



**SYNOPSIS OF BIOLOGICAL DATA
ON THE GRASS CARP
Ctenopharyngodon idella (Cuvier and Valenciennes, 1844)**

Prepared by
Jerome V. Shireman and Charles R. Smith



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Ctenopharyngodon idella (Cuvier and Valenciennes, 1844)

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PREPARATION OF THIS SYNOPSIS

This synopsis has been prepared in view of the growing importance of *Ctenopharyngodon idella* for aquaculture and for weed control which has resulted in its widespread introduction into waters throughout the world.

The study was funded by the US Fish and Wildlife Service, National Fisheries Research Laboratory, Gainesville, Florida, Dr James A. McCann, Director. Contract No. 14-16-009-78-912.

ABSTRACT

This synopsis compiles and reviews the presently available information on identity, distribution, bionomics, life history, population structure and dynamics, exploitation, aquaculture and weed control potential of the grass carp, *Ctenopharyngodon idella* (Cuvier and Valenciennes, 1844).

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1. IDENTITY

1.1 Taxonomy

- Suprageneric (Nelson, 1976)

Phylum Chordata

Subphylum Vertebrata (Crania)

Superclass Gnathostomata

Grade Pisces

Subgrade Teleostomi

Class Osteichthyes

Subclass Actinopterygii

Infraclass Teleostei

Division Euteleostei

Superorder Otariophysii

Series Otophysi

Order Cypriniformes

Suborder Cyprinoidei

Family Cyprinidae

Subfamily Leuciscinae

Genus *Ctenopharyngodon*

Steindachner

- Generic (Jordan, 1963)

Ctenopharyngodon Steindachner, 1866. Zur Fischfauna Kaschmirs und der benachbarten Landstriche. Verh. Zool. - Bot. Gesellsch. Wien, 16, p. 782 (orthotype: *C. laticeps*)

- Specific

Ctenopharyngodon idella is the sole member of the genus. No subspecies.

1.2 Description (Günther, 1868; Nichols, 1943; Berg, 1949)

1.2.1 Generic characters

Body oblong with moderate to large scales, rounded belly and broad head. Eye located in or above axis of body. Mouth subterminal to terminal and somewhat oblique; jaws with simple lips. Upper jaw slightly protractile and lower distinct only at angle of mouth. No barbels. Lateral line complete, running medially on side of the tail. Scales moderate (40-45). Dorsal and anal fins short and without spines. Branched rays about 7 and 8. Dorsal placed opposite to ventral fin. Origin of anal fin well behind posterior edge of dorsal. Branchial membranes attach to isthmus behind verticle from the orbit. Pseudo-branchiae present. Unfused gill rakers short, lanceolate, and widely set. Pharyngeal teeth biserial and 2.5-4.2, 2.4-4.2, 2.4-5.2, or 1.4-5.2. Crowns strongly compressed laterally and serrate, outer layer deeply folded, and grinding surface with a longitudinal groove.

1.2.2 Specific characters (see Figure 1)

D. 3/6-8, A. 3/7-8, V. 10, L.L. $38 \frac{6.5-7}{5}$ 45.

Depth in standard length (SL) 3.8-4.8. Head in SL 3.4-4.5. Eye in head 3.8. Suborbital ring very narrow; preorbital larger than hindmost suborbital. Forehead very broad; width of convex interorbital space equals the length of the head's postorbital portion and is

