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*Polskie Archiwum Hydrobiologii* publishes papers in every field of hydrobiology. Only works not submitted elsewhere are accepted.

Length. Succinctness of style is a prerequisite. In general, papers are limited to 16 printed pages, including illustration, references etc..

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Z. FISCHER\* and V. P. LYAKHNOVICH\*\*

BIOLOGY AND BIOENERGETICS OF GRASS CARP  
(*CTENOPHARYNGODON IDELLA* VAL.)

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1. INTRODUCTION

The grass carp — *Ctenopharyngodon idella* Val. — has in recent years become a very popular fish, being of considerable interest to both fish culturalists and biologists, mainly because of its ability to feed on various plants. Aquatic vegetation is usually poorly utilized (outside the natural geographic distribution of the grass carp) and forms a serious obstacle to the efficient management of ponds and lakes. The grass carp is rightly considered to be an effective remedy for this problem. In addition, the grass carp grows rapidly, has a large size, and is tasty. In pond culture it is an equal partner to carp and other fish in polyculture. These biological characteristics have prompted numerous attempts at acclimatization in freshwaters of Europe, Asia and North and South America.

However, still not enough is known about the grass carp's role in the productive processes of aquatic ecosystems. In addition to data indicating that the grass carp feeds exclusively on plants, there are numerous suggestions that it has a wide food spectrum. Animal food appears to play an important part both in the early and in the later stages of the grass carp's growth and development.

The ecological peculiarities of grass carp reproduction under natural conditions, such as in the Amur River floodplane, have produced serious difficulties in the grass carp's acclimatization. As a result, investigations have been made on the artificial reproduction and introduction of this species into new environments. Work has also been done on various aspects of the biology and physiology of this fish. Although much data has now accumulated, access to it is difficult since it is scattered among numerous journals and technical manuals, many of which are not widely distributed. There are over 500 published papers dealing with the grass carp. This monograph is the first attempt to provide a much needed review of the subject. The authors present, along with a summary of the literature, results of their own investigations of certain aspects of the biology of this fish which may elucidate the grass carp's role in the productive processes of aquatic ecosystems.

The authors wish to thank Professor R. Z. Klekowski for his lead and help in the execution of this work.

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## 2. GENERAL DESCRIPTION OF THE SPECIES

### TAXONOMIC POSITION

The grass carp — *Ctenopharyngodon idella* (Val.) — is the sole species of the genus *Ctenopharyngodon*, family Cyprinidae, Cypriniformes (Pisces). The species was first described by Valenciennes (1844) under the name *Lenciseus idella* on the basis of Chinese sources. Following a systematic analysis of ichthyological material collected in Chinese inland waters, Steindachner (1866) separated this species from the genus *Lenciseus* as an independent genus *Ctenopharyngodon*. Then the grass carp was described by Dybowski (1877) under the name *Pristodon siemianovi*. This description was based on material collected by Dybowski (1877) in the Amur River basin.

In accordance with Berg's (1949) classification, the systematic formula is as follows:

$$D \text{ III} - 7, A \text{ III} - 8, \text{I.I. } 43 \frac{6.5-7}{5} 45$$

where: D — dorsal fin (pinna dorsalis), A — anal fin (pinna analis), I.I. — lateral line (linea lateralis).

The Russian name "amur", or "white amur" is equivalent to the Chinese "van-yuy" (in South China and in other regions "tsao-yuy" or "kan-yuy"), English "grass carp", and German "Grasskarpf".

### MORPHOLOGY

According to Berg (1949) the grass carp is characterized by a spindle-shaped body, 3.8–4.8 times as long, without the caudal fin, as it is deep (Fig. 1). The body is 4 to 4.5 times longer than the head. The head is very broad, and the mouth is situated in the lower half. The hind corner of the mouth approaches a point vertically below the leading edge of the eye. The back, anterior to the dorsal fin, and the ventral surface, posterior to the pelvic fins, do not taper. The lateral line passes through the centre of the caudal fin and along it are found 40 to 45 scales. According to Nikol'skij (1956) the number can reach 47.

The colour of the grass carp's back is green-grey or yellow-grey, and that of its sides dark gold. The scales of the back and sides have a dark edge. The ventral surface is pale gold or white. The dorsal and caudal fins are dark, whereas the paired fins and oral fin are pale (Nicol'skij 1956).

The pharyngeal teeth are arranged in two rows, either 2.6–4.2 or 2.4–4.2 or 2.4–5.2



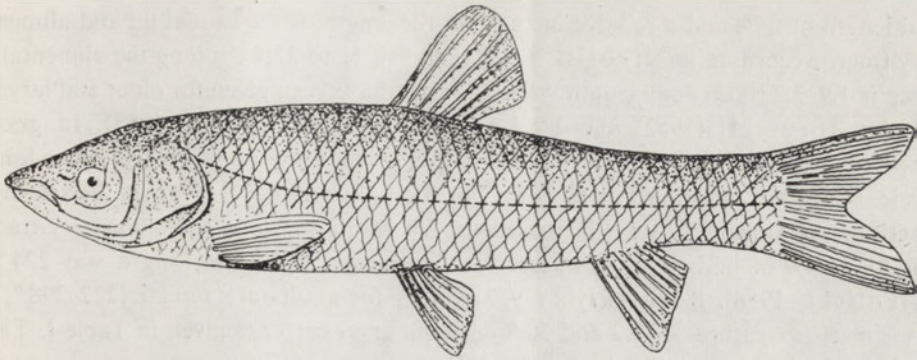


Fig. 1. Grass carp (*Ctenopharyngodon idella* Val.) (after Berg 1949)

or 1.4-5.2. Their crowns are strongly laterally compressed, and the sides heavily folded. The grinding surface of the teeth is deeply folded and furrowed Tchang 1933, (Chu 1935, Hickling 1966).

During the post larval stages, as the grass carp grows, there is a relative decrease in the length of the head, diameter of the eye, length of the mouth, depth of body

Table I. Change in size of biometric characters of grass carp as per cent of body length (acc. to Nikol'skij 1956)

Character	Body length (cm)	
	7.7	30.8
Longitudo capitis	29.0	25.1
Diameter oculi horizontalis	6.8	3.9
Summa altitudo corporis	26.7	17.8
Latitudo maxillae	9.7	8.7
Distantia postdorsalis	54.4	52.0
Altitudo pinnae dorsalis	23.1	18.7
Altitudo pinnae pectoralis	20.3	19.2
Longitudo pinnae analis	17.1	16.1

Table II. Weight of parts of grass carp body as per cent of total body weight

Age of fish	Mean weight (g)	Weight as % of total body weight						
		Head	Inner organs	Muscles and skin	Skeleton	Fins	Scales	Loss
One year old (Leonenko, Lyakhnovich 1968)	50.7	20.7	12.8	53.3	4.9	2.4	4.5	1.4
Two year old (Leonenko, Lyakhnovich 1968)	325.6	17.6	10.7	60.8	2.7	1.9	4.9	1.4
Three year old (Sukhoverkhov 1963)	794	16.4	12.4	61.2	—	—	—	3.6

— no data.

and length of fins, and a relative increase in the length of the caudal fin and alimentary tract. According to Nikol'skij (1956) in fish 11 to 32.4 cm long the alimentary tract is 1.9–2.2 times body length. Similar values have been given for older and larger fish by Borutskij (1952) and by Leonenko, Lyakhnovich (1968). In grass carp fry, however, the alimentary canal is shorter than the body. In fry 7 mm long the length of the intestine was 57% that of the body. As the fish grows the relative length of the alimentary tract increased. In fry 13–20 mm long the alimentary tract was 81–113% of body length, whereas in fingerlings 50–60 mm long it was 224% (Nicol'skij 1956). Borutskij's (1952) values for adults are similar (222–298%). Some meristic features of 7.7 and 30.8 cm long grass carp are given in Table I. The data on weight of particular body parts of grass carp of different age are presented in Table II.

#### GEOGRAPHIC DISTRIBUTION

The natural distribution of the grass carp extends from the Amur River basin in Eastern Asia to Southern China and Siam. This area lies between latitudes 20° and 50° north and between longitudes 100° and 140° east. In natural conditions the grass carp reproduces and overwinters in rivers with a summer rise of water level. It achieves large growth rates, however, in flooded areas and lakes which it reaches by canals and rivers. In many regions of China the grass carp has long been considered suitable for mass culture in fish ponds together with other fish species (Liu Chien-Kang 1954, Fidzimori 1958, Berg 1949). In the Amur River basin, on the northern boundary of its distribution, the grass carp is found in the region between Kymary and Liman. Greatest numbers are found from Habarovsk to Lake Udyl (Nicol'skij 1956).

The area inhabited by the grass carp has been greatly extended in recent years. The fish has been introduced into freshwaters of Central Asia, Eastern, Western and Central Europe, and of the Balkan and Arabian peninsulars. In some regions the grass carp has found conditions suitable for reproduction and full acclimatization (Fidzimori 1958, Bizyaev 1966), but over the greater part reproduction under fish culture conditions depends on artificially induced spawning. Nikol'skij (1956) concluded, from a study of the biology of grass carp in the waters of the Amur River basin, that this fish could be introduced to certain rivers in Central Asia and in Eastern and Western Europe.

#### LIFE CYCLE IN NATIVE WATERS

Information accessible to us concerning the biology of the grass carp in its native habitat is both scarce and lacking in detail. This may be due to a poor distribution of chinese journals abroad. Soviet data is better known, but invariably deals with the species on the edge of its natural distribution. Nikol'skij (1956) has written that the fish occurs in small numbers in the Amur River compared with the Yangtse and other large chinese rivers. Hundreds of millions of fry are



caught each year in these rivers for stocking farm ponds. This, however, does not appear to have fundamentally changed the grass carp population. Chinese research workers (Liu Chien-Kang 1955, Soin 1963, and others) have noted a large gathering of sexually mature grass carp in the spawning grounds of the rivers Yangtse, Sungari and SiKiang.

