their own kind, when other food fish are scarce. This is a characteristic of most fish predators and is regarded by Nikolsky (1950, 1960) as an adaptation for a greater utilization of the food base in a water body".

The information concerning the feeding of adult zander is considerable, mainly derived from work carried out in Eastern Europe and the U.S.S.R. Feeding can be considered under five headings:

a). Species composition

b). Food size

c). Method of swallowing

d). Daily consumption

e). Rate of digestion.

a). Species composition

The diet of adult zander seems to reflect the availability of each species. However Deedler and Willemsen (1964) state that, where smelt are available, zander may show an ~~outspoken~~ marked preference, being as much as the whole of the zander's diet. Otherwise the zander's diet may comprise any small fish available.

Work by Domrachev and Proudin (1926) on Lake Ilmen showed that zander feed mainly on smelt and ruffe (*Gymnocephalus cernua L.*). In the Sea of Asov, tyulka (*Clupeonella delicatula* Nordmann 1840), *Percarina* Sp., and *Benthophilus* sp. (a type of goby) are eaten. The Aral zander (Berg et al 1949) consume Aral roach (*Rutilus rutilus* sp.), common bream (*Abramis brama L.*), chekhon

(Pelecus cultratus L.) and other fish not exceeding 90-100 mm.

Milkulski (1964) states that zander eat whatever is available and increase in number with the increase in number of the food species. The type of fish in the zander's diet, depends considerably on the distribution and accessibility of the food.

Ivanova (1968), working on Rybinsk Reservoir, found that the zander's diet varied considerably. She found that zander fed most heavily during the summer-fall season.

At the beginning of the summer most of the predators stayed near the bottom, remaining scattered. Feeding was heaviest during the hours of darkness from 9 pm to 3 am. The distribution of the smelt affected the feeding of the zander. When the smaller smelt were distributed in the surface layers at night and the larger smelt deeper, the zander preyed on the larger ones. When the majority of smelt moved to the surface layers, the zander schooled to feed on the smelt. Schooling lasted about 2 hours, feeding from 6 to 9 pm and 12 to 3 am. When the smelt remained in the surface layers all the time the zander fed more extensively on ruffe (Gymnocephalus ceruna L.) and perch (Perca fluviatilis L.).

The water conditions also affect the zander's feeding. In low water years zander fed most heavily in spring on spawning roach and in summer on young perch. In high water years the main feeding occurred in spring on smelt and roach. In the autumn ruffe and young perch were eaten.

Pihu and Pihu (1974) working on the Pskov-Chudskoy Lakes, waters with similar fish compositions to Rybinsk found that, in all seasons, the main food was smelt. Zander occasionally resorted to eating ruffe and young perch. Further north, in the Karelian Lakes, vendace (Coregonus lavaretus L.) become more important.

Szypula (1964) working on the zander of north Polish lakes stated that the diet of zander (mature) was exclusively fish. He noted that they fed on fish species of little economic value. It therefore has great importance in the regulation of fish population composition, feeding on the competitors of economically important species. He states that the food most numerous in the zander's diet were in order, ruffe and perch. By weight the order was roach, ruffe and silver bream (Blicca bjoerkna L.). The total weight of the perch was low because the zander were eating small perch.

b). Food size

Popova and Sytina (1977) state that zander feed mainly on immature individuals, (ruffe, perch and young Cyprinids). When a prey species is abundant, adults are also eaten (Caspian roach, smelt, vendace and gobiids). These adults are usually the smallest slow growing fish, the sick, and specimens weakened after spawning, mostly males.

As the predator grows, certain food items are replaced by other larger food items. As the width of the mouth and the stomach size increases as the fish grows, the range of available prey increases, but the average length of prey changes only slightly. Zander prefer fish of 80 to 120 mm long (Popova and Sytina 1977). These prey are easiest to catch and are more rapidly digested and assimilated.

c). Method of swallowing

Pihu (1970) working on Lake Peipsi-Pskov examined the stomachs of 544 zander. She noted that: "The zander, a pelagic predatory fish, is a typical pursuer and, as a rule, swallows its prey tail first. Larger prey can, however, be swallowed head first only".

d). Daily consumption

Popova and Sytina (1977), noted that the daily ration of the zander during the most intensive feeding period (spring and early summer), constitutes 4.5 to 5.5% of the body weight and decreases to 0.5% during periods of less intensive feeding (winter). The annual ration is 200 to 250% of it's body weight. About 60% of the annual ration is consumed during spring, 15% during summer, 22% during autumn, 3% during winter. Their studies were carried out on the lakes, reservoirs and rivers of the U.S.S.R.

Steffens (1960) recorded the daily consumption of zander with regard to number consumed and found that the number decreased with increase in body length. Fortunatova and Popova (1973) came to the same conclusion. A 1-2 year old zander consumed as much as 264% of its body weight in a year, whereas a 3-4 year old fish consumed 224% and 5-6 year old 157%.

The wet weight conversion rate for zander of the Volga delta is 19.6% (i.e. 19.6 grams of zander produced from 100 grams of prey), while for pike the conversion rate is 11.4%. Fortunatova and Popova (1973) did not specify any differences in conversion for size (summary only available in English).

Salanki and Ponyi (1973), using Winberg's (1956, 1961) formulae for the relationship between food consumption, respiration (metabolism) and production, state that the consumed food is transformed into fish body with significant loss:

64% for respiration.

15-16% for flesh and gonads.

1.56% for reproduction.

e). Rate of digestion

Rate of digestion is temperature dependent. Molnar and Tolg (1961) fed zander of 250-300 mm on bleak (80-100 mm). They noted the following times to complete digestion:

TEMP C	5	10	15	20	23
TIME Hrs.	257	157	83	45	34

Popova and Sytina (1977) gave a table of digestion times for prey in zander stomachs (size unspecified).

TABLE 5: Rate of Prey Digestion by Zander

Water Temperature	Days (complete digestion)
Over 25 C	1
18-25	2
8-18	3
4-8	4
2-4	7
0.1-2.0	9

1.1.5. ENVIRONMENTAL PHYSIOLOGY

The zander can tolerate a considerable temperature range, but prefers warm rather than cool water. Temperatures allowing optimum growth range from 28C to 30C (Marshall 1977). The upper incipient lethal temperature is 35°C (Hokanson 1977).

The zander has a high oxygen requirement, 4.5 mg/l (temperature unspecified) being recorded as the lower limit of the optimum zone for adults and as the lethal limit for both embryos and fry (Kutznetzova 1955). The respiratory surface of the gills was measured by Byczkowska-Smyk (1960) and reported as being 18 cm^2/kg (compared to 5.3 cm^2/kg in the loach and 9 cm^2/kg in the eel).

Privolnev (1964) gives a maximum salinity tolerance of 12‰ for Russian zander. According to Deedler and Willemsen (1964) zander which wander into brackish water of 12-29‰ invariably die. In the Baltic Sea zander live with no apparent ill effect in water of 6‰ salinity (Neuhaus, 1934).

Auditory sensitivity was studied by Wolff (1969) and the frequency range (up to 200 cps) correlates well with the observations of intraspecific and interspecific aggression signals noted during the spawning season by Protasov et al (1965).

1.2. NATURAL DISTRIBUTION AND INTRODUCTION TO ENGLAND

Until the 16th century, the zander's distribution was limited to eastern and central Europe (Deedler and Willemsen, 1964). There it remains one of the most important commercial fishes (Berg, 1965). Since the 16th century, (particularly during the 19th century) numerous transplantations of zander have been made. Once in western Europe the zander extended its range considerably, by means of canals and other connecting water-courses. Further dissemination of zander has come about by the action of anglers and official bodies.

By the end of the 19th century the valleys of the Elbe and the Upper Danube formed the western limit (Armengaud 1962), the northern limit reaching to the middle of Scandinavia. By the 20th century the colonisation had reached western Europe, including all of the French valleys. Afterwards the zander increased its range beyond the edges of Europe. Introductions of zander have been documented by several authors: Denmark (Dahl 1962), Holland (Willemsen 1969), France (Goubier 1975) and Turkey (Aksiray 1961).

The first recorded English introduction was in January 1878, when the 9th Duke of Bedford released 23 zander, each of about 1 kg (Sachs 1878). These were placed in two lakes on the Woburn estates. These specimens originated from Bothkamper lake, Schleswig-Holstein. In 1910 another less well documented introduction was made.

After 1910 the zander appears to have become well established at Woburn. There then followed a number of subsequent introductions from Woburn to local waters. Populations were established in a number of stillwaters including Claydon lakes near Steeple Claydon.

All subsequent introductions of zander are believed to have derived from the original Woburn stock. However it must be noted that during 1960 a shipment of 500 Swedish zander were released into a small lake at Mepal in Cambridgeshire. These fish have bred and young zander have been seen (present author). It is thought that these fish have remained isolated from other zander populations since their introduction.

The recent rapid colonisation of river systems has occurred since the introduction of zander to an open ended watercourse. In 1960 mature zander were taken from Woburn to stockponds of the then Great Ouse River Authority. The stockponds were at Hengrave Hall near Bury St. Edmunds, Suffolk, and the zander placed in them bred successfully. When the lake was netted in 1963, 100 small zander, believed to be nearly one and two years of age (Cawkwell, pers, comms.) were obtained. Subsequently 97 of these fish were released in March 1963 into the Great Ouse Relief Channel at Stowbridge.

During the years after 1963, the zander quickly established itself in many new habitats by either natural movement or transplantations by anglers.

1.3. SPREAD OF THE ZANDER

All records of the spread of the zander are based on the first recorded and confirmed capture of a zander, usually by angling. In some cases zander may have been present in a particular water some time before the first recorded capture.

The listing of the first recorded capture dates in chronological order illustrates the rate and possible manner of colonisation. Information concerning the spread of the zander is presented in Table 6, mainly derived from Cawkwell and McAngus (1976). Figure 2 shows the extent of colonsation of the Fenland waters. Figure 3 shows the known area of colonisation of waters in the Coventry area.

TABLE 6: Date of First Recorded Capture of Zander and Location (adapted from Cawkwell and McAngus 1976)

Year	Captured at
1963	Introduction to Relief Channel
1965	First captures from Relief Channel
1966	Captures from tidal River Ouse
1967	Captures from Hundred Foot River Welney
1968	Captures from Great Ouse, Ten Mile Bank
1969	Captures from Great Ouse, Earith
1969	Captures from Great Ouse, Brownshill Staunch
1969	Captures from Great Ouse, Littleport
1969	Captures from Great Ouse, Ely
1969	Captures from River Wissey, Stoke Ferry
1969	Captures from Little Ouse, Brandon Bank
1969	Captures from River Lark, Prickwillow
1969	Captures from River Cam, Dimmocks Cote
1969	Captures from River Delph, Welmore
1969	Captures from Old Bedford River, Cock Fen
1970	Captures from Great Ouse, St. Ives
1970	Captures from Great Ouse, Huntingdon
1970	Captures from Roswell Pits, Ely
1970	Captures from Old West River
1970	Captures from Middle Level Drain, St. Germans
1972	Captures from Great Ouse, St. Neots
1972	Captures from Forty Foot Drain
1973	Captures from Great Ouse, Eaton Socon
1973	Captures from Sixteen Foot Drain
1973	Captures from Pophams Eau
1975	Captures from Old River Nene
1975	Captures from Twenty Foot River
1979	Captures from King's Dyke, Whittlesea

Figure 2.

Fenland Zander Waters

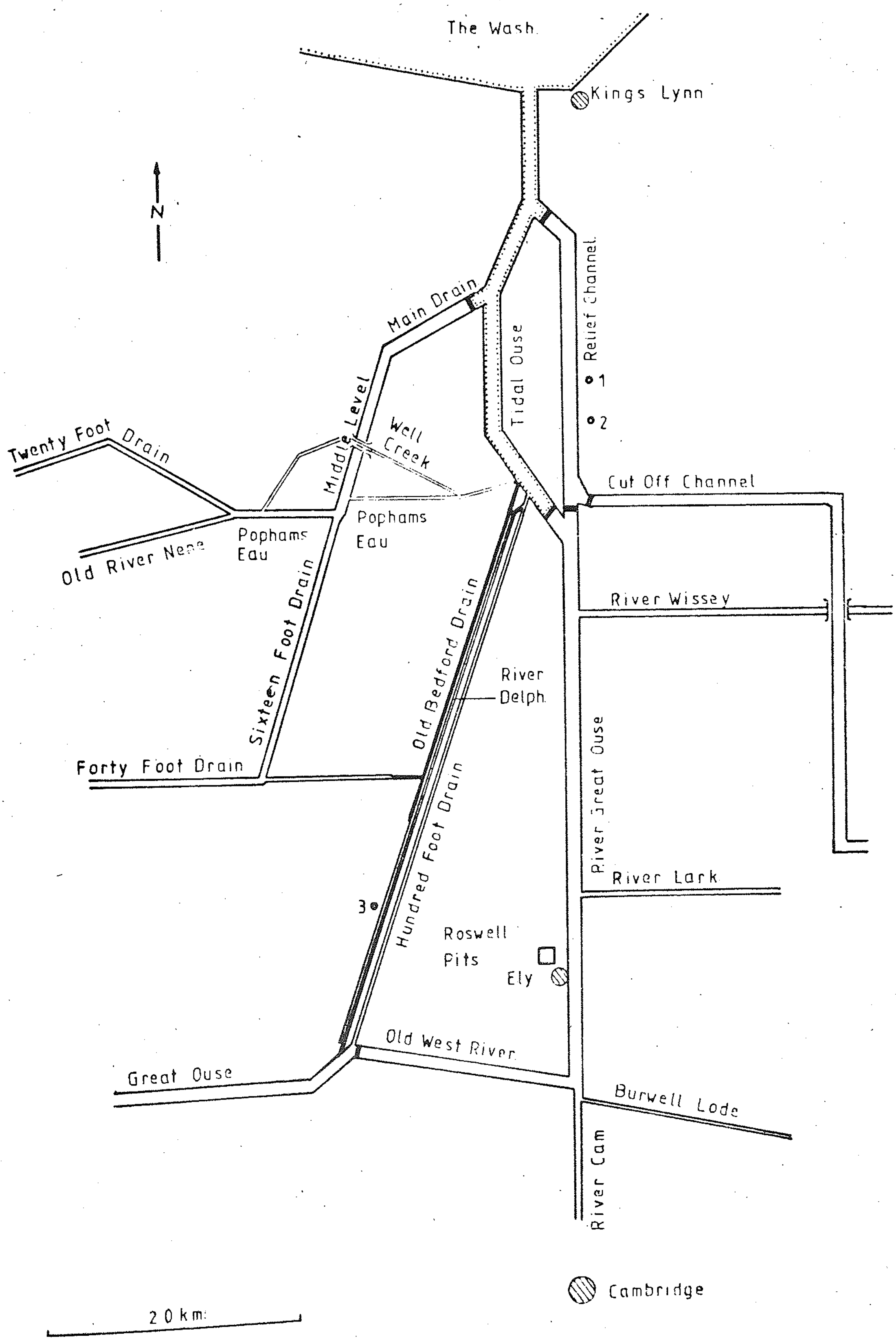
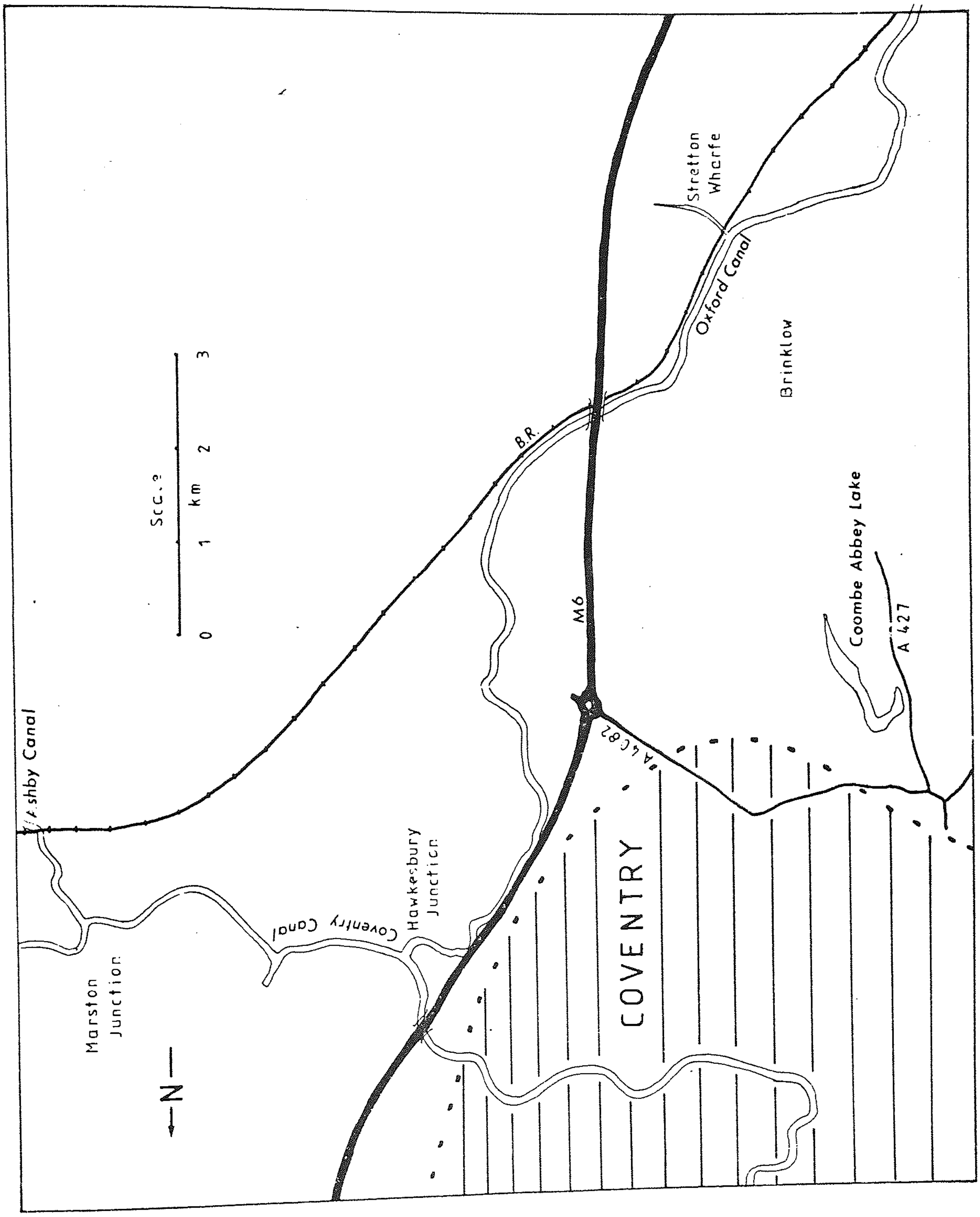


Figure 3.

Midland Canal and Lake Habitats of the Zander.



Further populations of zander have been noted:

In 1968 a zander of 0.65 kg was captured by angling from a small gravel pit at Watlington, Norfolk. The fish was thought to be one of several transferred from the nearby Relief Channel. The gravel pit has since been backfilled and any zander present destroyed.

In 1974 zander were noted in the Suffolk Stour. They are thought to have arrived there via the pipeline which connects the Cut-Off Channel with the Stour. From the Stour zander have been carried to Abberton Reservoir, with first reports noted in 1979 and confirmed in 1980 (Anglers Mail 1980).

In 1975 a dead zander of 3.2 kg was found after a fish kill at a gravel pit near Stowbridge, near to the Relief Channel. Zander were thought to have been introduced to the water in 1971 (present author).

In 1975 a breeding stock of zander were discovered and destroyed in a lake at Maxey near Peterborough. Age determinations suggested that these fish were stocked in 1973.

Also in 1975, zander were obtained from a lake at Woburn by a Mr. G. Rowles. These were placed into Old Bury Hill Lake near Dorking, Surrey. A breeding stock has since been established with the largest reported weighing in excess of 6 kg.

During 1976 a substantial number of young of the year zander were captured by anglers from Coombe Abbey Lake, near Coventry. These were subsequently found to be the offspring of 14 zander to 3 kg illegally transferred from Norfolk in 1973 and 1974.

Also in 1976 zander were noted in the Coventry and Oxford Canal near Coventry. Age determinations and the available information suggest that these zander were stocked in 1973 and originated from the Fenland waters. During 1979 zander were noted in the Ashby Canal, an arm of the same canal system.

During March of 1977 a zander of 2.4 kg was captured and returned to a gravel pit at Narborough, 10 miles east of King's Lynn, Norfolk.

In 1978 zander were captured from a large brick pit at Stewartby near Bedford. This introduction is thought to be dated 1973 or 1974 and be of Woburn origin.

In 1979 young of the year zander were captured from a gravel pit at Birstall near Leicester.

In 1980 mature zander to 2.2 kg were removed by the Thames Water Authority from a pond near London.

Also during 1980 two small zander were noted in the lower River Severn.

There is little doubt that further introductions of zander have been made. Zander are therefore likely to increase their range of habitats, by a combination of natural movement and illegal stocking. No pattern of movement has been determined and it is unlikely that predictions of the future distribution of zander will be possible.

1.4. OTHER MEMBERS OF THE GENUS STIZOSTEDION

One other member of the genus Stizostedion has been introduced to this country. The introduction of the walleye, Stizostedion vitreum vitreum, (Mitchell, 1818) was an accident. In 1925 twenty fingerlings hatched from American eggs supposedly of largemouth bass, Micropterus salmoides (Lacepede), were placed into the River Great Ouse at Earith bridge. Nine years later in 1934 a pike angler fishing in the River Delph at Welney captured a walleye of 5.3 kg. The fish was identified as a walleye by Dr. E.B. Worthington. No further examples have ever been noted.

In America the walleye's range is extensive. It ranges from near the Arctic coast in the Mackenzie River, south-east through Quebec to the St. Lawrence River and southwards to the Gulf Coat in Alabama (Scott and Crossman 1973). There is also a residual stock, apparently native along the Atlantic coast from Pennsylvania to North Carolina. It has been widely introduced outside its native range, particularly in the western reservoirs of the United States and along the Atlantic seaboard.

A sub species, S. vitreum glaucum (Hubbs), the blue walleye, inhabited the deeper and cleaner waters of Lake Erie, particularly in the eastern two-thirds of the lake, Regier et al. (1969) suggested that introgression with S. v. vitreum may have led to the disappearance of S. v. Glaucum in Lake Erie.

There is one other North American species, the Sauger, Stizostedion canadense (Mitchell 1918), which is found from the Hudson Bay basin, including the Saskatchewan, Red and Assiniboine rivers, the

Great Lakes and New Brunswick south to West Virginia. It is also found in the Tennessee River in Alabama, eastern Oklahoma, the Red River in Texas, eastern Kansas, Nebraska, Wyoming, south-western Iowa and Montana.

The two other species are both European, Stizostedion volgense (Gmelin 1785), being the Eastern Pikeperch. This species is much smaller in size than the zander and is restricted in distribution to the main rivers in the basins of the Volga (Kama and Vyatka), Ural, Don, Dnieper, Bug (rare), Dniester and Danube rivers. Stizostedion marinum (Cuvier and Valenciennes 1828), the sea pike-perch is the other European species, living in the brackish north-western part of the Black Sea and the Caspian Sea. It rarely enters rivers.

1.5. ECOLOGICAL IMPACT ON INTRODUCTION TO NEW HABITATS IN MAINLAND EUROPE

There is little doubt that the zander is a highly efficient predatory fish capable of colonising a wide range of differing habitats. As most predator and prey populations exist in a state of dynamic equilibrium, it is to be expected that both predator and prey will show changes in population number, age composition and biomass. These changes will cause interactions between the two populations, eventually resulting in a restoration of the "equilibrium". The degree of stability of predator prey relations may reflect the stability of the physical environment or the age and diversity of the fauna.

Poor survival or availability of prey fish is usually considered to be the most important factor affecting the growth and survival of a predatory fish species such as the zander (Biro 1972b). Svardson and Molin (1968) noted that the weight of Zander in Lake Hjalmaren during 1961 - 1965 was within corresponding length groups, lower than in 1955 - 1960. The zander were thin and in poor condition, the fishermen reporting that smelt were no longer present. They suggested that the zander were thin due to the scarcity of this preferred prey. This was probably correct as alternative prey was scarce and over predation may have occurred. Svardson and Molin (1968) also noted that when very strong year classes of zander were produced, growth was eventually retarded due to the zander reaching and superseding the limit of abundant forage fish.

Over predation has been noted in circumstances where the prey fish fauna is either poor in number or diversity. Popova and Sytina (1977) note regarding introductions of zander that "they have only been successful in water bodies with relatively good food supplies". In some waters of Middle Asia with a poor fish fauna the zander annihilated populations of local species which presumably had no adaptations to counter such high predation pressure. (Time scale not specified). Initially zander grew quickly and reproduced, but later, due to absence of other food, became cannibalistic and even ate zooplankton. Then the growth rate and abundance declined sharply (Dikansky 1974, Strelnikov and Dikansky 1975).

The impact of zander on its prey species is most easily studied when zander are introduced into new lakes.

Fortunately there have been a n mber of well documented introductions. Vallin (1929) describes the consequencies of the introduction of zander into Lake Ymsen, Sweden, (14.5 km^2) in 1911. The first catch of zander was in 1914 and the yield rapidly rose to 13 tons in 1918. Later the yield declined to about 4 tons. The population explosion of the new predator in Lake Ymsen heavily reduced the prey populations, especially that of perch. During the period 1918 - 1927 the annual catch of perch dropped from 1,175 kg to 87, that of bream from 2,435 to 69 and of roach from 285 to 5 kg.

Though there was some suggestion that changes in fishing intensity could have caused these trends, there is considerable additional data from a number of Swedish waters which suggests that introductions of zander could have a considerable effect on prey fish populations. In Lake Erken the introduction of zander had a very noticeable effect on the pike and perch population. The pike yield declined from 3-4000 per year to 1,500. Perch yield in gill nets fell from 1.2 kg in 1955 to 0.15 kg in 1962 (Agnedal 1969). Subsequent removal of large numbers of zander by the commercial fishery resulted in an increase in the number of pike and perch.

Not all introductions of zander have been considered to be detrimental to a fishery. Aksiray (1961), concerning the introduction of 10,000 100 to 150 mm zander to Lake Mermere in 1955, noted that the subsequent population of zander enhanced the value of the fishery. In October of 1959, 5,386 individuals were caught, nearly half of which were 360 mm in length and over 2 years of age. After zander were introduced, the wild fish population, mostly of little economic value, started to decrease. However common carp (Cyprinus carpio L.) a fish of high value increased in length and weight. There was an increase in total production of Lake Meremere.

Zander populations appear to rapidly fall to a low level of significance in diverse fish communities. Willemsen (1969), studying Lake Ijssel in Holland, during the period 1963 - 1967 noted that out of a total fish catch of 54 kg/ha/year only 0.4 kg/ha/year was composed of zander. He suggested that the low density of zander was due to either environmental changes or the phenomenon observed in other animals introduced in a new area where the initial extraordinary high density is followed by a decrease in abundance. Zander do not appear to maintain high densities for long and in established waters may comprise only a small part of the total predator population. Ivanova (1968) noted that in Rybinsk Reservoir, the stocks of roach, perch and ruffe exceeded the stocks of bream and zander by 20 - 30 times. From the Russian fisheries management point of view (Ivanova 1969), 35 - 40% of predators in the total fish stock, is considered to be an advantage. Low value fish are controlled and converted to valuable species.

Zander spawning success is said to vary considerably, German and Polish calculations suggesting that 0.01 to 1.5% of the number of spawned eggs grow up to reach adulthood. (Tesch, 1959, Wiktor, 1962). Bonar (1977) noted that in lakes having a small non-predatory fish component, cannibalism is considerably more frequent than in other water bodies.

In exceptional years, the zander's breeding results are excellent, leading to an abundance of young fish. Tesch (1962) suggested that the production of zooplankton, governed by water temperatures, prior to the zander's spawning season, was responsible.

There is some evidence that the introduction to or invasion of a new environment, by zander can result in decreases in the number of other predators such as pike and perch. Deedler and Willemsen (1964) stated that "As zander prefer to live in open water spaces and to prey upon small fishes, they have no serious interspecific competition, because predators following this pattern are not numerous. The perch could be the most serious competitor, with other species considered of minor importance."

However, Bouquet (1979) noted that Lake Velvne, once of low turbidity and high amounts of weedgrowth was famous as a fishery for large pike. However due to eutrophication and the associated increase in turbidity there occurred a decline in the number of pike and a loss of the pondweed. This coincided with an increase in the numbers of the previously scarce zander. In other waters where pike and zander co-exist, they tend to be spatially separated, the young pike preferring the weedy littoral zone while the large pike and the zander prefer the deeper water.

Dahl (1962) noted that on introduction of zander to Danish fisheries, changes occurred in the yield of other fish species (Table 7). Dahl, indicates that there is some doubt as to whether the zander was directly responsible for these changes as eutrophication was proceeding at the same time and this is known to have a considerable effect on species composition.

TABLE 7: Yield of fish from Danish Lakes

	Species				
	Eel	Pike	Perch	Blei	Zander
Average catch for years 1919-28 (kg)	7439	863	810	1356	0
Average catch for years 1942-51 (kg)	11640	233	0	13621	14060

In France where the zander has also been introduced, Goubier (1975) asks the rhetorical question "Has the zander had any negative effects on the resident fish species?" He notes that in the valley of the Seine, the zander has by predation removed certain bottom living herbivorous species. He goes on to say that this statement has not agreed with scientific observations made at the time.

Opinions differ considerably as to the zander's effect on prey fish populations. The data available is often limited and open to various interpretation. However there is enough evidence to suggest that the zander can in certain circumstances produce marked changes in native fish populations. This work seeks not to prove or disprove the idea that zander can change the fish populations of a fishery beyond recognition. Rather it attempts to identify specific traits of zander behaviour which differ from those of our native predators and in so doing identify factors which may be responsible for changes in fisheries populated by zander.

PART 2: FIELD STUDIES ON THE ECOLOGY OF THE ZANDER

2.1. THE COLLECTION OF MATERIAL

2.1.1. SITES

a). Great Ouse Relief Channel. NGR TF590012 to 612175

The Great Ouse Relief Channel is a manmade watercourse built to alleviate flooding of the land surrounding the River Great Ouse. It has a width averaging 91.4 metres, an average depth of 3 metres and is 16.6 km in length from its inflow at Denver Head Sluice to its outflow at Saddlebow Tail Sluice. For most of the year the Relief Channel has little flow, although during periods of heavy rainfall the water velocity may reach 0.7 m/sec (due to release of floodwater via the seven sluice gates at the Tail Sluice). (Klee 1979). Fluctuations in level of as much as 3 metres may be experienced in 24 hours. Inflow during flood-water diversion remains constant while run off of stored floodwater can only occur at times of low water in the tidal river Ouse. Therefore run off may occur only during the two periods of the day that see the main River Ouse at low or ebb tide.

The geology of the Relief Channel varies along its length. There are areas of peat, clay and gravel along the banks, however details of the underwater geology are unavailable.

The flora and fauna has changed since the water was flooded in 1959. Klee (1979) in the report on the survey of the Relief Channel described the flora of the channel as: "Apart from the extensive, but patchy fringe of reed (Phragmites spp) and sedges (Carex spp) there was very little macrophyte growth, whether emergent or submerged and very little filamentous algae, apart from a few beds of Enteromorpha spp."

Earlier in the history of the Relief Channel the present author noted a greater variety of aquatic plants. However, by the present time, this diversity has been much reduced.

No extensive study of the invertebrate fauna has been made, (Klee 1979) but numerous beds of zebra mussels (Dressensia polymorpha), are known to exist. Invertebrates typical of slow moving rivers or lakes are common, including Gammarus, Assellus, Daphnia, Cyclops and a wide range of insects and molluscs (authors observations).

The following list of fish species (Table 8) noted in the Relief Channel is a subjective assessment of those fish species present and their relative significance during three periods of the Relief Channel's evolution (present author). The list gives details of species occurrence for 1966, 1976 and 1979. The species composition of many other Fenland waters tends to be very similar to that of the Relief Channel in 1966, therefore such a collection of fish species will be referred to as the "Fenland Association". The "Fenland Association" could be further defined as an association of fish species typical of the slow moving or senile stage of a river, with the addition of species such as dace which are more typical of a rivers middle reaches. Water quality samples have not been taken from the Relief and Cut-off Channel for 2 years (Klee 1979a).

TABLE 8: Fish Fauna of the Great Ouse Relief Channel

Species	R/M	1966	1976	1979
Lampetra fluviatilis (River lamprey)	M	O	O	O
Salmo trutta trutta (Sea trout)	M	R	R	R
Osmerus eperlanus (Smelt)	M	O	O	O
Esox lucius (Pike)	R	C	C	C
Carassius carassius (Crucian carp)	R	R	R	R
Cyprinus carpio (Common carp)	R	R	R	R
Gobio gobio (Gudgeon)	R	C	P	P
Tinca tinca (Tench)	R	P	P	P
Blicca bjoerkna (Silver bream)	R	C	C	P
Abramis brama (Common bream)	R	C	C	C
Alburnus alburnus (Bleak)	R	C	R	R
Scardinius erythrophthalamus (Rudd)	R	C	R	R
Leuciscus cephalus (Chub)	R	R	R	R
Leuciscus leuciscus (Dace)	R	C	R	R
Cobitis Taenia (Spined loach)	R	R	R	R
Noemacheilus barbatus (Stone loach)	R	R	R	R
Anguilla anguilla (Eel)	MR	A	C	C
Rutilus rutilus (Roach)	R	A	C	C
Gasterosteus aculeatus (Three spined stickleback)	MR	C	C	C
Pungitius pungitius (Ten spined stickleback)	R	R	R	R
Lota lota (Burbot)	R	R	R	R
Perca fluviatilis (Perch)	R	A	P	P
Gymnocephalus ceruna (Ruffe)	R	P	P	R
Stizostedion lucioperca (Zander)	R	C	C	C
Pomatoschistus microps (Common Goby)	M	O	O	O
Platichthys flesus (Flounder)	M	O	O	O

KEY

M Migratory — MR Migratory or resident

R Rare — O Occasional — P Present — C Common — A Abundant

Klee notes in this report that previous occasional samples, indicated that the Relief Channel was "A fairly clean water with oxygen levels which are always satisfactory".

b). The Cut Off Channel. NGR TF591007 to TL700987

The Cut Off Channel is connected to the Relief Channel by a dividing sluice at Denver (Figure 2). This dividing sluice was completed in the early 70s - before this the two waters were continuous. Though this water extends into Suffolk as far as the River Lark, only a short section was used for this study. This particular section extends from the dividing sluice at Denver to the first syphon at Stoke Ferry, a distance of 13 km. The width averages 35 metres with a depth of 2 to 3 metres.

Generally this water is similar to the main Relief Channel with perhaps a more varied flora (Potamageton spp., Elodea spp.). Fish species composition is similar to that of the Relief Channel with the exception of some of the migratory species. The turbidity of the Relief and Cut-Off Channels varies with presence or absence of water flow, wind intensity and direction and time of year.

c). The Middle Level System.

This large and extensive drainage system comprises a number of waters, each connected to another and each similar in flora and fauna. Some are wider and deeper than others, but all are drained by means of one large pumping station at the end of the Middle Level Main Drain at Wiggenhall, St. Germans. Rate of flow varies with the speed of pumping and the distance away from the pump - maximum rate 0.5 m/sec. Emergent and marginal plants are more numerous than on the Relief Channel with extensive beds of Nuphar spp. and Potamageton spp.in many areas.

Invertebrate fauna is again typical of still or slow moving waters, with 14 to 40 groups represented, (Klee 1979b). The fish fauna is typical of the Fenland Association.

d). Middle Level Main Drain. NGR TF587140 to 505002

A maximum of 50 metres in width with a depth of 4 to 5 metres. There are few aquatic macrophytes at the lower end near Wiggenhall St. Germans with rather more found along the upper reaches.

e). Sixteen Foot Drain. NGR TF505002 to TL421873

A direct extension of the Middle Level, this water is narrower and shallower, with an average depth and width of 3 metres and 30 metres respectively. Aquatic weedgrowth is more extensive and varied than that found in the Middle Level.

f). Forty Foot Drain. NGR TL242881 to 422873

Crossing the Sixteen Foot Drain to form a T junction. Similar to the Sixteen Foot Drain.

g). Pophams Eau. NGR TF 469004 to 506002

A short drain connecting the Middle Level to the Old River Nene.

Similar to the Middle Level, but 30 metres wide. The Old River Nene in turn connects with the following drains: the Twenty Foot, Bevils Leam and King's Dyke. (The latter two not shown on Figure 2, but are direct extensions of the Twenty Foot Drain). The King's Dyke in turn, connects with the River Nene. The depth and width of these drains vary.

h). Great Ouse and Tributaries

River Great Ouse. NGR TL578876 to TF590011

The main river is mainly artificial in nature, the only part which is of concern to this work is the section between the Littleport A10 road bridge and Denver Head Sluice. The river is approximately 50 metres in width with a maximum depth of 7 metres. Water movement is usually slow. Aquatic plants are numerous, but restricted to the margins (present author).

Burwell Lode. NGR TL585679 to 548692

A small drainage cut or lode connected to the River Cam, which in turn is a tributary of the Great Ouse. The water is clear with luxuriant macrophyte growth, with a maximum depth of 1 metre and width of 10 metres. The length of the water studied was some 5 km. Fish species are again typical of the Fenland Association.

River Delph. NGR TL470859 to 572988

A drain of over 20 km in length, acting as a byepass for flood-water from the Great Ouse. The water averages 20 metres in width and 4 metres in depth. It has a varied flora and fauna.

i). Midland Zander Waters

Coventry and Oxford Canal, Ashby Canal. NGR SP400840 and SK363093 respectively

These canals form part of the extensive canal system connecting the Midlands with the North and South. The area from which zander were obtained on the Coventry and Oxford Canal was between Hawkesbury and Brinklow (Figure 3). Ashby Canal zander were obtained from near Snarestone (Leicestershire).

The canals are shallow and narrow, one and eight metres respectively. These canals are heavily used by various boat traffic especially during the summer. Aquatic plants are present, being more numerous in areas less extensively used by boat traffic. Fish species noted during Severn Trent Water Authority surveys include pike, perch, zander, roach, silver bream, common bream, ruffe, gudgeon and common carp.

Coombe Abbey Lake. NGR SP392792

A man made lake north of Coventry (Figure 3). Of approximately 35 hectares this shallow water (2 metres) has a small variety of fish species, though these are rather strongly represented numerically. Species present include; pike, perch, zander, eel, roach, common bream, crucian carp, tench and common carp. Roach and bream are particularly numerous and this water is regarded as a high quality fishery.

Stewartby Brick Pit. NGR TL010427

A large flooded brick pit, the water is mostly deep, (up to 20 metres) and is stocked with most of the common coarse fish. The water is situated near to Bedford.

2.1.2. COLLECTION OF MATERIAL AND THE SELECTIVITY OF METHODS USED

Studies of animals in their natural environment depend on the application of two approaches. One involves the collection of samples from the population, with detailed studies of the sampled animals to elucidate facts about the population as a whole. The second approach utilises direct observations of the animal in its natural habitat to yield the required information.

Fish are, particularly difficult to study in their natural habitat. Therefore most ecological studies of fish have been conducted by means of sampling programmes designed to provide information about the fish throughout its life.

Samples from a population depend for their representativeness on the methods used to obtain the samples. No one method (save complete draining and recovery of all fish) will give a true picture of a fish population. Each method of fish capture tends to be selective for fish of a particular age, size or physiological condition.

During the course of this work, zander were obtained by a number of methods. The selectivity of the capture methods and the application of no more than two capture methods at each sampling site meant that truly representative samples were difficult to obtain.

The methods used to obtain zander are described in the following text, Table 9, showing the contribution of each method to the supply of specimens used in this work. Where information is available the selectivity of the methods used is indicated. The utilisation of these specimens in subsequent investigations is outlined in Table 10.

TABLE 9. Numbers Caught and Methods Used to Obtain Zander

Water	1978		1979		1980	
Relief Channel	250r		180r	9s	46r	
Cut off	6r		7r	12s	1g	20se
Great Ouse	3r		2r	4s		
Middle Level	7r		101r	28s	18r	
Twenty Foot				2s		
King's Dyke				33e		4e
Forty Foot						16s
River Delph	24r		5r			
Burwell Lode				12e		
Coventry Canal		33e		6e		16e
Ashby Canal				12e	1r	1e
Coombe Abbey				60s	1r	30s
Stewartby					11r	
Wissey	1r					

Total	Rod and Line	(r)	663
	Seine Net	(s)	161
	Electrofishing	(e)	142
	Gill Net	(g)	1
	Siene Net and Electrofishing	(se)	20
	TOTAL		987

TABLE 10. Utilisation of Specimens

Water	1978		1979		1980		
Relief Channel	249t	1e	154ts	35as	6ts	28as	12as
Cut Off	6t			19as		15as	6ms
Great Ouse	3t		2e	4as			
Middle Level	5t	2e	63ts	66as	10as	2e	6ms
Twenty Foot				2as			
King's Dyke				40as	4as		
Forty Foot					12a	4e	
River Delph	24t		5t				
Burwell				12as			
Coventry Canal	21as	12e	4e	2a	16e		
Ashby Canal				12e	1a	1e	
Coombe Abbey			48as	22e	27as	4e	
Stewartby					11s		
Wissey	1t						

TOTAL	Tagged	(t)	516
	Marked	(m)	12
	Scales	(s)	583
	Autopsy	(a)	358
	Experimental	(e)	84

(a) Seine Netting

For the purposes of this work seine netting was the preferred method of obtaining zander. Little is known of the reaction of zander to a seine net, save that a preference is shown towards staying near to the bottom during the drawing of the net. This suggests that zander will escape under, rather than over the net. It does not, however, provide any information on differential selectivity due to size. The assessment of selectivity made here is therefore based on the mesh size employed. A knot to knot mesh of 7 mm was employed in most cases and according to Klee (1979) was effective in capturing roach and bream of 60 mm and greater fork length. As most nettings were carried out during the autumn, most young zander would have been considerably longer than 60 mm and therefore likely to be sampled effectively by seine netting.

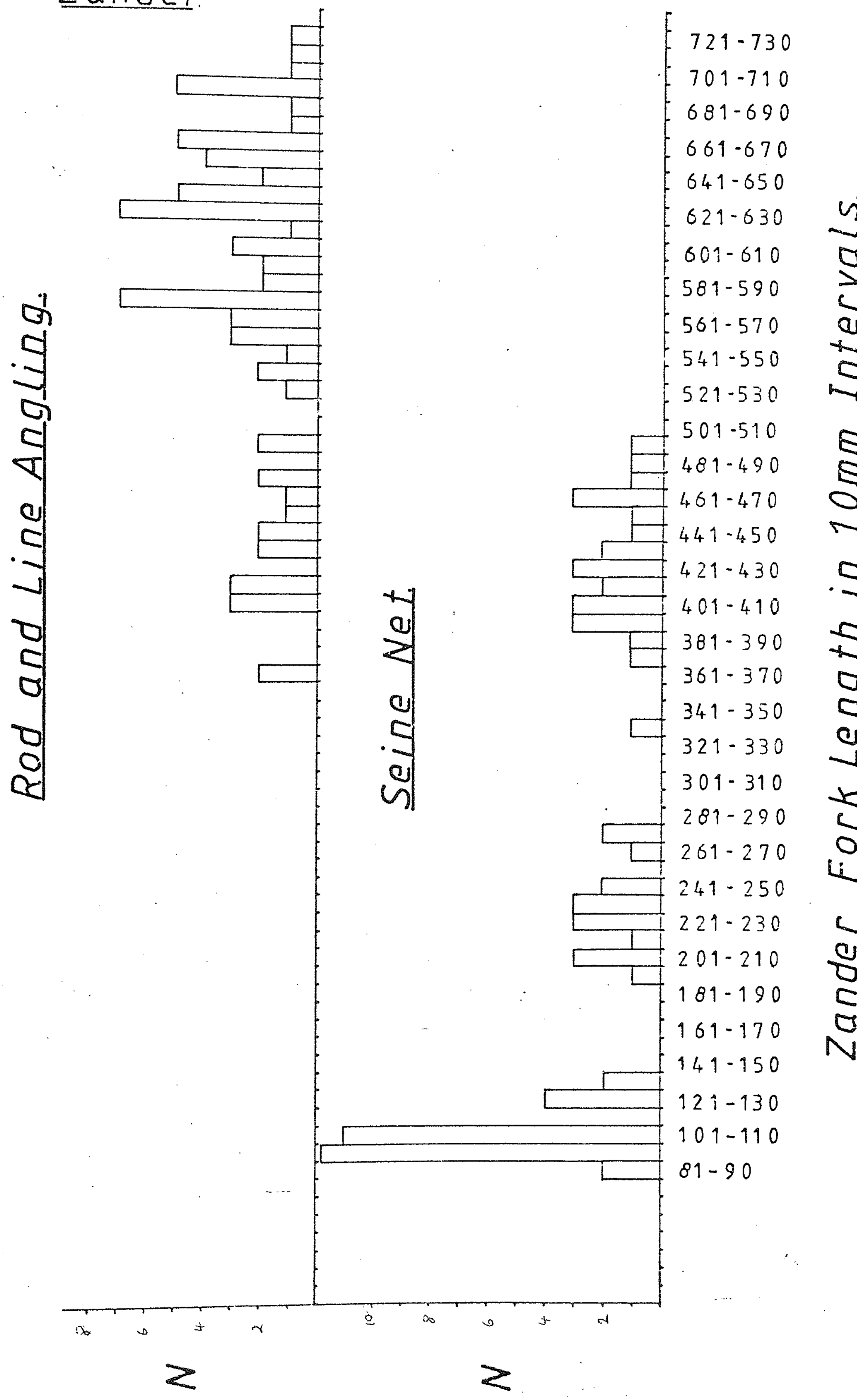
With low levels of fishing intensity the seine net tends to be very selective, especially where zander of different sizes are distributed unevenly. With only a small number of nettings the chances of making a representative sample is considerably reduced. In most cases, where seine netting was employed it was as a part of the Anglian Water Authority fishery monitoring programme. The waters which were seine netted in these surveys were generally large and therefore samples were obtained from only a small proportion of each water. The area surveyed on the Middle Level Main Drain was only 6% of the total. It is therefore possible that samples obtained were not representative. The available data from seine netting when compared with that obtained from rod and line angling (Figure 4) would tend to suggest this (see (d)).

(b) Electrofishing

Electrofishing methods vary in efficiency depending on the equipment employed. A.C. equipment was used to obtain zander, either during Anglian Water Authority surveys or Severn Trent Water Authority zander removal operations. Larger fish are generally stunned more easily than small fish due to the much larger potential difference across the larger fishes body. Very small fish also tend to be overlooked while large fish may

Figure 4.

Length Frequencies of Middle Level Zander



outrun or evade the electrical field. Specimens obtained by electrofishing came from the smaller, shallow canals and drains and were collected by working along the water to a stopnet or to a natural obstruction.

(c) Gill Netting

Gill netting is a passive method of fishing which relies on the fish encountering the net and becoming entangled. It is a very selective method (Nikolskii 1969), the selectivity depending very much on the shape of the fish and whether or not it has teeth or spines. Nets of 20 and 60 mm knot to knot mesh were set frequently during the summer, autumn and winter of 1979 in the Cut Off Channel near Stoke Ferry (see Figure 2). During this period only one zander was taken in these nets, while common bream and pike were frequently captured. Zander were however taken nearby (100 metres) on baited lines. No reference to such behaviour could be found in any literature studied. Zander are frequently gill netted in Sweden (Svardson and Molin 1968). The contribution of gill netting to sampling of zander populations was therefore for the purposes of this work, insignificant.

(d) Rod and Line Angling

The use of rod and line angling though seldom used for sampling fish populations in this country, has found applications in many situations worldwide (Scofield 1951a, 'Sinker' 1952, Kolganov 1959, Shakespeare 1962) where other methods of sampling prove impractical.

Many of the waters supporting a population of zander are large and extensive. These waters are difficult to sample by seine netting and electrofishing. The use of gill nets is prevented by the extensive damage to other fish species which are enmeshed along with zander. Such damage to fish stocks cannot be justified purely on the basis of obtaining fish for research.

Rod and line angling proved to be the most effective method of obtaining live zander for marking and for autopsy. The relative selectivity of the method is immediately apparent from Figure 4, relating to zander of the Middle Level system. This selectivity can be attributed to the size of baits and angling methods (bait size 100 mm and larger) employed (Rickards and Fickling 1978). During this work zander of less than 360 mm fork length were not obtained by angling. A comparison of the frequency of capture of zander of 361 to 500 mm by seine and rod and line, (23 and 18 out of total numbers of specimens obtained of 71 and 76 respectively) suggests that for zander of these lengths both methods of sampling are representative, hence the similarity between frequencies of capture.

Above 501 mm angling appears to be highly effective in obtaining zander. 76.3% of rod and line captures were greater than 501 mm. The inability of seine netting to sample such fish in the Middle Level system can be attributed to the very patchy distribution of zander of this size. Angling experience allows selection of areas inhabited by such fish and thereby results in a very high proportion of such fish being captured. Angling requires inordinate periods of time to enable capture of specimens and this does not allow a random approach to sampling. Once known "holding areas" (areas where zander are often to be found) are located angling effort tends to be concentrated there. This results in the type of selectivity shown in Figure 4. Because comparative data is not available from seine netting it is difficult to determine whether or not zander of greater than 501 mm have been sampled in a representative manner. However for this work an assumption will be made based on the similarity of seine and rod and line capture for fish of 361 to 500 mm. Because rod and line data was similar over these size ranges it is assumed that rod and line angling is selective for zander of less than 361 mm. Above 361 mm and up to 500 mm rod and line angling produces similar numbers of zander as seine netting. Above 501 mm rod and line caught zander would be similar to seine caught zander, if seine netting on a low intensity level was capable of sampling in a representative manner.

Selectivity can result from rod and line angling when a study of growth or feeding is to be made. It is very important to note the possibility of bias when such studies are being made as this might invalidate comparisons of data obtained by different methods. Rod and line angling is probably more likely to capture the hungry fish than the satiated ones. This might give incorrect information on frequency of feeding. There is a possibility that hungry fish are also slow growing, however the converse might also be true, that 'hungry' fish have greater appetites and therefore grow faster. Without meaningful observations such speculation is unlikely to be profitable.

For this work it has been necessary to pool data obtained by a variety of methods. Wherever this has been done, mention has been made of this in the text.

2.1.3. WEIGHING AND MEASURING OF ZANDER

The various methods used to obtain zander inevitably presented problems with the standardisation of measurements. In order to minimise error the following procedures were followed:

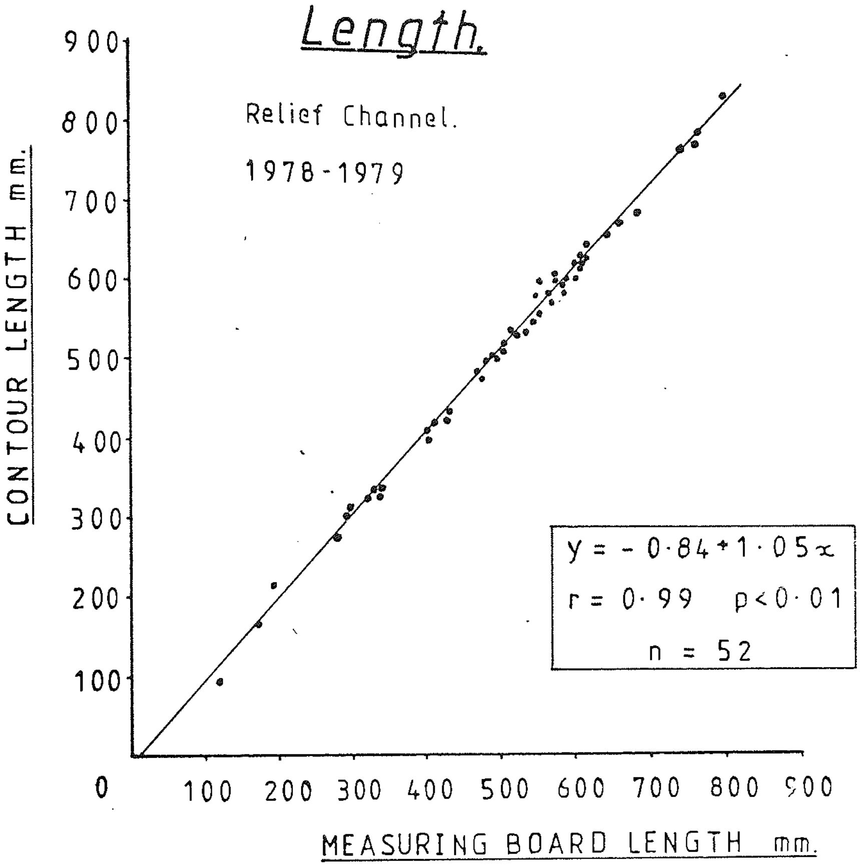
(a) Seven selected anglers were instructed how to tag, mark, weigh and measure zander.

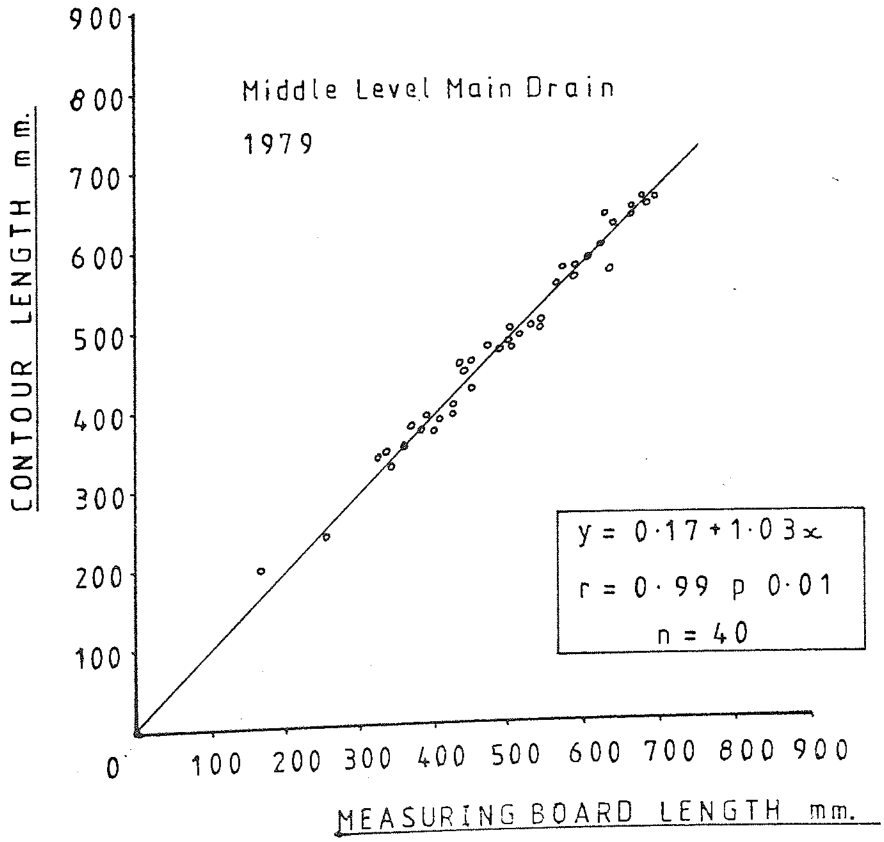
(b) In order to obtain recaptures of tagged zander, press releases were sent to all the major angling newspapers and magazines, including Angling Times, Anglers Mail, Coarse Angler, Coarse Fisherman and Angling. Information cards were also sent to all anglers interested in zander angling and these cards (Appendix III) were also placed at access points on the various fisheries.

Anglers were asked to record details of length and weight in the following manner:

Length recorded as fork length by means of measuring from the tip of the snout to the fork of the tail, the tape measure following the curvature of the body. This "contour" length is a different measurement from that obtained from a measuring board. Because the tape measure follows the body curvature the apparent length of the zander appears greater. Unfortunately this is the most common method used by anglers to measure fish. It was therefore decided to use this method and prepare a conversion scale, Figure 5, enabling the conversion of contour lengths to measuring board lengths. Such scales were prepared separately for Relief Channel and Middle Level zander.

Figure 5. Conversion Scale Contour/Measuring Board Length.





Once contour lengths had been obtained from recaptures it was then possible to convert where necessary to measuring board length. Comparisons of actual data for lengths with data derived from conversion scales indicated that the range of error was from -2.7% to 2.6% of the length of the zander. Therefore for studies of length change on recapture, all changes less than 3% of the body length were disregarded. (This effectively eliminates error due to conversion from contour to measuring board length).

Measurements were made wherever possible in mm, however some lengths were given in inches to an accuracy of $\frac{1}{4}$ inch. This represents a possible error of 1.7% (plus or minus) for 300 mm fish and somewhat less for larger fish (plus or minus 0.3 for 800 mm fish). This error comes within the range already allowed for and can therefore be disregarded. All non-metric units were converted to metric units.

Weight measurements were made in the laboratory using a top loading pan balance. In the field weighing was carried out using "Avon" dial scales, accurate to one ounce (28. 35 grams). A survey of several such balances indicated that an inaccuracy of plus or minus 2 ounces could be expected, or approximately 50 grams. Therefore for the purpose of recording the weights of recaptured zander, weight changes of plus or minus 50 grams and less were disregarded.

In order to enable comparisons of growth data for English zander with European mainland zander, (continental workers frequently employ body or total length rather than fork length), scatter diagrams of fork length and body length and fork length and total length were drawn and lines fitted by means of least squares (Figure 6).

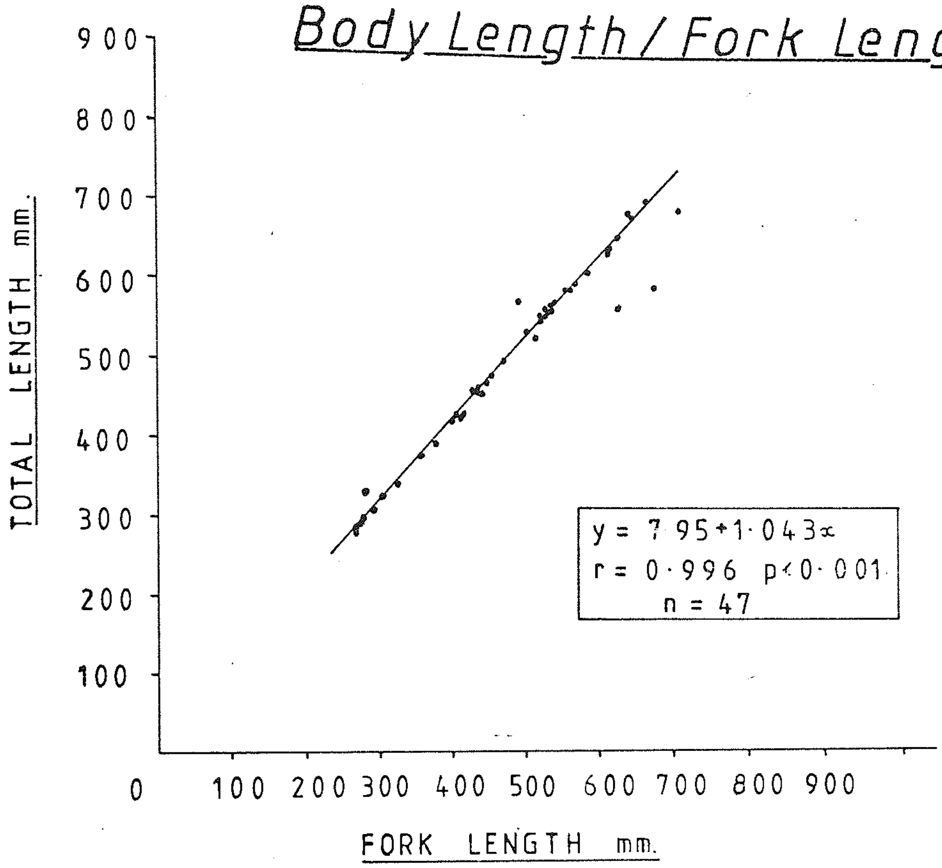
The three measurements of length are defined as follows:

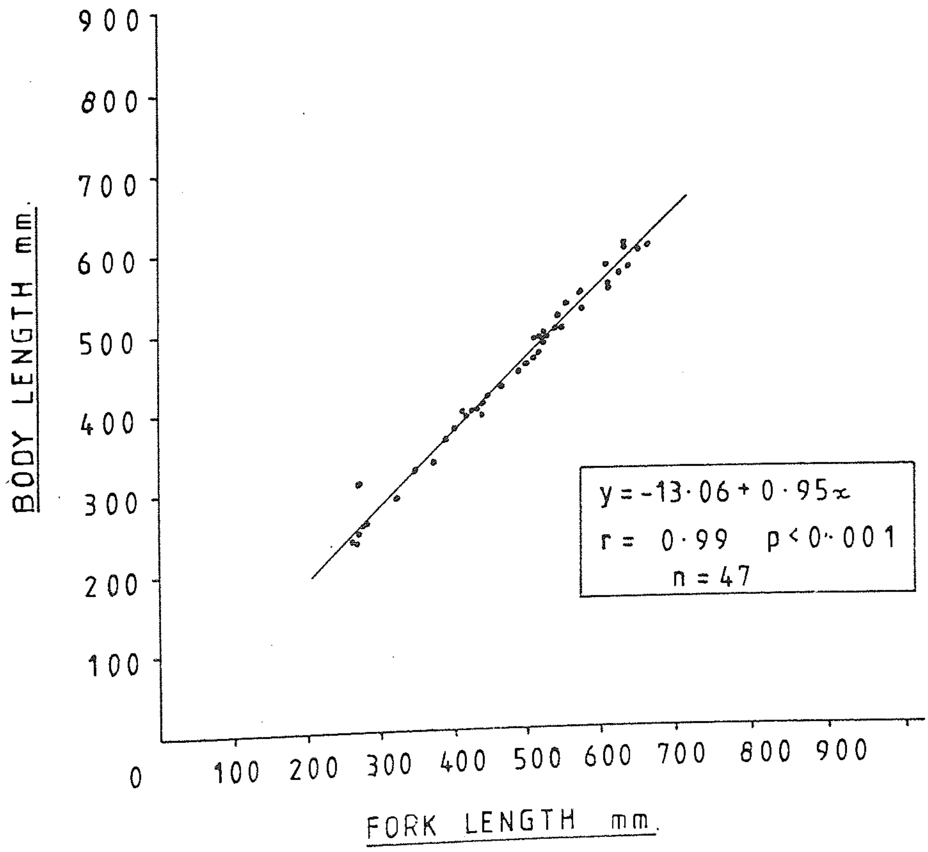
Total length, from the tip of the snout to the end of the tail fin.

Fork length, from the tip of the snout to the fork of the tail.

Body length (standard length), from the tip of the snout to the base of the tail fin rays.

Figure 6. Conversion Scale
Total Length / Fork Length, Body Length / Fork Length.





2.2. AGE AND GROWTH RATE OF ZANDER

Although numerous studies of the age and rate of growth of the zander have been made in Europe and the U.S.S.R., English zander have been the subject of only limited studies. (Fickling 1970 and 1976, unpublished, Linfield and Rickards 1979). These studies have all been subject to inaccuracies caused by shortage of data and the failure to validate the age determination techniques employed. This has resulted in the over-estimation of zander ages as presented in Linfield and Rickards (1979). The following section seeks to validate the methods of age determination which are most commonly employed and in so doing provide factual information on the age and growth of zander in a variety of different habitats. Such information is available from the following waters:

Great Ouse Relief and Cut Off Channel.

Middle Level Main Drain.

Burwell Lode.

Stewartby Brick Pit.

Coombe Abbey Lake.

Coventry, Oxford and Ashby Canal.

2.2.1. METHODS

Two structures were used for age determination. These were:

(a) Scales.

(b) Opercular bones.

These were obtained, handled and read in the following manner:

(a) Scales were removed from a key area on the "shoulder" of the fish (see Figure 7). This area is below the lateral line and just posterior to the operculum.

Samples of scales from other areas of the body indicated that the shoulder scales were more regular in shape and generally larger. This was found to be a considerable advantage when scale reading and therefore all scales used for age determination were removed from this key area.

In each case three well formed scales were removed and placed into small envelopes, suitably labelled. A code system using the year, sample number and water was used to identify material. For example ML 79/34 refers to fish number 34, collected in 1979, from the Middle Level Main Drain. All relevant data was recorded in a field notebook.

Before examination, scales were cleaned with a little water, dried and placed between two microscope slides which were taped together. Scale reading was by means of a "Projectina" overhead projection microscope. A magnification of x 30 was generally employed, though for very large scales x 10 was required, with multiplication by 3 to render the measurements compatible. The accuracy of the magnification was checked using a graticule and found to be satisfactory.

The distances to the edge of each annulus were recorded using a strip of mm graph paper laid across the projected image. At the edge of the outermost annulus, the number of circuli to the scale

Figure 7.

Area of scale removal.

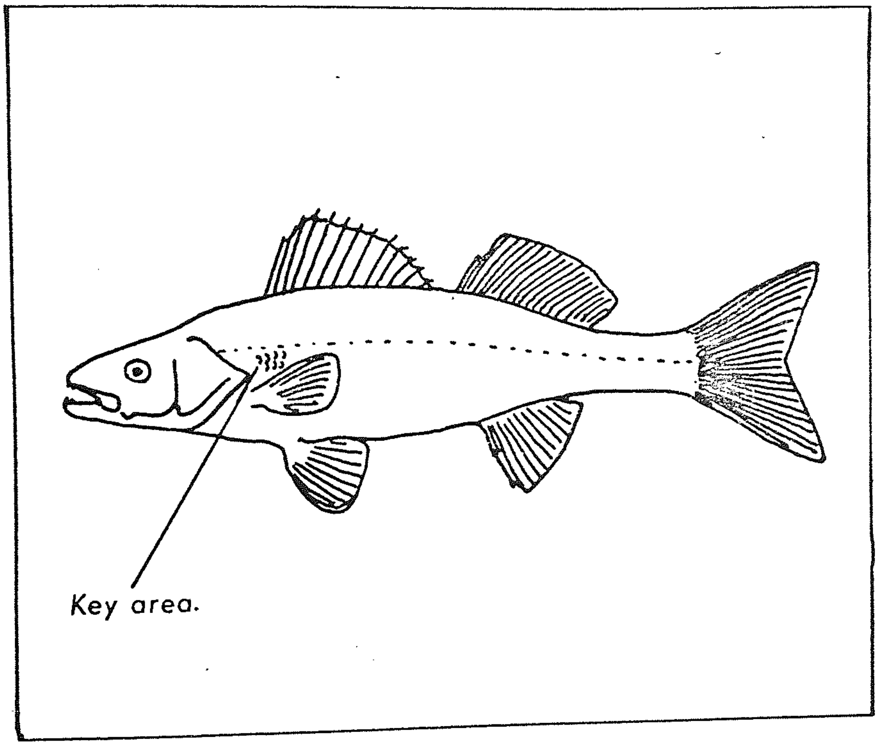
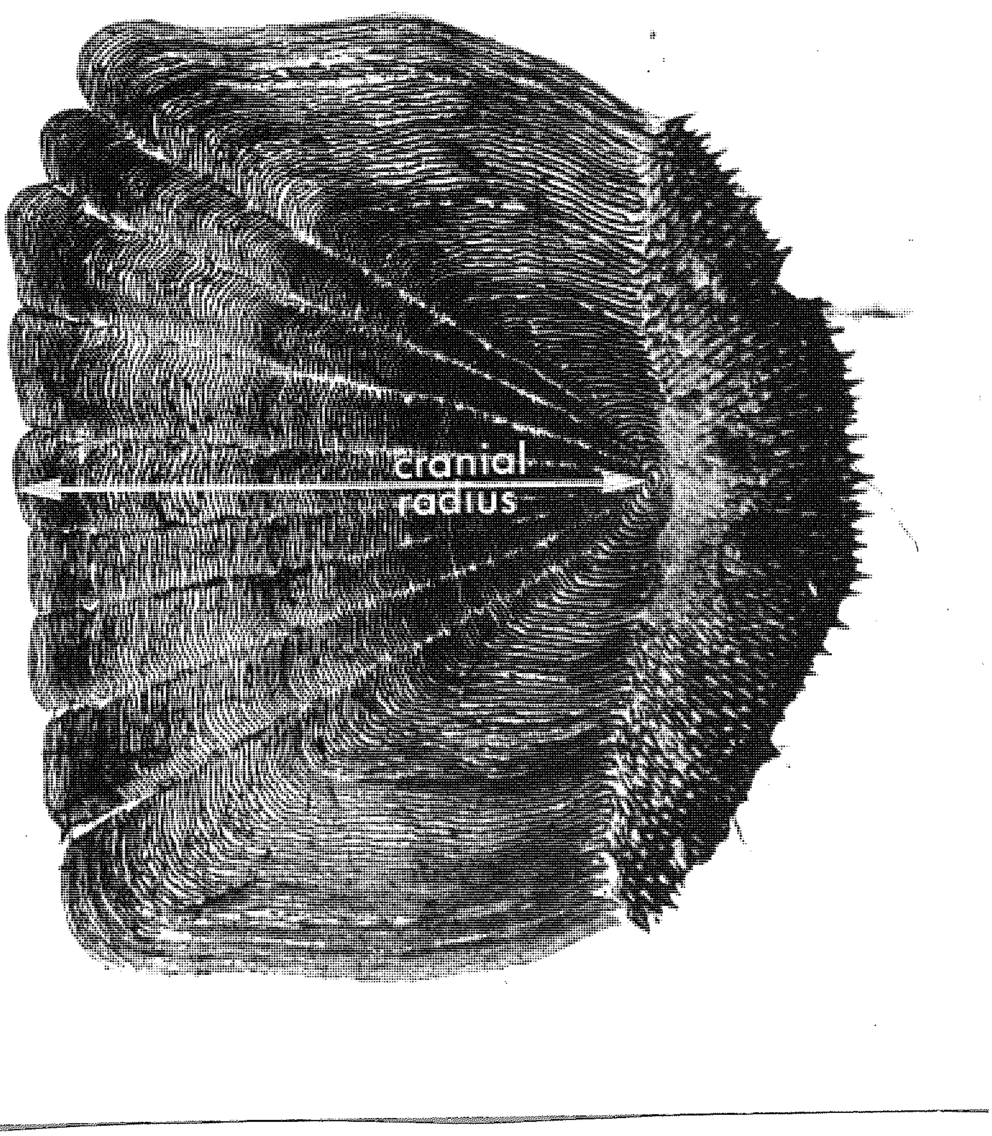


Plate 2.

Cranial Radius of Zander Scale.

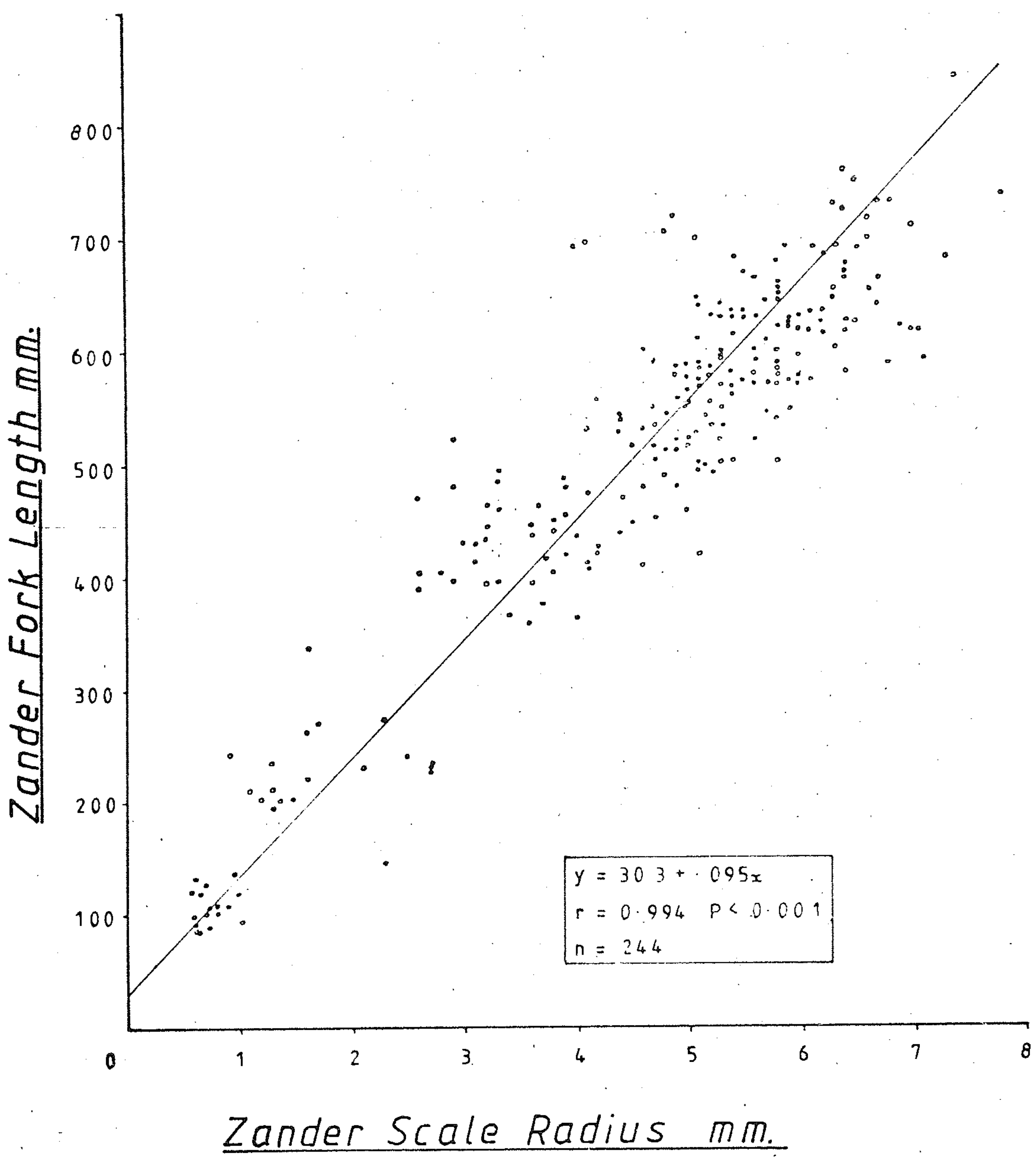


margin was noted. The cranial radius of the scale (Svardson and Molin 1973) was used for all age determination work. (Plate 2). The radius of each scale was obtained and this value plotted against the fork length of the fish concerned (Figure 8). Measurements were obtained from several zander populations and pooled. The high level of correlation ($P < 0.001$) suggests that the various populations have a common relationship, between fork length and scale radius. Regression lines were fitted by the method of least squares. An estimate of the zander length at the time of scale formation in the key area may be obtained from the intercept value on the y axis in the straight line relationship given.

The scales of slow growing or old zander can be difficult to read. The following precautions were taken to eliminate sources of error:

(i) Scales were examined in large numbers over short periods. Familiarity of the material proved to be helpful when locating annuli. A number of double annuli were noted. Biro (1970), working on zander, also described these double annuli referring to them as "pseudorings" and suggested that they may be the result of changes in growth produced by seasonal variations in food quantity or changes in climate. These changes being typified by two annuli very close together. It was difficult to discern which was the true and which was the false annulus. Therefore such double annuli were counted as one and the point mid way between the two used for back calculation. In this way a compromise was reached, between over-estimating or under-estimating the growth of zander with these double annuli.

Figure 8. Zander Scale Radius Fork Length Relationship.



(ii) Difficult scales, i.e. those which were badly damaged or worn were discarded. Wherever possible alternative scales were used from the same specimen, hence the requirement for at least three scales from each fish.

(iii) Where the 1st annulus was difficult to locate, a Walford Plot (Walford 1946) was used to determine the position of the 1st annulus.

(b) Opercular bones were dissected from the fish and placed into boiling water until the flesh was removed. By drying for 5 minutes at 105 C it was noted that the bones were ready for immediate reading. This dispensed with the requirement for storage before reading as advocated by Le Cren (1947) and Frost and Kipling (1959).

For the purpose of back calculation, the centre used by Le Cren (1947) for perch opercular bones was employed, (Plate 3). The measurement from the dorsal margin of the bone to the centre was used for the determination of distances between annuli. On the operculi of fish from temperate regions viewed by reflected light on a dark surface, summer growth appears as an opaque white zone, while the narrow transparent zones correspond with annuli. The opercular bone radius was plotted against fork length for each fish, to give the straight line relationship shown in Figure 9, the y intercept of which gives an estimate of the length of the fish at which opercular formation has taken place. Measurements were obtained from several zander populations and pooled. The high level

Plate 3.
Zander Opercular Bone.

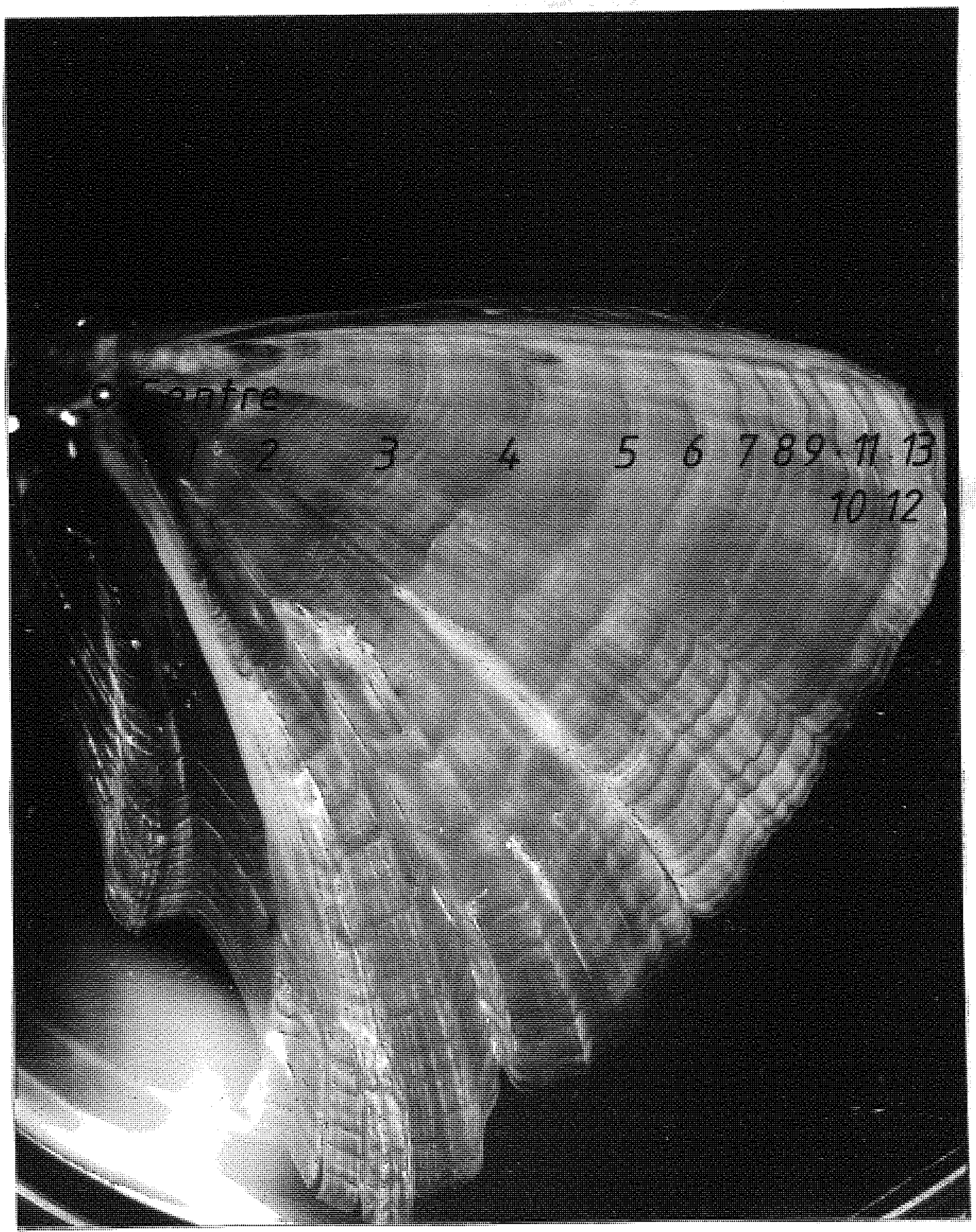
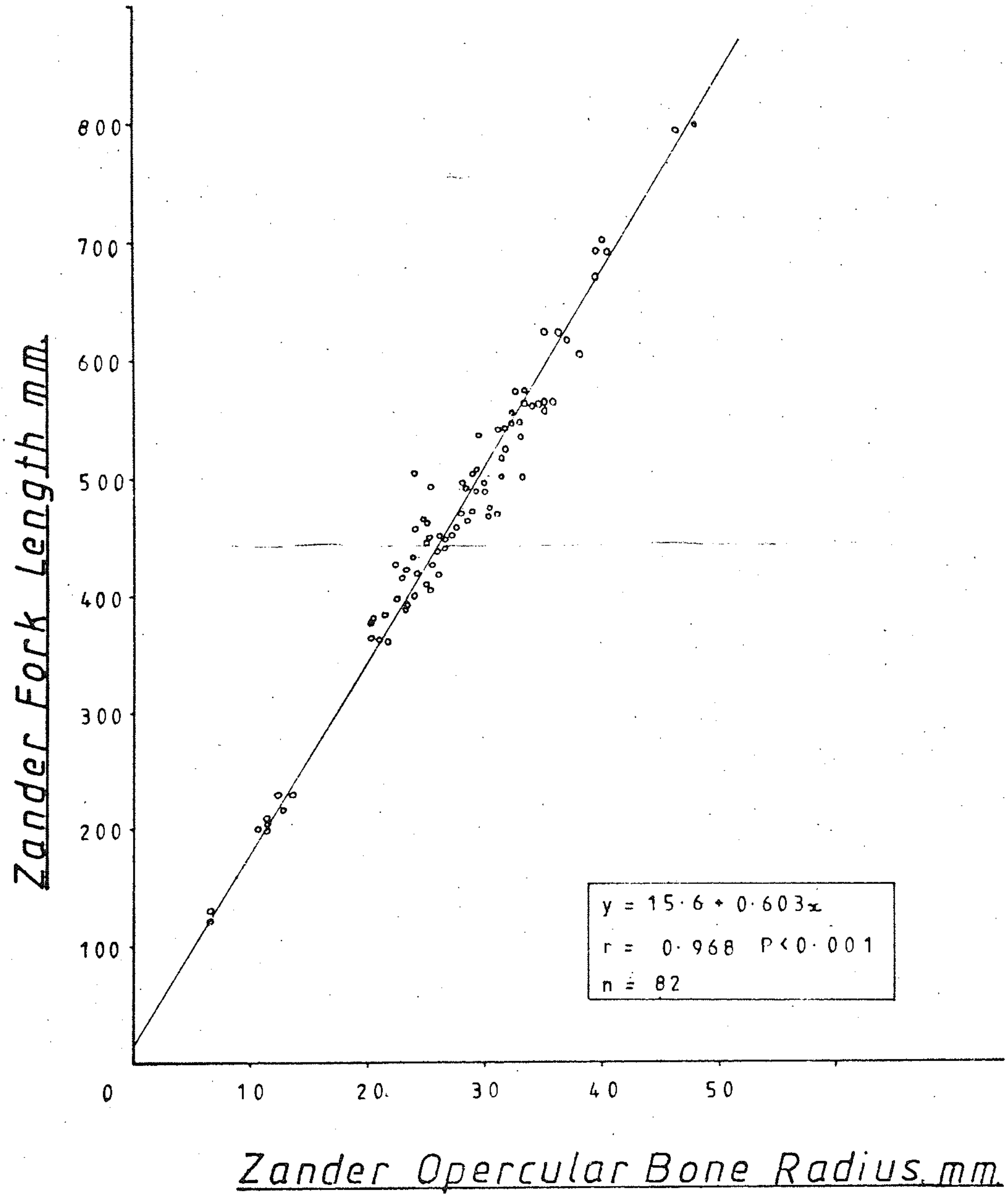


Figure 9 Zander Opercular Bone Radius, Fork Length Relationship.



of correlation ($P < 0.001$) suggests that the various populations have a common relationship between fork length and opercular width. Regression lines were fitted by the method of Least Squares.