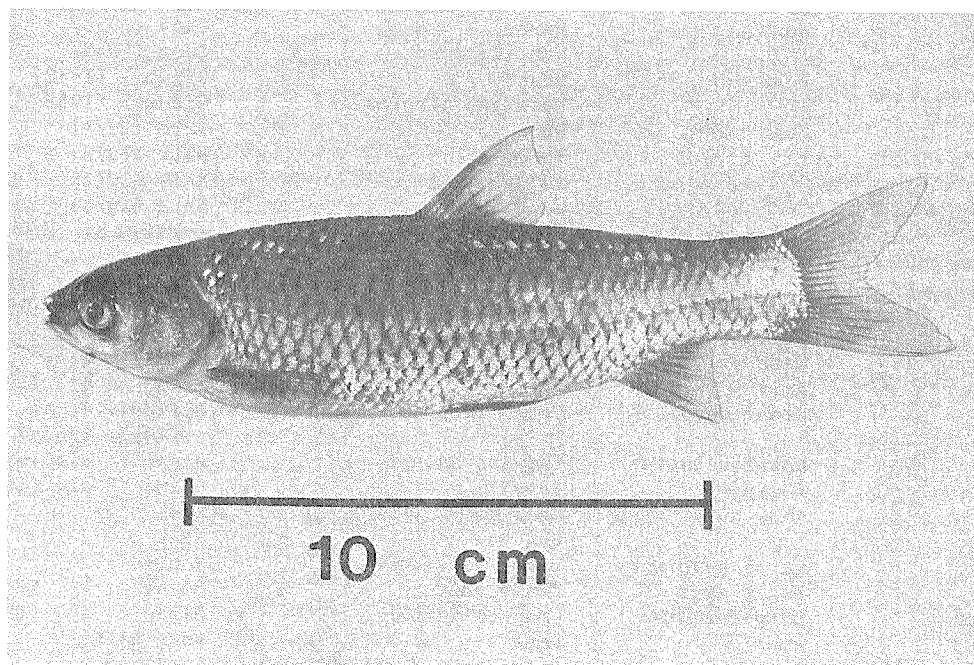


Figure 1 Grass carp (*Ctenopharyngodon idella* Val.)

greater than half the head length. Corner of mouth at vertical from anterior eye margin. About 12 short gill rakers. Sensory canal system highly developed on head. Opercular bone with radial striae. Scales have numerous radiating striae with transversely rugose interspaces. Dorsal and anal fins rounded; caudal deeply forked. Origin of dorsal somewhat in advance of ventral bases. Dark brown above, lighter below, sides with slight goldenish sheen. Fins dark. Base of each scale dark brown.

1.3 Nomenclature

1.3.1 Valid scientific name

Ctenopharyngodon idella (Cuvier and Valenciennes, 1844) Berg, *Fauna Rossii*, Ryby III, No. 1, p. 288, 1912. (Berg 1964).

1.3.2 Synonymy

Leuciscus idella Cuvier and Valenciennes, *Hist.Nat.Poiss.*, XVII, p. 362, 1844, China.

Leuciscus tschiliensis Basilewsky, *Nouv. Mém.Soc.Nat.Hist.Mosc.*, X, p. 233, 1855. (Günther, 1868).

Ctenopharyngodon laticeps Steindachner, *Verh.Zool.-Bot.Gesellsch.Wien*, 16, p. 782, 1866; Hong Kong. (Günther, 1868).

Sarcocheilichthys teretiusculus Kner, *Reise "Novara"*, Zool., I. *Fische*, p. 356, 1867; Shanghai. (Nichols, 1943).

Ctenopharyngodon idellus Günther, *Catalogue of the Fishes in the British Museum*, VII, p. 261, 1868; China.

Pristiodon siemionovi Dybovskii, *Izv. Sib. Otdel. Geogr. O-Va.*, 7, No. 1-2, p. 26 1877; Amur, Assuri, Sungacha, Lake Khanka, Sungari (Berg. 1964).

1.3.3 Standard, common and vernacular names

Today, the two most frequently used English common names are grass carp and white amur, with the former being more popular. Because of widespread introduction, vernacular names have proliferated and are presented below in Table I.