Table III. Growth of grass carp in water of the Amur River basin (acc. to Konstantinova 1956)

	Age (years)												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Minimum length (cm)	7.6	15.6	22.5	28.9	35.8	41.5	48.0	54.5	56.1	62.6	66.4	69.0	71.4
Maximum length (cm)	8.6	16.8	25.1	33.0	40.0	46.8	53.2	61.6	64.7	70.0	72.0	75.9	80.0

Table IV. Body length and weight of grass carp from Lake Udyl (acc. to Manizera, Booly after Nikol'skij 1956)

	Age (years)					
	6	7	9	10	12	13
Length (cm)	51.0	52.5	68.7	70.8	75.7	78.5
Weight (kg)	2.77	2.88	6.55	7.07	8.01	8.70

Konstantinova's (1956) data of growth in length of grass carp in the Amur River basin is outlined in Table III.

Nikol'skij (1956) has stressed that in the Amur River females are slightly larger than males of the same age. He quotes Manizera and Boolya's data for length and weight of grass carp from Lake Udyl (Table IV).

Berg (1949) has stated that the largest grass carp caught in the Amur was 110 cm long and weighed 15 kg. In the waters of Southern China, where the growing season is longer and warmer, the grass carp grows more quickly and reaches weights of 32 kg and lengths of 122 cm. For certain parts of the Amur River basin Suvorov (1948) has noted a length of 55.9 cm at 5 years of age and 68.7 cm at 6 years.

The grass carp reaches sexual maturity at 4-5 years of age in the Yangtse River and other Chinese waters (Chen, Lin 1935, Liu Chien-Kang 1955). In the Amur River basin sexual maturity occurs in the sixth year of life. According to Verigin (1963), in Southern China the grass carp reaches sexual maturity at 3-4 years of age, with males being a year earlier than females.

Sexually mature grass carp reproduce each year, spawning several times during the growing season. Spawning usually takes place in the swift currents of large rivers, in the water course, at the junction with tributaries, behind islands, or in shallows. It coincides with a rise in water level caused by summer floods (Liu Chien-Kang 1955, Nikol'skij 1956, Verigin 1963).

Information on the reproductive capacity of grass carp in native waters is incomplete. According to Liu Chien-Kang (1955) the roe of females caught in the Yangtse River had from 29,000-430,000 eggs. Chen, Lin (1935) have stated

that a 6 kg female (equivalent to 8–9 years of age) had about 100,000 eggs. Anishchenko (1939) has given a figure of 816,000 eggs for a female of 7.4 kg weight and 76 cm length. Since, like with other fish, reproductive capacity is proportional to body size, and since the grass carp can attain over 30 kg in weight, its reproductive capacity may be considered high.

The pelagic roe is shed into the current at a temperature of about 20°C and is carried down river. The diameter of the eggs is 4.2–5.0 mm, that of the yolk 1.25 mm, and that of the hatched embryo 6.85 mm. In Chinese rivers reproduction takes place from April to August (Chen, Lin 1935). Nikol'skij (1956) has stated that the 1949 spawning in the Amur River occurred on the 25–26 June and on the 10–12 July in the region above Leninsk. In 1948 embryos appeared in the Elaburg region between the 18th and 29th of June.

Embryonic and postembryonic development of grass carp has been investigated by Chen, Lin (1935), Lin (1935), Verigin (1950), Kryzhanovskij et al. (1951), Braginskaya (1951) and Inaba et al. (1957). The most detailed description is given by Soin (1963) who studied embryogenesis and early postembryonic development of grass carp in the Sungari River. Soin (1963) divides the development of the grass carp into phases and stages in accordance with Vasnetsov's (1953) theory. The "embryonic" phase he subdivides into 22 stages. During the first stage a fluid-filled space appears between the egg cytoplasm and the vitelline membrane and a blastodisc is formed. These processes take 40 minutes from fertilization at a temperature of 23–24°C. The second stage, cleavage, extends from the first division of the blastodisc into two blastomeres to further subdivisions into a blastula. Cleavage takes 5 hours and 50 minutes.

Stage 3. Gastrulation, formation of germ-layers and covering of yolk sac with blastoderm. Gastrulation starts 7 hours and 10 minutes and ends 12 hours and 10 minutes after fertilization.

Stage 4. Organogeny, involving the laying down of the nervous system, spinal chord, muscles, intestine, eyes and auditory vesicles. Division of the mesoderm into muscle segments continues as this stage ends 18 hours after fertilization.

Stage 5. The tail straightens away from the yolk sac and first body movements occur. Eye sockets and olfactory lobes become distinguishable.

Stage 6. Emergence of the embryo from the egg membrane, takes place 34 hours after fertilization and lasts for 4 hours at 23–24°C. The free embryo or prelarva has complete muscle segmentation and the beginnings of otoliths in the hearing apparatus. It is 5.2 mm long, shows little movement and in natural conditions, like the egg, is carried with the current.

Stage 7. Appearance of a developed and functioning circulatory system. The prelarva is still fairly inactive and feeds on its own yolk.

Stage 8. Appearance of gill-jaw apparatus and onset of gill function. The prelarva is 7.4 mm long. 76 hours after fertilization the mouth moves forward from its ventral position and shows signs of movement: Pigment cells appear. After 4 days the mouth is formed and active, and the gill-jaw apparatus starts to function as a breathing organ. First signs of a swim bladder appear. As the prelarvae approach 7.5 mm in



length they become more active and, although under natural conditions they are still carried by the current, start swimming towards the river banks.

The larval phase starts with the onset of mixed feeding at 4.5 days. Soin (1963) divides this phase into 5 stages.

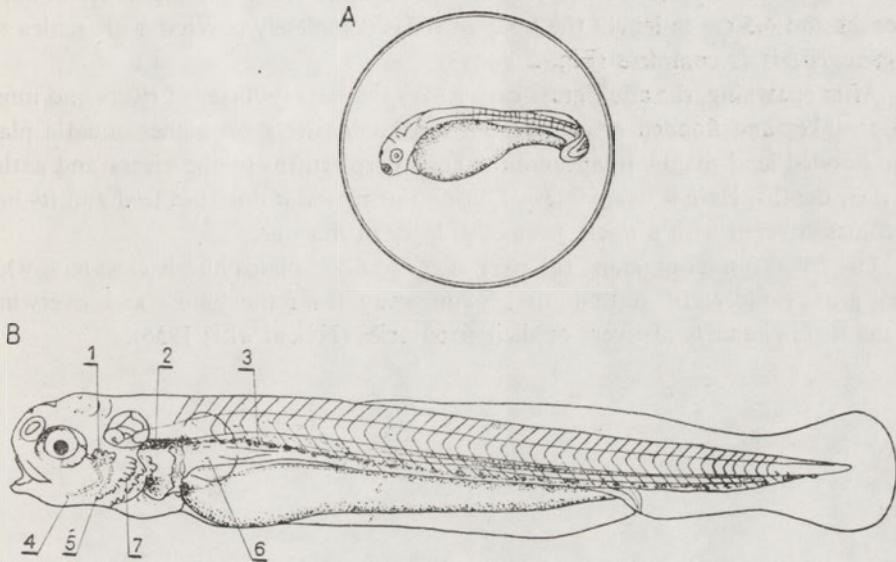


Fig. 2. Embryo development of grass carp (*Ctenopharyngodon idella* Val.) (after Soin 1963). A — beginning of embryo active separation (29 hr old), B — reduction of embryonic respiration organs, beginning of air-bladder (4 days old, 7.5 mm in length). 1 — pseudobranchia, 2 — beginning of pectoral vertebrae, 3 — air-bladder, 4 — arcus mandibularis aortae, 5 — arcus Hyoideum aortae, 6 — arteria subclavia, 7 — arcus visceralis aortae

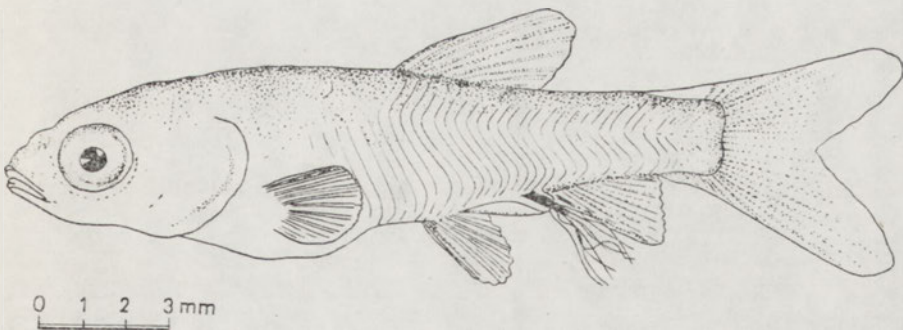


Fig. 3. Fry stage (about 1 month old, 2.1 cm long) (after Soin 1963)

Stage 1. Mixed endogenous and exogenous feeding. The larvae keep to the river banks and start to migrate upstream to quiet creeks and inlets. This stage ends at 6 days when the larvae reach 7–8 mm in length and feeding is completely exogenous.

Stages 2 and 3. Unpaired fins form and body length increases to 9 mm. The larvae (fry) feed actively on zooplankton.

Stage 4. The second chamber of the swim bladder appears.

Stage 5. 20–22 days after fertilization, when the larvae are 11.5–14.2 mm long, paired fins start to form.

The post larval phase (late fry — early fingerling) has been studied in less detail. At about one month and 2.1 cm in length scales start to tie up. In the absence of animal food the fry are able to feed on filamentous and other algae. At about 15 months and 4.5 cm in length the body of fry is completely covered with scales and organogenesis is complete (Fig. 2 and 3).

After spawning, the adult grass carp leaves the water courses of rivers and migrates to lakes and flooded areas where it feeds intensively on higher aquatic plants and flooded land plants. In autumn the grass carp returns to the rivers and gathers in their depths. Here it overwinters. During this period it does not feed and its body becomes covered with a thick, protective layer of mucous.

The fry also migrate along the river edges to flood plains and backwaters, where they grow rapidly. In autumn they swim away from the banks and overwinter in the main channels of rivers or their tributaries (Nikol'skij 1956).



Z. FISCHER

### 3. PHYSIOLOGY AND BIOENERGETICS OF GRASS CARP

#### ECOLOGICAL PLASTICITY

The ability of grass carp to adapt to a variety of ecological conditions is of interest on account of plans to introduce this fish into various waters. The ecological plasticity of this species should be considered foremost in relation to varying temperature, oxygen, salinity and food conditions.