The use of the opercular bone for age determination has one major disadvantage over the use of scales, in that the fish must be sacrificed. In many situations this is not desirable. Therefore wherever possible, scales have been used for age determination and the reading of opercular bones has been used for confirmation of these age estimates.

All lengths for ages determined were presented as lengths on May 1st, a date which corresponds with the time of new growth and annulus completion, (as determined from Coombe Abbey zander, see later). This enabled compatibility between samples obtained at different times of the year. Only data from the Relief Channel in 1968-70 had to be presented as zander lengths on May 1st with varied amounts of plus growth.

2.2.2. THE VALIDATION OF THE METHODS OF AGE DETERMINATION

According to Graham (1929) it is essential that whatever method of age determination is chosen, the time scale must be validated. He lists five criteria for validation as follows:

(a) Agreement with Petersen's method. Care must be taken that the modes represent age groups and not only particularly strong year classes.

(b) The seasonal record of the age of the ageing structure. If it is reliable, the supposed annulus will appear at the edge of the scale or bone only during a relatively short period of the year.

(c) The observation of year classes over a period of years. Recognisably strong and weak year classes should appear as successively older age groups each year.

(d) Marking experiments. Fish marked and later recaptured should show the number of annuli corresponding to the period of liberty.

(e) Tank or pond experiments. Fish reared in ponds or aquaria and of known age, should have annuli corresponding to this age.

Four of the five approaches mentioned above could possibly be used to validate age estimates from zander scales.

(a) Agreement with Petersen's Method

The first method compared the modes obtained from a plot of length frequency distribution (Figures 10 and 11) with the modes obtained from age determined samples. Cassie (1954) described a method of transformation using probability paper, which enabled normally distributed data to be expressed in a linear fashion. This procedure was followed for the transformation of data obtained from length frequency distributions and also age determined lengths, in the following manner.

All fish assigned to individual age groups, were grouped in divisions of 10 mm, thus giving the length distributions within age groups. Lengths for ages in each group conformed to a normal distribution, thus giving a series of modes corresponding to each age group.

Figure 10.

Frequency Distribution of Coombe Abbey Lake 1980 Seine Netted Zander.

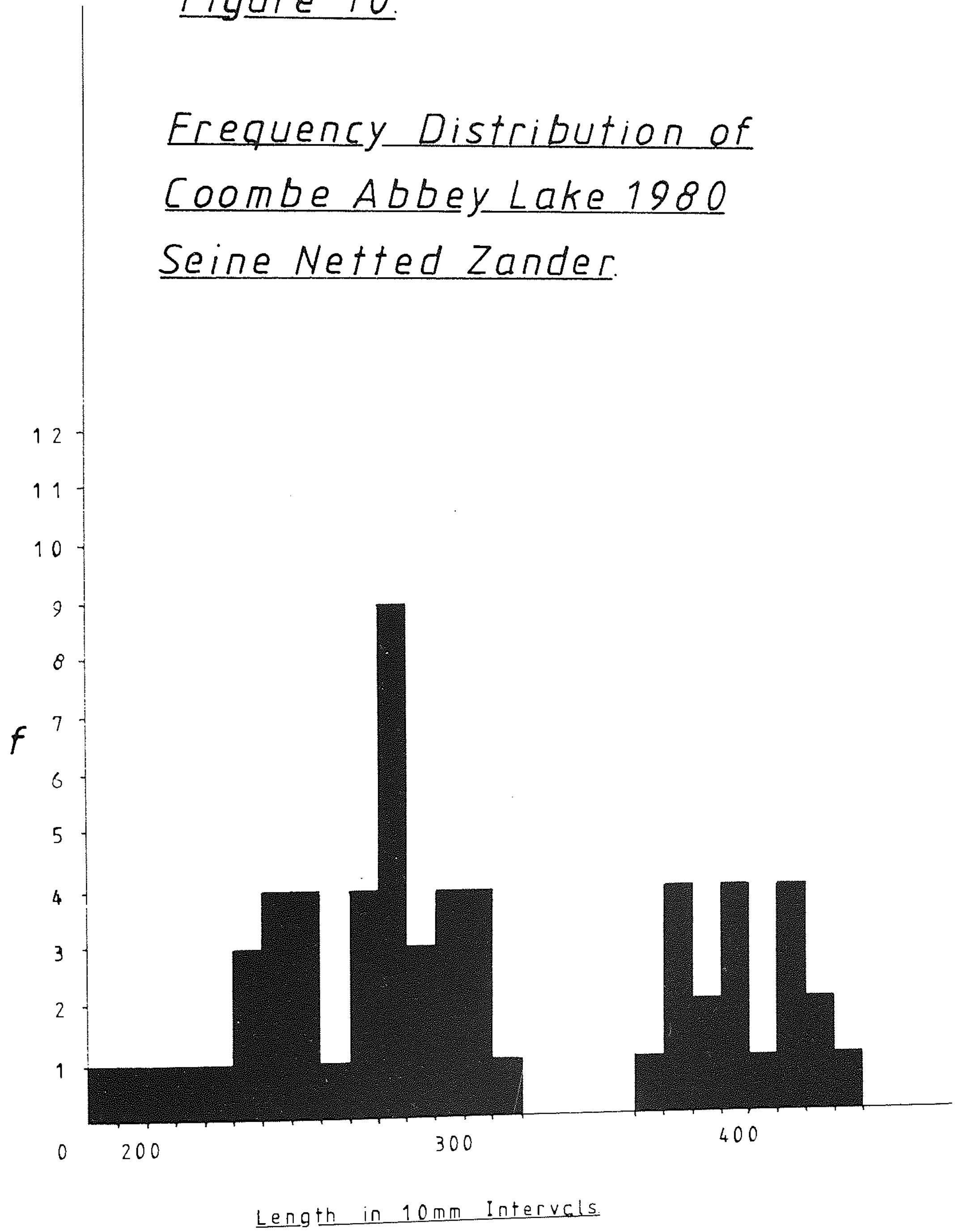
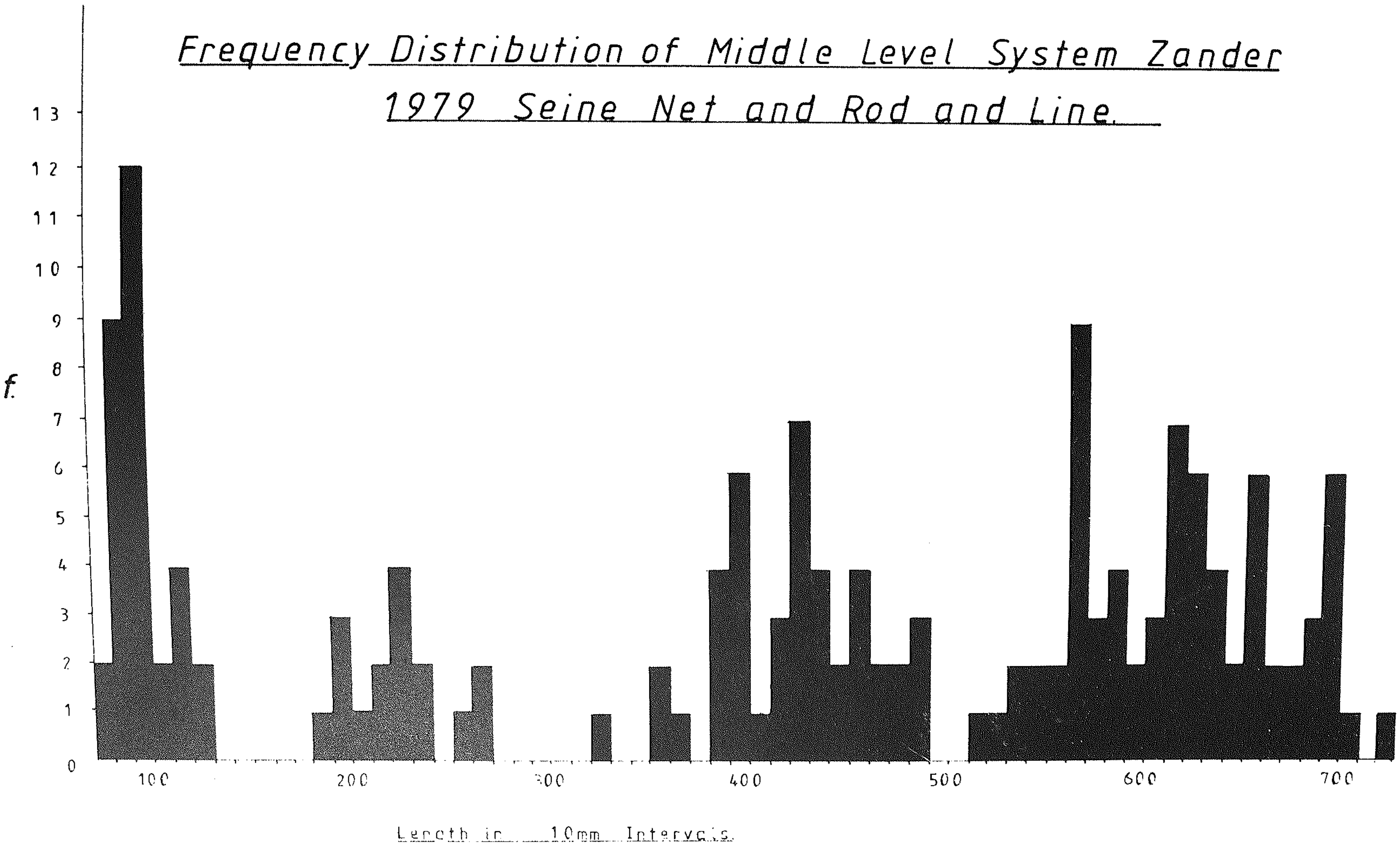


Figure 11.

Frequency Distribution of Middle Level System Zander 1979 Seine Net and Rod and Line.



These could then be compared with the length frequency modes shown in Figures 10 and 11, by conversion to percentage frequencies and plotting on probability paper. Straight lines were fitted to the points obtained. (Figures 12 and 13). The open circles shown in Figures 12 and 13 represented the plotting of cumulative frequencies, for the purpose of determination of the points on inflexion as explained by Cassie (1954).

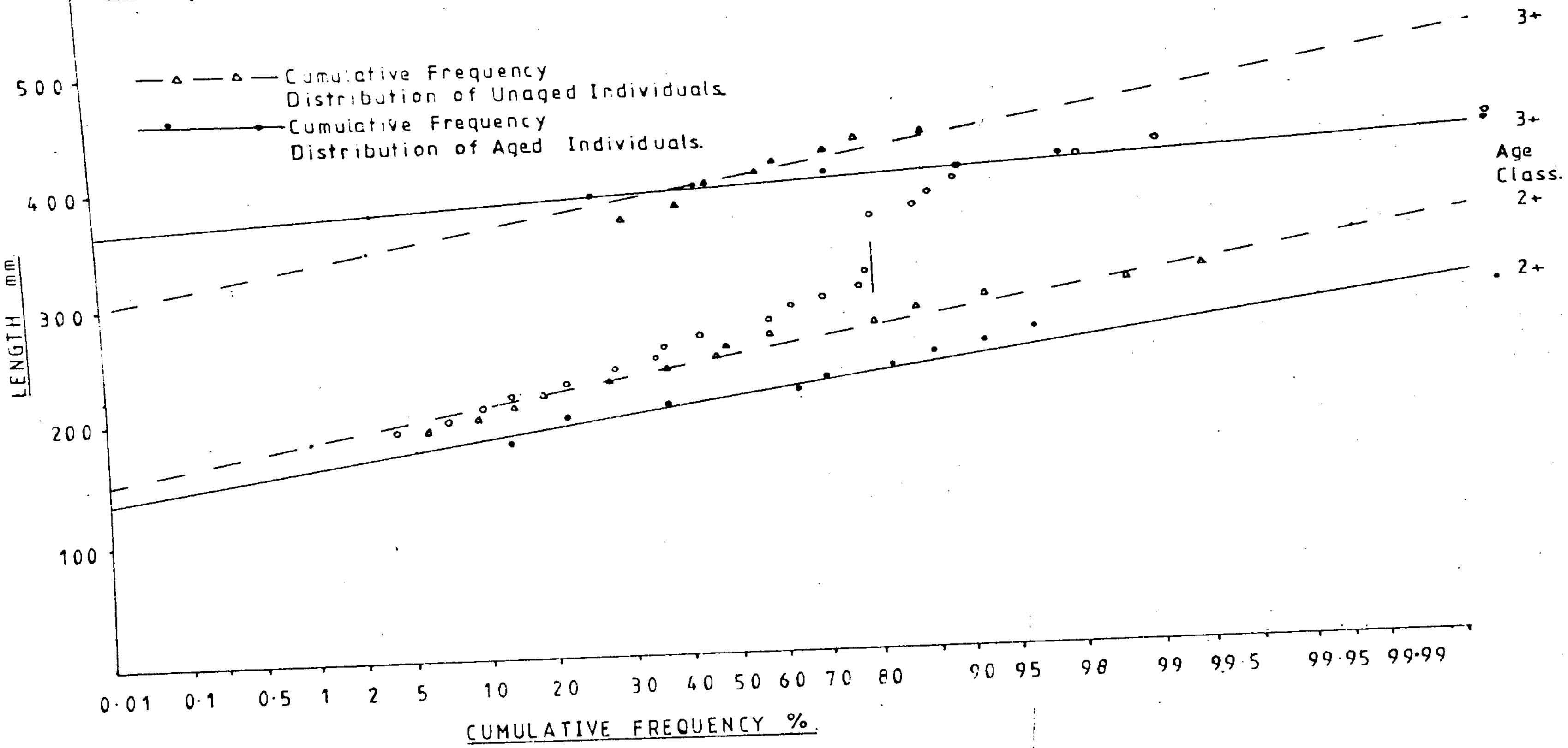
For Coombe Abbey data, ages 2+ and 3+ showed that there was, in fact no significant difference between the modes, (Table 11). Middle Level system data showed similarity between age determined length frequencies and length frequency distributions for the 0+, 1+, 3+, 4+ and 5+ year groups. Significant differences between age determined modes and those derived from length frequency distributions were not apparent (Table 12) suggesting that the age determinations agreed with the modes obtained using the Petersen method.

One anomaly was noted. For the Middle Level system, the 2+ lines shown in Figure 13 did not show similarity. This may have been due to the small number of fish available for this age group.

Beyond the age of 5 it is likely that considerable overlap in length occurs in age groups. This prevents further comparisons between modes, due to the difficulty in locating them precisely.

Figure 12.

Frequency Distribution of Coombe Abbey (1979) Zander.



<u>Figure 13.</u>

<u>Frequency Distribution of Middle Level (1979) Zander</u>

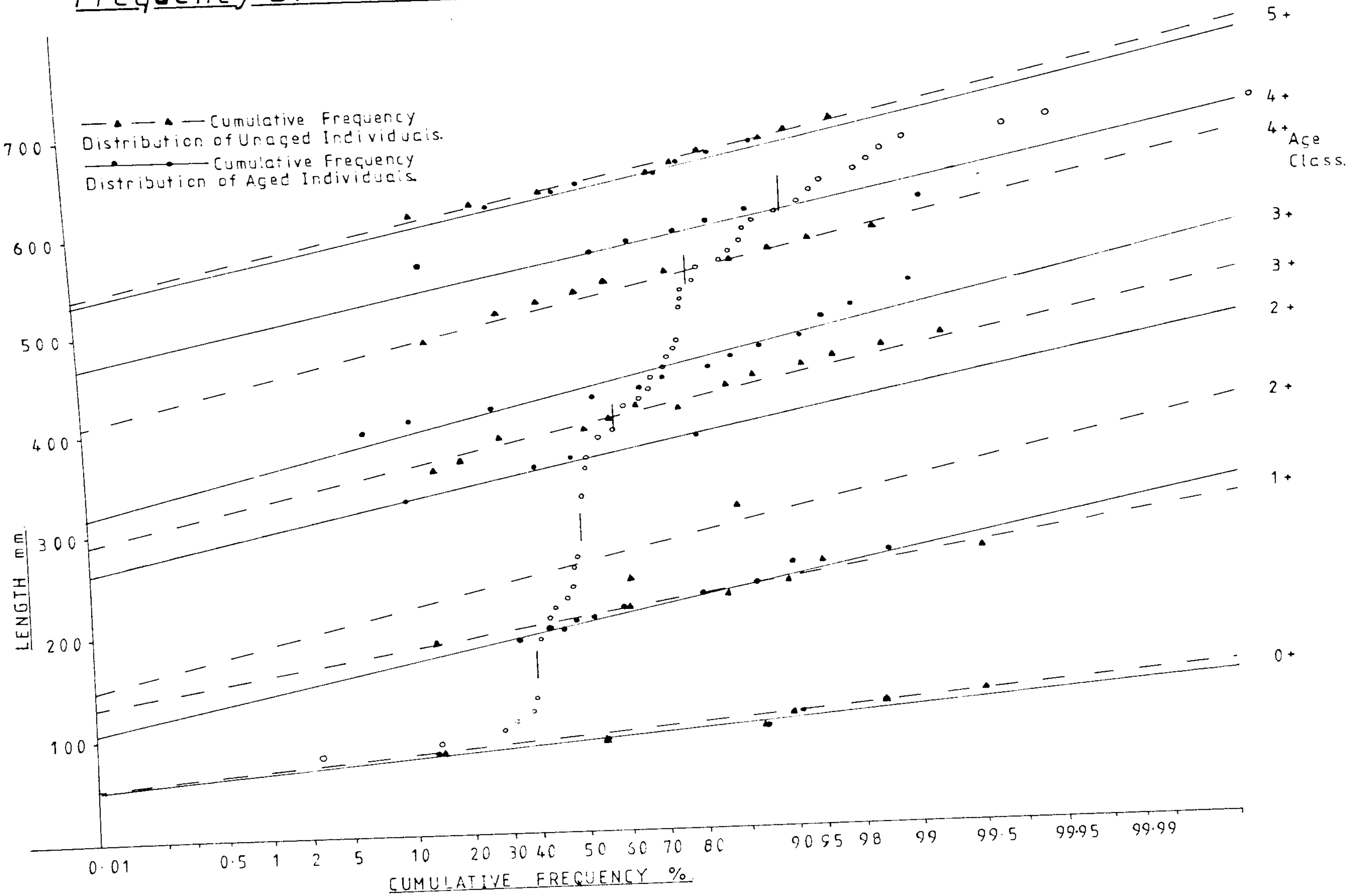


TABLE 11: Results of t tests between mean lengths of age determined and length frequency derived modes for Coombe Abbey Lake

Age	t	p	Degrees of Freedom
2+	1.1835	> 0.05	80
3+	0.268	> 0.05	36

TABLE 12: Results of t tests between mean lengths of age determined and length frequency derived modes for the Middle Level System

Age	t	p	Degrees of Freedom
0+	0.12	> 0.05	62
1+	0.645	> 0.05	31
3+	0.723	> 0.05	77
4+	0.86	> 0.05	36
5+	1.93	> 0.05	45
6+	0.899	> 0.05	30

(b) Time of Annulus Formation

Seasonal collections of zander scales from all waters studied were not possible, since availability of the species during the winter months was poor. Zander were also available from some waters over only limited periods (Table 13).

TABLE 13: Availability of zander scales

Water	Periods during which scales were available
Coombe Abbey	June 79. December 79. May 80.
Relief and Cut Off Channel	June 79. July 79. August 79. September 79. October 79. November 79. April 80. June 80.

Coombe Abbey zander are considered first. Three categories of scale development were identified:

No annulus formed
Annulus formed
Annulus formed and plus growth

(Zander available for this study ranged between 180 and 530 mm in length).

Table 14 presents the categories of scale development with the periods of sampling. Numbers in each group are expressed as percentages (actual numbers in brackets).

TABLE 14:

Period %	No Annulus formed	Annulus formed	Annulus with plus growth
June 79	0 (0)	41.2 (14)	58.8 (15)
December 79	0 (0)	0 (0)	100 (20)
May 80	4.2 (1)	79.2 (19)	16.7 (4)

In the majority of fish, annulus formation is complete by the end of May or beginning of June. In a large proportion of the fish examined plus growth was well advanced suggesting that new growth commenced sometime in May. By December all fish showed large amounts of plus growth. This suggests that annulus formation is an annual event which takes place during the spring.

According to Tschugunowa (1931), who studied zander from the Azov, immature zander form the annulus in the spring, whereas, in the case of older fish it originates in the last half of the year. This latter finding was not the case for Coombe Abbey zander. However the majority of Coombe Abbey zander were relatively young fish (93.4%, 3+ or younger), and it is possible that delayed annulus formation was not demonstrated here due to the lack of older fish. Annulus formation of Relief Channel and Cut Off Channel zander was examined to determine the existence or otherwise of this phenomena. Table 15 gives the number of zander with the various stages of scale growth expressed as percentages, (actual numbers in brackets).

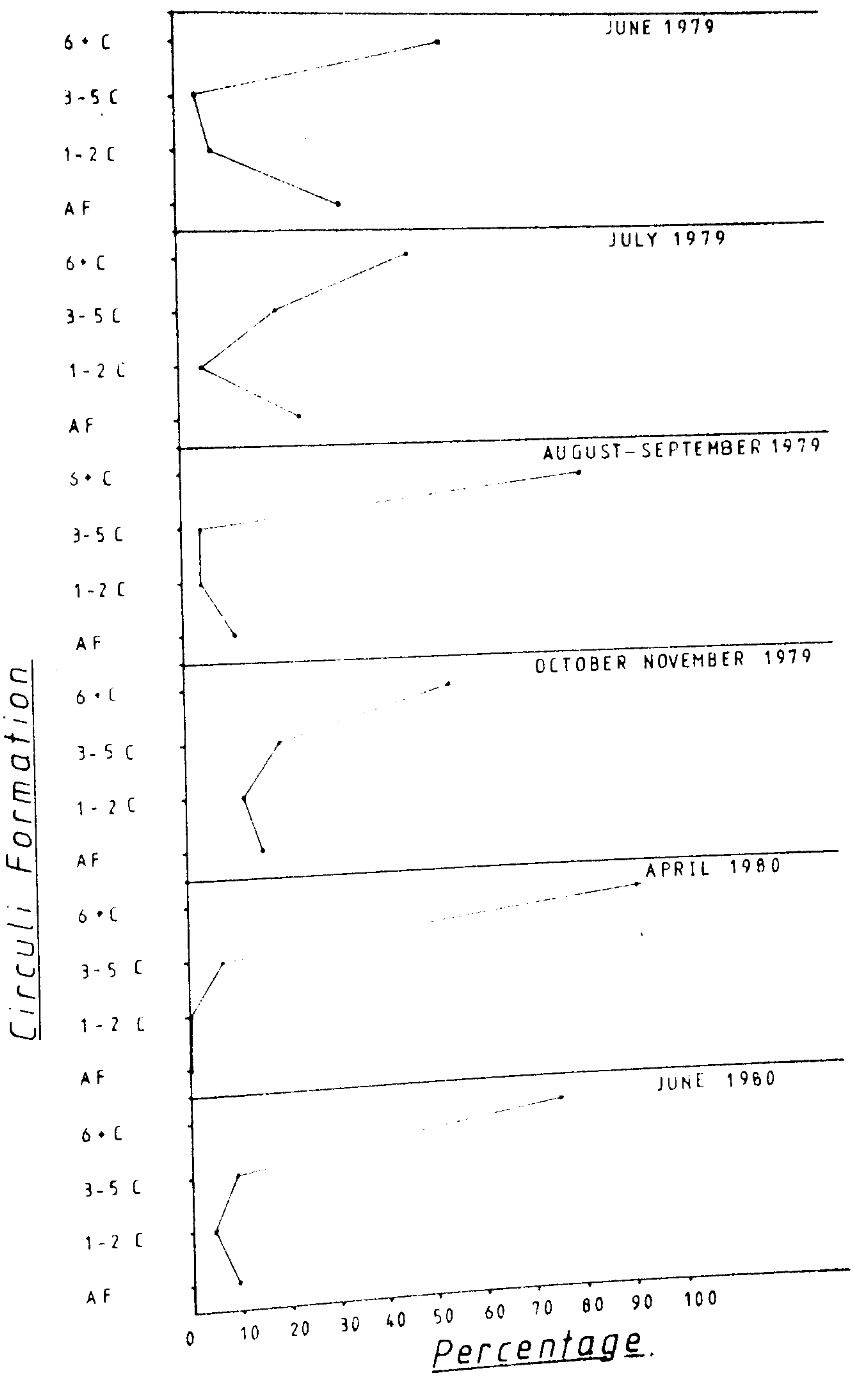
TABLE 15: Number of zander with stages of scale growth

Month	Number of Circuli from last annulus				Total Examined
	Annulus formed no plus growth	1-2	3-5	> 6	
June 79	33.3 (17)	7.8 (4)	3.9 (2)	54.9 (28)	51
July 79	25.7 (9)	5.7 (2)	20.0 (7)	48.6 (17)	35
Aug/Sep 79	10.7 (3)	3.6 (1)	3.6 (1)	82.0 (82)	28
Oct/Nov 79	15.4 (4)	11.5 (3)	19.2 (5)	53.8 (14)	26
April 80	0 (0)	0 (0)	7.7 (1)	92.3 (12)	13
June 80	9.5 (2)	4.8 (1)	9.5 (2)	76.2 (16)	21

The above results are described graphically in Figure 14. If annulus formation occurs in the same manner for both Coombe Abbey and

Figure 14

Circuli Formation on Zander Scales Examined During Different Months



Relief Channel zander, i.e. during May, it would be expected that from June to November, annuli would be present on Relief Channel zander scales in increasing numbers as these months progress. By April, plus growth should be almost complete with the annulus due to be completed in May. In the case of Relief Channel and Cut Off Channel zander, plus growth was still apparent in June with 33.3% of scales showing more than 3 circuli after the previous annulus. There did not appear to be any consistent trend towards increased plus growth with the progression of the months.

However from June 79 to April 80 there was a decrease in the number of fish having annuli without plus growth. This suggests that circuli were being added to the scales as the months progressed. The data obtained suggests that circuli formation was occurring, but for some reason the number of circuli added was not correlated with the passage of time. Two explanations for this could be suggested. Firstly it is suggested that the slow growth of the Relief Channel and Cut Off Channel populations (to be discussed in the following sections) may be responsible for wide variations in growth rate and therefore circuli formation. Nikolsky (1969) has suggested that well nourished fish populations show less variation in growth between individuals of the same sex and age than poorly nourished individuals.

Secondly, the age or length of the fish may have an influence on the number of circuli formed during a given period. A heterogeneous sample of zander would in this case give rise to wide variation in the number of circuli formed in each month. Scales for the Relief and Cut Off Channel study were obtained from zander of 300 to 840 mm. Therefore it was decided to subdivide the sample into two groups and ascertain any difference in circuli addition throughout the year. The two groups comprised fish of less than 550 mm and fish of 550 mm and larger. These groups corresponded to fish of 3 to 5 years and 5 to 12 years respectively.

Table 16 represents the number of fish with specific numbers of circuli expressed as a percentage, (actual numbers in brackets).

TABLE 16: Circuli formation as related to length of zander

Group	Number of Circuli after Annulus			
	Annulus formed	1-2	3-5	>6
550	24.6 (15)	3.3 (2)	4.9 (3)	67.2 (41)
550	25.8 (24)	5.4 (5)	8.6 (8)	60.2 (56)

Examination of the data contained within Table 16 indicates that there is, in fact, very little difference in circuli formation between the two groups. This would tend to suggest that the first explanation is the probable cause of the irregular circuli formation, since one would expect a much greater variation should the second situation apply.

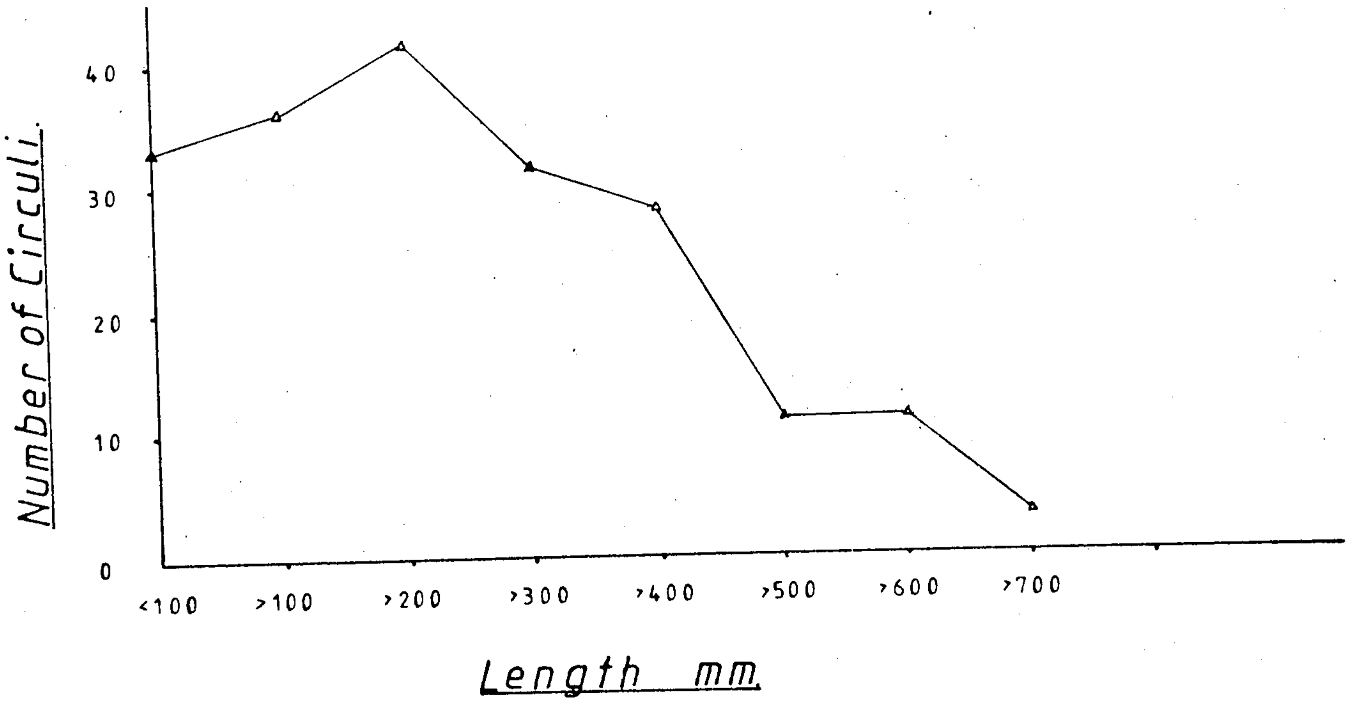
Slow growth in the fish population is therefore more likely to be responsible for the absence of a normal correlation between circulus formation and the time of year, observed in Relief Channel zander.

Examination of scales from zander obtained during October and November of 1979 from the Middle Level system showed that circuli formation was in this case clearly related to size and age. Figure 15 shows that circuli formation is greatest at a length of 200 mm or an age of approximately two years. Circuli formation occurs at a reduced rate before and after this length. Samples were limited to only a short period of the year and this prevented any conclusion being drawn as to the time of annulus formation. It is interesting to note that in all the fish obtained from the Middle Level system in October, annulus formation was followed by at least 6 circuli. This indicates growth since the spring check was laid down. The Relief Channel zander from the same month of the same year lacked circuli formation in 15.4% of the fish examined with a further 11.5% and 19.2% having 1 to 2 and 3 to 5 circuli respectively. This clearly indicates a differing rate of growth between the two populations, a point which will be considered at length later. It is also likely that irregular or slow growth of Relief Channel zander, has obscured the "normal" relationship between circuli formation and length as shown by a population exhibiting rapid growth (i.e. Middle Level zander).

(c) Zander were marked and recaptured over a period of one to two years. It was hoped that recaptures of zander marked and at liberty for a year or more, would show the addition of another annulus. Unfortunately it appeared that the tags used caused retardation of growth of the zander. This phenomena is dealt with in the section on growth.

(d) Zander held in aquaria or tanks for experimental purposes were generally fed on limited quantities of food compared with those living in the wild. Though growth was noted it was less than

Figure 15   The Relationship Between Zander Fork Length and Circulus Number Middle Level System October and November 1979



would have been expected from zander in a more suitable habitat. Examination of scales from zander held in captivity for a year indicated that circuli were being formed close to each other in much the same manner as would be expected during winter growth, even though water temperatures ranged as high as 21 C. This was attributable to the low food ration during captivity. Annulus formation corresponds to the commencement of new summer growth. The constant level of nutrition would not enable a period of increased growth, thus eliminating annulus formation and a seasonal record of growth.

Small zander of 50 to 150 mm were maintained on rations similar to that consumed in the wild. These fish showed rapid growth during the summer followed by slowed growth in the winter.

Plate 4 shows that formation of the annulus had commenced with the onset of winter feeding and reduced growth.

2.2.3. AGE DETERMINATION AND GROWTH

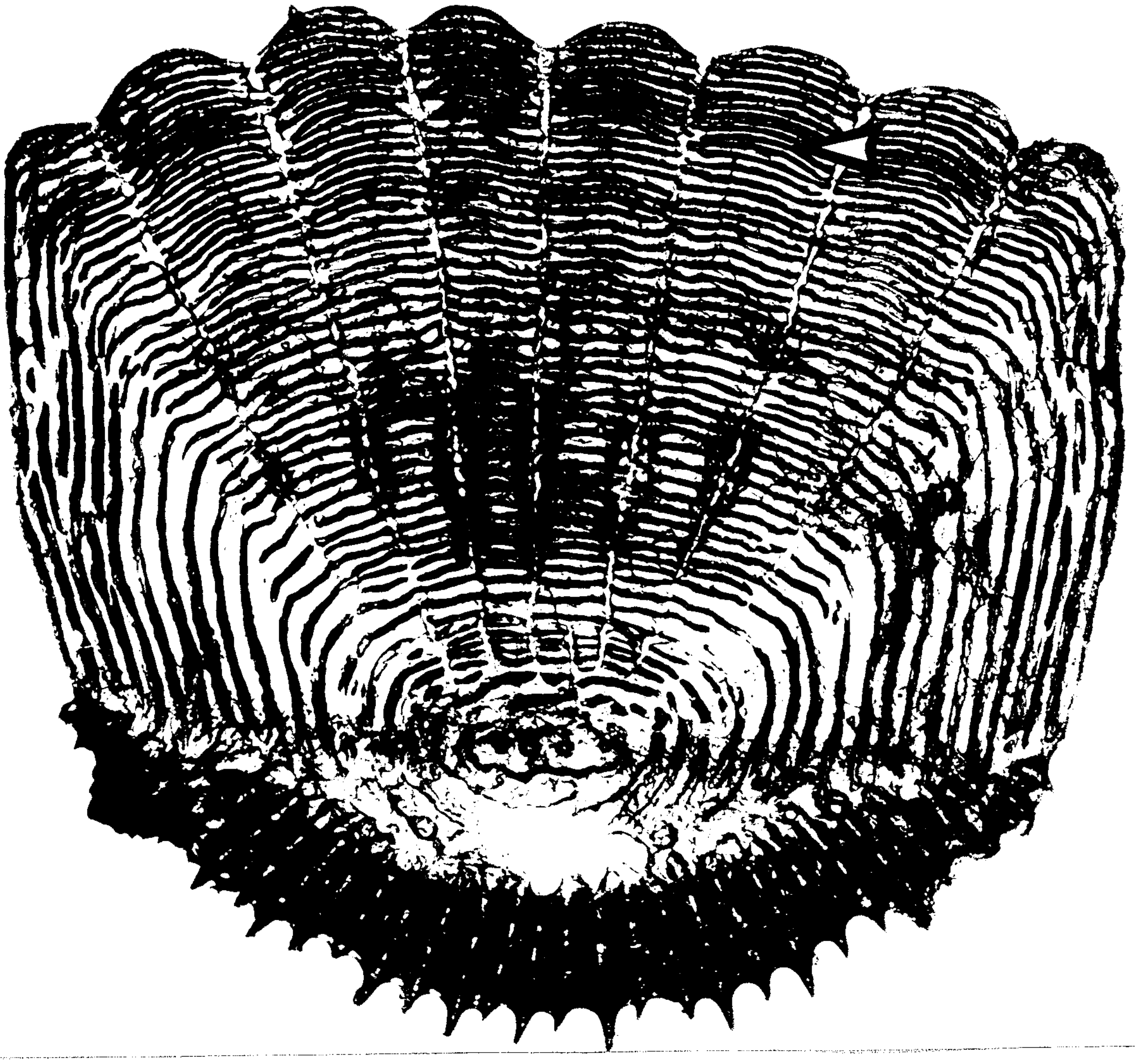
Introduction

Age determinations were carried out using the previously described methods and validation. Two types of evaluation could be made from scale determined ages. These were:

(a) Population growth rates. Here the length for age of each fish in the sample is determined. By finding the mean length of all the individuals of the same age and the 95% confidence limits, it is possible to produce a growth curve depicting the rate of growth of the fish population. The information contained within

Plate 4.

Scale from 150mm Zander January 1981 Showing Winter Circuli.



the curve is confined to the growth of the population as a whole. It does not give detailed information concerning differences in growth of individual age classes of zander.

(b) Individual growth rates. These can be obtained by the method of back-calculation. Using the relationship between scale growth and the increase in fish length enables the determination of the length of individual fish at any particular age (Lea 1910; Zamachaev 1941; Le Cren 1947; Koops 1979; Penaz and Tesch 1970; Reay 1972; Tesch 1977). By grouping year classes and then finding mean lengths for age at each year, it is possible to make comparisons of growth between year classes.

Growth data was treated in several ways to enable the extraction of as much information as possible. The following sections deal with each aspect of growth:

(i) Age for length, population growth.
(ii) Sex influenced differences in growth.
(iii) Differences in year class growth (Back-calculation).
(iv) Determination of L_∞ by means of Walford plots.
(v) Longevity.
(vi) Mortality.

(i) Population Growth Rates

Methods

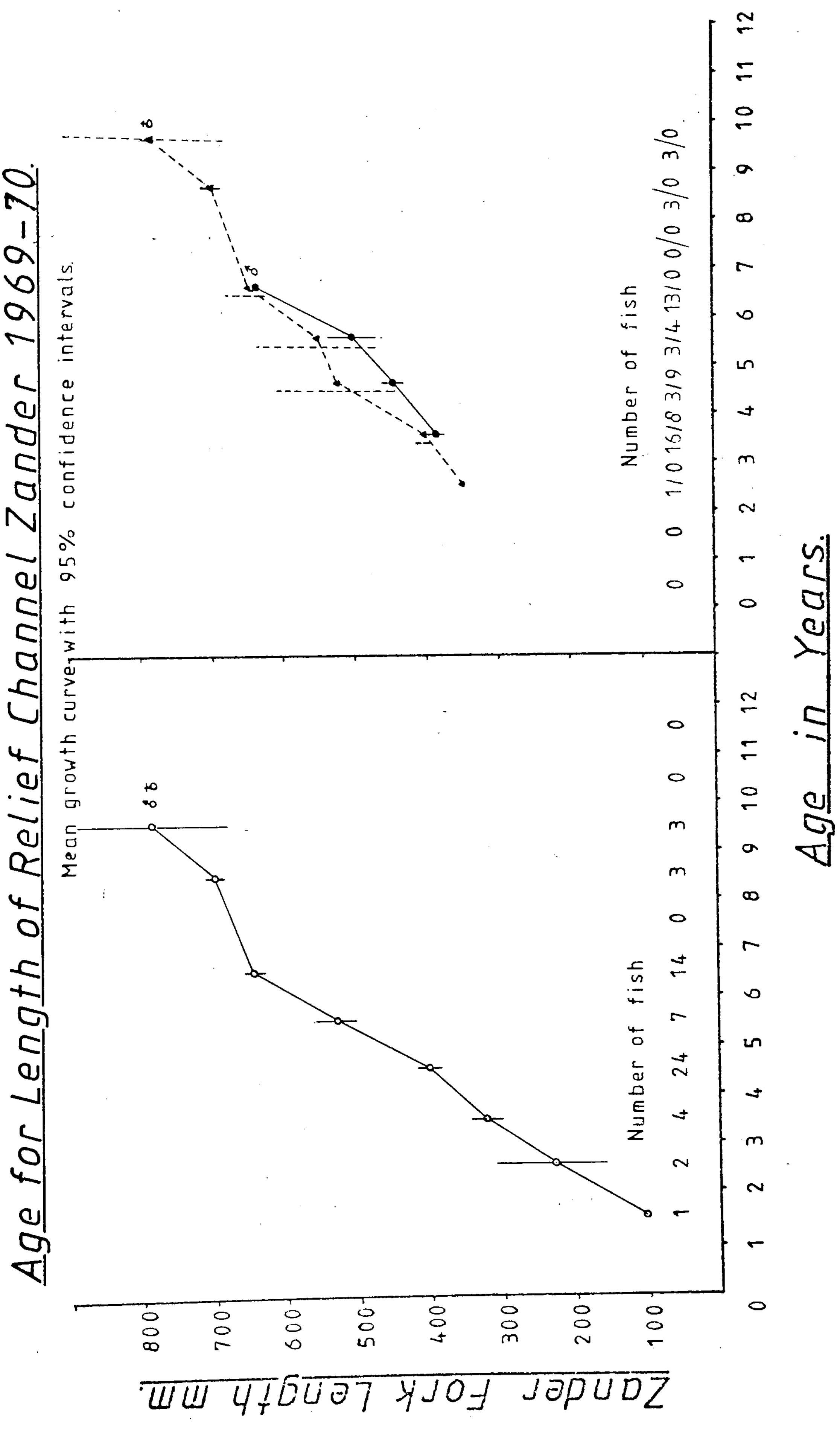
Population growth rates were used for comparisons of growth between samples of zander from different water. Where population growth rates were available for zander from one water, over a period of several years, comparisons were made between defined periods.

Results

All length for age data is presented in Appendix I and in Figures 16 to 22. Where sufficient data were available, male and female growth curves have been presented separately (see (ii)). As mentioned in section 2.2.1. the absence of May determined length for age data from the Relief Channel in 1969-70 means that plus growth has to be included in mean length for weight estimates for each age of zander. In order to enable comparison between this and the other populations, the 1969-70 zander were plotted on Figure 16 with plus growth.

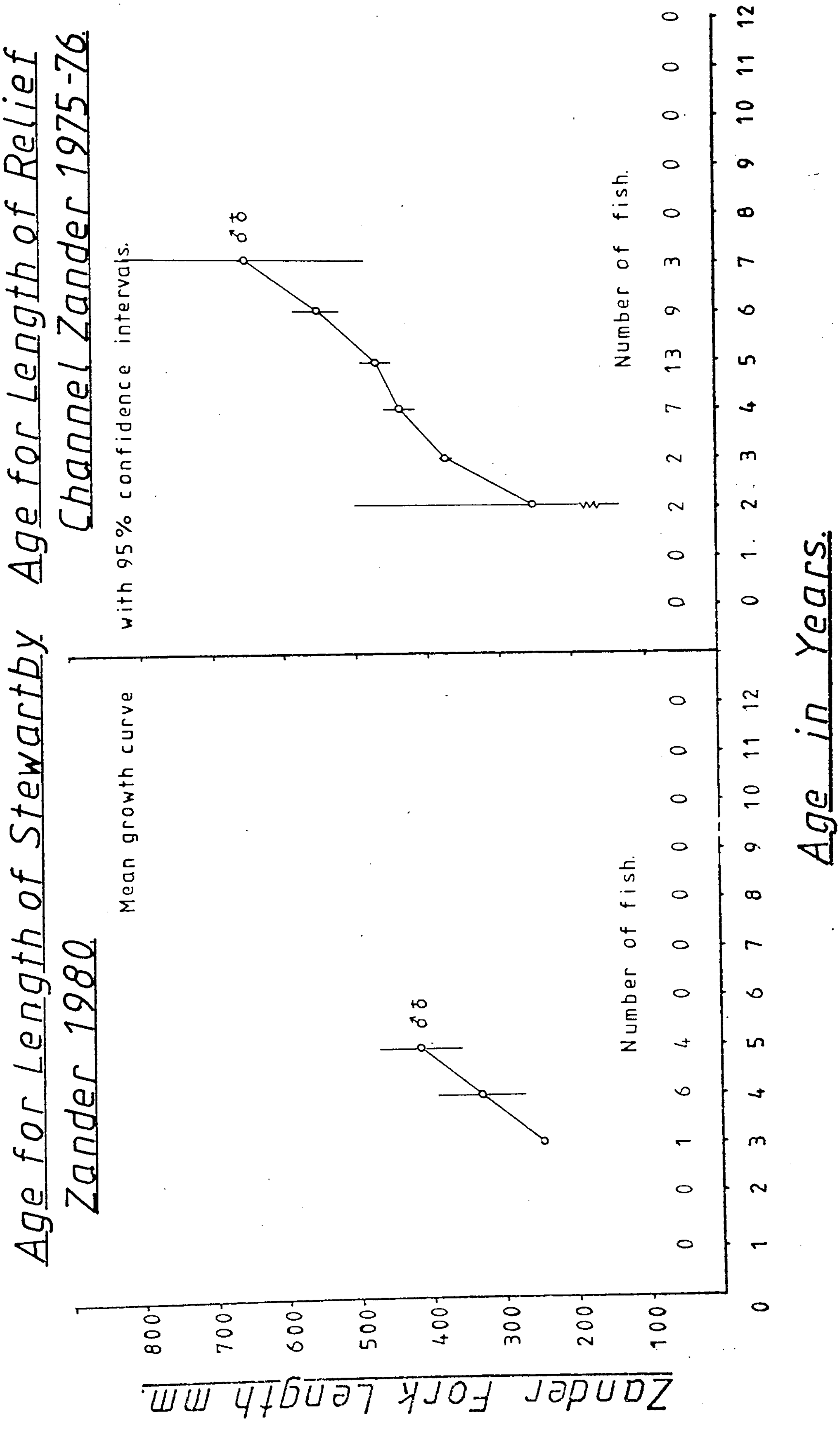
The growth curves obtained fell into two loosely defined groups which will be referred to here as fast and slow growers. Such categories are of a relative nature. Without comparison with the extremes of zander growth noted in other populations - the terms fast and slow are rather arbitrary. However as will be seen later the terms fast and slow do in fact correspond with fast and slow rates of growth noted in continental populations. The fast growers included the zander from the Middle Level in 1979-80, Coombe Abbey 1979-80, Relief Channel 1978-80, Burwell Lode 1979 and Relief Channel 1975-76. The slow growers were from the Coventry and Oxford Canal 1978-80 and Stewartby 1980 populations. The growth of Relief Channel 1975-76 zander appeared to slow considerably after the 4th year, however this trend was reversed by the 6th year where growth again became rapid. Such changes in growth curve shape are to be expected when growth data is derived from population growth rates. Such changes in rate of growth which are dependent on the fortune of the various year classes of zander will

Figure 16.



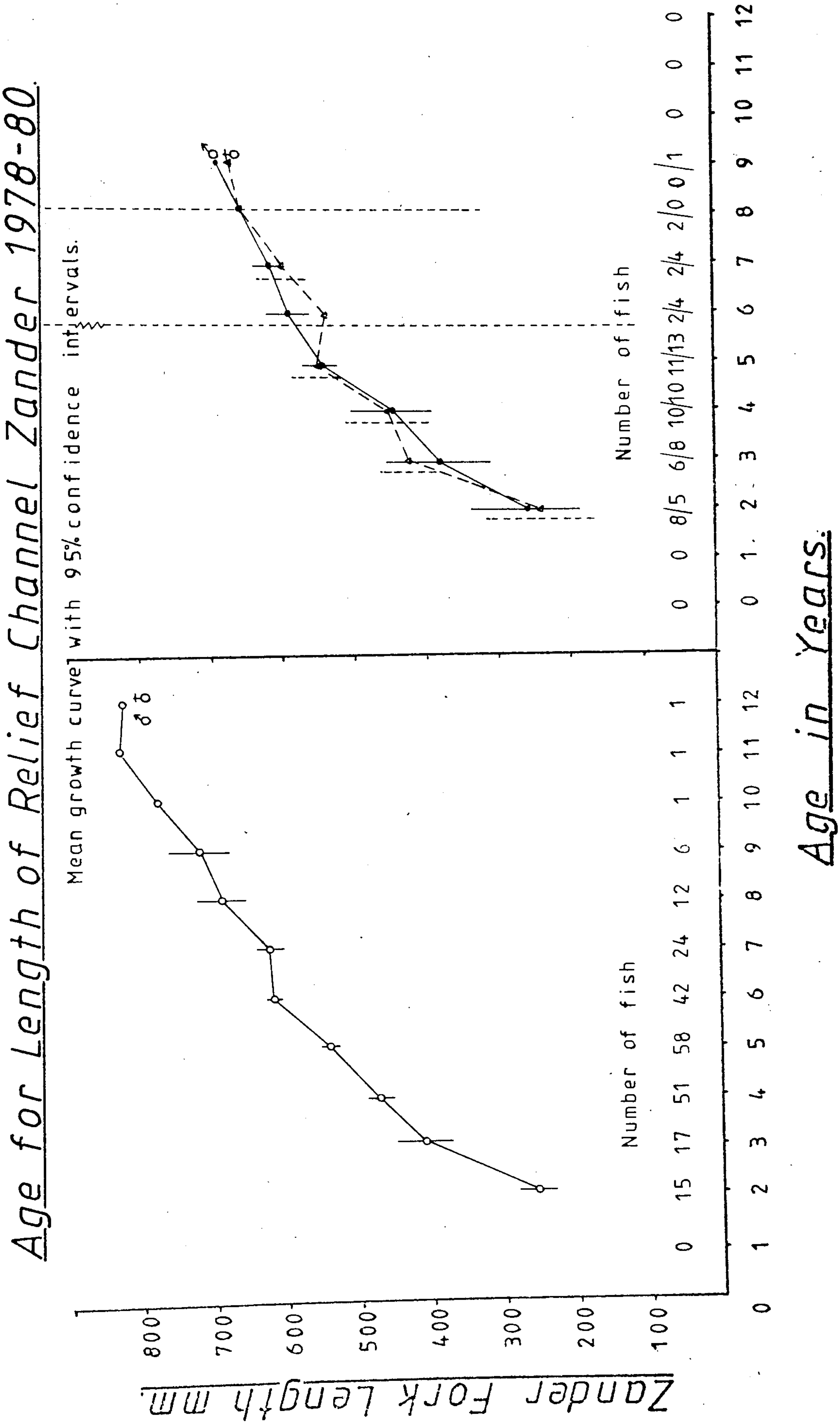
Age for Length of Relief Channel Zander 1969-70.
Mean growth curve with 95% confidence intervals.
Zander Fork Length mm.
800
700
600
500
400
300
200
100
0 1 2 3 4 5 6 7 8 9 10 11 12
0 1 2 3 4 5 6 7 8 9 10 11 12
Number of fish
1 2 4 24 7 14 0 3 3 0 0
Number of fish
0 0 1/0 15/8 3/9 3/4 13/0 0/0 3/0 3/0
Age in Years.

Figure 17



Age for Length of Stewartby Zander 1980
Age for Length of Relief Channel Zander 1975-76
Mean growth curve
with 95% confidence intervals.
Number of fish.
0 0 1 6 4 0 0 0 0 0 0
0 0 2 2 7 13 9 3 0 0 0 0 0
♂♀
Zander Fork Length mm.
800
700
600
500
400
300
200
100
0
1 2 3 4 5 6 7 8 9 10 11 12
Age in Years.

Figure 18.



Age for Length of Relief Channel Zander 1978-80.
Mean growth curve with 95% confidence intervals.
Zander Fork Length mm.
Age in Years.
Number of fish
0 15 17 51 58 42 24 12 6 1 1 1
Number of fish
0 0 8/5 6/8 10/10 11/13 2/4 2/4 2/0 0/1 0 0 0
♂ ♀
100 200 300 400 500 600 700 800
0 1 2 3 4 5 6 7 8 9 10 11 12

Figure 19

Age for Length of Middle Level System Zander. 1979-80.

Mean growth curve with 95% confidence intervals.

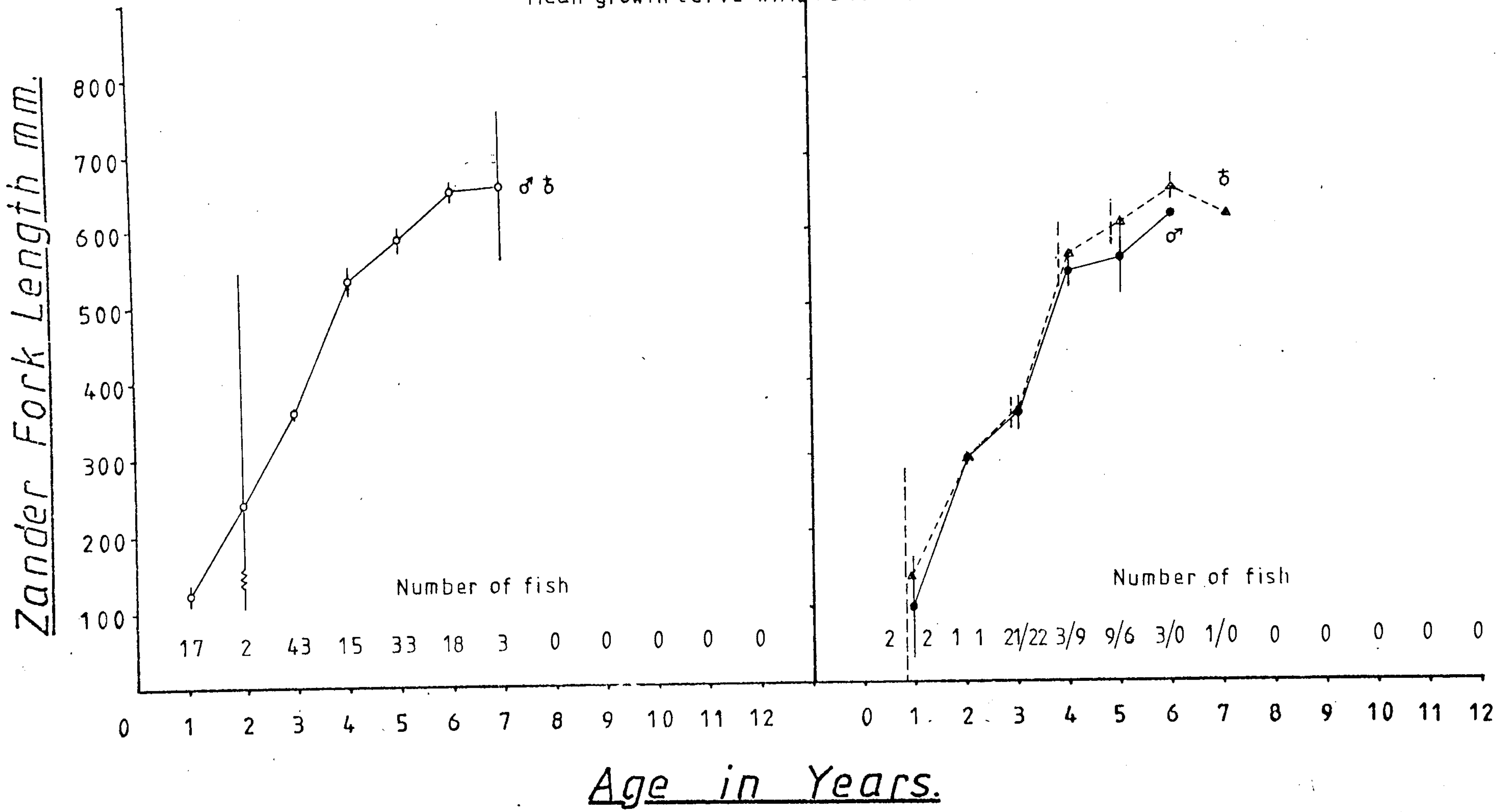


Figure 20.

Age for Length of Burwell Lode[1] and Oxford Canal[2] Zander.

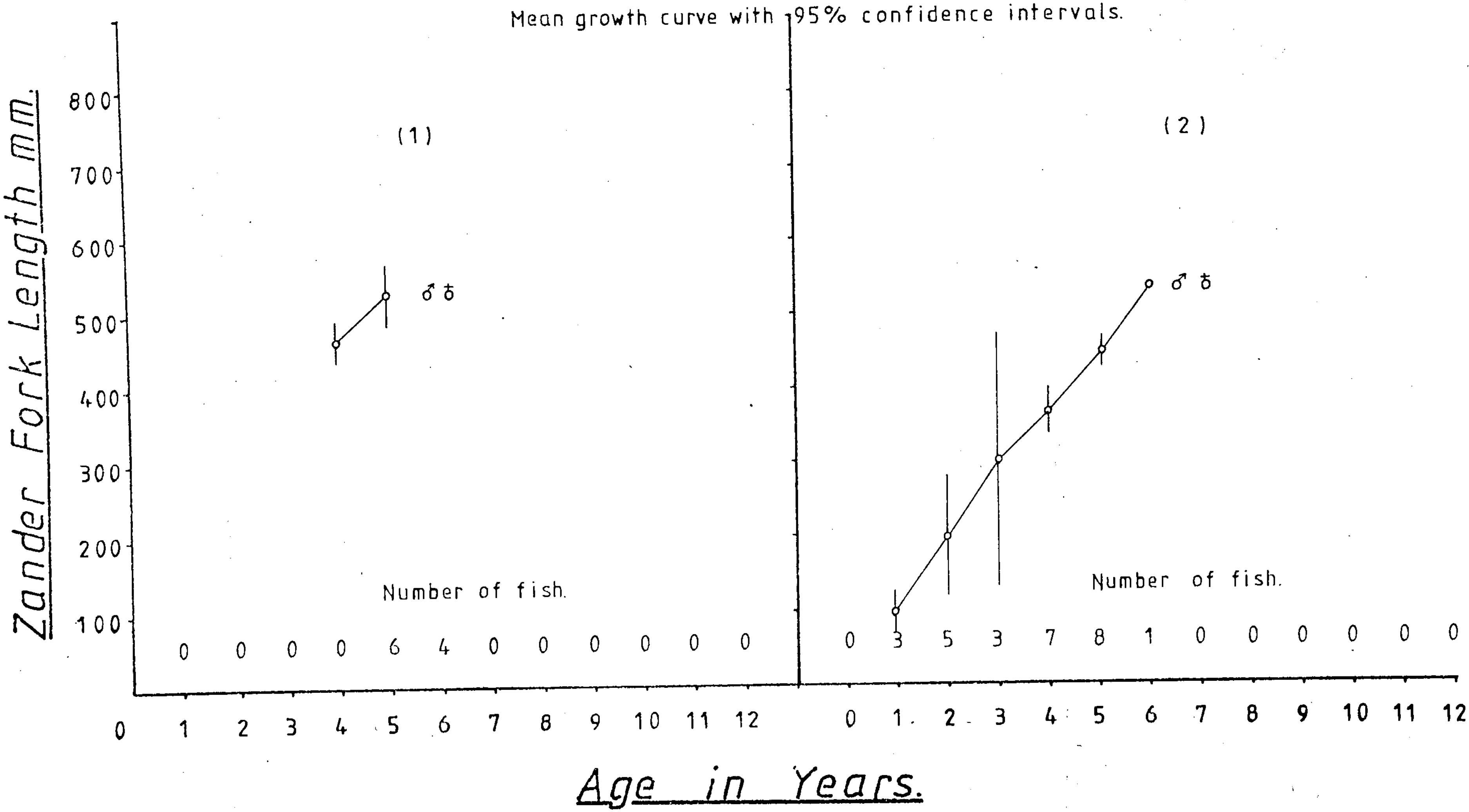


Figure 21.

Age for Length of Coombe Abbey Lake Zander 1979-80.

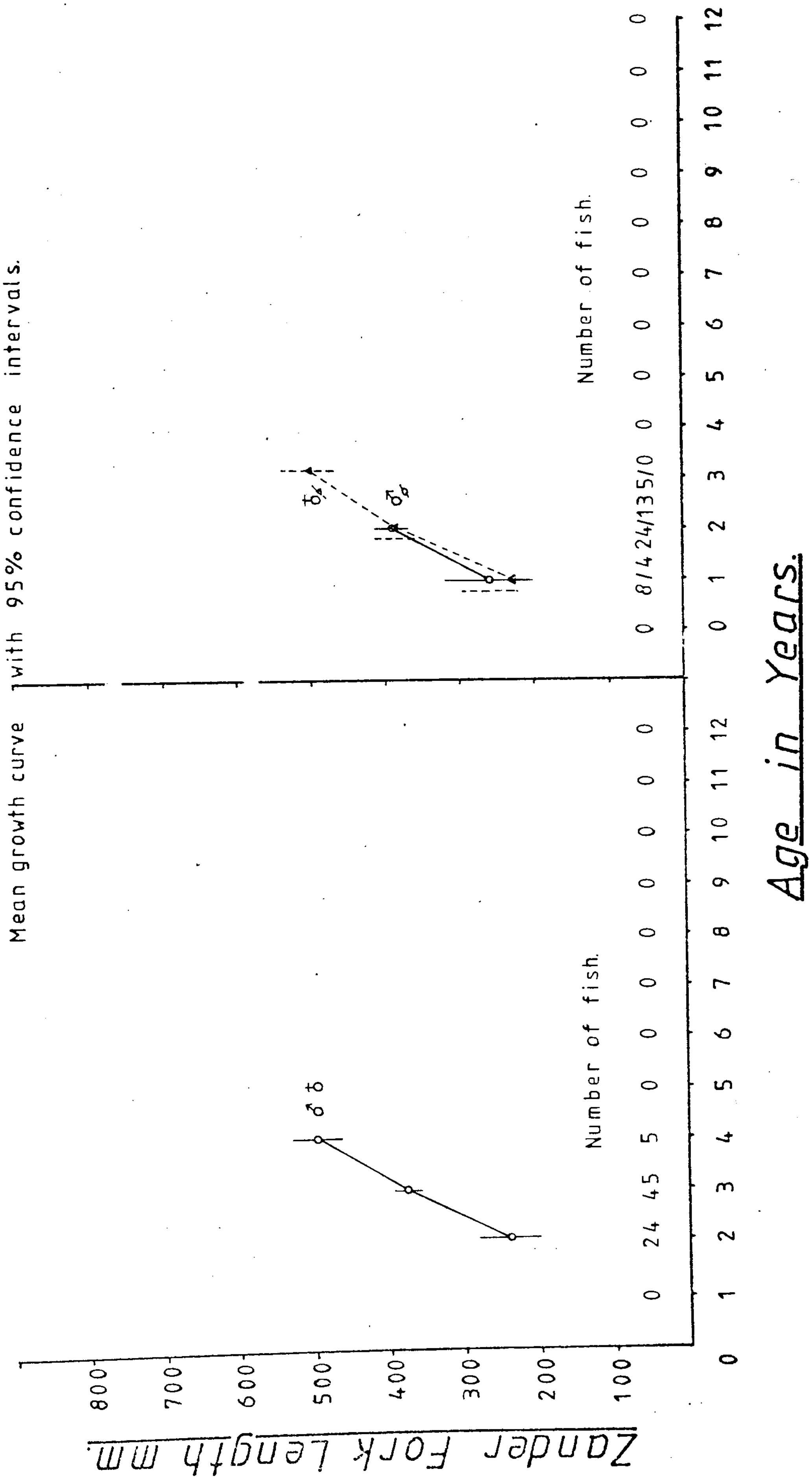
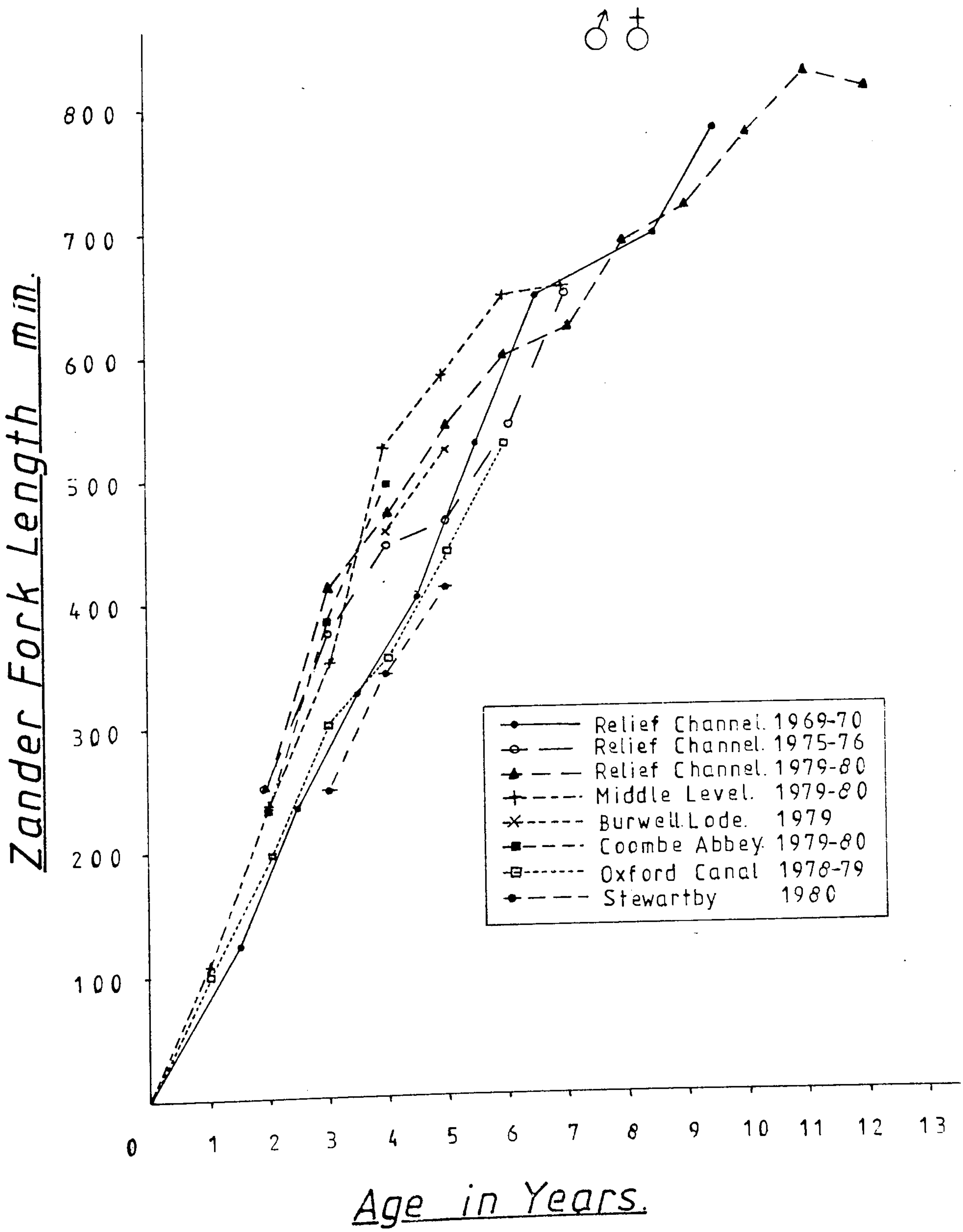


Figure 22.

Age for Length of Zander from all Waters Studied.



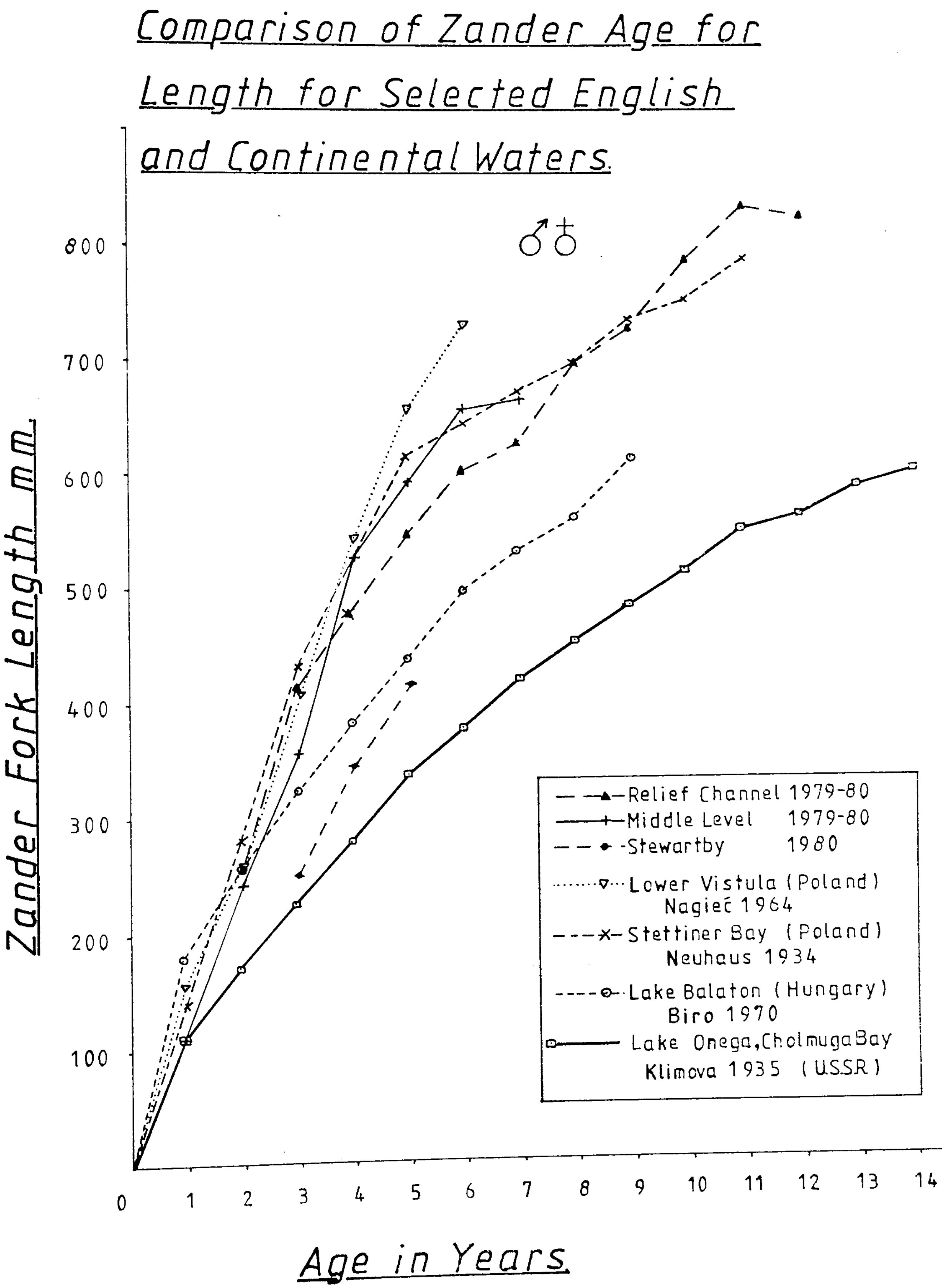
be examined in detail in sub-section (iii).

Despite this problem, population growth rates can be used to make interesting comparisons with other data derived in a similar manner. The growth curves of four different zander populations which have been obtained from continental waters are presented in figure 23. Selected English zander populations which are representative of the range of growth rates found in English zander are also included. All continental data was suitably converted to fork lengths by means of the relationship of fork length to body length and fork length to total length (Figure 6).

Continental zander lengths for ages could also be divided into fast and slow growers. Fast growers included two Polish populations, that of the Lower Vistula (Nagiec 1964) and Stettiner Bay (Neuhaus 1934). Slow growers included Lake Balaton in Hungary (Biro 1970) and Lake Onega in the U.S.S.R. (Klimova 1935). It can be seen from Figure 23 that none of the English populations studied so far have growth rates as low as Onega zander. Stewartby and Coventry and Oxford Canal zander showed respectively slower and similar growth to the zander of Lake Balaton. The remaining populations of English zander appear to show growth rates comparable to those of the faster growing continental zander.

The study of changes in population growth rates between periods could only be attempted for Relief Channel zander. Here data was available for three discrete periods, these being 1969-70, 1975-76 and 1978-80. It would appear that growth of zander up to 4 years was for 1975-76 and 1979-80, similar. Beyond 4 years, growth of the 1975-76 zander sample was erratic. Up until the age of 5 years,

Figure 23.


Comparison of Zander Age for Length for Selected English and Continental Waters.
♂♀
Zander Fork Length mm.
800
700
600
500
400
300
200
100
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Age in Years.
Relief Channel 1979-80
Middle Level 1979-80
Stewartby 1980
Lower Vistula (Poland) Nagieć 1964
Stettiner Bay (Poland) Neuhaus 1934
Lake Balaton (Hungary) Biro 1970
Lake Onega, Cholmuga Bay Klimova 1935 (USSR)

the 1969-80 zander were slow growers, however beyond this age growth increased rapidly. As mentioned earlier, such variations in growth, when caused by age class growth differences are best investigated by other means.

(ii) Sex Influenced Differences in Growth

Methods

Mean lengths for age of male and female zander were compared by means of a t test to determine whether there existed a significant difference in growth between the sexes.

Results

The result of the significance tests are shown in Table 17. It was noted that out of the 13 groups tested, only two showed significant differences. In both cases the males were smaller than the females.

TABLE 17: Results of Significance Test, Intersex Differences in Length

Water	Period	Age	Significance	P	df
Relief Channel	1969-70	3+	Males smaller	< 0.05	22
" "	"	4+	Males smaller	< 0.05	10
" "	"	5+	No sig. dif.	> 0.05	5
" "	1979-80	3	" "	> 0.5	10
" "	"	4	" "	> 0.5	18
" "	"	5	" "	> 0.5	22
" "	"	6	" "	> 0.05	4
" "	"	7	" "	> 0.1	4
Middle Level	1979-80	3	" "	> 0.1	41
" "	"	4	" "	> 0.05	10
" "	"	5	" "	> 0.1	13
Coombe Abbey	1979-80	1	" "	> 0.1	10
" "	"	2	" "	> 0.1	35

(iii) Differences in Year Class Growth (Back-calculation)

Methods

This study required the determination of individual growth rates and these were obtained by means of back-calculation. Scales were employed for back-calculation with the limited use of operculi for the confirmation of age estimates. Scatter diagrams for oral or cranial radius against fork length were fitted by means of the method of least squares (Le Cren 1947) to give a straight line relationship. Ricker (1973, 1975) recommends the G.M. functional regression equation which minimises the products of the distances on the x and y axes of a point from the line, rather than the standard predictive regression based on the least squares of the x axis. However according to Bagenal and Tesch (1978) this has not been generally accepted by statisticians. Therefore the method of least squares was employed throughout this work wherever regression lines had to be fitted.

Three types of scale radius, fork length relationships have been described;

(a) Linear. The line passing through the origin.

(b) Linear, but the line not passing through the origin.

(c) Curved. Slope increasing, S shaped or a combination of the two.

Figure 8 shows the relationship obtained for scale radius and fork length. This relationship was of the second type with the intercept on the y axis. When back-calculating lengths at each age it is therefore necessary to include an adjustment for the observed fact that scale formation from the key area selected, occurs at a length of 30.3 mm. This length is similar to the length of 40 m (body length) suggested by Biro (1970) for the formation of scales in the lateral key area. Scalation of zander was noted as being complete at a length of 55 mm, based on a small sample of 0 plus zander obtained from the Forty Foot Drain during the summer of 1980.

A similar type of relationship was noted between opercular bone width and zander fork length (Figure 9). Here the intercept on the y axis was 15.6 mm.

Correlation coefficients of the regressions for scales and opercular bones were both high and signified a strong correlation between scale radius and fork length, $r = 0.994$ ($P < 0.001$) df 242 and opercular width and fork length, $r = 0.968$ ($P < 0.001$) df 80.

For cases where the fitted line does not pass through the origin, a modification of the direct proportion formulae (Fraser 1916; Lee 1920) should be used.

$$ln = \frac{a\ Sn}{S}\ (1-a)$$

Where ln is the length of the fish when annulus 'n' was formed,

l is the length of the fish when the scale sample was taken,

Sn is the radius of annulus 'n' (at fish length ln),

S is the total scale radius,

a is the intercept on the y axis (fork length).

Axes are reversed compared with normal convention, after Norden (1967).

Before any comparisons of growth could be made the possibility of Lee's phenomenon (Lee 1920) being present was considered, since this would result in an underestimation of the mean lengths of older fish. (Bagenal and Tesch 1978). Four possible causes of this phenomenon have been suggested:

(a) Incorrect back-calculation procedure.

(b) Non-random sampling of the population, for example the sampling method tends to select the larger members of the younger ages.

(c) Selective natural mortality, favouring greater survival of the smaller fish.

(d) Selective fishing mortality, similarly biased (Lee, 1920).

To ascertain which causes are involved requires intimate knowledge of the fish population and the sampling procedure. Lee's phenomenon is not always present in back-calculated lengths, and occasionally the reverse effect has been observed (Bagenal and Tesch 1978). The latter could be caused by size selective mortality that bears most heavily on the smaller fish of any age group. There is also the possibility of changes in growth rate occurring over a period of years, due to changing environmental conditions.

In order to make comparisons between lengths for ages of zander of different year classes, the following procedure was adopted. Back-calculated lengths for age of each age class were grouped together and the mean lengths at each age subsequently determined with the 95% confidence limits. The means thus obtained could be compared between year classes. This would enable any differences in growth rate between year classes to be demonstrated.

Results

The mean back-calculated lengths for age of Relief Channel 1979 and Middle Level 1979-80 zander are to be found in Tables 18 and 19

TABLE 18: Relief Channel 1979 Mean Back Calculated Lengths for Year Class

Year Class		Age 1	2	3	4	5	6	7	8	9	10	11	12
1976	$\bar{x}$	138	295	431									
	95%	121-155	273-317	389-473									
	n	8	8	8									
1975	$\bar{x}$	113	212	351	482								
	95%	98-128	190-234	324-378	465-519								
	n	31	33	33	33								
1974	$\bar{x}$	109	198	341	477	543							
	95%	99-119	186-210	321-361	465-490	530-556							
	n	35	42	45	45	45							
1973	$\bar{x}$	98	217	336	452	535	602						
	95%	85-111	199-235	317-355	437-467	529-550	591-613						
	n	25	29	31	31	31	31						
1972	$\bar{x}$	90	222	322	430	503	561	621					
	95%	84-96	202-242	301-343	400-460	481-525	540-582	599-643					
	n	15	15	15	15	15	15	15					
1971	$\bar{x}$	101	226	320	433	511	593	658	703	715			
	95%	83-119	190-262	290-350	395-471	479-543	552-634	614-702	661-745	676-754			
	n	7	8	9	9	9	9	9	9	5			
1970	$\bar{x}$	102	217	324	414	522	572	628	674	764	811	836	
	95%	3-201	185-249	287-361	385-443	471-573	527-617	584-672	635-713				
	n	2	4	5	5	5	5	5	5	1	1	1	
1969		No 1969 year class representatives											
1968	$\bar{x}$	-	202	380	508	585	665	688	746	749	782	815	826
	n	0	1	1	1	1	1	1	1	1	1	1	1
1967	$\bar{x}$	-	218	340	505	561	627	671	715				
	n	0	1	1	1	1	1	1	1				

TABLE 19: Middle Level Main Drain 1979 Mean Back Calculated Lengths for Year Class

Year Class		Age 1	2	3	4	5	6	7
1976	$\bar{x}$	139	238	368				
	95%	128-150	214-262	340-396				
	n	18	18	18				
1975	$\bar{x}$	129	293	448	526			
	95%	97-161	264-322	429-467	507-545			
	n	12	13	13	13			
1974	$\bar{x}$	137	291	459	544	593		
	95%	118-156	276-306	447-483	531-557	590-606		
	n	26	27	28	28	28		
1973	$\bar{x}$	159	331	470	566	617	656	
	95%	80-238	344-355	447-493	545-587	600-634	639-673	
	n	13	14	14	14	14	14	
1972	$\bar{x}$	179	317	434	538	599	636	663
	95%		277-357	352-516	384-692	519-679	549-723	571-755
	n	1	3	3	3	3	3	3

TABLE 20: Coombe Abbey Lake 1979-80 Mean Back-Calculated Lengths for Year Class

Year Class		Age 1	2	3	4
1975	$\bar{x}$	128	208	314	466
	95%				
	n	1	1	1	1
1976	$\bar{x}$	97	247	407	509
	95%	92-102	236-259	401-413	477-540
	n	28	29	29	4
1977	$\bar{x}$	102	238	369	
	95%	96-108	228-250	338-401	
	n	43	43	19	

respectively; similar data for Coombe Abbey 1979-80 being presented in Table 20. These back-calculated lengths for age were then grouped into year classes, and this plotted graphically for Relief Channel 1979, Middle Level 1979-80 and Coombe Abbey 1979-80 data. (Figures 24, 25 and 26 respectively). Dealing with each zander population individually, the mean lengths of each year class at each age were compared by means of a t test. The values of t obtained and their significance are to be found in Appendix II.

The comparisons of mean lengths for year class at each age confirmed the trends noticeable in Figures 24, 25 and 26.

Before any conclusions could be made, it was necessary to eliminate if possible, any other factor which might have given rise to these trends. The most immediate point of concern was the possibility that rod and line angling was selecting the larger individuals of the younger fish. This selectivity was referred to under item (b) of the factors which might contribute to the appearance of Lee's phenomenon in the data. It has already been established that rod and line angling is selective for zander of greater than 361 mm. Where a zander age group such as the three year olds would vary between 300 and 400 mm it is obvious that angling would select the larger individuals. This must be considered when sampling includes fish near to the selectivity limit of the method being used. Fortunately most of the fish obtained from the Relief Channel and Middle Level were much larger than the selectively limit and only 3rd year fish would be likely to show any selectivity induced "largeness". In the case of the Middle Level zander, it was possible to compare seine and electrofished zander with rod and line caught zander and determine whether or not there was a significant difference

Figure 24.

Relief Channel Back-Calculated Lengths for Year Class from 1979.

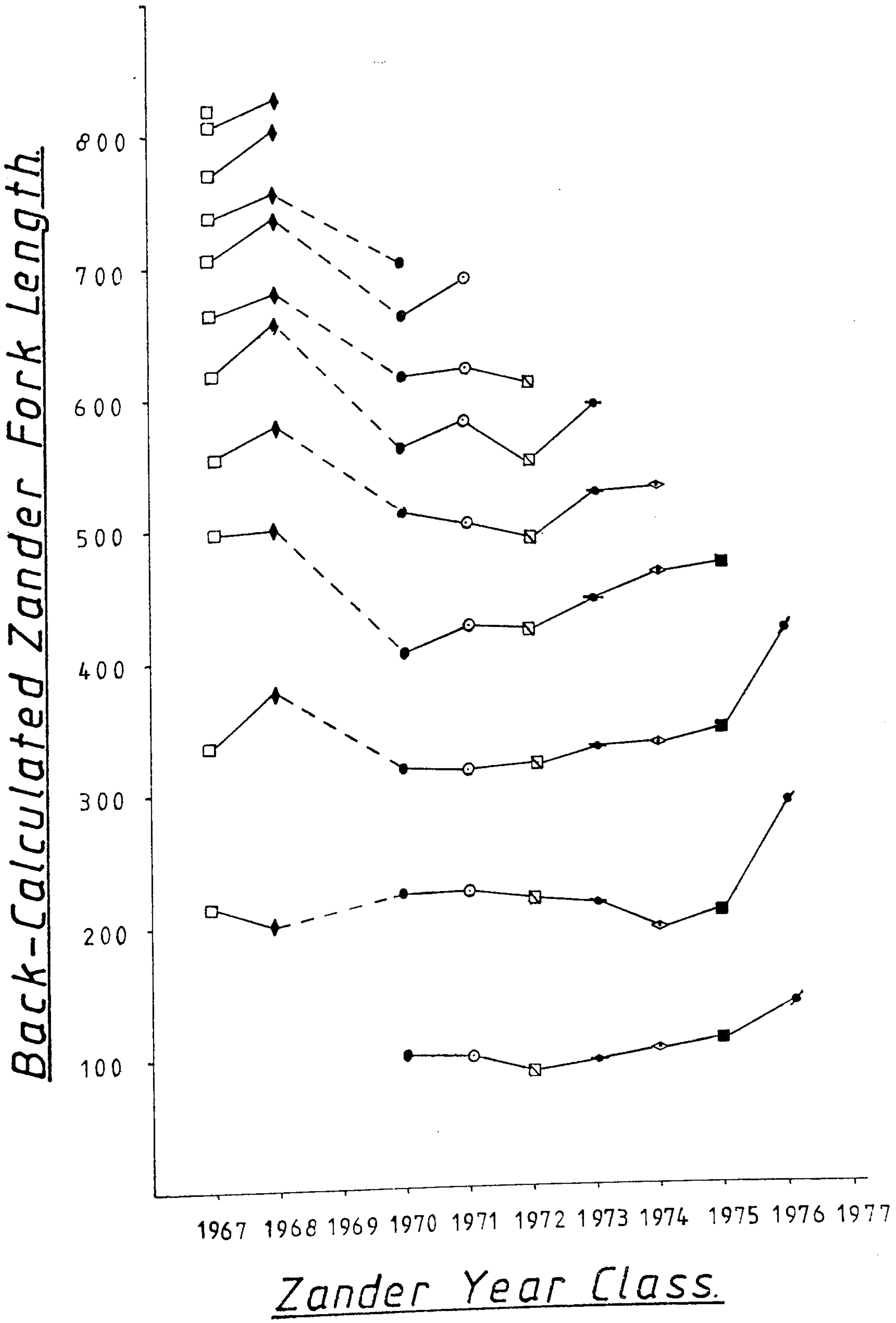


Figure 25.