Table I

Standard common and vernacular names

COUNTRY	STANDARD COMMON NAME	VERNACULAR NAME	AUTHORITY
China	Hwan yu	Hwan yu	Richardson (1846)
		Hwan u	Richardson (1846)
	Chow hu	Chow hu	Birtwistle (1931a)
		Waan ue	Lin (1935a)
	Huan	Huan	Chow (1958)
		Wan (Cantonese)	Chow (1958)
	Huan-yü	Huan-yü	Gidumal (1958)
		Waan yue (Cantonese)	Gidumal (1958)
	Wuan yu	Wuan yu	Naik (1972)
		Ts'ou	Naik (1972)
Ts'oyu		Naik (1972)	
Waan yu		Naik (1972)	
Czechoslovakia	Ts'ao-yu	Ts'ao-yu	I-kui et al. (1966, 1973)
	Amur bily	Amur bily	Blanc et al. (1971)
		Amur biely (Slovakian)	Blanc et al. (1971)
Denmark	Graeskarpe	Graeskarpe	Blanc et al. (1971)
Germany	Graskarpfen	Graskarpfen	Molnár (1969)
Hong Kong	Waan yu	Waan yu	Naik (1972)
Hungary	Amur	Amur	Blanc et al. (1971)
India	Grass carp	Grass carp	Alikunhi et al. (1962, 1963a)
Israel	Karpion haesef	Karpion haesef	Blanc et al. (1971)
Japan	Sogyo	Sogyo	Ojima et al. (1972)
Malaysia	Chow hu	Chow hu	Naik (1972)
		Wan yu	Naik (1972)
Mexico	Carpa herbivora	Carpa hervivora	Rosas (1976)
Poland	Bialy amur	Bialy amur	Blanc et al. (1971)
Romania	Crap-de-iarba	Crap-de-iarba	Blanc et al. (1971)
USSR	Amur	Amur	Berg (1964)
		Belyi amur (Lake Khanka)	Berg (1964)
United States	Grass carp	Grass carp	
	White amur	White amur	
Vietnam	Ca cham	Ca cham	Naik (1972)

1.4 Morphology

1.4.1 Gross morphology and anatomy

Little variation in gross morphology has been reported and no subspecies are known. Berg (1964) states that small (< 108 mm total length) grass carp from Harbin (Haerhpín), China have larger scales (L.L. 38-42) and deeper bodies (3.4-3.5 SL) than others examined. Berry and Low (1970) give the following meristics for 20 specimens (SL 9.1-18.5 cm): D. 1-2/8; P. 1/14-16; V. 1/7-8; A. 2/8-9; C. 5-6/17/4-6; L.L. 50 $\frac{6-7}{42}$, \bar{x} snout length (SL) 14.3; \bar{x} head length (SL) 3.4; \bar{x} head width (SL) 5.3; \bar{x} interorbital width (SL) 6.7; \bar{x} body breadth (SL) 4.2; \bar{x} caudal peduncle length (SL) 6.7; and \bar{x} caudal peduncle height (SL) 7.7. The cycloid scales have a central focus, slightly scalloped anterior margin, and completely scalloped posterior edge.

According to Inaba and Nomura (1956), the buccal cavity has a few anterior transverse folds and many low, longitudinal folds on its roof. A labial fold runs along the upper lip. The tongue is not free. Its mucus membrane rises in a semi-triangular shape and has many fine transverse folds. The mouth has thick lips. The jaws, vomer, palatines and tongue-lack teeth.

The fifth branchial arch is well developed, its length being twice its breadth and having two rows of large, laterally compressed and sharply serrated pharyngeal teeth. The tooth formula is 2.5-4.1. The inner teeth are more strongly developed than the lateral teeth. Small compressed accessory replacement teeth are embedded in the mucus membrane of the pharynx near the pharyngeal jaw. The horny pad or molar, which provides a masticatory surface for the teeth, is oval with rugose patterns on the free surface. Each branchial arch has slender, tapering gill rakers arranged biserially on the margin. Each raker consists of a basal plant for attachment, and a pliable shaft with striations, covered with a thin layer of mucus. They are small and dispersed (Berry and Low, 1970).