In grass carp, as in other organisms, the youngest individuals (fry) are most sensitive to environmental changes. Vinogradov, Erokhina (1967) have reported that the optimum temperature for development of grass carp roe is 18–19°C. It is interesting to note that the temperature distribution is of a modal and not of a normal type, so that an increase in temperature to 28–30°C is not harmful, whereas a slight drop in temperature by 2°C below the optimum (16–18°C) not only slows down development, but also increases roe mortality. First postembryonic stages show a similar response. Resistance to temperature variation increases with development of fish. According to Opuszyński (1967a) grass carp in the first year of life can even survive a temperature of 36°C, with the lethal temperature ranging from 34.2 to 41.2°C in various seasons. Both fry and two-year-old grass carp endure well a lowering of temperature, nearly as well as carp. When the temperature dropped to 0.2°C the survival rate was 76–96% for grass carp as compared with 84–98% for carp bred in the same ponds (Okoniewska, Opuszyński 1969). The higher the individual weight of fish, the better its survival. The possibility of prolonged endurance to low temperature can be inferred from (1) a small, usually smaller than in carp, loss of proteins during hibernation (1.0 g/100 g of body in grass carp versus 1.5 g/100 g of body in carp), and from (2) a high fat content in spring (5.2% of body weight in grass carp, 2.2% in carp (Okoniewska, Opuszyński 1969)). This suggests that grass carp can easily overwinter under the climatic conditions of Central Europe.

The resistance of grass carp to deteriorating oxygen conditions is also high. At low temperatures (6–7°C) it has survived an oxygen content as low as 0.5–0.9 mm/l (Gierałtowski 1963). According to Opuszyński (1967a) the average lethal threshold of oxygen content is 0.43 mg/l for fry and 0.32 mg/l for one-year-olds.

However, Chesnokova (1971) has found that grass carp are highly vulnerable to pesticides. She studied the effect of 2,4-D and propamide on survival of 4-day-old larvae. Small amounts of these toxins (4 kg propamide per ha, 1.8 kg 2,4-D per

ha) caused 20% mortality, and larger doses (7 kg propamide per ha, 5 kg 2,4-D per ha) 70% mortality.

The ability of grass carp to feed on different types of food will be discussed in detail in "Diet and food assimilation". By and large the grass carp has a vast food range, its diet depending on the conditions in which it finds itself and on the food available. As early as the first larval stages the grass carp's choice of food is largely governed by availability. With further development, when its ability to consume different types of food increases, it feeds on higher plants, grasses, zooplankton, small aquatic animals, pelleted foods, and even on bread.

That the grass carp reveals a high ecological plasticity can be inferred from the fact that it is able to adapt to a saline environment (Rykova 1964). The spermatozooids of grass carp remain mobile in fresh water for 1–1.5 minutes, at a salinity of 3.5‰ for 7.8 minutes, and at 6‰ for 32 minutes. However, at salinities of 7.5‰ and above the spermatozooids lose their activity almost instantaneously. Embryonic development is normal at salinities of up to 4.9‰, but above this level it is hindered. The same holds for postembryonic stages: they survive the salinity of the Black Sea (4.9‰) but at higher salt concentrations deaths occur. Larval mortality begins at salinities above 7.6‰.

It appears, therefore, that one may conclude from the above data that the grass carp shows a high ecological plasticity and an ability to adapt to various environmental conditions. Adaptation, however, takes time. The acclimatization of fish brought from natural conditions to a laboratory is a long process. It has been observed by Fischer (1970a). During the first 2 to 4 weeks after being transferred from ponds to aquaria the fish lost weight in spite of being offered food to excess. Then there was a period of static weight, followed eventually by growth. Growth was taken as an indication of completed acclimatization. The whole process lasted 2–3 months, its duration varying with individual fish. Acclimatization periods of other species are shorter, for example in perch (*Perca fluviatilis*) and eel (*Anguilla anguilla*) about one month, in *Leucaspis delineatus* and carp (*Cyprinus carpio*) about 2 weeks.

#### CHEMICAL COMPOSITION AND CALORIFIC VALUE

The basis of many investigations, both in the field of physiology and in general biology, is the variation in energy value of the organism examined. Lyakhnovich (in print) has obtained direct measurements of calorific content of roe and of developing larvae. These measurements were carried out at the author's request in the Department of Bioenergetics and Bioproductivity at the Nencki Institute of Experimental Biology in Warsaw. Lyakhnovich found that the calorific value of embryos just after fertilization was 6.5 cal/mg dry weight. In hatching larvae it dropped to 4.7 cal/mg, while in larvae up to 12 days old it ranged from 4.5 cal/mg to 5.3 cal/mg dry weight.

The calorific value of one-year-old fish was found to be closely related to food and living conditions. It ranged from 4.3 cal to 6.47 cal/mg (Fischer 1972a).

It is also possible to estimate calorific values of grass carp from data on the chemical composition of its body. The chemical composition of the grass carp's body



Table V. Chemical composition of grass carp as percentage of wet body weight

Author	Water (%)	Protein (%)	Fat (%)	Ash (%)
Klejmenov (1962)*	73-75	16.1-18.7	5.2-6.1	1.4-1.6
Sukhoverkhov (1963)*	73	17.6	6.3	3.1
Okoniewska, Okoniewski (1969)*	76.8	17.9	4.2	1.2
Dem'yanko (1971)				
2-year-old	76.3	18.04	4.55	1.09
3-year-old	73.1	18.10	7.27	1.03
Mann (1968)				
(72.7-1370 g)	77.2-79.4	—	1.4-0.4	—
Joshev, Boyadzhiev (1969)				
(880-2440 g)	74.5-77.1	18.8-19.9	3.1-6.1	0.8-1.0

\*Age of fish unknown.

Table VI. Fat content in various body parts of grass carp as percentage of wet weight (after Mann 1968)

Body length (cm)	Dorsal muscles	Ventral muscles	Head	Skin	Spine
18.0	0.4	0.5	3.5	10.8	4.5
48.0	1.4	22.1	20.4	11.4	17.1

Table VII. Composition of lipids in various body parts of grass carp as percentage of total lipids (after Rimsh 1968)

Lipid	Liver	Muscles	Adipose tissue
Phospholipid	11.1	13.9	5.4
Cholesterol	9.1	10.8	8.6
Free fatty acids	3.2	7.5	4.0
Triglyceride	37.2	27.2	63.7
Vitamin A	12.5	13.7	5.1
Stearic esters	10.0	6.2	6.7
Hydrocarbons and other components	16.9	20.7	6.5

varies with culturing conditions and with geographic location (Table V). Different parts of the body have a different chemical composition. Mann (1968) has reported on the fat content of various organs of the grass carp (Table VI). Rimsh (1968) has given the composition of lipids in the body tissue of 2-year-old grass carp (Table VII).

All the above data pertain to immature fish. Mature fish weighing 18,760 g were investigated by Kizeveter (1942) who found that lipids formed 5.14% of wet weight. Palmitic acid was the main component, this finding being supported by Rimsh (1968) (Table VIII).

Table VIII. Fatty acids and triglycerides composition (as per cent of the total content) in various body parts of 2-year-old grass carp (after Rimsh 1968)

Fatty acid	Abbreviated formula	Liver	Muscles	Adipose tissue
Myristic	14 : 0	6.6	3.7	2.1
Myristoleic	14 : 1	1.6	2.1	0.5
Palmitic	16 : 0	38.4	38.8	40.2
Stearic	18 : 0	6.8	1.4	5.2
Oleic	18 : 1	35.8	29.0	31.1
Linoleic	18 : 2	9.2	14.8	19.1
Linolenic	18 : 3	1.6	10.2	1.8

Table IX. Characteristics of grass carp blood (Leonenko, Lyakhnovich 1968)

Season	Haemoglobin (g%)	Hematocrit (%)	Erythrocyte number (million/mm <sup>3</sup> )
Spring	8.6	31.7	1.798
Summer	9.4	32.1	1.832
Autumn	9.2	33.3	1.850

Another important study is that of grass carp blood. Leonenko, Lyakhnovich (1968) and Lyakhnovich, Leonenko (1971) have examined it extensively. They have estimated the volume of one erythrocyte in grass carp blood to be 170–180  $\mu^3$ . Blood characteristics show seasonal variation, as indicated in Table IX.

According to Leonenko, Lyakhnovich (1968) the blood constitutes from 2.60 to 4.68% of body weight in 2 year-old grass carp, with mean haemoglobin concentration being 9.6%. These authors have also described the relationship between body weight and erythrocyte number, haemoglobin concentration and total blood cell volume. Figure 4 shows relationship between blood specific weight, erythrocyte number, hematocrit and haemoglobin concentration. Lyakhnovich, Leonenko (1971) have noted total blood cell volume (Fig. 4). Lyakhnovich, Leonenko (1971) have noted continuous amitotic divisions of erythrocytes in grass carp blood. Such divisions are often observed when fish are kept in poor conditions (e.g. lack of proteins, poisoning). They may have indicated a shortage of valuable protein due to an inadequate supply of exogenous animal proteins in the diet.

Data on blood characteristics in grass carp, other than that given by Lyakhnovich, Leonenko (1971), is scarce. Syrov (1969) has studied blood properties in relation to sex differences in fish. Haemoglobin content and erythrocyte number were higher in males than in females, whereas erythrocyte sedimentation rate was lower. Blood composition was affected by the application of a hormone preparation: the number of lymphocytes decreased, and that of monocytes, multinuclear leucocytes and neutrophils increased.