Middle Level Back-Calculated Lengths for Year Class from 1979.

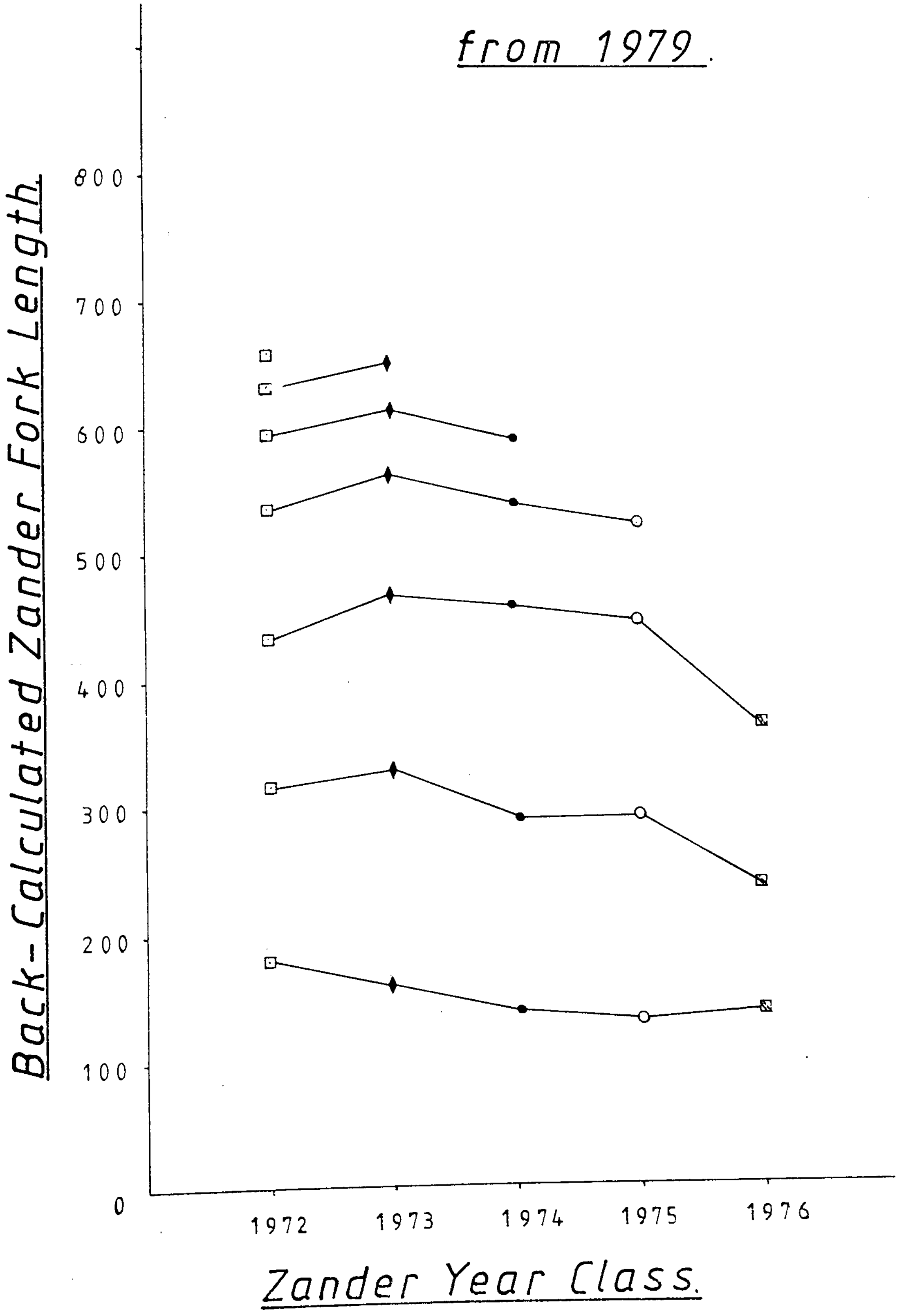
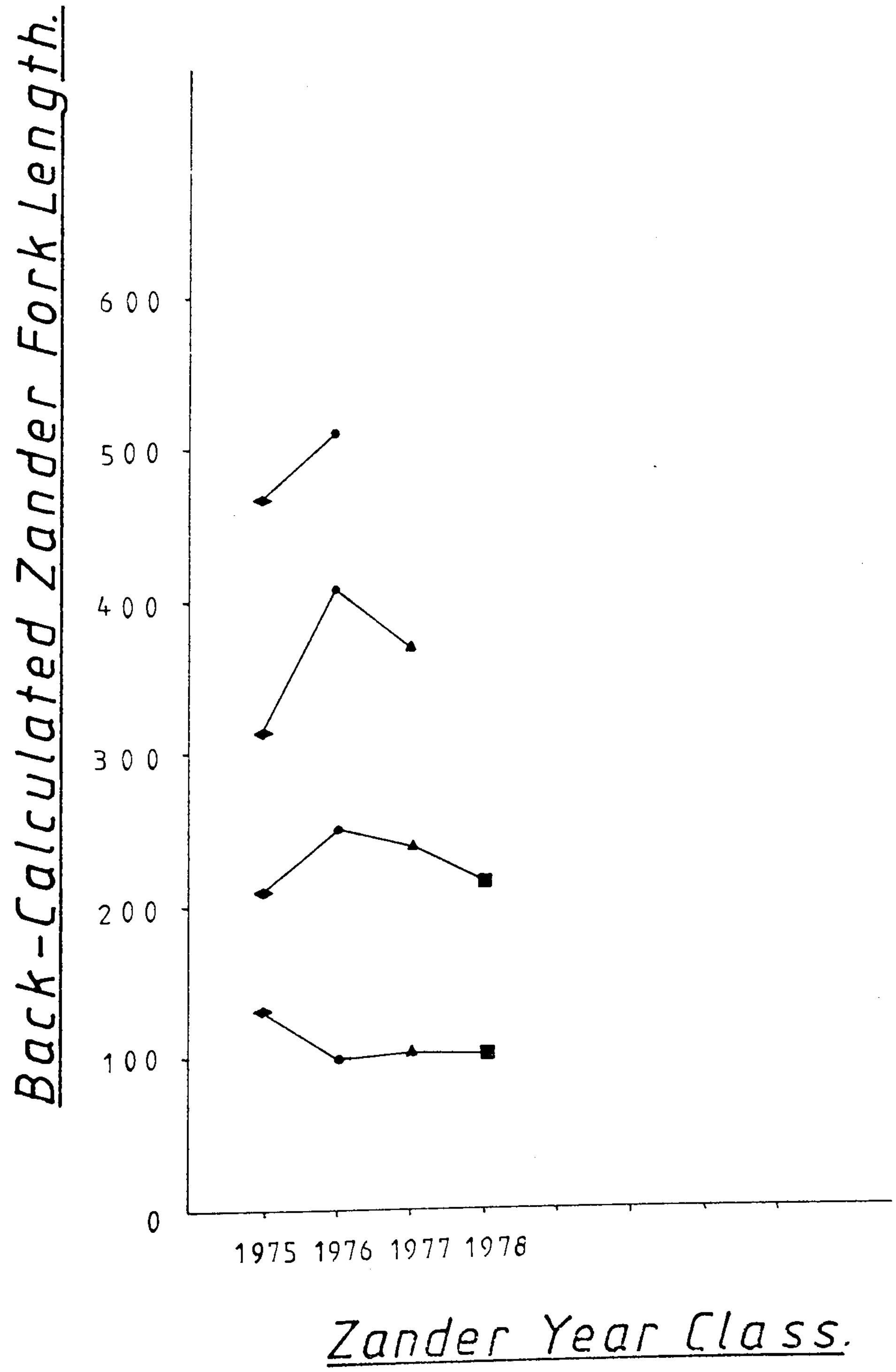


Figure 26.

Coombe Abbey Back-Calculated Lengths for Year Class from 1979-80.



in lengths for year class at each age, using two different capture methods. Zander from the connected Twenty Foot Drain and King's Dyke caught by electrofishing and seine netting were grouped into age classes and the mean length of each age class at each particular age was compared with the corresponding mean length, for Middle Level zander obtained by rod and line angling. (The back-calculated lengths for ages for this comparison are to be found in Appendix I). No significant difference was noted (at the $P > 0.05$ level) between the 1976 year class of each water at year 1, 2 or 3. Provided the waters involved were similar growth rates for each zander population, it would appear that rod and line angling is not noticeably selective for larger individuals of 3 year old zander. (Marking studies suggested that there was an interchange of zander between these waters and this would be liable to result in uniform growth rates between waters). In the case of Middle Level zander it is apparent that the younger fish are smaller at any particular age than were their predecessors at the same age. If rod and line selectivity were selecting the larger individuals, it would presumably have disguised this trend. It is therefore suggested that rod and line angling has not selected to any noticeable degree the larger individuals of the younger fish. All fish obtained from Coombe Abbey were obtained by seine netting and this was suggested as being selective against only the very young zander. The selectivity limit of 60 mm was never approached by zander samples obtained from this water.

The following differences in year class growth were noted for the three populations studied.

Relief Channel 1979

The Relief Channel zander showed the following differences in growth between year classes. The 1976 year class was at all ages (1, 2 and 3), significantly larger than all other year classes. Such consistant significant differences were not apparent with any other year class. The 1975 year class was at year 4 significantly larger than the 1970, 1971, 1972 and 1973 year classes. The 1974 year class was at year 4 significantly larger than the 1970, 1971, 1972 and 1973 year classes. At year 5 it was also significantly larger than the 1971 year class. The 1973 year class was at year 4 larger than 1970 and at year 6 larger than 1972.

At years 1, 2, 3, 4, 5, 6, 7 and 8 the 1970 year class showed little difference in length when compared with similar ages from the 1971 and 1972 year classes. This similarity of growth between the three year classes suggests a fairly uniform and low rate of growth when compared with later age classes. By 1973, some acceleration of growth becomes noticeable, with significantly greater lengths noted for years 4 and 6 when compared with 1970 and 1972. The 1974 year class were significantly longer at year 4 than 1970, 1971, 1972 and 1973. At year 5 the 1974 year class was significantly longer than the 1971 year class. The 1975 year class was at year 4 significantly longer than the 1970, 1971, 1972 and 1973 year classes.

These findings serve to confirm the impression gained from Figure 24, that the more recent year classes were showing increased growth compared to their predecessors.

Middle Level 1979-80

Middle Level zander also showed differences in growth between year classes. In this case the opposite trend to that noted with the Relief Channel 1979 zander was apparent. Middle Level zander year classes showed the following differences in growth.

At year 1 there were no significant differences in growth between any year class. However by year 2, it becomes clear that many of the earlier year classes were greater in length than the later year classes. The 1972 year class was at year 2 larger than the 1976 year class. This was also the case at year 3. The 1973 year class was at year 2 larger than the 1974, 1975 and 1976 year classes. At year 3, 1973 was significantly larger than 1976. At year 4 larger than 1975. The 1974 year class was at years 2 and 3 significantly larger than the 1976 year class. The 1975 year class was at years 2 and 3 significantly larger than the 1976 year class. In no cases were the later year classes longer than the earlier year classes. This suggests that the later zander year classes were showing slowed growth when compared with the earlier ones.

Coombe Abbey 1979-80

The zander population of this water is still relatively young, therefore comparisons between year classes is restricted to only two years, 1976 and 1977. There were no significant differences between the year classes at year 1 and 2. At year 3 the 1976 year class was significantly larger than the 1977 year class.

(iv) Determination of L_∞ by Means of Walford Plots

Methods

Walford (1946) described a graphical method of depicting the growth of a variety of animals including fish. The method entails the plotting of the length of the fish at time 't' against the length at time 't' +1. The points obtained may then be fitted with a straight line using a least squares regression. The intercept with the 45 degree slope is the point of ultimate length L_∞ and this is the estimate of the maximum length which can be attained by the fish population.

Results

Walford plots for all the populations studied were presented in Figure 27. These were derived from population growth rates. A number of the Walford Plots failed to reach L_∞. This was thought to have been caused by differences in growth, of the various year classes found within the population. These could not be used for interpretation. Where data was available, Walford Plots for individual age classes were drawn. This eliminated the effect extreme changes in growth would have on the slope of the line to L_∞. These Walford Plots are to be found in Figures 28a and 28b. The values of L_∞ obtained were tabulated and presented in Table 21.

Figure 27.
Walford Plots.

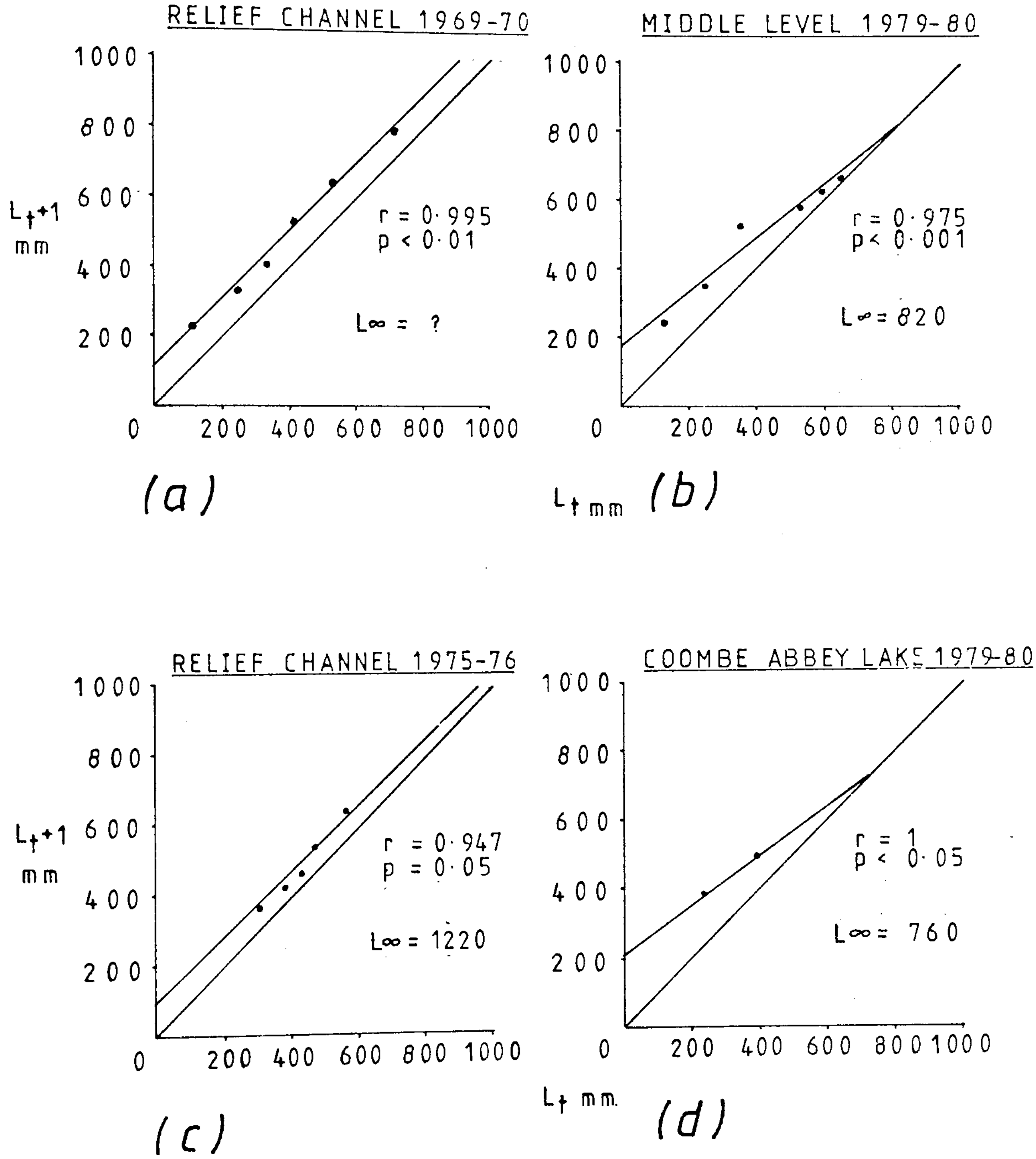
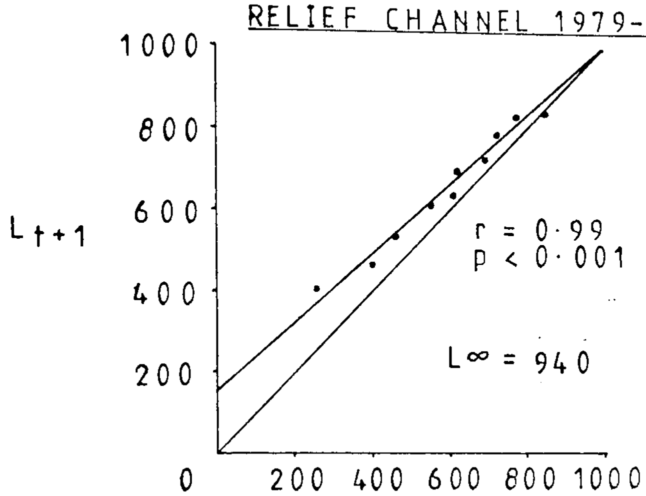
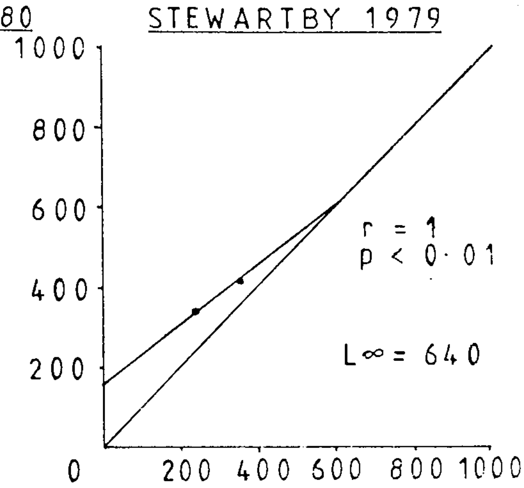


Figure 27.

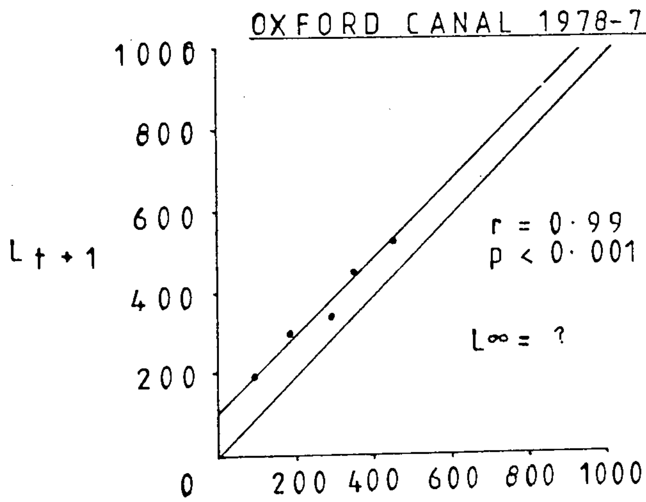
Walford Plots.



(e)



L_t mm. (f)



L_t mm. (h)

(g)

Figure 28.a
Walford Plots.

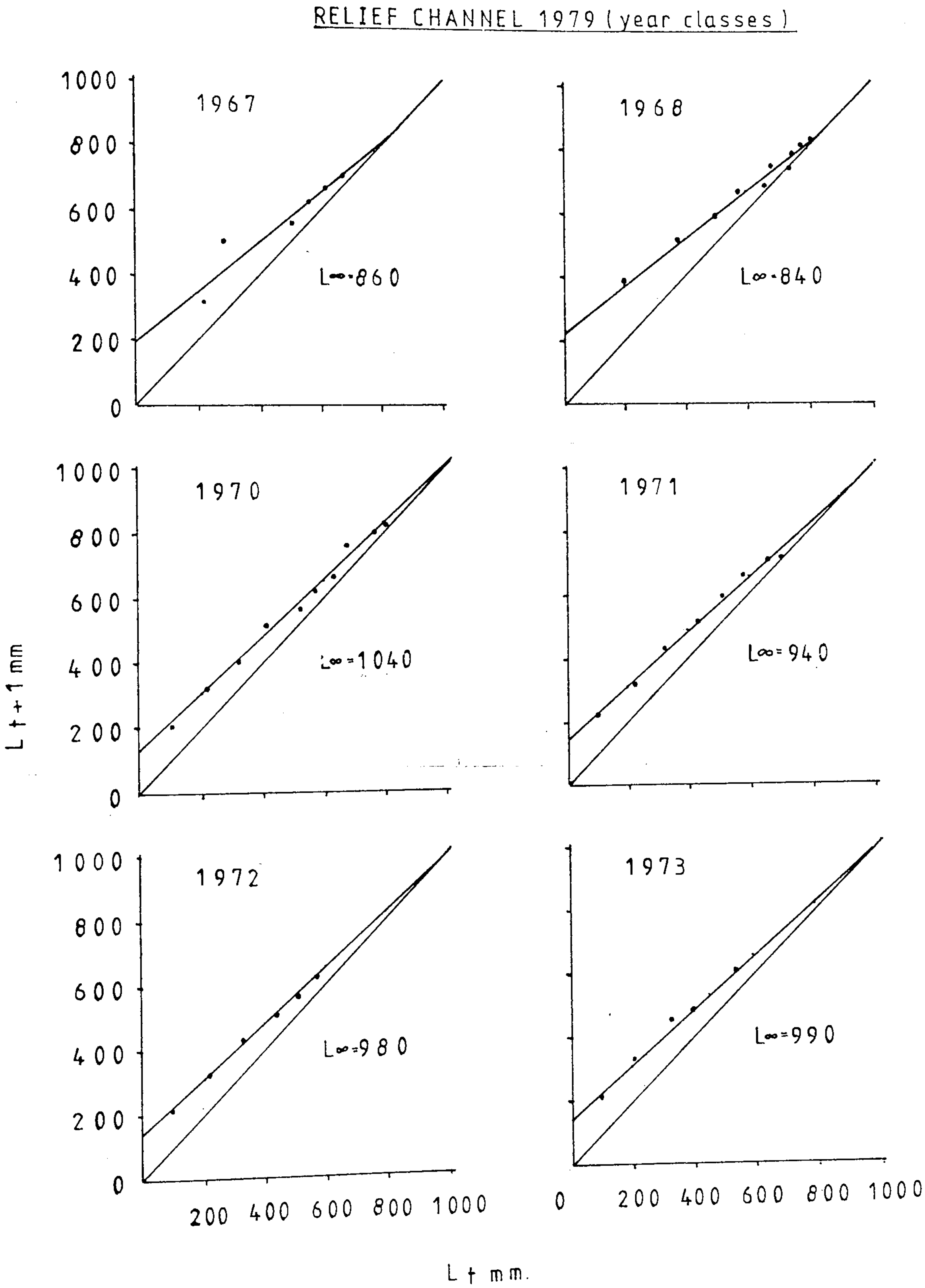


Figure 28b
Walford Plots.

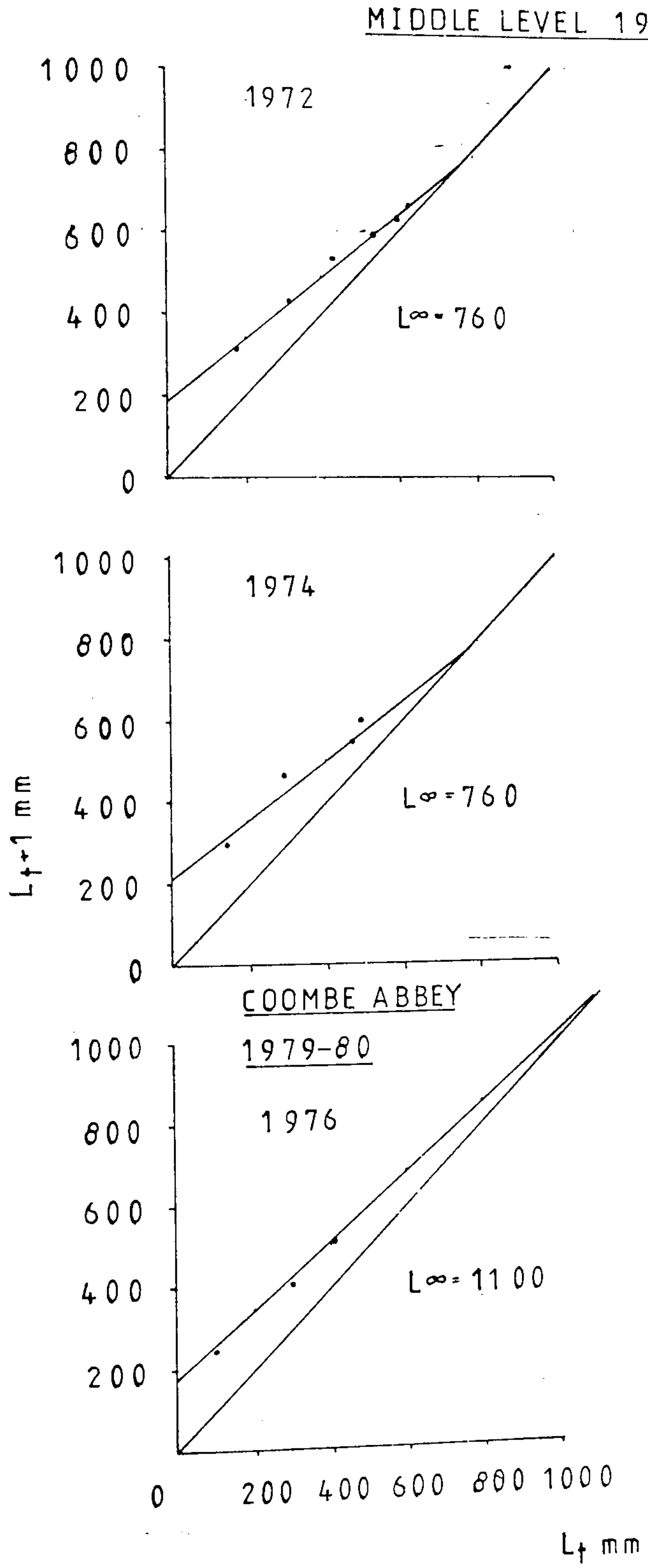


TABLE 21: Values Obtained from Walford Plots

Water	Year	L ∞	Number of Sample
Relief Channel	1979-80	940	216
Middle Level	1979-80	820	131
Coombe Abbey	1979-80	760	72
Stewartby	1980	640	11
Water	**Year Class**		**Number in Sample**
Relief Channel	1967	860	1
Relief Channel	1968	840	1
Relief Channel	1970	1040	5
Relief Channel	1971	940	9
Relief Channel	1972	980	15
Relief Channel	1973	990	31
Middle Level	1972	760	3
Middle Level	1973	800	14
Middle Level	1974	760	28
Middle Level	1975	820	13
Coombe Abbey	1976	1100	29

The Walford Plots of population growth showed that the Relief Channel zander of 1979-80 were likely to attain the greatest length, compared with the other waters. L∞ values were for the Middle Level zander 820 mm, Coombe Abbey 760 mm and lastly Stewartby 640 mm.

Year class Walford Plots showed some variations as expected. There was a slight trend towards increasing L∞ with the more recent Relief Channel year Classes. Middle Level zander year classes showed less obvious variation and values of L∞ were fairly constant. Coombe Abbey zander could only be examined for one year class and this resulted in a very high value for L∞ of 1100 mm. This suggested that growth was fast to a projected large ultimate length.

(v) Longevity

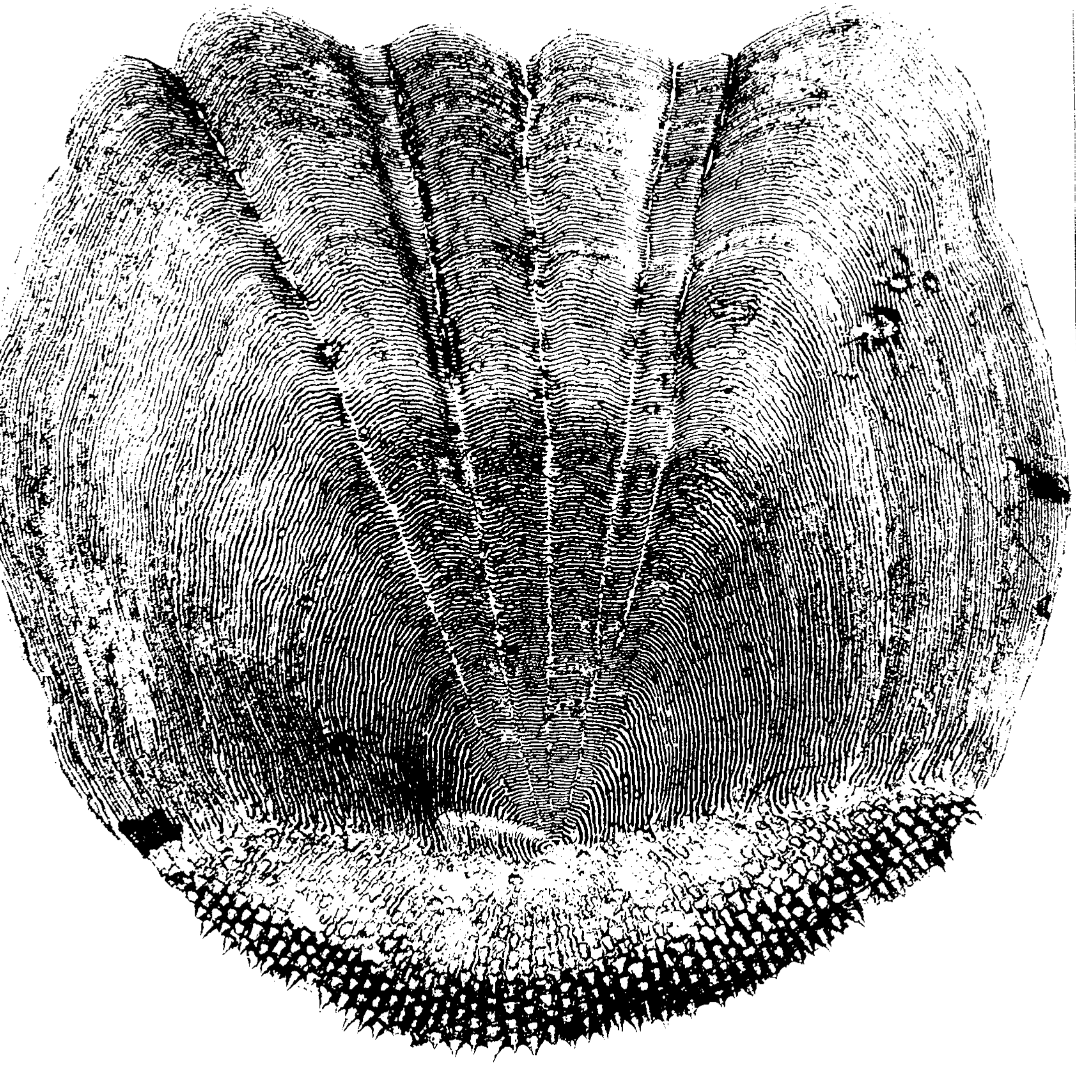
Methods

Maximum ages of male and female zander were derived from scale readings with confirmation obtained from opercular bones where these were available. Age determination of fish depends on the formation of annuli every year. Once growth ceases, circuli and subsequently annulus formation ceases. There have been several cases of fish ceasing to grow, meanwhile continuing to live without apparent ageing when the scales have been examined. Harris (1973) noted this phenomenon with brown trout (Salmo trutta L). The Royal Zoological Society kept in their London aquaria a large common carp (Cyprinus carpio L), for a number of years. The age of the fish when acquired, was determined and subsequently found to be the same on its death some years later. Such continued existence of common carp without linear growth and apparent ageing is thought to occur in the wild. (Clifford pers. comms.). Evidence obtained from the tagging of zander suggested that this might also occur with zander.

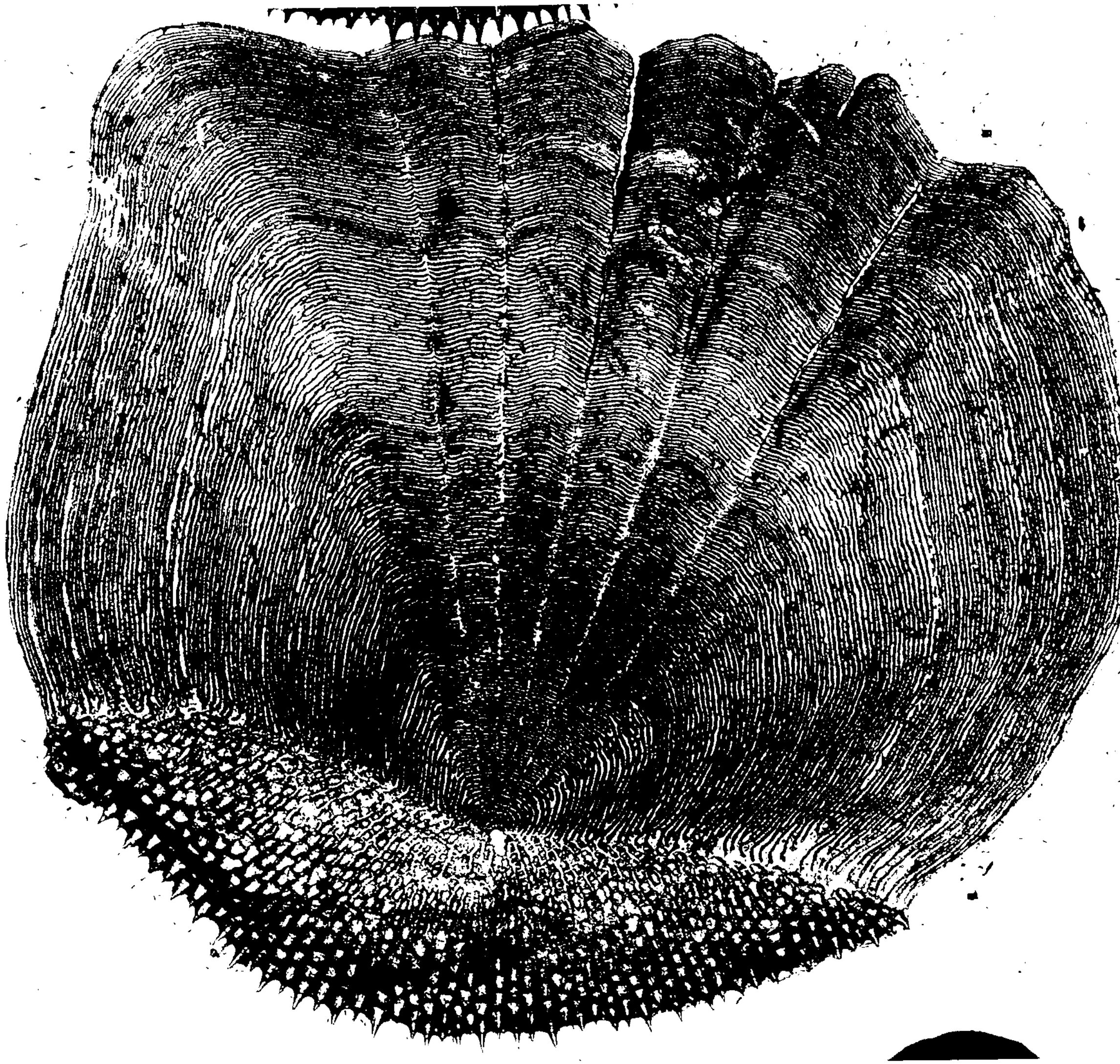
Zander which had been tagged or marked, with removal of scales for ageing were recaptured and scales again removed for ageing. This enabled examination of the scales from each period thus showing whether or not additional annuli had been formed. Periods of at least one winter and spring elapsed before recapture. Photographs of such scales were also obtained along with examples which showed specific features associated with slowed growth (Plates 5 to 8).

PLATE 5

Two scales from Middle Level zander number 264629. Scale (a) was removed on 23.10.79. when the zander weighed 3756g, measured 667 mm and was 6 plus years old. Scale (b) was removed on 25.6.80. when the zander weighed 3303g, measured 683 mm and was again apparently 6 plus years old. This zander had shown very limited growth and a substantial weight loss this resulting in a lack of a discernible seventh annulus.



a



b

Plate 5.

PLATE 6

A scale from Relief Channel zander number six of 1980. This was a female of 1502g and 532 mm. Capture was in June.
The enlarged cranial radius of the scale shows that this individual of 4 plus years showed reduced growth in its third year (point A) and subsequently this was continued into the fourth year. A fast growing zander would not normally show such an extensive area of close spaced circuli, particularly when relatively young.

Plate 6.

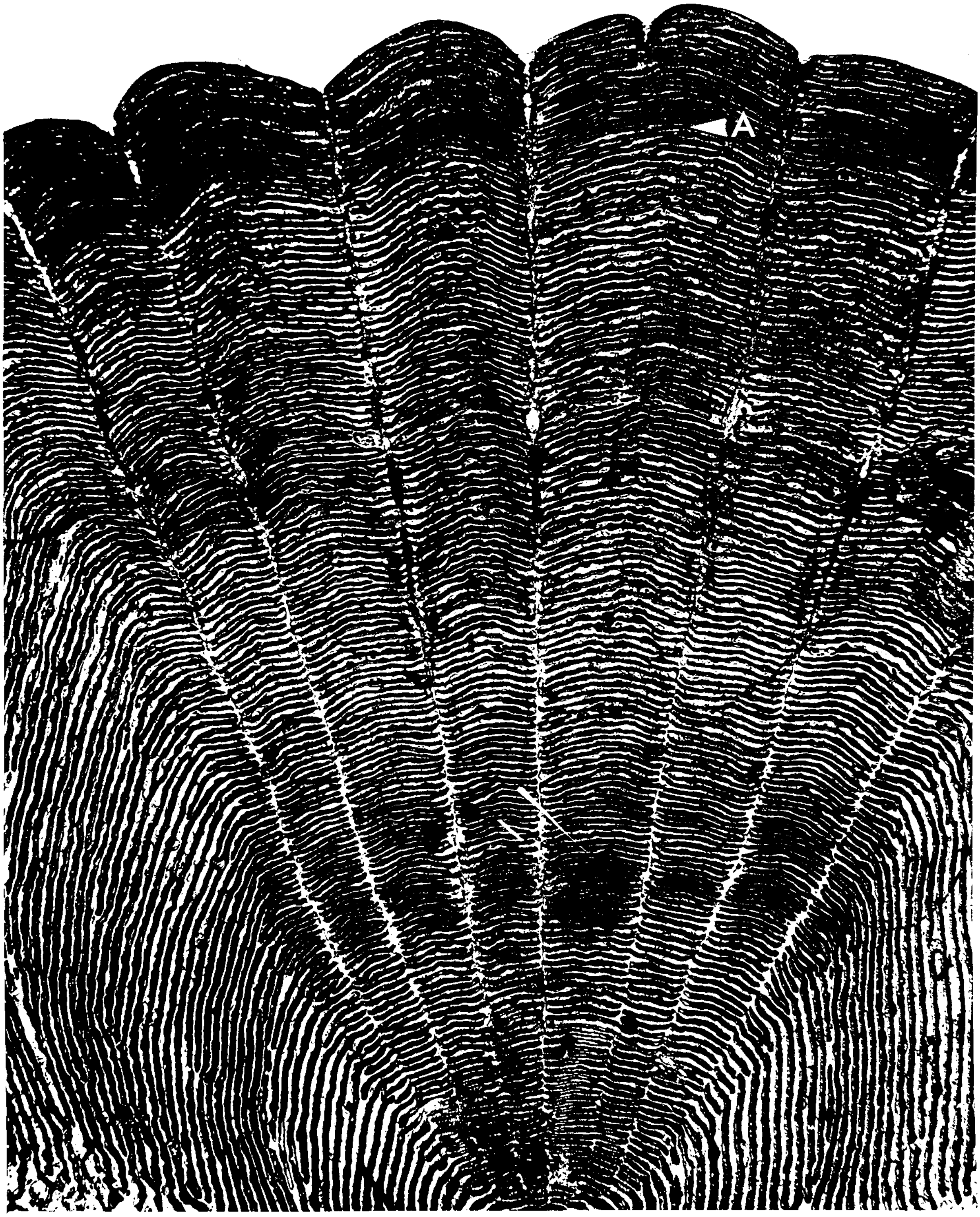


PLATE 7

A scale from Relief Channel zander number seventeen of 1980. This was a female of 851g and 452 mm. Capture was in June. This individual of 4 plus years shows remarkably clear annuli at year 2, 3 and 4. Again reduced growth is evident, circuli being closely spaced.

PLATE 8

A scale from Relief Channel zander number one of 1980. This fish was thought to be a female and weighed 5698g and measured 795 mm. Capture was in June. This scale demonstrates the difficulty likely to be encountered when attempting to determine ages of older fish. This fish was considered to be 10 plus years old.

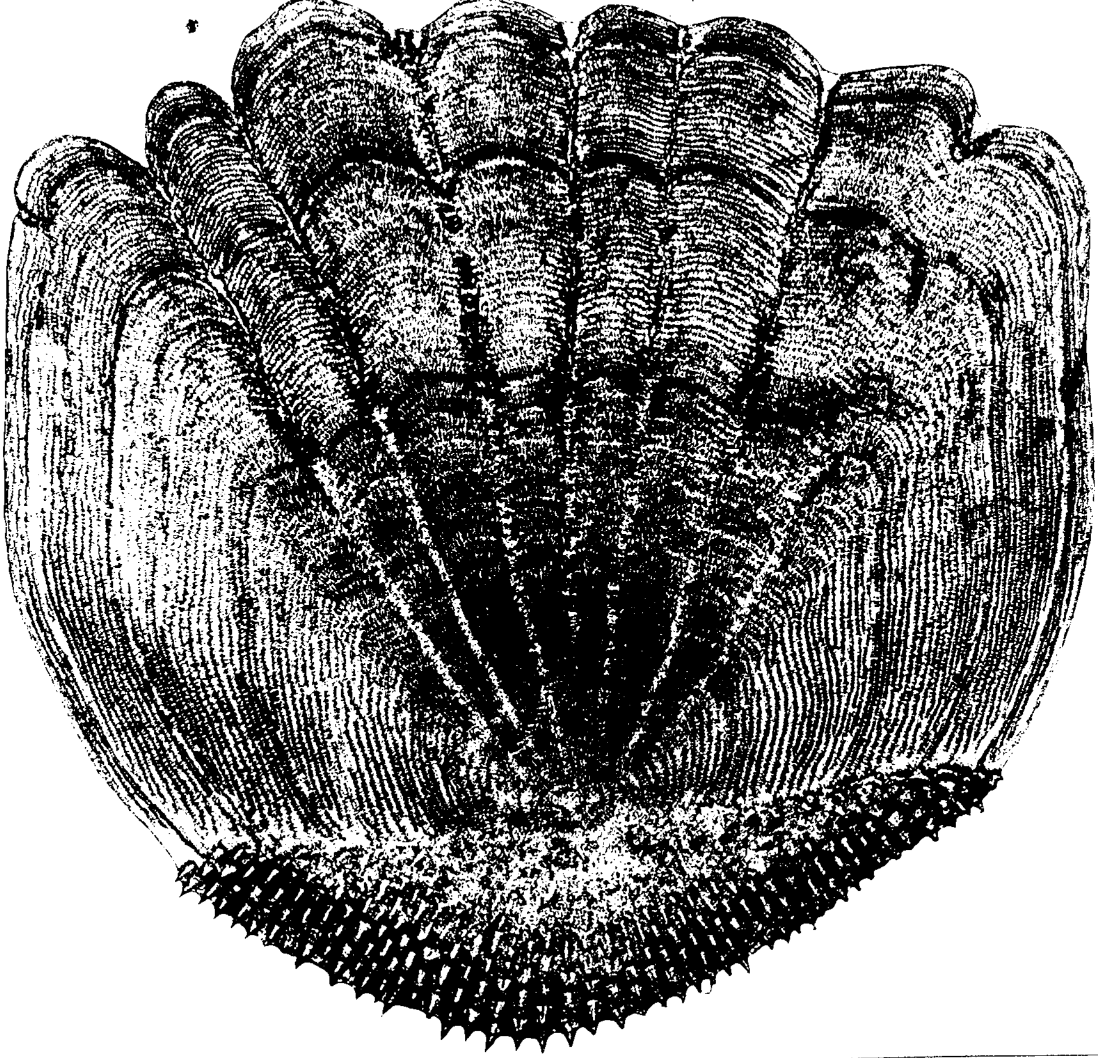
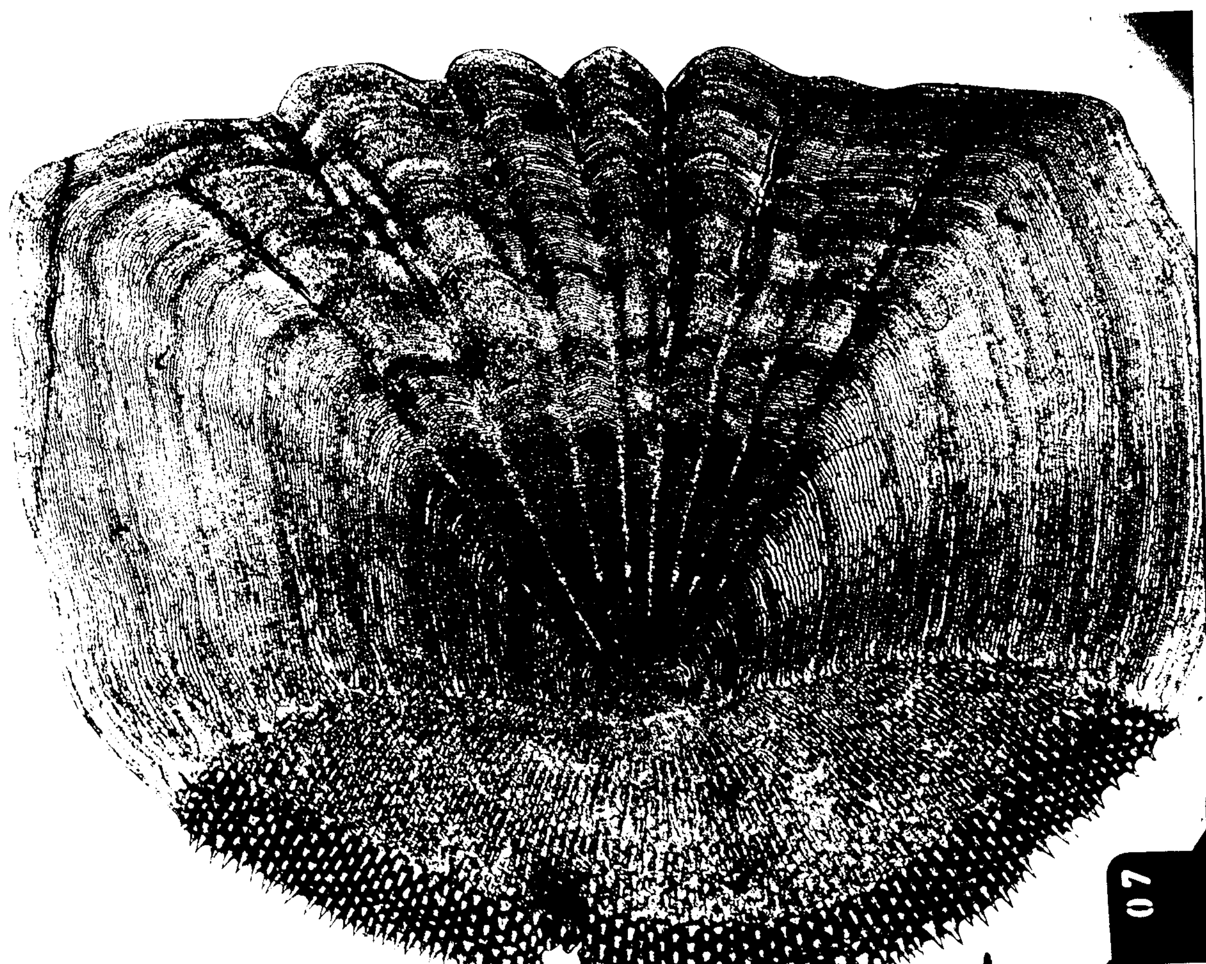


Plate 7.

Plate 8



Results

From observations made using direct data, the oldest female noted was 12 plus years at 826 mm. and the oldest male 9 plus years at 698 mm. Both these fish were from the Relief Channel and captured in 1979. The oldest fish noted by the present author prior to this study was a fish of 13 plus years of 838 mm from the Relief Channel in 1978. Fish of similar ages were not obtained from other waters due to the relatively recent colonisation by zander (See spread of the zander for dates of first capture).

The oldest zander noted in this study was subsequently recaptured in 1980 and found to have decreased in weight, remained a similar length and showed no additional annulus formation. However precise age determinations using scales from large fish are particularly difficult (Plate 8 shows a scale from a zander of 10 plus years and 795 mm). Therefore ages and lengths of zander were compared at time t and time t + 1. The mean ages and lengths were then tested using a t test. Table 22 presents 10 fish from the Relief Channel and Table 23 presents 5 fish from the Middle Level.

TABLE 22: Zander ages and lengths at time t and t + 1 from the Relief Channel

Tag Number	Length 1979	Length 1980	Age 1979	Age 1980
264161	750 (16/10)*	720 (5/7)*	8+	8+
264417	710 (25/6)	720 (6/6)	9+	8+
264345	523 (24/6)	535 (23/7)	4+	4+
264602	665 (3/9)	655 (16/6)	6+	7+
264634	645 (25/10)	641 (16/6)	6+	5+
264079	552 (25/6)	577 (16/6)	4+	4+
264439	776 (21/7)	770 (16/6)	9+	11+
264096	691 (24/6)	670 (16/6)	8+	7+ Erosion
264309	576 (28/7)	595 (16/6)	4+	4+
1558	840 (25/10)	851 (9/8)	11+	10+
Mean	672.8	673.4	6.9+	6.8+

*Day and Month in Brackets

TABLE 23: Zander ages and lengths at time t and t + 1 from the Middle Level Main Drain

Tag Number	Length 1979	Length 1980	Age 1979	Age 1980
264650	666 (23/10)	690 (20/7)	5+	6+
264636	590 (23/10)	600 (20/7)	4+	5+
264610	595 (23/9)	605 (29/6)	5+	5+
264611	700 (22/9)	710 (29/6)	7+	6+
264629	667 (23/10)	683 (25/6)	6+	6+
Mean	643.6	657.6	5.4+	5.6+

*Day and Month in Brackets

The mean lengths of Relief Channel zander on recapture were only slightly greater than the mean lengths on the occasion of initial capture. Mean ages showed a slight decrease and this can be explained by erosion of scale material, something which was particularly noticeable in zander number 264096. Middle Level Main Drain zander showed a greater increase in mean length between recaptures, though the periods at liberty only varied slightly. There was also a slight increase in mean age between first capture and recapture.

Plates (5a and b) show zander scales from 1979 captures and 1980 recaptures. Annotations describe specific features on these scales and Plates 6 and 7 which show examples of slower growth and other characteristic features of zander scales.

Length increases when expressed as percentages of the original length proved to be small. Relief Channel zander showed an increase of 0.09% while Middle Level zander increased in length by 2.2%. Both of these figures fall within the 3% margin of error mentioned in Section 2.1.3. It was therefore concluded that increases in length were negligible for Relief Channel zander tagged in 1979 and recaptured in 1980. Length increase of the Middle Level zander though more significant, did not exceed the limit placed on the measurement of length data. Therefore it cannot be said that the length increases were due to growth rather than measuring error.

Age increase was also very slight for both Middle Level and Relief Channel zander, though the former did suggest an increase rather than the decrease shown by the latter. Assuming the accuracy of ages determined from scales it is apparent that little increase in age has occurred. This suggests that both samples of tagged zander, showed negligible ageing on recapture 8 and 12 months after the initial capture.

(vi) Mortality and Survival

Methods

Mortality and survival were expressed using the method described by Mann (1975). The number of each age group of zander was converted to a percentage of the total. The percentages obtained were plotted as natural logs against age. A least squares regression line was fitted to the points and this was used to calculate the mean instantaneous mortality rate, Z ($= \log_e Nt - \log_e Nt\ \ 1$) and annual survival rate,

$$S = \left(\frac{Nt + 1}{Nt}\right)$$

The limited data available, required the pooling of data. All Relief Channel years were combined, from 1969 to 1980 to give the mean mortality and survival of the population. Any attempts at determining differences in mortality and survival between years was impractical because of the small amount of data. Middle Level and Coombe Abbey data was also examined. All Relief Channel and Middle Level data used was derived from rod and line angling, with no fish younger than 3 years (approximately 400 mm) included in calculations. This eliminated the effect of rod and line selectivity. Coombe data was from seine netting only and fish younger than 2 years were excluded (approximately 200 mm). No fish younger than two years were obtained in Coombe samples, therefore the whole sample could be utilised. Combinations of sampling methods could not be used, due to the possible bias caused by such combination.

Therefore the methods which have produced the majority of zander were used for this study.

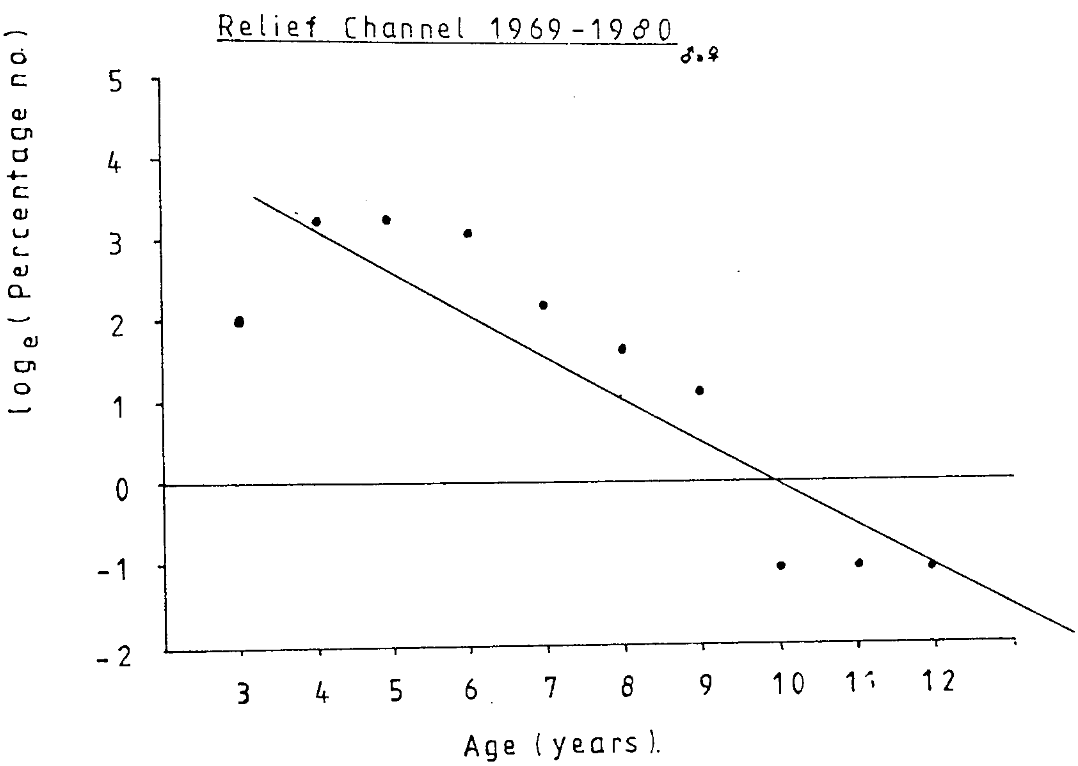
Results

The percentage age group composition of the samples studied is presented in Table 24. The data has been transformed to a plot of log percentage survival against age, in Figures 29a and 29b. The mortality and survival rates derived from the regressions are presented in Table 25.

TABLE 24: Percentage Composition of Zander Age Groups

Water	Time	Percentage Composition of Age Groups										
		2	3	4	5	6	7	8	9	10	11	12
Relief Channel	1969-1980		7.8	24.7	26.7	22.3	9.3	5.1	3.1	0.34	0.34	0.34
Relief Channel (Male)	"		19.6	32.1	30.4	8.9	7.1	0	1.8	0	0	0
Relief Channel (Female)	"		9.6	35.6	19.2	20.6	2.7	6.9	5.5			
Middle Level	1979-1980		38.4	13.4	29.5	16.1	2.7					
Middle Level (Male)	"		2.6	56.4	23.1	15.4	2.6					
Middle Level (Female)	"		44.7	27.7	19.2	6.4	2.1					
Coombe Abbey	1979-1980	32.4	60.8	6.8								

Figure 29a.
Survival of Relief Channel Zander.



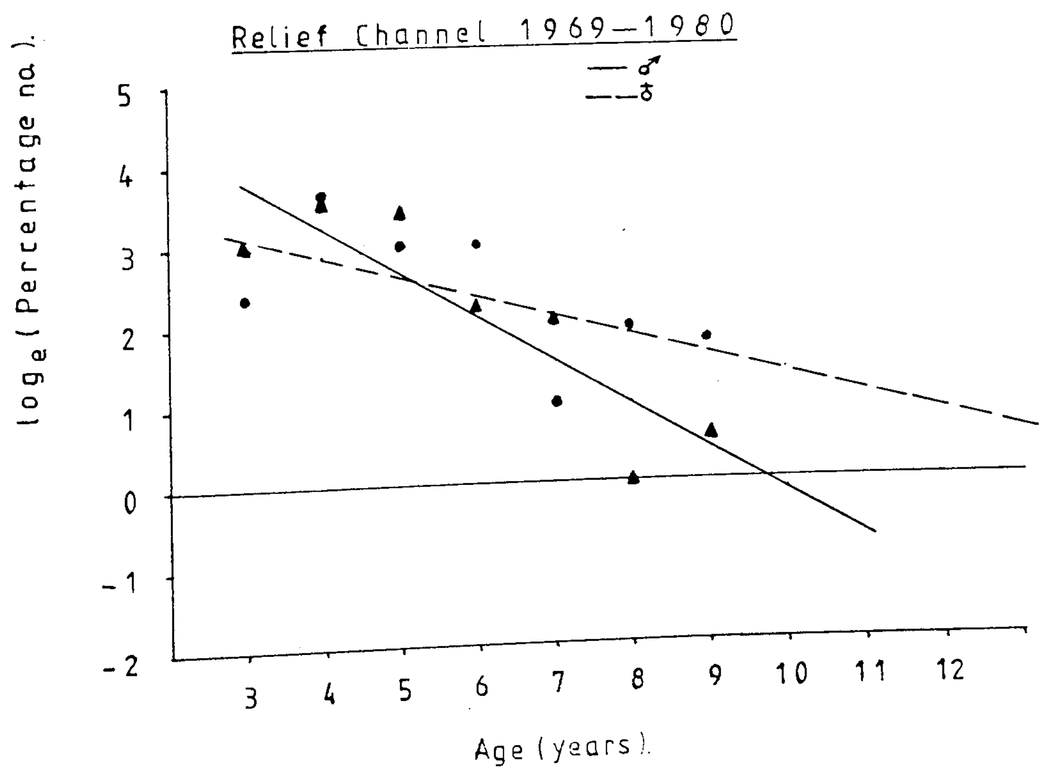
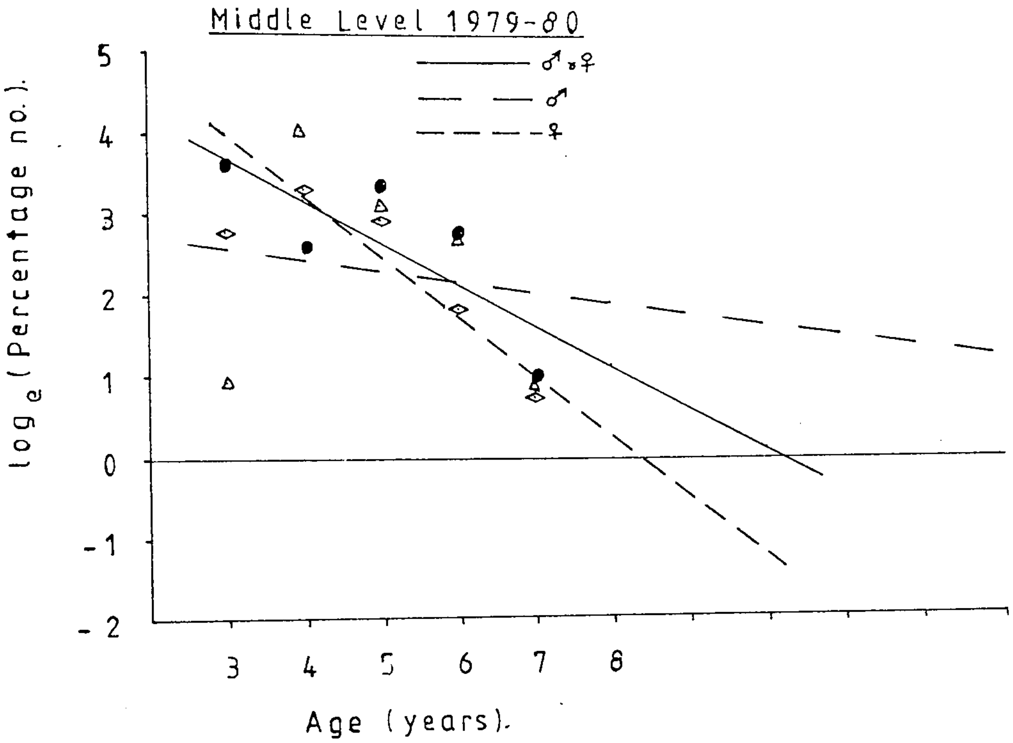


Figure 29b.

Survival of Middle Level and Coombe Abbey Zander.



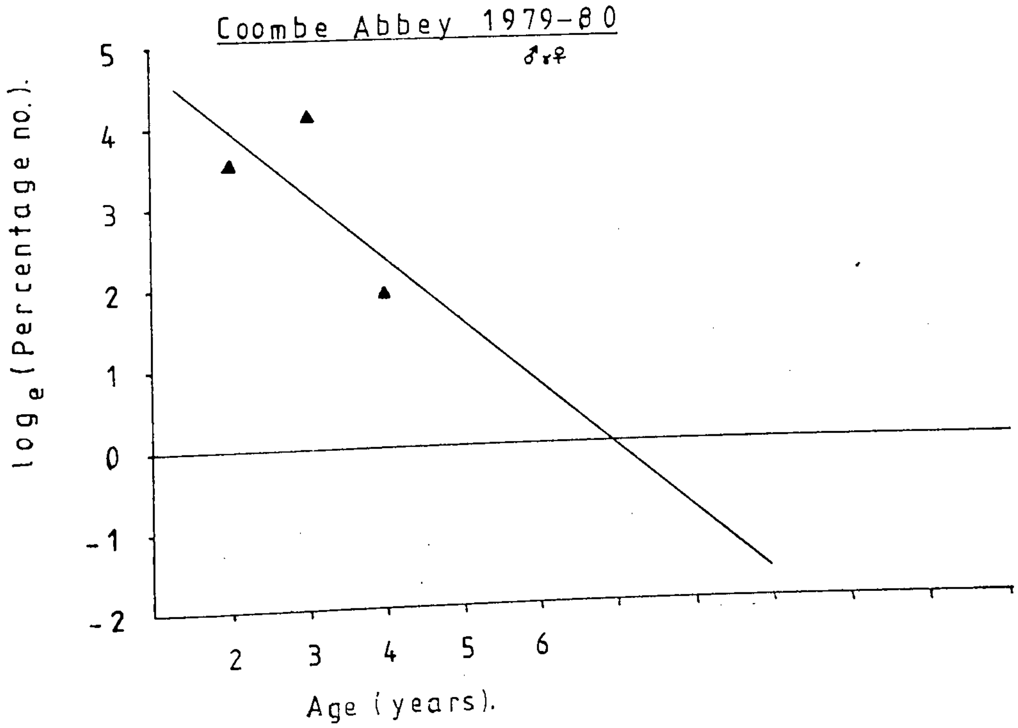


TABLE 25: Values of Mortality Rate Z and Survival Rate S

			Z	S
Relief Channel	1969-80	Male and Female	0.53	0.59
"	"	Male	0.56	0.57
"	"	Female	0.26	0.77
Middle Level	1979-80	Male and Female	0.51	0.6
"	"	Male	0.13	0.33
"	"	Female	0.76	0.47
Coombe Abbey	1979-80	Male and Female	0.8	0.45

Table 25 shows that the mortality rates and survival rates of zander from the Relief Channel (pooled) and Middle Level 1979-80 were very similar. Coombe Abbey zander showed a higher rate of mortality and a lower level of survival. Relief Channel Male zander showed very similar mortality and survival rates to the whole population. Females however had reduced mortality and higher survival. On the Middle Level this trend was reversed with males showing increased survival and reduced mortality while the females had increased mortality and reduced survival.

2.2.4. DISCUSSION

The growth data presented in this section represents the most comprehensive study made on this aspect of the ecology of the English zander. The validation of the method used for age determination (scale reading) is a particularly important point which is often overlooked in growth studies. Here scale reading was shown to be valid for the age determination of zander up to 6 years of age. Beyond the age of six years, it is suggested that scale reading continues to provide valid estimates of growth, but the possibility of over or underestimation of zander growth does increase with increasing age. For particularly old zander, opercular bones may provide confirmation of ages. However where conservation of large zander for angling purposes is desirable, the removal of opercular bones is not practical.

The study of population growth rates and the subsequent comparisons between zander populations and periods of time, allows categorisation of the growth of zander. Because population growth rates reflect the growth of zander year classes, which are in themselves subject to variation in rate of growth, the growth curves derived from population growth rates will show variations due to this. Most continental workers appear to adopt a similar approach and the comparative data presented in Figure 23 is by necessity composed of zander growth rates derived from population growth rates. The growth curves obtained from the various continental sources, Neuhaus (1934), Klimova (1935), Nagiec (1964) and Biro (1970) show with one exception, (that of Neuhaus 1934) a characteristic growth curve, with length increment slowly decreasing with increasing age. The zander studied by Neuhaus (1934) showed a decrease in growth after 5 years which was not continuous with the remainder of the growth curve. It is suggested that the older zander were growing slower than the younger fish. The growth rates of the other continental zander appeared consistent, suggesting fairly stable environmental conditions resulting in typical growth curves. This is probably a feature of many zander populations which have become well established and equilibrated over a long period of time.

By comparing the zander growth rates obtained in this study, with continental growth rates which represent extremes of rapid and slow growth, English zander growth rates can be categorised as relatively slow or fast growers. Such categorisation can then be used to provide an indication of the availability of food in the environment since according to Woynarovich (1959, 1968) the rate of growth is a function of the available quantity of food.

The growth curves of some of the English zander studied showed considerable variation in growth, both between populations, and also within populations. It was apparent that the majority of English zander were growing at rates approaching the faster growing populations of continental zander. This suggests that the majority of English waters now supporting populations of zander are suitable for the rapid growth of zander. The variations in growth rate exhibited within populations suggest that though growth may be rapid, it is also subject to considerable variation.

The first example dealt with here showed precisely this pattern of fast, but variable growth within the population. Relief Channel data was available for 3 periods. During 1969-1970 (Figure 16) scale readings indicated that zander of 6 years and older were growing faster than the younger fish. This conclusion is based on the observation that the growth curve for this period showed increased growth in length for age when compared with the younger fish.

The reverse situation was noted in 1975-1976 (Figure 17). Here the younger zander were growing faster than the older fish. The zander of 1979-80 (Figure 18) showed a similar trend. Overall the Relief

Channel zander growth rates were similar to the faster growing continental zander, with the exception of the young zander of 1969-1970, which showed ~~slowed~~ growth more typical of the slower growing continental zander. Age class comparisons of growth were available for the Relief Channel in 1979-1980. This comparison showed that the younger year classes were significantly greater in length at each age than the older year classes. The possibility of this being an artifact caused by Lee's phenomenon was discounted, the following points being noted:

(1) Back-calculation procedure was based on a linear relationship between scale radius and zander fork length. The intercept value of y was 30.3 mm a value which is similar to that noted for key area scale development (Biro 1970).

(2) The possibility of non random sampling of the population was considered. The result of this would be the selection of the larger individuals of the younger year classes. Comparisons with seine net and electrofished samples, showed that the mean lengths were for the age groups examined the same as rod and line samples, (Middle Level Main Drain). Because angling methods were standardised it was assumed that there was no difference in selectivity between waters. The majority of zander examined in this study were larger than the selectivity limit.

(3) Selective natural mortality, favouring the smaller zander cannot be discounted. However in an environment with a high proportion of large predators it is suggested that small predators are likely to suffer increased rather than reduced mortality.

(4) Selective fishing mortality favouring the smaller fish was unlikely as the majority of zander anglers, in favour of killing zander, kill all sizes. Others prefer to remove the small fish only.

Changes in growth rates of Relief Channel zander were thought to be due to variations in prey availability. Only in 1979 were prey fish biomass estimates, available. If 1979 is considered as part of the most recent period of zander colonisation of the Relief Channel, three other periods could be identified. These were based on the writers experiences of the Relief Channel since 1963.

1. Pre 1968 prey fish abundant *
2. 1968-74 preyfish scarce *
3. 1975-77 prey fish abundant
4. post 77 prey fish scarce **

* confirmed by Linfield and Rickards (1979)

** confirmed by AWA survey, Klee (1979a).

The prey fish biomass for 1979 was less than 0.1 g/m^2 with an estimated zander biomass of 0.6 g/m^2 (Klee 1979a). Both these figures represent very low biomass figures. The irregularity of circuli formation and the poor growth of individual fish marked and at liberty for periods of 1 to 2 years suggest that the recent growth of Relief Channel zander has been slow or negligible. The fact that the 1976 year class and to a lesser extent the 1974 and 1975 year classes showed relatively fast growth suggests that either zander density was low or prey fish were numerous. The large number of individuals of the 1974, 1975 and 1976 year class suggests that the year classes were strong and that rapid growth was influenced by the high biomass of prey available.

Earlier age classes of Relief Channel zander, such as those of the late sixties and early seventies would have lived through several periods of alternating food shortage and abundance. Such inconsistent food supplies are unlikely to result in optimum growth.

These large fluctuations in growth would appear to be a characteristic of zander populations in this country. This may be attributable to the fact that zander have been present in the Fenland waters for only a short time (18 years). The variation in circuli formation and the lack of a relationship between circuli number and zander size, suggests a varied rate of growth and this has been suggested by Nikolski (1969) as a feature of fish populations with poor food supplies or intense competition for what should be adequate food supplies.

The cause of variations in growth over a period of time, rather than between individuals is probably due to predator prey oscillations as described by Gause (1934) and McNaughton and Wolf (1979). A cycle of prey increase is followed by predator increase. Subsequently over predation reduces prey numbers, eventually inhibiting predator survival and growth. With reduction of predator numbers, prey fish are again able to increase. Such oscillations are typical of unstable populations lacking factors which would serve to buffer the predator prey reaction. It is suggested that such oscillations have taken place in the Relief Channel resulting in distinct changes in predator and prey populations.

The mortality rate of 0.53 noted for Relief Channel zander during the period 1969-1980 is relatively low. This may contribute to the increasing "wavelength" of the oscillations. If as suggested mortality occurs at approximately 50% per year on the whole of the zander population and recruitment was non-existent, it would take 3 years for a 75% reduction in zander numbers to occur. (This figure derived by subtracting 50% from the estimated number of zander in the Relief Channel once a year for 3 years). A further 3 years for a reduction to 90% (based on a provisional estimate of 2000 zander greater than 360 mm). Even if few young zander survive to be recruited to the adult population, it would still take a long time for predation pressure to be reduced to a level where the prey fish would rapidly increase in numbers.

Once predator numbers had decreased, the build-up of prey fish with rapid growth rates (due to plentiful food) would take several years. Predator numbers would then start to increase again. Altogether such cycles would appear to take 6 to 10 years. Though the quantification of such changes is based on considerable amounts of speculation, it is hoped to demonstrate elsewhere, in an appropriate manner that zander numbers have been subject to changes induced by oscillation of predators and prey.

One of the most interesting aspects of Relief Channel zander of 1979-80, is the apparent lack of growth. This is supported by the tagging of zander and a very small number of zander and pike which had recognisable markings. On recapture growth over a period of 1 to 2 years proved to be negligible. Unfortunately many workers De Roche (1963), Moller Christensen (1961), Eschmeyer (1959) and Shetter (1967) have already demonstrated that tagging may reduce the growth of fish. It is interesting to note that the reduction in growth of tagged Relief Channel zander was greater than that noticed for the Middle Level zander bearing the same type of tag.

Confirmation of zero or little growth could only be achieved by the marking of zander by means of dye marks, Hart and Pitcher (1969) or by freeze branding, Mighell (1969). These methods having as far as is known, no retarding effect on the fishes growth. Unfortunately this approach was not available.

Middle Level Main Drain zander were examined during one period, 1979-1980. These zander showed rather different growth characteristics compared with the Relief Channel zander of the same period. The older Middle Level zander were growing faster than the younger ages. This was confirmed by the comparison of age classes. Middle Level zander growth resembled the faster continental zander. It is suggested that the older age classes of Middle Level zander were growing faster than the younger ones, due to the lack of intraspecific competition during the early history of zander in the Middle Level (colonisation was thought to have commenced in 1970). Also prey fish levels were probably higher prior to 1977. The writers observations and the changes in anglers catches of prey fish would tend to suggest that prey fish have decreased in numbers. The recent AWA survey of 1979 (Klee, 1979b) noted prey biomasses of 0.7 g/m^2 which is very low when one considers that zander biomass was 0.3 g/m^2. A full scale pike and zander removal exercise has just been completed on this system and it is now unlikely that oscillations will occur to the same extent as has been noted on the Relief Channel.

Coombe Abbey zander were among the faster growing populations noted. Their growth was similar to that of the Vistula and Stettiner Bay populations. Growth of the Coombe zander was over the limited range examined comparable to that of the Middle Level and Relief Channel in 1979-80. Prey fish estimates were not available for this water, however it was noted that roach of a suitable size (100-160 mm) were plentiful, during seine nettings.

Burwell Lode zander appeared to show similar growth to Relief Channel 1979-80 zander and are therefore typified as fast growers. Prey fish populations as noted by Gregory (1979), were for roach and bream 3.8 g/m^2 with zander biomasses of 1.1 g/m^2. Zander removal was carried out on this water and changes in prey populations are not likely to be caused by zander, unless imigration from the River Ouse occurs.

All the zander populations described so far were described as fast growers. The wide variation in environment and prey density suggests that zander are adaptable and capable of rapid growth in a variety of water types. Only two populations of zander so far described, showed slow growth similar to that of the slower growing continental populations. One of these was from Stewartby Brick Pit. These had growth rates similar to the zander of Lake Balaton. Biro (1970) noted that Lake Balaton zander were often poorly nourished. Stewartby Brick Pit is known to be deep and lacking in extensive littoral zones (Beat and Johnson Pers Comms). Prey fish are said to be large and few in number (Johnson pers comms). This may account for the slow growth of this population.

The zander of the Coventry and Oxford Canal have a growth rate intermediate between the Stewartby zander and the slow growing year classes of the Relief Channel zander of 1969-70. During electro-fishing work on this canal, prey fish were found only in modest numbers.

This canal is used heavily by boats during the summer and there is evidence to suggest that the frequent passage of boats decreases the productivity of a water (Murphey, Eaton 1981).

The determination of L_∞ by means of Walford Plots was affected by the varied rates of growth shown by many of the zander populations studied. Walford Plots depend on the assumption that growth of a fish continues at a constant rate, having been predetermined by the early years growth. Length increments decrease progressively until L_∞ is reached. If growth is variable the fitting of a Walford Plot and the estimation of L_∞ is not possible.

Walford Plots of population growth exhibited extreme variation in the case of Relief Channel 1969-70, 1975-76 and Coventry and Oxford canal 1978-79, thus preventing realistic estimates of L_∞. Values of L_∞ were highest for the Relief Channel and Middle Level during 1979-80, followed by Coombe Abbey 1979-80. Stewartby 1979-80 showed the lowest value of L_∞. When Relief Channel 1979-80 and Middle Level 1979-80 data was presented as year class plots, L_∞ values were rather variable, which suggests variation in growth within year classes. Middle Level zander showed much less variation in L_∞ values, though these were generally indicative of slower growth. It is suggested that growth of the year classes of Middle Level zander was more consistent within year classes than was the case with Relief Channel zander. The solitary Walford plot for the one Coombe Abbey year class suggested that growth of this year class was rapid with a large L_∞ reached rapidly.

It is suggested that the variability within year classes was in the case of the Relief Channel zander, due to the periodic oscillations between predator and prey. Less variability was noted within Middle Level year classes and this possibly reflects a greater stability of the prey populations during the periods studied.

The longevity of zander still remains uncertain. Female zander of 13 plus years (838 mm) and males of 9 plus (698 mm) have been noted. However fish of 12 plus years have been recaptured a year later, while showing no significant ageing or growth. It is suggested that the maximum period of growth notes in zander is 13 plus years, but that longevity may be greater than 13 plus years, due to survival after the cessation of growth. Ages of 15 to 24 years as noted by authors such as Berg et al (1949), Balagurova (1963) and Biro (1977) have not been noted in this country, probably due to the comparatively recent nature of zander introductions. Poor survival of old fish due to poor feeding and angling mortality may have been responsible for this.

Sex related differences in growth were not demonstrable in English populations. Svardson and Molin (1968) noted that males grew at a slower rate than females and were also shorter lived. Sampling of larger, older zander might have revealed differences in growth related to sex. Deductions based on simple statistical tests, when samples are small do not preclude the possibility of sex related differences in growth. The present level of sampling failed to reveal sex related differences in growth in the majority of populations studied.

Mortality rates of zander were for male and females combined, very similar for the Relief Channel 1969-80 and Middle Level 1979-80, being 0.53 and 0.51 respectively. Survival rates were also similar being 0.59 and 0.6 respectively. This suggests that mortality and survival rates in these two Fenland waters were very similar. Mann (1976) found that mortality and survival of Dorset Stour pike was 0.57. Zander mortality rates in Fenland waters are slightly lower than for Stour pike and survival slightly higher. Mann (1976) also found that male mortality was higher than female mortality. Relief channel male mortality was higher than for females, being 0.56 and 0.26 respectively. This large difference in mortality was reversed for Middle Level zander, being 0.13 for males and 0.76 for females.

Coombe Abbey zander had a high mortality rate for males and females combined which could be attributed to successive removals of zander by means of seine netting. Further discussion of all the data presented in this section will be found in Section 4 where the other aspects of this study will be discussed.

2.3. THE FOOD OF THE ZANDER

2.3.1. INTRODUCTION

The majority of previous studies of the feeding of the zander have been made on populations existing in Eastern Europe and the U.S.S.R. (Ivanova 1968; Biro 1969, 1973, 1977; Pihu and Pihu 1970; Popova and Sytina 1977). Studies in England have been limited to that of Linfield and Rickards (1979). The present study examines the feeding of zander from a number of different waters and, in so doing, attempts to identify specific characteristics of zander feeding behaviour. The experimental approach, (section 3), seeks to investigate further the characteristics of zander feeding noted in this section.

2.3.2. METHODS

Zander stomachs were removed intact and either frozen within two hours of capture (being kept at less than 5 C in a cool box, on removal) or examined immediately. The temperature at the time of capture was recorded. The contents of the stomachs were washed with water into a white dissecting tray. Individual food items were separated and the following details noted;

(a) Species of prey
(b) Number of food items
(c) Length of food items
(d) Weight of prey
(e) Maximum size of prey which can be ingested
(f) Direction of swallowing of prey, head or tail first
(g) Feeding periodicity
(h) Number of empty stomachs.

The methods of treatment of the data obtained from the observations were as follows:

(a) Species of prey

Prey fish eaten by zander were easily identified when undigested. With advancing stages of digestion, identification became increasingly difficult. Cyprinid fish were identified by either their scales or pharyngeal teeth (Maitland 1972). Non-cyprinid fish were identified by means of any remaining calcified tissues including scales. Where a precise identification was not possible, the prey remains were categorised as far as possible, usually as either cyprinid, non-cyprinid, percid or unidentified. Invertebrate prey was identified by reference to whole animals, or distinctive parts such as limbs or jaws. No attempt was made to identify invertebrates to more than genera level.

Irregular sampling precluded any study of seasonal changes in prey preference. Attention was therefore concentrated on the species composition and size of prey eaten by the zander as compared to the size and species composition of the prey population. Anglian Water Authority reports on the Relief Channel, (Klee 1979a), Middle Level Main Drain (Klee 1979b) and Burwell Lode (Gregory 1979), were used to obtain information on the size and species composition of prey fish in these waters. In addition to this data, the available prey fish in Coombe Abbey Lake were sampled by means of a seine net in the spring of 1980.

An important assumption has to be made regarding the possibility of species specific selectivity of the prey fish sampling methods. Because of the possibility of different species being selected or avoided by the fishing method in use, there is a possibility that survey obtained species compositions are different from the actual prey fish populations. Because little can be done to ensure that fishing methods are truly representative, it was assumed that selectivity was negligible. This assumption has to be considered seriously in any interpretation of the results.

Selectivity for the size of fish sampled was possible. According to Klee (1979ab) sampling was quantitative for roach and bream greater than 60 mm fork length when seine netting (mesh 7 mm square). Gregory (1979) gave a higher quantitative sampling limit for roach and bream of 115 mm when using electrofishing as the sampling method on Burwell Lode.

For Coombe Abbey, quantitative sampling limits were probably similar to those for the Middle Level (net mesh again 7 mm square). The number of prey fish captured in surveys which were inaccessible to zander predation was less than 0.5% of the total and was therefore considered as insignificant when prey fish percentage compositions were calculated.

Available prey estimates were made either at the time of zander sampling, i.e. Coombe Abbey 1980 and Burwell Lode 1979, or during the zander sampling year, i.e. Relief Channel 1979 (October) and Middle Level 1979 (November).

(b) Number of Food Items

The number of prey items consumed was ascertained by counting whole prey items. Digested prey remains were ascribed to groups until all remains were accounted for. It was a relatively simple task to "reconstruct" prey items in this manner.