Intestinal length relative to SL ranges from 1.6 to 2.0 (Hoa, 1973) to 1.6-2.6 (Berry and Low, 1970) to 1.9-2.7 (Hickling, 1966). Chang (1966) states that relative intestinal length increases from 0.5 in larvae to 2.5 in adults. Berry and Low (1970) present the most detailed account of grass carp internal anatomy. The gut is differentiated into a short esophagous, pyloric sphincter, poorly defined intestinal swelling, intestine proper, and rectum. Coiling of the gut follows a constant pattern. The liver lies on the dorsal surface of the gut and its lobes usually extend the length of the abdominal cavity. Closely associated with the liver is a diffuse pancreas from which several small ducts join the bile duct to form the hepatopancreatic duct, which enters the gut immediately posterior to the pyloric sphincter. The large gall

bladder lies between the liver and intestine. The narrow, dark red spleen occurs in two or three parts. The swim bladder is located between the alimentary tract and kidneys, and is divided into two chambers, the bulbous anterior chamber being half the length of the tapering posterior one. A pneumatic duct originates from the anterior end of the posterior chamber, passes forward and swells into a pneumatic bulb before entering the esophagus. A diffuse adrenal gland is located in the pronephros of the kidney (Mezhnin, 1975). The gonads of immature specimens are located above the swim bladder and adhere closely to the peritoneum. Gonadal differentiation occurs at a mean total length of 58 mm (50-60 days old). The presumptive ovary flattens from its oval cross section and becomes attached to the peritoneum at two places with a coelum separating the gonad and abdominal wall; the testis remains the same (Shelton and Jensen, 1979). Unlike many other fish, anatomical differentiation of the gonads into sex-specific shapes precedes cytomorphological differentiation in the grass carp (Bobrova, 1972). Slack (1962) examined a mature 476-day-old female with a gonadosomatic ration of 0.04 and ovarian weight of 290 g. The ovaries had expanded into lateral lobules and were orange in colour.

In a review of the percent composition by weight of various constituents in grass carp, Jähnichen (1971) cited the following ranges: body 61.2-67.5, head 11.5-19.9, skeleton 2.9-8.3, fins 2.1-2.3, scales 2.8-5.2, gut 6.2-13.0, and gonad 0.6-0.8. Okoniewska and Okoniewski (1968) found the weight components in percent to be 19.9 for the head, 62.0 body, 55.0 fillet, 10.2 gut, 7.0 skeleton and 7.9 for fins and scales together.

In spite of overlapping spawning seasons and habits, natural hybridization of the grass carp with the silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*) has not been documented. Under artificial conditions, however, the grass carp has been crossed, not only with these species, but also with the black carp (*Mylopharyngodon piceus*), goldfish (*Carassius auratus*), common carp (*Cyprinus carpio*), black bream (*Megalobrama terminalis*), eastern bream (*Abramis brama orientalis*), white bream (*Parabramis pekinensis*), rohu carp (*Labeo rohita*), *Labeo ariza*, catla (*Catla catla*), mrigal (*Cirrhina mrigala*), and pla-tapien or puntius carp (*Puntius gonionotus*) (Section 3.1.6).

The hybrid cross presently causing the most interest is that with the bighead carp. Aliev (1967) obtained two progeny from a grass carp female fertilized by a bighead male. The predominantly matroclinous young deviated significantly toward the paternal phenotype only in possessing one less caudal vertebra and a pale bluish-grey colour. In the opposite cross, that involving bighead roe fertilized by grass carp milt, Verigin, Makeeva and Shubnikova (1975) produced truly

intermediate hybrids (mean length 8.1 cm). Number of trunk myotomes, scale size, head size, eye position, and body depth fell between the parental types. Of 19 characters analysed, 11 differed significantly from both parents and 7 from either the father or mother. The majority of characters deviated either 46-96 % toward the female or 13-80 % toward the male. The pharyngeal teeth and bones were intermediate in formula and general structure. Berry and Low (1970) described the morphology of hybrids resulting from female bighead crossed with male grass carp. The origin and number of dorsal and pectoral fin rays in the hybrid approached the maternal type while ventral fin ray number was closer to that of the paternal parent. Hybrid anal fin ray counts were intermediate between those of the parents. Lateral line and transverse scale series were intermediate between and more variable than in the parents. Other intermediate characters included scale size and shape, dorsoventral profile, and jaw and head lengths. The hybrid resembled the grass carp with a terminal mouth, elongate body, and round short snout. Hybrid features similar to bighead were a high and long caudal peduncle, wide head, and abdominal keel. Unlike the bighead, the grass carp and hybrid had asymmetrically arranged pharyngeal teeth. Otherwise, the size and shape of these teeth and the molar were intermediate in the hybrid. Mean length and density of hybrid gill rakers were more than in grass carp, but less than in bighead. They also tended to be irregularly bent in different directions and their insertion on the arches differed from the parental types. Gill filaments were shorter than in either parent. The relative length and coiling pattern of the hybrid gut were identical to grass carp. Diameters of gut regions in the hybrid were closer to those in bighead. The hybrid swim bladder had a 1:1.2 length ratio between anterior and posterior chambers, a condition intermediate between the 1:2 ratio in grass carp and the 2:1 ratio in bighead. Shape of the posterior chamber more closely resembled that of the grass carp.