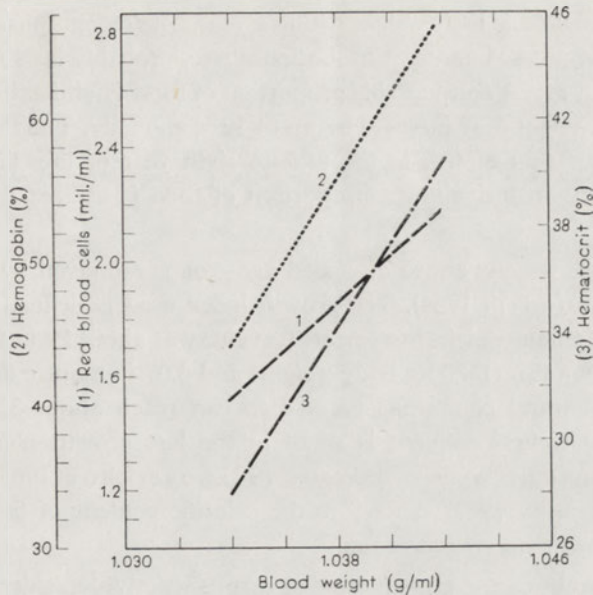


Fig. 4. Interrelationships between specific weight of blood and erythrocyte number, haemoglobin concentration and hematocrit (acc. to Leonenko, Lyakhnovich 1968). 1 — erythrocyte number, 2 — haemoglobin concentration, 3 — hematocrit

Giurcă (1970) and Giurcă, Rădulescu (1971) have described the maturation of gonads and the hatching of fry in relation to typical seasonal changes in RNA and DNA content. They found that the quantity of RNA depended on the degree of maturation of oocytes. From April to September small changes in gonads were correlated with minimum quantities of nucleic acids. A negative correlation was ascertained between the quantity of RNA and DNA and gonad maturation. The ratio of RNA to DNA in grass carp gonads was found to be 1:10.

Summing up, the grass carp has a relatively high fat content (reaching 6% of wet body weight) and a fairly high water content (about 75%). As in other fish the greatest quantities of adipose tissue are found in the belly muscles. Blood characteristics are similar to those of carp blood.

#### GROWTH

It is well known that the growth rate of any organism varies with environmental conditions. Growth is thus affected by quality and quantity of food available, oxygen content, and so on. The optimum temperature for growth of grass carp, according to Prikhod'ko (1967), ranges from 22 to 27°C. Prikhod'ko (1967) has reported annual weight increases of 1.2 kg near Kiev (Ukraine) and of 2.5 kg in the Krasnodar region (Caucasus).

Three growth phases can be distinguished in the grass carp life cycle. During the first phase growth rate is intense with most of the food being utilized for growth (growth to food intake ratio of 10%). It appears that in grass carp this phase lasts for the first two years of life (Suvorov 1948, Nikol'skij 1956). According to the

literature, fish can double their weight within a year. The second phase, when growth is still intense but not as intense as in the first phase, probably lasts from the second to the fifth year of life. A considerable proportion of food is still utilized for growth (3%), and body weight may increase by up to 30% annually. The third phase starts with sexual maturation of fish in the fifth to sixth year of life. Growth is small, often nil, and only an insignificant proportion of food is utilized for body growth (about 1%).

Growth indices for the above discussed age-groups are given by an anonymous Chinese paper (Anonym 1964). The growth index used is defined as the ratio of body weight to 24 hour weight increment. Its value was about 29 in fry (0–1 g body weight), 2 in young fish (1–200 g body weight) and 0.07 in mature fish (above 200 g weight). Under natural conditions grass carp can reach about 32 kg in weight. Although body weight increment is small in the last growth phase, fat content increases and moisture content decreases (Sukhoverkhov 1963, Mann 1968, Joshev, Boyadzhiev 1969). Therefore the calorific content of fish still increases even though growth may have ceased.

As mentioned above, the growth of grass carp is strictly dependent on the quantity and quality of food. Growth rate varies considerably between fish fed exclusively with plants, those fed exclusively with animal food, and those receiving a mixed diet. This is a controversial issue deserving detailed discussion.

Krupauer (1967) has observed a lack of growth in fish fed only with plants and has suggested that such a diet must soon lead to death. This observation is, in part, confirmed by Fischer who found in her experiments that although one-year-old grass carp (thus being in the first phase of most intense growth) did not die, their growth was almost nil, being 50 mg/24 hr for fish weighing about 40 g. The relationship between growth rate and body weight could be described by the formulae  $P = 11.5W^{0.46}$ , where  $W$  is fish weight in grams and  $P$  is growth in cal/24 hr. The calorific value of the fish ranged between 4.34 cal/mg and 5.02 cal/mg dry weight. These results are contrary to those obtained by Opuszyński (1967 b) who cultured grass carp under laboratory conditions for 17 days (acclimatization period included) at the same temperature. He obtained growth rates ten times higher than those observed by Fischer (1970 b). The discrepancy in results may be due to the difference in duration of the experiments: 17 days versus 8 months. The possible cause of growth cessation when plant food alone is supplied may lie in the specific properties of plant proteins. Lack of even minute quantities of animal proteins can retard growth. It is possible that the harmful effects of animal protein shortage only appear after a prolonged period on a monotonous diet.

Migita, Hashimoto (1949), feeding grass carp with various diets in laboratory conditions, calculated growth indices according to the formula:

$$x = \frac{z (W_n - W_0)}{n (W_n + W_0)} \cdot 100$$

where:  $W_0$  — initial weight of fish,  $W_n$  — final weight of fish,  $n$  — number of fish,  
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$z$  — coefficient of proportionality. Their results (Table X) indicate that grass carp fed animal food grew better than those fed plants.

The growth of grass carp kept on an exclusively animal diet is, according to Fischer (1970 b) ten times faster than that on an exclusively plant diet. She describes the relationship between growth and body weight for fish on an exclusively animal

Table X. Growth index for grass carp cultured at various temperatures and fed with various diets in excess (after Migita, Hashimoto 1949)

Food		Temperature (°C)				
		20	22	29		
		Body length (cm)				
		10-12	7-10	3.03-3.06	3.16-3.27	10-12
Animal	<i>Chryomyia megacephala</i> larvae	0.78	1.97	—	—	4.17
	<i>Moina sp.</i>	—	—	14.3	11.5	—
	Spirodela	0.19	1.29	—	—	4.22
Plant	<i>Eichhornia crassipes</i>	—	—	—	—	0.62
	<i>Wolffia arrhiza</i>	—	—	8.2	7.3	—
	Linseed	—	—	4.9	—	—

— no data.

diet by the formula:  $P = 1.92 W^{1.18}$ , where  $W$  is weight in grams and  $P$  is growth in calories /24 hr. Mints, Efimova (1970), however, observed very intense growth of grass carp in peaty waters where there were on vascular plants. They have suggested that the fish fed on peat.

Numerous papers deal with growth rates of grass carp under natural conditions (Lukanin 1959, Verigin 1961, Babayan 1962 and many others). However, increments are given in various units, which makes comparison difficult. After much recalculation (Fischer 1970 b) it appears that fish in the phase of intense growth, weighing about 200 g, gained nearly 1000 calories in 24 hours. This is a high value. Such an increase would not have been possible if the fish had fed only on plants. The rapid growth of grass carp in peaty waters also may have been due to the consumption of some animal food.

The conclusion can be drawn that the growth rate of grass carp depends first and foremost on the diet. This dependence is clearer than in other fish, since the grass carp's food is more variable and since it can attain a very high body weight. The growth phases in the grass carp's life cycle follow the general pattern common to other fish.

#### DIET AND FOOD ASSIMILATION

As mentioned above, fish growth depends closely on the quality and quantity of food eaten. Diet composition shall be considered first. There is a lot of information on this subject. Many authors (Borutskij 1952, Nakamura 1958, Verigin

1961, Tsyun I-Chun et al. 1963, Pavlovskij 1966, Scheer et al. 1967, Opu-szyński 1967 b and others) consider the grass carp a herbivorous fish and give long lists of plants consumed by it.

Fry (up to 30 mm in length) are thought to feed on zooplankton, rotifers, cru-staceans, and chironomid larvae. On reaching a length of 30 mm the grass carp shifts to plant food, according to the authors mentioned above. Scheer et al. (1967) consider that this shift depends closely on temperature: up to a temperature of 15°C the grass carp feeds on zooplankton and above this temperature on plants. Bo-brova's (1968) results, however, show that below 15°C both feeding rate and growth decrease considerably (to about half of that at 22°C). This is difficult to reconcile with Scheer et al. (1967), since animal food has a higher calorific value and is more readily assimilated than plants (Fischer 1972 b).

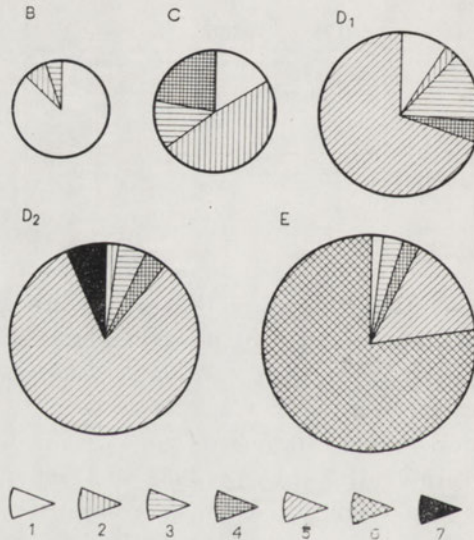


Fig. 5. Food of grass carp larvae in successive stages of development in per cent. B-E — stages of larvae. 1 — Rotatoria, 2 — Arcella, 3 — Copepoda, 4 — Cladocera, 5 — Chironomidae, 6 — Aphidiidae, 7 — Heleidae (after Bessmertnaya 1968)

A detailed study of the diet of grass carp larvae (early fry) has been made by Bessmertnaya (1968). She states that larvae feed throughout the day and night and that their diet changes as they grow. She divides the life of larvae into 5 stages, based on differences in diet composition, namely: B — 1-4 days after hatching, C — 5-6 days after hatching, D — 7-8 days, D<sub>2</sub> — 9-10 days and E — 11-15 days (Fig. 5). The author considers that changes in larval diet do not depend on food preference, but rather on anatomical accessibility or on the presence or absence of a given species in the habitat. Bessmertnaya (1968) notes that 37.5% of stage E fry consumed plant food. Kornenko (1971) points to the important role of infu-soria during early larval stages.