(c) Length of Food Items

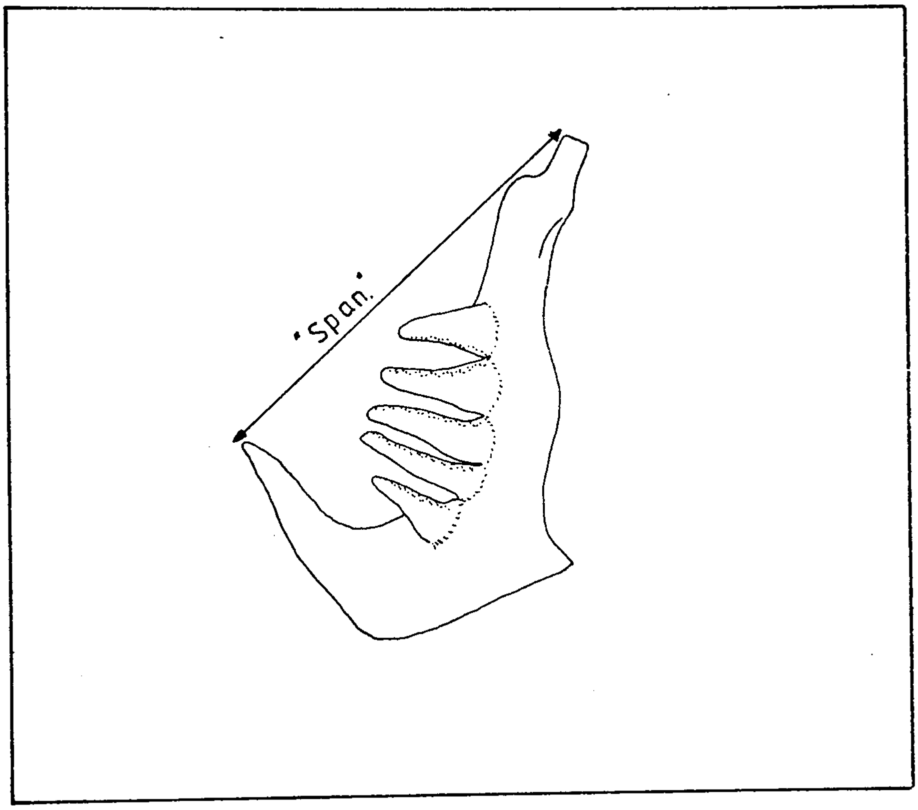
The fork length of fish prey and total length of other prey was measured using either a measuring board or a vernier, depending on the size of prey. Prey fish which were partially digested presented a problem when attempting to estimate their original lengths. The length of fish with pharyngeal teeth, such as members of the cyprinidae, could be estimated by means of the fork length, pharyngeal tooth relationship. Specimens of roach and common bream were obtained from a variety of sources and were generally the mortalities occurring during seine netting, trawling or electrofishing. 38 roach of 34 - 210 mm and 18 common bream of 62 - 250 mm were dissected to remove pharyngeal bones. Measurements were made across the points shown in Figure 30. The distance between these points is described as the "span". Pharyngeal tooth span was then plotted against fish length for the two different species and a regression line fitted by the method of Least Squares. The relationships obtained are given below.

Roach	$Y = 9.7 + 12.5x$	$r = 0.98$	$(P < 0.001)$
Common Bream	$Y = 1.93 + 13.3x$	$r = 0.99$	$(P < 0.001)$

From this relationship the original length of roach and bream could be determined. No other cyprinid species were regularly encountered in zander stomachs, therefore similar regressions for other species were not required.

Figure 30.

Pharyngeal Tooth Measurment.



In many cases pharyngeal teeth could not be found. This was due either to the prey fish being too far advanced in its state of digestion, or the prey species being a non-cyprinid and therefore lacking pharyngeal teeth. Another method of estimating prey lengths was devised, based on the relationship between prey length and state of digestion. Dead roach of known weight and length were force fed to zander held at 15°C and stomach flushed at intervals of 10 hours (Section 3).

An arbitrary scale of digestion on a scale of I to X was used (Fickling and Lee 1981) to denote the stage of digestion and the length of the roach remaining was noted at each stage. This relationship is presented in Table 26. From this relationship it was possible to derive the estimated original length of any digested prey species, with the normal body shape for a freshwater fish (eels are excepted here).

Reconstructed prey fork lengths were calculated by adding the percentage length loss noted at each stage to the observed prey length. The estimate of original prey length was therefore:
For the remains of a prey fish at stage VII and length of 120 mm,

$$120 + \frac{120}{100} \times 17.5 = 141$$

The accuracy of the method was tested with a sample of 19 roach; and a sub sample of 10 roach obtained from zander stomachs. In each case pharyngeal bones were present enabling a direct comparison of reconstructed length estimates obtained from the percentage length digested relation, with pharyngeal bone, fish fork length regression estimates. With a sample of 19 fish the error was

TABLE 26

STAGE	DESCRIPTION OF STAGE OF DIGESTION	% LENGTH DIGESTED
I	No digestion	0
II	10% of scales removed by digestion. Tail slightly digested.	2
III	30% of scales removed by digestion. Tail fin rays separated but still only partially digested.	3.5
IV	60% of scales removed by digestion. Tail fin rays breaking down.	6.0
V	100% descaled, no tail rays.	9.0
VI	Head digesting, root of tail digesting, all epidermal cover destroyed.	13.0
VII	Bodywall digested, viscera exposed and being digested, head consisting of loosely connected bones.	17.5
VIII	Viscera partially digested, head remains indistinct, tail root exposed.	24.0
IX	Musculature around vertebral column only remaining.	35.0
X	Digestion complete, breaking down of vertebral column.	100.0

-0.7% (SD 10.1). A further sub-sample of 10 fish gave an error of 0.22% (SD 10.1). Considering the arbitrary nature of the scale employed this was considered to be a satisfactory low level of error.

Caution has to be shown when attempting to estimate the size of prey fish beyond stage IX. A recourse to a study of vertebral or otolith sizes may be required for digested material beyond stage IX. In this work very few stomach contents were at this stage and any noted were not included in this work, owing to the difficulty of obtaining satisfactory length estimates. Fickling and Lee (1981) dealt with the mentioned procedure and is shown in the Appendix. Information obtained on prey fish length, was used to investigate the relationships between prey-length and zander length and available prey length and length of prey eaten. Lengths of prey fish noted in zander stomachs during 1968-1970 were estimated without recourse to the more refined methods used for later work.

(d) Weight of Prey

The weights of prey items were estimated in the following manner. Invertebrate prey items, removed whole from zander stomachs were weighed. Small invertebrates such as Daphnia were weighed in sub-samples and then the number of individual organisms was counted.

Undigested prey fish could be weighed directly, while digested prey lengths were estimated from reconstructed prey lengths using the length-weight relationships described by Gregory (1979), (Table 27). These were derived from samples obtained from Burwell Lode in August of 1979 and therefore represent fish in a non-reproductive condition (i.e. not containing large quantities of eggs and milt). Some difference in the length-weight relationship is likely during the course of the year, however without recourse to a detailed study of the prey fishes length-weight relationship, throughout the year this would be impossible to quantify.

TABLE 27: Length-Weight Relationship of Roach and Bream from Gregory (1979)

						Number
Roach	< 20g	$\log_{10}a$	-4.4222	b	2.8061	23
	20-100g	$\log_{10}a$	-4.6072	b	2.9346	47
	> 100g	$\log_{10}a$	-4.2983	b	2.8193	19
Common bream		$\log_{10}a$	-5.2581	b	3.2211	69

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Information on digestion rates derived from experimental work (Section 3) could be used to estimate the weight of prey consumed during a given period of time. Similarly the feeding periodicity of zander could be studied (see g).

The period of time elapsed since prey ingestion was estimated by means of timed digestion experiments conducted in the laboratory at specific temperatures (Section 3). With an estimated time of digestion, it was possible to establish the time elapsed since the ingestion of the earliest food item. The weight of the food organisms was estimated, therefore the estimated rate of feeding could be established. This was expressed as grams per hour, percentage of the zanders bodyweight per hour and percentage of the zanders bodyweight per day (or 24 hours).

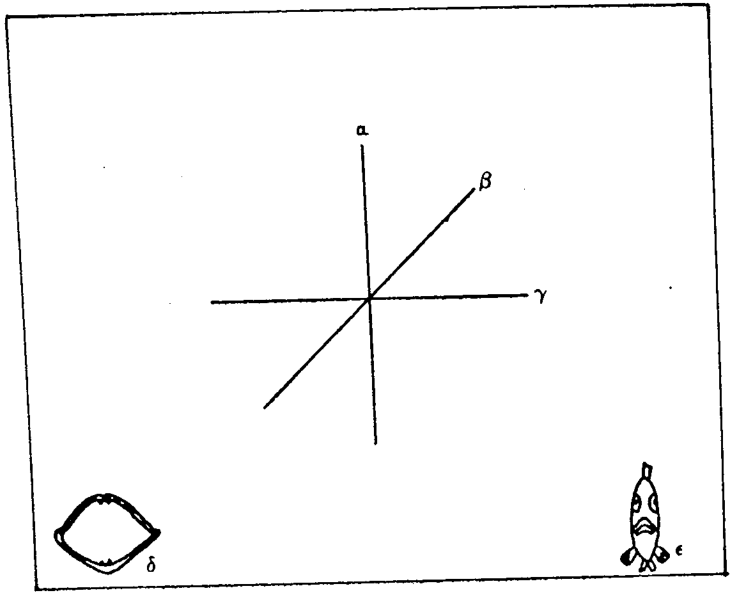
(e) Maximum Possible Prey Size

Observation of zander in the laboratory indicated that the gape of the mouth was the factor limiting the size of prey fish consumed. This subject will be examined in more detail in Section 3, and it is sufficient at this point to note that all food items which passed through the zander's jaws were subsequently swallowed. This suggests that the dimensions of the jaws is the limiting factor in the process of prey ingestion. A number of workers have studied the relationship between mouth size of predators and the size of prey eaten. Lawrence (1957) estimated the size of prey that Largemouth bass (Micropterus salmoides, Lacepede 1802) could consume by measurement of jaw size. Pearre (1980) carried out similar studies on species of Chaetognatha, measuring head width and prey size. This study involved the measurement of mouth width (gape) and mouth depth of zander and the measurement of prey body depth. Zander mouth gapes and depths were measured using a Vernier. Figure 31 shows the points measured. All measurements were made on fresh specimens and at maximum extension of the jaws. Jaw gape was measured from the premaxilla, dentary intersection to the same point on the other side of the jaw. Jaw depth was measured from the premaxilla centre to the dentary centre. A total of 65 jaws were measured over the zander length range of 45 to 710 mm. The points were plotted, mouth gape and depth against zander fork length and a least squares regression line fitted. (Figures 33 and 34 respectively). The relationships obtained were:

Mouth depth	$y = -2.3 + 9.5x$	$r = 0.99$	$p < 0.05$	$n = 65$
Mouth gape	$y = -0.9 + 8.33x$	$r = 0.99$	$p < 0.05$	$n = 65$

From the slopes of the regressions it was apparent that mouth gapes were greater than mouth depths. This suggests that the maximum size

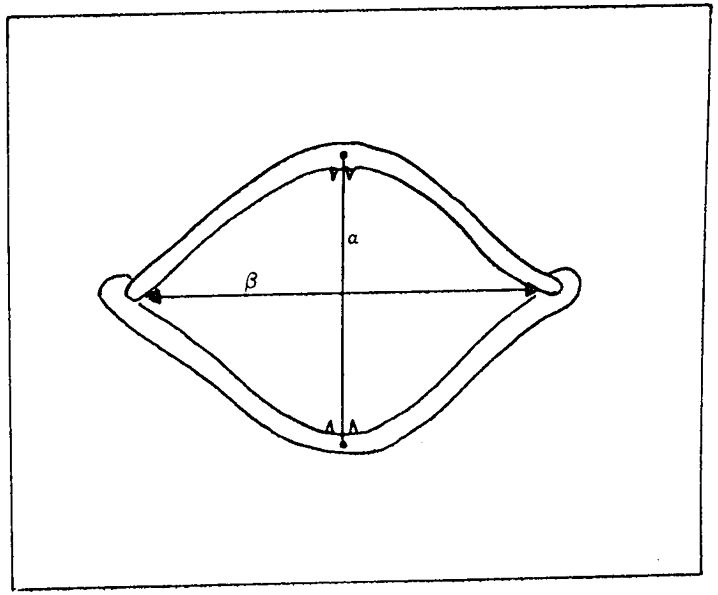
Angle of Prey Ingestion.



α Vertical.
β Diagonal.
γ Horizontal.
δ Jaw ⎤
ε Prey fish. ⎦ In relation to α β γ

Figure 31.

Dimensions of Zander Jaws Measured.



α Mouth depth.
β Mouth gape.

Figure 32.

Zander Mouth Dimensions.

Figure 33.

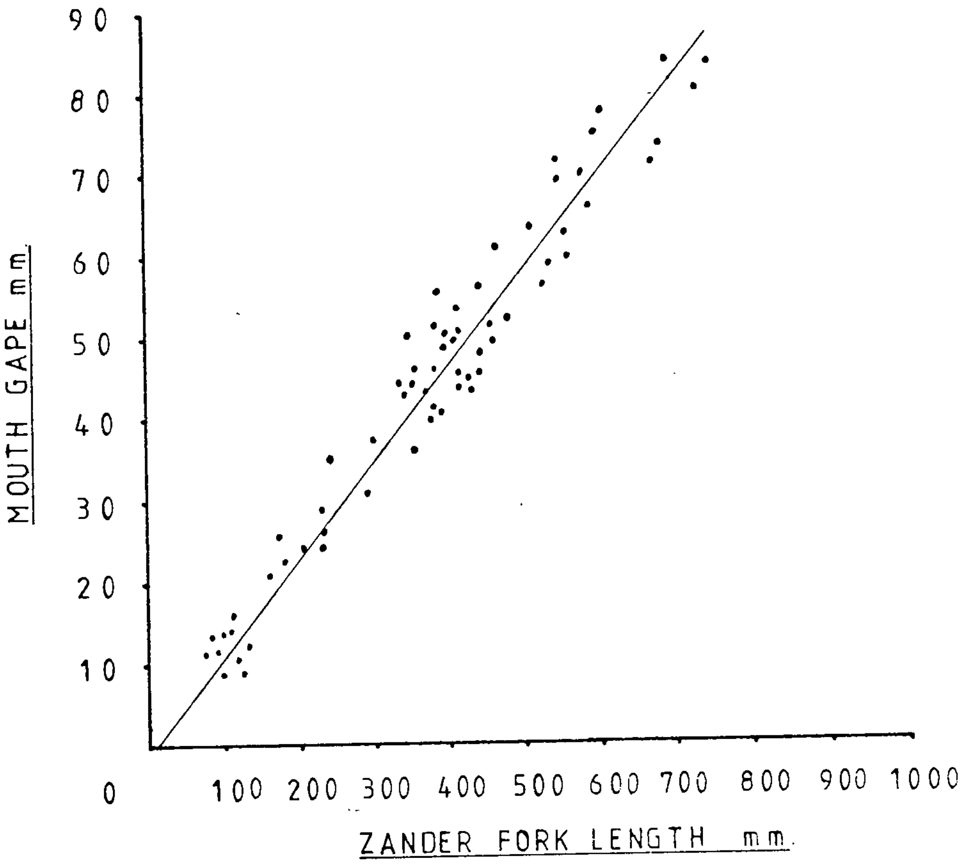
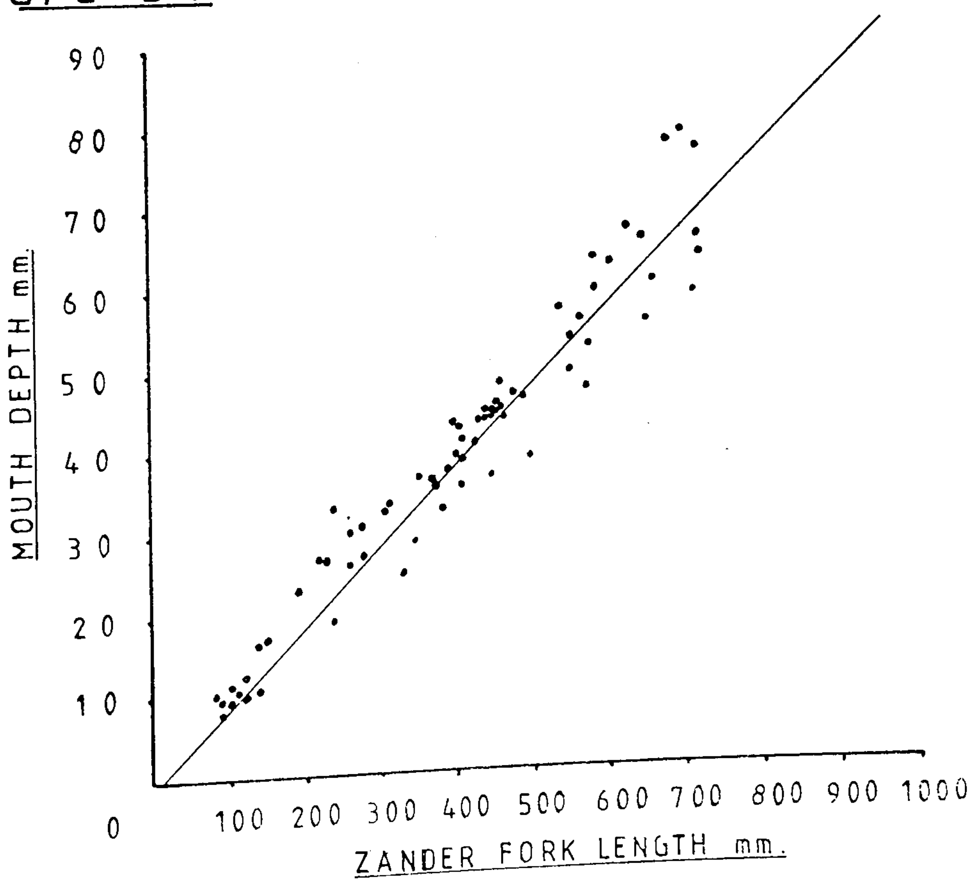


Figure 34.



of prey is limited by mouth gape. Aquarium studies suggest that prey is normally swallowed in the horizontal plane as opposed to any other. Figure 32 shows the planes of swallowing available to the zander.

Prey fish depths were measured using a Vernier and the depth, fork length relationship of each prey fish species was determined. Prey depths were measured from the base of the dorsal fin to the base of the pelvic fin. This was the deepest part of the prey fishes body. Fish with spiny dorsal fins were also measured with the dorsal fin erect, from the tip of the extended dorsal fin to the base of the pelvic fin. Prey fish lengths as noted in zander stomachs were then expressed as percentages of the maximum prey size ingestible. These percentages were summed according to prey species for each zander population and means calculated.

(f) Direction of Swallowing of Prey

Prey fish were either swallowed head or tail first. According to Molnar and Tolg (1962) prey is not rotated in the stomach, therefore the position of the prey in the stomach is indicative of the method of swallowing. The lengths of prey fish swallowed hear or tail first were noted. Prey fish lengths were expressed as the percentage of the maximum size ingestible and means for each direction of swallowing. The means were then tested for significant differences using a "t" test.

(g) Feeding Periodicity

Two approaches were employed for this study. Firstly during a short period of June 1980, the time of capture of zander using rod and line angling was recorded on the Relief Channel. The number of zander captured was expressed as number of zander caught per one hour period. In this way the differences in angling effort per day were equalised, allowing a true representation of zander feeding.

Secondly, rates of digestion obtained by digestion studies were used to estimate the time of consumption of prey items. (The methods used to obtain the digestion data are presented in Section 3). If the digestion time of a prey item of known size is known at a given temperature, it is possible to estimate the time of ingestion of a prey item found in a zander's stomach.

(h) The Number of Empty Stomachs

The number of empty stomachs was noted. Comparisons between zander populations were only valid when sampled using the same capture method. Rod and line angling captured zander could be compared with each other, while electrofishing and seine netting were comparable. This was because rod and line caught zander were thought more likely to have empty stomachs than those obtained by other means.

2.3.3. RESULTS

(a) Species of Prey

The percentage species composition of zander prey fish are presented as histograms in Figures 35 and 36. Data for the Relief Channel 1968-70, 1975-76, 1979 and 1980, were presented with data for the Middle Level Main Drain 1979-80, Burwell Lode 1979, Coombe Abbey Lake 1979-80 and Coventry and Oxford Canal 1978-79.

Figure 35.

Percentage Species Composition.

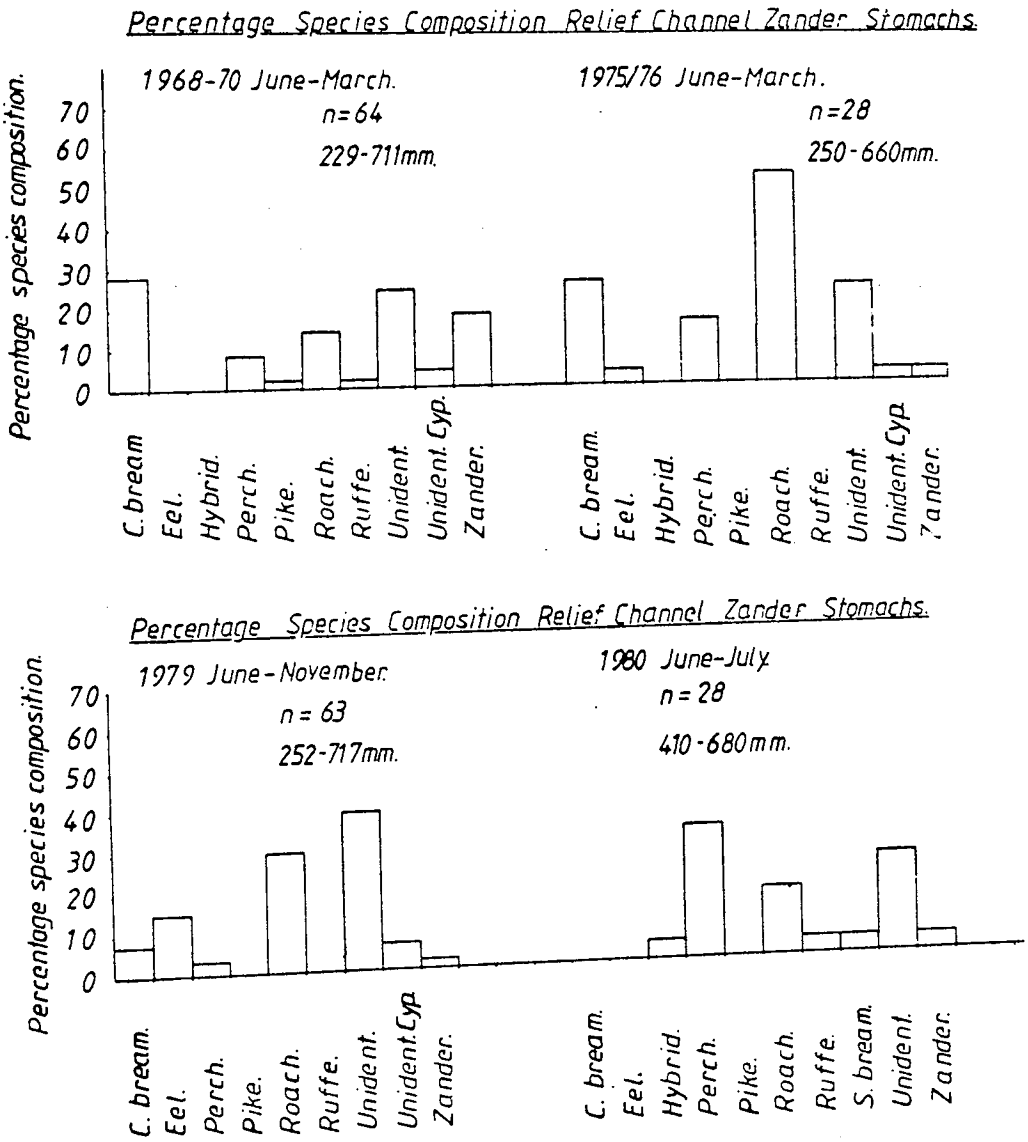


Figure 36.

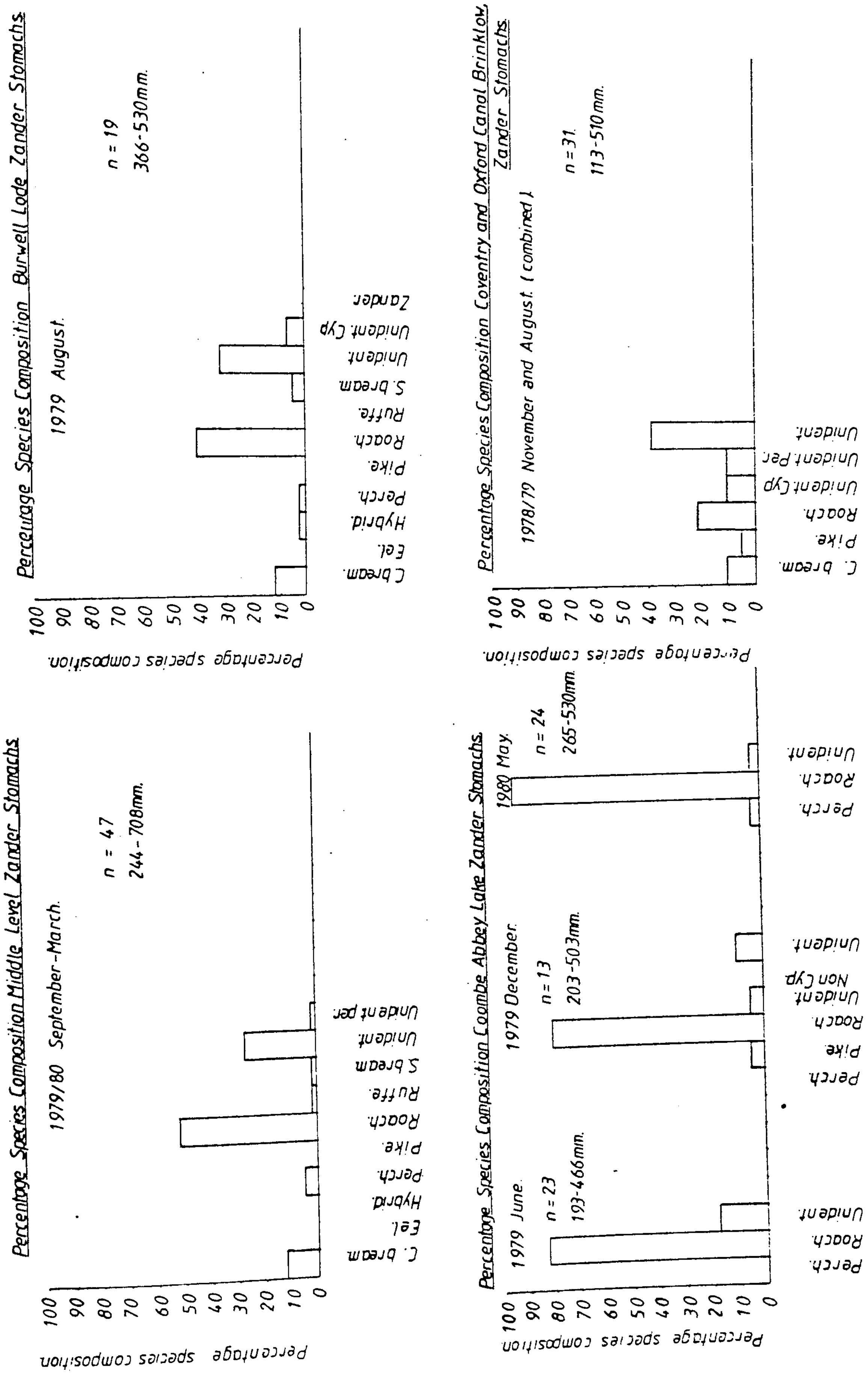

Percentage Species Composition Burwell Lode Zander Stomachs
1979 August.
n = 19
366-530mm.
Percentage Species Composition Coventry and Oxford Canal Brinklow, Zander Stomachs
1978/79 November and August. (combined)
n = 31.
113-510mm.
Percentage Species Composition Middle Level Zander Stomachs
1979/80 September-March.
n = 47
244-708mm.
Percentage Species Composition Coombe Abbey Lake Zander Stomachs
1979 June.
n = 23
193-466mm.
1979 December.
n = 13
203-503mm.
1980 May.
n = 24
265-530mm.
Percentage species composition.
C. bream.
Eel.
Hybrid.
Perch.
Pike.
Roach.
Ruffe.
S. bream.
Unident.
Unident. Cyp
Unident. Per.
Unident. Non Cyp
Zander.
100 90 80 70 60 50 40 30 20 10 0

Figure 37 presents the percentage species composition of the available prey fish. Data was presented similarly to that of the prey fish noted in zander stomachs. Data was available from the Relief Channel 1979, Middle Level Main Drain 1979, Burwell Lode 1979 and Coombe Abbey 1980. The data used in these histograms was presented in Appendix IV, except for survey data which is available in the relevant reports (Klee 1979ab and Gregory 1979).

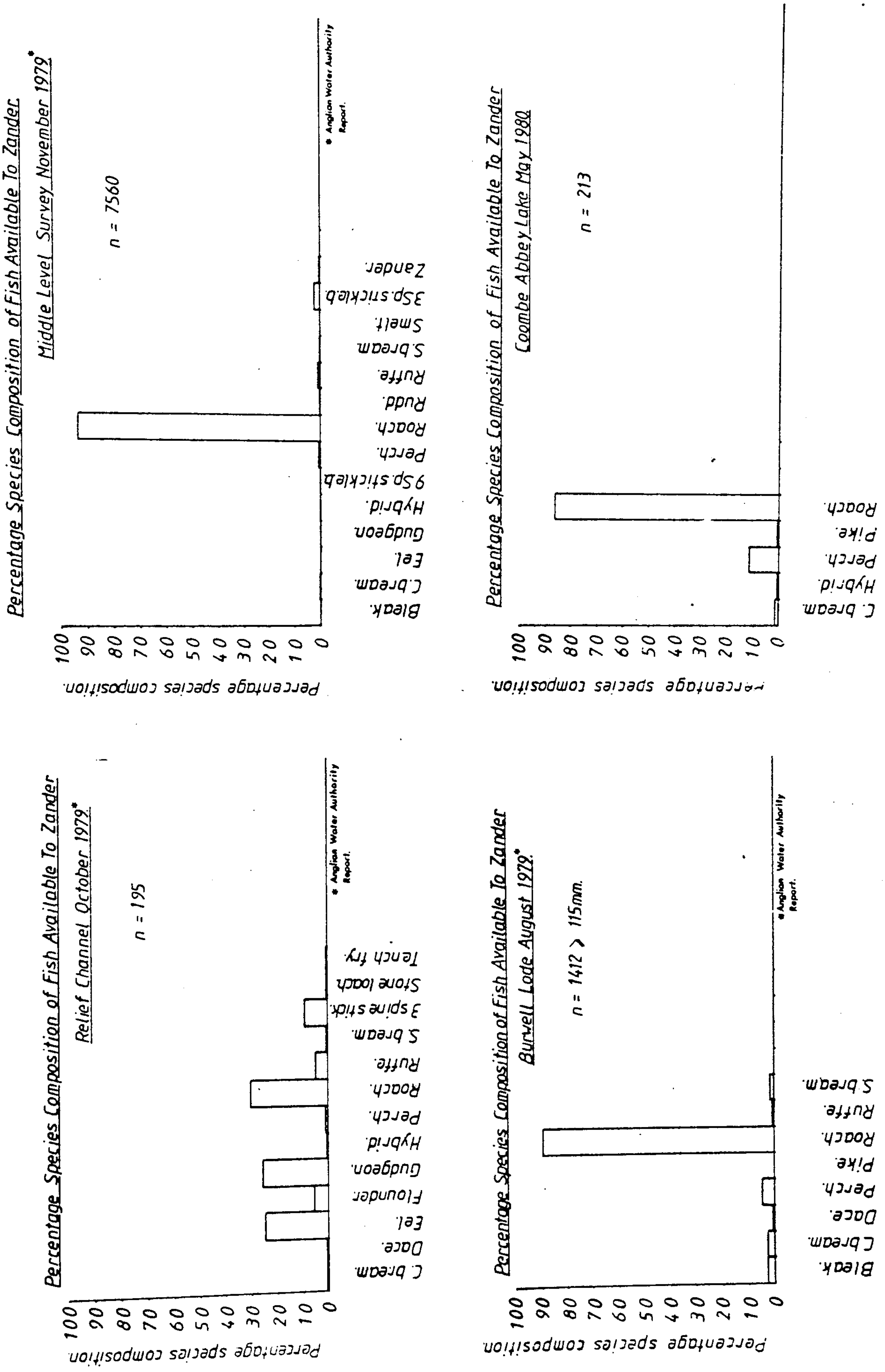
Percentage species composition as obtained from zander stomachs and survey results were ranked and tested for significance using the Wilcoxon Matched Pairs test (Siegal 1956). (Table 28). No significant difference was noted between the two percentage species composition. This suggests that zander were preying on each prey species in proportion to its availability or abundance.

TABLE 28: Results of Wilcoxon Matched Pairs Test

Water	Period	N	N negative	P
Relief C	1979	14	25	> 0.05
Middle Level	1979	8	19	> 0.05
Burwell Lode	1979	7	14	> 0.05
Coombe Abbey	1980	5	5	> 0.05

Initial consideration was given to zander samples which could be compared with the available prey fish population. The Relief Channel zander of 1979 (Figures 35 and 37) were feeding most heavily on roach, which were also the predominant available prey fish. Eels were the second most important prey fish consumed and were also well represented as available prey fish. Common bream were the third most important prey followed by perch. Young zander were the least numerous of the identifiable prey species.

Figure 37.



Percentage Species Composition of Fish Available To Zander
Middle Level Survey November 1979*
n = 7560
Bleak.
C.bream.
Eel.
Gudgeon.
Hybrid.
9Sp.stickleb.
Perch.
Roach.
Rudd.
Ruffe.
S.bream.
Smelt.
3Sp.stickleb.
Zander.
* Anglian Water Authority Report.
Percentage species composition.
Percentage Species Composition of Fish Available To Zander
Coombe Abbey Lake May 1980
n = 213
C. bream.
Hybrid.
Perch.
Pike.
Roach.
Percentage Species Composition of Fish Available To Zander
Relief Channel October 1979*
n = 195
C. bream.
Dace.
Eel.
Flounder.
Gudgeon.
Hybrid.
Perch.
Roach.
Ruffe.
S. bream.
3 spine stick.
Stone loach.
Tench fry.
* Anglian Water Authority Report.
Percentage Species Composition of Fish Available To Zander
Burwell Lode August 1979*
n = 1412 > 115mm.
Bleak.
C.bream.
Dace.
Perch.
Pike.
Roach.
Ruffe.
S.bream.
* Anglian Water Authority Report.

Unidentified prey fish and unidentified cyprinid fish formed a large proportion of the prey fish noted in zander stomachs. If it is assumed that this unidentified portion corresponds in composition with the identified prey percentage composition, then comparison between prey eaten and available prey will be valid. A number of prey species were encountered in survey samples, which were not noted in zander stomachs. These included gudgeon, ruffe, three spined sticklebacks and flounders.

Middle Level 1979 zander (Figures 36, 37) were eating mainly roach which were also the predominant available prey species. Common bream were next most abundant in zander stomachs, followed by perch, silver bream and ruffe. However roach were by far the most important prey fish. All other prey species which were available to zander as prey fish were very few in number compared with roach. Eels, though known to be common (authors observation) in the Middle Level, were neither well represented in survey samples or zander stomachs.

Burwell Lode zander (Figures 36 and 37) were also feeding predominantly on roach, which were again the most abundant prey species, Perch, though the second most common prey available, were not well represented in zander stomachs. Bleak, though the third most abundant prey species, were not noted in zander stomachs. Common bream, on the other hand, though not well represented in survey samples, were the second most important fish species in the zander's diet. Silver bream were also more prevalent in zander stomachs than in survey samples.

Coombe Abbey Lake zander in May of 1980 (Figures 36 and 37) were feeding almost exclusively on roach, which were also the most important prey species noted in seine net samples. Perch were second most important in the diet and in the prey fish population. Common bream, though available as prey in relatively small numbers, were not noted in zander stomachs.

An examination of zander feeding data from other waters and periods, suggests similar emphasis on predation of the most numerically abundant prey fish. Oxford canal zander (Figure 36) preyed mainly on roach and common bream. These were the most abundant fish, as noted while electrofishing. Relief Channel zander at 1968-70 (Figure 35) appeared to be preying on mainly common bream, with zander second most common. Roach were unusually third most abundant in zander stomachs. Perch, pike and ruffe were also eaten. There are no records of prey fish species composition from this period, however it is known that most common fish species were present at this time. Eels, though available to zander, again were not noted in stomach contents.

During the period 1975-76 (Figure 36) on the same water roach were the predominant prey species, followed by common bream and perch. Young zander were again noted in zander stomachs, but not as often as during the previous period. Zander from the same water in 1980 (Figure 35) were feeding most heavily on perch (mainly young of the year) which, though numerically important, would compose a very small proportion of the zanders diet in weight. Roach were second most important, followed by roach bream hybrids, ruffe, silver bream and zander.

Coombe Abbey Lake zander were, for the two other periods considered, preying to a similar extent on roach as the zander from May of 1980. Roach were again by far the most important prey species, with other prey fish such as young pike, noted on only one occasion.

Invertebrate prey were noted in zander stomachs. However, though these were in some cases numerically important, they were seldom significantly important when considered in terms of weight. The following invertebrates were noted in zander stomachs:

Daphnia sp.
Chironomid sp.
Gammarus sp.
Asellus sp.
Sialis sp.
Dragonfly larvae.
Dreissensia polymorpha (zebra mussels)
Oligochaetes
Tricoptera sp.

Because of the inappropriate nature of a numerical comparison of zander feeding on invertebrates and fish, further reference to invertebrate feeding was left until the section on weight of prey items (d).

(b) Number of Food Items

The relationship between the number of prey fish and zander length was investigated by means of a regression line (least squares) and tested for correlation . All data was pooled into groups dependent on the period sampled and/or the populations studied (Table 29).

TABLE 29: Tests for Correlation Between Number of Prey Items and Zander Fork Length

Water	Period	Number	r	p
Relief Channel	1968-70	26	0.35	> 0.05
"	1975-76	11	-0.38	> 0.05
"	1979	26	0.25	> 0.05
"	1980	14	0.26	> 0.05
Middle Level	1979-80	26	0.23	> 0.05
Burwell Lode	1979	14	0.19	> 0.05
Coventry and Oxford Canal	1978-80	17	-	-
Coombe Abbey	1979-80	47	0.33	< 0.05
Relief Channel (AWA)	1969-70	23	-0.008	> 0.05
Cut Off Channel	1980	8	-0.29	> 0.05

At the present level of sampling, it appeared that there was no significant correlation between number of prey fish and zander length for the majority of populations studied. Only Coombe Abbey zander showed correlation between number of prey fish and zander length, significant at the $p < 0.05$ level.

The number of zander eating a specific number of prey fish was expressed as a percentage and presented in Table 30.

TABLE 30: Percentage Number of Zander eating 1 to 10 Prey Fish

Number of Prey	Number of Zander	Percentage Number
1	107	50.2
2	53	24.9
3	26	12.2
4	14	6.6
5	2	0.9
6	1	0.5
7	2	0.9
8	3	1.4
9	1	0.5
10	4	1.9

Half the zander examined had eaten one prey fish prior to the period of sampling, nearly 25% had eaten two prey fish, while 12% had eaten 3 prey fish. 6.6% had eaten 4 prey fish. This progressive and apparently predictable trend in the number of prey fish eaten was not continued beyond 5 prey fish. This suggests that zander, when feeding, consume prey in varied numbers. The mean number of prey fish noted in zander stomachs was 2.1, suggesting that prey fish were generally consumed in small numbers.

(c) Length of Food Items

The lengths of prey fish, were plotted against zander length. Eels because of their unique body shape were plotted separately, as were also invertebrates. Regression lines were fitted to the points and the degree of correlation (if any) noted. A summary of the results obtained is presented in Table 31. Figures 38 to 45 present the data as plotted with the regression line fitted (where appropriate).

Figure 3.8.

Zander/Prey Length Relationship. Relief Channel 1968-70

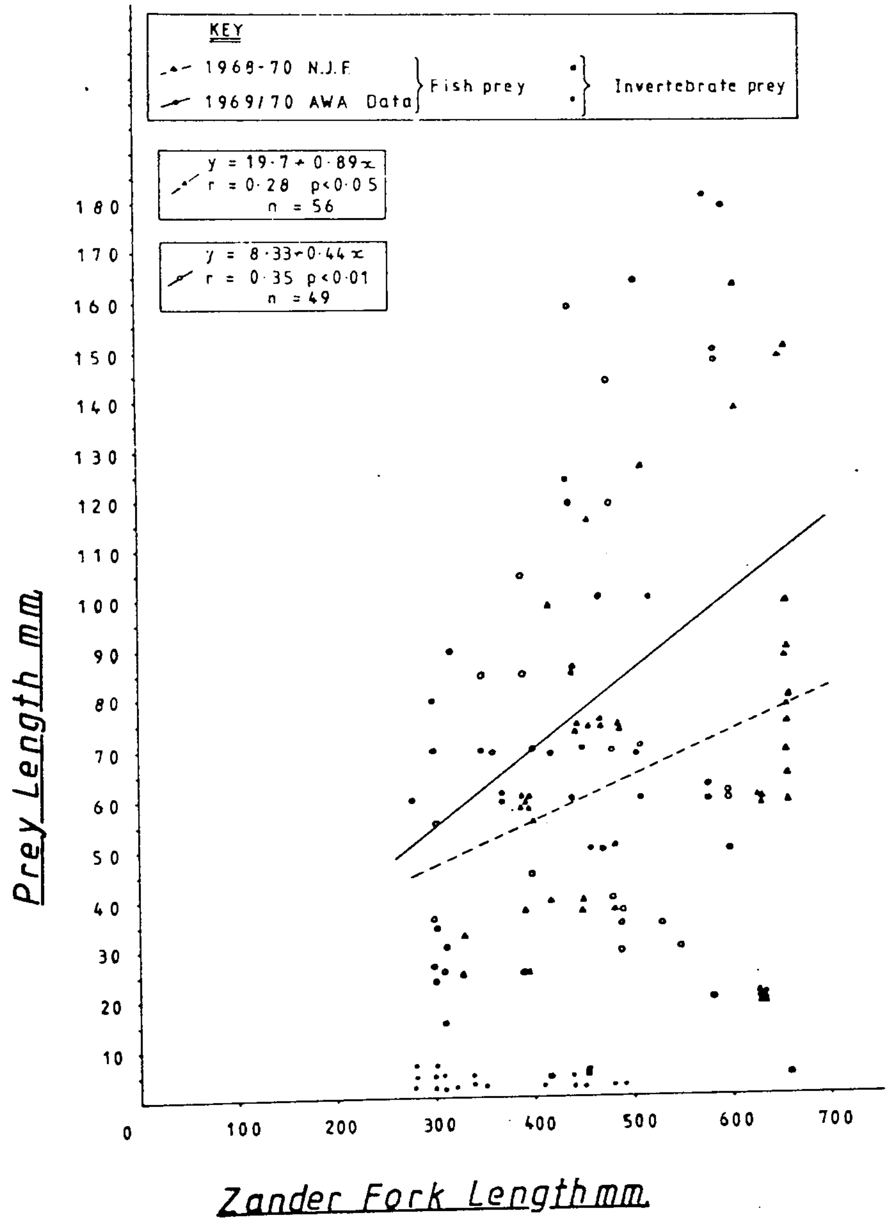
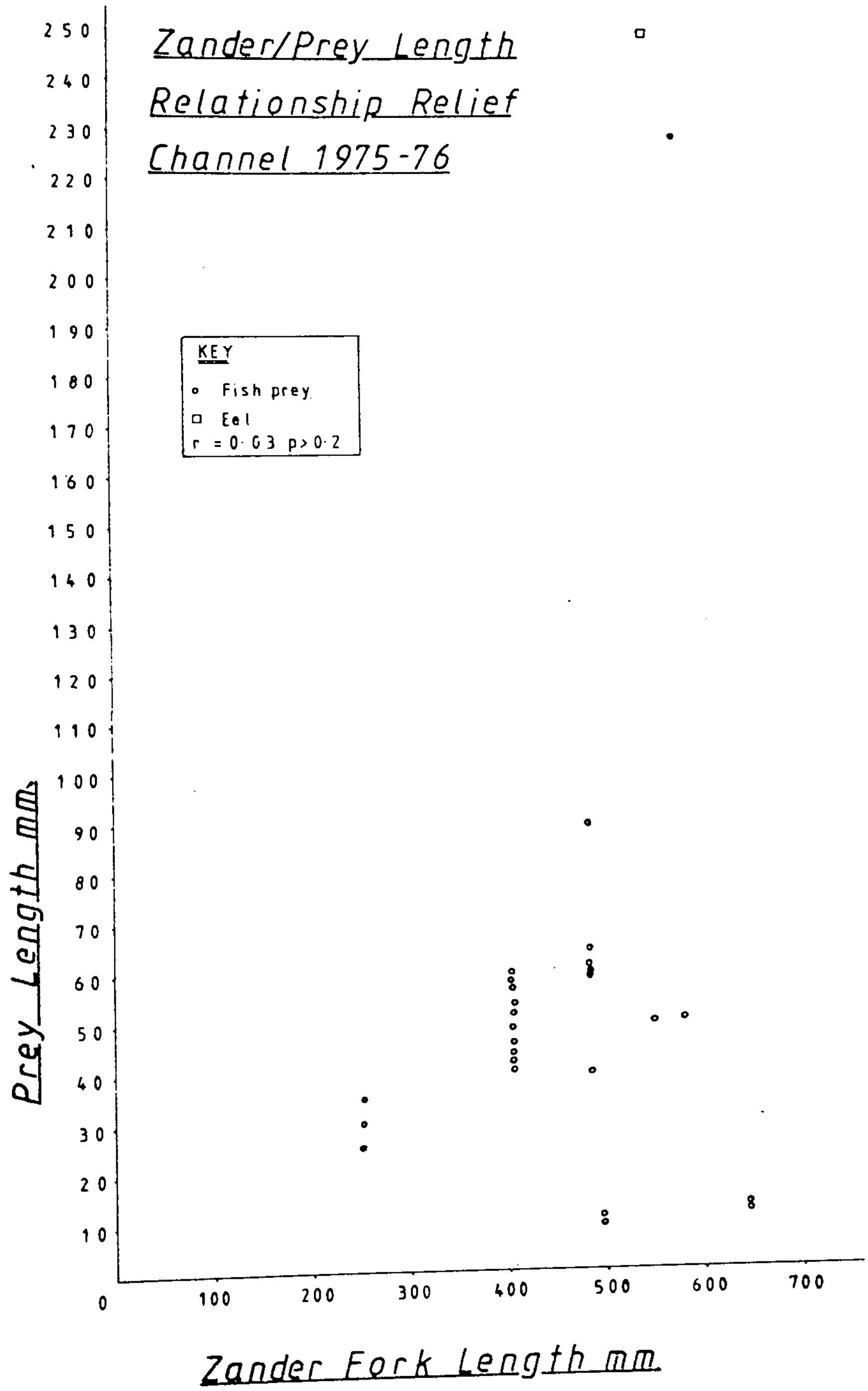
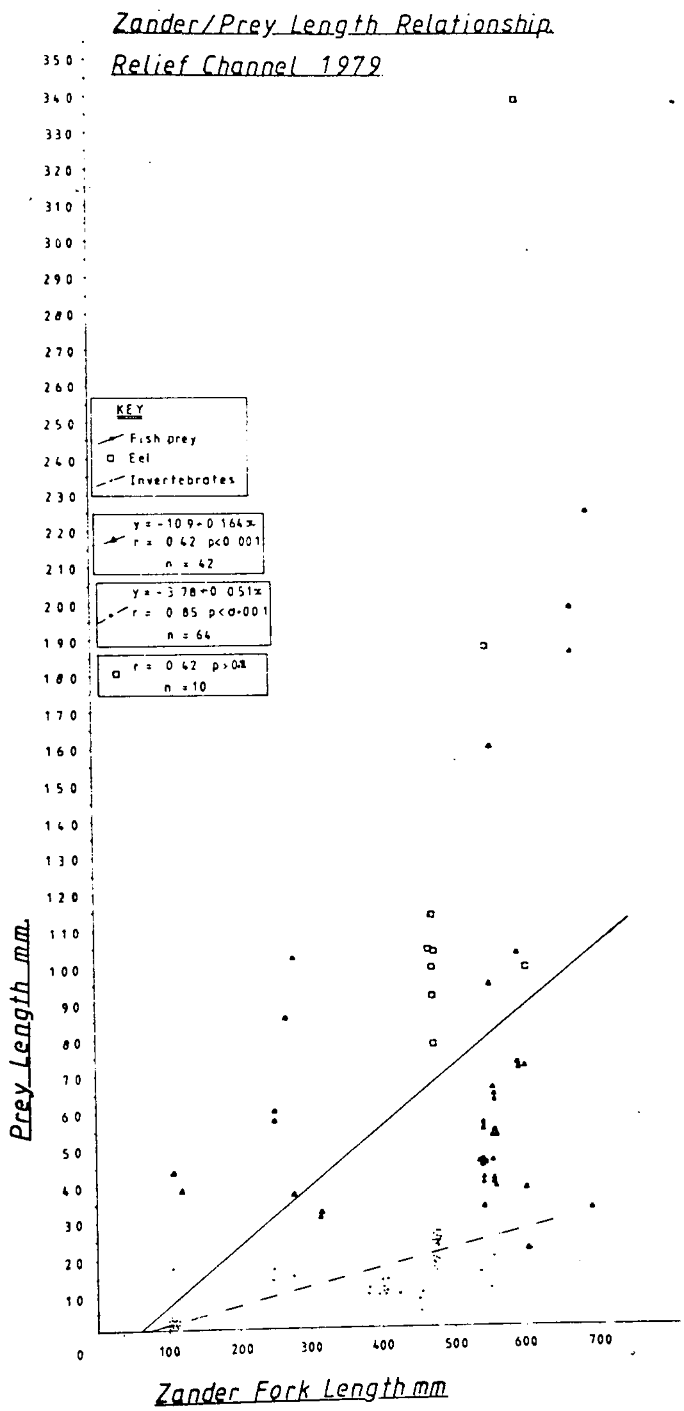


Figure 39



Zander/Prey Length
Relationship Relief
Channel 1975-76
KEY
Fish prey
Eel
r = 0·03 p>0·2
Prey Length mm
Zander Fork Length mm
250
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
100
200
300
400
500
600
700

Figure 40.



Zander/Prey Length Relationship
Relief Channel 1979
KEY
Fish prey
Eel
Invertebrates
y = -10 9 + 0 164x
r = 0 42 p<0 001
n = 42
y = -3 78 + 0 051x
r = 0 85 p<0·001
n = 64
r = 0 42 p>0.1
n = 10
Prey Length mm
Zander Fork Length mm
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
240
250
260
270
280
290
300
310
320
330
340
350
100
200
300
400
500
600
700

Figure 41

Zander/Prey Length Relationship
Relief Channel June-July 1980

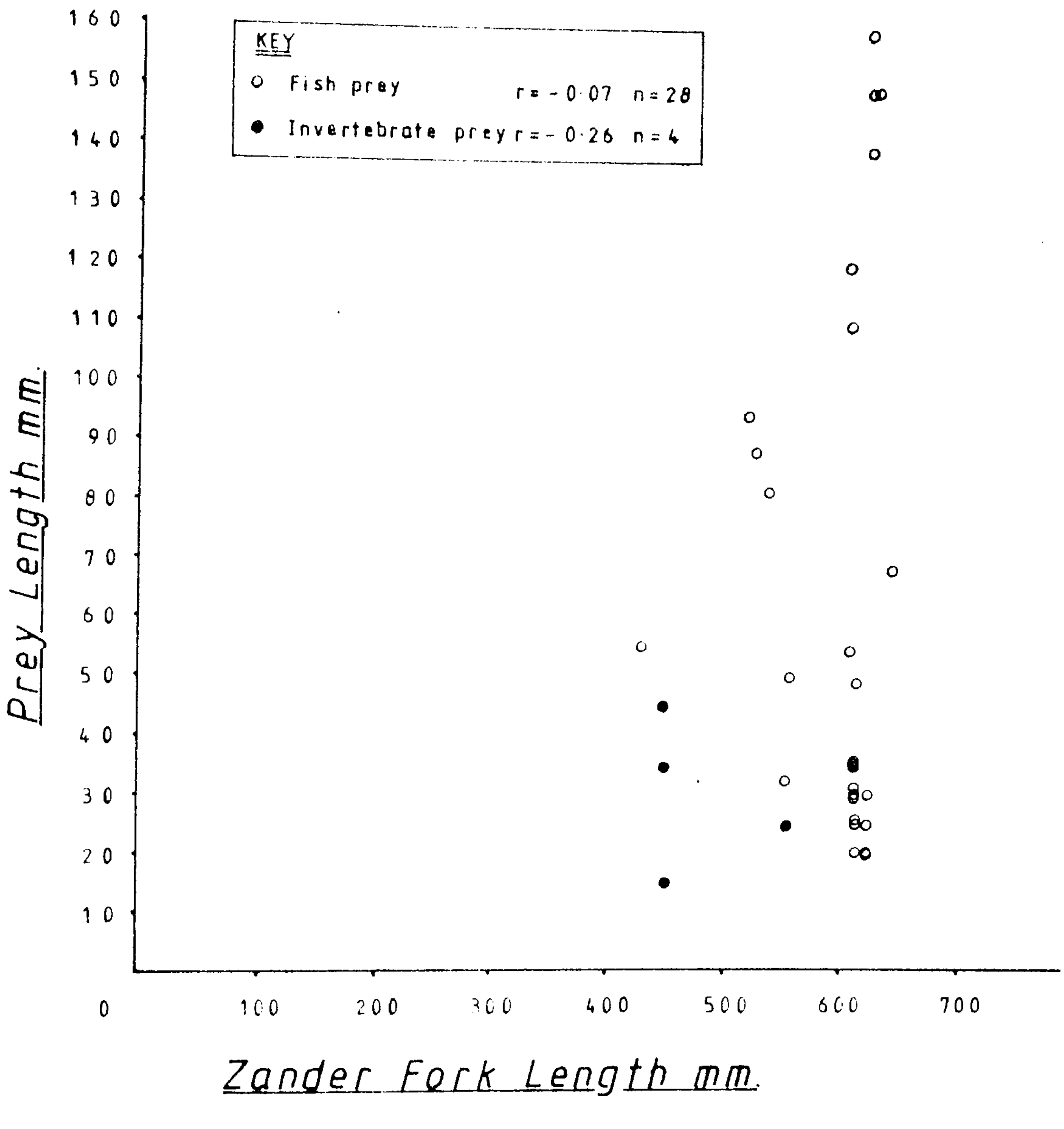


Figure 42.

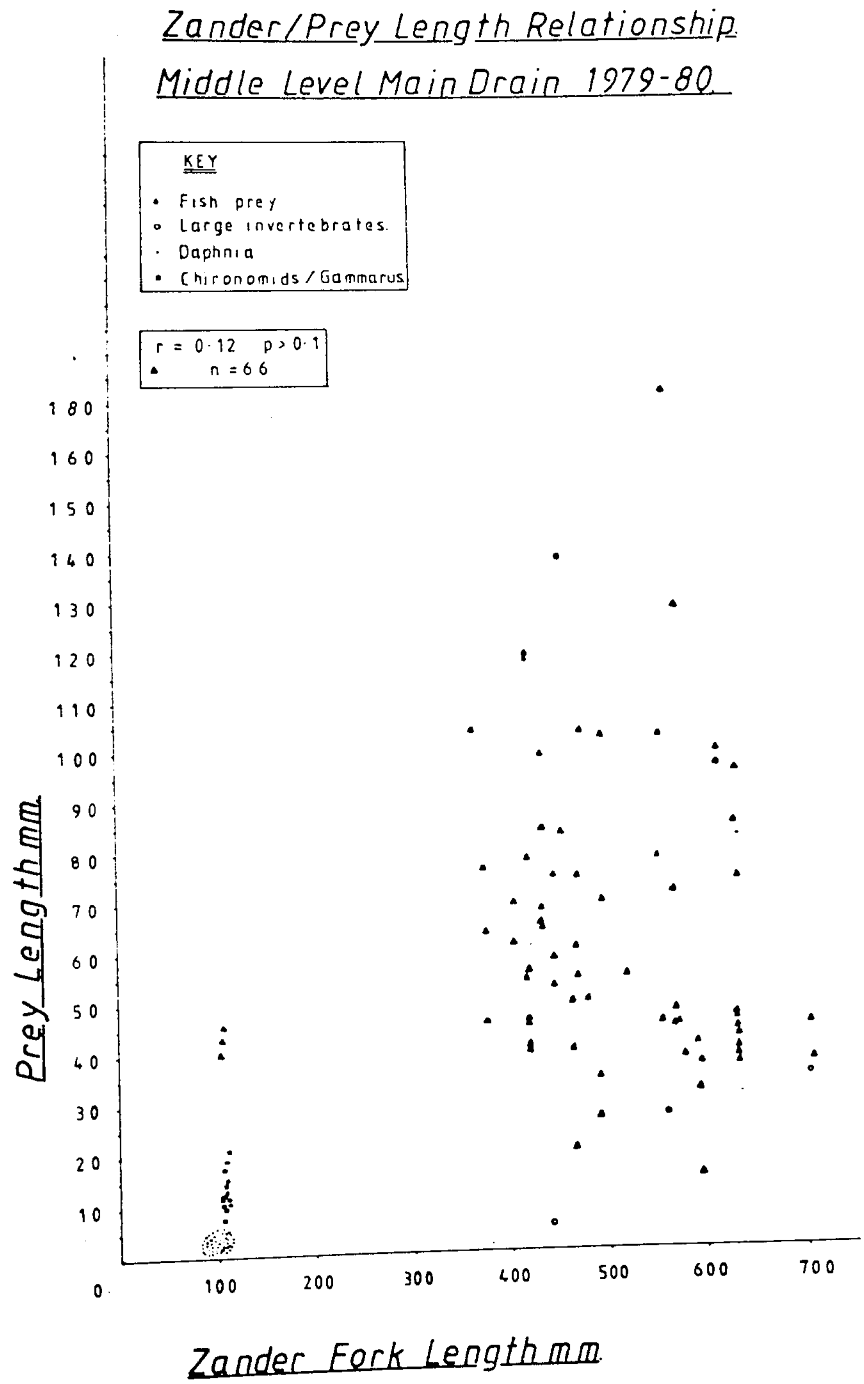
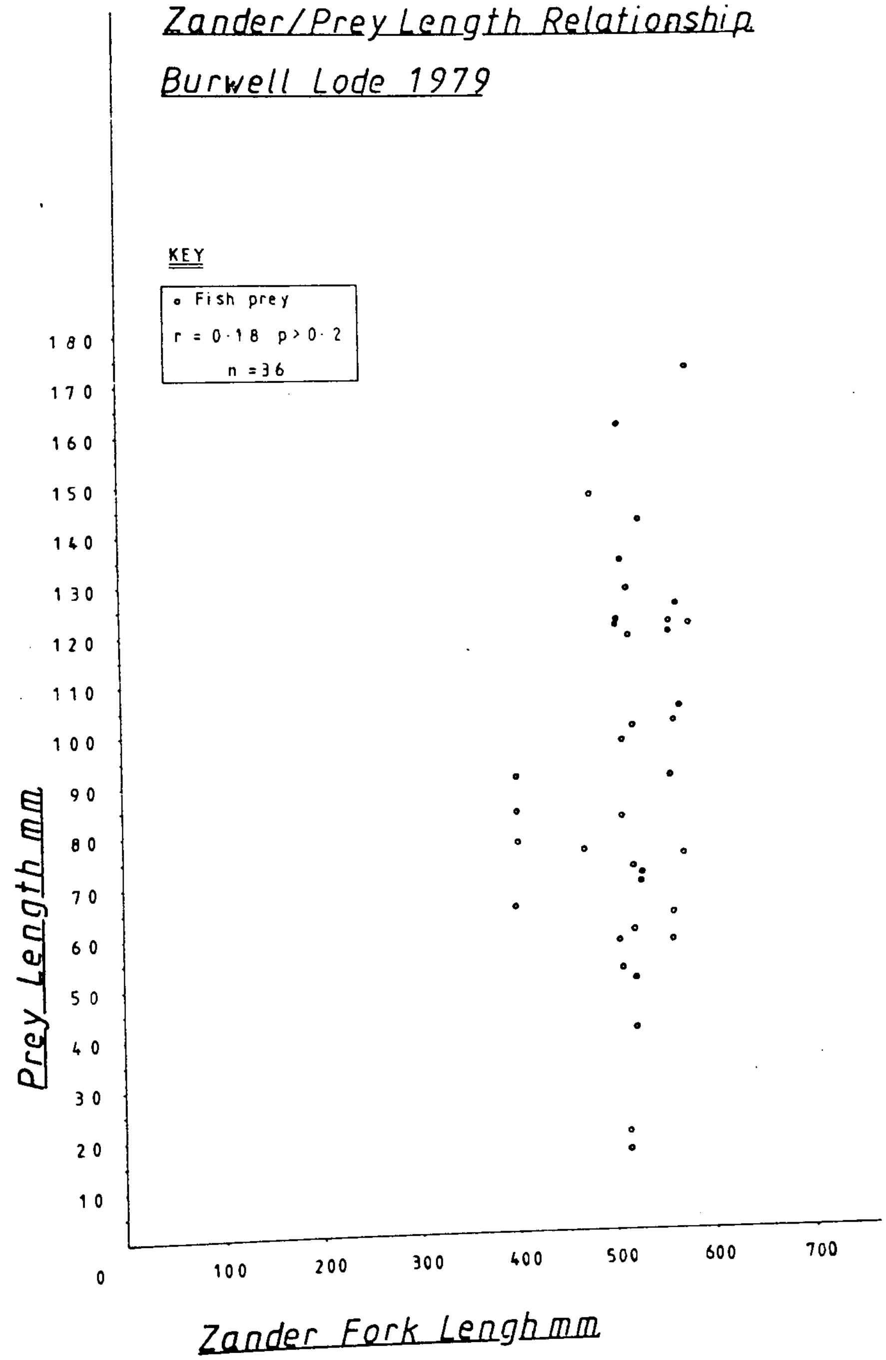

Zander/Prey Length Relationship.
Middle Level Main Drain 1979-80.
KEY
Fish prey
Large invertebrates.
Daphnia
Chironomids / Gammarus
r = 0·12 p > 0·1
n = 66
Prey Length mm
180
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
100
200
300
400
500
600
700
Zander Fork Length mm

Figure 43



Zander/Prey Length Relationship
Burwell Lode 1979
KEY
Fish prey
r = 0·18 p > 0·2
n = 36
Prey Length mm
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
100
200
300
400
500
600
700
Zander Fork Lengh mm

Figure 44.

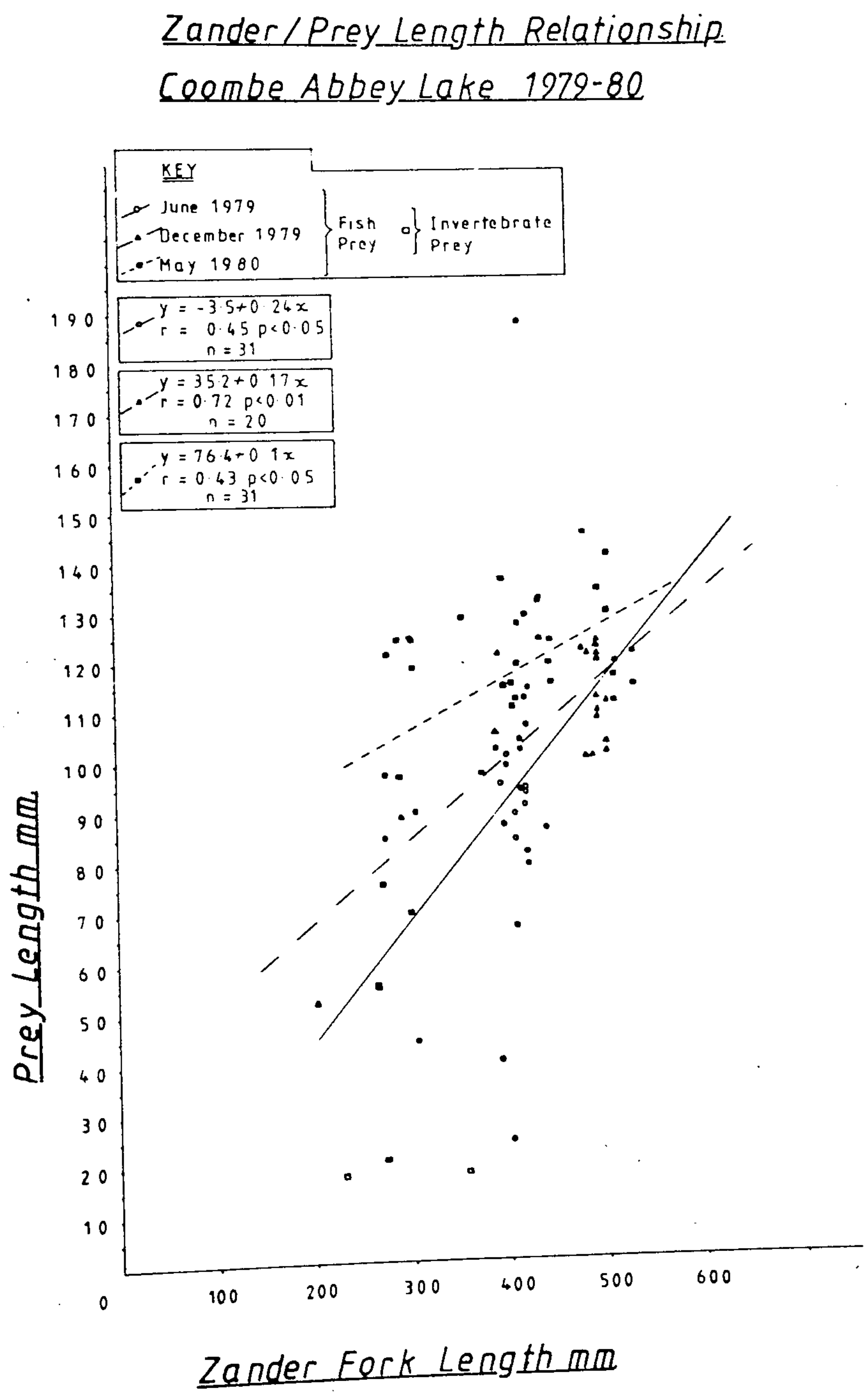
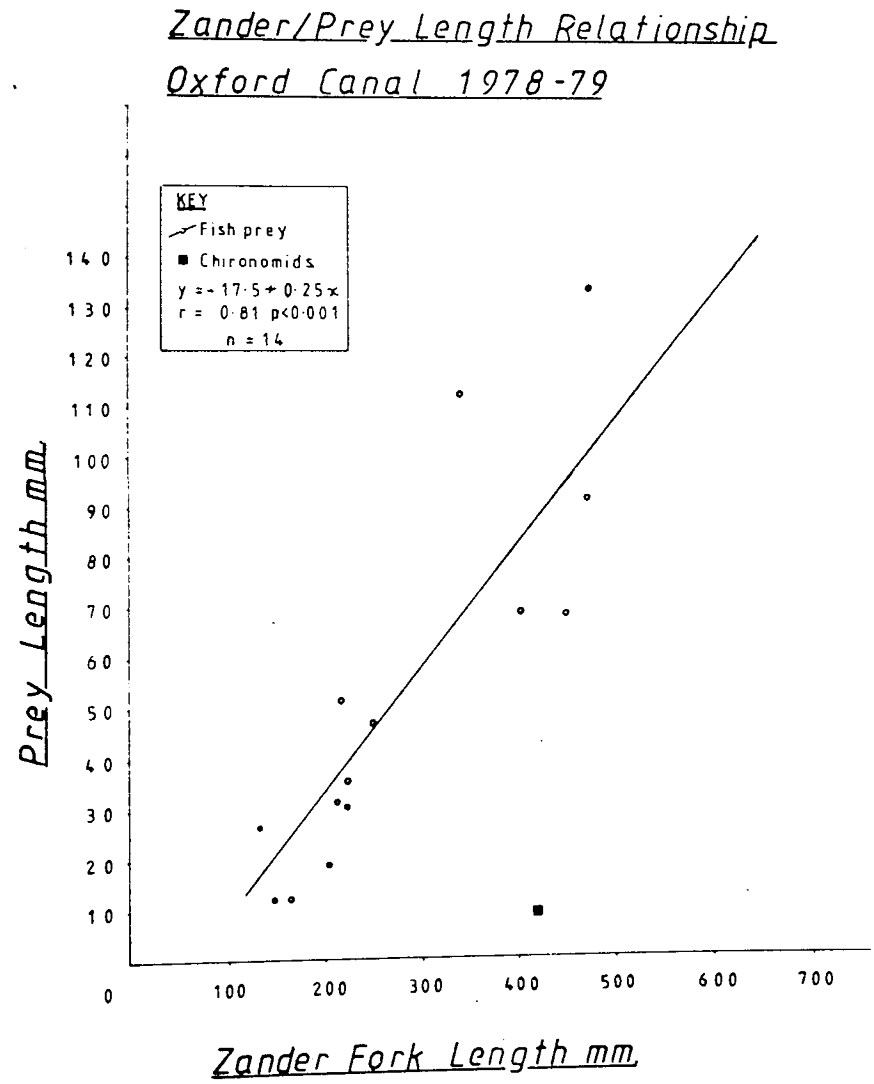

Zander/Prey Length Relationship
Coombe Abbey Lake 1979-80
KEY
June 1979
December 1979
May 1980
Fish Prey
Invertebrate Prey
y = -3·5+0·24x
r = 0·45 p<0·05
n = 31
y = 35·2+0·17x
r = 0·72 p<0·01
n = 20
y = 76·4+0·1x
r = 0·43 p<0·05
n = 31
Prey Length mm
Zander Fork Length mm
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
100
200
300
400
500
600

Figure 45.



Zander/Prey Length Relationship
Oxford Canal 1978-79
KEY
Fish prey
Chironomids
y = -17·5 + 0·25x
r = 0·81 p<0·001
n = 14
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
100
200
300
400
500
600
700
Prey Length mm
Zander Fork Length mm

TABLE 31: Zander Length, Prey Length Relationship

Water	Period	Prey	r	n	p	y = a+bx
Relief Channel	1968-70	fish	0.28	56	< 0.05	y = 19.7+0.89x
"	1969-70 (AWA)	fish	0.35	49	< 0.05	y = 8.3+0.44x
"	1975-76	fish	0.03	27	> 0.05	
"	1979	fish (excl. eel)	0.42	42	< 0.05	y = -10.9+0.16x
"	1979	eel	0.42	10	> 0.05	
"	1979	invert.	0.85	64	< 0.05	y = -3.78+0.051x
"	1980	fish invert.	-0.07 -0.26	28 4	> 0.05 > 0.05	
Middle Level	1979-80	fish	0.12	66	> 0.05	
Burwell Lode	1979	fish	0.18	36	> 0.05	
Coombe Abbey	June 1979	fish	0.45	31	< 0.05	y = -3.5+0.24x
"	Dec. 1979	fish	0.72	20	< 0.05	y = 35.2+0.17x
"	May 1980	fish	0.43	31	< 0.05	y = 76.4+0.1x
Coventry & Oxford Canal	1978-79	fish	0.81	14	< 0.05	y = -17.5+0.25x

Where data was obtained from very similar periods such as the three samples from Coombe Abbey in 1979 and 1980, the Relief Channel 1968-1979 and AWA results for the Relief Channel 1969-70, the slopes were tested for significant difference using Analysis of Variance (Blalock 1972). Regression coefficients for Coombe Abbey were found to be not significantly different at the < 0.05 level of significance. The two sets of Relief Channel data were significantly different from each other at the < 0.05 level fish lengths. Despite this, it is apparent that in many cases a positive correlation exists between zander length and prey length. In other cases correlation does not exist and it can be seen that zander prey on a wide range of prey fish sizes. Even when correlations were noted, which suggest an increase of prey fish size with zander length, it could be seen that zander were preying on very small prey fish, independent of zander size.

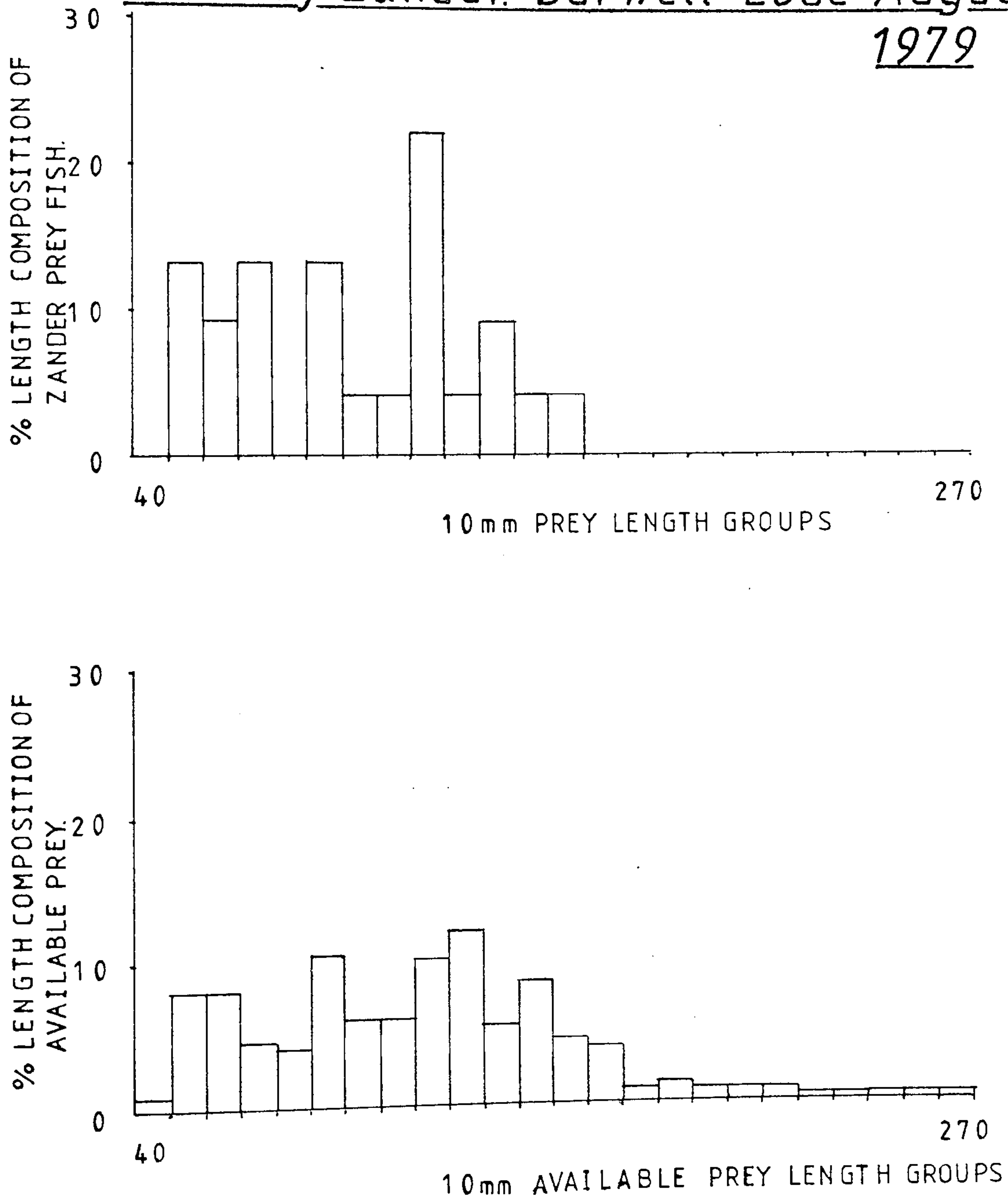
If the length distribution of available prey fish is compared with the length distribution noted in zander stomachs, it is possible to determine whether or not zander are removing prey fish from the population in direct proportion to the availability of the various sizes of prey. Three zander populations were studied in this manner. These were the Coombe Abbey Lake population of 1980 and those from the Middle Level and Burwell Lode in 1979.

The mean length of prey fish available to zander was tested against the mean length of the prey found in zander stomachs, using a t test. (Table 32).

Figures 46 and 47 present the frequency distributions of available prey and zander prey as noted for Burwell Lode in August of 1979 and for the Middle Level Main Drain in 1979-80. Gregory (1979) working on Burwell Lode found that electrofishing did not sample the available prey fish representatively, below the length of 115 mm. In order to allow a comparison between zander prey size and available prey size this point was noted while a comparison of prey and available prey lengths was made. This included many fish of less than 115 mm.

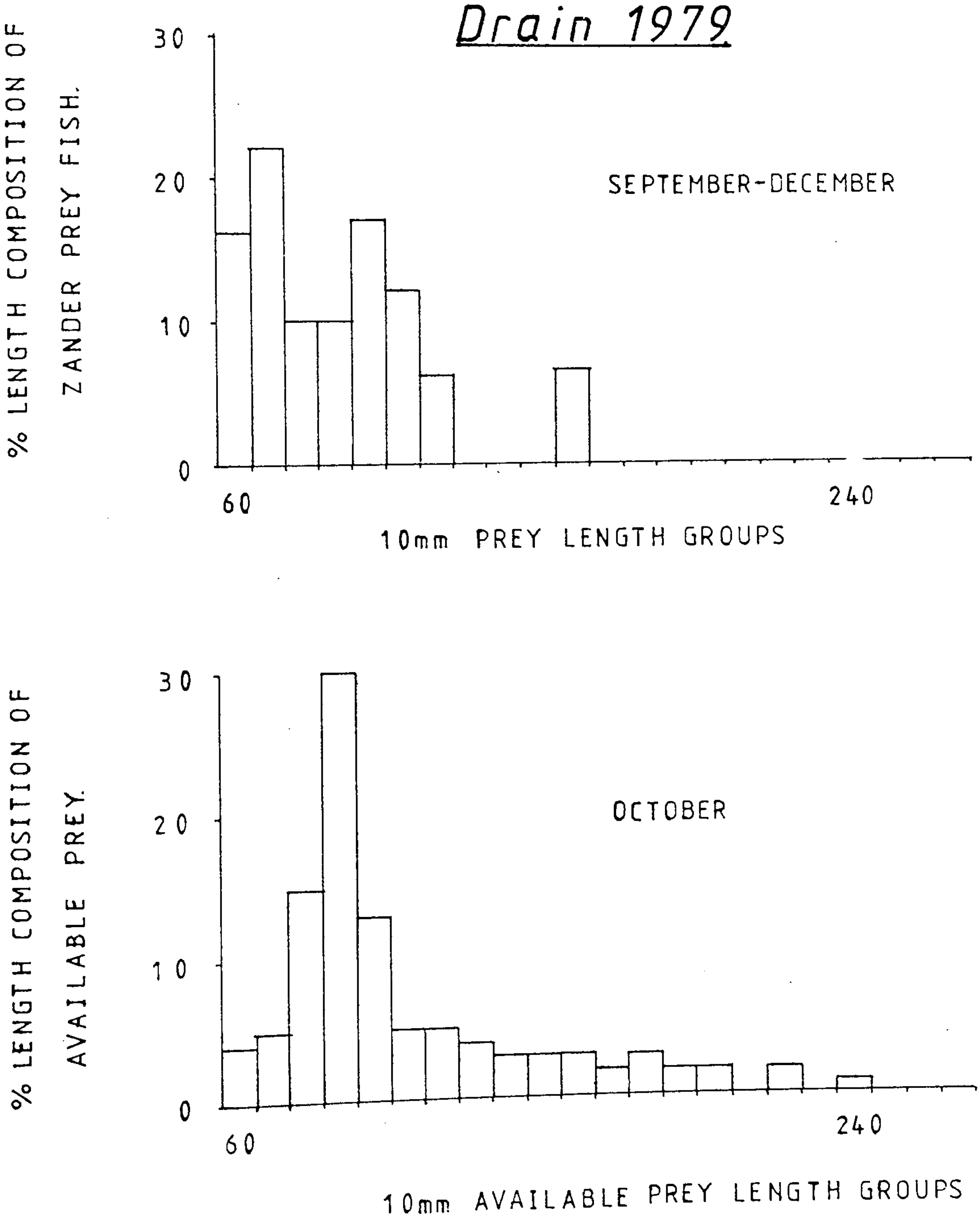
Figure 46.

The Percentage Length Composition of Available Prey Fish and Prey Fish Eaten by Zander. Burwell Lode August 1979



from Gregory 1979 (AWA)

Figure 47
The Percentage Length Composition of Available Prey Fish and Prey Fish Eaten by Zander. Middle Level Main Drain 1979



from Klee 1979b (AWA)

TABLE 32: Results of t tests, comparing the means of available zander prey fish (roach) lengths and the prey fish lengths noted in zander stomachs (roach).

Sample Method	Available Prey size Range	Mean		Prey size Range	Mean	n	t	p
Seine Coombe 80	94-165	132.9	184	70.5-146	118.7	29	3.05	< 0.05
Zander size range from May 80 273-530 n 24								
Electro-fished Burwell 79	40-280	94.97	2034	50-179	104.8	23	1.039	> 0.05
Zander size range from Burwell Lode August 1979 366-530 n = 19								
Seine Middle Level 79	60-240	106.6	914	60-179	106.3	66	0.2	> 0.05
Zander size range from Middle Level September-March 1979-80 244-708 mm n = 47								

For the Middle Level study, sufficient samples of zander prey and available prey fish were obtained to enable a comparison, excluding all fish less than 60 mm. This was the minimum size of fish which Klee (1979b) considered was sampled representatively by his chosen fishing methods.

Figures 46 and 47 suggest that both Burwell Lode and Middle Level Main Drain zander were feeding on the smaller sizes of available prey fish. Feeding was concentrated between 60-120 mm on the Middle Level and 50-160 mm in Burwell Lode.

(d) Weight of Prey

The following weights were recorded for invertebrate prey eaten by zander. Weights were expressed as means of up to 30 weighed individuals. (Table 33).

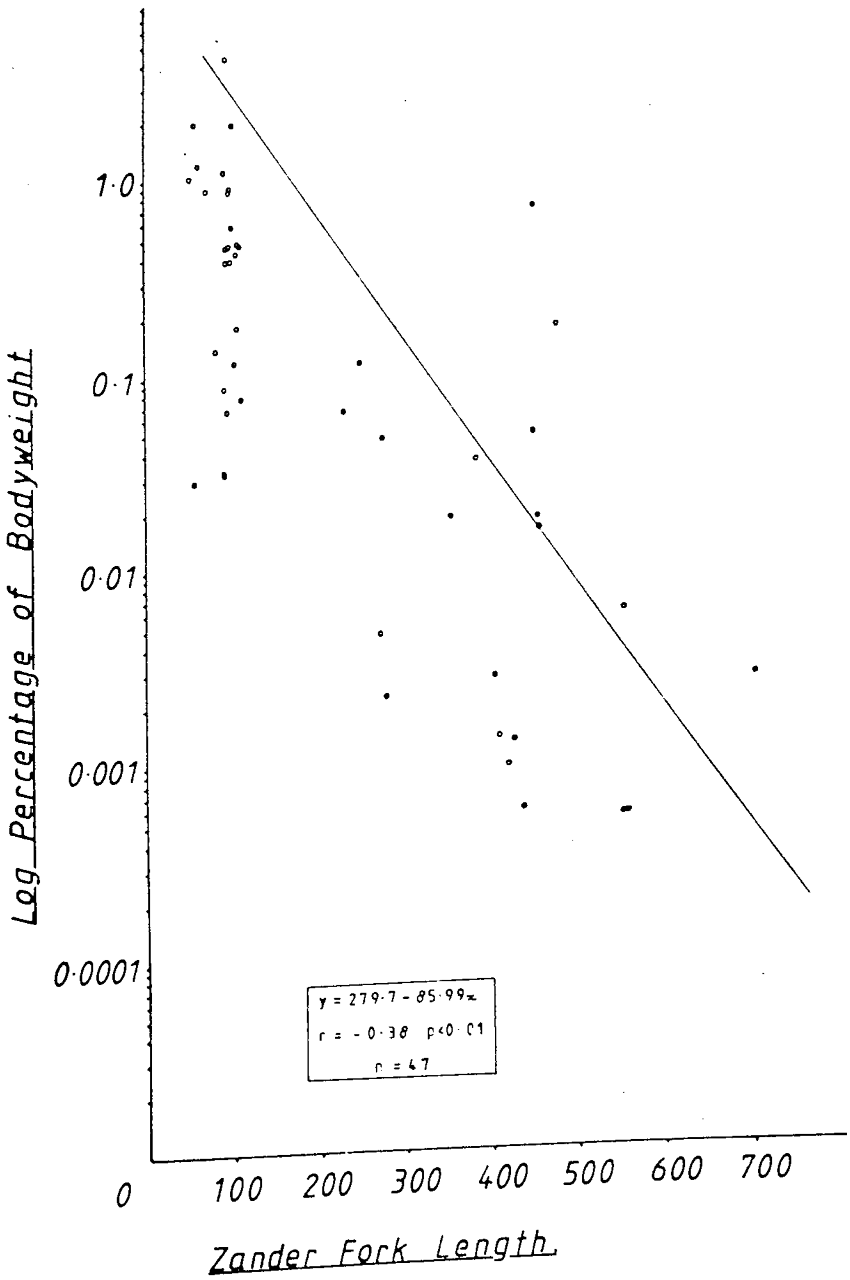
TABLE 33: Mean Weights of Invertebrate Prey

Invertebrate	Mean Weight	Number in Sample
Daphnia sp.	0.001g	30
Chironomid sp.	0.009g	14
Gammarus sp.	0.051g	15
Asellus sp.	0.057g	1
Ephemera sp.	0.045g	1
Odonata sp.	0.12g	2
Hirudinia sp.	0.12g	2
Trichoptera sp.	0.15g	1

The total contribution in weight, of the invertebrates to the zanders diet was in most cases negligible. Only in the case of zander less than 100 mm was it clear that invertebrates formed a significant part (by weight) of the diet. Figure 48 shows the relationship between zander fork length and the precentage of the body weight of the zander, consumed in the form of invertebrate prey. The smallest prey fish noted in zander stomachs were 30 mm in length and weighed 0.2 grams. This exceeds the heaviest invertebrate noted in this study. It would appear that young zander of less than 100 mm consume large numbers of invertebrate prey, with as many as 60 Daphnia noted in some individual stomachs. This may form a substantial part of the diet, by weight. However similar sized zander would also consume small fish, presumably fulfilling the nutritional requirements at one feed. As the zander

Figure 48.