Makeeva and Verigin (1974) obtained a small number of progeny from degummed common carp roe fertilized with grass carp milt. Surviving hybrids had 25 trunk myotomes as in the common carp. Fingerling morphology deviated toward the maternal parent in 15 of 20 characters, of which 8 exceeded the parental value. Of 5 characters more similar to those of grass carp, the heights of dorsal, anal and pectoral fins exceeded the paternal value. The pharyngeal teeth in the hybrid had a triserial formula of 1.2.3-3.2.1 versus 1.1.3-3.1.1 in common carp and 2.4-5.2, 1.4-5.2, etc., in grass carp. Their structure resembled more closely that of the maternal parent. Two matroclinous specimens were obtained in addition to the true hybrids. Nevertheless, they showed paternal influence in head length, eye diameter, and pectoral and pelvic fin lengths (Makeeva, 1976). Stanley and Jones (1976) produced hybrids from the same cross which had intermediate numbers of dorsal fin rays,

lateral line scales, and gill rakers. Basal length of the hybrid dorsal fin was intermediate between the parental values. Hybrids had pharyngeal teeth structure and identical anal fin ray numbers to those in common carp.

Artificial crosses with other species have not been fully investigated. Aliev (1967) hybridized female silver carp with male grass carp and obtained patroclinous young which lacked abdominal keels. The position of the pectoral and base length of the anal fin in the hybrid were intermediate between the parental types. He also produced hybrid fingerlings by crossing female grass carp with male black bream. Characteristics tending toward the paternal phenotype were long antedorsal and pectoral-ventral intervals, high dorsal fin, long pectoral and ventral fins and long anal fin base. Characters in common with black bream were dorsal fin position, ventral-anal keel, and a small, terminal mouth. Head dimensions and ventral-anal distance approached those in the grass carp. The anal fin formula (III-17) fell between those of the parents. Ryabov (1973) crossed a female grass carp with eastern bream and obtained hybrid embryos which all died within 8 days. Embryos with maternal characteristics survived longer. They had 27-29 trunk myotomes and cigar-shaped yolk sacs similar to grass carp, but their pigmentation resembled that of the eastern bream. Alikunhi, Sukumaran and Parameswaran (1962, 1963b, 1973) performed reciprocal crosses of the grass carp with rohu carp and catla. All hatchlings died in the first day after emergence, with the exception of those involving the cross between male grass carp and female rohu carp. These specimens survived as long as 2 weeks, but were not described. Stanley (1973a) produced feeding hybrid larvae by fertilizing goldfish roe with grass carp milt. These fish had a deep body, small eyes, and fins similar to goldfish (Stanley and Sneed, 1973a, 1973b). Fisheries Division researchers of the Joint Commission for Rural Reconstruction, Taiwan, crossed female black carp with male grass carp, which resulted in viable hybrids with feeding habits similar to grass carp (Chen, 1969).

Stanley and Jones (1976) obtained androgenetic and gynogenetic grass carp by crossing female common carp with male grass carp and by fertilizing grass carp roe with irradiated common carp milt, respectively. These progeny were identical to grass carp and differed significantly from common carp and hybrids in all the variable characters examined. Additionally, all gynogenetic fish were female (Stanley, 1976a, 1976d).