The following plant species have been found in the alimentary tracts of adult grass carp: *Fontinatis sp.*, *Equisetum sp.*, *Ceratophyllum demersum*, *Polygonum amphibium*, *Trifolium repens*, *Myriophyllum sp.*, *M. spicatum*, *Trapa natans*, *Lysimachia vulgaris*, *Stachys palustris*, *Bidens tripartita*, *Butomus umbellatus*, *Alisma plantago-aquatica*, *Elodea canadensis*, *Hydrille sp.*, *H. verticillata*, *Hydrocharis morsus ranae*, *Valisneria spiralis*, *Potamogeton crispus*, *L. filiformis*, *P. natans*, *P. pectinatus*, *P. obtusifolius*, *P. perfoliatus*, *Eichhornia crassipes*, *Calla palustris*, *Lemna sp.*, *L. minor*, *Spirodella polyrrhiza*, *Wolffie arrhiza*, *Juncus articulatus*, *J. effusus*, *J. filiformis*, *Typha latifolia*, *T. angustifolia*, *Carex nigra*, *C. hudsonii*, *C. pseudocyperus*, *Scirpus sp.*, *S. silvaticus*, *Calamagrostis epigeios*, *Glyceria fluitans*, *Phragmites communis*, *Poa palustris*, *Zizania latifolia*, *Sphagnum sp.*, *Hottonia palustris*, *Galium palustris*, *Chara sp.*, *Elodea canadensis*, *Cladophora sp.*, *Spirogyra sp.* (Verigin 1961, Gaevskaya 1966, Prikhod'ko, Lupacheva 1967, Krupauer 1967, Fischer 1968, Opuszyński 1969).

This huge number of species suggests that the grass carp feeds on an assortment of plants depending on the habitat it occurs in. Shorygin (1952) states that, from the point of view of food preference, food may be divided into preferred, exchanged and normal, while in terms of practical significance into main, secondary and tertiary. Stroganov (1963) points to the fact that under unfavourable nutritional conditions even tertiary food can become the main one. Verigin *et al.* (1963) divide plants into three groups according to grass carp preference:

1. Well eaten. *Phragmites communis*, *Potamogeton pectinatus*, *Ceratophyllum demersum*, *Elodea canadensis*, *Lemna trisulca*, *Hydrocharis morsus ranae*, *Poa palustris*, *Typha latifolia*, *Trifolium pratense*, *T. medium*, *Agropyron repens*, *Chelidonium majus*, *Polygonum aviculare*, *Achillea millefolium*, *Trifolium repens*, *Potentilla anserina*.

2. Moderately eaten. *Vallisneria spiralis*, *Myriophyllum sp.*, *Calla palustris*, *Polygonum amphibium*, *Juncus effusus*, *Bidens tripartita*, *Butomus umbellatus*, *Juncus lamprocarpus*, *Scirpus silvaticus*, *Carex nigra*, *Erigeron canadensis*, *Agrostis alba*, *Galeonis speciosa*, *Linaria vulgaris*, *Calamagrostis epigeios*, *Equisetum palustrae*, *Potentilla crantzi*, *Vicia sepium*, *Mentha arvensis*, *Pteridium aquilinum*, *Glechoma hederacea*, *Melandrium album*, *Matricaria chamomilla*, *Tussilago farfara*, *Lappa nemorosa*.

3. Poorly eaten. *Stachys palustris*, *Odontites rubra*, *Juncus filiformis*, *Carex pseudocyperus*, *Sonchus arvensis*, *Tanacetum vulgare*, *Chamaenerion angustifolium*, *Lisimachis vulgaris*, *Teraxacum officinale*, *Zepidium ruderales*, *Capsella bursa pastoris*, *Lotus corniculatus*, *Sisymbrium officinale*, *Trifolium arvensis*, *Chenopodium album*.

Under laboratory conditions grass carp showed no clear preference when supplied ad libitum with 10 common plant species (Fischer 1968). By offering various assortments of plants, a slight preference was noted for three species, namely: *Lemna minor*, *Lactuca sativa* and *Glyceria fluitans* (Table XI). However, this does not imply that the grass carp stopped feeding in the absence of preferred plants. Low food preference was indicated by low values for Ivlev's (1955) coefficient. Fischer's (1968) experiments were carried out with one-year-old fish. There is no doubt, however, that the grass carp modifies its food preference with age. Young fish with

Table XI. Food preference, calorific value and ash content of different plant food components (from Fischer 1968)

Plant	Ivlev's (1955) index		Calorific value of dry wt. (cal/g)	Ash content (%)
	Mean <i>K</i>	Standard error		
<i>Lemna minor</i>	+0.222	0.0342	3.6582	17.0
<i>Lactuca sativa</i>	+0.217	0.0445	3.8570	15.0
<i>Glyceria fluitans</i>	+0.008	0.0497	4.1128	10.0
<i>Potamogeton natans</i>	-0.109	0.0572	4.0925	17.0
<i>Juncus effusus</i>	-0.128	0.0485	3.9294	13.0
<i>Sphagnum sp.</i>	-0.232	0.0583	3.9963	7.3
<i>Hottonia palustris</i>	-0.346	0.0727	4.0630	10.0
<i>Carex hudsonii</i>	-0.498	0.0564	4.0542	3.0
<i>Galium palustre</i>	-0.540	0.0615	4.0542	10.0
<i>Typha latifolia</i>	-0.610	0.0524	4.2368	5.7

poorly developed pharyngeal teeth prefer soft plants, avoiding hard ones such as *Typha latifolia* which, according to Verigin (1961) is willingly eaten by somewhat older grass carp. According to Stroganov (1963) and Verigin (1963) food preference varies with temperature. Stroganov (1963) notes decreasing selectivity with increasing temperature.

On the other hand, Cure (1970) maintains that grass carp show a clear preference for certain foods (*Potamogeton pectinatus*, *Lemna trisulca*, *Typha* and *Phragmites*), which does not contradict the results previously described. He also states that grass carp feed on a wide range of plant species. Applying Ivlev's (1955) formulae it would appear that the grass carp's diet depends chiefly on availability and only slightly on food preference.

Contrary to the common view that grass carp feeds only on aquatic plants, it willingly consumes Tubificidae, Chironomidae and, when fed supplementally, oats, tree leaves, grass, various grains, and bread (Stroganov 1955, 1963). The latter paper, Chinese works quoted by Nikol'skij (1956), as well as papers by Cure (1970) and Fischer (1972b) suggest that the grass carp is an omnivorous species. One-year-old grass carp show excellent assimilation and growth rates when fed only with animal food, whereas when kept only on plant food for a prolonged period they do badly. Body weight increments are extremely low, even at a very high food intake.

The amount of food eaten, viz. daily food ration, should, ideally, be expressed in calories per 24 hours. Unfortunately such data are scarce. Food intake is often given as a percentage of body calorific content, or as a ratio of wet weight of food eaten to wet weight of fish, or simply as wet weight of food consumed. Cure (1970) maintains that the grass carp eats its own weight of plants a day at a temperature of 20–28°C. Lukanin (1959) reports that grass carp weighing about 2000 g consume 500–2300 g of fresh vegetation. Zolotova (1971) states that the average daily intake of grass carp on a plant diet is 30% of fish body weight. Experimenting under natural



conditions, Verigin (1963) ascertained that daily intake varied from 115 to 1350 g fresh weight per kilogram of fish, depending on the species of plant eaten. Conversion of such data into energy units is difficult and inevitably involves large errors. Thus, in spite of much data on grass carp feeding under natural conditions, it is almost impossible to estimate the food intake in calories. Relevant literature is scarce and only gives results for plant food. The energy value of animal food consumed under natural conditions has not been determined. Fischer (1968) investigated the daily ration of one year old grass carp kept under laboratory conditions and fed various plants normally eaten by it. The values obtained varied from 660 to 9786 calories per individual, depending on the species composition of the diet. The daily intake of grass carp weighing 20–50 g was 3000–56,000 calories, when fed on a pure plant diet of one species, while that of 86–107 g fish on a pure animal diet was 3000–10,000 calories. However, a mixed animal-plant diet gave astonishing results (Fischer 1973) — the intake being higher than for animal food alone (Fig. 6). Assuming

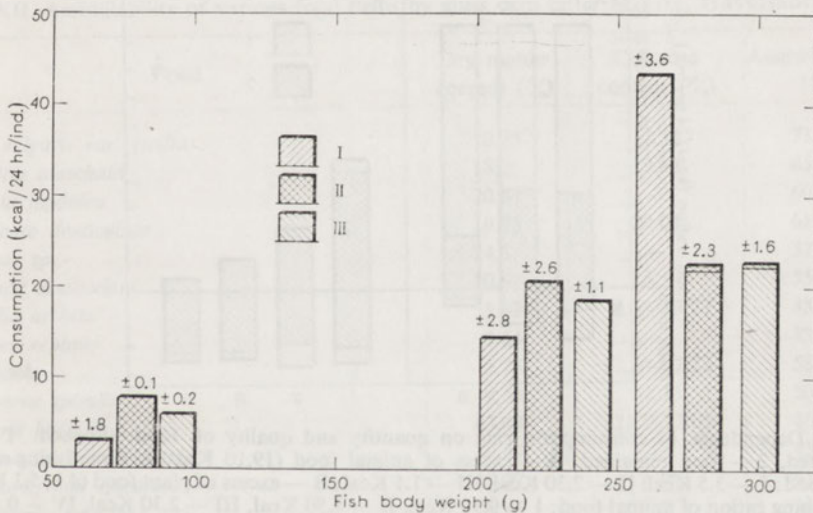


Fig. 6. Dependence of consumption rate on the type of food supplied. I — excess of plant food, II — excess of plant + animal food, III — excess of animal food

that 40% of the animal food is assimilated (Fischer 1972 b), and calculating the theoretical energy loss for respiration (Fischer 1970 a), we can conclude that growth rates on ad libitum mixed and animal diets should be similar. This probably results from the fact that tubificids were chiefly consumed when a mixed diet was fed in excess. Animal food constituted 76% of total intake. Food intake increased uniformly with fish body weight when a mixed animal-plant diet was fed to excess (Fig. 6). However, when plants only were supplied food intake increased considerably with change of fish weight from about 240 to 300 g. Within this relatively narrow weight range daily intake increased threefold from 16 to 45 Kcal. Assuming a constant assimilability of 20% for plant food (Fischer 1972b), the 300 g grass carp on an all plant diet should have used about 7 Kcal for growth, which would

have been similar to the growth rate on an animal diet. This, however, did not happen: in a 10 day experiment the fish gained about 4% in weight on animal food and lost about 2% on plant food. Therefore, either respiration increased considerably in fish fed plants, or assimilation decreased. The latter seems most probable. It is possible that after reaching a weight of about 300 g there is an increased demand for some "minimum factor" (a vitamin or an aminoacid) which results in an increased food intake and retarded growth.