The Invertebrate Weight, Zander Length Relationship.



grows, more invertebrates would be required to sustain the young fish. This it is suggested is the reason why zander become predatory on young fish at an early stage in life. Field samples of zander of 50 to 60 mm revealed that some zander (approximately 30%) had eaten young fish in addition or instead of invertebrates.

Early adaptation to feeding on other fish would provided suitable prey was available, ensure a supply of suitable prey sizes, thus eliminating the need for the capture of large numbers of small invertebrates.

The weight of fish prey eaten by zander was studied wherever enough data was available. Samples were examined from:

Relief Channel June-August 1979
Relief Channel October 1979
Relief Channel June and July 1980
Cut Off Channel April 1980
Middle Level Main Drain September, October and November of 1979
Burwell Lode August 1979
Coombe Abbey June 1979, December 1979 and May 1980.

The mean weight of prey fish eaten by zander was expressed as grams per hour for each sampling period. Temperatures noted during the sampling periods ranged from 3 to 21 C. Daily temperature fluctuations usually ranged around + or -3°C (field observations). Therefore temperatures were approximated to 5° divisions. A 24 hour estimate of the weight of prey eaten by zander was also made, however such an estimate does not give a true estimate of daily feeding as it is in fact based on an hourly feeding rate. Zander are unlikely to feed continuously at the estimated hourly rate. The weights of prey eaten were expressed as percentages of the zanders bodyweight for both hourly and 24 hour estimates with 95% confidence limits. Table 34 presents the estimated mean feeding rates of zander from the periods and populations studied.

TABLE 34: Feeding Rates of Zander

Number of Zander	Temperature	% Bodyweight eaten in 1 hr	95% Confidence limit	% Bodyweight eaten in 24 hr	95% Confidence limit
RELIEF CHANNEL June-August 1979					
19	20°C	0.12	0-0.28	2.87	0-6.7
RELIEF CHANNEL October 1979					
13	15°C	0.02	0-0.44	0.51	0-1.07
RELIEF CHANNEL June-July 1980					
28	20°C	0.05	0.01-0.09	1.16	0.7-1.61
CUT OFF CHANNEL April 1980					
15	10°C	0.02	0-0.038	0.38	0.12-0.65
MIDDLE LEVEL September 1979					
13	15°C	0.16	0.019-0.3	3.9	0.47-7.32
MIDDLE LEVEL October 1979					
14	15°C	0.014	0-0.036	0.345	0-0.86
MIDDLE LEVEL November 1979					
4	10°C	0.002	0-0.006	0.053	0-0.15
BURWELL LODE August 1979					
14	20°C	0.28	0.14-0.422	6.73	3.34-10.12
COOMBE ABBEY June 1979					
22	20°C	0.13	0.086-0.17	3.15	2.09-4.2
COOMBE ABBEY December 1979					
13	5°C	0.02	0.01-0.029	0.476	0.26-0.69
COOMBE ABBEY May 1980					
24	20°C	1.05	1.22-3.00	25.1	3.65-46.6

The feeding rates shown in Table 34 suggest that feeding is more intensive during the warmer months, on the waters where data is available for different periods. Summer feeding of Coombe Abbey zander was more intensive than Relief Channel zander. Burwell Lode zander were feeding more intensively than Coombe Abbey zander in June 1979 and Relief Channel zander in the summer months. All winter, autumn and spring feeding rates were lower than summer rates (where comparisons were possible).

(e) Maximum Size of Prey Which can be Ingested

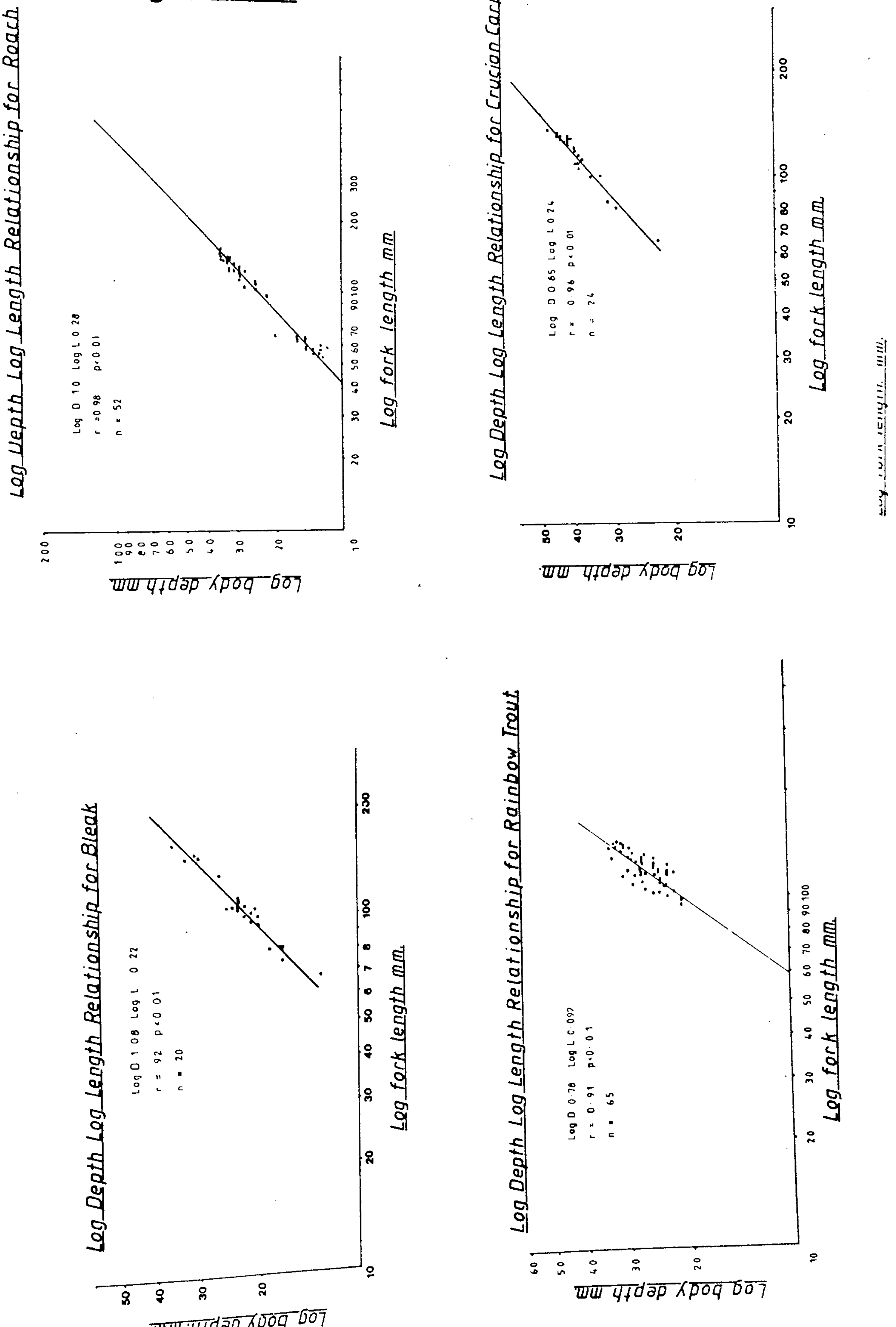
A variety of prey fish species were measured in the manner described earlier and prey depths plotted against prey fork lengths. Regression lines were fitted using the Method of Least Squares (Figures 49 and 50, Table 35). Zander mouth gapes were fitted to prey depths to enable an estimate of maximum prey lengths ingestable, for zander of any given length consuming, prey fish of any given species. The influence of prey fish depth on the maximum size of prey fish a zander can consume could be determined by reference to Figure 51. The extrapolations shown in Figure 51 are based on the assumption that the prey fork length-zander length relationships remains constant with increasing size. Small samples of larger prey fish were found to approximate to the extrapolated line, therefore it was considered that the extrapolated line could be used for the purposes of this work. Fish with "shallow" body forms could be consumed at greater fork lengths than prey fish with "deeper" body forms. Spiney dorsal fins a feature of Percid fish such as the perch and ruffe, tend to increase the apparent depth.

Prey fish lengths noted in zander stomachs were then converted to percentages of the "maximum prey length ingestable" as derived from Figure 51. The means of these percentages were calculated for each zander population studied, each period and the four most commonly noted prey fish species. These means are presented in Table 36.

TABLE 35: Estimated Maximum Prey Lengths for Zander

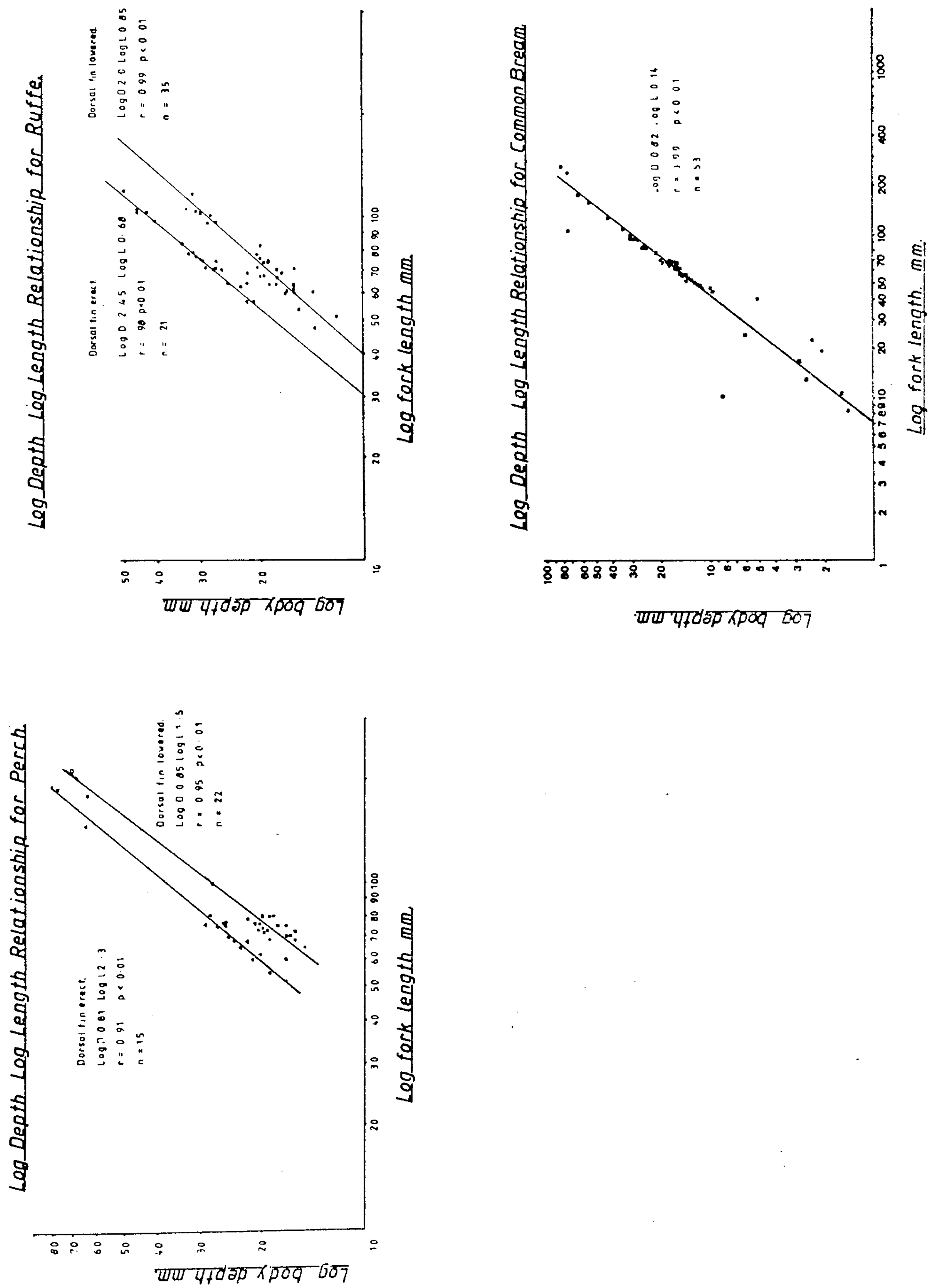
Zander Length mm	Bleak mm	Rainbow Trout mm	Roach mm	Ruffe Dorsal Fin lowered mm	Perch Dorsal fin Lowered mm	Crucian Carp mm	Common Bream mm	Perch Dorsal fin Erect mm	Ruffe Dorsal fin Erect mm
50	(8)	(18)	(11)	(10)	(25)	-	14	(17)	(15)
100	(38)	(46)	(36)	(31)	(43)	(16)	33	(32)	(28)
150	67	73	61	51	61	(36)	51	(46)	(41)
200	97	101	86	72	79	(56)	69	61	54
250	126	128	110	93	97	76	87	75	67
300	156	155	135	113	115	96	105	89	81
350	(186)	(183)	160	134	133	116	123	104	94
400	(215)	(211)	(185)	155	151	136	141	118	107
450	(245)	(238)	(210)	175	169	(156)	160	132	(120)
500	*	(266)	(235)	196	187	(176)	178	147	(133)
550		(293)	(260)	(216)	205	(196)	196	161	(146)
600		(321)	(285)	(237)	(223)	(216)	(214)	176	(159)
650		(348)	(310)	(257)	(241)	(236)	(232)	190	(172)
700		(376)	(335)	(278)	(259)	(256)	(250)	204	(186)
750		(403)	(360)	(299)	(277)	(276)	(268)	(219)	(199)
800		(431)	(385)	(320)	(295)	(296)	(287)	(233)	(212)
850		(458)	(410)	(340)	(313)	(316)	(305)	(247)	(225)
900		(486)	(435)	(361)	(331)	(336)	(323)	(262)	(238)

Figure 49



Log Depth Log Length Relationship for Roach
Log D 1 0 Log L 0 28
r = 0 98 p < 0 01
n = 52
Log fork length mm
Log body depth mm
Log Depth Log Length Relationship for Crucian Carp
Log D 0 65 Log L 0 24
r = 0 96 p < 0 01
n = 24
Log fork length mm
Log body depth mm
Log Depth Log Length Relationship for Bleak
Log D 1 08 Log L 0 22
r = 92 p < 0 01
n = 20
Log fork length mm.
Log body depth mm.
Log Depth Log Length Relationship for Rainbow Trout
Log D 0 78 Log L 0 92
r = 0 91 p < 0 01
n = 65
Log fork length mm.
Log body depth mm

Figure 50.



Log Depth Log Length Relationship for Ruffe.
Dorsal fin erect
Dorsal fin lowered
Log fork length mm.
Log body depth mm.
Log Depth Log Length Relationship for Common Bream.
Log fork length. mm.
Log body depth mm.
Log Depth Log Length Relationship for Perch.
Dorsal fin erect.
Dorsal fin lowered.
Log fork length mm.
Log body depth mm.

Figure 51.

The Estimated Maximum Lengths of Several Prey Fish Species Accessible to Zander.

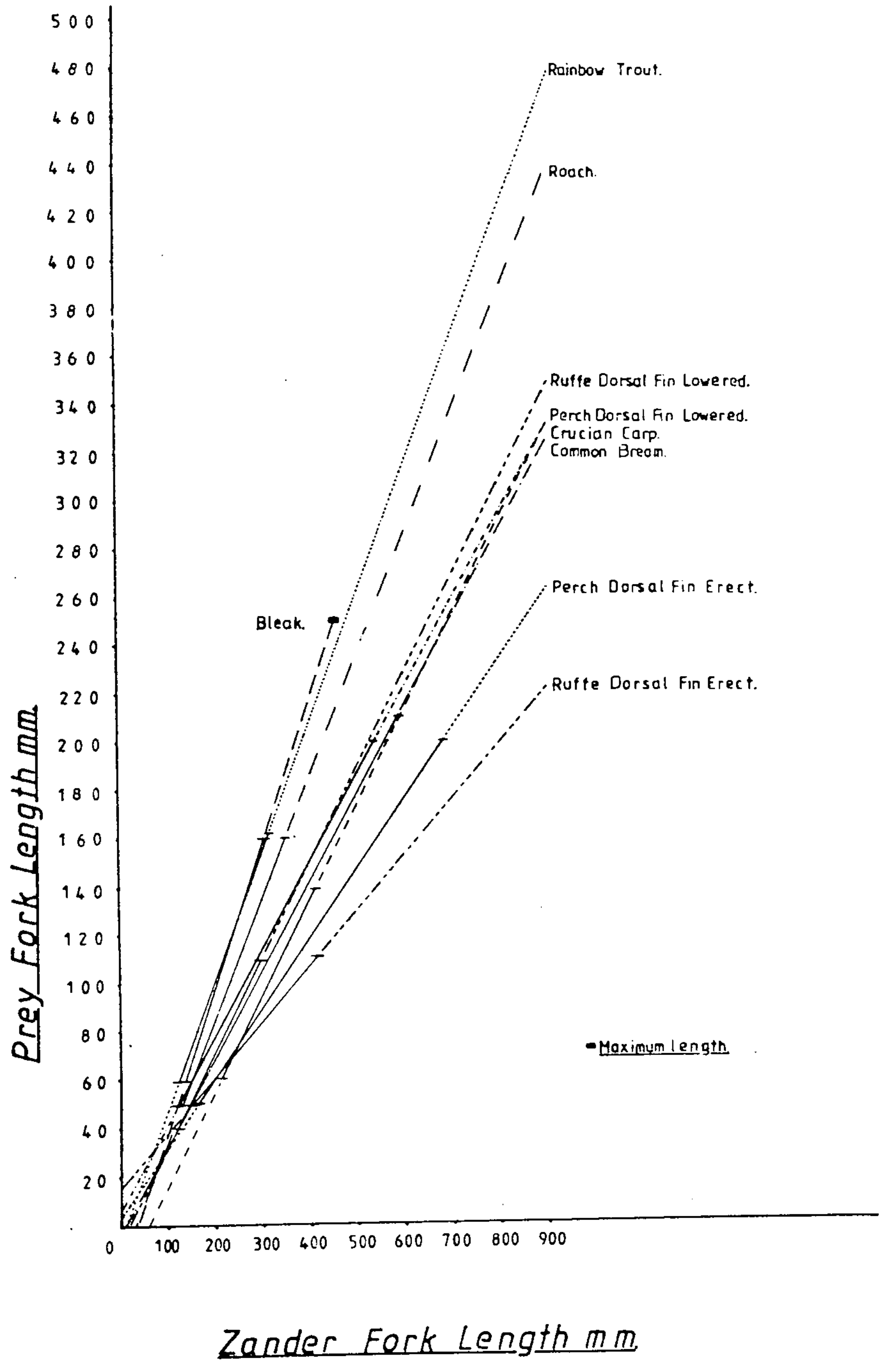


TABLE 36: Zander Prey Lengths Expressed as a Percentage of the Maximum Length Ingestible

Location	Period	Mean Zander Length	n	mean %	95% cl
		ROACH			
Coombe Abbey	June 79	399	22	50.9	47.3 - 54.5
" "	Dec. 79	431	15	51.2	47.2 - 55.2
" "	May 80	390	29	66.8	64.1 - 69.5
Relief Channel	1968-70	456	17	27.4	33.4 - 52.0
" "	1975-76	521	16	24.6	14.9 - 34.3
" "	1979	498	14	36.4	21.3 - 51.5
" "	1980	519	7	42.0	25.2 - 58.8
Burwell Lode	Aug. 1979	506	15	42.6	35.8 - 49.4
Middle Level	1979-1980	429	26	33.0	21.4 - 44.5
		COMMON BREAM			
Relief Channel	1968-1970	543	14	19.8	14.3 - 25.3
" "	1975-1976	515	6	63.0	48.3 - 77.7
" "	1979	651	4	66.2	2.1 - 130
" "	1980	512	2	51.4	43.1 - 59.7
Middle Level	1979-1980	515	11	41.8	6.9 - 76.6
		PERCH DORSAL FIN LOWERED			
Coombe Abbey	1980	265	1	79	
Relief Channel	1968-1970	502	4	58.5	19.4 - 97.6
" "	1975-1976	250	3	31.0	0 - 108
" "	1980	568	10	14.9	0 - 55
Middle Level	1979-1980	406	2	50	11.9 - 88
Burwell Lode	Aug. 79	470	1	43.1	
		PERCH DORSAL FIN RAISED			
Coombe Abbey	1980	265	1	102.4	
Relief Channel	1968-1970	502	4	72.0	35.2 - 108.1
" "	1975-1976	250	3	40.0	22.6 - 57.4
" "	1980	568	10	19.2	13.9 - 24.5
Middle Level	1979-1980	406	2	63.5	48.4 - 78.6
Burwell Lode	Aug. 79	470	1	55.1	

TABLE 36: Continued

Location	Period	Mean Zander Length	n	mean %	95% cl
		RUFFE DORSAL FIN LOWERED			
Relief Channel	1968-1980	457	1	42	
Middle Level	1979-1980	365	1	75	
		RUFFE DORSAL FIN RAISED			
Relief Channel	1968-1970	457	1	62	
Middle Level	1979-80	365	1	107	

(f) Direction of Swallowing

Zander were found to swallow the majority of prey fish tail first. Of the total number of roach noted in stomachs (n = 117) 66.6% were swallowed tail first and 33.3% head first. The other prey species were swallowed head and tail first in similar proportions. These prey fish included bream, perch, ruffe, eel, zander and pike. No significant effect on the direction of swallowing could be attributed to the presence or absence of spiney fins.

All prey lengths were expressed as percentages of the maximum size ingestible, the mean percentages were then tested for significance, head first against tail first. Table 37 presents the results, there being no significant difference in prey length swallowed head or tail first for three of the zander populations. Only Coombe Abbey zander showed a significant difference.

TABLE 37: Results of Significance Tests, Mean Roach Lengths Expressed as percentages of the Maximum Size Ingestible Swallowed Head or Tail First

Site	Mean Percentage of the maximum prey length ingestible Head first	SE	n	Mean Percentage of the maximum prey length ingestible Tail first	SE	n	t	Significance	df
Coombe Abbey 1979/80	58.7%	4.3	13	47.9%	1.5	45	2.99	$p < 0.05$	56
Burwell Lode Aug.1979	38.7%	12.8	3	48.9%	3.43	14	1.12	$p > 0.05$	15
Relief Channel 1979-80	49.0%	5.7	8	40.5%	6.5	12	0.92	$p > 0.05$	18
Middle Level 1979-80	27.8%	3.7	13	39.3%	6.7	13	1.42	$p > 0.05$	24

(g) Feeding Periodicity

Rod and line angling results, (336 rod hours fished), based on the number of zander captured per number of particular hours of the day fished (Figure 52a), showed a diurnal pattern consisting of two peaks during June-July 1980 for Relief Channel zander. Both feeding peaks were close to the period of maximum change in light intensity, dawn and dusk. The corresponding estimate of feeding periodicity derived from stomach contents (Figure 52b) showed a similar periodicity. The reasonable agreement between the two methods of estimating zander feeding periodicity suggested that the times of feeding of the zander were being estimated correctly. Angling observations were not obtained in detail for the other periods, however casual observations tended to agree with the estimated feeding times using stomach contents.

The summer feeding of Relief Channel zander appeared to be similar during 1979 (June to August, Figure 53a) and 1980 (June to July, Figure 52b). Feeding was centred around dawn and dusk, with an additional feeding period situated in the late afternoon. Such late afternoon feeding was regularly encountered during angling efforts and could be narrowed down to a very restricted period of time on most days. Illumination levels could be high with cloudless skies, yet this did not appear to deter zander from feeding. Water depth and suspended matter may have been important in the regular appearance of the afternoon feeding period.

October feeding on the Relief Channel, (Figure 53b) was again centred around dawn, with less feeding at other periods. Cut Off Channel zander during April of 1980 (Figure 53d) showed a pre-dawn

Figure 52. Feeding Periodicity.

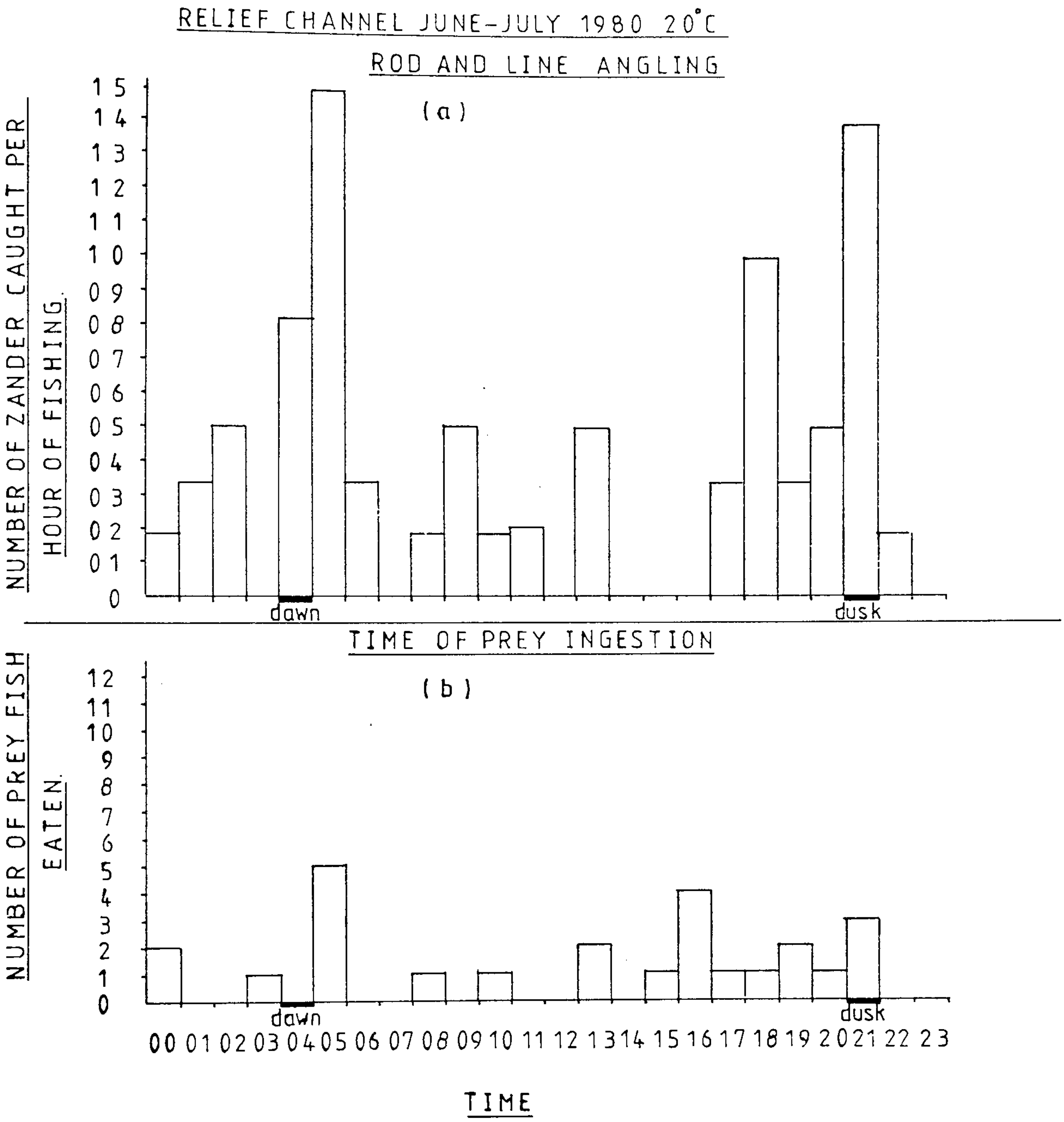
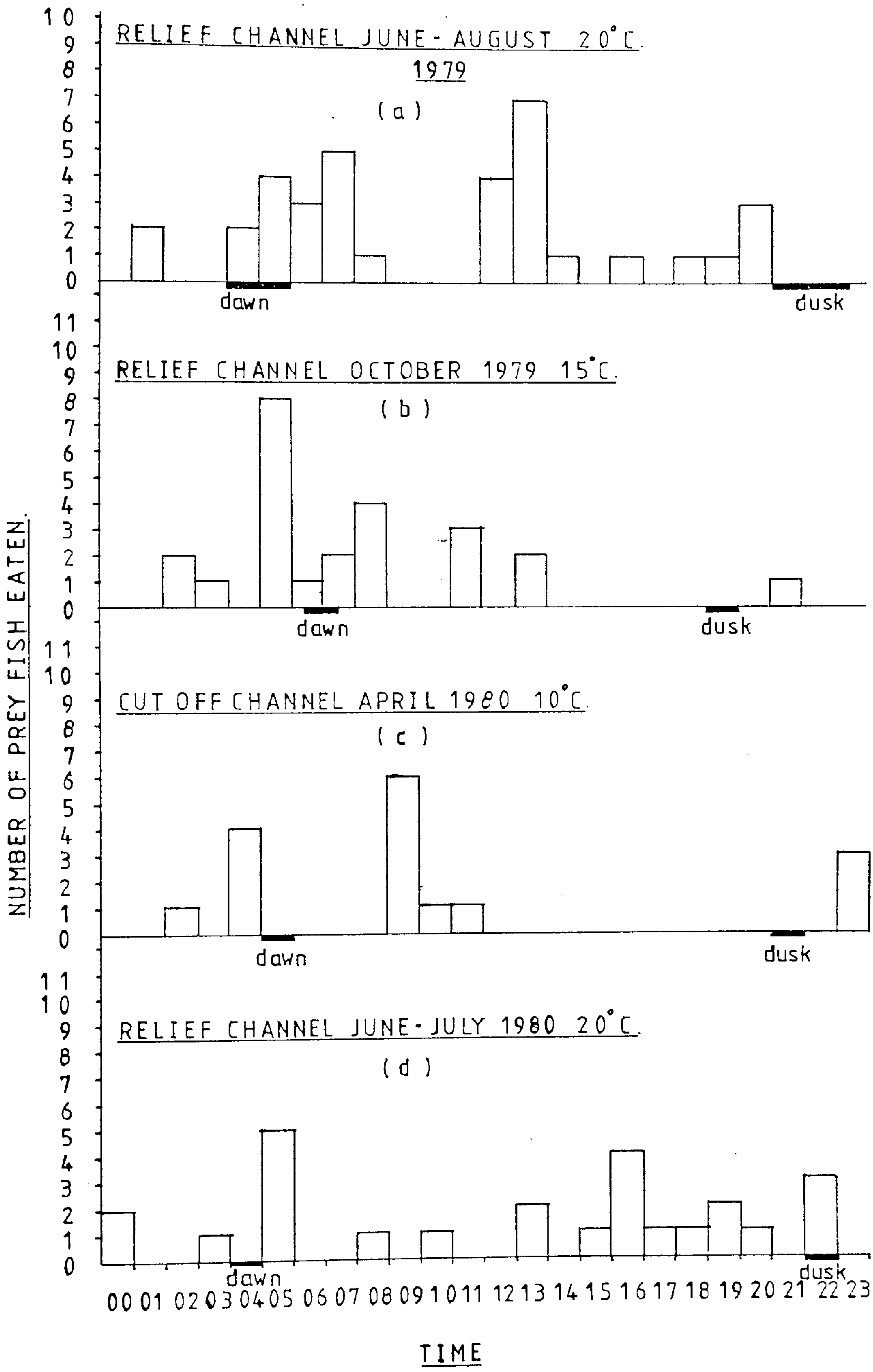


Figure 53. Feeding Periodicity.



and late morning feeding period, with a short post dusk feeding period.

Middle Level (Figure 54) zander were studied for a limited period only. Of interest was the almost continuous feeding throughout the day during September. Very little data was available for October and November.

Coombe Abbey zander showed during June 1979 and late May 1980 (Figure 55a and c) similar feeding periodicity. Here feeding was particularly marked around 9.00 hours. Dusk saw a smaller peak of feeding activity. During December of 1979, feeding was occasional throughout the day and night. (Figure 55b).

Burwell Lode zander showed peaks in feeding activity before dawn and after dusk. Some day time feeding was also noted (Figure 55d).

(h) Number of Zander with Empty Stomachs

Amongst the Rod and Line caught zander, the number of empty stomachs remained remarkably constant, between 50 and 60 percent of the total examined. The numbers of empty stomachs appeared to increase the earlier the sampling period. Middle Level 1979/80 zander showed a relatively high incidence of empty stomachs. All electrofishing and seine netted samples showed a much lower incidence of empty stomachs, 20 to 28 percent. Percentages of empty stomachs for the zander obtained by electrofishing or seine netting were remarkably similar. Apparent differences in the food availability in each water did not appear to influence the number of empty stomachs.

Figure 54. Feeding Periodicity.

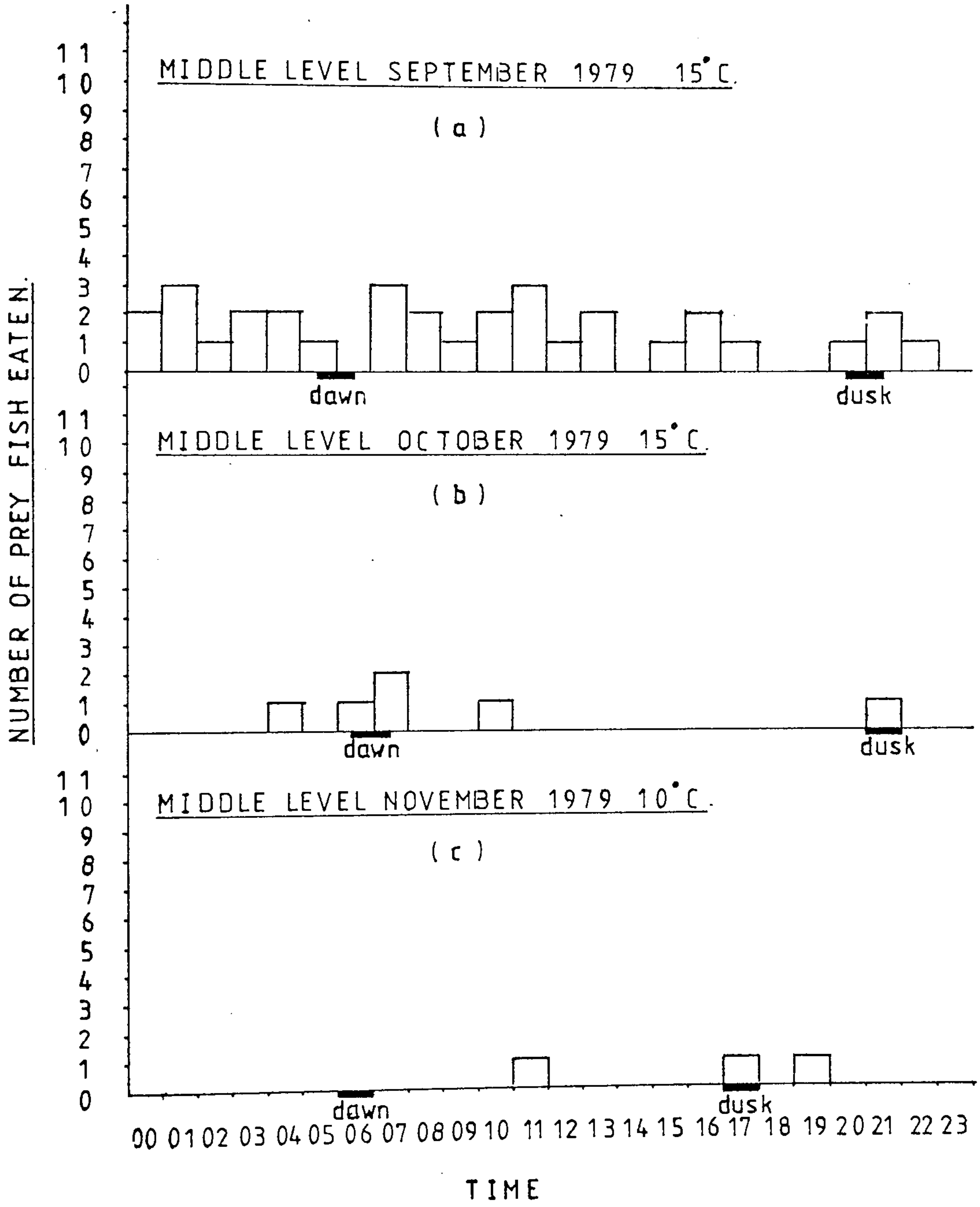


Figure 55 Feeding Periodicity.

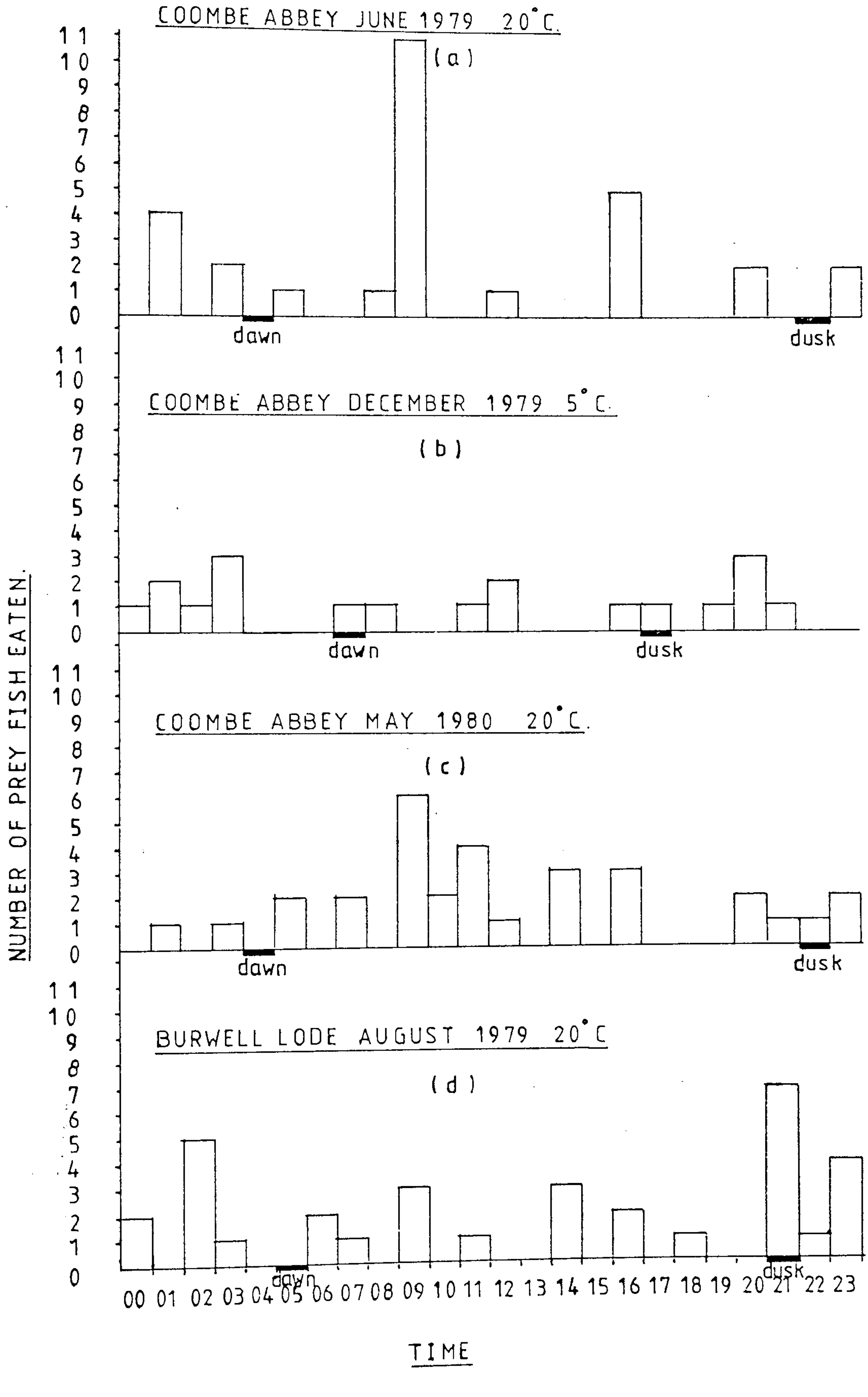
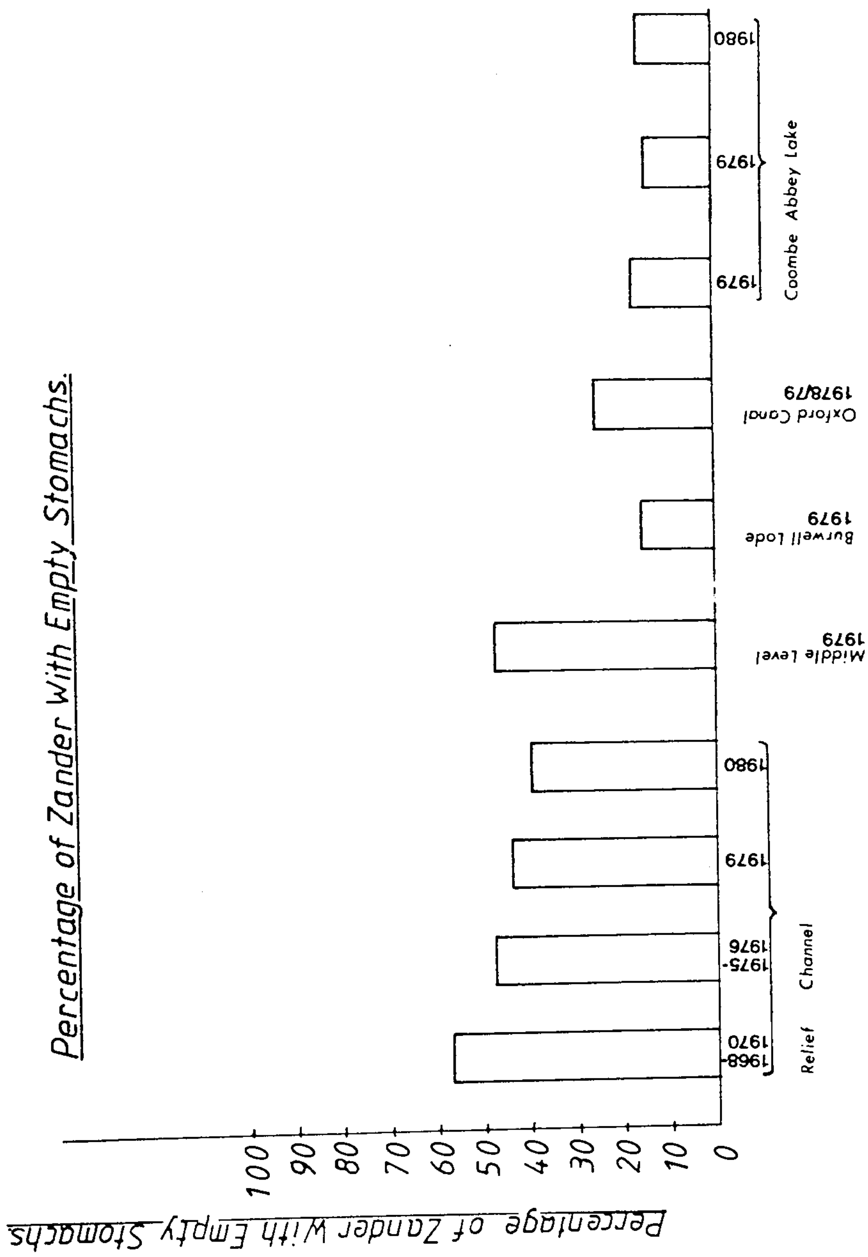


Figure 56.

Number of Zander With Empty Stomachs.



Discussion

The investigation of the zander's feeding habits was conducted along 8 related lines, some of which have counterparts in the literature of Eastern Europe and the USSR. This section has investigated zander feeding in more detail than previously noted and in places covers new lines of investigation.

The difficulty experienced in obtaining large numbers of zander on a regular basis has precluded studies of a seasonal nature. However it has been possible to clarify some of the facets of zander feeding behaviour which were not of a seasonal nature.

Various workers, notably Deedler and Willemsen (1964) and Mikulski (1964) are agreed that the zander's diet consists mainly of fish in proportion to the availability of individual fish species.

The word availability needs to be defined in the context of this work. Where sampling of a food fish population is representative (the basic assumption of part of this work), those food fish small enough to be eaten by the zander, comprise the available prey. The behavioural adaptations of the varied fish species are likely to result in differential availability to zander. Fish which live in the littoral region, or utilise the cover of water plants for much of their lives may be less liable to zander predation than those living outisde of the littoral zone. Therefore when comparisons of available zander prey fish and those eaten by zander are made, any differences between the two could be attributable to either preference by the zander or prey behaviour.

All the zander populations studied in 1979 and 1980 were preying on the most abundant prey fish recorded in survey work, the roach. With some exceptions the other prey fish species were consumed in proportion to their abundance. Where this was not the case, the behaviour of the prey fish may have been responsible. This was noted by Ivanova (1968) working on Rybinsk Reservoir. The distribution of the smelt (Osmerus eperlanus L) affected the zander's feeding habits. When the smelt were in the surface layers all the time, ruffe and perch were eaten instead.

Eels in particular may be more accessible to zander during periods of intense feeding or during autumn migration. At other times the eel's benthic habit and ability to burrow into the substratum may make it less accessible to zander predation. This may account for the sporadic appearance of eels in the zander's diet, in spite of the widespread occurrence of eels in the Fenland waterways.

Flounders are another benthic fish species, well camouflaged and adapted to a semi concealed existence. Their shape may also preclude serious predation by the zander. Sticklebacks may because of their littoral habits, be unavailable to zander. Their spines may also prevent predation by the smaller zander.

The majority of the other common prey species should show similar degrees of availability, being midwater or bottom living shoal fish. Differences in predation would then be attributable to preference by the zander.

Observations of the Relief Channel zander, during the 4 periods studied showed that there was some variation in the species composition of the zanders diet. Variation occurred in the predominance of common bream, roach, perch and eels, the most important prey fish species. This could be attributed to changes in the availability of the prey fish. This may also have accounted for the fluctuation in the importance of young zander in the adult zanders diet. Yearly fluctuations in survival of yearling zander would have a strong influence on the number of such fish in the adults diet.

There was no evidence to suggest that specific prey species were sought in preference to others. The smelt, the zanders favoured prey fish, (Deedler and Willemsen 1964) was not available in large numbers, (only two were encountered in AWA surveys) therefore this preference if it existed, could not be demonstrated. It would appear that most of the available species of fish are consumed by zander. Similarly a variety of invertebrates were eaten, but with no apparent preference, except for the fact that the smaller invertebrate forms such as Daphnia were generally taken by the smaller zander of less than 100 mm.

Prey species compositions based on numerical representation give information on the zander's predation on each species, by number. It does not take into account the prey species weight. Some of the smaller fish species such as bleak and sticklebacks do not reach a large size (Maitland 1977). Therefore their contribution to the nutrition of the zander is only likely to be significant if large numbers are eaten. Fortunately in this work, the major prey fish species were all capable of growing to a large size (greater than 400 mm). Therefore a wide range of prey sizes were available to the zander, obviating any need to eat large numbers of the smaller prey species.

Invertebrates formed a significant part of the diet for individuals of less than 100 mm. Though larger zander in excess of 700 mm had eaten invertebrates, the contribution to the zander's diet was insignificant. Daphnia, when eaten in numbers by young zander, formed a significant part by weight of the young zander's diet. Pisciverous feeding was noted as starting at a length of 50 to 60 mm, in 30% of the young zander examined (25). It is possible that pisciverous feeding started earlier as samples of younger zander were not obtained. Huet (1970) and Szalay (1973) quote 40 mm and 25-30 mm respectively as the time of commencement of pisciverous feeding. (No indication was given whether or not feeding was entirely pisciverous). Due to the rapid growth of the young zander the available invertebrates soon become very small in comparison to the young zander. In order to continue growth a switch to fish feeding is desirable. Poltavsuk (1969) notes slower growth of young zander when fed on invertebrates rather than small fish.

Zander of a greater length than 100 mm were invariably found to have eaten fish prey. Where invertebrates were the sole prey of zander larger than 100 mm it is suggested that food fish might have been in short supply. Food fish were plentiful in Coombe Abbey and invertebrate feeding by zander was rare. The reverse was the case in the Relief Channel during 1979.

The hypothesis that the number of prey fish noted in zander stomachs per period of feeding, was related to zander length was considered, but found to be unsubstantiated. The reasoning behind this line of investigation was that larger zander might increase the number of prey consumed rather than increase the size of prey. It was noted that the majority of feeding zander (75%) had eaten 2 or more prey fish before capture and that 25% had eaten 3 or more. This suggested that zander did in fact feed to some extent on quantities of prey rather than a fewer large individuals. However it did not indicate that this was correlated with size. The intake of several prey items in a feeding period was a general habit of zander of all sizes.

A trend towards the consumption of large numbers of 0 and 1 plus roach and perch was noticeable during limited periods, such as June and July of 1980, on the Relief Channel. The consumption of large numbers of 0 and 1 plus fish (less than 70 mm) probably coincided with the localised abundance of these small prey fish, at this particular time of year. When very small fish were eaten, zander tended to eat between 2 and 10 of these fish and were generally consumed during a short period. This indicates a short period of feeding devoted to the capture of numbers of small fish. Where such shoals were present on the Relief Channel, the numbers were often considerable. Zander might make successive feeding forays into these shoals until satiated. 0 and 1 plus prey fish were seldom eaten singly by zander larger than 200 mm. It would appear that very small fish are not worth the feeding effort of the zander unless available in numbers.

One of the factors which may have influenced the results of the study of prey sizes eaten by the zander, was the differential rate of digestion of different sized prey fish. Section 3 demonstrates that the smaller prey fish are digested faster than the larger prey items.

Swenson and Smith (1973) noted that rate of digestion was negatively correlated with prey size, when working on the gastric digestion of the walleye. This means that small prey fish are resident in the zanders stomach for shorter periods than larger prey fish. Bias therefore results, possibly giving an underestimate of the number of small prey in the diet. This section of the work could not quantify the degree of bias caused by differential digestion rates. However the laboratory studies carried out later, were designed to eliminate such bias while attempting to demonstrate preference for certain prey sizes.

The length of prey fish eaten was for most zander populations, positively correlated with zander length. There were however cases where no correlation was noted. Such examples included zander obtained from Burwell Lode August 1979, Middle Level 1979-80, Relief Channel 1975-76, June-July 1980 and for zander eating eels, Relief Channel 1979. The presence of a strong positive correlation suggests that zander prey size increases with increasing zander size. However reference to the various figures describing the relationship, show that the scatter is very wide. Zander seem to prey on a large range of prey sizes, with an increased capability for consuming larger prey items as the zander increases in size. Where correlations were not noted, two factors may have been influencing zander feeding. Firstly prey fish sizes may be restricted to a limited size range, thus precluding the establishment of a zander zander length prey length relationship. Secondly zander may have been feeding on prey fish in proportion to their availability. This might result in smaller fish being consumed more often, by all sizes of zander. Generally in most waters where correlation did not occur, zander prey was available in a wide range of sizes. It is therefore suggested that the smaller prey fish, were the main food of all sizes of zander, thus precluding the zander length, prey length relationships noted in other samples. Furthermore it is suggested that a correlated zander length and prey length relationship is a feature of zander populations with a restricted food supply. The word restricted refers in this context to either a very low population of prey fish or a very limited size range of prey.

Relief Channel 1968-70, 1979, 1980, Oxford Canal 1978-80 and all Coombe Abbey zander samples, indicated that zander were having to utilise either a low density prey fish population or a population with a limited size range of prey. As zander size increased, prey fish size increased. This presumably helps larger zander to avoid intraspecific competition from younger zander feeding on smaller prey fish. However there the smaller sizes of prey fish were numerous, zander of all lengths concentrated their feeding on these fish, therefore precluding any correlation.

The difference in slope of the regression lines obtained for zander prey lengths from the Relief Channel in 1969-70 (AWA) and my own data from 1968-70 could be attributed to either the slight difference in the sampling period or differences in the methods used to estimate prey lengths. In both cases a positive correlation existed between zander length and prey length, indicating that larger zander were preying on prey of a greater mean length than the smaller zander.

The comparison of the length composition of the available prey (roach) population and zander prey (roach) showed that in the case of Burwell Lode and Middle Level zander, mean prey fish lengths corresponded to the mean available prey lengths. Only the largest prey fish appeared to be absent in zander stomachs though present in the prey population. This tends to confirm the observation made earlier, that zander when given a choice tend to consume the smaller and presumably younger members of the prey fish population.

Coombe Abbey zander were consuming prey fish (roach) of a mean length, significantly less than the mean length of available prey fish (roach). It would appear that the roach of Coombe Abbey were somewhat larger than the zander prefer. This may have been caused by very poor recruitment to the roach population, during recent years. Scale reading suggested that the 1976 year class was particularly strong and that those following were very poorly represented. While the 1976 year class of zander would have "grown up" with the 1976 roach year class, later year classes of zander would have found many of the 1976 roach year class to be inaccessible due to their relatively large size.

Predation on roach would therefore be selectively directed at the smaller individuals of the 1976 year class and any of the less numerous subsequent year classes.

The estimation of feeding rates of zander indicated that zander from the Relief Channel in June - August 1979 and June - July 1980 were feeding at a lower rate than zander from Coombe Abbey in June of 1979 and May of 1980. This difference may have been attributable to seasonal differences in feeding. Popova and Sytina (1977) note that up to 80% of the zander's annual ration may be eaten in April and May during the post spawning period. However as indicated in the section on age and growth (2:2), Relief Channel zander were at the time of this study showing slowed growth while Coombe Abbey zander were showing rapid growth. It would seem likely that these differences in growth were due to differences in food availability and feeding rate. The low feeding rates of Relief Channel zander provide some confirmation of the low prey density.

Winter feeding levels were invariably lower than summer rates, for all populations studied. This confirms angling observations which indicate the temperatures of less than 8°C see reduced zander feeding. This was to be expected as digestion rate is influenced by temperature. Molnar and Tolg (1962) note that zander stomachs emptied 8 to 10 times more rapidly in summer than winter. Assimilation being slower at low temperature means that rate of growth may be reduced. The time taken to evacuate the stomach is longer in winter and therefore one could expect fewer prey to be taken in the winter. Despite this, the daily feeding rate of Coombe Abbey zander (0.476% of the bodyweight) was very close to or greater than the feeding rate of other populations in the autumn and spring. The high level of feeding of the Middle Level zander is September of 1979 was almost certainly due to very intense round the clock feeding (as noted in the study of feeding periodicity). This was rather exceptional and angling observations suggest that this was not repeated in September of 1980.

Some of the samples were obtained during very limited periods and it is possible that these were not representative of the zanders usual feeding rate. The trends noted did fortunately correspond with the findings noticed elsewhere in this work.

The estimated 24 hour feeding rates tended in most cases to be lower than the quoted 4.5 - 5.5% of the bodyweight noted as being consumed by zander. (Popova and Sytina 1977). Only one of the Fenland populations Burwell Lode in August of 1979 exceeded 5% at the 95% confidence level. Coombe Abbey feeding rates were during the summer either close to or in excess of this level of feeding. Both these zander populations would appear to have a plentiful supply of prey and this was confirmed by Gregory (1979) and the present authors observations. Anglian Water Authority reports suggest that prey fish were at a low density in the Relief Channel, and Middle Level. The zander feeding rates would tend to agree with their findings, except for Middle Level zander in September of 1979. Here the intensive feeding, probably on a large concentration of prey fish (one was noted at Three Holes in 1979 and appears in the results of the Middle Level survey, Klee 1979b) resulted in a high daily rate of feeding of 3.9% (0.47%-7.32% at the 95% level).

The measurement of prey depths showed that different species of prey fish had different length depth relationships. It is suggested that the deeper prey fish become unavailable to zander predation at lesser lengths than fish with narrower or more shallow bodies. Because of the limited selection of prey fish species noted in quantity in zander stomachs the influence of prey fish depth was not demonstrable. The size of prey eaten by zander was generally between 30 and 50% of the maximum size ingestible. This method of expressing the size of prey eaten by the zander, though more complicated than simply expressing prey length or weight as a percentage of the zanders body weight or length, takes into account not only the size of the zander, but also the depth of the prey. For predators with moderate sized jaws this must be of considerable importance.

Spiney finned fish such as perch, ruffe and zander were eaten by zander in most waters and generally swallowed head first. A few were swallowed tail first. The effect of the spines of a Percid fish species should be significant when the predator considered tends to swallow prey tail first. The spines of small percids are relatively soft, however larger percids have strong spines and these may be erected and prove most difficult to depress when applying force from the posterior of the fish. Therefore zander would have difficulty swallowing relatively large percids tail first and would supposedly swallow such fish head first. Experimental work in the laboratory was to later provide additional evidence to support these ideas.

The swallowing of prey fish was in the majority of cases tail first. Pihu (1970) working on Lake Peipsi - Pskov noted that larger prey can be swallowed head first only. The tail-first method of swallowing is consistent with the zanders method of prey capture. Aquarium observations have shown that attacks are frequently to the posterior of the prey. Turning of the prey had not been noted and therefore prey seized by the tail is always swallowed tail first. Of some importance was the demonstration that the mean length of prey swallowed tail first was less than the mean length swallowed head first. This suggests either a deliberate preference for a head first approach of larger prey or a higher failure rate for tail first attacks on larger prey.

The study of feeding periodicity demonstrated that zander have defined periods during which feeding is most intense. The pattern noted was in many cases diurnal, but feeding periods at other times of the day and night were also noted. Light levels were not recorded during this study, however dusk and dawn were for many zander populations the time of greatest feeding activity. The zander's American relative the walleye has been shown by Ryder (1977) to be strongly influenced by levels of light penetration. The walleye has a very well developed <u>Tapetum</u> <u>lucidum</u> (Moore 1944) which gives very good vision in levels of low illumination. Zander are less well equipped than the walleye (Moore 1944) for scotopic vision and it is therefore not surprising that this study showed that zander were quite capable of feeding at a variety of light levels. It should be noted that zander caught by rod and line angling were invariably captured from 3 to 4 metres of peat stained water and it is likely that the turbidity of the water has a mollifying effect on the zanders response to high levels of illumination.

Angling experiments conducted by Ryder (1977) on the walleye showed that feeding was most intense during the evening or before night fall. This was ascertained by experimental fishing for several 24 hour periods. Only the occasional intermittent catches were made during day time and the night. High levels of disturbance of the water, wind and increased turbidity of the water stimulated earlier feeding. The grestest capture rate of walleye occurred at the point of greatest light change, dusk. Zander feeding followed a similar pattern on some waters, however in September of 1979 on the Middle Level, feeding became almost continuous, throughout a 24 hour period through much of September. This may have been a seasonal feature, perhaps similar to the pre-winter feeding period described by Popova and Sytina (1977). Angling experiences tended to confirm that zander generally fed most intensely at dawn and dusk. Angling together with the study of stomach contents showed that outside of the peak feeding periods zander fed sporadically. Coombe Abbey zander were noted as feeding during the summer, most intensely well after dawn and at dusk. This may have been due to the varying turbidity of the lakes water, tending to delay feeding until light penetration had reached an optimum level. It is suggested that zander being less well equipped for scotopic vision are therefore much more adaptable regarding feeding periods than the walleye.

The percentage number of empty stomachs noted in samples of zander obtained by seine netting and electrofishing was for Coombe Abbey relatively low. Tanasiychuk (1974) working on Kremenchug Reservoir in April-May (the peak feeding period) gave 18% as the lowest percentage of zander with empty stomachs. The highest level was 56%. The fact that Coombe samples were consistent, being between 15.4 and 19.1% suggests that feeding was intense at all times of sampling (December, June and May). Burwell Lode zander were similarly feeding intensively in August of 1979. Oxford Canal zander showed a higher percentage of empty stomachs and this may indicate less intensive feeding due perhaps to lower food densities.

All other samples were mainly rod and line derived and showed similar percentages with empty stomachs. It is suggested that this is caused by rod and line caught zander reaching a similar degree of hunger before sucumbing to angling methods. This would tend to equalise the number of empty stomachs regardless of nutrition.

In conclusion, the feeding habits of the English zander would appear to be similar to the zander of the European mainland. Most English waters lack the prey fish species diversity found in Europe and the USSR. This is probably the reason why the roach is the main food of the English zander. The zander's preference for smaller prey fish has been confirmed. Zander feed less intensively during the winter and generally swallow prey tail first.

In order to make meaningful comparisons between the zander's feeding and that of other freshwater predators such as the pike and perch, studies along similar lines to this would be required.

2.4. THE MARKING OF ZANDER AS A MEANS OF STUDYING MOVEMENT

2.4.1. INTRODUCTION

A mark is defined as any factor which makes a fish identifiable either as an individual or as a member of a batch. Marks may be artificial, e.g. mutilation of fins or addition of tags, or natural, e.g. genetic markers or parasites. (Laird and Stott 1978).

The ideal marking method would make any fish permanently and unmistakably recognisable individually to anyone examining it. It would be inexpensive, easy to apply in the field and have no effect on the fishes growth, mortality, behaviour, liability to capture by predators or fishing gear, or it's commercial value. Unfortunately no such "ideal" method has been developed. Nevertheless an investigator can select a method which complies as far as possible with the above requirements in his particular circumstances.

Without continual monitoring of the zander population, a precise indication of eventual zander population density is impossible to make.

There have been a number of marking studies carried out on the zander, notably those of Puke (1952), Kracziewicz (1969), Vostradovska (1974) and Goubier (1975). Marking studies have been much more extensive on the American genus of Stizostedion the walleye, Stizostedion vitreum vitreum (Mitchell 1818). These studies have highlighted the more extensive movements of the walleye compared with the zander. Movements and homing of walleye (Crowe 1962, Olson and Scidmore 1962, Forney 1963 and Wolfert 1963), are largely related to spawning migrations. Goubier (1975) did not note any seasonal movements of zander in French rivers and could find no association of movement with spawning.

Kraczkiewicz (1969), however notes that "Migrations of adult fish between the Firth of Szczecin and the Pomeraninan Bay were of an active nature caused by biological factors such as spawning and nutrition".

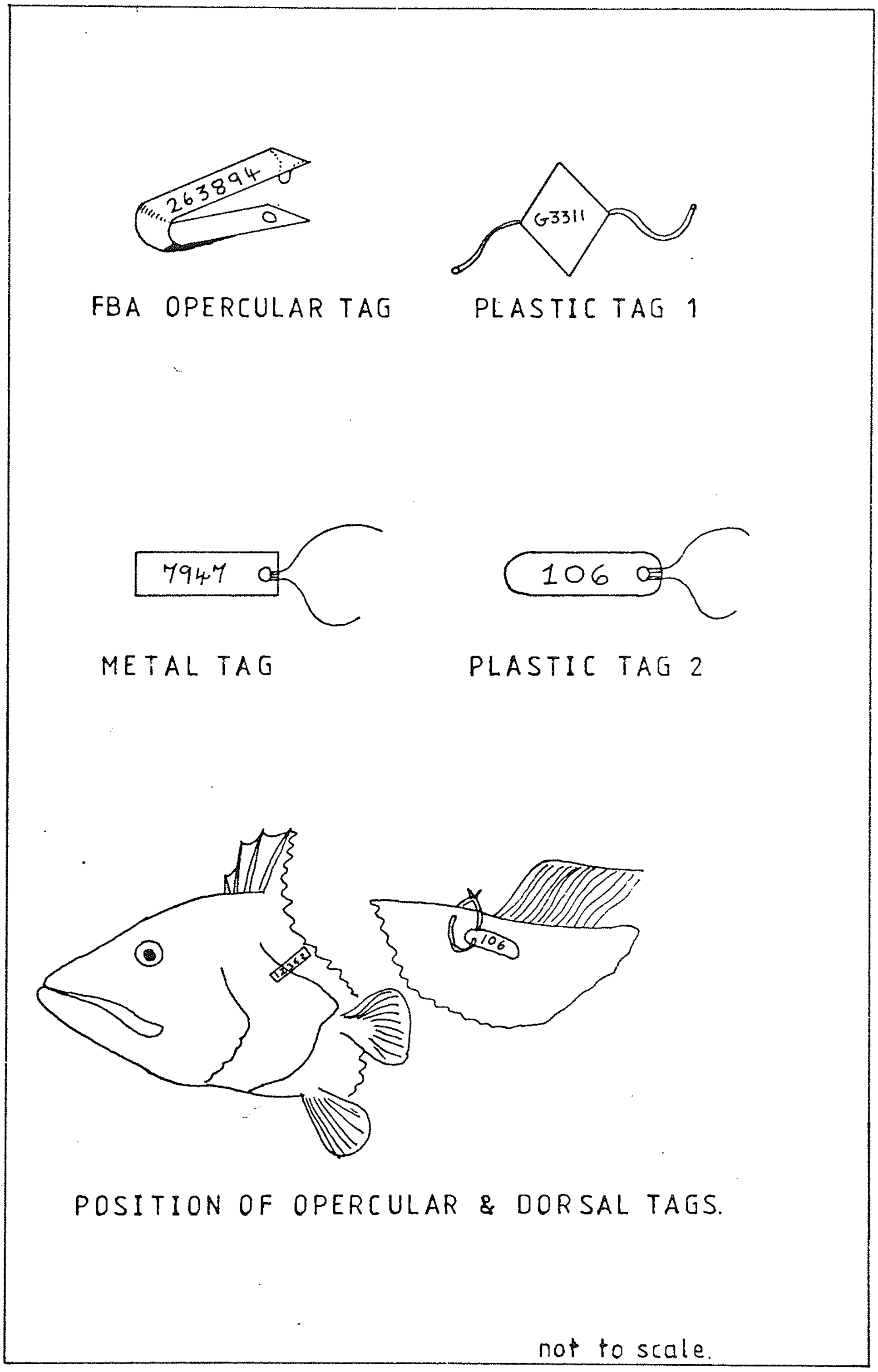
Though the Great Ouse River catchment is relatively small compared with the large river systems of mainland Europe and the U.S.S.R., zander are thought to move considerable distances through the system. The aim of this work is to quantify this movement and suggest the reasons for it. It was also hoped to obtain population estimates of zander from certain waters. This is dealt with in Section 2.5.

2.4.2. METHODS

The means used to obtain zander have been described in section 2.1.2. Zander were marked using two types of tag (Figure 57). The majority of fish were marked using a Freshwater Biological Association opercular tag. Made of stainless steel, these tags carried a six figure number. They were attached to the operculum by inserting the point of a scalpel into the operculum 10 mm from the posterior edge, above the root of the pectoral fin. The tab of the tag was then inserted in the hole made and folded over.

Figure 57.

Tag Types.



The marked fish were then released and the surrounding area observed, should a tagged fish float to the surface. Such fish were killed and the tag removed. Zander with obvious disease or severe angling damage due to unhooking were not tagged. The alternative tags were attached to the anterior base of the second dorsal fin. Insertion of the wire was by means of an hypodermic needle. Once the needle had been pushed through the base of the fin, the wire was inserted into the bore of the needle and the needle withdrawn. The wire was then threaded through the zander's body. The two wires were then twisted together and cut short. The security of both types of tag was checked before release.

The following details were noted for each marked zander:

(1) Weight

(2) Fork length

(3) Date

(4) Capture site

(5) Condition of the fish

(6) Tag number

Recaptures were dealt with in a similar manner. After June 1979 scales were removed from tagged fish.

When the use of tags was discontinued, zander were marked with Alcian Blue dye (Hart and Pitcher 1969), injected subcutaneously with a hypodermic syringe. This was required for the work on population estimation to avoid counting individual fish twice.

2.4.3. RESULTS

The marking of zander commenced in June of 1978 and was concluded in August 1980. Recaptures were recorded until August 1981. The number of zander, tagged, with months, tag types and water are presented in Table 38. The following points were considered before interpretation of the results:

(1) Degree of tag loss using the various tags
(2) Mortality of tagged fish
(3) Number of tags removed and the number of tagged zander removed from the population by anglers.

The degree of tag loss when using the FBA opercular tag was considered to be very low. Because the tag has to be inserted through the bone, the loss of the tag will leave either a split or a hole in the operculum. A sample of 28 zander examined in June and July of 1980 were in 3 cases found to have holes in the operculi consistent with tag loss. Tag loss using opercular tags was therefore estimated as being 10.7% during the period June 1978 to July 1980 (25 months).

Tagged fish which subsequently died on release were noted on 3 occasions. Only tagged fish which died and remained on the bottom of the river bed could not be accounted for. The number of such fish could not be quantified. During seine netting work no dead zander were recovered, even though a large number of zander had been tagged recently. It is suggested that the majority of dead zander were noted when floating on the surface.

TABLE 38: Zander marked and the Sites, June 1978 to July 1980

				1978								1979								1980	
Water	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Feb	Mar	Jun	Jul
Relief Channel.	1 22*	81 11*	34 0	61 16*	13 0	24 0	1 0	0 0	0 0	2 0	63 0	50 1*	11 8*	4 0	7 3*	0 0	0 0	0	0	5	0
Cut off Channel	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Middle Level	0	0	0	0	0	3	2	0	0	0	0	0	0	37	27	2	0	0	1	4	1
River Delph.	0	0	9	11	4	0	0	0	0	1	0	2	1	0	1	0	0	0	0	0	0
Great Ouse.	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Totals	1978/79	1979/80	SUM
Relief Channel	264	154	418
Middle Level	5	72	77
Cut Off Channel	6	0	6
River Delph	25	4	29
Great Ouse	3	0	3
TOTAL	303	230	533

*Denotes non standard tag.

Tags were removed by anglers, however tag loss by this cause could be determined in a similar manner to natural loss. The removal of tagged zander from the water was also difficult to quantify, however for this section it is sufficient to know that the removal of tagged zander did not prevent the obtaining of satisfactory recovery rates for tagged fish. One tagged fish of 2.9 kg captured from the River Delph almost doubled it's size in less than six months. It is suspected that this fish was either weighed incorrectly by the captor or the tag had been exchanged by persons unknown. A similar experience was noted by Goubier (1975).

The non standard tags attached to the dorsal fin base were found to be unsatisfactory for this study. On several occasions these tags fell from the fish during handling. A fish held in captivity lost such a tag after 3 months. Also the ratio of opercular tags to dorsal tags was quite different.

	Number captured	to	Number tagged
Opercular tag	1	:	13.7
Dorsal tag	1	:	49

Generally the tagging of zander was carried out with the minimum amount of damage to the zander. Few tags were found to be inflicting damage to their carriers.

The majority of recaptures of marked zander were obtained from the Relief Channel, Middle Level and River Delph. Very few recaptures were obtained from the Cut Off Channel and none from the Great Ouse. This was probably a reflection of the very small number of marked zander released into these waters. The major capture and recapture sites were presented in Table 39 and Figures 58, 59 shows the position of these sites. The time period, distance moved and rate of movement were presented in detail in Appendix IV Peg Nos. refer to permanent numbered fishing positions for angling. The length of the Relief Channel was 16 km and that of the Middle Level 17.3 km.

The study of the zanders movement by means of marking provided information on the following points:

(i) The zander's range and rate of movement

(ii) The influence of size on distance, moved by zander

(iii) Catchability of zander and an estimate of mortality

(iv) Weight and length changes of marked zander.

(i) The zander's range and rate of movement.

The marking and recapture data was presented as graphs showing distances moved up and down stream with time (Figures 60-63). The Relief Channel zander released in 1978 and 1979 and subsequently recaptured in 1978, 1979 and 1980 showed fairly uniform movements up and down-stream from release points. The percentages of zander which moved upstream and downstream or remained static was very similar for 1978 fish whether they were recaptured in 1978 or 1979 (Table 40).

TABLE 39: Ordnance Survey Grid References of Capture Sites

Site	NGR
Relief Channel	
Denver Sluice	TF 591 012
Denver 1st drain E	TF 593 015
Downham Bridge	TF 601 032
Downham Stones E	TF 603 038
Downham Drain 24E	TF 604 045
Downham Stow 40E	TF 604 046
Stow Downham 85E	TF 604 053
Stow Downham 164W	TF 604 060
Stow Downham 127E	TF 605 064
Stowbridge	TF 605 070
Stow Magdalen 13E	TF 604 072
Runcton Holme E	TF 603 095
Magdalen Rail Bridge Stow 157W	TF 602 010
Magdalen Rail Bridge Stow 168W	TF 602 011
Magdalen Rail Bridge	TF 600 013
Magdalen Rail Bridge - Road Bridge 192E	TF 600 105
Magdalen Road Bridge - Rail Bridge 210E	TF 603 113
Magdalen Road Bridge North Side	TF 603 114
Polver Outfall	TF 608 127
St. Germans Zander Area	TF 609 136
St. Germans Bridge	TF 609 142
Middle Level Main Drain	
Three Holes to Cottons Corner	TL 502 999
Three Holes Pophams Junction	TF 505 002
Three Holes Poplars	TF 513 009
Berries Bridge	TF 516 012
Magdalen Railway Bridge - Road Bridge	TF 572 111
Peters Bridge	TF 581 128
River Delph	
Welmore Sluice	TL 570 987
Welney Bridge	TL 528 937
Great Ouse	
Southery	TL 930 610
Cut Off Channel	
Hilgay-Roxham Bridge	TL 625 008

Figure 58.
Principal Capture and Recapture Sites for the Relief and Cut Off Channels.

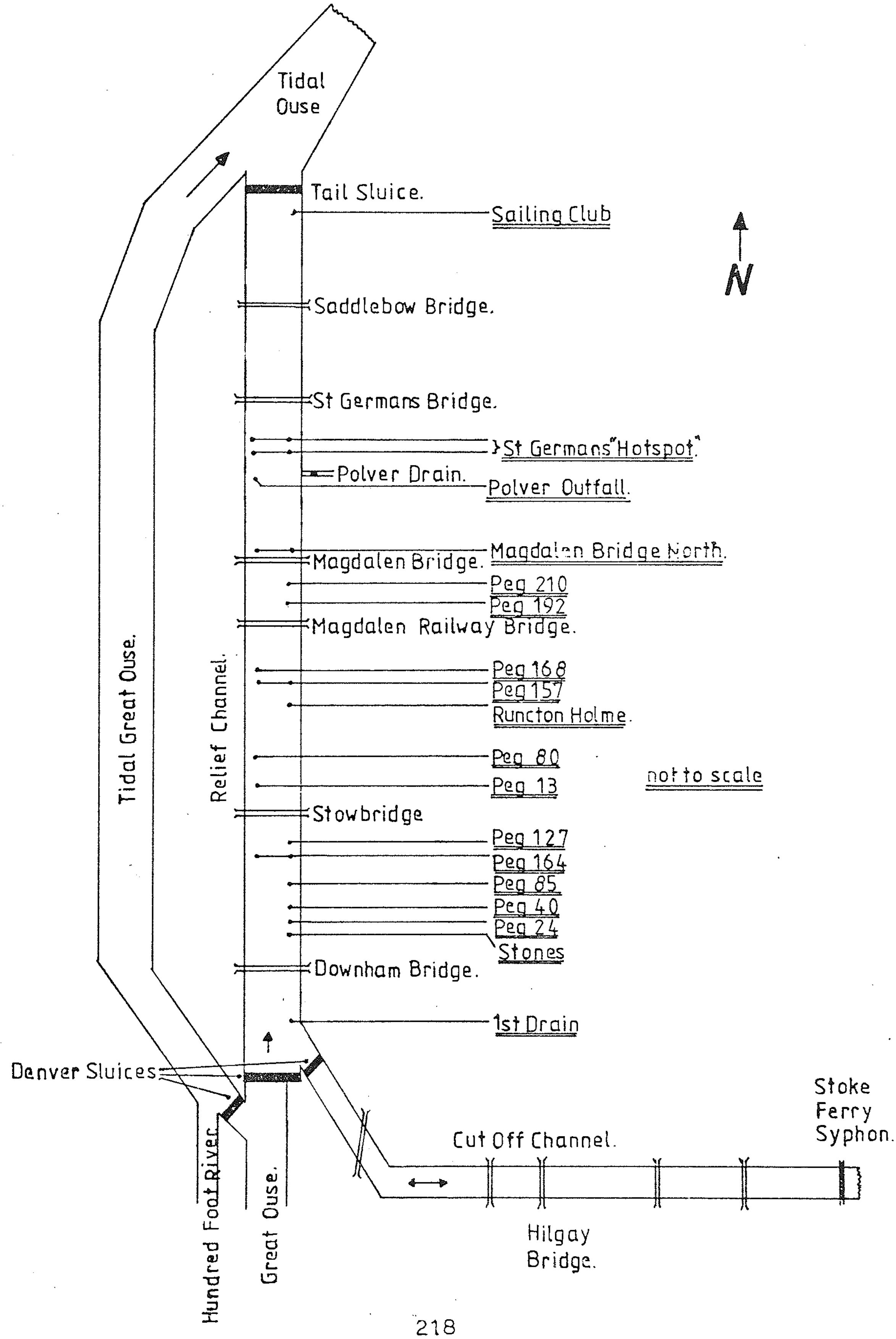


Figure 59.

Principal Capture and Recapture Sites for the Middle Level System.

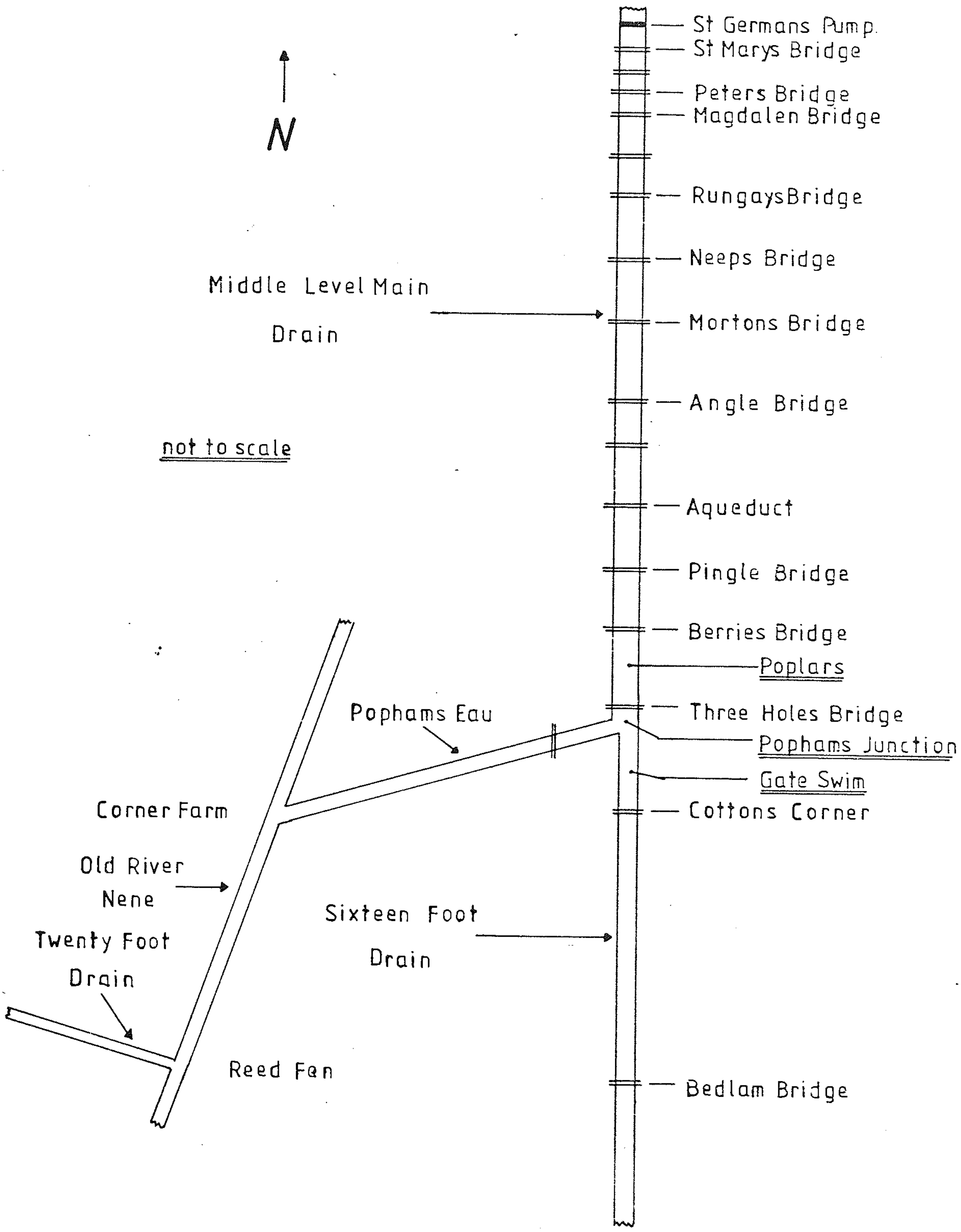


Figure 60.

Movement of Marked Zander Relief Channel.

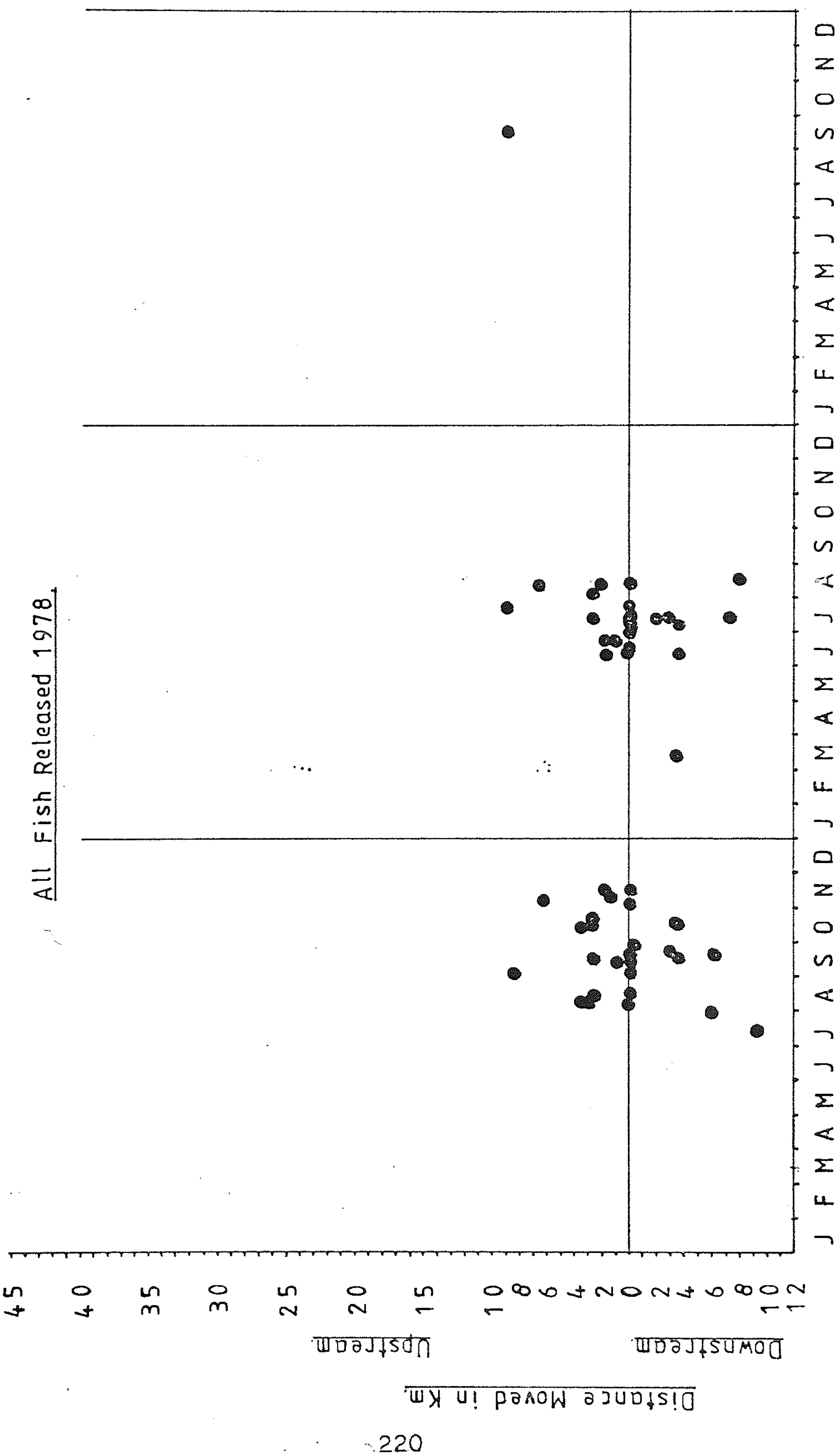


Figure 61.
Movement of Marked Zander
Relief Channel.