1.4.2 Histology

Berry and Low (1970) thoroughly described the gut histology. A thin serosal layer surrounds the esophagus. The next layer, a thick muscularis, has an outer part of striated circular muscles and an inner one of striated longitudinal and oblique muscles. Connective tissue and scattered bundles of longitudinal

striated muscle comprise a compact submucosa. The mucosa has broad shallow folds of variable size bordered by pseudostratified epithelial cells with scattered saccular mucus cells. The pneumatic duct is formed of a thin serosal layer, striated longitudinal and circular muscle layers, a thick layer of fibrous connective tissue, and finally, a layer of cuboidal epithelial cells lining the lumen. In the transition zone from the esophagus to the intestinal swelling, the mucosa develops high, ramulous folds. In the intestinal swelling, the muscularis becomes reduced and is composed of smooth muscle layers with longitudinal fibres overlapping the inner circular fibres. The submucosa forms finger-like extensions between the mucosal folds. Tall columnar cells, scattered goblet cells, and a reduced number of saccular mucus cells constitute the mucosal epithelium. The intestine proper resembles the intestinal swelling, but the muscosal folds are reduced in number and size. Tall columnar absorptive cells and goblet cells occur in the mucosal epithelium. Small lymphocytes and granular cells are embedded in the submucosa. The rectum has features similar to the intestine, but the submucosa is extensive and richly vascularized. The size and number of mucosal folds are further reduced. The mucosal epithelium is composed primarily of goblet cells with rare saccular mucus cells. Hybrids resulting from female bighead crossed with male grass carp have alimentary tracts which are histologically more similar to those of the grass carp.

Shelton and Jensen (1979) found histological differentiation of the gonads in grass carp to be a protracted and a variable process. Nested oogonia and rare primary oocytes appeared in fish 94-125 days old. From 180 to 232 days of age, the ovaries were transitional with oogonia transformed into oocytes. Between the ages of 240 and 405 days, basophilic oocytes occurred in half of the ovaries examined. Of the four oldest females (675 days), three had ovaries dominated by primary oocytes and with distinct ovigerous lamellae. Germ cells proliferated between 150 and 300 days of age in males. Spermatogonia dominated in 300-675-day-old fish, but never formed primary spermatocytes. The efferent duct network and vascular system began development from 90 to 125 days of age. In central USSR, Bobrova (1972) observed oocytes to begin protoplasmic growth at age three and trophoplasmic development in 6-7 years. Spermatogenic waves appeared in the second year for males and mature sex cells in spermatogonia dominated the testes in 27-28 months. Primary and secondary spermatocytes occurred at 37-38 months and a few ampullae with mature sperm developed in 39-40 months. In Malaysia, Slack (1962) described a set of relatively mature ovaries from a large specimen, which had 2 % of the ova in the yolk vesicle stage, but none in the primary yolk stage, presumably due to a pause in the maturation cycle. In Malaysian hybrids, produced by crossing female bighead with male grass carp, Berry and Low (1970) found 9-11-month-old females with young

oocytes and 20-month-old males with seminiferous lobules producing spermatozoa.

The blood has 2.0×10^6 erythrocytes/mm³, 2.4×10^4 leucocytes/mm³, a hematocrit of 43 %, 9 g % hemoglobin, and pH of 6.9 (Molnar, 1969). Lyakhnovich and Leonenko (1971) discovered age-related and seasonal variation in the blood characteristics of acclimatized grass carp. Blood volume and hemoglobin concentration rose in mid-summer. Concentration of hemoglobin averaged 9.6 g % of the blood. The total amount was highest in 1+ fish (3.85 g/kg fish) and lowest in underyearlings (2.75 g/kg fish).

The adrenal gland is composed of adrenocortical and adrenomedullary cells located near the cardinal vein and its branches in the kidney pronephros. The adrenomedullary cells may be localized in the walls of the post-cardinal vein and its branches, or bunched into islets in the adrenocortical mass and near the sinusoidal capillaries. A vascular wall separates the cells from the blood vessel lumen, except in the sinusoids where only an endothelial layer is present (Mezhnin, 1975).