From the above it appears that an optimum diet for grass carp should consist of 75% animal and 25% plant food. The first component would ensure growth of fish, whereas the second would supply necessary vitamins and large amounts of carbohydrates used mainly for respiration (Fischer 1972 a, b). The results of experiments in which grass carp were fed different quantities of animal and plant food are, therefore, interesting (Fig. 7). The figure shows clearly that, when animal food

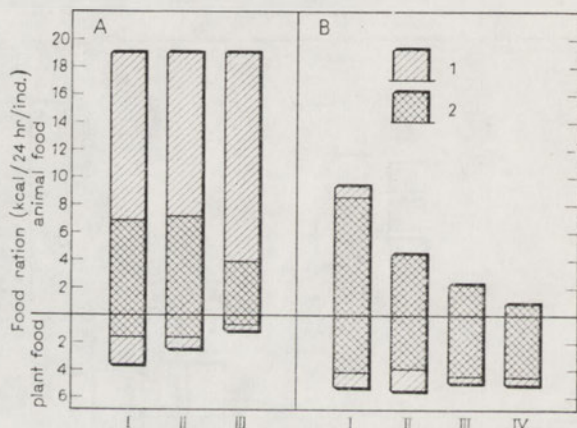


Fig. 7. Dependence of consumption rate on quantity and quality of food supplied. 1 — food consumed, 2 — food remained. A — excess of animal food (19.10 Kcal) + diminishing ration of plant food: I — 3.5 Kcal, II — 2.30 Kcal, III — 1.1 Kcal; B — excess of plant food (4.9–5.3 Kcal) + diminishing ration of animal food: I — 9.30 Kcal, II — 4.50 Kcal, III — 2.30 Kcal, IV — 0.90 Kcal

was limited and plant food was in excess, the amount of plant food eaten remained unaffected (Fig. 7A). In the reverse situation, however, when animal food was in excess and plant food restricted to 500 cal, there was a clear reduction (almost half) in the amount of animal food eaten. Therefore, it may be concluded that the grass carp needs a certain minimum of plant food, which facilitates the ingestion and probably digestion of large amounts of animal food, which, in turn, is responsible for a high body growth rate. Thus both animal and plant food is essential for good growth of this fish.

Migita, Hashimoto (1949) have carried out a series of experiments in which different proportions of animal (*Chryomya*) and plant food (*Spirodela*) were supplied. They found that in fry and young fish animal food, rather than plant food, was responsible for growth. They concluded that to ensure a good growth rate the grass



carp should be fed at least 30% animal food. According to them a mixed diet improves food utilization in grass carp.

A mixed plant-animal diet has been commonly used in Chinese pond culture (Anonym 1964) and has yielded good results.

In this light, Penzes, Tölg's (1966) conclusion that animal proteins are not necessary for normal growth of grass carp appears debatable. Hickling (1966) has reported the presence of active proteases in the midgut of grass carp. In addition, besides amylase he also found lipases. This may suggest that the grass carp is adapted to the consumption and assimilation of both plant and animal food.

The assimilation of different types of food by grass carp was first investigated by Migita, Hashimoto (1949). They supplied known amounts of food and collected the faeces by hand every 20 minutes to avoid their disintegration. From this they calculated the quantity of food assimilated and expressed it as a percentage of food intake (Table XII). Growth rates were also recorded and the ratio of food

Table XII. Assimilability of various food items by grass carp (after Migita, Hashimoto 1949)

Food	Dry matter content (%)	Cellulose content (%)	Assimilability (%)
<i>Beta vulgaris</i> var. <i>cicilia</i>	10.75	12.36	73.6
<i>Curbitia moschata</i>	18.2	12.68	65.9
<i>Leersia japonica</i>	20.34	—	60.21
<i>Medicago denticulata</i>	19.73	29.03	61.35
<i>Bromus</i> sp.	24.3	—	57.3
<i>Lactuca denticulata</i>	10.6	26.5	55.4
<i>Wolffia arrhiza</i>	3.62	8.03–13.27	83.5
<i>Impoeca reptans</i>	8.54	—	73.4
Spirodela	3.76	13.24–22.22	58.93
<i>Valisneria spiralis</i>	9.5	31.33	50.3
<i>Ziziana latifolia</i>	43.48	21.5–22.01	46.7
<i>Potamogeton maaskianus</i>	19.49	—	45.95
<i>Myriophyllum spicatum</i>	10.07	17.38	41.54
<i>Eichhornia crassipes</i>	6.95	70.2	31.17
Linseed	83.72	6.33	75.7
Rice mixture	89.5	12.84	73.8
<i>Chryomyia megacephala</i> larvae	13.57	—	90.78
<i>Lumbricus terrestris</i>	23.09	—	87.29

— no data.

intake to growth (food conversion ratio<sup>1</sup>) calculated. The results for different food items are gathered in Tables XIII, XIV and XV. The authors also state that the grass carp does not possess cellulase and that, therefore, digestibility is closely related to the amount of fibre in the food. They consider that the grass carp can digest all but cellulose. Although this conclusion is most probable, it is not fully proved by their paper since no supporting studies of enzymes were made.

<sup>1</sup> The reciprocal of gross production efficiency index *K*.

Table XIII. Weight growth index of young grass carp (4.5–17 g) fed with mixed food (Chryomyia — animal food, Spirodela — plant food) (according to Migita, Hashimoto 1949)

Diet	Ratio of animal to plant food eaten during the experiment	Weight growth index (%)		
		20°C	22°C	29°C
1 day: Chryomyia 2 days: Spirodela	3 : 7	—	2.07	3.98
1 day: Chryomyia 4 days: Spirodela	2 : 8	—	1.03	—
1 day: Chryomyia 6 days: Spirodela	1.5 : 8.5	—	—	1.94
Chryomyia and Spirodela given simultaneously	3 : 7	0.71	—	—
	1 : 9	0.60	—	—

Table XIV. Food conversion coefficients of grass carp fed with different food and at different temperatures (after Migita, Hashimoto 1949)

Fish weight (g)	Food	Temperature (°C)		
		20	22	29
4.5–17	<i>Chryomyia megacephala</i> larvae	11.8	7.54	6.03
	Spirodela	40.63	25.48	15.63
0.5–1.99	<i>Moina sp.</i>	—	—	6.49
	<i>Wolffia arrhiza</i>	—	—	11.30
	Linseed	—	—	14.10

— no data.

Borutskij (1955), mentioning the assimilation efficiency of grass carp, has stated that about 50% of consumed nitrogen is excreted. Stroganov (1963) has reported that digestion by grass carp is incomplete and can amount to about 70% of the food eaten. In an experiment with fish fed the aquatic plant *Enhydris angustipetala* and Tapioca leaves, Hickling (1966) recorded an assimilability of about 50% for food and of about 43–47% for nitrogen. He found that reduction of ingested material occurred mainly in the posterior part of the gut. The activity and seasonal variation of digestive enzymes (amylase, trypsin and lipase) has been mentioned by Bruzinov (personal communication) at the All-state Meeting of U.S.S.R. Hydrobiologists in Kishiniov.

The first radio-isotope study of grass carp nutrition appeared in a small paper by Tsaj Zhen'da, Hua-Yao (1962) in which they concluded that 14–16 cm long individuals are unable to assimilate *Microcystis* cells. However, they do not state whether grass carp eat these algae at all.

Panov et al. (1969) have performed a detailed radioisotope study in which they determined assimilability and conversion ratios for plant and animal food. They report that grass carp weighing 5 g assimilated 69% of animal food (*Daphnia*) on a calorific basis and 15–18% of plant food (*Potamogeton spp.*). Food conversion



Table XV. Index of food efficiency (food: growth ratio) in young grass carp 4.5–17 g in weight fed with mixed diet (Chryomyia — animal food, Spirodela — plant food) (according to Migita, Hashimoto 1949)

Diet	Ratio of animal to plant food eaten during the experiment	20°C			22°C			29°C		
		Index		Difference (%)	Index		Difference (%)	Index		Difference (%)
		Theoretical*	Experimental**		Theoretical*	Experimental**		Theoretical*	Experimental**	
1 day: Chryomyia	3 : 7	—	—	—	12.84	10.68	16.82	9.58	8.61	10.12
2 days: Spirodela		—	—	—	14.33	22.84	60.08	—	—	—
1 day: Chryomyia	2 : 8	—	—	—	—	—	—	—	—	—
4 days: Spirodela		—	—	—	—	—	—	10.99	19.48	77.25
1 day: Chryomyia	1.5 : 8.5	—	—	—	—	—	—	—	—	—
6 days: Spirodela		22.24	7.49	66.32	—	—	—	—	—	—
Chryomyia and Spirodela given simultaneously	1 : 9	22.24	11.94	55.29	—	—	—	—	—	—

100

\* Calculated according to the following formula:  $x = \frac{100}{(I+Z) + (I_1+Z_1) + (I_2+Z_2) + \dots}$ , where  $x$  — food efficiency index of mixed food;  $I, I_1, I_2$  — percentage incidence of each food item in mixture;  $Z, Z_1, Z_2$  — food efficiency index of each food item.

\*\* Real food efficiency index calculated from experimental data.

was 7 for zooplankton and 26.6–32.2 for plant food. These values are similar to those given by Verigin et al. (1963), Sobolev (1966) and Prikhod'ko (1962). Food conversion ratios given by Prikhod'ko, Lupacheva (1967) are greater, however, than those reported by Panov et al. (1969) and other authors, reaching as much as 57. The differences most probably result from different feeding conditions.

Migita, Hashimoto (1949) obtained food conversion ratios for grass carp at different temperatures (Table XIV).