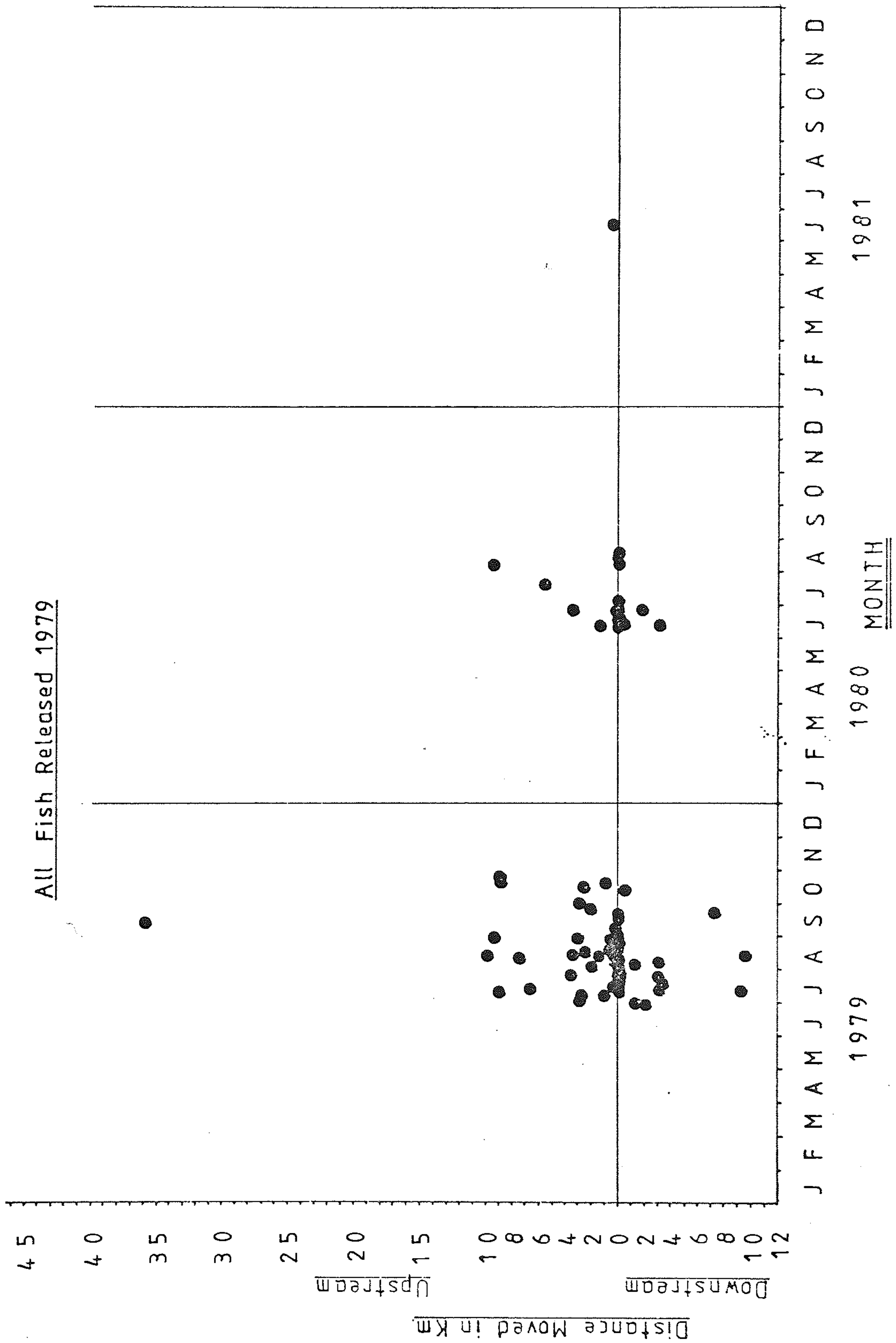
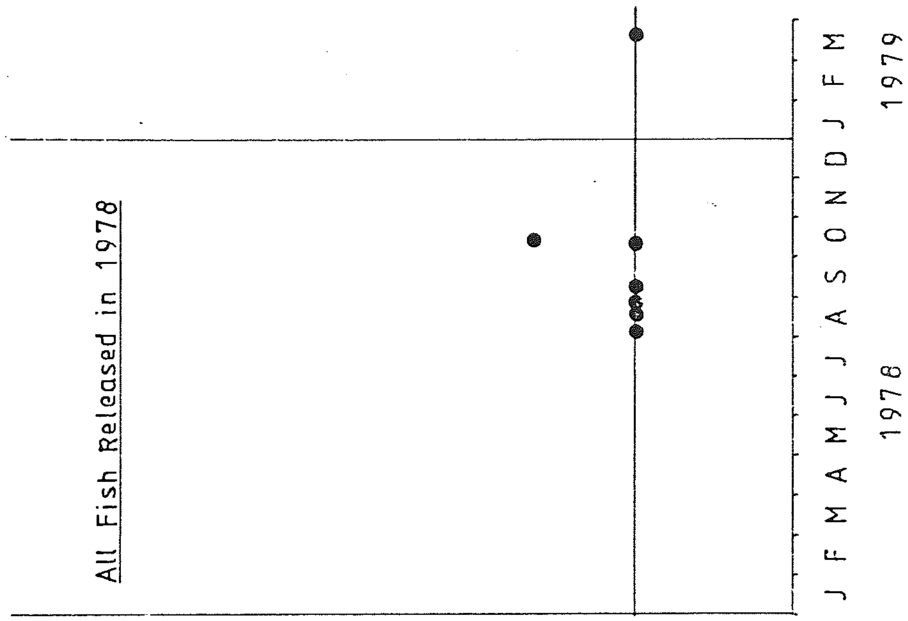


Figure 62.

Movement of Marked Zander River Delph.



Movement of Marked Zander Relief Channel.

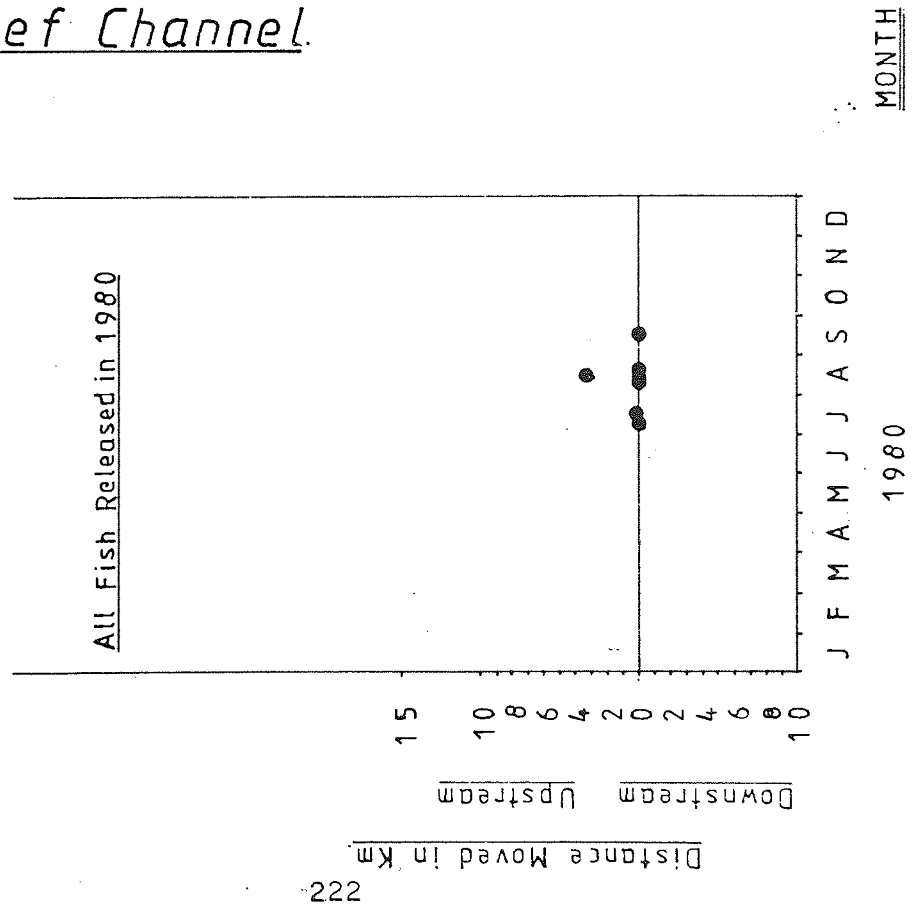


Figure 63.
Movement of Marked Zander
Middle Level System.

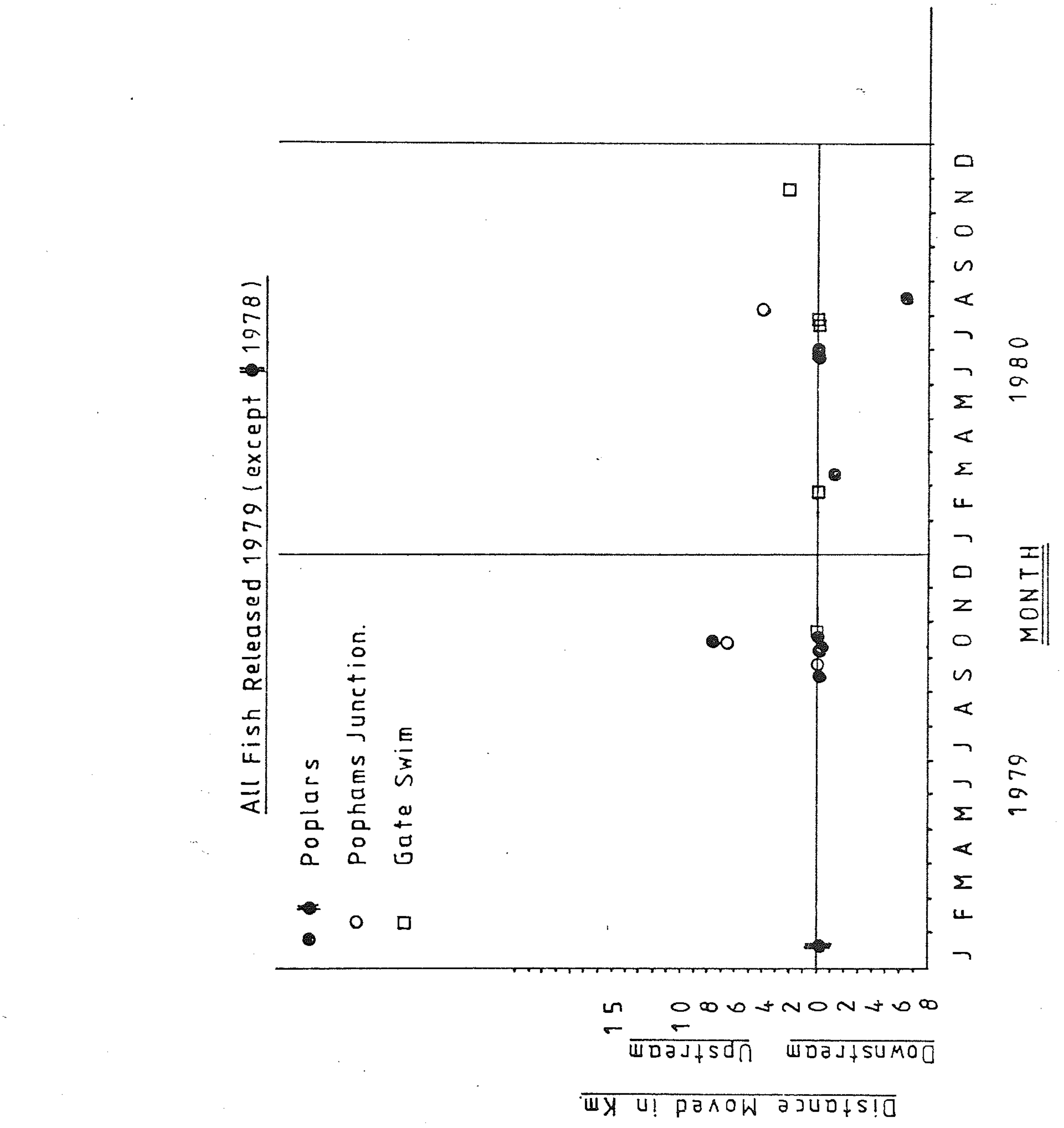


TABLE 40: Range of Zander Movement Relief Channel 1978

Mean Distance Moved	Upstream	Downstream	Static
Recaptured in 1978	4.05 km	4.14 km	0
n	12	9	8
Percentage	41.4	31.0	27.6
Recaptured in 1979	3.15 km	4.3 km	0
n	10	7	6
Percentage	43.5	30.4	26.1

Range of Zander Movement Relief Channel 1979

Mean Distance Moved	Upstream	Downstream	Static
Recaptured in 1979	4.99 km	3.69 km	0
n	26	12	30
Percentage	38.2	17.7	44.1
Recaptured in 1980	2.97 km	1.91 km	0
n	7	3	11
Percentage	33.3	14.3	52.4

Zander released in 1979 appeared to have a greater percentage of upstream movers compared with downstream. Static zander were more numerous in the recaptures of 1979 zander than 1978 zander.

Distances moved up and downstream were compared by means of a t test between years. No significant differences in upstream and downstream movements were noted, ($P > 0.05$) between years. Relief Channel zander appeared to range freely over the entire length of the fishery. Two zander were recaptured outside of the Relief Channel. One from the Hundred Foot River near Earith. A distance of 35.8 km (minimum) was recorded by this fish which travelled this distance in 59 days of the summer of 1979. Another zander of 5.3 kg was captured from the Cut Off Channel at Stoke Ferry. The tag number was mislaid by the would be informant, however as no large zander were tagged in the Cut Off Channel it must be assumed that the tagged fish was one of several marked and released in the Relief Channel. The maximum rate of movement recorded by Relief Channel zander was 2.87 km/day during September of 1979. On one occasion two marked zander released on consecutive days at the same site were recaptured on one day at a site 2.87 km upstream.

Distances travelled by Relief Channel zander were categorised into 2 km divisions (Table 41).

Table 41: Distance Moved by Relief Channel Zander

Distance Moved on Release	Number 78	%	Number 79	%
0	14	25.5	47	49.0
0.1-1.9	9	16.4	18	18.8
2.0-3.9	21	38.2	18	18.8
4.0-5.9	1	1.8	1	1.04
6.0-7.9	5	9.1	2	2.1
8.0-9.9	5	9.1	8	8.3
>10	0	0	2	2.1
	n = 55		n = 96	

Table 42: Range of Zander Movement Middle Level 1979

Mean Distance Moved	Upstream	Downstream	Static
Recaptured in 1979			
	7.2 km	0.2 km	0
n	2	1	6
Percentage	22.2	11.1	66.7
Recaptured in 1980			
	3.0 km	3.9 km	0
n	2	2	7
Percentage	18.2	18.2	63.6

The percentage composition of zander which had moved various distances showed some similarity between periods. Between 25.5 and 49% of the population was static, 16.4 to 18.8% moved up to 1.9 km, 18.8 to 38.2% 2.0-3.9 km. Small percentages moved more than 4 km. There appeared to be a slight decrease in the number of long distance movers in 1979 compared with 1979.

Middle Level zander movement data was less comprehensive than that obtained from the Relief Channel. Table 42 presents the upstream and downstream movements of zander released in 1979 and recaptured in 1979 and 1980.

Upstream movements were greater in distance and number in 1979. Recapture in 1980 showed similar degrees of up and downstream movement with the same proportion moving in each direction. The number of static zander for both periods were very similar. The greatest distance moved by Middle Level zander was 7.7 km in 11 days during September and October in 1979. The maximum rate of movement was 0.7 km/day. Middle Level zander were recaptured from several linked waters, namely the Sixteen Foot Drain, Pophams Eau and Old River Nene. Two zander released in different areas were recaptured 11 and 31 days later in the same area on the same day. Two zander released at the Poplars swim on the 22nd and 23rd of September 1979 were recaptured on the same day in the same location in June of 1980. Insufficient data was available for statistical comparisons of distance moved in relation to year recaptured. Table 43 indicates that the majority of Middle Level zander (41%) showed no movement. Small numbers of zander moved up to 7.7 km. Overall 1979 Relief Channel and Middle Level zander showed a similar proportion of statics and movers.

TABLE 43: Distances Moved by Middle Level Zander

Distance Moved on Release 1979	Number	%
0	12	48
0.1-1.9	3	15
2.0-3.9	1	5
4.0-5.9	1	5
6.0-7.9	3	15
8.0-9.9	0	0
>10	0	0

Distances of recapture from release points were plotted at 1 km intervals on arithmetic probability scale as cumulative percentages of the total frequency (Stott 1967, Hunt 1974) (Figure 64.). A normal distribution when treated in this manner produces a straight line. However a Sigmoid curve was noted, similar to that obtained by Stott (1967) and Hunt (1974). This indicates the presence of two normal distributions of differing dispersions, consisting of a large static component and a smaller population which wanders more widely. Such patterns of movement were noted for both Relief Channel and Middle Level zander populations.

River Delph zander were recaptured in the original capture area in 7 cases out of 8 (87.5%). One example was recaptured 6.5 km upriver. Another undetailed recapture was made 2 km upriver. The rate of movement for the 6.5 km mover was 0.16 km/day.

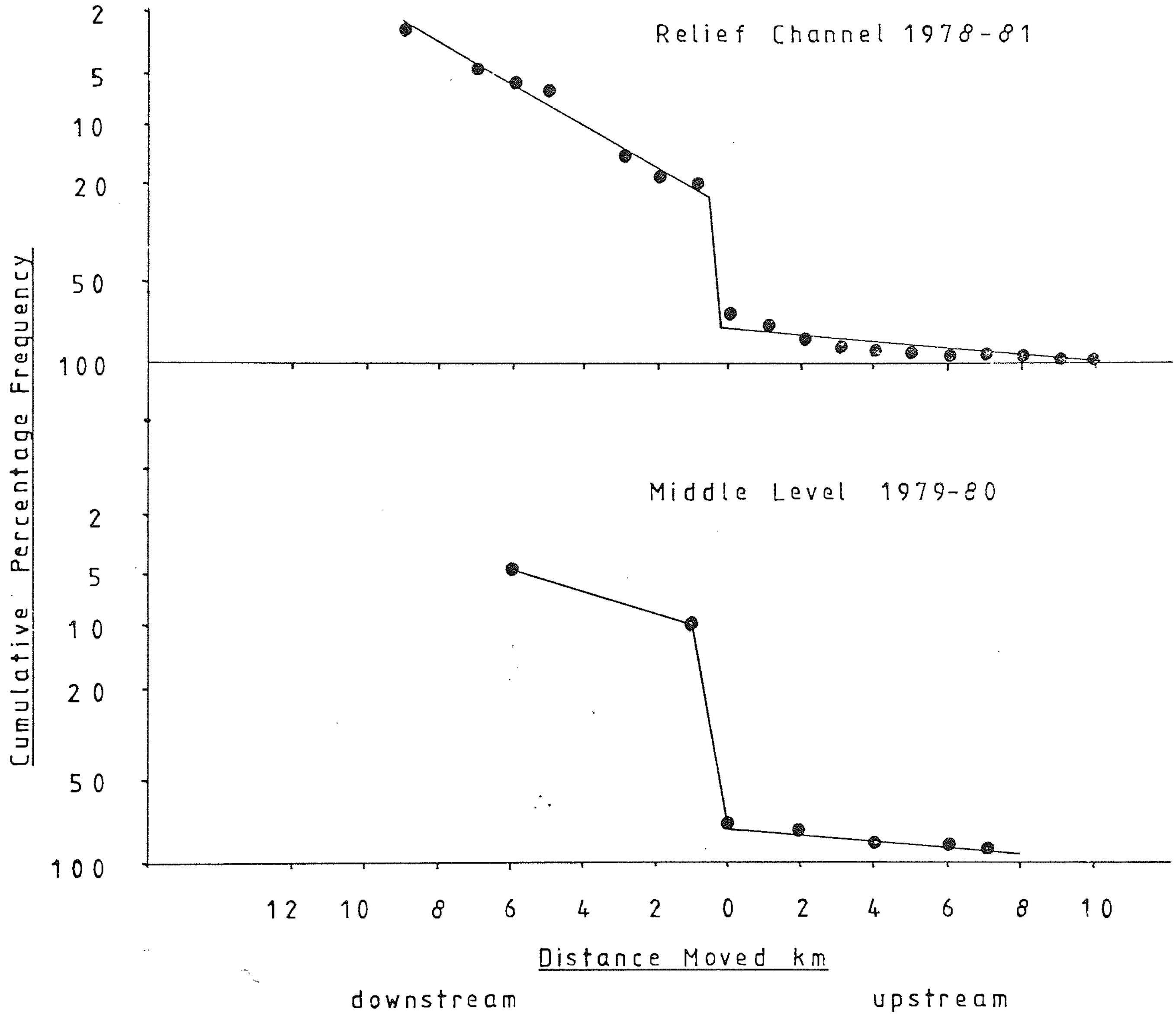
No significant correlation as noted between zander length and distance moved for Middle Level zander, r = -0.1 (df 17) or for zander length and rate of movement, r = 0.05 (df 17). Insufficient data prevented a similar study of River Delph zander movement.

(ii) The Influence of Zander Size on Distance Moved

Zander length and distance and rate of movement were tested for correlation using the method of least squares. No significant correlation was noted for Relief Channel zander, the correlation coefficient for zander length and distance moved being -0.1 (df 145). For zander length and rate of movement r = -0.092 (df 143).

Figure 64.

Relative Capture Frequency with Distance from Release Point



(iii) Catchability of zander and an Estimate of Mortality

Table 44 presents the recapture rate and Table 45 the number of multiple recaptures noted from each fishery. The percentages of zander recaptured twice, three times, and four times were higher for zander released in 1979 than 1978 (Relief Channel). Recaptures of zander released in 1980 and recaptured twice in that year were greater than in the preceding years. This trend is apparent in spite of marked zander releases being greater in 1978 than 1979 and 1980. Overall recapture rates were fairly high with 24.3% of marked zander subsequently recaptured once again, 5.6% two more times, 4.7% 3 times and 0.75% were recaptured 4 more times after the initial capture. The recapture data is considered with reference to population estimation in the following section (2.5). It is sufficient to mention that percentage returns of marked zander were higher for zander released in 1979 and recaptured in the same year than zander released in 1978 and recaptured in the same year. Recaptures of zander released in 1978 remained at an almost identical level during 1978 and 1979, falling rapidly in 1980. Zander recaptures from 1979 released showed a steady decline through 1980. Recaptures of zander released in 1979 on the Middle Level showed a slight increase the following year. No 1981 returns were noted. River Delph recaptures declined rapidly from 1978.

The estimation of the rate of mortality of tagged zander required the subtraction of the estimate of tag loss. A yearly rate of 5.1% tag log was estimated for Relief Channel zander and this was used for the Middle Level also. All zander tagged were greater than 400 mm therefore mortality estimates refer to fish of greater than 3 years of age.

TABLE 44: Zander Recaptures Related to Year Tagged

Relief Channel

Year Tagged	No. Tagged	Rec 78	%	Rec 79	%	Rec 80	%	Rec 81	%	Total	Rec %
1978	215	26	12.1	25	11.6	1	0.47	0	0	52	24.2
1979	137	0	0	43	31.4	12	8.8	1	0.7	56	40.9
1980	5	0	0	0	0	2	40	0	0	2	40
All	357	26	7.3	68	19.1	15	4.2	1	0.3	110	30.8

Middle Level

Year Tagged	No. Tagged	Rec 78	%	Rec 79	%	Rec 80	%	Rec 81	%	Total	Rec %
1978	5	0	0	1	20	0	0	0	0	1	20
1979	66	0	0	8	12.1	12	18.2	0	0	20	30.3
1980	6	0	0	0	0	0	0	0	0	0	0
All	77	0	0	9	11.7	12	15.6	0	0	21	27.3

River Delph

Year Tagged	No. Tagged	Rec 78	%	Rec 79	%	Rec 80	%	Rec 81	%	Total	Rec %
1978	25	6	24	4	16	0	0	0	0	10	40
1979	2	2	0	0	0	0	0	0	0	0	0
All	27	8	29.6	4	14.8	0	0	0	0	10	37

Cut Off Channel

Year Tagged	No. Tagged	Rec 78	%	Rec 79	%	Rec 80	%	Rec 81	%	Total	Rec %
One fish recaptured from 6 tagged										1	16.7
Total All pooled	467	35	7.5	81	17.3	27	5.8	1	0.2	142	30.7

TABLE 45: Multiple Recaptures of Tagged Zander

Relief Channel (standard tags)

Year Tagged	Captured Once	Twice	Three Times	Four Times	Five Times
1978	182	29	6	3	2
% of Recaps.	-	15.9%	3.3%	1.65%	1.1%
1979	82	34	9	10	0
% of Recaps.	-	41.5%	11%	12.2%	0
1980	3	2	0	0	0
% of Recaps.	-	66.6%	0	0	0
All	267	615	15	13	2
% of Recaps.	-	24.3%	5.6%	4.7%	0.75%

Multiple recaptures did not occur elsewhere, except for two examples on the River Delph. One recaptured on 2 occasions, one once. This gave an overall percentage recapture of 3.7% two times and 3.7% three times.

Estimated mortality rates based on the number of tagged zander recaptured in consecutive years was presented in Table 46.

Mortality estimates based on this method depend on the assumption that recaptures are proportional to the number of zander present. This was obviously not the case for the Middle Level.

(iv) Weight and Length Changes of Marked Zander

Weight and length changes of marked zander were grouped by seasons, corresponding to the June to March open period for angling. Weight and length changes were expressed as percentages of bodyweight and length (Table 47).

All 1978 zander released into the Relief Channel had an average lost weight, while all 1979 releases on average gained weight. Middle Level releases showed a mean weight increase in 1979, but on recapture in 1980 had lost weight. River Delph recaptures in 1978 had on average gained weight. Mean length changes were in the majority of cases less than the margin or error noted in section 2.1.3.

TABLE 46: Estimated Mortality of Tagged Zander

Year Released	% Not surviving until 1979	% Not surviving until 1980	% Not surviving until 1981
Relief Channel			
1978	0	96.0%	no estimate
1979	-	70.7%	97.6%
Middle Level			
1979	More recaptures were recorded in 1980 than 1979		

TABLE 47: Mean Weight and Length Changes of Tagged Zander

Water	Year Released	Year Recaptured	% Wt. Change	Range	n	% L Change	Range	n
Relief Channel	1978	1978	-1.38	-9.3 - +6.2	23	+0.89	-1.06 - +4.57	17
"	1978	1979	-4.43	-23.2 - +14.5	25	-0.72	-8.8 - +4.1	23
"	1979	1979	+1.88	-18.1 - +53.4	63	+0.28	-10.3 - +5.4	46
"	1979	1980	+5.05	-12.1 - +31.3	16	+1.37	-4.35 - +5.4	12
Middle Level	1979	1979	+3.89	-2.7 - +18.1	7	-0.39	-5.9 - +2.5	6
"	1979	1980	-4.06	-15.1 - +1.3	11	+2.8	-11.6 - +3.9	5
River Delph	1978	1978	+15.6	-6.7 - -1.3	6	-1.47	-1.12 - +0.65	5

All fish greater than 3 years of age and sexually mature

2.4.4. DISCUSSION

Before discussing the movement of zander, some definition of the types of movement shown by fish would be appropriate. Movement itself simply refers to a change in position of a fish, a displacement of a lower order of magnitude than migration. Migration as defined by Nikolski (1963) is: "A sometimes passive though usually active mass movement from one habitat to another". Homing is according to Gerking (1959): "The choice that a fish makes between returning to a place formerly occupied instead of going to other equally probable places". Home range, defined by Gerking (1953) is "The area over which an animal normally travels".

The movements of zander were studied most comprehensively on the Relief Channel. Recaptures were recorded from all sections. (Figure 58). Angling returns, with the assistance of press publicity were obtained from a wide variety of areas mainly within but also outside, of the Relief Channel. However the majority of recaptures of tagged fish were made in two areas, roughly defined as Downham Market and St. Germans. Both areas are 2-4 km from the impounding sluices as the southern and northern ends of the fishery respectively.

The overall recapture rate for the Relief Channel zander was high, 30.8%. This indicated that this zander population was the subject of intensive angling and individuals were likely to be recaptured on more than one occasion if returned to the water alive. It also suggests a low mortality due to angling. The recapture rate obtained in this study compared favourably with Goubier's (1975) study of French zander. His highest annual recapture rate was 20% from the Vidourle river in 1961. Mean recapture rates were however much lower, 7% in 1961/63 for the same river and 8.4% for the River Orb.

The reasons for the higher recapture rate during this study can be suggested as:

(a) Goubier though releasing a larger number of zander (5,937) did so, into much larger river systems (Orb 145 km, Vidourle 95 km) as opposed to the Relief Channel's 16.6 km.

(b) His zander were frequently small (100-300 mm) as opposed to mainly greater than 350 mm for this work. Goubier noted that small zander were more likely to suffer from the application of tags than larger zander.

(c) The semi enclosed nature of the Relief Channel and the release of a larger number of tagged individuals which remained mainly in the same watercourse.

(d) A high level of angling effort and widespread knowledge amongst anglers of this work.

The high recapture rate experienced enabled a worthwhile study of zander movement. For Relief Channel zander upstream movements were more numerous than downstream movements, (Figures 60-62), though the distances involved were similar. This trend eventually resulted in a reduction in the number of recaptures from the lower Relief Channel, (northern end), until in 1980 returns of tagged zander ceased, despite equal angling effort by the author and helpers. Tagged zander continued to be recaptured at the sites towards the upstream section of the Relief Channel (southern end). It would appear that by late 1979 zander had ceased to inhabit the lower Relief Channel in sufficient numbers to enable recaptures to be made. Many of the zander tagged at St. Germans subsequently arrived in the Downham Market area and were recaptured later, still in the same area. Meanwhile no tagged zander were noted moving back to St. Germans. The upper Relief Channel has always been the most prolific area for the capture of zander (Rickards and Fickling 1979). While zander numbers were high as determined from the population estimate for 1978 (2.5) it appears that zander were present in many areas of the fishery. However as zander numbers declined it would appear that zander continued to inhabit the upper "favoured" stretches of the Relief Channel creating a vacuum in the lower lengths. This accounts for the increase in the proportion of static zander, from 26.1-27.6% (78) to 44.1-52.4% (79). The Anglian Water Authority survey of 1979 (Klee 1979a) confirmed this with zander captures confined to the upper Relief Channel. It is interesting to note that the majority of prey fish noted during this survey were to be found in the upper reaches of the Relief Channel and this in itself may have been sufficient reason for a redistribution of the zander population.

The actual process of capture and tagging may have been the reason for some zander movements, however in many cases zander did not move or if movement had occurred, the return to the original capture site was effected before recaptures elsewhere could be made.

The movements of zander within the Relief Channel suggests that the home range of this zander population is variable. Stott (1961 and 1967) working on the roach (Rutilus rutilus L) and Gudgeon (Gobio Gobio L) of the River Mole noted that the population could be divided into a large (61-70%) static population and a smaller (21-39%) mobile population. Such findings have been repeated with other fish species notably the barbel (Barbus barbus L) Hunt (1974). There would certainly appear to be a static element (Table 41) in the Relief Channel zander population and an element which wanders within the confines of the fishery. A very small proportion moved out of the Relief Channel and travelled considerable distances upriver. Attempts to correlate movement and zander size proved unproductive there being no apparent correlation between size and distance moved, or rate of movement. The zanders home range would appear in some cases to be very restricted, yet in others a simple reflection of the artificial barriers which for much of the time prevent movement in and out of the Relief Channel. The significance of the impounding Head and Tail sluices cannot be overlooked, for it is quite possible that these set the limits of some of the zanders home ranges. On the other hand for much of the winter period both sluices are open, so there is no apparent reason why zander should not roam further afield than the Relief Channel. The small number of fish recaptured outside of the Relief Channel suggest that the majority of zander have a restricted range. The fact that only around 10% (Table 41) of the zander recaptured had moved 8 to 10 km suggests that a home range exists independent of the impounding sluices.

Because displacement studies were not a part of this work it is unclear whether or not Relief Channel zander show homing tendencies. One particular fish (264448) did show a degree of homing by moving from Downham Market to St. Germans in 9 days and then returning to Downham Market after 97 days. However this zander may well have travelled to many other areas before or after its final recapture and its occurrence in the original capture area may have been the result of a fortuitous meeting between zander and angler, while enroute to other areas. Generally zander recaptures were for the mobile element unpredictable except for the general upstream movement mentioned earlier.

The 35.8 km movement of one zander in 59 days (264485) indicates that zander are capable of long distance movements and if this is accompanied by the long distance movement of other zander the term migration might be suggested. This ability to move such long distances has a considerable ecological implication. Zander could rapidly move to new areas and colonisation of unpopulated areas could be effected in very short periods. The rapid spread of the zander since its introduction to the Relief Channel in 1963 confirms this suggestion. Such movements could also give rise to temporary concentrations of zander in certain areas, perhaps where food fish are more numerous. The resulting increase in predation pressure would presumably have a serious effect on localised concentrations of prey fish. Areas vacated by zander would of course be relieved of such pressure. It is unclear whether or not the movement of this particular zander was directed or the result of chance wandering. Once having passed through the Relief Channel sluice (Head or Tail), return may have been prevented, resulting in further wandering. Alternately, the food shortage in the Relief Channel may have induced migration to more hospitable areas. The Hundred Foot River, (Figure 2) the recapture site of this fish, though having not been surveyed is said to be reasonably well populated with prey fish (McAngus pers comms.).

The highest rate of movement was acredited to another zander (26213), 2.87 km in one day. This exceeds Goubiers (1975) maximum rate of movement of 1.6 km per day. Goubiers fastest mover was in a downstream direction as opposed to upstream for the fastest mover of this study. It might be suggested that downstream movements are less significant than upstream movements due to the possibility of passive movement. Ferguson and Derhsen (1971) noted a 9.1 km/day movement of a walleye tagged in the Great Lakes system. The direction up or downstream was not indicated, however the movement was associated with a spawning migration. It is therefore evident that the Genus Stizostedion is capable of rapid movement over considerable distances.

The distance accredited to 264485 was a minimum distance based on the assumption that the zander moved in the most direct fashion to its recapture point. It is quite possible that this zander had travelled by a less direct route and the distance suggested must be considered as a minimum estimate of movement. Goubier (1975) noted a maximum downstream movement of 200 km on the River Herault and a maximum upstream movement of 30 km upstream on the Orb. The presence of weirs and locks appeared to offer greater obstruction to upstream movers than downstream movers. Relief Channel zander could not effect downstream movements of greater than 20 km due to the saline nature of the tidal River Ouse. Even if penetration of the saline waters was possible the lack of anglers fishing for zander in these waters would make recaptures unlikely.

Relief Channel zander and indeed zander from the Middle Level and River Delph were frequently captured in considerable numbers from restricted areas. 21 zander were recaptured from one small area (30 m x 50 m) of the Relief Channel, tagged and released on the same day. Subequent recaptures of these fish did not indicate that these fish were in any way associated. Recaptures showed no discernable pattern. Similarly 15 zander captured and released into an area of 20 m x 50 m on the Middle Level, failed to show associated movements to other areas, though recaptures in the original capture area were noted over a period of several months. This indicates that zander though forming large shoals, do not appear to retain a shoal identity.

Occasionally zander released in different areas were recaptured from the same area, on the same day. It would appear that zander during their movements will at times converge on certain areas, regardless of the original capture point.

Middle Level zander provided less data due to the smaller number of fish released. However recapture rates were again high (27.3%) and very similar to that obtained from the Relief Channel. A greater proportion of static zander (Table 43) was noted compared with the Relief Channel in 1978, but the proportion of static zander showed little different to that noted for the Relief Channel in 1979. The data for up and downstream movement was rather sparse, but there was an indication of movement of a similar order to that noted for Relief Channel zander. Though the Middle Level system is much more extensive than the Relief Channel and with few barriers, movement was fairly limited, a distance of

7.7 km being the maximum recorded. Maximum rates of movement were fairly high, 0.7 km/day, indicating that the limited distances moved were accomplished rapidly. As mentioned earlier associated recaptures were noted, but only for static zander. On one occasion zander were released from two different areas at a 25 day interval and one fish from each release was subsequently recaptured in the same area on the same day, (upstream, 6.6 to 7.7 km).

Of particular interest was the lack of interchange between the two principle capture and recapture sites. No zander released at the Poplars moved to the Gate Swim and vice-versa (Figure 59). Yet both areas were very close (less than 2 km) and there was no restriction to zander movement. It is suggested that the majority of Middle Level zander have a much more restricted home range than Relief Channel zander. A mobile element exists and this appeared to be in similar proportion to the Relief Channel, however movement was less extensive. It should be noted that the with less recapture data and a shorter period at liberty, the chances of the recapture of a long distance mover would probably be reduced.

River Delph zander provided only a small number of recaptures but a high recapture rate of 37%. The proportion of non movers as the highest noted, however once again a small mobile element existed. During 1978 zander number 264135 was recaptured 3 times in the same area, despite angling efforts in other areas. Some zander certainly appear to have a very restricted home range.

The results of this study suggested that each zander population consists of individuals with varying tendencies to move or remain static. It is difficult to define the extent of the zanders home range, however movements in excess of 10 km were seldom noted and it can therefore be suggested that zander have a large home range. This home range appears to differ depending on the population. It would be somewhat speculative to suggest that zander movements are related to food supply, however it was apparent that the greatest movements were effected by zander living in waters with low prey densities (Relief Channel). Though no surveys have been carried out on the River Delph, a minor pollution in 1980 indicated that prey fish were at the time of the study relatively numerous. It is interesting to note that River Delph zander showed the most restricted movements. Where prey fish are few in number it is logical to suggest that a predator will have to search further and longer before finding prey (Ivtev 1961). The higher the prey density the greater the likelihood of an encounter and presumably a capture.

This might account for the lower levels of static zander in the Relief Channel as compared with the Middle Level and River Delph.

The possibility of movements associated with spawning could not be investigated, however Goubier (1975) failed to note any movement associated with spawning. It is likely that a migratory urge as exhibited by the walleye is the result of restricted spawning areas. Zander were probably able to spawn successfully in many areas. The widespread distribution of 0 plus zander during surveys on the Middle Level drains would confirm this.

The catchability of zander varied between waters and periods. Relief Channel zander were particularly prone to multiple recaptures. The increase in catchability of tagged fish might be attributed to either an increase in hunger or an increased accessibility to angling. Both explanations are probably to some extent true. Relief Channel zander appeared to be in poorer condition in 1979 compared with 1978 (2.6). This suggests increased hunger. The redistribution of the remaining zander in the Downham Market area and the subsequent increase in the proportion of static zander would also increase the chance of multiple recaptures. Multiple recaptures declined in 1980 probably due to mortality and decreased angling intensity (ref. AWA permit sales).

The estimated mortability rate from the decline in tag returns appears high in comparison with the mean mortality rate for the Relief Channel of 0.53, however the food shortage which occurred in the Relief Channel would probably increase mortality rates, hence the loss of 96% of 1978 releases due to natural and fishing mortality combined. 1979 releases faired little better with 97.6% dead by 1981.

The increase in tag returns from Middle Level zander released in 1979 may have been due to a low mortality rate, however by 1981 no returns were obtained. This was probably due to the organised removal of zander from this fishery. The mortality rate though unquantified was probably very high.

The changes in length of zander between captures provided no worthwhile information as the majority of data was exceeded by the margin of error introduced in section 2.1. Weight changes were however more significant. Percentage weight losses were high for Relief Channel zander released in 1978 and recaptured in 1978 and 1979. This situation was reversed in 1979 when all 1979 and 1980 recaptures had gained weight. It would appear that the zander were now able to show some degree of weight gain. This could be attributed to either increased prey availability or reduced competition for prey from other zander. Middle Level zander showed weight increases for fish released in 1979 and recaptured in 1979, but weight losses for zander recaptured in 1980. This might partially have been attributed to zander gonad production during the winter of 1979 or alternatively, because of a reduction in prey availability. River Delph zander increased in weight after release in 1978 and recapture in 1978. This may again be attributable to gonad production. These changes in weight will be discussed with reference to other sections of this work in part 4.

2.5. THE ESTIMATION OF THE DENSITY AND BIOMASS OF THE ZANDER POPULATION OF THE GREAT OUSE RELIEF CHANNEL

2.5.1. INTRODUCTION

The marking or tagging of zander and their subsequent recapture has been used in this study to note the movement and changes in weight and length of zander. The information from marking studies was also used to obtain density and biomass estimates of Relief Channel zander. Such mark-recapture exercises depend on the observation of the following rationale: (Ricker 1975, Youngs and Robson 1978 and Begun 1979).

(i) Marked fish should not lose their marks. If marks are lost then some estimate of mark loss is required.

(ii) The mortality of marked fish should be the same as for unmarked fish.

(iii) The marked fish should mix with the unmarked fish, so that subsequent sampling selects marked and unmarked fish in proportion to their occurrence in the population. Marked fish should be equally susceptable to recapture compared with unmarked fish.

(iv) Recruitment to the catchable population should be nil or at least estimable.

(v) Migration of marked fish should be the same as for unmarked fish.

(vi) Immigration of unmarked fish should not occur.

(vii) Recaptures should number greater than 3 or 4 to reduce statistical bias and allow the calculation of realistic confidence limits.

These assumptions are basic to all of the simpler population estimation methods which employ various modifications of the Peterson estimate (Petersen 1896).

2.5.2. METHODS

Zander were marked using the numbered tags described in the previous section. Marking and recapture was carried out by 4 groups of anglers (including the present author) all of whom were instructed in the procedure required. A record was kept of all fish tagged, the number of tagged fish recaptured and the total number of zander recaptured with and without tags. A note was made of all tagged fish removed from the population by anglers during each period. Furthermore an estimate of tag loss was obtained as detailed in the previous section. This was found to be 5.35% per annum. When the application of tags was discontinued, unmarked zander were dye marked on the ventral surface of the body using Alcian Blue dye. This prevented the counting on more than one occasion of recaptured zander.

Population estimation was based on the release of tagged individuals in 1978 and recapture in 1979 and the release of tagged individuals in 1979 and their subsequent recapture in 1980. Further estimates were hoped for based on the return of 1980 releases in 1981, however none of the anglers assisting made recaptures during 1981, probably due to the very small number of zander captured.

The majority of population estimation techniques employ modifications of the Petersen technique. The estimate is derived from the ratio of marked individuals recaptured from a known number of unmarked individuals, when the total number of marked individuals in the population is known. The basic Petersen estimate only provides a valid estimation if all the assumptions noted earlier are upheld. More sophisticated methods such as the Fisher Ford (1947) method provide some estimation of mortality and allow longer periods between recaptures. Unfortunately such methods require more data than was available here. Begon (1979) notes that when the more sophisticated methods cannot be employed, a modification of the Petersen estimate, the Weighted Mean, can be used to provide an estimate, provided the results are interpreted with a certain amount of caution. The Weighted Mean uses a number of Petersen estimates and seeks to provide a mean of these estimates, suitably weighted towards the mean, based on the largest number of recaptures. For details of the formulae used, see 2.5.3. Results.

The assumption most likely to be violated during a mark-recapture exercise which runs for a period of 16 months is that of there being no recruitment of unmarked individuals to the population. Youngs and Robson (1978) note that by selecting specific parts of the population it is possible to eliminate recruitment. This was effected in this study by eliminating all three year old fish recaptured in the recapture period. This eliminated any 2 year old fish present during the marking period, which would not have been captured and marked and which might then have appeared in the subsequent years captures as unmarked individuals. Few 3 year old fish were captured in this study and even fewer were marked. Individual Petersen estimates were made in order to obtain estimates for calculation of a weighted mean, for the following months in each period; Recaptured in 1979 June, July, August and October and August and October were combined to provide a recapture total of 4.

Recaptured in 1980 June, July and August. Population estimation was restricted to fish larger than 400 mm (older than 3 years).

2.5.3. RESULTS

The following terminology was employed:

- M The number of marked fish in the population
- n The total number of fish recaptured
- m The number of marked fish recaptured.

Table 48 presents the values obtained during the marking and recapture exercise.

Using the formulae for the Weighted Mean:

$$N = \frac{Mn}{(\ m+)1}$$

and for the standard error: $SE = N \quad \frac{1}{m_1+1} + \frac{2}{(\ m_1+1)^2} + \frac{6}{(\ m_1+1)^3}$

the following estimates were obtained for zander of 400 mm and over:

1978	2206	or with 95% confidence limits:	1086 - 3326
1979	621	" " " "	315 - 927

TABLE 48: Values Obtained During Mark-Recapture Exercise

	M 78	Adjusted M 78	n 79	m 79	M 79	Adjusted M 79	n 80	m 80
June	213	201.6	77	5	144	136.3	49	10
July	213	201.6	68	7	144	136.3	11	4
August	213	201.6	21	2	144	136.3	22	3
September	213	201.6	4	0	-	-	-	-
October	213	201.6	20	2	-	-	-	-

The surface area of the Relief Channel can be calculated as 16,000 m x 91.4 m or 1462400 m/^{2} (Ordnance Survey).

The density of zander in 1978 was therefore:	0.0015 per m^2
or with 95% confidence limits:	0.000745 - 0.00227 per m^2
The density of zander in 1979 was therefore:	0.000425 per m^2
or with 95% confidence limits:	0.00022 - 0.00063 per m^2

A biomass estimate can be derived by multiplying the density figures by the mean weights of the zander in 1978 and 1979. Mean weights derived from weights of all zander marked. These were respectively 2033 $\pm$ 131 and 2004 $\pm$ 133.7.

Biomass estimates were therefore in the range: 1.42-4.91 gm/m^2 for 1978
and: 0.41-1.35 gm/m^3 for 1979.

2.5.4. DISCUSSION

The biomass and density estimates obtained here suggest a decrease in the number of zander during the period 1978 to 1979. The decrease in biomass is due to the reduction in the number of individuals, the average weight of the zander having declined only slightly (1.4%). The reduction in zander numbers amounted to 71.2% of the total present in 1978. Confirmation and validation of the estimate was sought. In October of 1979 the Anglian Water Authority carried out a seine net survey of the whole Relief Channel, with sample sites at random along this fishery. The results of the survey are given by Klee (1979a), however the density and biomass estimates obtained during this survey are reproduced here by kind permission of the AWA. (Table 49). The data from this study is also included.

TABLE 49: Density and Biomass of the Relief Channel Fish Population

	Species	Density No/m^2	Biomass gm/m^2
AWA 1979	Roach	0.0021	0.03
	Pike	0.0011	1.25
	Eels	0.0018	0.37
	Gudgeon	0.0019	0.02
	Zander · 100 mm	0.0003	0.61
Present Study	Zander 1978	0.000745-0.00227	1.42-4.91
Zander of greater than 400 mm	Zander 1979	0.00022-0.00063	0.41-1.35

The similarity between density and biomass estimates for 1979 was suggestive of an accurate assessment of the zander population. Seine netted zander were all larger than 400 mm, except for 3 small 0+ specimens of around 100 mm. The weight of these fish 28-32g contributes very little to the biomass estimate obtained by the Anglian Water Authority. The AWA figure is based on seine net sampling and the assessment of the number and weight of zander caught in the area sampled. The higher values obtained during 1978 should be a valid estimate providing any violation of the basic assumptions is of equal magnitude for each year. The most likely violation, that of immigration of unmarked individuals into the population remained unquantified. The survey of the Great Ouse below Littleport, carried out in 1979 by the Anglian Water Authority (Klee 1979c) produced no zander. The likelihood of large numbers of zander migrating to the Relief Channel from this watercourse must be considered unlikely. The Cut Off Channel and Tidal River Ouse may have contributed some marked individuals, and this would have tended to increase the estimates of density and biomass. The results obviously indicate a large reduction in numbers of zander and even if the actual precision of the estimates are open to criticism, the considerable difference between the 1978 and 1979 estimates cannot be ignored.

Several possible reasons for the considerable decrease in zander numbers can be put forward:

(i) Emigration of zander. Two individuals were noted outside of the Relief Channel, one in the Cut Off Channel another in the Hundred Foot River. It is likely that a number of zander have invaded other waters during 1978 and 1979. Tag returns from these other waters would probably be at a lower rate, due to the large area of water and the lack of local publicity concerning this work.

(ii) Natural mortality and fishing mortality.
These two forms of mortality could not be separated, but it has been demonstrated in Section 2.2. that a combined mortality of 0.53 was noted on the Relief Channel in the past 12 years. The extremes of mortality were 15.4 to 90.3%, with a mean of 71.2%. Such wide limits do not offer confirmation of the mortality estimates obtained elsewhere, however the mean mortality rate derived from the mean population estimates for each period does suggest a higher than average mortality rate.

Any population estimate derived from a non-enclosed population should be considered cautiously, however the overall trend in decline in zander numbers is confirmed by angling results.
Recruitment appeared to be of a low order, zander of 0 plus being captured at only one site of the Relief Channel during AWA survey (3 individuals). On other waters such as the Middle Level, such fish were encountered at many sites (Klee 1979b). Similarly 1 plus and 2 plus zander were not noted at all on the Relief Channel. In previous years such fish were regularly captured by anglers fishing for other species. It is therefore suggested that the zander population of the Relief Channel is a declining one.
As far as can be deduced, recruitment of zander to a size which

can be captured on rod and line, using conventional zander angling methods, is of a low order of magnitude. If mortality continues at present rates with no increase in recruitment then a further contraction of the zander population is likely.

2.6. THE LENGTH WEIGHT RELATIONSHIP AND THE VISCERAL FAT CONTENT OF ZANDER

2.6.1. INTRODUCTION

The relationship between the length and weight of fish has been studied in great detail for many species of fish. This length, weight relationship can be described by the formulae:

$$W = al^{b}$$

a and b are two constants, b being the exponent of l usually between 2 and 4, depending on the sample studied (Hile 1936, Martin 1949, LeCren 1951). a depicts the weight of a fish of unit length. A logarithmic transformation of the weight and length measurements, allows the fitting of a straight line by the method of least squares. This gives:

$$\log_{W} = \log_{a+b}\log_{l}$$

Differences in the coefficient a between different periods and populations of the same species can be attributed to a number of factors:

(1) State of sexual development and whether male or female. Seasonal cycles of gonad production produce changes in the length-weight relationship.

(2) Fullness of stomach. The degree of fullness of the stomach will influence the length weight relationship.

(3) The "condition" or fatness of the fish. Fish which store substantial amounts of fat in the visceral cavity, will have different length weight relationships, dependent on how much fat is stored at this site. Changes in the amount of musculature will tend to have a similar influence on the "condition" of the fish.

The coefficient b indicates isometric growth when the value is 3. Values of greater than 3 indicates that growth in weight is proportionately greater than growth in length. Values of less than 3 indicate that growth in weight is proportionately less than growth in length. In either cases where growth in weight is not directly proportional to growth in length, growth is said to be allometric (Le Cren 1951).

The study of the length-weight relationship of the zander was conducted in the hope of determining differences in "condition" between the populations studied. The hypothesis being that the fatter fish will be of "better condition" and presumably of faster growth and better nourished. (Bagenal and Tesch 1978). Various studies such as those of Le Cren (1951), Weatherly (1972) and Ricker (1975) confirm that provided the state of gonad development, stomach contents and genetic variation are taken into account, length weight relationships can provide an indication of the physiological state of the fish.

Because of the variables noted above and the fact that it is often difficult to eliminate all of them in a study such as this, another method of expressing the "condition" or fatness of the zander was considered. The method used involved the estimation of the amount of visceral fat carried by the zander. Shulman (1974) states that, "the fat deposits of the zander were found in the abdominal cavity as part of the mesentary. These fat deposits play a leading role in the endogenous feeding of the zander during wintering and spawning migration starvation". The fat also has a conserving action on body proteins during such periods. Because a fish can only store fat, when the available food intake is more than sufficient for metabolic and reproductive needs, large fat deposits may be thought of as indicative of adequate feeding. Low fat deposits would indicate a lower level of nutrition. It should be noted that fat deposits may vary with the seasons (Shulman 1974) and that comparisons between populations should if they are to result in valid conclusions be made at similar times of the year, unless evidence to the contrary is available. Insufficient specimens were available on a seasonal basis to enable a seasonal study of fat content, therefore comparisons were made using pooled samples from similar periods wherever possible.

Studies of visceral fat content have not be carried out in English speaking countries, though Craig (1977) conducted a detailed study of the total body composition of the perch of Lake Windemere. He demonstrated an inverse relationship between water and fat content and seasonal variations associated with gonad production. Craig worked on the total body composition of the perch, notably the water, protein, fat and ash content. Zander are however much larger fish than perch, thus precluding a study using whole fish. Instead the viscera of the zander were used to determine the fat content of the visceral fat stores.

2.6.2. METHODS

Zander weights and lengths were converted to natural logs and the straight line relationship calculated using the method of least squares (Le Cren 1951). The relationships obtained were then tested for significant difference of the coefficient "b" using analysis of Covariance (Sokhal and Rolfe 1967). The following samples were available for comparison: (Blalock 1972)

		Length Groups of:
Relief Channel	1969, 1970, 1975, 1976, 1978, 1979, 1980	330-840 mm
Middle Level	1979, 1980	321-730 mm
Burwell Lode	1979	380-510 mm
River Delph	1978	410-810 mm
Coombe Abbey		180-540 mm

Le Cren (1951) working in perch noted that O+ and mature male and females had differing length weight relationships. In this study very young zander were not available and the sex of older fish was only observed in dissection. Therefore all data was pooled and considered as male and females combined.

The period of data collection was for the majority of samples June to November. Burwell Lode zander lengths and weights were obtained in August and Coombe Abbey samples in May, June and December. Length weight relationships were compared on the basis that samples were not obtained during the pre-spawning gonad development period. Figure 67 of Section 2.7.2. shows that gonad size increases did not commence until after November. All zander would therefore have a length weight relationship independent of gonad development. (Gonad development is discussed in the following section).

Visceral fat contents were determined in the following manner. The viscera were removed. Gonads were removed for further investigation and the viscera was portioned with scissors into pieces of approximately 10 mm cubed, and placed into a weighed foil tray. The viscera consisted of the empty stomach, liver, spleen, intestine, gall bladder and attached fat deposits. The fat content of these organs was found to be negligible when compared with the visceral fat contents, being less than 0.001% of zander bodyweight as opposed to 0.05-6.0% of zander bodyweight. Therefore to enable rapid processing of material, (visceral fat did not have to be dissected from the other organs) fat analysis was conducted on the entire viscera, minus gonads. Once the wet viscera had been weighed with the foil tray, it was dried to a constant weight in an oven at 105 C. This was found to require a period of 48 hours and then the dried viscera was cooled in a dessicator before reweighing. The dried viscera was then extracted with petroleum ether using the Soxhlet method (Horowitz 1970). This gave the ether extractable fat content of the viscera. This was termed the "crude fat content of the zander viscera".

Three zander populations were examined in this manner and these consisted of pooled data from several months. These were:

Relief Channel	1979, 1980	(June-November)
Middle Level	1979	(September-December)
Coombe Abbey	1979, 1980	(May, June and December)

Fat weights of male and female zander were pooled to enable statistical comparisons between populations.

2.6.3. RESULTS

The length weight relationships for each population studied were compared with each other and tested for significant difference using Analysis of Covariance. All were found to be significantly different at the $p < 0.001$ level. Table 50 presents the equations of the length weight relationships obtained, ranked in ascending order of increasing slope, and therefore increasing "fatness". Table 51 presents the results of the significance tests.
Table 50 shows that Relief Channel 1975 had the poorest condition while Relief Channel 1976 zander were in the best condition.

If the coefficients of condition for Relief Channel zander are plotted against the year, as in Figure 65 it can be seen that changes in condition have followed a cycle, with high points in 1969 and 1976 respectively and low points in 1975 and 1979.

Visceral fat weights were expressed as a percentage of the zanders bodyweight. These were then plotted against zander weight and regression lines fitted by the method of least squares. (Figure 66). Table 52 presents the equations of the fitted lines, and their significance. Original data, Appendix V.

The percentage fat weight - zander weight regressions were tested for significant difference using Analysis of Covariance (Table 53).

Figure 65

Changes in the Coefficient of Condition of Relief Channel Zander 1969–1980.

Male and females combined June – November.

Figure 66.
Visceral Fat Content

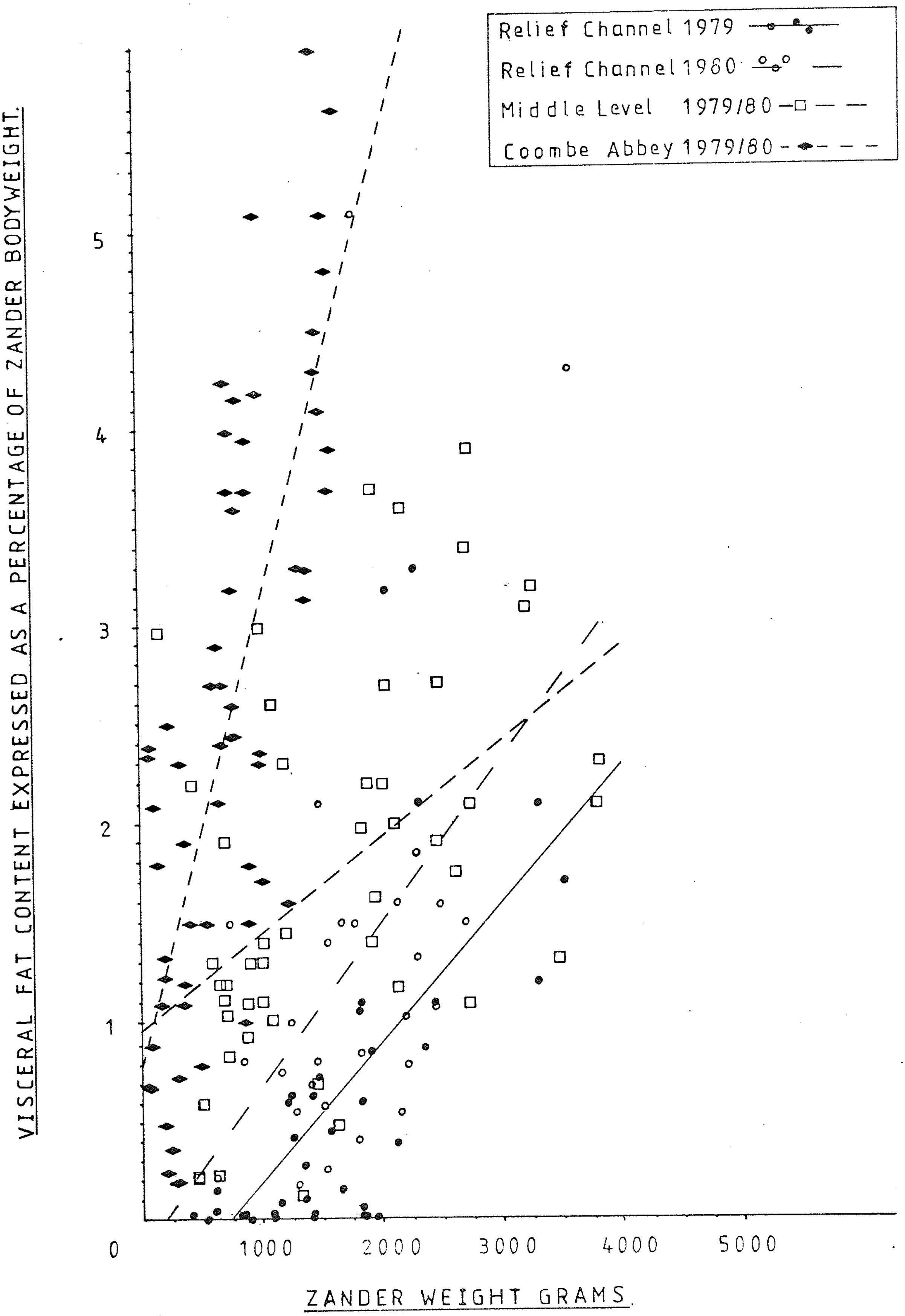


TABLE 50: Equations for Zander Length Weight Relationship

Location	Year	Log W = b	Log L + Log	r	No.	$S_E = \frac{1-r^2}{n}$
Relief Channel	1975	Log W = 2.68	Log L -3.75	0.98	60	0.005
River Delph	1978	Log W = 2.98	Log L -11.4	0.80	25	0.072
Burwell Lode	1979	Log W = 2.99	Log L -11.46	0.97	18	0.014
Relief Channel	1970	Log W = 3.04	Log L -4.5	0.99	55	0.003
Relief Channel	1980	Log W = 3.09	Log L -10.05	0.97	39	0.009
Relief Channel	1979	Log W = 3.1	Log L 3.1	0.99	176	0.001
Coombe Abbey	1979	Log W = 3.23	Log L 12.76	0.98	62	0.005
Middle Level	1979	Log W = 3.27	Log L -12.8	0.99	106	0.002
Middle Level	1980	Log W = 3.28	Log L -13.8	0.99	15	0.005
Relief Channel	1978	Log W = 3.3	Log L -5.6	0.98	227	0.003
Relief Channel	1969	Log W = 3.35	Log L -6.0	0.99	62	0.002
Relief Channel	1976	Log W = 3.6	Log L -5.2	0.99	21	0.004
				Total	866	

Weight in grams, Length in mms

All correlations significant at the $p < 0.001$ level.

TABLE 51: Results of Analysis of Covariance of All Length Weight Relationships

	S.S	D.F	V	
Amount of variation in weight unexplained by length, X, assuming no interaction	28.8	853		
Explained by interaction	24.31	11	2.21	$F_{11,842} = 442$
Error	4.49	842	0.005	

Significantly different at $p < 0.001$ level ($F_{11,842}$ at $p = 0.001$ between 2.74 - 3.02).

TABLE 52: Regression Equations and Correlation Coefficients for Visceral Fat, Zander Weight Relationship

Population		Equation	r	p	n
Relief Channel	1979	$y = -0.51 + 0.0007x$	0.59	< 0.05	38
Relief Channel	1980	$y = -0.163 + 0.0008x$	0.48	< 0.05	28
Middle Level	1979/80	$y = 0.95 + 0.0005x$	0.49	< 0.05	49
Coombe Abbey	1979/80	$y = 0.723 + 0.002x$	0.77	< 0.05	62

x zander weight

y visceral fat expressed as a percentage of zander bodyweight

TABLE 53: Results of Analysis of Covariance, Percentage Fat Weight - Zander Weight. All samples.

	S.S	D.F	V
Unexplained by X, assuming no interaction	170.72	172	
Explained by interaction	18.32	3	6.11
Error	152.4	169	0.9

$F_{3.169} = 6.8$

Significantly different at $p < 0.001$ level. ($F_{3.169}$ at $p = 0.001$ was between 5.42 - 5.79).

The statistical test showed that when all four samples were compared a significant difference existed between them. Further closer examination using the same test revealed that Coombe Abbey zander were the cause of this difference and that Relief Channel and Middle Level fat contents did not show sufficient differences to be considered as significantly greater or lesser than each other. Table 54 presents the results of the further tests.

TABLE 54: Results of Analysis of Covariance, Percentage Fat Weight - Zander Weight

Relief Channel 1979, 1980 and Middle Level 1979/80

	S.S	D.F	V	
Unexplained	78.08	111		
Explained	1.4	2	0.695	$F_{2.109} = 0.988$
Error	76.7	109	0.703	

Not significantly different at the p = 0.05 level.

($F_{2.109}$ 3.07 - 3.15 at p = 0.05)

Relief Channel 1979 and 1980

	S.S	D.F	V	
Unexplained	42.1	63		
Explained	0.075	1	0.075	$F_{1.62} = 0.11$
Error	41.99	62	0.677	

Not significant at the $p < 0.05$ level. (F_{162} at $p = 0.05 = 4.0$).

The visceral fat contents of the Fenland fish were therefore significantly lower than those noted in the Coombe Abbey samples.

There was some suggestion that Relief Channel 1979 zander had the lowest visceral fat contents, however as already mentioned this could not be described as a significant difference using the available tests.

2.6.4. DISCUSSION

In previous sections it has been suggested that there exists a considerable difference in nutrition and growth between some of the zander populations in this country. The existence of such differences should also allow demonstration by other methods apart from direct growth studies using scales etc. Length-weight relationships ought to be influenced by the zander's standard of nutrition and similarly the visceral fat content should provide an indication of a zander population's circumstances.

Length-weight data is most comprehensive for the zander of the Relief Channel. By plotting coefficients of condition against year, (Figure 65) it was possible to demonstrate that the condition of the Relief Channel zander showed quite marked changes over the period of study. Condition reached a peak in 1976. It is important to note that the number of zander sampled in 1976 was only 21. This may have caused, due perhaps to sampling of the "fattest" fish, an exaggerated estimation of condition. 1969 was also a year which saw zander in relatively "good condition". Both these years also correspond to periods of rapid growth in length as determined from scale reading. Condition reached its lowest level in 1975 and was also poor during 1979 and 1980. The latter two years were periods of very poor growth as already mentioned in the section on age and growth. In 1979 Anglian Water Authority survey work (Klee 1979a), revealed a very low density of prey fish. Though no quantitative data is available regarding prey fish densities in 1976, the authors own observations would suggest that suitable prey fish, particularly roach and silver bream of 100 mm were particularly numerous. The fact that the condition coefficient was the highest recorded would tend to confirm this.

Having established that Relief Channel zander have shown condition changes of an extreme nature, it is possible to utilise this range in order to make judgements regarding the condition of zander from other populations, (3.2 being the approximate central point or average on Figure 65). The River Delph and Burwell Lode zander both have coefficients of condition which correspond to the Relief Channel zander of 1970. Such a coefficient of condition will be described here as below average. Coombe Abbey, Middle Level 1979 and 1980, all have slightly above average coefficients of condition, corresponding to the Relief Channel in 1978. None of the existing zander populations appear to have as high levels of condition as have been noted in past years on the Relief Channel. In broad terms the data suggests that River Delph and Burwell Lode zander were poor in condition and perhaps suffering from a food shortage, while the Middle Level and Coombe Abbey zander were relatively fat and presumably well nourished.

According to Nikolskii (1969) "The state of vitality of a fish population may be judged from the character of the growth and the quantity and quality of the fat in the various organs". Having suggested that good condition equals fatness and therefore adequate feeding, the studies of visceral fat content provide useful evidence to substantiate this statement. The Coombe Abbey population was the most heavily endowed with fat deposits, while Middle Level and Relief Channel zander showed significantly smaller deposits. Figure 66 suggests that Relief Channel zander in 1979 had smaller fat deposits than Middle Level and Relief Channel 1980 zander, however the statistical test, though sensitive could not discern a significant difference. The inability to demonstrate significant differences may be due to the limited sizes of the samples. Length-weight data on the other hand generally employed much larger samples, this probably accounting for the demonstration of significance.

Visceral fat studies do enable, provided samples are large enough, a direct estimation of "fatness" and therefore state of nutrition. This approach avoids the restrictions of the length-weight study which depends to some extent on the fullness of the predators stomach. Unfortunately no comparative studies of zander fat content are available. The only study of length-weight relationship, that of Goubier (1975) employs a different method of measuring the zander (total rather than fork length), therefore without access to his original data, a transformation and subsequent comparison is not possible. (He obtained b values of 2.5 to 3.4).

Further consideration of the findings of this section will be made in conjunction with the previous sections in Part 4.

2.7. SEXUAL DEVELOPMENT AND REPRODUCTION

2.7.1. INTRODUCTION

The reproduction of the zander is well documented (Deedler and Willemsen 1964). This study sought to investigate those aspects of the zanders reproduction liable to modification due to the relatively new environment. Factors likely to influence reproduction, include climate, latitude and zander growth rate. These aspects were as follows:

(i) Seasonal changes in Gonad weight.

(ii) Time of spawning.

(iii) Sex ratio.

(iv) Age of maturity.

(v) Fecundity.

Most of these lines of study require fairly large samples of fish. Such large samples of fish were never available for prolonged periods; therefore, in order to obtain seasonal records of, for instance, gonad development, pooling of data from a wide variety of sources was required. It was appreciated that different populations of zander may have had differing rates of gonad development, presumably influenced by nutrition or local differences in water temperatures, however some information was required on this subject and a generalised study could perhaps be considered as better than no study at all.

2.7.2. METHODS

Zander sacrificed for other associated studies were used in addition for this study. These were obtained from a variety of waters, see Table 10, for zander autopsied. The following details were noted:

(a) Sex, the ratio of male to female.

(b) Gonads were examined for state of maturity.

(c) The weight of the gonads were obtained by weighing on a pan balance to an accuracy of 1g. The weight of gonad was expressed as a percentage of the zanders bodyweight.

(d) The Fecundity of the zander was estimated by means of egg counts. Ovaries were removed and weighed samples of eggs then counted. Samples were in triplicate and usually weighed 0.5 grams. The method followed closely that used by Kipling and Frost (1969) for the pike. The surrounding tissue was removed and weighed, from this the total weight of eggs could be calculated as follows:-

gonad wt - wt surrounding tissue = wt. eggs.

2.7.3. RESULTS

Zander weight and gonad weight as a percentage of bodyweight was thought to be negatively correlated, however insufficient data was available to enable this to be conclusively demonstrated.

(i) Seasonal changes in gonad weight.

Gonad weights expressed as a percentage of zander weight were plotted against the month sampled. Lines were drawn through means. Figures 67 and 68 show the seasonal cycle of gonad development for male and female zander respectively. It can be seen that female ovary weight (expressed as % of zander bodyweight) starts to increase after the end of the summer, increasing slowly

Figure 67.

Seasonal Changes in Zander Ovary Weight.

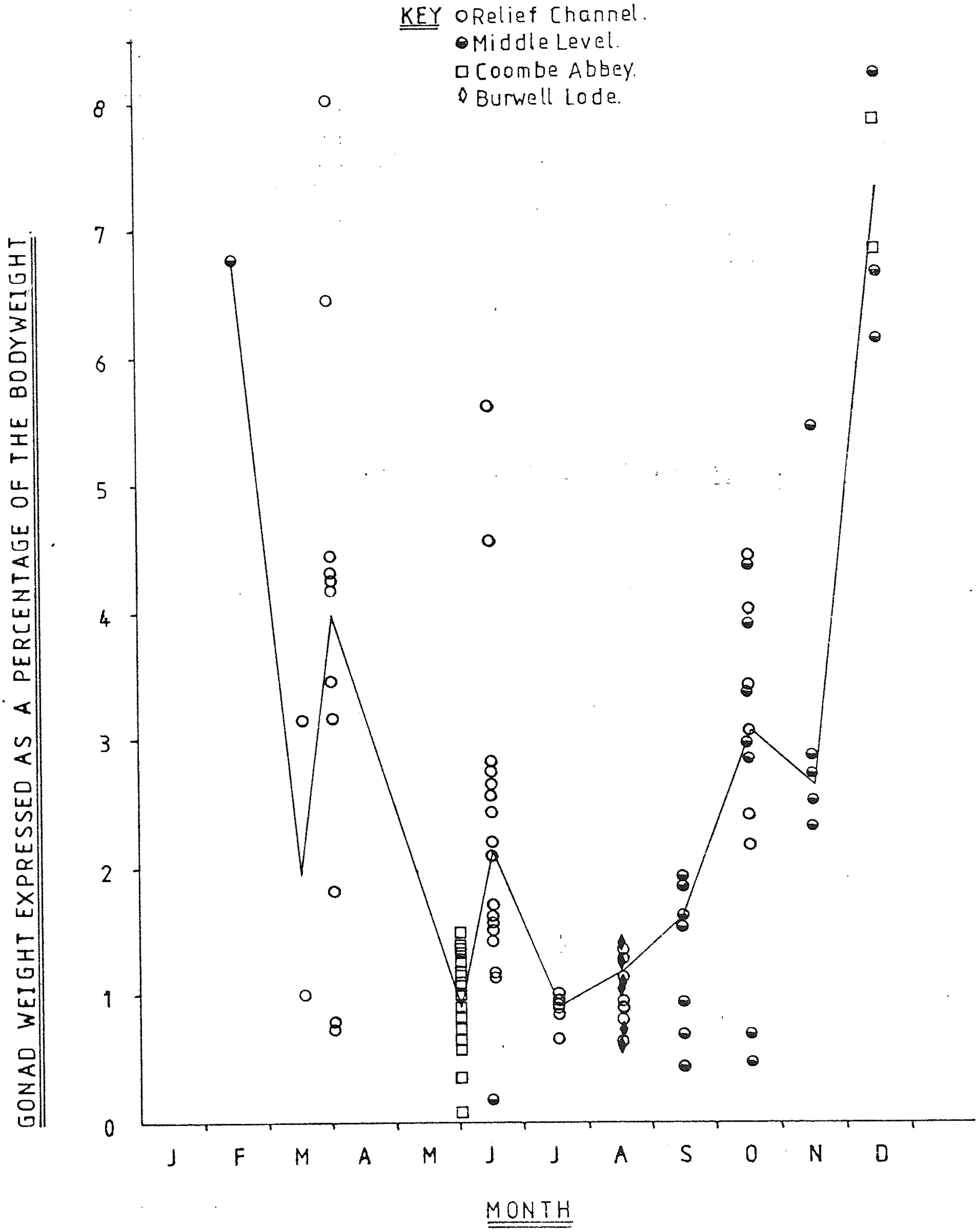
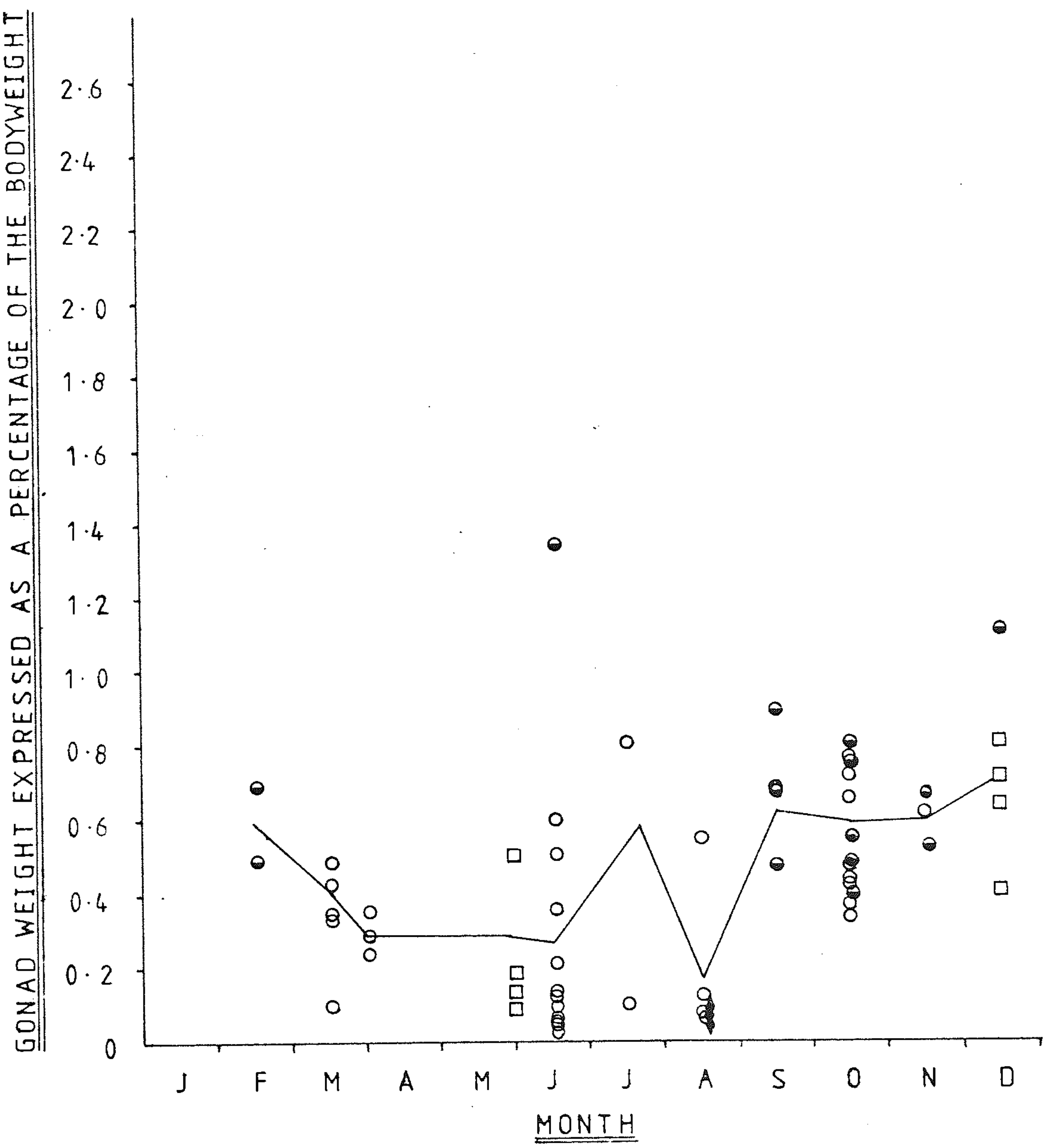


Figure 68.

Seasonal Changes in Zander Testes Weight

KEY As for females



until November when ovary weight increases rapidly to reach a peak in December. Thereafter the data is scanty and the most noticeable change in weight occurs at sometime during May or late April when presumably spawning takes place. Ovaries were noted as comprising as much as 8% of zander weight in December. Males showed less distinct changes in testes weight, but a general increase in testes weight towards December was noticeable. Testes weights ranged up to 1.4% of zander bodyweight.

During June and July of 1980, a number of female zander were obtained from the Relief Channel. Of the 15 examined, 4 had ovaries which were obviously unspent. Though showing some reabsorption, the ovaries still contained large numbers of eggs and were clearly different from ovaries of zander which had spawned. This high percentage of non spawners (27.7%) was not noted at any other time or in any other zander population.

(ii) Time of spawning.

Unfortunately samples of zander ovaries and testes were not available throughout the close season for angling (March to June). It was therefore impossible to determine precisely when spawning occurred. It can however be suggested that, as zander had not spawned by the 14th of April and this has occurred by May 31st, that spawning occurs in late April or May. During this period water temperatures ranged from 8 to 19°C.

(iii) Sex Ratio.

The overall sex ratio of zander from all the populations studied was 1.2 females to 1 male. This was similar to that noted by continental workers Alm (1959) and Filuk (1962), who noted an even proportion of males and females.

(iv) Age of maturity.

Male zander were noted as being sexually mature at 2 years of age (smallest fish 277 mm from Coombe Abbey). Female zander were noted as being mature at 2 plus years of age, spawning presumably on their third birthday. (The smallest sexually mature zander came from the Cut Off Channel, 340 mm). Of the 306 fish available for the study of maturity only one female failed to reach maturity by its third year, this being a 398 mm specimen from Coombe Abbey. All males were sexually mature by their 2nd year.

(v) Fecundity.

Relatively few zander were available for fecundity studies (i.e. few contained eggs). Table 55 presents the estimates of egg number.

TABLE 55: Number of Eggs Noted, Zander Ovaries

Source	Zander Weight g	Zander Length mm	Number of Eggs	95% CL
Oxford Canal	1236	475	192,856	191,851 - 193,861
"	1085	456	302,500	299,850 - 305,150
"	1392	481	275,808	269,586 - 282,030
"	1114	455	222,347	221,287 - 223,407
Middle Level	625	415	32,456	27,155 - 37,757
"	935	455	62,529	58,527 - 66,531
"	929	450	61,933	53,624 - 70,242
"	956	452	82,551	80,101 - 85,001
"	1010	463	110,379	107,713 - 113,045
Relief Channel	1985	590	235,334	133,333 - 337,335

The data from Table 55 was tested for correlation, length with egg number and weight with egg number. The length with egg number relationship was not significant at the $P > 0.05$ level of significance ($r = 0.48$, df 8), while the zander bodyweight with egg number relationship was significant, at the $P < 0.05$ level ($r = 0.66$, df 8) (Figure 69).

2.7.4. DISCUSSION

Seasonal studies of gonad development are not available for zander from England and are not available as English translations in foreign literature. Le Cren's (1951) study of the perch of Lake Windermere is therefore considered alongside the present study since the zander and perch are related and are both spring spawners. The changes in ovary weight noted during this study, followed closely that of the perch, with an increase in weight after October, followed by a rapid increase after December. Ovary weight falls rapidly between April and May during spawning. Testes weight again follows the pattern typified by the male perch, that is, a period of weight increase after August, with a sustained peak weight from October to March, followed by a steady decrease in weight before and during the spawning period. Though the data presented was based on limited observations, the similarity with the related perch suggests that the basic nature of the gonad development cycle has been demonstrated.

The 27.7% incidence of non-spawning noted amongst female zander from the Relief Channel in 1980 could be explained perhaps, by a low level of nutrition leading to spawning being postponed in favour of inhanced survival of the adult fish. However, this is far from proven and other variables, such as the lack of suitable spawning areas, mates, or unfavourable temperatures may have been responsible.

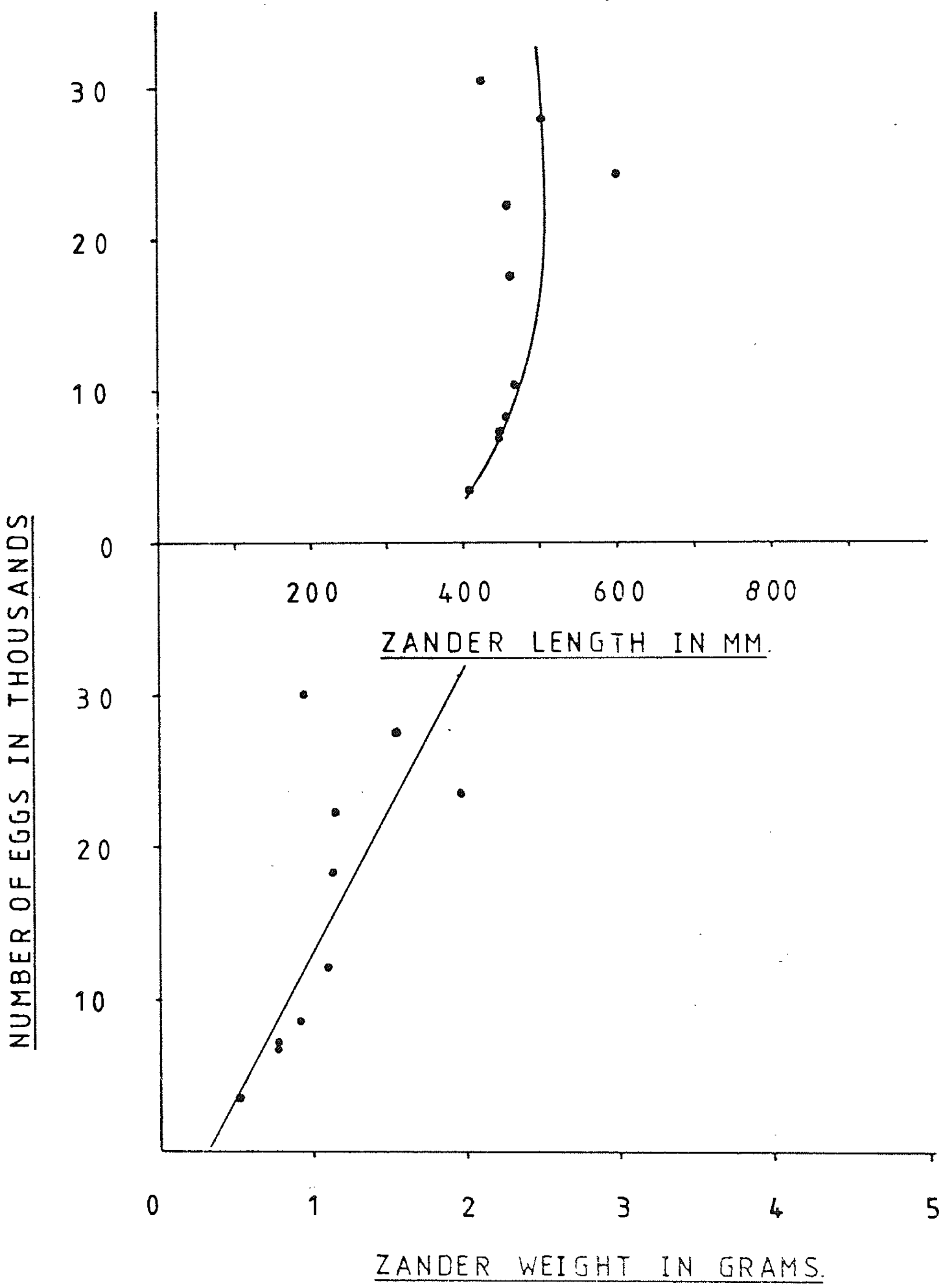
Variations in sex ratio were apparent in different samples, however it was felt that this was due to the small size of the samples. Pooling resulted in a sex ratio which showed the females as being slightly more numerous than the males. This may be due to a higher level of mortality in males.

Zander mature in English waters at the age of 2 years in the case of males, and 3 years in the case of females. Deferred maturity in slow growing individuals as noted by Wiktor (1954, 1962) and Romanycheva (1962), was not noted in this study.

Fecundity was correlated with zander weight and a straight line (Figure 6 relationship was noted. This corresponds with Havinga's (1945) observations of zander and that of Johnson (1971b) and Wolfert (1969) who observed a straight line relationship for the walleye. Zander length and fecundity produced a curvilinear relationship similar to that obtained for the walleye by Wolfert (1969), implying that fecundity increases disproportionately as the zander increases in length. Leonte and Ruga (1955) failed to show a relationship between length and fecundity.

Figure 69

Relationship Between Zander Weight Length and Fecundity.



The projected fecundity of a 1 kg zander as derived from the weight fecundity regression was 135,181 (130,483 - 162,284 at the 95% confidence limit). This is a lower fecundity than that quoted by Deedler and Willemsen (1964). They indicated 200,000 per kg. The zander fecundity noted here was however higher than that quoted for the pike, 26,400 - 31,900 per kg, Kipling and Frost (1969) and also higher than that of the related walleye, 29,700 per kg, Smith (1941), or 82,700 per kg quoted by Wolfert (1969). This suggests that the zander has a greater reproductive capability than certain predators, though this of course does not necessarily imply that the zander would be more successful in establishing itself or maintaining its numbers than other predators.

PART 3

LABORATORY STUDIES

3.1.1. INTRODUCTION

The study of the zander in the laboratory enabled the elucidation of certain facets of the zander's physiology, ecology and behaviour. Wherever possible, laboratory studies have been designed to complement field studies. This enabled comparison of observations based on field and laboratory studies. Laboratory studies investigated the following three subjects:

- 3.2 The feeding behaviour of zander
- 3.3 The rate of digestion of prey fish
- 3.4 The conversion rate and maintenance requirement of zander.

As all studies employed the same facilities and method of handling of specimens these are described under Materials and Methods. The three individual studies are then dealt with separately, with the methodology described for each study.

3.1.2. MATERIALS AND METHODS

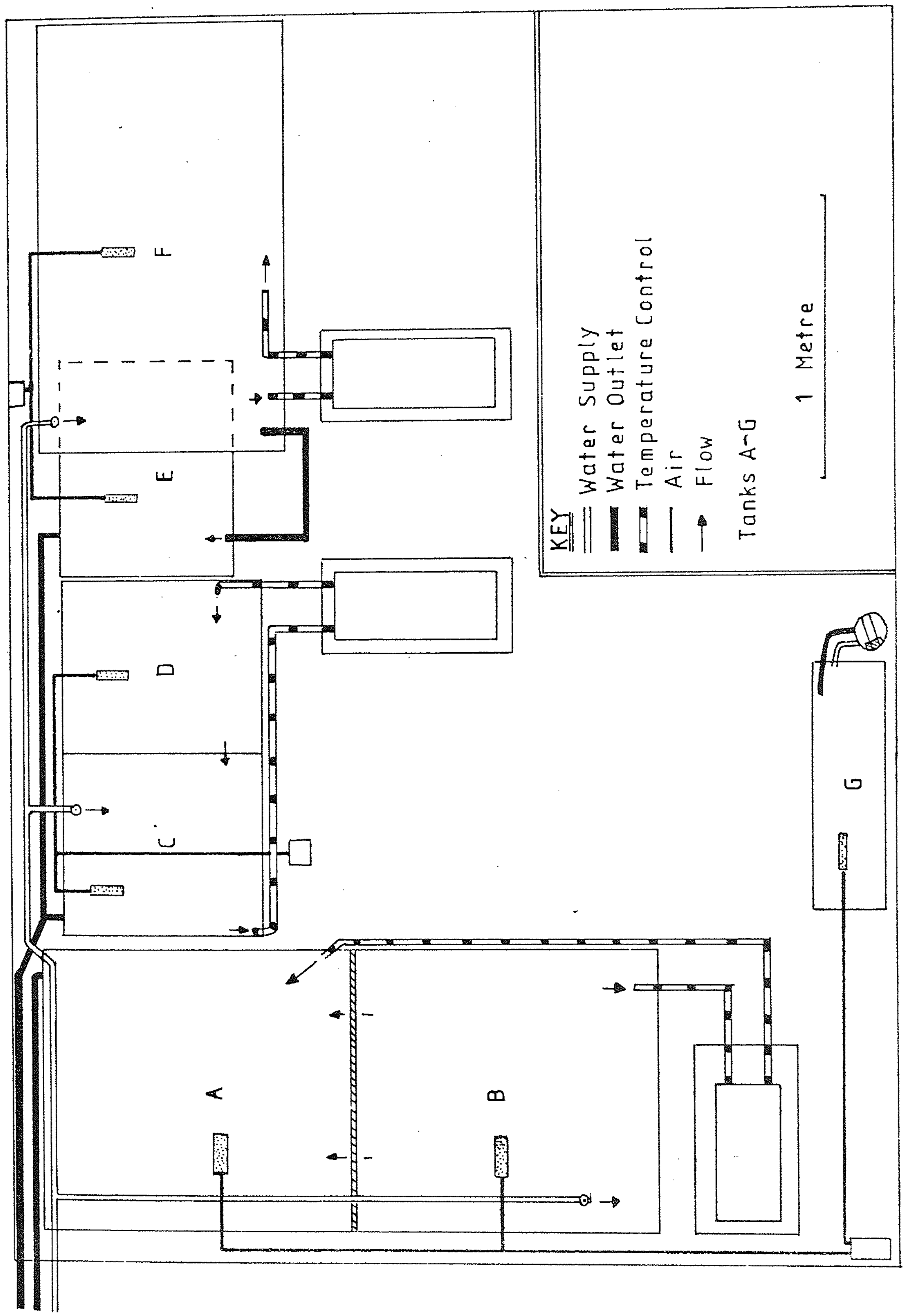
Zander were obtained from a variety of sources (Table 10) and ranged in size from 97 mm (7.27g) to 487 mm (1360g). A total of 84 zander were used for experimental work during the period November 1978 to January 1981. Before the zander obtained from the field could be transferred to the experimental tanks a period of quarantine was required to reduce the chance of infection being brought into the laboratory. Quarantine facilities consisted of previously sterilised and flushed glass fibre tanks with covers and a through flow of approximately 2 litres per minute. The zander were held for a period of three weeks and treated on two separate occasions with each of malachite green (3 ppm) and formalin (100 ppm), before transfer.

Figure 70 shows the laboratory arrangement of tanks. These were glass fibre tanks or glass aquaria. All large tanks had a throughflow of mains water at approximately 1 litre per minute. Aeration was supplied to each tank via airlines supplied by diaphragm type pumps. Temperature control was by means of Grant Flow Coolers linked to a Grant heating unit. The flow produced by the unit was sufficient to enable thorough mixing of the water in each tank. All tanks were positioned away from direct natural illumination, but with overhead lighting which when in use enabled observation and manipulation of the specimens.

While the zander were held in quarantine, feeding usually ceased. In order to stimulate feeding once in the laboratory, the zander were force fed small roach on two occasions. Feeding usually recommenced shortly afterwards. Natural feeding was carried out in the following manner in order to condition the zander to feeding when required. Live food fish were introduced and left in the tank for no longer than 30 minutes. The remaining food fish were then removed. After this procedure had been followed for several feeding periods (usually once per day) the zander became conditioned to feed when prey were presented to them. Zander in captivity would eat only live prey fish. Dead prey fish were not eaten. It is thought that high levels of stimuli (presumably movement) are required to elicit a feeding response from captive zander. The capture of zander by angling is primarily and

Figure 70.

Facilities for Laboratory Studies.



successfully accomplished by means of the use of dead fish, which suggests that the zander's laboratory preference for live fish is not typical of the zander in the wild.

While in some experiments temperature regimes were varied out of phase with seasonal changes, the photoperiod experienced was natural.

Prior to the commencement of experiments, each zander was identi-field by means of natural variation in scalation or fin formation. Where no characteristic features were present, individual fish were fin clipped in a specific manner, the posterior dorsal fin and the caudal fin being chosen for clipping. Up to 24 zander were held for experiments at any one time. A period of acclimatization followed transfer to the experimental tanks. This period lasted 4 weeks and was sufficient to enable conditioning. During this period temperatures were adjusted to those required for experiments. Changes of one degree C were made each day until the required temperature was reached. Temperatures of 5, 10, 15 and 20 degrees C were used for the various experiments. Temperature fluctuations were slight, plus or minus one degree. Higher temperatures were not used, because of the lack of relevance to English water temperatures. During the 4 week acclimatization period feeding was carried out at approximately 2-3% of the zander's bodyweight.

All manipulations carried out with the experimental animals were with anaesthetised fish using a 50 ppm solution of Benzocaine

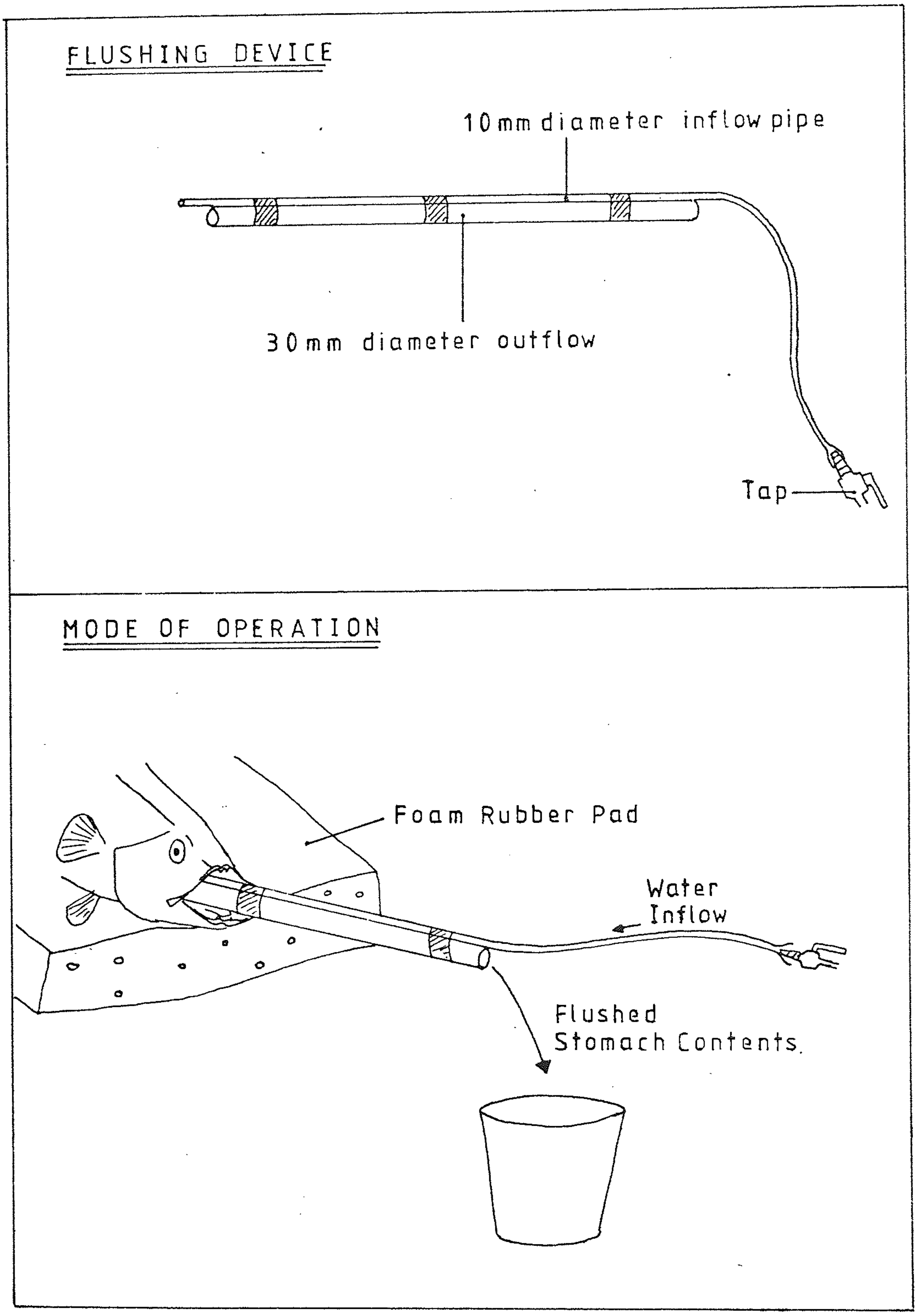
(Ethyl P-Aminobenzoate, Laird and Oswald 1975). Zander were not held in the solution for longer than 5 minutes and in all cases recovery was rapid. Generally the larger the zander the longer the period of contact with the anaesthetic required. All prey fish were similarly treated to enable weighing and measuring.

Zander were weighed using a top loading balance after all excess moisture had been removed using a hand towel. Weights were recorded to an accuracy of 1g for all fish heavier than 250g and an accuracy of 0.1g for smaller fish. Lengths were determined using a measuring board to record the fork length to the nearest mm.

Force feeding required the anaesthetisation of the zander. Small dead fish, usually of 50 to 100 mm were placed headfirst into the zander's mouth. Using blunt forceps the prey was pushed down inside the zander's throat. Finally the prey was pushed out of sight using a 300 mm plastic tube of 5 mm diameter. Occasionally rejection of the prey fish occurred; in this case the zander was fed again in the same manner. Force feeding was only used for pre-experimental feeding. All experimental feeding was natural and initiated by the zander. Swenson, Lloyd and Smith (1973) found that force fed walleye digested their prey more slowly than naturally fed specimens. The mixing of feeding methods was therefore avoided.

Prey fish were removed from the zander using a simple device for stomach flushing (Figure 71). It consisted of a 30 mm diameter plastic tube of 600 mm to which was attached a 5 mm diameter rubber pipe. When inserted into the zander's stomach, a stream of water

Figure 71
Stomach Flushing.



via the pipe flushed the stomach contents out via the larger tube. This device was effective and used on zander of greater than 350 mm using prey items of less than 130 mm. (undigested).

Behavioural studies were conducted in two sizes of glass aquaria. The larger measured 2 x 0.6 x 0.6 metres while the smaller was 1 metre by 0.3 metres wide and deep.

3.2. THE FEEDING BEHAVIOUR OF THE ZANDER

3.2.1. INTRODUCTION

Field studies of the zander's feeding habits suggested that zander usually preyed on comparatively small prey fish, swallowing them tail first. This is confirmed by the observations of Berg (1965), Goubier (1975), Popova and Sytina (1977) and Willemsen (1977).

These observations have led to the suggestion that zander are primarily adapted to the pursuit and capture of prey fish from the posterior. It is suggested that this behaviour is responsible for zander preying on prey fish smaller than the maximum size ingestible, the hypothesis being that small prey fish are swallowed tail first with greater ease than larger prey fish. This, it is suggested, results in a preference for comparatively small prey fish (less than 60% of the maximum prey size ingestible, as defined in section 2.3. Various workers including Popova and Sytina (1977) and Willemsen 1977 have suggested that zander prefer "small" prey fish.

Beyerle and Williams (1968) used two terms to describe the feeding behaviour of predatory fish. Selectivity was defined as: "the extent to which a predator eats one size or species of food item rather than another". Preference was described as "The inherited, instinctive desire to consume one size or species of prey rather than another".

The differences between the two terms, though seemingly small, are in reality considerable. The effect of predation by a species which selects for availability, must be different to that of a predator which shows a preferred food size. This study sought to classify the zander's feeding behaviour accordingly. Is the zander, like the pike, a selective feeder, its diet corresponding closely to relative abundance or availability of prey, (Allen (1939), Johnson (1959)? Or, does the zander prefer and actively seek to obtain certain sizes of prey fish?

In the wild, variations in prey availability may disguise certain patterns of feeding behaviour. Lewis et al (1961) notes that any selection for a particular type of food may in itself alter selection trends, by removing the more desirable food items first. Therefore, there is a possibility that stomach contents obtained from fish in the wild may show selection for food items which are less desirable. Since having removed the desired food, the predator switches to the next choice. A laboratory study under controlled conditions is more likely to provide an accurate assessment of a predators feeding. Many workers have carried out laboratory studies, notably on the large-mouth bass, (Micropterus salmoides Lacepede), Lawrence (1957), Lewis (1961), Espinosa and Deacon (1973) and the pike, Beyerle and Williams (1968) and Mauck and Coble (1973).

In a natural environment it is difficult to determine the extent to which a number of variables are involved in any particular manifestation of selectivity or preference by a predatory fish. However, by confining predator and prey to tanks it is theoretically possible to control to a large extent variables caused by factors other than preference. Therefore any selection of specific prey types or sizes should be the result of preference.

3.2.2. METHODS

Zander were held in large tanks as used for the other laboratory studies. The tanks were of a sufficient size to allow pursuit of food over short distances (500 mm). Cover for zander or prey was minimised, consisting only of airlines and temperature control in and outflows. Temperatures were maintained at a constant 15 C. A large aquarium offering a similar environment to the large tanks was used for studies which required the observation of the zander. Behavioural observations made using the aquarium were with the observer seated 2 metres from the tank in diffuse daylight. Artificial illumination was not used for behavioural observations. Three experiments were conducted and the methods for each experiment are described below.

Experiment A. Observation and Typing of Zander behaviour.

Zander were observed regularly during the 1½ year period and all non-feeding behaviour was noted. During a total of 673 feeding occasions, observations were made and the results noted. Zander size varied from individuals of 60 mm to individuals of 450 mm.

Experiment B. Influence of Prey Size on Method of Swallowing.

Roach of varying lengths from 11 to 35% of the zanders bodylength were presented to zander of between 380 and 450 mm. Experiments were carried out during three periods of each day, mid morning, midday and mid afternoon. If food was not eaten within the 30 minute observation period it was removed and represented at the next feeding time. In this manner the zander were conditioned to feed each time observation was in progress. The direction of swallowing of each prey fish was observed. Swallowing was in some cases very fast, however the direction of swallowing was never in doubt. A wide range of sizes were presented. Fish greater than 35% of the zanders bodylength were presented on thirteen occasions but were not eaten. It was therefore concluded that meaningful observations concerning the direction of swallowing of prey fish would not be obtained using large prey fish. (It should be noted that this did not apply to zander of less than 150 mm).

Experiment C. Prey Size Preference of Zander.

Four groups of zander were used for this experiment. The fish used were of similar lengths (see Table 56). Grouping of fish was based mainly on those fish which would coexist with each other. Aggressive individuals were retained alone. Two species of prey fish were used for these experiments, roach and rainbow trout (Salmo gairdneri, Richardson 1836). Experiments were carried out using either species, but never in combination. Before introduction of the prey fish the zander were disturbed using a hand net. This effectively stopped an immediate feeding reaction. (Lewis et al (1961) working on largemouth bass found that many food items were taken on hitting the surface of the water). Prey fish were therefore given time to adjust to the new environment and were presumably equally susceptible to predation. Two sizes of prey fish were presented on each occasion. Each fish was weighed and measured and equal numbers of two difrerent sizes presented. The mean prey lengths presented were at all times significantly different (using a t test) at the $P < 0.001$ level. Feeding time was 2 to 4 hours before darkness. Feeding was most intense during this period and during darkness.

TABLE 56: Zander Size Groups used for Prey Size Preference Experiment

Fish Code	Fork Length	Weight		Group Code
A	445-448	918-937		1
B	418	716		
C	423	749	± 19g	2
D	385	582		
E	419	755	± 70g	3
F	448	1014		
G	442-445	772-829		4

Length and weight changes due to growth or weekly fluctuations due to ration size.

In order to eliminate the possibility of the zander consuming all of the preferred prey sizes and then consuming the other prey sizes, each size of prey fish was presented in excess of the zanders daily ration of 5% of the zander's bodyweight (Popova and Sytina 1977). Prey fish of each size were presented in numbers which amounted to 6-8% of the bodyweight of the zander in each group.

The presentation of 5 fish of each size generally met the above criteria, though when small prey fish were used larger numbers up to 10 of each were required to exceed the zanders daily ration. The following morning the remaining prey fish were removed, weighed and measured, and the fish eaten noted. The experiment was continued the following day. A total of 30 prey fish eaten was aimed for, before termination of each experiment. In some cases a shortage of suitable prey fish resulted in slightly lower numbers of prey fish being used.

Whenever prey fish were presented to zander, every effort was made to avoid mixing fish which had been used before and naive fish. Avoidance behaviour was noticeable in fish which had previous experience of zander predation from early experiments. Conditioned prey fish were therefore presented with other conditioned prey fish and naive fish were similarly segregated. This prevented differential prey fish avoidance from influencing the experimental results.

Ivlev (1961) suggests using selectivity indices to demonstrate degrees of selection of prey fish. Windell and Bowen (1978), however, suggest that the application of indices of a varied nature as suggested by many workers, can be replaced by one or two statistical tests, thereby increasing uniformity and compatibility of data. They suggest either the X^2 or G test (Sokal and Rholf 1967). For this work the X^2 test was used to validate the selection experiments (2 X 2 contingency table). All results for each size range experiment were continuously pooled until the target number of prey fish was reached.

Zander of 100-150 mm were fed on roach of two sizes, corresponding to 13.3-40% of the body length. Experiments were continuous, with equal numbers of prey fish in excess of the daily ration maintained for 4 weeks. The number of each prey size eaten each day was noted. Prey size ranges were between 20 and 40 mm, with means of 21.2 mm and 38 mm for each size group. Size groups were significantly different using a t test at the $P < 0.001$ level. (53 and 10 fish in each size range respectively).

3.2.3. RESULTS

Experiment A. Observation and Typing of Zander Behaviour

The component parts of zander behaviour were categorised in order to provide reference points for other studies. The following items of behaviour were noted and coded accordingly. The terminology was an adaptation of that used by Holmes (1979).

Non Feeding Activity

YAWNING (YN) Body arches, first dorsal fin erect, all other fins spread out from the body. Mouth wide and gill covers flared. Lasting 3-5 seconds.

BELLYSWIMMING (BG) Swimming along the bottom of the tank in short bursts with rapid tail beats.

DOMINANCE (DE) Usually one zander deters another conspecific which is approaching food or simply encroaching into the dominant zander's water space (distance less than 50 mm). Dominance is demonstrated by "mock stabbing". This consists of a stab made by the dominant's jaws, usually close to the intruding zander's head. Sometimes the head of the dominant jerks in a horizontal plane on the approach of the intruder. The intruder retreats quickly. The dominant zander does not completely raise its first dorsal fin, a partial erection being the usual response. The intruders dorsal fin remains folded.

RELATIVE POSITIONING (CONSISTANCY OF) (RP) During the experimental period which lasted for 1½ years, each zander usually adopted a favoured position in the tank. When several zander were retained together, positions were often maintained in relation to the other zander. Out of 156 daily observations made on zander in aquaria, made during the day (10.00 to 14.00) prior to experiments, on 141 occasions zander were noted in their usual positions. This amounted to 90.4% of all observations. At other times the zander were either swimming actively or at rest in different positions.

FREE SWIMMING (FG) Rarely noted during the day, but noted regularly at night, particularly with zander of 100-150 mm which had proportionately more living space than larger zander. The zander swim against the glass with dorsal fin erect. Of 63 observations during the hours of darkness, free swimming was noted 52 times for zander of 100-150 mm and of 47 observations of zander of 350-450 mm free swimming was noted 31 times.

RESTING (RG) Zander resting on tank floor. Dorsal fin folded, little movement. Of 121 daylight observations (9.00-16.00 hrs) resting was noted 111 times for zander of 100-150 mm and of 143 observations of zander of 350-450 mm, resting was noted 135 times. All observations prior to feeding.

AGGRESSION (AN) Certain zander, particularly those held in captivity for longer than 6 months, became aggressive towards fellow zander. Aggression was exhibited as a strong physical attack on the other zander. This consisted of tail biting and stabs to the head. Such attacks were likely to be serious if allowed to continue. A life size model of a zander was made and attached to a glass rod. This was presented to an aggressive zander (A) and was repeatedly attacked. Attacks were made to mainly the head end of the model. Removal of the models eyes and tail resulted in attacks to either end. Aggression appeared then to be based on recognition of the head of the model due to the presence of eyes. Moving the eyes to the tail brought an increased response to the tail of the model.

After several presentations of the model, teeth marks across the dorsal surface of the model were visible. Such aggression was not of a predatory nature as both zander and model zander were either of a similar size to or larger than the aggressive zander. Aggression was not species specific for when a large rainbow trout, 400 mm long was placed in the tank with the aggressive zander attacks occurred. Similarly prey fish of various sizes were, on occasions, attacked without being ingested.

The aggressive tendency was not reduced by removal of the aggressive zander to another tank. Aggression continued regardless of the aggressive zander being in its own tank or not. Aggressive zander were by necessity retained in tanks of their own.

Feeding Behaviour

COLOUR CHANGE (CE) A visible change in colouration (a lightening) was noted pre and post feeding.

FIXATION (FN) Dorsal fin raised, eyes show movement to focus on prey.

APPROACH (AH) Dorsal fin lowered, tail propelling.

ATTACK (AK) Dorsal fin lowered, body sometimes moved from vertical towards 45 degree angle.

TAKE (TE) Dorsal fin raised, prey seized.

SWALLOW (SW) Rate of swallowing dependent on method of take. In all cases dorsal fin raised. Prey fish swallowed in direction taken.

(i) Taken across vent or by tail, swallowed tail first. Handling time increases with size of prey. Swallowing immediate with prey less than 15% of the zander's body-length. Handling time appears less for narrow prey compared with deep prey (not quantified).

(ii) Taken across back or under head, swallowed head first. Time taken to swallow increases with size of prey and position of take. Large prey items taken almost halfway along the prey's body take the longest to swallow.

(iii) Taken tail first, but eventually rejected. Prey were usually greater than 30% of the zanders body length.

Manoeuvering of prey was limited to partial release and subsequent suction of prey due presumably to reduction of water pressure in the buccal cavity. Table 57 presents handling times for prey fish of various sizes and direction of swallowing.

TABLE 57: Mean Handling Times for Roach of Varying % Bodyweight

Prey size	Head first	SE	n	Tail First	SE	n
% of BL	Mean handling time in seconds					
15	0	-	12	0		36
15-25	12.5	1.2	6	14.9	4.2	15
25	162	6.3	4	391	25.1	3

No significant difference in handling time was noted using a t test at the $p > 0.05$ level for prey swallowed head or tail first, up to a percentage length of 15%. Above 15% of the body length there was a significant difference at the $p < 0.05$ level.

Experiment B. Influence of Prey Size on Direction of Swallowing.

Table 58 presents the mean lengths of prey fish (roach) expressed as % of zander body length swallowed by zander for each direction. Differences between the means were tested for significance using a t test and there was a significant difference at the 0.05 level. It was therefore suggested that prey swallowed head first were larger than prey swallowed tail first.

TABLE 58: Mean Percentage Lengths of Prey Swallowed Head and Tail First

	Head First	Tail First
Mean % of bodylength	31.65	28.04
Standard deviation	4.7	5.7
Number	23	26

$t = 3.27$ at 47 dF $p < 0.05$

Tail first swallows comprised 77% of the prey ingestions of zander of 350-450 mm feeding on prey of 4-28% of zander body length. Head first swallows comprised the other 23% of swallows.

During experimental observation it was noted that zander sometimes made a specific approach towards the head end of larger prey fish (greater than 25% of the zanders bodylength). The success rate of head first attacks was higher for prey fish greater than 25% of the bodylength than for tail first attacks. (95% and 86% respectively). The mean overall success rate for zander of 89.5% is somewhat lower than that noted by Hart (1981 pers comms), working on pike. He noted a success rate of 99.5%, for pike feeding on minnows. (Phoxinus phoxinus L). However the size of prey in relation to the pike was not specified.

Experiment C. Prey Size Preference of Zander.

The results of this experiment are presented in Tables 59 and 60. There the mean prey length of the large and small prey fish are recorded along with the number of each eaten. The significance or otherwise of the zander's predation is established by means of a X^2 test, using a 2 x 2 contingency table to compare size distribution of prey eaten for each group.

TABLE 59: Result of Preference Experiment. Zander Presented with Two Sizes of Roach

Mean Length mm Small	Mean Length mm Large	Percentage Difference	Number Small	Number Large	Eaten Small	Eaten Large	X^2	P
65	94	44.6	27	27	24	3	32.7	< 0.001
SE 0.6	0.56							
94	104	10.6	34	34	24	8	15.1	< 0.001
SE 0.5	0.45							
106	125	16.1	40	40	22	4	18.5	< 0.001
SE 0.6	0.7							
106.5	116	8.9	30	30	12	12	-	-
SE 0.2	0.3							
114.1	127.6	11.8	42	42	15	10	29.9	< 0.001
SE 0.7	0.7							

TABLE 60: Result of Preference Experiment. Zander Presented with Two Sizes of Rainbow Trout

85	103.3	21.5	55	55	18	9	3.97	< 0.05
SE 0.3	0.3							
92.6	103.3	11.5	56	56	17	16	0.04	> 0.5
SE 0.2	0.3							

By ranking the percentage difference in prey lengths in descending order it was apparent that zander ceased to show significant preference for the smaller prey fish sizes at between 8.9 and 10.6% difference in body length for roach and between 11.5 and 21.5% for rainbow trout (Table 63).

TABLE 61: Percentage Difference in Prey Lengths Offered to Zander and Significance

Percentage Difference in Length of Prey Fish	Significant/Not Significant
ROACH	
44.6%	Significant
16.1%	"
11.8%	"
10.6%	"
8.9%	Not significant
RAINBOW TROUT	
21.5%	Significant
11.5%	Not significant

Zander appeared to be able to discern the difference between two sizes of prey fish and consistently chose the smaller prey fish, except when the difference in prey fish sizes was slight. The point at which zander showed preference for the smaller prey fish was at a lower percentage length difference for rainbow trout than roach. This suggests that some other effect was the cause of the different threshold of preference.

It would have been useful if the point at which preference is noticeable had been more closely defined, particularly for rainbow trout. Fortunately the ranges given show no overlap, therefore it is obvious that the zander were showing preference for the smaller prey at different percentage length differences for roach and rainbow trout.

The result of the experiments using the smaller zander were very clear cut. None of the larger prey fish were eaten. There were no signs of the larger prey having been attacked. The smaller prey fish were eaten throughout the four week period and 53 were consumed. The preference threshold for the small zander was evident for roach with a difference of 79.2% in bodylength. Unfortunately the size ranges of roach were limited and further studies could not be attempted. However this does show clearly that when the difference in prey length is very great, the smaller prey fish are preferred to the exclusion of the larger prey, even though both prey sizes are theoretically liable to zander predation.

3.2.4. DISCUSSION

Laboratory observations of predatory fish are dependent for their accuracy on the suitability of the environment. The ideal laboratory environment probably approaches the natural habitat in size. Obviously the constraints placed on research require more modest surroundings for the experimental animals. The important question when considering the results of a series of experiments, is whether or not the zander's natural behaviour is retained in captivity? The zander used for this work showed limited growth and appeared with the required amount of attention to feed regularly. Swenson et al (1973) notes that fish which show growth are probably not highly stressed. The increase in zander activity as illumination levels decreased and the preferred method of swallowing prey fish tail first, confirmed observations made in the field and suggested that these behaviours were not modified unduly by being in captivity.

If any credence is to be given to the experimental results, it must be assumed that the zanders natural behaviour patterns are maintained in the laboratory. Unfortunately one major difference in feeding behaviour was noted. Zander are regularly captured in the wild using dead fish, fished in a static manner (Rickards and Fickling 1979). Laboratory zander steadfastly refused to take dead prey fish, resting on the tank bottom. It seems that the artificial environment produces a higher threshold of stimuli. A food item must provide a high level of stimuli to evoke a predatory response. Movement and the escape response appeared important in producing a zander feeding response.

Modification of the zander's feeding habits by conditioning showed that the zander was quite adaptable and certainly able to capture prey in the confines of the tanks, even in high levels of illumination. However if allowed to lapse back into a more natural feeding regime, feeding was carried out during darkness. Such crepuscular feeding is said to be typical of the generalised carnivore (Huntsman 1979), daylight feeding being more difficult and requiring further adaptations in predator behaviour.

The various types of behaviour displayed by the zander could in some cases be explained and related to observations derived from the field studies. Yawning has been noted in a number of fish species. Morris (1954) suggested that yawning in bullheads

(*Cottus gobio* L) occurred when the fish were unoccupied. He also noted that yawning was more frequent amongst fish with strong jaws. Rasa (1971) working on the jewel fish (*Microspathodon chrysurus*) states that yawning in this species was initiated by high levels of excitement and low levels of kinetic activity. Tugendhat (1960) in her study of the feeding behaviour of the three spined stickleback (*Gasterosteus aculeatus* L) found that yawning was associated with "excess initiative to feeding and with a slow build up of feeding motivation". It was found to occur at moments of balance between feeding and interrupted feeding and also when balance was maintained for some time.

Yawning activity of zander was noted before and after feeding, therefore it is difficult to offer a similar explanation to those mentioned, except that the zander may have been excited and unable because of the space restriction to indulge in swimming activity. Yawning behaviour appears to be a feature of many fish species and would seem to have little significance, regarding the ecological role of the zander.

The other zander behaviour which defied a meaningful explanation was "bellyswimming". This appeared to be some form of searching pattern, perhaps associated with locating food. Unfortunately such behaviour was never associated with feeding. The dominance behaviour noted at times is probably a natural trait common in the wild, perhaps during feeding or whilst the male guards the spawning nest. On the other hand the close confinement of the zander may have caused this behaviour. Frost and Kipling (1967) noted that pike fry did not become aggressive until crowded. Out of the 84 fish used during the study, only 6 individuals showed dominance. The same can be said for relative positioning and without the use of some form of telemetry in the wild the existence of territorial behaviour cannot be confirmed. Aggression on the other hand does occur in the wild. On numerous occasions zander have been captured bearing lacerations, almost certainly caused by the stabbing teeth of another zander. Such parallel cuts can only have been caused by zander. The zander noted with such attack damage have ranged in size from 350 mm to 650 mm. Such aggression cannot be based solely on the desire to eat a fellow zander. Similarly large bream have been noted with similar marks, the present author having found a 1.75 kg bream with typical zander stab marks. Such events though rare have been recorded before (Linfield and Rickards 1971). It is suggested that aggression occurs without a desire to eat the attacked organism. In some cases zander probably attempt to devour prey which is larger than their swallowing capacity and these fish are released. Such fish do sometimes survive and these have been noted by the present author on several occasions.

The laboratory feeding behaviour of the zander, appears to conform to Popova and Sytina's (1977) definition of an ambush pursuit predator. Though tank space was for the larger zander limited preventing the long distance pursuit of prey fish, the small zander of around 100 mm were less restricted yet failed to show pursuits of more than 8 zander body lengths. Prey capture was tail first after a short burst of speed with the subsequent grabbing of the prey. The two pairs of stabbing teeth one on the upper and lower jaws appear to be important in this seizure of prey, often by only an extremity of the preys body. Laboratory studies revealed a higher incidence of tail first feeding (77.2%) compared to that noted in the wild (66.6%). This could be attributed to the larger prey items eaten in the wild. Laboratory zander were seldom fed prey of greater than 30% of the body length.

Handling time increased with increasing prey size and further increased if the prey was swallowed tail first, when prey was greater than 15% of the zanders bodylength. Handling time showed no significant difference for prey swallowed head or tail first under 15% of zander bodylength. It is therefore suggested that smaller prey require less handling time and can be swallowed in either direction easily. Larger prey require increasing periods of handling and it is easier for the zander to swallow these head first rather than tail first. The zanders preferred method of attack appears to be from the preys tail, therefore it is to its advantage to predate on smaller prey. This entails a minimum of effort in capture and the shortest possible handling time and therefore requires predation on prey fish which are easily swallowed tail first.

The study of the actual feeding behaviour of the zander revealed a number of interesting points. As previously noted by Elshoud-Oldenhave (1979) the zander captures its prey using a combination of suction and grasping. This study also noted that once the prey had been grasped, only a limited amount of movement was possible. Observations of the feeding of the pike (authors observation and Hart pers comms) have revealed an ability to position prey fish so that they can in most cases be swallowed head first. The zander lacks this ability and therefore relies on the fact that the prey it has taken can be swallowed without difficulty. Zander appear to change their feeding strategy if the prey fish becomes too large to swallow easily tail first. The point at which this change in strategy occurs was not determined. In the laboratory prey fish which were released were only seized a second time if they showed activity. Dead fish were not seized. In the wild zander may reposition prey by releasing and seizing a second time.

The train of events leading to seizure of prey was fairly stereotyped. The significance of the erection of the first spiney dorsal fin is a matter for conjecture. Excitement appears to govern its erection, usually caused by the fixation of the prey, however the approach and attack sees this fin lowered. It could be suggested that the obvious dorsal fin is lowered on approach to the prey to avoid scaring the prey. The erection of the dorsal fin prior to approach and on capture of prey may be part of the zanders shoal behaviour. The dorsal fin may signal and convey information to other zander.

The experiments investigating the prey size preference of zander showed conclusively that zander will, when given the choice show a preference for smaller prey fish, provided the difference in prey sizes is sufficient to exceed the preference threshold. This threshold is lower for deep bodied fish compared to shallow bodied species.

Factors likely to invalidate the preference experiments have to be considered. Firstly there was the possibility of differential availability of the two sizes of prey. However apart from differences in swimming speed and manoevreability both sizes of prey were equally available to the zander. These factors were investigated using a perspex box with one prey size in each of two equal divisions. It was hoped that the zander would indicate its preference for either size of prey on the basis of size alone, each fish being restricted in its range and speed of movement. Unfortunately despite 12 trials, individual fish showed varying levels of activity which tended to evoke a predatory reaction from the zander, based on whichever was the most lively. The influence of prey size could not therefore be tested in this manner. Observations of the prey fish presented to zander during the preference experiments indicated that behaviour was similar regardless of size. It was therefore decided to accept that preference shown by the zander was based on other factors apart from rate of movement etc.

As detailed in Section 2.3 (Figure 51) the rainbow trout has a different body shape to the roach. Roach are deeper bodied than rainbow trout and it is suggested that it is this that affects the threshold of preference. There would appear to be no other morphological factor which could cause the difference in preference thresholds. Parsons (1971) working on the walleye found that body shape was not important in prey selection. He found that prey were selected by length, not shape and that prey length increased with walleye length. If this was the case for zander then it is difficult to explain the different preference thresholds for the two different prey species. If zander were similar to walleye the preference threshold should be the same regardless of prey species. This was obviously not the case. Further experimentation would have helped to add weight to the suggestion that prey body depth has an influence on prey size preference. Limited trials with a very deep bodied species, the crucian carp (Carassius carassius L) suggested that zander preferred to eat roach or rainbow trout of a similar size, when presented together. Unfortunately comparisons between three very different prey species are open to criticism due to the different colouration, swimming actions and behaviour, all of which could overide the zanders preference based on body depth. Such experiments would have been valid, if prey fish of similar behaviour and the same length, etc. yet with different body depths had been available. Model fish were considered for this work, each with a different length-depth ratio, however the zanders refusal to attack dead fish precluded this approach.

3.3. EXPERIMENT ON THE RATE OF DIGESTION OF PREY FISH

3.3.1. INTRODUCTION

The rate of digestion of prey fish was determined to enable estimation of prey ingestion times and feeding periodicity of fish obtained in the field. Swenson, Lloyd and Smith (1973), working with walleye, noted that no significant difference in rate of digestion could be attributed to the different sources of walleye. Similarly repeated handling was shown not to have any significant effect on digestion rates. Using fathead minnows (Pimephales promelas) at 14.5 and 20°C. The zander used in these studies showed growth throughout the study and it is therefore suggested that the fish were in a relatively unstressed state.

3.3.2. METHODS

Swenson, Lloyd and Smith (1973) demonstrated that, in the case of walleye, rate of digestion of similar sized prey items increased with walleye length. In order to eliminate bias caused by differences in zander length, all experiments were conducted using the same experimental fish, thus rendering each experiment comparable. The experimental fish numbered 14 and were 402 mm to 440 mm in length.

The following experimental approach was adopted in the determination of digestion rates. The zander were fed with roach of known weight and length. Roach fed to groups of zander were marked with coloured threads inserted under the dorsal fin using a hypodermic needle. This enabled each roach to be identified when removed from the zander's stomach (after Swenson et al 1973). After 30 minutes remaining uneaten prey were removed and timing of digestion commenced from the time of food removal. Zander were stomach flushed at varied intervals and temperatures of 5, 10, 15 and 20°C to enable estimates of digestion rate (Section 2.1).

A range of prey fish sizes 101.7-112.4 mm (16.2-22.g) were fed to the zander, thus enabling the relationship between prey length and rate of digestion to be demonstrated. Flushed remains were strained from the flushing water using a tea strainer and weighed to 0.1g. The length of remains were measured to the nearest 1 mm. Before return to the tank each zander was force fed with a 80 mm prey fish. In order to maintain natural feeding (see section 3.4). Feeding commenced again some 2 to 6 days later depending on temperature.

3.3.3. RESULTS

The mean prey lengths and weights of prey fish fed to the experimental zander were tested for significant difference using a t test. No significant differences existed at the $P > 0.05$ level. Therefore the range of prey fish fed to the zander was comparable. Graphs of prey length and weight digested with time were plotted with lines or curves fitted by eye. These are presented in Figures 72-75 at temperatures of 5, 10, 15 and 20°C. These graphs were used to estimate times of total prey digestion.

Table 62 presents the estimated time for total digestion (i.e. less than 1g). This is based on the reduction in weight of the

Figure 72.

Rate of Prey Fish Digestion.

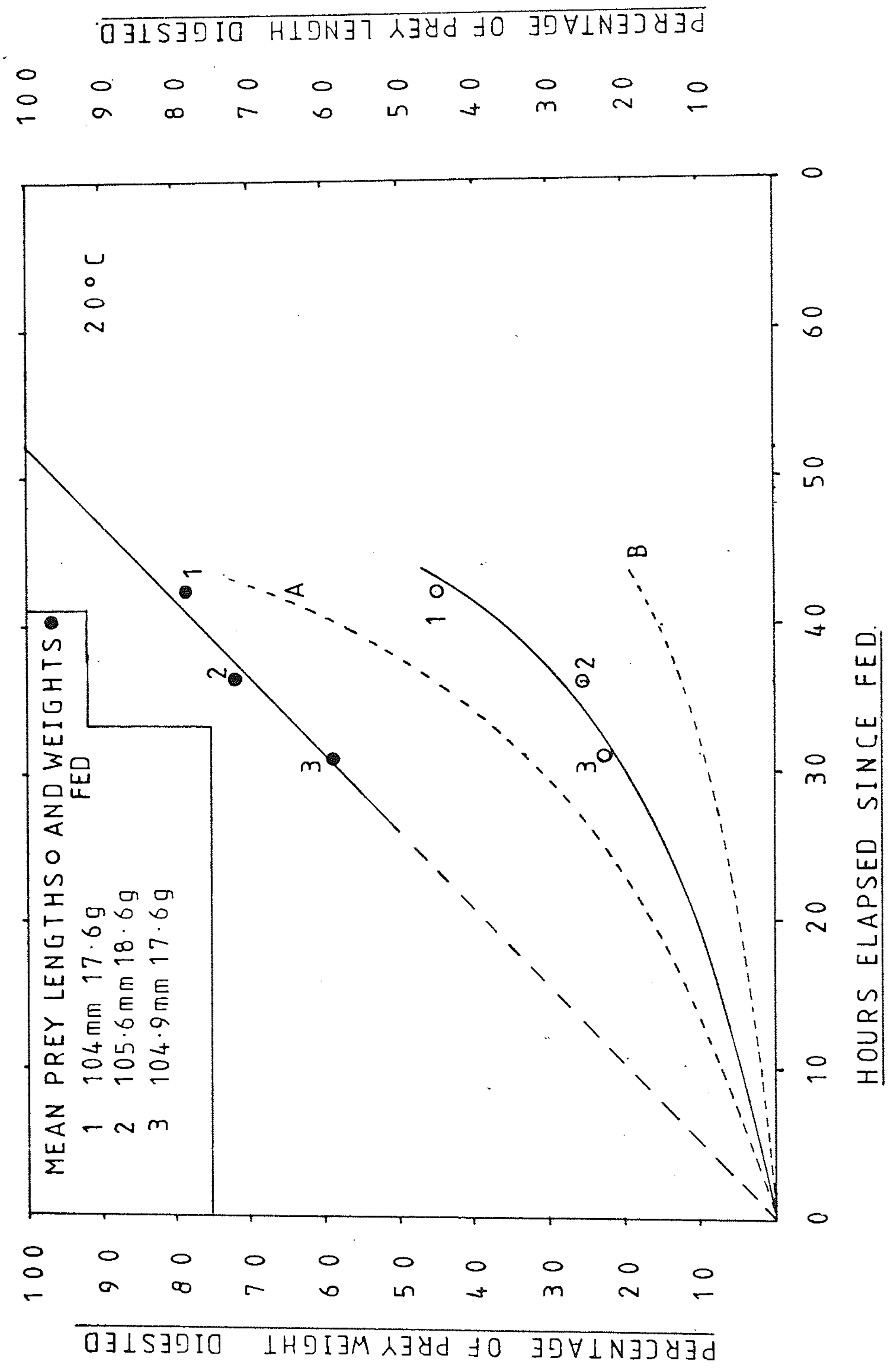


Figure 73.

Rate of Prey Fish Digestion.

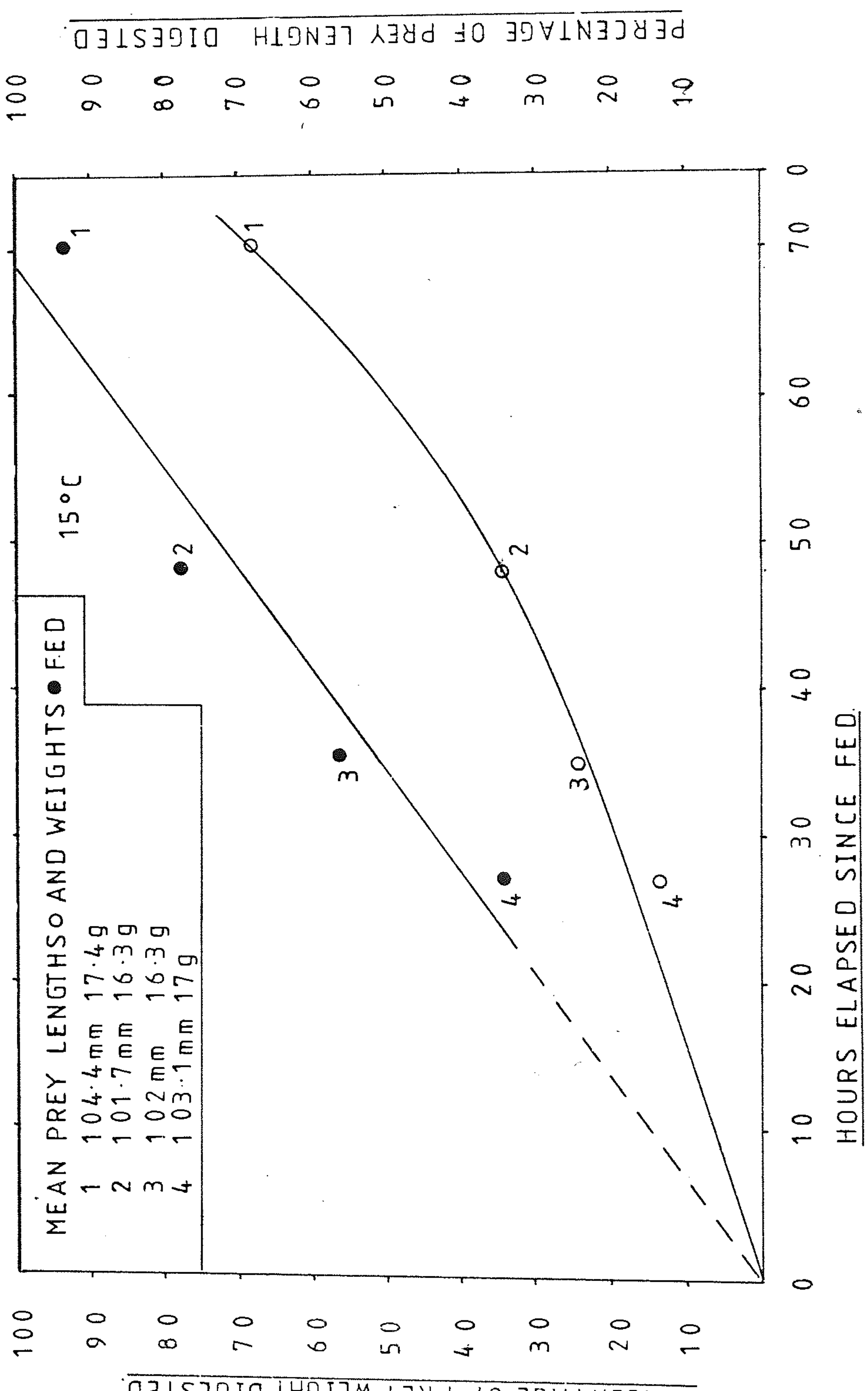


Figure 74.

Rate of Prey Fish Digestion.

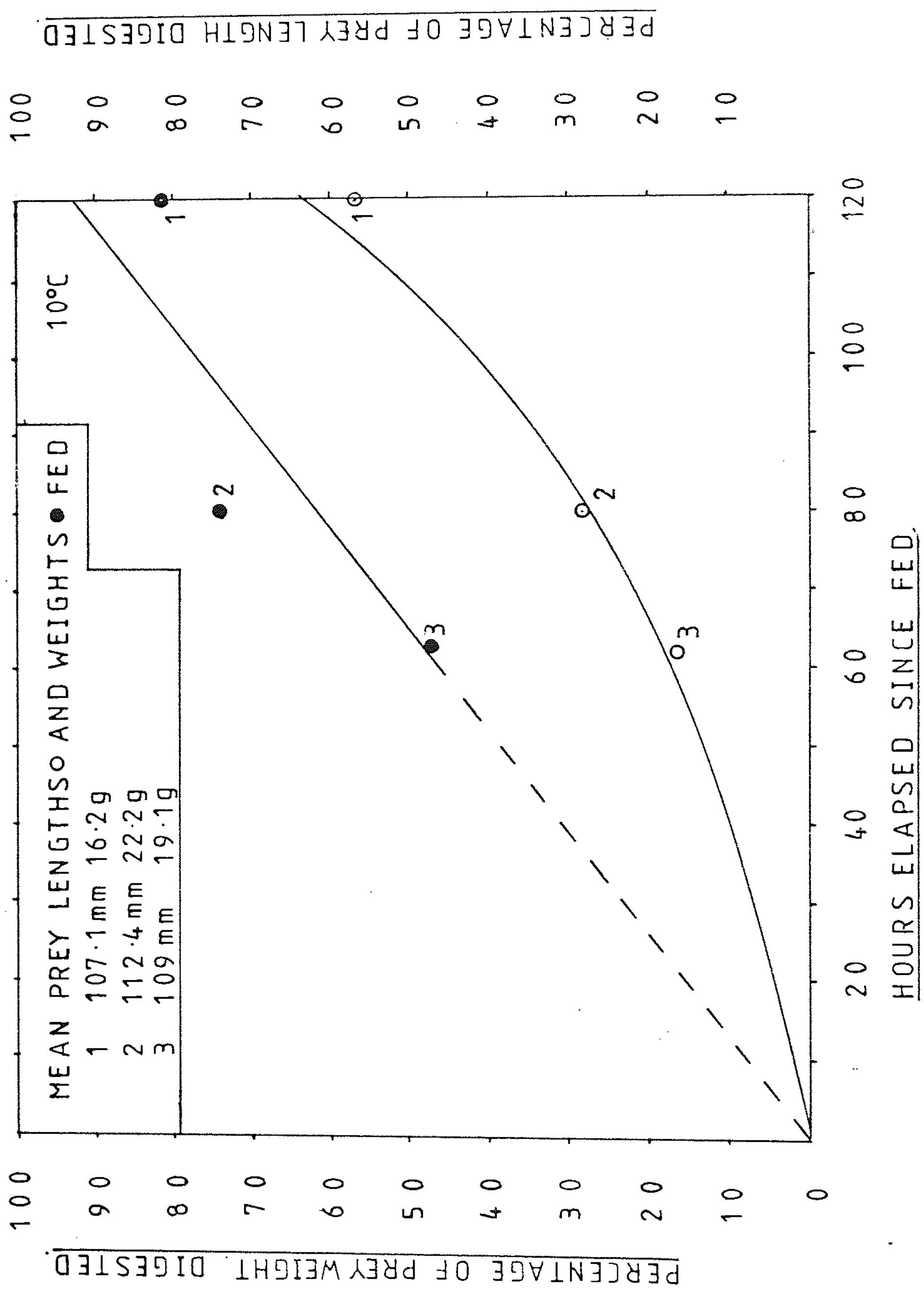
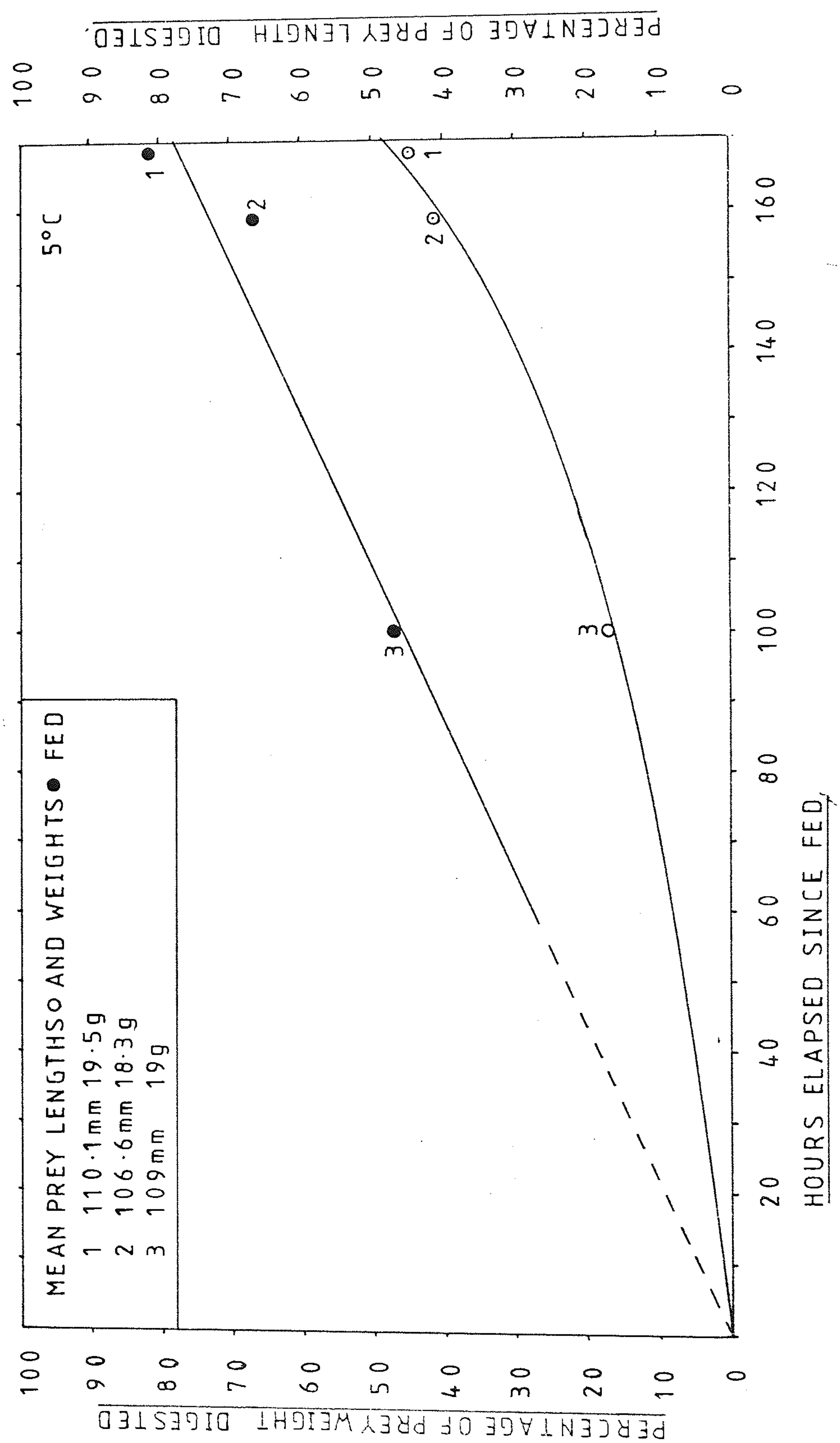


Figure 75.
Rate of Prey Fish Digestion.



prey item with time. Prey weight decreases in a linear fashion with increasing digestion time. Prey length however gives a curvilinear relationship, until the point is reached when fragmentation of the prey prevents an estimate of length. This point occurs between 45 and 68% digestion. Prey weight is therefore the better parameter, beyond 45% digestion.

TABLE 62: Estimated Time of Total Digestion of Roach

Temperature	Sample Size	Prey L Range mm	Prey W Range g	Time to Total Digestion
20 C	42	104-105.6	17.6-18.6	52 hrs
15 C	56	101.7-104.4	16.3-17.4	69 hrs
10 C	42	107.1-112.4	16.2-22.2	130 hrs
5 C	42	106.6-110.1	18.3-19.5	215 hrs

A 5 degree temperature decrease from 20 to 15 C resulted in a 32.7% increase in digestion time. A further 5 degree drop in temperature results in a 88.4% increase in digestion time. Finally a decrease in temperature from 10 to 5 C results in a 65% increase in digestion time. Overall the rate of digestion decreases by a factor of 313% with a 15 degree C temperature decrease.

Prey fish digestion proceeds more slowly the larger the prey fish. This was also noted by Swenson (1973). To enable estimation of prey ingestion times (2.4.) for prey fish of varied lengths, the effect of prey length was estimated. From this work it was estimated that a 12% increase in prey length resulted in a 58% increase in digestion time. Curves A and B on Figure 72 show the effect of a 12% increase or decrease in prey length. Further curves for further increases or decreases in prey length are easily derived, but are not included on Figure 72 for clarity.

3.3.4. DISCUSSION

The purpose of this section was primarily to enable the estimation of the time of ingestion of prey fish noted in zander stomachs during fieldwork (2.2.4.).

The results of this work were studied in comparison with the work of Molnar and Tolg (1962a), the only published study at present available (Table 63). The estimated times of total digestion were obtained from figures 72-75, based on the point of reduction or prey fish to less than 1g.

TABLE 63: Time of Prey Digestion Estimated by Molnar and Tolg Compared with Present Study

Temperature	Time to Complete Digestion This Study	Time to Complete Digestion Molnar and Tolg
23	-	34 hrs
20	52 hrs	45 hrs
15	69 hrs	83 hrs
10	130 hrs	157 hrs
5	215 hrs	257 hrs

Molnar and Tolg's prey fish were bleak (Alburnus alburnus L) of 80-100 mm, while in this study roach were the prey fish, of 101.7-112.4 mm.

Molnar and Tolg's experimental zander appeared to digest prey fish slower than those used for this study except at 20°C. This is despite the fact that their prey fish were smaller than those used here. Some explanation for this difference, although small, is required. One possible explanation is that stress caused the digestion of Molnar and Tolg's zander to be depressed, since their work required the retention of the zander in a fixed position for X-ray photography of the stomach contents.

Zander were also force fed during the Molnar and Tolg study. Swenson and Smith (1973) have demonstrated the depression of digestion due to force feeding in their own study of the walleye. Because of this, the present study sought to present prey fish in as natural a manner as possible. This restriction was unfortunately very time consuming as the experimental zander did not always consume prey fish when required. Force feeding between experiments was important as this provided the experimental fish with food, as stomach flushing during the experiments invariably deprived the zander of much of their food. Also force feeding had the advantage of encouraging feeding. It was noted that experimental zander would frequently lapse into periods of non feeding, which became almost permanent unless action was taken. Zander were therefore fed either naturally during experiments or by force feeding between experiments. Windell (1967) noted that periods of food deprivation resulted in lowered metabolic level, and anatomical changes in the alimentary canal and especially the pyloric caecae which result in a slower rate of food progression. It was therefore very important to ensure that the experimental fish were fed regularly.

3.4. THE CONVERSION RATE AND MAINTENANCE REQUIREMENT OF ZANDER

3.4.1. INTRODUCTION

Studies of the conversion rate and maintenance requirements of predatory fish have been extensive. Notable studies of relevance to this work include Johnson's (1966) study of pike (Esox lucius L), Brett, Shelbourne and Shoop's (1969) study of the sockeye salmon (Oncorhynchus nerka Walbaum 1792) and the previously mentioned work by Swenson et al (1973) on the walleye. The study of the coho salmon (Oncorhynchus kisutch Walbaum 1792) made by Carline and Hall (1973) showed that growth efficiencies of fish in laboratory and semi natural environments were very similar. For the purpose of this work it will be assumed that laboratory studies can be used to provide information about the food utilisation of wild populations.

The term 'maintenance' has been taken to mean the weight of food required to maintain a constant bodyweight. This weight of food is utilised in swimming, standard metabolism, processes of digestion and the assimilation and storage of food materials. Conversion rate refers to the total or gross efficiency of the utilisation of food materials. The partial or net efficiency of utilisation may be calculated by subtracting the maintenance requirement from the total ration. This then provides information on the food utilisation when in excess of the maintenance requirement.

3.4.2. METHODS

Experiment A

A long term experiment (18 months) was conducted to enable estimation of the zander's conversion rate and maintenance requirement. The experiment required the feeding of zander with a variety of ration sizes at different temperatures. Seven zander as used in the study of feeding behaviour (3.2., Table 53), were utilised during and after the feeding behaviour studies. The experimental zander were obtained from Coombe Abbey Lake and were subject to the quarantine procedure noted in 3.1.2. Experiments were conducted 4 weeks after removal from quarantine with surplus prey fish provided before experiments began. The seven zander used for this study were placed into four groups and retained in separate tanks due to the aggressive tendencies of certain fish. These groupings were: Group 1A, Group 2B, C, D, Group 3E, F, Group 4G. The mean weights and lengths of each group is presented in Table 64.

TABLE 64: Mean Weights and Lengths* (where applicable) of Zander Groups 1 to 4

Fish Code	Group	Mean Weight g	Mean Length mm
A	1	918	445
BCD	2	682.3	408.7
EF	3	884.5	433.5
G	4	772	442

*Weights and lengths at start of experiments.

Each group of fish was presented with 80 mm to 110 mm roach on a daily basis, the number of prey fish presented being varied to obtain different ration sizes. Feeding was usually during mid morning and mid afternoon, or once during mid morning depending on the ration size desired. Prey fish were weighed before presentation and the weight of the remainder noted on withdrawal of prey an hour later. Ration size ranged from 0 to 14% of the zander's body-weight calculated on a weekly basis. (50% of two week ration). Percentages of the zanders bodyweight were based on the mean of initial and final zander weights. The percentage of the zanders bodyweight fed, was therefore based on the zander's estimated weight during the middle of the 2 week experiment.

Each feeding experiment required a two week period. During this period time was allowed for the zander to be fasted, allowing emptying of the stomach and evacuation of the gut. From Section 2.3., times for complete digestion at each temperature were used to calculate the fasting period. An additional 24 hours was allowed for evacuation of faeces based on aquarium observations of the time required for the cessation of defecation. Zander were weighed and measured on Monday mornings, thereby eliminating the requirement to feed during weekends. Table 65 presents fasting periods at each temperature.

TABLE 65: Length of Fasting Period at Each Temperature

Temperature	Fasting Period
20 C	72 hrs
15 C	94 hrs
10 C	154 hrs
5 C	244 hrs

3.4.3. RESULTS

Experiment A

Using the methods described the maintenance, optimum and maximum rations of zander were determined for temperatures of 5, 10, 15 and 20 degrees C. Percentage of zander bodyweight fed was plotted against percentage of zander bodyweight, loss, no change or gain. Curves were fitted to the points by eye (Figures 76 - 78). The point of intersection with the x axis gave the estimate of the maintenance ration. By drawing the tangent to the curve from the origin, the optimum growth ration was determined (Brett et al 1969). The asympote of the curve represents the maximum ration which results in an increased addition of bodyweight. Beyond the maximum feeding rate, no further additional weight increase can be expected. Table 66 presents the values obtained for maintenance, optimum and maximum rations at 10, 15 and 20 degrees C. Only the maintenance requirement could be estimated at 5 degrees C due to the limited number of points.

TABLE 66: Maintenance, Optimum and Maximum Rations of Zander

Temp.	No. of 2 week experiments	Maint. Ration	Optim. Ration	Max. Ration
(All expressed as percentages of zander bodyweight in grams)				
5 C	8	0.6	-	-
10 C	10	1.4	4.6	7.8
15 C	41	3.6	10.0	16.6
20 C	24	9.1	19.6	25.0
		Zander Groups 1 to 4		

Figure 76.

7Day Maintenance, Optimum and Maximum Ration of Zander of 346–1070g, 405–458mm at 20°C.

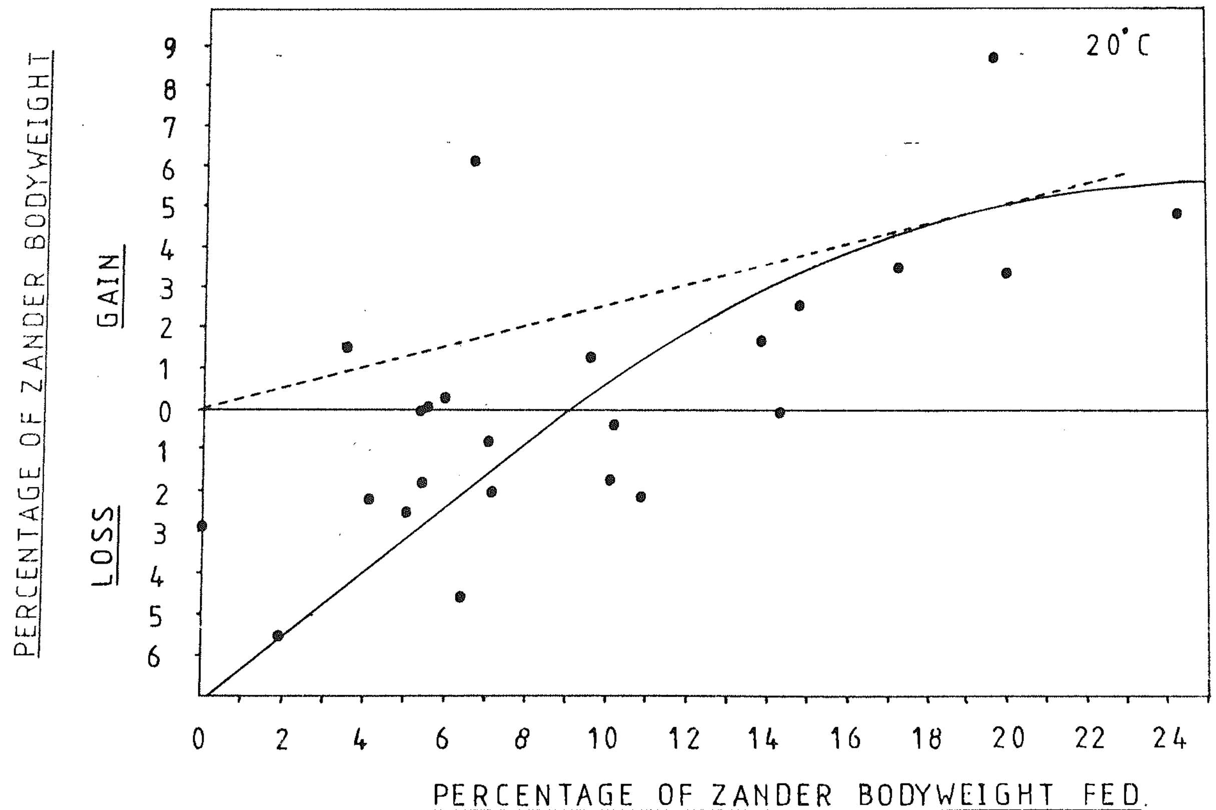


Figure 77.

7 Day Maintenance, Optimum and Maximum Ration of Zander of 346-1070g, 405-458mm at 15°C.

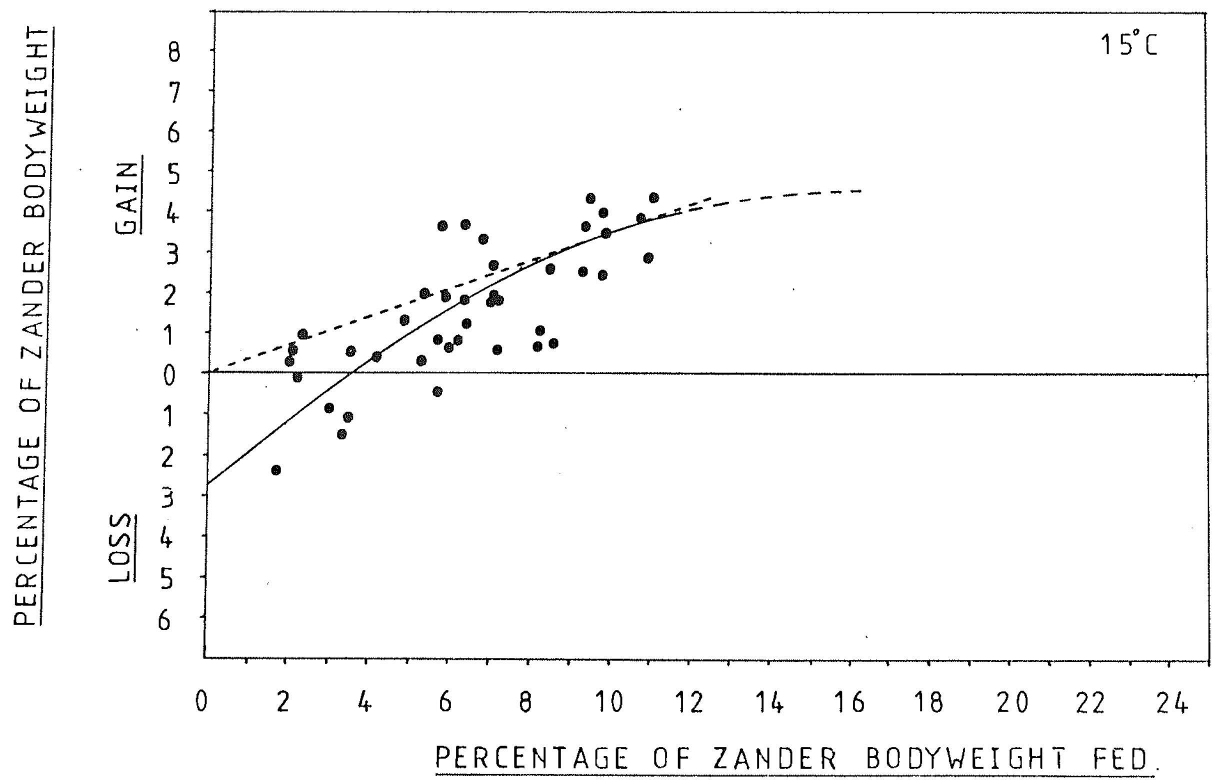
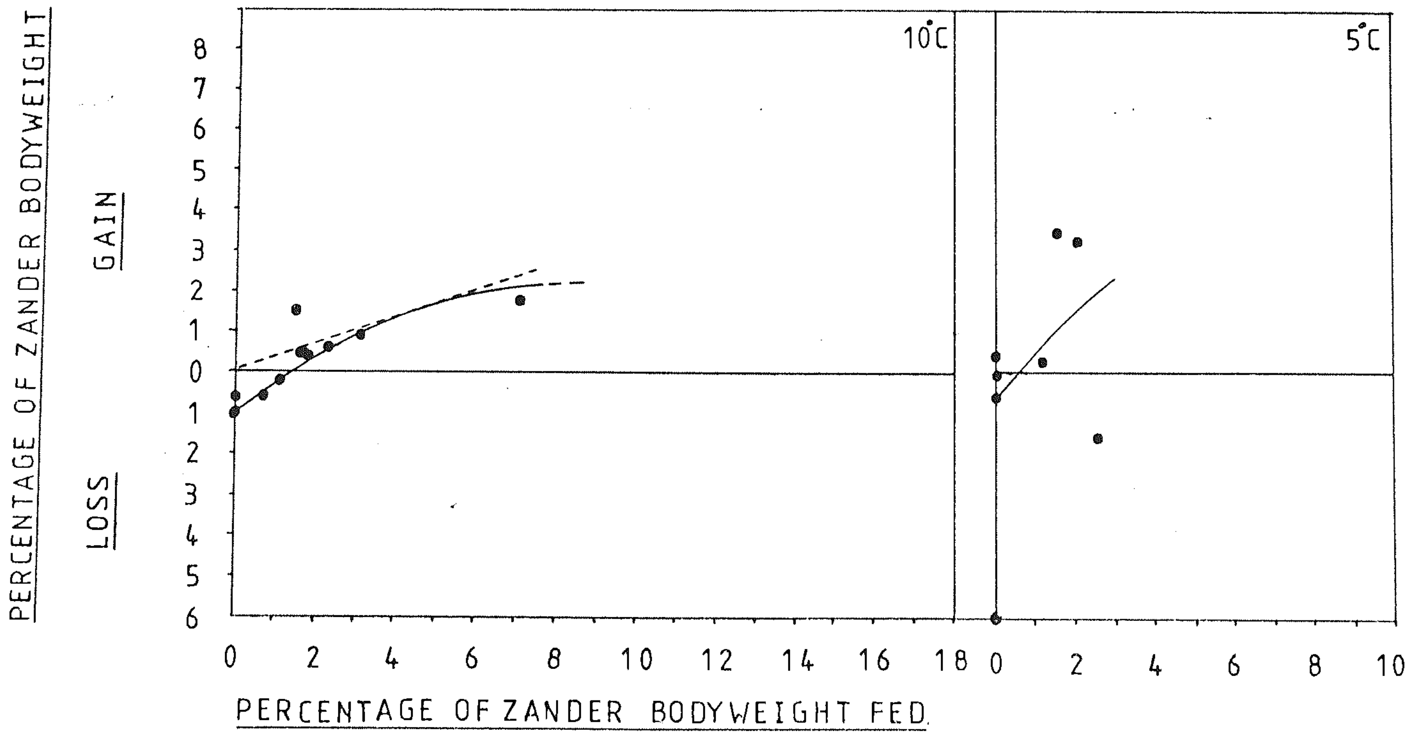


Figure 78.

7 Day Maintenance, Optimum and Maximum Ration of Zander of 346-1070g., 405-458mm at 10 a 5°C.



The relationship between maintenance, optimum and maximum ration and temperature is presented as Figure 79.

The gross conversion efficiency was calculated using the formulae:

$$E_g = \frac{G}{I} \times 100$$

where G is growth and I is food intake.

Growth and food intake are both expressed as percentages of the zander bodyweight. E_g is therefore an estimate of the efficiency of utilisation of food.

The gross efficiency of the zander at the four temperatures studied was plotted against percentage of zander bodyweight fed. Figure 80 presents the curves obtained. Similarly the net conversion efficiency was presented as Figure 81. The net conversion efficiency was derived from the formulae:

$$E_n \quad \frac{G}{I - M} \times 100$$

where M is the maintenance ration subtracted from the food intake, E_n is an estimate of the efficiency of utilisation of food surplus to the maintenance requirement.

Experiment B

Table 67 presents the mean weights and lengths of the small zander at the beginning and end of each two week period with the mean weight of prey eaten.

Figure 79.

Effect of Temperature on Maintenance, Optimum and Maximum Ration.

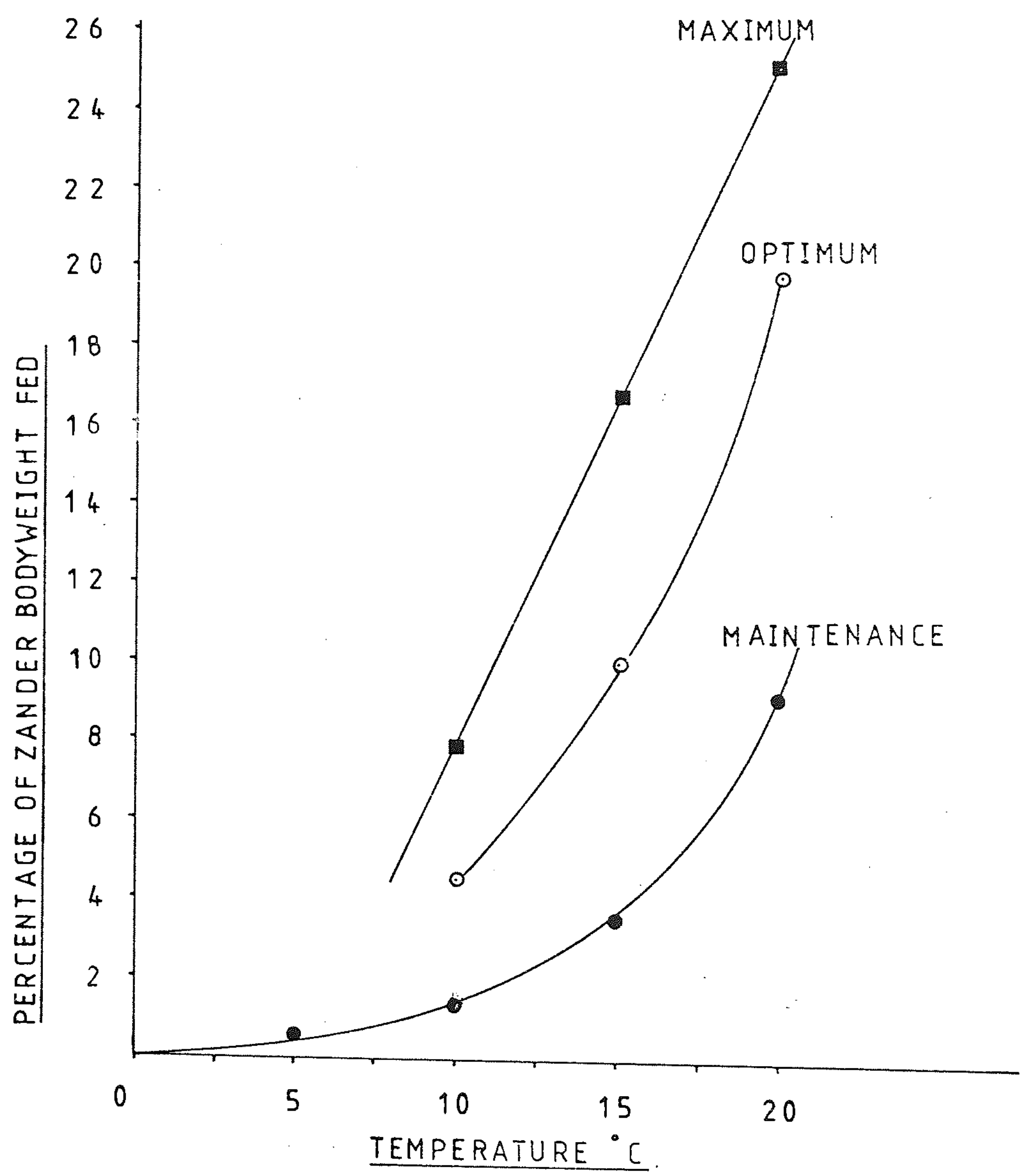


Figure 80.
Gross Conversion Efficiencies of Zander at 5, 10, 15, 20 °C.

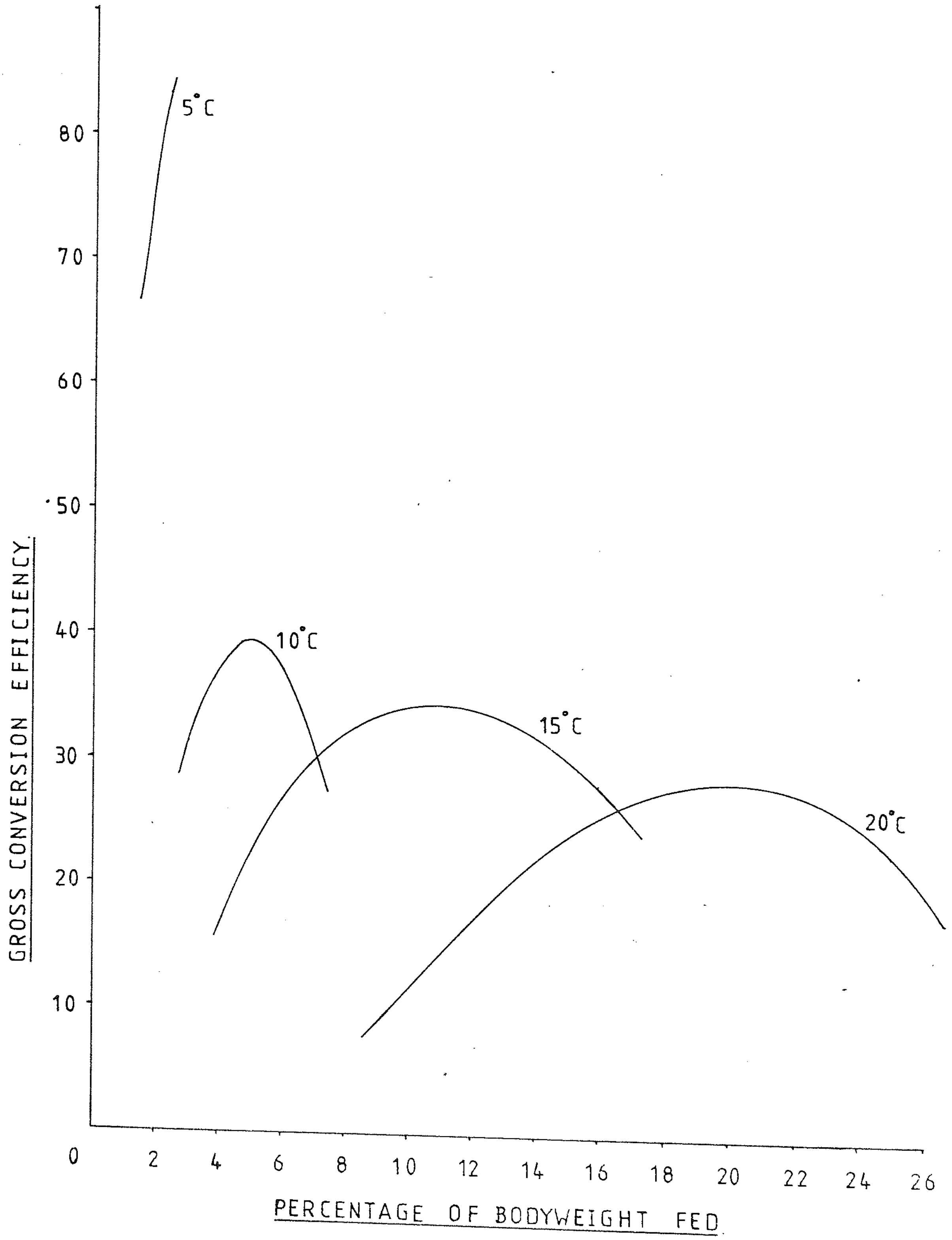


Figure 81.