Fidzimori (1958) reported that food conversion in grass carp varied with age, being 15 for fry, 30 for one year old fish, 78.9 for two year old fish, and 101.8 for 3 year old fish. Thus, the food conversion ratio is very variable, depending both on age of fish and type of food. According to Stroganov (1963) the most commonly reported food conversion ratios for grass carp range between 14 and 21, with extremes reaching 54. He also states that this coefficient can be as small as 5. In the latter case, a higher proportion of animal food in the diet is to be expected.

Fischer (1972 b) has confirmed results obtained by Panov et al. (1969) that grass carp fed exclusively with plants (*Lactuca sativa*) assimilate only 20% of ingested food. This low assimilability is due to a large cellulose fraction in the diet. Hydrolyzable carbohydrates were 75% assimilated, proteins 41% and lipids 36%. According to Fischer (1972 b) the assimilated proteins from plants are used mainly for respiration and only to a small extent for growth. This may explain the small growth rate of fish fed with plants. When animal food alone was supplied the assimilability of energy amounted to about 40% and that of proteins to only 26%. The proteins were utilized mainly for growth, with  $K_{2p} = 60\%$  ( $K_{2p} = P/A$ , the ratio of protein incorporated into body tissues to those assimilated). About 44% of lipids and 92%

Table XVI. Indices of proteins, carbohydrates and lipids in budget of matter in grass carp. Food: *Tubifex tubifex* (from Fischer 1972 b)

Character	Proteins	Lipids	Carbohy- drates	Ash	Total	Calorific value (cal/mg)	
						from chem- ical com- position	from com- bustion
Fish (%)	56.5	16.7	2.6	14.2	90.0	4.9279	5.9419
Food (%)	51.6	20.0	3.8	6.2	81.5	5.6192	3.072
Faeces (%)	48.9	15.3	9.8	8.7	82.7	4.6522	4.8047
$U^{-1}$	26.1	44.3	92.3				
$K_1$	15.2	13.9	0.32				
$K_2$	60.1	30.1	0.32				
$C_{exp} - C_{P+R+F}$	%	+16.0	+16.0	-148.8			
	mg	+115.7	+44.7	-80.4			

of carbohydrates were assimilated. The proportions of proteins, carbohydrates, and lipids in budget experiments performed on grass carp fed different foods is given by Fischer (1972 b) (Tables XVI and XVII). The tabulated results should be



Table XVII. Indices of proteins, carbohydrates and lipids in budget of matter in grass carp. Food: *Lactuca sativa* (from Fischer 1972b)

Character	Proteins	Lipids	Carbo- hydrates		Ash	Total	Calorific value (cal/mg)	
			Glucose	Cellulose			from chemical composition	from combustion
Fish (%)	63.5	5.0	3.1	—	17.2	88.8	4.2192	4.4767
Food (%)	15.3	5.8	6.3	53.4	19.2	100.0	5.0217	4.8918
Faeces (%)	8.3	17.0	3.3	48.4	23.0	100.0	4.2672	3.5372
$U^{-1}$	41.0	36.6	75.4					
$K_1$	6.5	23.8	0.003					
$K_2$	15.9	39.2	0.003					
$C_{exp} - C_{P+R+F}$	%	+16.5	-25.3					
	mg	+26.9	-1.7					

considered merely as a means of comparison of the main pathways of utilization of various substances by fish fed such diverse food. The results of the nitrogen balance in grass carp deviate considerably from general data on nitrogen transformation in fish (Ivlev 1939b, Karzinkin 1952, Chalupova, Blažka 1960). These authors point to the tendency for very efficient utilization of proteins by organisms (up to 90%) and to the considerable role of protein transformation in the overall processes occurring in organisms. Data on nitrogen transformation in grass carp (Nikol'skij 1956, Stroganov 1963, Hickling 1966, Fischer 1972 b) indicate a lower assimilability of proteins. Fischer's values produced under laboratory conditions with excess food and a strict monospecific diet are probably lower than those for natural conditions. Nevertheless, it can be concluded from the above mentioned data that under natural conditions the grass carp assimilates only 30–50% of proteins, depending on diet composition, and not 80–90% like other organisms (Tables XVI and XVII).

The carbohydrate balance differs considerably from the nitrogen balance (Fischer 1972 b). Fischer (1972 b) found that assimilation of hydrolyzable carbohydrates was high for both plant and animal diets, being 75 and 92% respectively (Tables XVI and XVII). Energy metabolism requires relatively large amounts of carbohydrates as compared with growth and excretion processes. The quantities of carbohydrates metabolically combusted exceed those ingested in food, which suggests that glyco-genesis must take place on a large scale in the grass carp.

Fischer's (1972 b) lipid balance showed that lipids from an all plant diet were used mainly for growth (Table XVII). This is understandable because of the lesser usefulness of plant proteins for fish growth. The utilization of lipids in grass carp fed animal food was lower on a percentage basis ( $K_{1L} = 13.9\%$  and  $K_{2L} = 30.1\%$ ) but much higher in terms of weight, since the lipid content of animal food was 20%, compared with only 5.8% for plant food.

From data thus compiled, one can assume that under natural conditions, where

the fish consume both plant and animal food, growth is covered mainly by animal proteins and by lipids of both animal and plant origin. It is most likely that carbohydrates in the diet (mostly in plants) and proteins of plant origin are chiefly used in energy metabolism. Glycogenesis probably occurs to a marked extent.

To summarize, it appears that the composition of the diet of grass carp depends chiefly on the availability of food. In this light the herbivorous nature of grass carp should be considered facultative rather than obligative. For optimum growth the proportion of plants in the diet should only be about 25%. Presumably there is an increase in the proportion of plants in the diet and in overall food intake when animal food becomes less available due either to its scarcity or to competition. Increasing the proportion of plant food, however, no doubt results in reduced growth rate.

#### GASEOUS EXCHANGE

Lyakhnovich (unpubl.) has studied the respiration of embryos and first larval stages of grass carp. He found that during embryonic development an individual consumed about 0.03  $\mu\text{l O}_2/\text{hr}$  2 hours after fertilization and 0.75  $\mu\text{l O}_2/\text{hr}$  after 35 hours. After hatching respiration decreased to 0.55  $\mu\text{l/hr}$  at a weight of about 1 mg and then slowly increased. 19 day old larvae (16.5 mg) consumed about 16  $\mu\text{l/hr}$ .

Of the many possible approaches to the study of energy metabolism, the most adequate seems to be to investigate the relationship of oxygen consumption and carbon dioxide production to body weight. This may be expressed by the formula  $Q = a \cdot W^b$ , where  $Q$  is the quantity of oxygen consumed or carbon dioxide evolved per individual per hour,  $a$  is the quantity of oxygen consumed or carbon dioxide evolved per hour by a fish weighing 1 g,  $b$  is the slope, and  $W$  is fish weight in grams.

Winberg (1961) described this relationship for fish in general by the formula:  $Q = 0.307 W^{0.81}$ , where  $W$  is fresh weight in grams and oxygen consumption is in mg  $\text{O}_2/\text{hr}$ . Among deviations from the rule he quotes a chinese formula for grass carp and silver carp:  $Q = 0.152 W^{0.84}$ . Unfortunately we could not reach the original paper, and therefore do not know such details as age of fish, whether they were taken from their natural habitat, or whether reared in a laboratory, and what they were fed with. The regressions obtained by Fischer (1970 a, 1972 b) under laboratory conditions differ considerably from the chinese one: for fish fed with animal food  $Q = 0.300 W^{0.77}$ , and with plant food  $Q = 0.487 W^{0.61}$ , expressed in the same units as Winberg (1961). In both cases  $a$  values are higher and  $b$  values lower than those cited by Winberg (1961). Kalashnik (1971) has obtained a similar regression for grass carp ranging in weight from 14 to 250 g:  $Q = 0.335 W^{0.77}$ . His experiments were done on fish collected directly from ponds and therefore presumably feeding on natural food. The similarity of Kalashnik's (1970) results to Fischer's (1972 b) for fish fed with animal food suggests that under natural conditions the grass carp is not a typical herbivor. A Chinese author, Yen Ye-Tsu (1959), has given values for respiration of grass carp weighing 1.1 and 9.6 g. In Table XVIII these are compared with theoretical values for oxygen consumption at these



weights calculated from the regressions mentioned above. From the differences shown in this table it may be concluded that the Chinese regression quoted by Winberg (1961) ( $Q=0.152 W^{0.84}$ ) has been confirmed by Kalashnik's (1971) experiment and by Fischer's (1972 a) with Tubificidae as food. The data of the latter two authors are similar to those of Winberg (1961) for all fish. Deviations from his formula ( $Q=0.307 W^{0.77}$ ) are to be expected, as he himself thoroughly explained, due to the ecological properties of the species. Such deviations as occur between the general regression for fish and the regressions for grass carp, as well as between regressions within the species, seem to be of little significance.

Table XVIII. Theoretical oxygen consumption ( $\mu\text{l O}_2/\text{hr}$ ) by grass carp of different weight calculated from regression equations:  $R=aW^b$  (where  $R$  respiration in  $\mu\text{l/hr}$ ,  $W$ —wet weight in g,  $a$ ,  $b$ —proportionality factors) according to different authors

Fish weight (g)	Yen Ye-Tsu (1959) No formula	Chinese data (after Winberg 1961) $0.152W^{0.84}$	Winberg (1961) $0.307W^{0.77}$	Fischer (1970 a, b, 1972a)	
				Food	
				Tubificidae $0.300W^{0.77}$	<i>Lactuca sativa</i> $0.487W^{0.61}$
1.1	416.2	165.9	332.0	323.0	520.0
9.6	2658.3	1016.0	1929.0	1705.0	950.0

The literature on carbon dioxide production by grass carp is exceptionally scarce. Yen Ye-Tsu (1959) was the first to deal with this topic. He obtained a mean value of  $187 \mu\text{l/g}\cdot 1 \text{ hr}$  of  $\text{CO}_2$  for fish weighing 9.6 g. Unfortunately he does not give data for other weights. Fischer (1970 a, b, 1972 a) has also studied carbon dioxide production by grass carp under experimental conditions fed with different types of food. For fish ranging between 20 and 120 g in weight and fed with animal food she obtained the regression  $Q\text{CO}_2=456.6 W^{0.68}$ , where  $W$  is fish weight in grams and  $Q\text{CO}_2$  is the volume of carbon dioxide produced in  $\mu\text{l/hr}$ . Using this formula the theoretical carbon dioxide production for a fish weighing 9.6 g is  $220 \mu\text{l/g/hr}$ , only 33  $\mu\text{l}$  more than the figure measured by Yen Ye-Tsu (1959). The similarity of their results suggests that these authors have correctly described a regular trend.