Net Conversion Efficiencies of Zander at 5, 10, 15, 20°C.

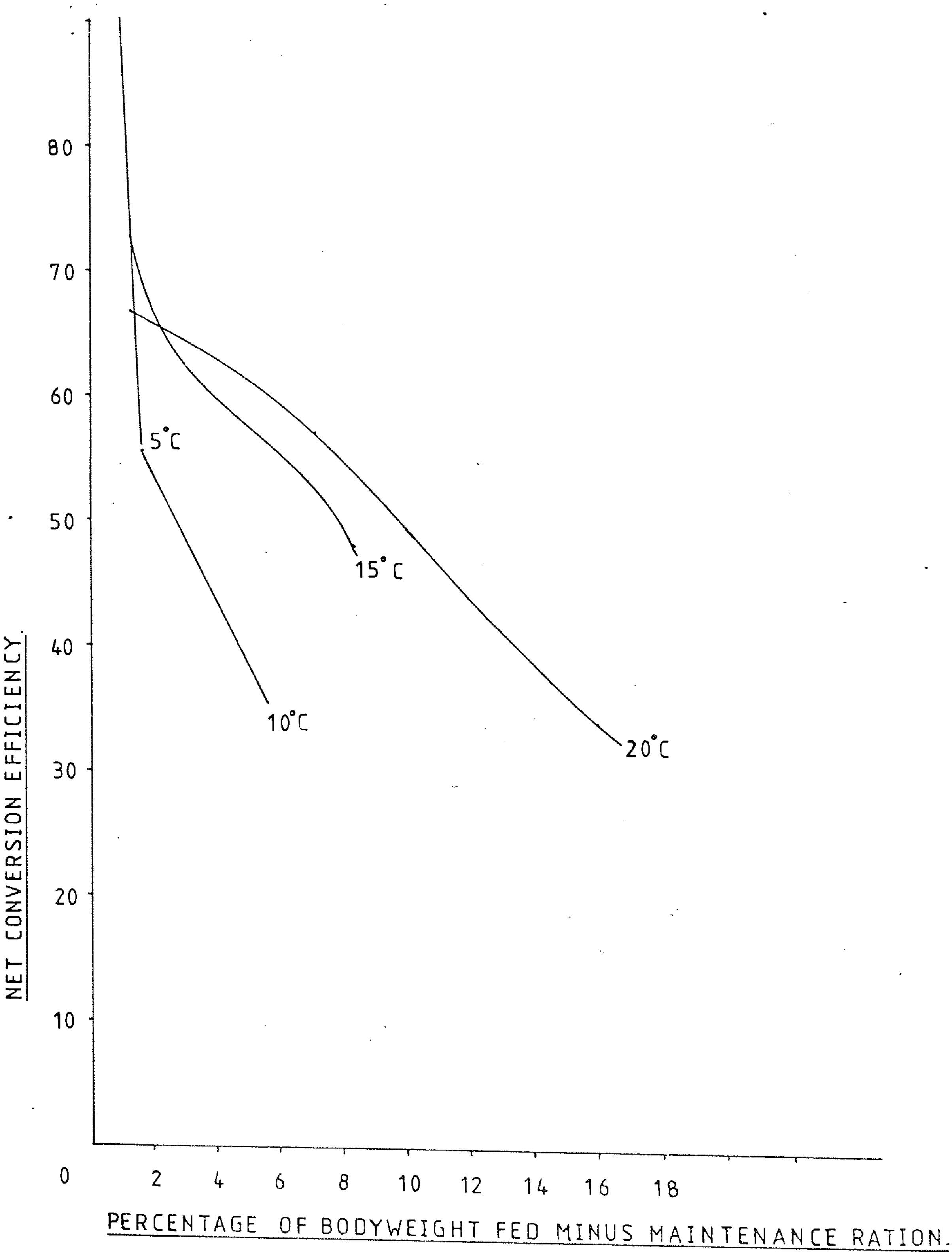


TABLE 67: Weight, Length and Food Intake of Small Zander

Two week period	Initial Weight	Initial Length	Final Weight	Final Length	Weight Fed	Temp.	No. of Zander
1	7.9	100	12.8	114	27.5	22	2
2	12.8	114	14.4	123	13.8	20	2
3	14.4	123	17.7	131	23.7	19.4	2
4	16.3	125	17.3	128	18.9	15.4	3
5	17.3	128	18.1	130	17.7	14.4	3
6	15.0	121	15.6	123	29.0	14.9	4
7	15.6	123	17.3	127	31.0	14.9	4
8	17.3	127	18.9	130	31.0	14.1	4
9	18.9	130	19.6	132	18.0	11.4	4
10	19.6	132	19.4	132	6.1	7.8	4
11	19.4	132	19.1	133	7.2	9.0	4
12	19.1	133	19.1	133	6.8	8.0	4

Percentage of bodyweight fed was plotted against temperature (Figure 82). Food intake was at a high level at 22 C and decreased with the lowering of the temperature. Percentage weight and length change were also plotted against temperature (Figure 82) and it was apparent that percentage weight and length increases were greatest at higher temperatures. This was presumably caused by the higher level of food intake at higher temperatures. When percentage weight change and percentage length change was plotted against percentage bodyweight, (Figure 83) a least squares regression line could be fitted which showed a high level of correlation:

Weight $r = 0.97$ $p < 0.05$ (n 12) $y = -6.1 + 0.37x$

Length $r = 0.95$ $p < 0.05$ (n 12) $y = -11.3 + 0.11x$

Figure 82.

Growth of Zander 91-158mm

August 1980 - January 1981.

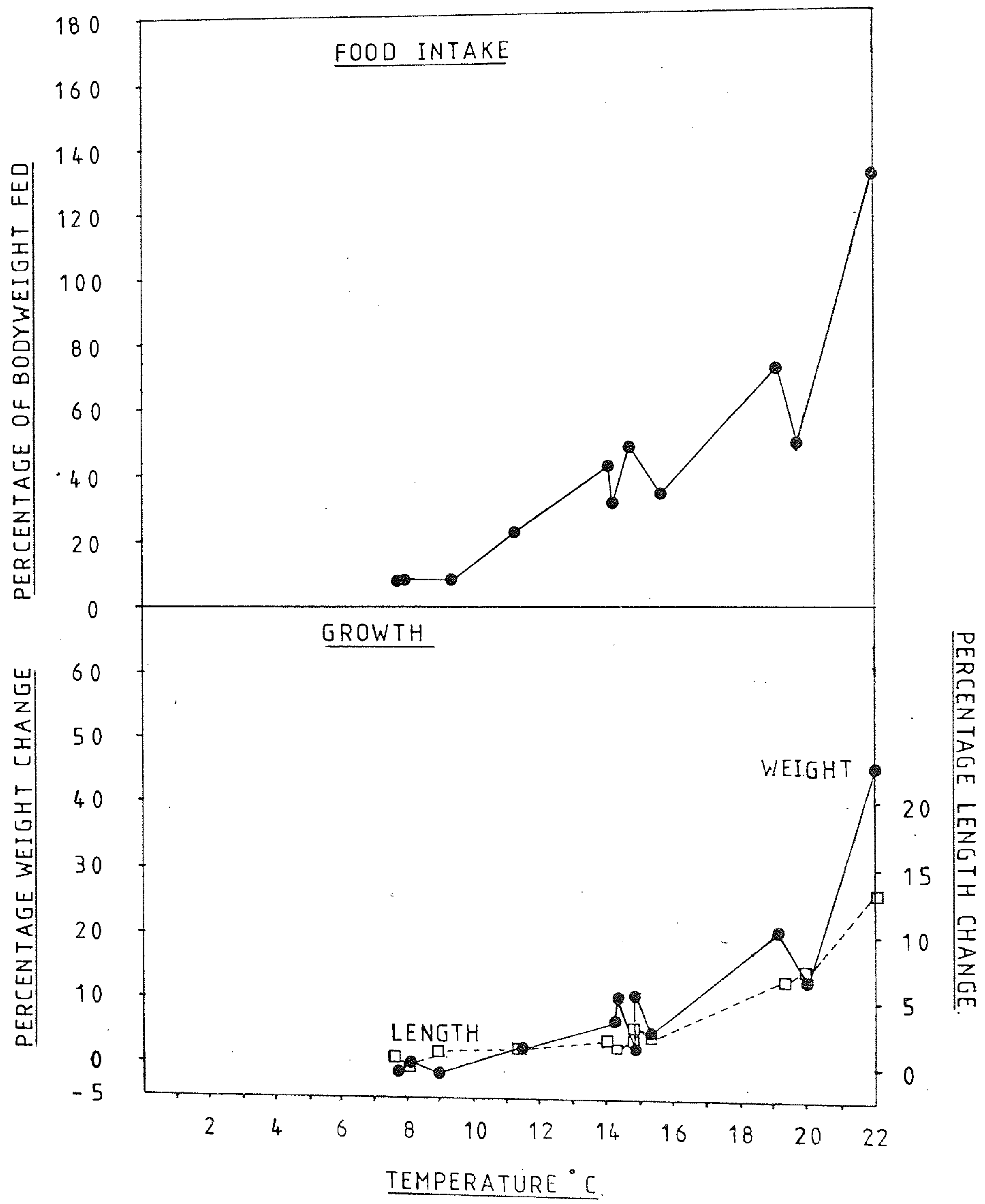
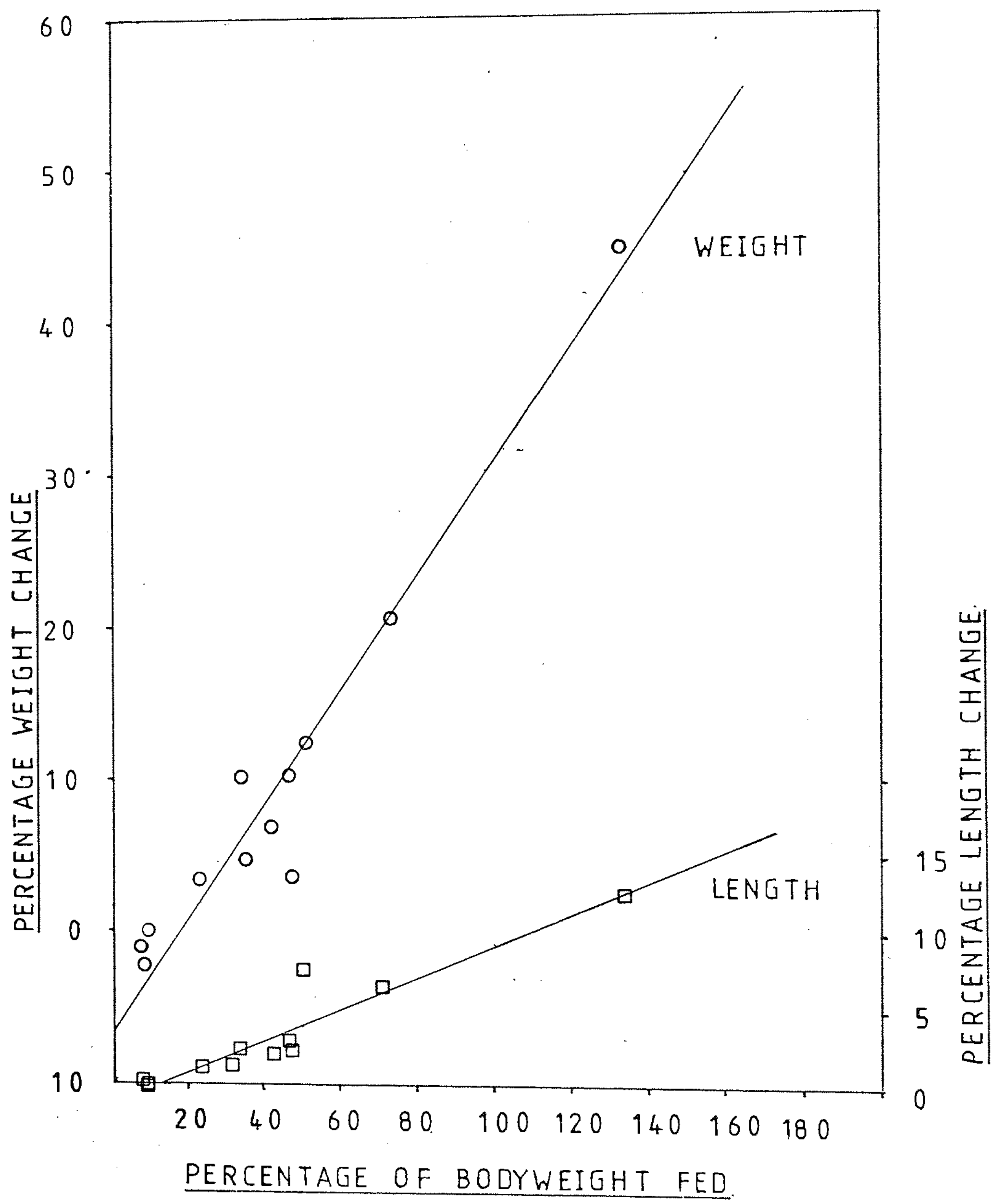


Figure 83.

Percentage Weight and Length Change of Zander (91-158mm) in Relation to Percentage of Bodyweight Fed.



This suggested that the growth of young zander is related to food intake and this in turn is related to temperature.

The mean maximum food intake for individual zander during this study consisted of 133% of the zander's bodyweight during a 14 day period. This is a daily food intake of 9.5% per day (at 22 C). The mean total food intake per individual zander during the 24 week period was 484.7% of the bodyweight. This gave a mean daily food intake from August to January of 2.9% of the bodyweight. A total of 189 roach of a mean weight of 0.37g were eaten per zander during the 24 week period.

The gross conversion efficiencies of the small zander at the two week mean temperatures, during the 24 week period were calculated (Table 68).

TABLE 68: Gross Conversion Efficiencies of Small Zander

Temp.	G.E.
22 C	35.1%
20 C	23.9%
19.4 C	28.3%
15.4 C	15.0%
14.4 C	29.7%
14.9 C	6.9%
14.9 C	22.5%
14.1 C	20.6%
11.4 C	14.9%
7.8 C	0
9.0 C	0
8.0 C	0.9%

Experiment B

While the major study of the zander's maintenance requirements and conversion rates was progressing, (Experiment A) a smaller size range of zander became available and these were the basis of a 2nd experimental study. Initially eight 0 plus zander were obtained from the Forty Foot Drain (see Figure 2). However 6 failed to survive longer than two weeks due to damage incurred during netting. Two further additions from the same water were made, eight and twelve weeks into the experiment, after a two week acclimitisation period in another tank. The small zander were retained in an aquarium of 1000 mm x 300 mm x 300 mm with filtration and aeration. Feeding was in excess of the daily requirement (5% of the bodyweight per day, Popova and Sytina 1977) with ten 0+ roach available per zander every day. Each day at 11 a.m. the number of small roach was checked by counting and the number brought up to ten per zander by the addition of new fish. Approximately 25% of each zanders bodyweight was available per day. The small zander measured 91 mm to 158 mm and weighed 5.96g to 31.2g during the experimental period which lasted 24 weeks. The experiment consisted of 12 two week periods during which feeding was allowed for 12 days followed by two days fasting and then the small zander were measured and weighed as described earlier (3.1.2.). At the end of each two week period the weight of roach fed to the small zander was transformed to a percentage of the zanders bodyweight. This in effect gave the mean percentage weight of food eaten per zander. The estimated weight of the zander at day 7 (the mean of the weights on day 1 and 14) was used for this transformation. The small zander were dealt with collectively at all times, data being expressed as mean weights, lengths and weights of food eaten, for either 2, 3 or 4 fish.

The temperature regime followed that of the daily air temperature, though being slightly elevated due to the indoor positioning of the tank (approximately 2 to 4 degrees C above ambient). Temperatures were recorded using a maximum - minimum thermometer and the mid point between maximum and minimum was estimated as the mean daily temperature. A mean two weekly temperature was derived from the mean of the 14 daily observations.

3.4.4. DISCUSSION

The discussion of the study of the conversion rate and maintenance requirement of the zander can be considered as a comparative discussion, relating existing studies of predatory fish to the present study and as a theoretical discussion of the zanders likely demands on the prey fish population of the habitat.

Most laboratory studies of predatory fish have involved the use of a restricted size range of experimental animals. The present study is no exception and it must be accepted that conclusions derived from this study might not be applicable to zander of different weight, length, age or state of sexual maturity, to those used here.

Johnson (1966) did not notice a significant difference in the maintenance requirement of the two sizes of pike he studied. However the size range used in his work was very small and no fish greater than 250 mm were utilised. Prather (1951) working on largemouth bass (*Micropterus salmoides* Lacepede) and Williams (1959) working on largemouth and smallmouth bass (*Micropterus dolomieu* Lacepede) noted that the smaller and younger experimental fish had lower maintenance requirements and also converted food more efficiently. The availability of zander for this study was such that a limited size range was employed during experimental work.

Long term studies of conversion rates and maintenance requirements should also take into account the production and shedding of gonad products. This may result in a periodic net loss of energy each year amongst sexually mature individuals. During this study the majority of experimental animals were immature at the start of the experiments though all would have been old and large enough to reach maturity during the experiments. Examination of 6 individuals in January of 1981 (4 males, 2 females, all 2+) indicated that gonad development was not in an advanced state. Gonad products were never shed during the experiments (this would have resulted in a sudden weight loss). The influence of gonad production is therefore considered to be negligible.

Johnson (1966) noted during his study of the pike that the maintenance requirement, though influenced by temperature, was also influenced by the time of year. During this study, temperatures approximated the normal regime and therefore could be considered as being similar to conditions in the natural environment.

The most detailed study of the maintenance and conversion rate (Table 69) of a predatory fish was conducted by Brett et al (1969) on the sockeye salmon (*Oncorhynchus nerka* Walbaum 1792).

TABLE 69: Values for Food Utilisation of Sockeye Salmon Compared with Zander

Temp.	Maintenance % of Bodyweight		Optimum % of Bodyweight		Maximum % of Bodyweight	
	S.Salmon	Zander	S.Salmon	Zander	S.Salmon	Zander
1 C	0.4	-	0.16	-	0.24	-
5 C	0.5	0.08	0.37	-	0.74	-
10 C	0.95	0.2	1.02	0.66	1.34	1.1
15 C	1.5	0.51	1.22	1.4	1.38	2.3
20 C	2.6	1.3	1.5	2.8	1.2	3.6

It is noticeable that the zander has a much lower maintenance requirement than the sockeye salmon, and also that the zander has a lower optimum and maximum utilisation requirement below 10 C. Above 10 C the zander requires a higher level of food intake to enable optimum and maximum utilisation. The sockeye salmon were fed on a diet consisting of 51-63% moisture while the zanders diet of natural food (roach and bream) invariably had a much greater moisture content 76.7 - 82.9%. The zander therefore makes a much better use of its food than the sockeye salmon or itself has a higher water content. Data from Brett et al (1969) on the water content of sockeye salmon suggest a range of 71 - 86.9% while zander used in this work ranged between 73.8 - 77.4%.

(95% confidence range of a mean of 75.6% water content), therefore the differences in conversion must be due to more efficient utilisation.

The gross conversion efficiencies of the zander were high compared with most other predatory species, though compatibility was often lacking in water temperatures and fish size (Table 70).

TABLE 70: Gross Conversion Efficiencies of Predatory Fish

Species	Size	Month	Temp.	Conversion Efficiency
Walleye *	300-500mm	June-Sept.	20 C	26.1%
Pike **	250mm	Jan-Dec	8 C	30.6%
S.Salmon ***	200mm	lab	11.5C	25.0% maximum at any temp.
L. bass ****	150mm	"	27-32 C	41.7%
" "	250mm	"	"	23.8%
L..bass *****	300mm	"	19.5-25 C	15.2 - 47.6%
S. bass	300mm	"	"	22.2 - 38.5%
Zander @	405-458mm	"	5 C	66.7 - 83.3%
"	"	"	10 C	28.2 - 39.1%
"	"	"	15 C	20.0 - 35.0%
"	"	"	20 C	9.4 - 25.8%
"	"	"	Mean of all temps.	31.2 - 45.8%
Zander *@	-	Jan-Dec	?	19.6%

* Swenson et al (1973) Estimated from wild fish in natural environment

** Johnson (1966)

*** Brett et al (1969)

**** Prather (1951)

***** Williams (1959)

@ Present study

*@ Fortunatova and Popova (1973)

The very high conversion efficiency at 5 C may have been caused by the artificial conditions and ease of finding food. There is little doubt (if Table 65 is consulted) that zander do not feed heavily below 7-8°C in the most natural environment available during this study (Experiment B). If food is easily available in captivity it requires relatively little effort to ingest sufficient food to exceed by a considerable amount the very small maintenance requirement. This can then lead to some very high conversion efficiencies.

The gross conversion efficiencies obtained during this work can be compared with those obtained in other studies. Fortunatova and Popova (1973) noted a mean gross conversion efficiency of 19.6% for the zander. The temperature regime noted during their work is unknown, however such a conversion efficiency would correspond with the results obtained during this study for 15 to 20 C. Swenson et al (1973) noted a mean gross conversion efficiency for walleye of 26.1% at approximately 20 C (again precise temperatures are not specified). This is again similar to the observations obtained in this work. Johnson (1966) figure of 30.6% obtained for pike throughout a year is similar to this works mean value for the four temperatures. The zander appears to be able to convert food more efficiently than the pike. Zander appeared to be slightly more efficient than sockeye salmon at 11.5 C. Generally the Centrachid fish such as the small and largemouth bass appeared more efficient than the zander at the high temperatures studied by workers such as Prather (1951) and Williams (1959). This is not surprising, for the Centrachid fish are natives of somewhat warmer areas than the zander and are probably adapted for life in relatively warm waters. This suggests that zander are adapted to a temperature climate, where water temperatures tend not to fluctuate beyond 0-20 C.

The study of the small zander provided further information on the effect of temperature on gross conversion efficiency. There was a somewhat erratic, but still distinct, decrease in gross conversion efficiency down to 9°C when gross conversion efficiency became negligible, due to a very reduced food intake. This was rather different from the results obtained using the larger zander and is suggested to be further evidence that the larger zander were probably feeding more than they would in a natural situation. The small zander were retained in a large tank, when compared with the larger zander. It is suggested that 8-9 C is the point at which feeding is so reduced that enough food is eaten to satisfy only the maintenance requirement. The periods of lowered temperature were, however, short, only six weeks being below 9°C and it is possible that adaptation to lower temperatures may be required for increased feeding.

At 22 C gross conversion efficiency was at its highest, again the reverse of the experience gained with the larger zander. It is possible that the maintenance requirement of small zander is significantly less than that of larger zander, as noted by other workers working on the various species of bass. This might account for the much higher conversion efficiencies of the smaller zander at high temperatures. However, without further experiments with small zander, it will be impossible to determine the reason for these differences, although this does act as a cautionary warning when attempting to relate laboratory studies on limited size ranges of zander to the natural environment.

The small zander may have continued to show increasing conversion efficiency as temperature increases, but it is likely that a peak would be reached between 22 and 35 C, the incipient death point (Hokanson 1977).

The use of data gathered in the laboratory to estimate factors such as food consumption rates cannot really be considered valid unless the laboratory study seeks to examine the fishs behaviour and metabolism in conditions equally varied as those found in the wild. This study obviously failed to satisfy such criteria, although this does not prevent a brief investigation onto the likely food requirement of the zander. Having worked with fish approaching 1000 grams it will be permissible to investigate the food requirements of a hypothetical 1000 gram zander living during 1980 (presuming this hypothetical fish to be immature). Mean monthly temperatures obtained from a maximum minimum thermometer kept in an outside holding tank were used to enable monthly estimates of temperatures in 1980. Table 71 presents the estimated monthly maintenance requirements of a 1000g zander, using estimates of maintenance requirements derived from Experiment A (Figure 79).

TABLE 71: Estimated Maintenance Requirement of 1000g Zander Based on Laboratory Study

Month	Temp.	Monthly Maintenance Requirement % of Bodyweight
January	5 C	1.77%
February	7 C	2.8%
March	8 C	5.3%
April	10 C	6.4%
May	13 C	11.5%
June	18 C	30.0%
July	19 C	35.4%
August	19 C	35.4%
September	16 C	18.0%
October	12 C	9.3%
November	8 C	5.1%
December	5 C	1.81%
	TOTAL	162.7%

In 1980 a 1000g zander would require 162.74% of its bodyweight to enable it to maintain its existing bodyweight. Estimating the amount of food required to enable growth is rather more difficult due to the differences in gross conversion efficiencies each month. The only information available is that of Popova and Sytina (1977) who noted from field observations that up to 60% of the annual ration is eaten during the spring, 15% during the summer, 22% during the autumn and 3% during winter. Typically a 1000 gram zander would be three years old and could expect in a productive water to show a 40% increase in weight, reaching 1400g by year 4 (2.2). Knowing the amount of food it takes at optimum feeding levels to produce zander flesh at various temperatures (Figures 76-78) it can be calculated that a zander of 1000g would require the following amounts of food (Table 72). The yearly ration (excluding maintenance) is allocated per month in a ratio corresponding to Popova and Sytina (1977) findings. By trial and error it was possible to demonstrate a hypothetical 40% increase in weight during a year (May-April) with food intake corresponding to the quoted seasonal pattern.

TABLE 72: Monthly Food Intake Expressed as Percentage of a 1000g Zanders Bodyweight, to enable a 40% Increment in Weight

Month	Temp.	Estimated Monthly Intake as a Percentage of Bodyweight in addition to maintenance ration	Increments starting at 1000g
May	13 C	30%	1036.9 g
June	18 C	5%	1072
July	19 C	5%	1108
August	19 C	5%	1145
September	16 C	7.65%	1190
October	12 C	7.65%	1229
November	8 C	7.65%	1256
December	5 C	1.0%	1266
January	5 C	1.0%	1276
February	7 C	1.0%	1283
March	8 C	10%	1322
April	10 C	20%	1401

1000g food equals 401g increment

In order to show a 40.1% weight increment, typical of a well nourished zander population, a 1000g zander would require 1627.4g of prey for maintenance plus 1000g of additional prey. This gives a requirement of 263% of the bodyweight per year. This conforms well with Popova and Sytina's estimate of 200 - 250% of the bodyweight. Fortunatova and Popova (1973) notes that 3 to 4 year old zander consume 224% of their bodyweight in a year. The possibility that Russian zander show slower growth may account for a reduced food requirement compared with the zander in this study.

Though such a hypothetical investigation of the zander's food requirement fails to take into account many variables, such as type of food, individual genetic variation and the age and sexual maturity of the fish, it is apparent that the figures derived in the laboratory can be combined with the available data on zander feeding, to give confirmation of earlier studies such as those of Fortunatova and Popova (1973) and Popova and Sytina (1977).

PART 4

CONCLUDING DISCUSSION

The various aspects of the ecology of the zander require consideration in relation to each other rather than in isolation. It is also necessary to consider the zander in relation to the other major predatory fish native to this country, the pike.

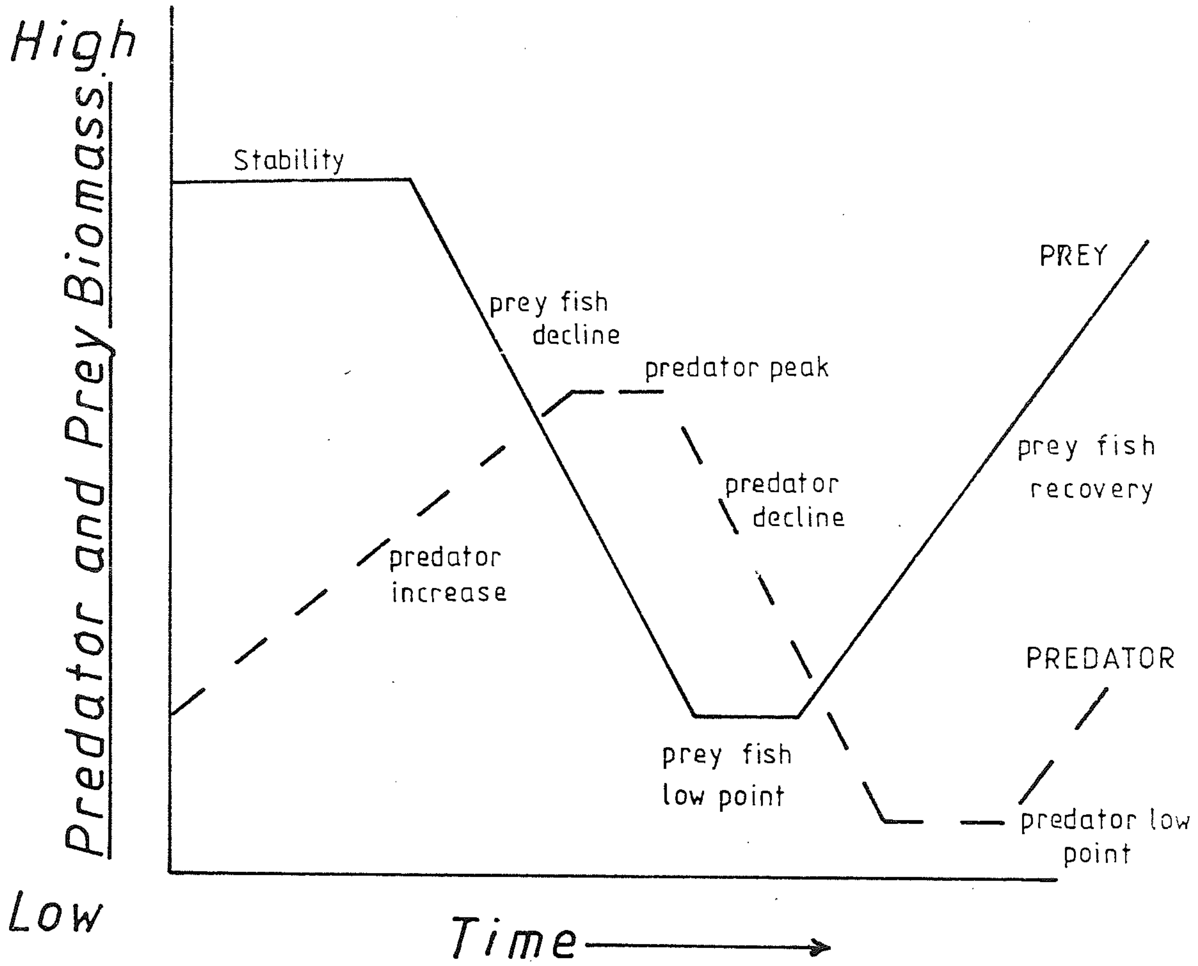
The most obvious underlying theme, noticeable throughout this work, was the variation in growth, condition and feeding of the zander populations studied. It has been mentioned earlier (1.2) that many of the zander populations existing in this country are relatively new, few except the Woburn and Claydon populations having been in existence for longer than 21 years. It might be suggested that the wide variations in growth and condition of zander may be due to a comparative lack of stability between predator and prey populations. This instability may have been caused primarily by the introduction of the zander. Unfortunately drastic changes in zander growth and condition are also typical of well established zander populations, notably Lake Balaton in Hungary (Biro 1969, 1970, 1972, 1973 and 1977). Neither is the existence of predator prey imbalances confined to fish populations containing zander. Instances of predator prey imbalances have been noted by the present author in fisheries where pike are the major predator. The loss of large numbers of perch due to an Aeromonad bacterial infection would appear to have caused predator prey imbalance in some of the water storage reservoirs of North London (Palmer pers. comms.)

Instability of predator-prey populations lead inevitably to oscillations in predator and prey numbers and biomass. During the period of study, several different waters appeared to be in stages of oscillation (Figure 84). It is suggested that the Relief Channel in 1979 and 1980 was in the decline phase for both predator and prey. This phase was typified by slowed growth (2.2) of zander and poor condition and fat content (2.6). Prey fish numbers were low (Anglian Water Authority Survey Data). Zander numbers were also in decline (2.5). The nearby Middle Level system would also appear during 1979 and 1980 to have been in the decline phase for prey fish, although the downward fall in fishing results is likely to be halted due to remedial action taken by the Anglian Water Authority. This involved the removal of 80% of the predators in the system. The other fisheries studied, such as Coombe Abbey Lake, appeared to be too recently colonized by zander to enable identification of any changes in the predator prey dynamic equilibrium. With continued removal of zander from this fishery it is unlikely that any meaningful pattern will emerge.

It is perhaps too early in the zander's history in this country to determine whether or not instability will eventually give way to relative stability without man's intervention. The time scale to the achievement of relative stability is also unclear. So far the length of each complete oscillation has, for the Relief Channel, been 6 to 10 years, (based on changes in zander condition, 2.6) with no signs as of yet of a reduced magnitude to each oscillation. In future when zander colonise new waters it will be important to monitor the developments within a fishery in an attempt to prevent changes in the predator-prey equilibrium. This study has provided sufficient base line data on the growth and condition of the zander to enable conclusions to be made on the growth and condition of

Figure 84.

Predator-Prey Oscillation.



future zander populations. This it is hoped will lead to more efficient fisheries management strategies aimed at optimising both predator and prey stocks.

It is interesting to speculate as to why zander should contribute to instability in a fishery. Assuming that most well established fisheries with pike as the major predator are fairly stable, why should the introduction of another predator, the zander, lead to changes in the predator-prey equilibrium? The means by which pike and prey fish populations maintain themselves in equilibrium are poorly documented, although it is likely that mortality and recruitment of pike is dependent on abiotic factors, such as temperature and water conditions affecting the pike directly, and also indirectly via the prey fish (Le Cren 1965). Mortality and recruitment of pike is likely to depend on the availability of food and the degree of self control of pike populations is likely again to be influenced by prey fish availability.

Cannabalism by pike is likely to be most intense when the ratio of young pike to other prey fish is high, leading effectively to population control. The stability of a predator-prey population is likely to be maintained provided recruitment of predators or prey remain within limits. Poor prey fish recruitment may cause a temporary increase in cannabalism amongst pike and increased mortality due to starvation amongst older fish. The introduction of another predator such as the zander may change the type or degree of predation on the prey fish population.

Any differences in the type of predation will also cause changes in the prey fish population. One of the most important differences between the pike and the zander, is the size of prey consumed. Pike have larger jaws than zander, and this means that, for any given length, a pike will be able to consume a larger prey fish than a zander. Keast and Webb (1966) found that pike have a mouth gape of 14.5% the bodylength, while perch have a mouth gate of only 8%. From this present research it was noted that zander have a mouth gape of 11.3% of the bodylength. Pike have also been noted by various authors to swallow prey fish in excess or near to their own bodylength. Lawler (1965) notes that one pike of 380 mm swallowed a burbot (Lota lota L.) of 460 mm while another pike consumed a whitefish (Coregonus sp.) of 30 mm less than its own length of 360 mm. Such large swallows have never been noted during this study of the zander and it is obvious that jaw size is of considerable importance in the swallowing of large prey. The larger jaw size of the pike means that a wider range of prey sizes can be consumed. This may mean that the pike is a more versatile predator than the zander. However the zanders preference for small prey fish may mean that it is more highly specialised in the capture of small prey. It can therefore be suggested that certain types of prey populations will favour either predator. Unfortunately neither predator is so specialised that it has a totally different prey fish size requirement, therefore an element of competition is bound to exist between pike and zander.

The selective predation of the smaller prey fish by zander may cause changes in the structure of the prey fish population.

This may have been the cause of the unusual prey fish population noted by Linfield and Rickards on the Relief Channel (pre 1975). Here the population consisted of mainly large cyprinids presumably too large to be eaten by zander though not entirely inaccessible to pike predation. Very strong year classes of prey fish followed by weak ones has also been a feature of the Relief Channel prey fish populations. It is suggested that this may lead to strong year classes of zander. However once a large population of zander has come into existence it is likely that zander numbers will not fall quickly enough to avoid serious overpredation on small prey fish. This lag behind the prey fish population is shown in Figure 84. A feature of zander populations which are existent during a period of prey fish scarcity is the wide range of prey fish eaten and the larger quantities of invertebrates consumed. Unusually, eels form a large proportion of the zanders diet in such situations (2.3), and it is possible that such feeding is as a last resort. Eels are certainly not an important part of the zanders diet in waters where other prey fish are still fairly common.

Competition for food between pike and zander might result in a decrease in numbers or biomass of both predators. The population estimates obtained during this study suggest that zander numbers and biomass have decreased and angling returns seem to indicate a similar decline in pike numbers/biomass.

There is little evidence to suggest that zander as yet contribute a major proportion of the predator biomass in the waters studied.

Anglian Water Authority surveys of the Relief Channel, Great Ouse and Middle Level systems have shown that pike are more strongly represented than zander. Competition between the pike and zander would therefore appear not to be to the exclusion of either species.

The food requirements of zander populations cannot at present be precisely determined, due to the limited size range of fish used in experimental work. Further experimental work is required to enable determination of any differences in maintenance requirements and conversion efficiencies. However it has been shown that the Relief Channel zander population of 1979 required approximately 0.43 to 2.07 gm/m^2 of prey fish to meet their maintenance requirements. This estimate is based on the maintenance requirement of a hypothetical 1000g zander during a year. The available prey fish biomass as ascertained from Anglian Water Authority surveys was 0.42 gm/m^2. If the assumptions that survey results were realistic and that 1000g zander have similar maintenance requirements to those existing in the Relief Channel in 1979 hold true, then it is apparent that prey fish were available in sufficient numbers to meet the maintenance requirement of the zander alone. The fact that other predators such as pike were in competition for these prey fish suggests that the zander population was likely to continue to be short of prey. This was confirmed in 1981 when very few zander were captured and it is suggested that many zander died or migrated during the winter of 1980-1981.

The zanders large home range and ability to move considerable distances, suggests that invasion and colonisation of new waters will continue to be rapid. Whether such rapid movement over long distances is a specific trait of zander and atypical of pike is unclear, as similar marking studies have been few and limited mainly to those of the present author. The observations made indicated that pike could move $1\frac{1}{2}$ to 3 km during periods of 30 to 60 days, with maximum rates of movement of 1.02 km/day compared to the zanders maximum of 2.87 km/day on the same water (Relief Channel). Without more detailed research into the movements of pike in rivers and drains, comparisons between pike and zander are unlikely to prove useful.

This study provided basic information on most aspects of the zanders ecology. Where information is scarce and available data limited, little could be done to improve the input to this work, at least with the resources available. Further studies of the zander will no doubt concentrate on particular aspects of the zanders ecology and in so doing will investigate these aspects in greater detail. Originally this study had intended to carry out additional lines of investigation and it will be worthwhile mentioning these.

During the early stages of this study a suitable lake was found with an owner willing to have zander introduced as an experiment. The water located near to the River Severn was well concealed and on private land. It was anticipated that a complete survey of the water would precede the introduction of a known weight and number of zander. The water would then be monitored in order to discern any changes in the prey fish populations caused by the zander. Such a study was likely to be a long term research project, but it was felt that some data would have been available after two years, with the option of other research workers carrying on the work. Unfortunately the projected study failed to proceed beyond the outline stage, due partly to the sensitive nature of new zander introductions and the difficulty in obtaining sufficient zander for all research requirements.

Due to the difficulty in obtaining zander it is likely that further research will be of a mainly experimental nature, confined to the laboratory. Studies of zander populations in the wild, on a comparable scale to Lawler's (1966) work on pike will demand considerable numbers of zander. Lawler examined 29,000 (American) pike during his work and it is unlikely that this quantity of zander exists in any one water. Furthermore without considerable funds, the collection of such numbers of zander would be impossible. Laboratory studies will hopefully establish the importance of prey fish preference caused by the individual body depth-length relationships. Also in extensive controlled conditions it might also be possible to confirm or deny, the selective predation on certain species of prey fish.

Field studies need not be totally discounted as there are some approaches which can be pursued provided suitable equipment is available. The use of sonic tracking equipment has already been used extensively to study the pike of Staunton Harold Reservoir in Derbyshire (White unpublished). A similar study conducted on the zander would give a greater insight into the zanders daily activity and also its longer term movements.

ACKNOWLEDGEMENTS

This study of the Ecology of the Zander would not have been possible without the help of a large number of individuals, public bodies and angling clubs. Foremost amongst the individuals I must thank my supervisor Dr. R.L.G. Lee for his guidance of my work and his constructive criticism through the study. Mr. F. Hargreaves and Mrs. H. Barbour duly thanked for assistance with the final manuscript and production of most of the plates. My wife Dr. K. Fickling provided invaluable assistance, translating several German and French scientific papers and helping with statistical analysis of the data. The work in the field would not have been possible without the help of many anglers. I would like to mention individually those who made the most significant contribution to this work. These were Dr. D. Moore and Mr. B. Moore, Mr. M. Brown, R. Jackson, D. Phillips, L. Strudwick, G. Whilley, P. Burton, A. Johnson and A. Beat.

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APPENDIX I: Population growth rates with 95% confidence limits
Figures in brackets denote sample numbers

Water	Period	Sex	Fork Length for Age with 95% Confidence Limits 1	2	3	4	5	6
Relief Channel	1969-70	M&F	114 (1)	235 (2)	329 (4)	406 (4)	533 (7)	651
			-	159-311	300-357	396-417	488-579	637-
	1969-70	F	-		349 (1)	414 (16)	569 (3)	652
			-	-		400-427	435-704	636-
	1969-70	M	-	-	392 (3)	450 (8)	507 (4)	641
			-	-	377-408	434-466	465-548	---
	1975-76	M&F	-	255 (2)	376 (2)	439 (7)	470 (13)	549
			-	± 494	370-382	417-461	448-492	514-
	1979-80	M&F	-	255 (15)	414 (17)	477 (51)	547 (58)	602
			-	225-285	381-467	459-495	537-557	591-
	1979-80	F	-	243 (8)	427 (6)	455 (10)	549 (11)	540
			-	202-284	392-463	415-495	515-583	58-1
	1979-80	M	-	279 (5)	390 (8)	446 (10)	545 (13)	595 (
			-	200-358	321-459	389-503	525-565	569-
Middle Level	1979-80	M&F	110 (17)	240 (2)	356 (43)	532 (15)	589 (33)	65[illegible] (
			98-122	± 616	349-363	514-550	574-604	641-
	1979-80	F	145 (2)	288 (1)	353 (21)	547 (3)	603 (9)	654 (
			± 279	-	332-374	335-759	573-633	616-
	1979-80	M	102 (2)	288 (1)	355 (22)	540 (9)	564 (6)	617 (
			± 134	-	327-383	518-562	516-612	-
Burwell Lode	1979	M&F	-	-	-	463 (6)	526 (4)	
			-	-	-	436-490	486-566	
Oxford Canal	1978-79	M&F	100 (3)	198 (5)	301 (3)	358 (7)	445 (8)	534 (
			72-128	123-283	130-472	325-391	422-468	--- -
Coombe Abbey	1979-80	M&F	-	234 (24)	389 (45)	500 (5)		
				218-319	375-404	468-532		
	1979-80	F	-	229 (8)	394 (24)	500 (5)		
			-	191-267	373-415	468-532		
	1979-80	M	-	258 (4)	395 (13)			
			-	202-314	374-416			
Stewartby	1980	M&F	-	-	250 (1)	345 (6)	416 (4)	
			-	-		286-404	358-474	

APPENDIX I

Back-calculated lengths for year class of Relief Channel (1979) Zander

1967	1	2	3	4	5	6	7	8	9	10	11	12	years
	---	218	340	505	561	627	671	715	749	782	815	826	

1968	1	2	3	4	5	6	7	8	9	10	11	years
	---	202	380	508	585	665	688	746	764	811	836	

1970	1	2	3	4	5	6	7	8	9	years
	--	206	312	427	525	585	626	687	762	
	110	220	306	392	466	532	618	647	681	
	--	199	311	438	553	589	655	710	725	
	--	--	377	426	566	616	666	689	698	
	94	244	315	386	499	539	577	638	710	

1971	1	2	3	4	5	6	8	8	years
	95	236	314	470	545	616	679	730	
	93	170	281	378	483	570	646	691	
	81	174	326	489	571	628	690	725	
	87	199	243	333	427	465	514	561	
	--	--	306	454	530	616	672	717	
	136	242	346	427	506	567	655	720	
	99	260	347	443	523	627	683	745	
	--	295	366	473	517	622	687	709	
	119	234	349	427	501	624	698	728	

1972	1	2	3	4	5	6	7	years
	80	189	264	332	430	485	546	
	97	246	336	445	481	541	574	
	92	248	365	409	523	581	643	
	77	158	279	423	467	544	609	
	88	235	316	374	460	513	563	
	101	206	327	459	506	546	647	
	77	237	337	479	518	572	632	
	81	202	304	450	486	544	620	
	90	210	298	387	497	601	658	
	84	222	322	457	503	563	627	
	88	196	305	382	509	597	639	
	--	295	366	473	517	622	687	
	99	191	291	464	512	585	661	
	118	311	420	560	612	634	683	
	87	250	329	412	530	571	625	
	83	230	340	415	504	536	589	

APPENDIX I (continued)

Back-calculated lengths for year class of Relief Channel (1979) Zander

1973	1	2	3	4	5	6	years
	74	224	340	455	547	593	
	95	192	315	467	545	596	
	77	175	316	472	551	613	
	70	198	310	410	551	623	
	90	163	295	352	460	550	
	85	222	293	441	509	605	
	--	141	318	436	510	561	
	79	218	299	386	463	523	
	95	192	315	467	545	596	
	91	196	311	434	539	583	
	96	220	338	406	462	571	
	--	317	461	526	579	644	
	--	193	349	462	550	632	
	88	215	348	465	582	652	
	90	193	285	411	451	568	
	--	--	344	454	524	600	
	220	287	347	487	557	628	
	85	178	268	420	524	615	
	106	301	451	494	572	626	
	85	240	297	445	543	605	
	91	203	305	466	567	655	
	96	168	312	498	561	570	
	--	--	318	418	510	589	
	139	331	484	555	611	631	
	82	182	294	423	526	572	
	--	173	284	441	541	604	
	86	200	359	421	598	589	
	116	229	411	487	592	642	
	146	294	407	472	580	616	
	87	220	317	496	544	605	
	91	230	309	486	531	601	

1974	1	2	3	4	5	years
	76	155	251	380	450	
	93	204	357	508	547	
	97	197	333	496	567	
	160	283	353	512	568	
	111	177	313	491	508	
	124	243	379	528	570	
	176	256	430	485	562	
	86	184	309	473	552	
	--	--	273	449	522	
	69	140	297	492	542	
	--	236	317	420	484	
	77	174	271	397	515	
	91	172	320	485	566	
	98	191	388	484	548	
	111	177	312	458	506	
	151	224	365	445	511	
	92	173	324	501	566	
	135	225	322	477	540	
	114	166	250	374	453	
	101	195	349	511	571	
	100	174	290	460	538	
	--	250	432	531	596	
	76	152	318	447	520	
	90	174	294	451	534	
	167	258	423	551	627	
	80	173	320	496	578	
	--	--	318	497	555	
	111	191	330	494	578	
	91	170	310	494	564	
	96	213	352	528	586	
	79	190	343	476	557	
	--	228	408	527	599	
	106	176	301	446	505	
	134	236	399	483	559	
	--	191	325	492	560	
	--	166	312	464	519	
	179	254	376	443	484	
	--	171	308	468	549	
	119	250	444	495	528	
	--	--	292	472	540	
	136	237	376	555	672	
	87	205	333	455	561	
	89	183	329	469	534	
	88	200	308	463	541	

APPENDIX I (continued)

Back-calculated lengths for year class of Relief Channel (1979) zander

1975	1	2	3	4 years
	162	296	482	566
	106	192	315	484
	85	188	317	471
	85	159	290	477
	113	327	443	502
	166	285	466	523
	82	145	271	422
	--	151	259	454
	85	207	334	512
	141	207	316	401
	133	165	293	446
	168	265	338	488
	74	123	269	456
	94	191	314	472
	74	123	269	453
	--	180	333	469
	91	174	314	490
	111	189	286	425
	111	209	335	504
	67	154	323	430
	104	170	321	471
	171	298	477	494
	103	350	529	593
	102	161	245	373
	98	175	293	441
	86	177	317	503
	153	270	406	550
	81	192	316	501
	115	262	392	521
	76	139	321	441
	122	262	438	484
	88	247	398	535
	112	250	414	501

1976	1	2	3 years
	130	270	352
	122	274	453
	156	310	410
	145	346	457
	114	277	395
	174	310	485
	123	277	396
	138	295	496

APPENDIX I (continued)

Back-calculated lengths for year class of Coombe Abbey Lake zander

1975	1	2	3	4	Sex
	128	208	314	466	F
1976	1	2	3	4	
	85	232	403		F
	81	220	420		F
	103	229	398		F
	82	228	401		F
	103	257	422		F
	108	257	425		M
	97	251	422		F
	90	234	401		M
	129	383	420		F
	98	269	415		M
	92	216	400		M
	95	241	418		F
	93	230	390		F
	93	234	390		M
	93	243	410		F
	100	249	419		?
	102	251	421		?
	98	247	417		?
	95	231	364		M
	116	249	404		M
	97	238	402		F
	97	254	396		M
	107	256	405		F
	83	241	392		M
	103	250	416		M
	127	290	431	530	F
	73	216	372	482	F
	--	241	410	512	F
	76	232	407	510	F

APPENDIX I (continued)

Back-calculated lengths for year class of Coombe Abbey Lake zander

1977				1978		
1	2	3	Sex	1	2	Sex
91	260		M	100	215	F
91	244		F			
83	219		M			
126	306		F			
83	182		F			
108	251		I			
62	226		I			
112	246		I			
72	186		I			
77	198		?			
81	209		?			
83	214		?			
83	214		?			
85	219		?			
92	236		?			
135	288	430	M			
122	291	419	F			
100	239	369	M			
83	174	265	I			
141	319	440	F			
119	275	413	M			
94	257	425	F			
133	290	446	F			
130	282	435	F			
111	252	410	F			
101	235	355	F			
106	200	305	I			
116	268	410	F			
106	261	400	F			
88	193	273	F			
109	187	276	F			
96	230	355	M			
99	244	325	M			
79	192	266	F			
78	179		M			
131	267		?			
120	281		?			
119	262		F			
114	250		M			
135	225		F			
102	238		F			
100	304		M			
90	160		F			

APPENDIX I (continued)

Back-calculated lengths of year class of Middle Level (1979) zander

1972

1	2	3	4	5	6	7 years
--	306	445	569	617	665	686
179	335	460	578	619	646	683
--	309	397	466	562	598	620

1973

1	2	3	4	5	6 years
179	347	514	626	671	708
111	332	476	556	617	660
--	304	458	564	590	623
179	337	485	590	607	650
114	342	479	587	629	687
108	316	454	562	608	635
142	293	461	548	618	639
114	299	360	484	551	602
200	356	464	549	653	691
186	349	511	578	621	650
183	347	518	613	646	678
176	329	485	576	616	638
199	362	433	515	597	676
174	324	475	574	613	649

1974

1	2	3	4	5 yrs
154	204	469	567	605
99	253	454	528	598
84	297	440	507	547
269	329	452	529	592
93	270	441	519	549
114	318	510	598	626
135	235	409	506	580
140	293	468	564	630
--	257	440	516	569
151	294	433	553	597
151	282	429	515	563
68	256	438	510	560
149	278	421	473	558
109	262	452	528	579
211	325	511	568	625
175	333	472	573	622
190	343	496	565	638
165	319	467	567	601
96	281	471	537	579
98	256	439	553	603
150	361	474	590	651
180	335	468	564	598
103	234	417	502	533
106	278	473	562	603
189	363	514	599	647
89	231	420	510	552
93	279	453	526	559
--	--	516	597	656

1975

1	2	3	4 years
--	246	373	478
240	429	503	544
205	289	423	462
155	334	466	547
98	295	441	531
84	258	441	525
101	271	485	571
161	318	467	544
91	261	447	510
92	256	458	553
127	300	429	501
103	269	456	545
85	277	439	532

1976

1	2	3	1	2	3	1	2	3 yrs
118	225	332	142	263	377	150	279	417
170	303	461	154	294	439	192	222	337
141	280	425	106	148	280	160	273	399
136	275	420	147	189	336	113	188	308
131	270	416	111	161	257	92	164	298
149	248	367	106	178	293	168	281	407
158	202	317	160	224	336			

1977

1	2 yrs
151	288

1978

1 yr
108
95

APPENDIX I (continued)

Back-calculated lengths for year class of Twenty Foot Drain and King's Dyke zander (1979)

1976	1	2	3	1	2	3	1	2	3 yrs
	76	136	199	147	239	335	--	214	363
	127	263	356	126	219	397	150	248	345
	168	282	399	166	274	377	123	266	427
	141	233	335	150	265	377	125	232	357
	135	222	313	128	225	361	144	281	437
	135	235	357	--	175	315	159	275	368
	143	234	341	--	186	307	127	219	347

1977	1	2 yrs
	130	191

1978	1	1 yrs
	159	167
	131	92
	121	113
	123	96
	106	96
	95	103
		103

APPENDIX II

Results of Significance Tests

Relief Channel 1979

Year classes compared	t	p	df	significance
		YEAR 1		
1970-1971	0.04	> 0.5	7	
1970-1972	1.52	> 0.1	15	
1970-1973	0.16	> 0.5	25	
1970-1974	0.3	> 0.5	31	
1970-1975	0.3	> 0.5	31	
1970-1976	2.37	< 0.05	8	1976 > 1970
1971-1972	1.86	> 0.05	20	
1971-1973	0.24	> 0.5	30	
1971-1974	0.59	> 0.5	40	
1971-1975	0.58	> 0.5	36	
1971-1976	3.57	< 0.01	13	1976 > 1971
1972-1973	1.08	> 0.1	38	
1972-1974	2.37	< 0.02	38	1974 > 1972
1972-1975	2.39	< 0.05	44	1975 > 1972
1972-1976	7.55	< 0.001	21	1976 > 1972
1973-1974	1.25	> 0.1	58	
1973-1975	1.22	> 0.1	54	
1973-1976	3.01	< 0.01	41	1976 > 1973
1974-1975	0.01	> 0.5	64	
1974-1976	2.66	< 0.02	41	1976 > 1974
1975-1976	2.59	< 0.02	37	1976 > 1975
		YEAR 2		
1970-1971	0.39	> 0.5	10	
1970-1972	0.46	> 0.5	18	
1970-1973	0.01	> 0.5	31	
1970-1974	0.95	> 0.1	43	
1970-1975	0.29	> 0.1	37	
1970-1976	5.2	> 0.001	10	1976 > 1970
1971-1972	0.52	> 0.5	22	
1971-1973	0.58	> 0.5	35	
1971-1974	1.91	> 0.05	47	
1971-1975	0.79	> 0.1	39	
1971-1976	3.86	< 0.01	14	1976 > 1971
1972-1973	0.68	> 0.5	43	
1972-1974	2.48	> 0.02	55	
1972-1975	1.09	> 0.1	47	
1972-1976	4.44	< 0.001	22	1976 > 1972
1973-1974	1.71	> 0.05	70	
1973-1975	0.62	> 0.5	62	
1973-1976	4.43	< 0.01	35	1976 > 1973
1974-1975	0.74	> 0.1	72	
1974-1976	8.4	< 0.001	47	1976 > 1974
1975-1976	3.95	< 0.001	39	1976 > 1975

APPENDIX II (continued)

Relief Channel 1979

Year classes compared	t	p	df	significance
		YEAR 3		
1970-1971	0.22	>0.5	12	
1970-1972	0.04	>0.5	19	
1970-1973	0.47	>0.5	34	
1970-1974	0.52	>0.5	49	
1970-1975	0.67	>0.5	36	
1970-1976	4.26	<0.01	11	1976 > 1970
1971-1972	0.32	>0.5	23	
1971-1973	0.81	>0.1	38	
1971-1974	1.04	>0.1	51	
1971-1975	1.05	>0.1	40	
1971-1976	5.13	<0.001	15	1976 > 1971
1972-1973	0.7	>0.1	45	
1972-1974	0.8	>0.1	58	
1972-1975	1.12	>0.1	47	
1972-1976	5.8	<0.01	22	1976 > 1972
1973-1974	0.02	>0.5	73	
1973-1975	0.82	>0.1	75	
1973-1976	4.52	<0.001	37	1976 > 1973
1974-1975	0.82	>0.1	75	
1974-1976	5.24	<0.001	50	1976 > 1974
1975-1976	3.01	<0.01	39	1976 > 1975
		YEAR 4		
1970-1971	0.79	<0.1	12	
1970-1972	0.76	<0.1	19	
1970-1973	2.06	>0.05	34	1973 > 1970
1970-1974	3.57	>0.001	47	1974 > 1970
1970-1975	3.12	>0.01	36	1975 > 1970
1971-1972	0.005	<0.5	22	
1971-1973	1.25	<0.1	38	
1971-1974	3.01	>0.01	51	1974 > 1971
1971-1975	2.68	>0.02	40	1975 > 1971
1972-1973	1.78	<0.05	45	
1972-1974	3.6	>0.001	58	1974 > 1972
1972-1975	3.2	>0.01	47	1975 > 1972
1973-1974	2.6	>0.001	73	1974 > 1973
1973-1975	2.43	>0.05	62	1975 > 1973
1974-1975	0.24	<0.5	75	
		YEAR 5		
1970-1971	0.46	>0.5	12	
1970-1972	0.91	>0.1	19	
1970-1973	0.91	>0.1	34	
1970-1974	1.27	>0.1	47	
1971-1972	0.49	>0.5	23	
1971-1973	1.84	>0.05	38	
1971-1974	2.4	<0.01	54	1974 > 1971
1972-1973	2.94	<0.01	45	1973 > 1972
1972-1974	3.65	<0.001	58	1974 > 1972
1973-1974	0.71	>0.1	73	

APPENDIX II (continued)

Relief Channel 1979

Year classes compared	t	p	df	significance
		YEAR 6		
1970-1971	0.77	> 0.1	12	
1970-1972	0.38	> 0.5	19	
1970-1973	0.58	> 0.5	34	
1971-1972	1.51	> 0.1	23	
1971-1973	0.23	> 0.5	38	
1972-1973	0.31	> 0.5	45	
		YEAR 7		
1970-1971	1.06	> 0.1	12	
1970-1972	0.16	> 0.5	19	
1971-1972	1.69	> 0.1	23	
		YEAR 8		
1970-1971	1.06	> 0.1	12	

Middle Level 1979-80

Year classes compared	t	p	df	significance
		YEAR 1		
1973-1974	1.48	> 0.1	37	
1973-1975	1.71	> 0.05	23	
1973-1976	1.77	> 0.05	29	
1974-1975	0.12	> 0.5	36	
1974-1976	0.16	> 0.5	42	
1975-1976	0.7	> 0.1	28	
		YEAR 2		
1972-1973	1.05	> 0.1	15	
1972-1974	1.16	> 0.1	28	
1972-1975	0.83	> 0.1	14	
1972-1976	2.56	< 0.02	19	1976 > 1972
1973-1974	3.62	< 0.001	39	1973 > 1974
1973-1975	2.67	< 0.02	25	1973 > 1975
1973-1976	6.2	< 0.02	30	1973 > 1976
1974-1975	0.14	> 0.5	38	
1974-1976	3.9	< 0.001	43	1974 > 1976
1975-1976	2.97	< 0.01	29	1975 > 1976
		YEAR 3		
1972-1973	1.46	> 0.1	15	
1972-1974	1.35	> 0.1	29	
1972-1975	0.69	> 0.5	14	
1972-1976	2.79	< 0.02	19	1972 1976
1973-1974	1.00	> 0.1	40	
1973-1975	1.58	> 0.1	25	
1973-1976	5.29	< 0.001	30	1973 1976
1974-1975	1.07	> 0.1	39	
1974-1976	6.6	< 0.001	44	1974 1976
1975-1976	4.2	< 0.001	29	1975 1976

APPENDIX II (continued)

Middle Level 1979-80

Year classes compared	t	p	df	significance
		YEAR 4		
1972-1973	1.08	> 0.1	15	
1972-1974	0.27	> 0.5	29	
1972-1975	0.5	> 0.5	14	
1973-1974	1.96	> 0.05	40	
1973-1975	3.06	< 0.01	25	1973 > 1975
1974-1975	1.64	< 0.05	39	1974 > 1975
		YEAR 5		
1972-1973	0.41	> 0.5	15	
1972-1974	1.75	> 0.1	29	
1973-1974	1.58	> 0.1	40	
		YEAR 6		
1972-1973	1.05	> 0.1	15	

Coombe Abbey 1979-80

Year classes compared	t	p	df	significance
		YEAR 1		
1976-1977	1.16	> 0.1	71	
		YEAR 2		
1976-1977	0.99	> 0.1	72	
		YEAR 3		
1976-1977	2.97	< 0.001	46	1976 > 1977

Appendix III

ZANDER RESEARCH

The following information would be appreciated on the capture of any tagged zander :

(1) Exact Weight

(2) Length to fork of tail

(3) Number of tag. It pays to write the number down if possible as many helpers have muddled numbers.

(4) Place and date of capture (precise location as near as you feel able).

(5) Condition of fish, live or dead.

Information should be sent to :

Neville Fickling,
Dept. of Biological Sciences,
University of Aston,
Gosta Green,
Birmingham B4 7ET.

Postage will be refunded and the helper will be kept informed of zander movements.

APPENDIX IV.

Mark and Recapture Data Presented Under Original Capture Sites.

RELIEF CHANNEL.

Denver - Downham 1st Drain.

TAG NO.	DISTANCE MOVED KM	DAYS AT LIBERTY	RATE OF MOVEMENT	DIRECTION	FORK LENGTH	DATE OF RELEASE
264213	2.87	1	2.87km/d	downstream	570	22-9-78
264401	1.2	7	0.41km/d	downstream	610	25-6-79
263983	3.2	316	0.01km/d	downstream	635	10-7-79
264429	3.3	20	0.17km/d	downstream	641	30-6-79
Downham - Stow Stones E.						
263971	6.08	62	0.1km/d	downstream	533	22-7-78
263890	0.16	59	0.003km/d	downstream	798	3-8-78
264309	0.31	286	0.001km/d	downstream	597	28-7-79
264311	0	1	0		559	22-7-79
264602	0.5	37	0.014km/d	downstream	680	3-9-79
Downham - Stow Drain 24E.						
263981	5.77	25	0.23km/d	downsteam	589	11-7-78
263983	2.87	74	0.04km/d	upstream	635	10-7-78
263984	2.87	74	0.04km/d	upstream	558	11-7-78
263992	2.87	24	0.12km/d	upstream	445	10-7-78
263994	9.51	No details.		downstream	533	10-7-78
263996	9.2	19	0.48km/d	downstream	678	10-7-78
264414	3.0	15	0.20km/d	downstream	540	26-6-79
263993	0.31	356	0.001km/d	upstream	533	10-7-78
264401	3.1	7	0.4km/d	upstream	610	25-6-79
263895	2.87	367	0.008km/d	upstream	530	9-7-78
263990	2.7	372	0.007km/d	downstream	608	10-7-78
1571	2.9	59	0.05km/d	upstream	590	4-8-79
264441	0	28	0		629	1-7-79
264448	9.2	9	1.02km/d	downstream	775	30-6-79
264483	3.4	31	0.11km/d	upstream	695	20-7-79
264489	7.4	52	0.14km/d	downstream	660	4-8-79
264496	0.3	18	0.017km/d	upstream	545	22-7-79
264418	0.5	67	0.008km/d	upstream	660	25-6-79
264427	0.31	10	0.031km/d	upstream	603	1-7-79
264429	3.3	20	0.17km/d	upstream	641	30-6-79
264431	0.31	No details.		upstream	622	30-6-79
264433	9.51	49	0.19km/d	downstream	591	1-7-79
264401	2.87	7	0.41km/d	upstream	610	25-6-79
264406	0	22	0		533	30-6-79
264409	3.37	32	0.11km/d	upstream	573	30-6-79
264411	0	26	0		622	27-6-79
264411	1.63	7	0.23km/d	upstream	622	22-7-79
264411	1.32	15	0.09km/d	downstream	622	5-8-79
264077	0	132	0		584	11-3-79
264077	0	9	0		584	20-7-79
264077	0.31	11	0.028km/d	upstream	584	29-7-79
264306	0	8	0		675	28-7-79

APPENDIX IV.(continued)

TAG NO.	DISTANCE MOVED KM	DAYS AT LIBERTY	RATE OF MOVEMENT	DIRECTION	FORK LENGTH	DATE OF RELEAS
Downham - Stow Drain 24E.						
264309	0.31	36	0.009km/d	upstream	597	28-7-79
1558	0	259	0		840	25-10-79
1558	0	6	0		840	9-8-80
264491	0	383	0		730	20-7-79
263983	0	286	0		635	21-10-78
264079	0	356	0		572	25-6-79
264079	0	17	0		572	16-6-80
264079	0	42	0		572	3-7-80
264161	0	247	0		750	10-10-79
264332	2.22	354	0.006km/d	downstream	690	7-7-79
264332	0	30	0		690	28-6-80
264439	0	340	0		800	21-7-79
264439	0	19	0		800	16-6-80
264602	0	54	0		690	16-6-80
264423	0.6	776	0.001km/d	upstream	641	25-6-79
264634	1.32	10	0.132km/d	upstream	642	25-10-79
264602	0	244	0		665	12-10-79
264485	35.8	59	0.61km/d	upstream	500	20-7-79
		via Denver Sluice.				
			0.8km/d	upstream		
		via Tail Sluice.				
Downham - Stow 40E.						
264551	0.1	17	0.006km/d	upstream	697	22-7-80
264634	0.15	231	0.001km/d	upstream	642	23-10-79
264432	0.75	60	0.013km/d	upstream	641	22-7-79
Stow - Downham 85E.						
1566	1.2	69	0.017km/d	upstream	610	5-8-79
264297	7.9	262	0.03km/d	downstream	600	28-10-78
264296	1.3	243	0.005km/d	upstream	660	28-10-78
264293	1.6	19	0.086km/d	upstream	645	28-10-78
Stow - Downham 164W.						
264209	1.9	282	0.007km/d	upstream	620	19-9-78
264212	7.3	294	0.025km/d	downstream	680	19-9-78
264247	1.9	313	0.006km/d	upstream	580	20-9-78
263919	2.3	391	0.006km/d	upstream	690	24-7-78
Stow - Magdalen Railway Bridge 52W.						
264551	3.5	30	0.17km/d	upstream	697	23-6-80
Runcton Holme.						
263888	3.44	54	0.064km/d	upstream	628	28-7-78
Magdalen Railway Bridge - Stow 168W.						
264073	0.1	44	0.002km/d	upstream	658	5-8-78
264345	5.77	295	0.02km/d	upstream	530	24-6-79
264412	3.55	365	0.01km/d	upstream	552	28-6-79
264413	3.2	5	0.64km/d	downstream	546	26-6-79
264414	3.0	26	0.16km/d	downstream	540	26-6-79
264424	0	32	0		584	26-6-79
Magdalen Railway Bridge - Stow 157E/W.						
264200	3.43	282	0.012km/d	downstream	690	10-9-78
264201	3.43	290	0.012km/d	downstream	585	21-9-78
264218	2.8	328	0.009km/d	upstream	625	10-9-78
264243	0.6	42	0.014km/d	downstream	495	15-7-79

APPENDIX IV. (continued)

TAG NO.	DISTANCE MOVED KM	DAYS AT LIBERTY	RATE OF MOVEMENT	DIRECTION	FORK LENGTH	DATE OF RELEASE
Magdalen Railway Bridge - Stow 157E/W						
264106	0	305	0		572	24-9-78
264276	3.43	303	0.011km/d	downstream	767	20-10-78
7931	6.68	46	0.15km/d	upstream	633	21-9-78
263905	3.43	50	0.07km/d	downstream	635	6-8-78
264143	0	46	0		705	7-8-78
264196	0	2	0		560	10-9-78
264202	3.43	32	0.11km/d	downstream	585	21-9-78
264205	2.85	10	0.29km/d	downstream	630	17-9-78
264054	8.64	23	0.38km/d	upstream	552	12-8-78
264221	3.43	176	0.02km/d	downstream	545	17-9-78
Magdalen Railway Bridge - Magdalen Road Bridge 190E.						
264324	6.88	260	0.027km/d	upstream	750	2-12-78
264324	2.5	14	0.18km/d	upstream	750	1-8-79
264415	2.0	5	0.4km/d	downstream	591	28-9-79
Magdalen Road Bridge North Side.						
264316	1.91	249	0.008km/d	downstream	620	1-11-78
264316	0	3	0		620	7-7-79
264316	0	4	0		620	10-7-79
264316	0	2	0		620	14-7-79
264316	0	1	0		620	17-7-79
St. Germans Zander Hotspot.						
264212	0	6	0		680	19-9-78
264297	0	1	0		600	28-10-78
264448	9.1	97	0.094km/d	upstream	775	30-6-79
263881	9.2	361	0.026km/d	upstream	538	24-7-78
263905	0	11	0		535	24-9-78
263905	0	283	0		535	6-8-78
263914	0	323	0		495	24-7-78
264451	8.9	9	0.99km/d	upstream	610	26-8-79
264465	9.0	56	0.16km/d	upstream	711	26-8-79
264463	2.04	29	0.07km/d	upstream	622	27-8-79
264495	0	30	0		638	2-8-79
264342	2.63	103	0.026km/d	upstream	585	26-6-79
264346	0	13	0		584	26-6-79
264346	0	8	0		584	8-7-79
264421	0	19	0		597	28-6-79
264421	0	10	0		597	16-7-79
264434	0	17	0		680	30-6-79
264434	0	20	0		680	4-8-79
264435	0	16	0		597	30-6-79
264498	0	5	0		563	10-7-79
263914	0	17	0		495	30-6-79
8440Y	10	27	0.37km/d	upstream	705	4-8-79
7947	9.5	15	0.63km/d	upstream	622	18-8-79
264192	0	301	0		683	24-9-79
264090	0	219	0		603	10-11-79
264090	0	10	0		603	16-6-79
264092	0	246	0		616	11-11-78
264096	0	33	0		718	24-6-79

APPENDIX IV. (continued)

TAG NO.	DISTANCE MOVED KM	DAYS AT LIBERTY	RATE OF MOVEMENT	DIRECTION	FORK LENGTH	DATE OF RELEASE
264096	0	52	0		718	26-7-79
264294	0	39	0		730	25-6-79
264337	6.8	20	0.34km/d	upstream	555	26-6-79
264445	0	9	0		584	30-6-79
264450	0	7	0		432	30-6-79
264450	1.91	16	0.12km/d	upstream	432	6-7-79
264450	7.54	19	0.4km/d	upstream	432	21-7-79
263914	0	27	0		495	16-7-79
264906	3.18	14	0.23km/d	upstream	490	22-7-78
263914	0	20	0		495	30-6-79
264058	0	60	0		640	3-9-78
264059	0	42	0		591	1-10-78
264117	1.91	39	0.05km/d	upstream	665	24-9-78
264119	3.43	28	0.12km/d	upstream	545	24-9-78
263886	3.43	19	0.18km/d	upstream	635	21-7-78
264068	0	81	0		570	23-8-78
264096	0	271	0		718	15-9-79
264098	9.2	689	0.013km/d	upstream	591	11-11-78
264346	9.2	389	0.024km/d	upstream	550	15-7-79
264435	0	331	0		597	15-7-79
264058	0	244	0		640	1-11-78
MIDDLE LEVEL MAIN DRAIN.						
Poplars.						
264601	1.25	161	0.008km/d	downstream	745	23-9-79
264610	0	277	0		620	23-9-79
264611	0	278	0		725	22-9-79
264158	0	252	0		645	5-10-79
264459	6.5	365	0.018km/d	downstream	648	28-9-79
264471	4.0	299	0.013km/d	upstream	654	20-10-79
264171	7.7	11	0.7km/d	upstream	705	5-10-79
264190	0	12	0		590	4-9-79
264607	0	17	0		590	22-9-79
264265	0	16	0		700	16-9-79
264268	0.2	24	0.008km/d	downstream	630	16-9-79
264357	0	31	0		580	16-12-78
Pophams Junction.						
264254	0	21	0		405	15-9-79
264258	6.6	31	0.22km/d	upstream	463	15-9-79
Pophams - Cottons Corner Gate Swim.						
264174	0	17	0		710	6-10-79
264626	0	127	0		650	23-10-79
264629	0	250	0		697	23-10-79
264636	0	267	0		612	23-10-79
264642	2	395	0.005km/d	down/up	594	23-10-79
264650	0	267	0		690	23-10-79
CUT OFF CHANNEL.						
Hilgay - Roxham.						
264056	0	28	0		450	20-8-78
RIVER DELPH.						
Welmore - First Corner.						
264127	0	45	0		510	26-8-78
264132	0	33	0		650	20-8-78
264135	0	29	0		810	5-8-78
264135	0	19	0		810	2-9-78
264141	0	36	0		775	2-9-78
264266	6.5	42	0.16km/d	upstream	710	9-10-78
264252	0	215	0		680	11-3-79

Appendix V.

Coombe Abbey Lake. Visceral Fat Content.

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat Content.
June 1979.					
1250	466	F	41.8	20.0	1.6
820	403	F	52.7	20.0	2.44
1040	442	F	47.1	24.4	2.35
680	398	F	56.2	14.4	2.12
750	401	F	54.5	31.8	4.24
851	422	F	51.9	35.3	4.15
921	425	M	50.1	16.5	1.79
943	422	F	49.6	37.3	3.95
893	410	M	50.8	8.93	1.00
1049	420	F	46.9	18.2	1.73
936	424	M	49.8	14.0	1.5
766	400	F	54.2	30.6	4
254	277	I	67.0	6.4	2.5
140	240	I	70.0	2.9	2.1
126	223	I	70.3	3.0	2.39
365	306	I	62.0	8.4	2.3
84	182	I	73.2	0.6	0.7
202	265	I	64.1	2.7	1.34
137	230	F	71.8	3.2	2.34
165	253	I	69.1	3.0	1.8
89	215	I	73.7	0.8	0.9
923	418	F	49.0	13.8	1.5
923	418	F	50.1	33.7	3.7
804	390	F	53.1	20.7	2.6
795	410	F	53.3	25.4	3.2
330	342	F	72.9	0.9	0.2
December 1979.					
1510	485	M	38.8	68.8	4.3
1600	495	M	49.9	59.0	3.7
1550	496	F	43.9	63.3	4.1
1510	487	M	11.5	88.9	5.9
690	398	F	42.3	18.6	2.7
650	390	M	48.0	17.5	2.7
388	342	F	48.5	7.2	1.9
205	284	M	75.7	0.5	0.24
74	203	F	80.0	0.5	0.68
378	341	M	50.8	4.5	1.2
1400	490	F	50.6	44.1	3.15
1520	493	M	63.5	67.7	4.5
1620	503	M	51.0	63.3	3.9
May 1980.					
1701	530	F	34.5	95.3	5.6
1347	482	F	48.2	45.0	3.3
1603	515	F	35.4	77.0	4.8
1389	510	F	44.0	45.7	3.3
978	425	F	44.5	36.6	3.7
560	375	M	56.8	8.6	1.5

Appendix V.

Coombe Abbey May 1980 (continued)

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat Content.
170	265	I	77.4	0.5	1.1
999	440	F	68.7	22.5	2.3
702	413	M	52.5	17.1	2.4
1573	514	F	35.9	80.8	5.1
1035	446	F	40.0	52.7	5.1
1014	435	F	39.2	43.0	4.2
822	410	F	40.9	29.7	3.6
503	355	F	70.8	4.2	0.8
276	305	M	79.2	0.5	0.19
766	410	F	68.0	18,6	2.43
652	400	F	46.9	19.0	2.9
213	273	F	77.7	0.5	0.23
248	290	F	75.5	0.9	0.36
355	375	M	65.9	3.7	1.1
325	340	M	65.1	2.4	0.75
206	275	F	71.1	1.1	0.5
220	281	F	62.8	2.7	1.23

Middle Level Main Drain.

September 1979.

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat Content.
1871	555	M	45.6	36.8	1.97
1021	466	M	43.8	36.5	3.0
2211	570	M	22.5	80.3	3.6
1219	498	F	64.2	17.7	1.45
723	420	F	70.0	8.5	1.18
1219	495	F	46.0	28.3	2.32
1021	466	F	49.6	11.8	1.11
893	445	M	60.1	8.3	0.93
482	365	M	77.4	1.1	0.23
1110	470	F	65.0	12.0	1.01
461	366	F	45.2	10.2	2.2
688	406	M	52.3	7.8	1.13
1340	520	M	77.9	1.8	0.13
1970	565	F	39.8	73.3	3.7

October 1979.

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat Content.
723	405	M	54.6	7.5	1.04
695	420	F	56.5	9.2	1.3
780	440	M	60.9	6.6	0.85
3501	692	F	59.3	46.2	1.32
2155	592	F	47.9	43.6	2.0
1928	560	M	43.1	41.6	2.2
1134	480	M	50.1	29.2	2.6
2098	580	M	38.0	56.4	2.7
2778	635	F	42.2	58.4	2.1
2055	573	M	40.8	45.1	2.2
688	406	M	49.7	8.2	1.19
482	382	F	77.4	1.1	0.23

Appendix V.

Relief Channel. Visceral Fat Content.

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat content.
June/July 1979.					
822	458	M	79.3	0.3	0.037
1400	550	F	83.8	1.3	0.093
1106	540	F	75.0	0.11	0.009
1843	570	F	81.3	1.2	0.065
631	411	M	84.3	0.32	0.051
1814	555	F	59.3	18.97	1.05
2381	618	M	59.3	21.24	0.89
1559	540	F	69.6	7.03	0.45
425	310	M	44.11	0.1	0.024
624	410	M	80.6	0	0
610	405	M	77.5	0.9	0.15
1084	505	M	81.0	0.3	0.028
1290	520	M	75.6	5.5	0.43
879	480	M	49.2	0.2	0.02
2055	580	M	55.7	42.2	2.1
August/September 1979.					
1460	555	M	80.7	0.4	0.027
3289	675	M	46.3	67.6	2.1
1829	570	M	75.1	11.16	0.61
1200	505	F	67.9	7.74	0.65
1106	540	M	85.1	0.1	0.009
1985	615	M	81.9	0.2	0.01
1200	505	M	67.9	7.74	0.65
1450	555	F	64.2	9.5	0.66
November/October 1979.					
1843	548	M	45.3	58.2	3.2
1497	534	M	62.4	11.3	0.76
1400	550	F	82.6	1.6	0.114
1701	560	M	77.0	2.6	0.15
1814	594	M	82.0	0.38	0.021
1985	590	F	34.6	17.21	0.87
2189	580	M	69.2	8.46	0.39
1871	573	M	71.7	0.31	0.017
1491	625	M	83.4	0.3	0.02
2325	622	M	34.9	77.1	3.3
1304	510	M	72.9	3.5	0.27
3289	694	F	59.4	39.7	1.2
1814	560	M	35.1	20.0	1.1
2450	630	M	64.2	26.8	1.1
3544	698	M	48.6	59.4	1.7

Appendix V.

Visceral Fat Content.

Cut-Off Channel.

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat content.
April 1980.					
715	436	F	73.7	2.5	0.35
992	502	F	68.4	3.4	0.34
638	438	F	66.9	2.96	0.46
1361	525	F	80.9	0.34	0.025
397	359	M	70.9	2.26	0.57
666	425	F	71.5	2.72	0.41
326	340	F	75.2	1.08	0.33
525	382	M	55.0	10.76	2.1
1006	495	F	74.7	2.94	0.29
539	380	F	54.6	10.38	1.93
1191	511	F	80.3	0.6	0.05
369	341	F	62.8	3.17	0.86
822	478	M	68.3	5.15	0.63
780	426	F	73.2	3.58	0.46
1559	549	F	81.7	0.62	0.39

Relief Channel.

June/July 1980.

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat content.
2445	649	F	65.5	26.28	1.08
1318	535	F	76.2	2.18	0.17
2552	645	F	74.1	40.0	1.6
3643	680	F	33.4	157.9	4.3
1573	535	F	31.5	21.2	1.4
1503	532	F	37.3	31.4	2.1
1432	530	M	67.1	9.82	0.69
2296	684	M	55.2	30.5	1.33
2693	645	M	20.8	39.2	1.5
1843	670	F	53.4	93.9	5.1
2140	595	F	57.1	34.0	1.6
1531	557	F	64.4	4.0	0.26
751	430	F	28.4	11.4	1.5
1800	591	M	55.5	27.2	1.5
1822	580	F	24.7	15.7	0.86
1276	527	M	66.9	7.0	0.55
851	452	F	61.9	7.1	0.83
1673	556	M	50.5	24.5	1.5
2233	685	M	50.6	30.4	0.8
2234	615	M	58.7	23.0	1.03
2311	607	F	52.2	43.2	1.87
2155	618	M	30.8	12.1	0.56
1177	491	F	62.4	9.0	0.77
1517	540	M	66.9	9.0	0.59
1262	520	M	61.3	12.7	1.0
1446	532	M	60.9	11.9	0.83
638	410	M	29.2	1.4	0.22
1800	608	M	76.9	7.6	0.42

Appendix V.

Middle Level Main Drain continued. Visceral Fat Weights.

Weight.	Length.	Sex.	% Moisture.	Fat Weight.	% Fat content.
November 1979.					
541	378	I	57.5	33.0	0.61
191	273	I	54.0	5.7	2.96
641	395	I	62.3	1.5	0.23
2878	632	M	36.1	112.8	3.9
3813	708	F	46.1	81.2	2.1
1956	580	M	44.2	32.1	1.64
2509	625	M	42.2	67.2	2.7
610	408	F	51.6	8.0	1.3
1020	460	F	46.7	13.6	1.33
723	423	M	42.7	13.6	1.9
December 1979.					
2750	632	M	35.9	94.1	3.4
3686	695	F	35.6	84.8	2.3
2552	615	F	40.8	48.2	1.9
1956	575	F	36.2	27.1	1.4
February 1980.					
936	478	F	51.2	10.4	1.1
2750	675	M	64.4	30.2	1.1
1446	530	F	52.7	9.6	0.7
June 1980.					
1659	555	M	37.2	8.1	0.49
1049	480	F	56.6	14.1	1.4
3246	656	F	38.4	100.7	3.1
3303	667	F	30.6	106.7	3.2
2665	624	F	43.5	46.6	1.75
2155	598	M	26.0	25.1	1.17
Burwell Lode.					
August 1979.					
1285	512	M	59.0	40.8	3.18
1330	497	F	56.6	16.6	1.25
1420	520	F	32.7	19.29	1.36
570	366	M	78.6	2.7	0.47
1005	480	M	41.1	22.8	2.3
660	400	F	55.1	8.0	1.21
1880	560	F	51.0	21.6	1.12
2040	580	F	60.2	21.7	1.06
2010	567	F	56.7	24.5	1.3
1540	520	M	78.6	2.7	0.47
1510	530	F	55.3	19.8	1.31
1390	510	F	59.9	42.3	3.04
1380	519	F	55.9	19.6	1.42
1120	482	M	57.1	19.0	1.7
1300	505	F	56.3	21.8	1.7
840	470	M	62.2	17.7	2.1
1531	511	M	48.1	17.3	1.13
1503	507	F	48.3	15.6	1.04

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