Lyakhnovich (unpubl.) has measured carbon dioxide production as well as oxygen consumption by embryonic and early larval stages of grass carp. During embryonic development changes in  $\text{CO}_2$  production were proportional to those in  $\text{O}_2$  consumption. They amounted to  $0.02 \mu\text{l CO}_2/\text{hr}$  in the first two hours and to  $0.42 \mu\text{l CO}_2/\text{hr}$  just before hatching 34 hours after fertilization. Directly after hatching a decrease in the amount of carbon dioxide produced was observed. On the 16th day after hatching one larva of about 13 mg in weight produced  $1.5 \mu\text{l CO}_2/\text{hr}$ . However, on the 17th day and thereafter  $\text{CO}_2$  production increased, amounting to  $12.3 \mu\text{l CO}_2/\text{hr}$  for larvae weighing 17–20 mg.

Calculation of respiratory quotient is necessary for indirect calorimetry determinations. Theoretically  $RQ$  values should range from 0.7 to 1.0. This quotient is very

unstable and changes with diet composition, size of ration, ambient temperature, body weight, and even with time of day.

According to Lyakhnovich the  $RQ$  for embryonic stages is low and amounts to about 0.6. Such a low value is understandable because of the starved state of embryonic stages. An  $RQ$  as low as this, or even lower, is typical during metamorphosis and first stages of larval development when the organism depends on food stored in the yolk sack. However, after 17 or 18 days of life the  $RQ$  reaches a value of 0.76.

According to Yen Ye-Tsu (1959) the respiratory quotient in mature grass carp ranges from 0.88 to 0.91 depending on fish age. He accepts 0.91 as a mean value. This differs from the values obtained by Fischer (1970 a, b, 1972 a, b) both for plant and for animal food. For grass carp fed with animal food the average  $RQ$  was 0.80, this relatively low value resulting from the properties of the food itself. A different situation was observed when only plant food was supplied — the  $RQ$  was higher and amounted to 0.96 on average, reflecting enhanced carbohydrate transformation.

The relatively large variation in metabolic processes of grass carp can be accounted for by the diversity of food consumed. Since the grass carp, depending on its age and environment, feeds mainly either on animals or on plants, its energy metabolism may shift from the lipid to the carbohydrate type. This is reflected by the large changes observed in  $RQ$  values (0.76–0.96).

#### ENERGY BUDGET

Calculation of energy budgets aims at describing species as converters of energy form food into body biomass. Unfortunately there is little data on energy budget parameters for animal species under natural conditions. Such investigations are exceptionally difficult and often impossible unless preceded by laboratory experiments. Fischer (1970 b, 1972 b) has produced, for one-year-old grass carp, an instantaneous energy budget (i.e. one covering a part of the life, cycle as opposed to the whole life cycle as in a cumulative budget). The experiments aimed at describing energy transformation by this fish and its role in energy flow to other links of the trophic chain in aquatic reservoirs. She found that food intake in calories was large, irrespective of food quality and that, after appropriate recalculation it, was higher than that reported by Ivlev (1939 b) and Karzinkin (1952). This may be connected with the fact that Fischer fed to excess in her experiments.

The growth rates (in calories) of fish fed with animals were about ten times as great as those of fish fed with plants. The quantity of faeces was very high when both types of food were given.

The index  $U^{-1}$  describes the proportion of energy that is assimilated. The efficiency of assimilation by grass carp was first studied by Migita, Hashimoto (1949) (Table XII). They obtained values ranging from 31% for plant food to 90% for animal food, depending on the type of food consumed. Fischer (1972 b) has calculated the assimilability of various types of food in three different ways (Table XIX).



Table XIX. Mean values of energy indices (from Fischer 1972 b)

Fish body weight (g)	Food	Indices				
		$U^{-1}$			$K_1$	$K_2$
		$\frac{P+R}{C}$	$\frac{C-FU}{C}$	Conover's (1966) method		
86-107	Tubificidae	39.50	40.10	41.82	12.53	40.40
20-55	<i>Lactuca sativa</i>	17.20	24.81	20.72	2.22	14.47

The values obtained by different methods of calculation vary little among themselves, but are about half of those reported by Migita, Hashimoto (1949). Presumably this discrepancy is due to the prolonged nature of Fischer's (1972 b) experiments in which the fish were kept in aquaria for many months and to the fact that Migita, Hashimoto (1949) experimented with younger fish (up to 17 g). It is known that young organisms tend to assimilate more efficiently than older ones. Techniques used in the two studies also differed. In the Japanese work faeces were collected by hand, whereas in Fischer's (1972 b) they were centrifuged out and dissolved proteins were also taken into account. According to Fischer (1972 b) the assimilability of animal food by grass carp was about 40%. This value is most similar to that for assimilability in less active predators (Klekowski et al. 1972) such as *Actinia* (Ivleva 1964) and larvae of *Lestes sponsa* (Fischer 1972 c) where it ranges from about 35 to 65%. Thus, it appears that the grass carp kept in experimental culture and fed with animal food can be considered as an inactive carnivore. This inactivity may result from a certain restriction of movement of fish by the culture chamber. Under natural conditions, when movement of fish is unrestricted, assimilation is probably higher. The low assimilation may also have been caused by ad libitum feeding. Davies (1964) has reported diminishing assimilation with increasing food intake in his study of the bioenergetics of crucian carp.

With fish fed plants Fischer (1972 b) obtained an assimilability of about 20%. Such low assimilation is typical for filtrating organisms (Richman 1958, Monakov, Sorokin 1961) and for detritus feeding organisms, such as *Asellus aquaticus* (Prus 1971) and *Tubifex tubifex* (Ivlev 1939 a). Both these groups of organisms fed on plants or on detritus. It can be concluded, therefore, that assimilation efficiency is so closely dependent on the type of food eaten that when an organism switches to another diet its assimilation efficiency changes also. Fischer's (1973) work suggested that grass carp could assimilate both the types of food given, the animal food being better assimilated than the plant food.

The gross production efficiency index  $K_1$  describes the proportion of food intake used for fish growth. Its value is 12.5% for grass carp fed with animals and 2.2% for those fed with plants. These values are lower than those given by Ivlev (1939 b) for carp and by Karzinkin (1952) for other fish.

The  $K_1$  index for grass carp fed exclusively with plants is astonishingly low. Such low values have only been found in *Asellus aquaticus* (Prus 1971) where  $K_1$  was 5.32 on average. From Migita and Hashimoto's (1949) data it is possible

to calculate  $K_1$  indices for grass carp fry and fingerlings to 17 g in weight (Table XX). They are similar to those obtained by Fischer (1972 b) (Table XIX). A  $K_1=12\%$  with animal food was determined both by Fischer (1973) and by Migita, Hashimoto (1949). With plant food Fischer obtained a  $K_1=2\%$ , whereas Migita and Hashimoto (1949) obtained 3%.

Table XX. Gross production efficiency index  $K_1$  (%) for grass carp fed with different food (recalculated from data given by Migita, Hashimoto 1949)

Food		Fish weight (g)		
		4.5-17		0.52-0.9
		Temperature (°C)		
		20	22	29
Plant	Spirodela	2	3	6
	Eichornia			2
	Wolffia			8.9
	Linseed			7
Animal	Chryomyia	8	12	16
	<i>Moina sp.</i>			15

The net production efficiency index  $K_2$ , denoting the proportion of assimilated food used for growth, is also low for fish fed with plants, amounting to 14.5%. Similar values are given by Prus (1971) for *Asellus aquaticus* (17%) and by Klekowski, Duncan (in print) for some long-living poikilotherms. The  $K_2$  index for grass carp fed with animals is 40.4%. This value is close to that obtained by Ivlev (1939 b) for carp and to those commonly found in aquatic poikilotherms (Klekowski, Duncan in print).

To sum up, one can suppose that the bioenergetic processes in grass carp fed with animal food are similar to those in carp — the fish assimilates animal food to an average degree, grows rapidly, and shows a broad food preference. On the other hand, grass carp fed with plants assimilate to a minimal degree and shows very low growth rates. That the grass carp feeds on vascular plants under natural conditions can probably be explained by the fact that these plants form a “free” food supply not utilized by other animals and for which the grass carp does not encounter any competition. It is beyond doubt that the grass carp feeds also on plants under natural conditions. This ties in closely with its important role in preventing the over-growth of water bodies. Simultaneously, one has to bear in mind that, as well as destroying vegetation, grass carp will also feed to a great extent on the fauna of these bodies of water. Plant food can even increase the grass carp’s requirement for animal proteins from which it derives most of the energy for growth. 15% of animal proteins is used for growth, whereas only 6% of plant protein is thus used. This fish can only utilize aquatic vegetation to a small extent. About 80% of the energy accumulated in consumed plants is voided in faeces that sink to the bottom as partly digested plant debris. Such “fertilization” must cause a thorough



change in bacterial populations inhabiting the body of water, which in turn will strongly affect the plankton and benthic fauna — in other words, it will affect the biocenosis of the reservoir. Cure (1971) has described the increased eutrophication following introduction of grass carp to a pond. Its character changed dramatically (1967 — about  $1.00 \text{ g O}_2/\text{m}^2/24 \text{ hr}$ , 1970 —  $11.1 \text{ g O}_2/\text{m}^2/24 \text{ hr}$ ).

On the other hand, animal food consumed by grass carp is assimilated to a degree similar to that found in the majority of omnivorous fish (40%). When there is an abundant fauna this type of food most probably forms the main source of energy for grass carp. It may be assumed that under natural conditions where there is severe competition for food or animal food is scarce the grass carp can shift to plant food and feed on it almost exclusively. Under such conditions very poor growth of its biomass is to be expected.

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