In thermal-stability and alcohol resistance experiments on muscle tissue from interpopulation hybrids and a parental form of grass carp, Andriyasheva (1969) found no significant differences, indicating a depression of heterosis.

1.4.3 Cytology

Much attention has been directed toward the karyology of grass carp and the hybrids produced by crossing it with common, bighead and silver carp. Ojima, Hayashi and Ueno (1972) determined the diploid chromosome number of grass carp to be 48 and the arm number to be 84, with 10 submetacentric or subtelo-centric chromosomes, 8 metacentrics, and 6 telecentric or acrocentric chromosomes. Manna and Khuda-Bukhsh (1977) and Máriań and Krasznai (1978, 1979) obtained similar results with small differences in the number of chromosome types. Beck, Biggers and Dupree (1980) found 15 metacentric, 9 submetacentric, and no acrocentric chromosomes. They suggested that excessive contraction of chromosomes caused by overexposure to colchicine would obscure the short arms of the small submetacentrics and might explain the differences of their results from those of previous workers.

In crosses of female grass carp with male bighead ($2n = 48$), a hybrid resulted with triploid karyomorphology; diploid number equaled 72 and number of arms was 126-128 (Máriań and Krasznai, 1978). Beck, Biggers and Dupree (1980) analysed comparative chromosome morphology and hypothesized that the triploid hybrid probably resulted from retention of a polar body in the zygote, because it possesses two maternal sets and one paternal set of chromosomes. By fertilizing common carp ($2n = 100-104$) roe with grass carp milt,

Vasil'ev, Makeeva and Ryabov (1975, 1978) obtained allotriploid larvae ($2n = 124-128$) and inviable diploid embryos ($2n = 74-76$). The reciprocal cross yielded only inviable diploid embryos. Mantelman (1973) investigated the karyology of hybrids from reciprocal crosses of grass and silver carp ($2n = 46-56$). Most hybrids were diploid but others had much higher (uncounted) chromosome numbers, indicating polyploidy.

Shelton and Jensen (1979) identified oocytes by their basophilic staining. Chen, Chow and Sim (1969) identified minute cells which were embedded in the ovigerous lamellae throughout the year and corresponded to the chromatin-nucleus stage of development. Slack (1962) described the differentiation of ova in grass carp. All oocytes in immature fish and 60-70 % in mature females were in the perinucleolus stage (size range 50-250 μ). Numerous peripheral nucleoli occurred in the central nucleus. Perinucleolus oocytes initially were strongly basophilic, but became weakly basophilic at larger sizes. They identified a rudimentary zona radiata at this stage. A peripheral ring of oil droplets appeared just within the zona radiata at the beginning of the yolk-vesicle stage. Yolk vesicles formed and increased centripetally. During the primary yolk stage, yolk globules multiplied to fill the cytoplasm. The steadily thickening zona radiata became radially striated and yolk globules obscured the yolk vesicles at the secondary yolk stage. Ova in this stage were 1.3 mm in diameter. In the tertiary yolk stage, Chen, Chow and Sim (1969) described further increases in yolk globules, reductions of the vesicles, and redifferentiation of the irregular nucleus. The nucleus moved toward the animal pole near the micropyle during the migratory-nucleus stage. The nucleus reached the micropyle and the nuclear membrane disappeared in the final prematuration stage. Berry and Low (1970) found the young oocytes of 9-11-month-old bighead-grass carp hybrids to be 33.0-132.0 μ in diameter with densely staining cytoplasm and chromophobic nuclei.

Bobrova (1972) described early egg development from fertilization to first cleavage,

a period of 1 h at 21-23°C. The first polar body and its division were described. The spindle of the second maturation division occurred at the very edge of the plasma at the animal pole near the micropyle and extended exactly perpendicular to the oocyte surface. The sperm head appeared near the female telophase group during the second maturation division, and division of the second polar body began. The male and female pronuclei united in 25-30 minutes and fused in 40-45 minutes. The metaphase stage of the first cleavage division took place at 50-55 minutes with the spindle perpendicular to the axis and extending over the animal and vegetable poles of the egg. Telophase commenced at the 55-60th minute. In reciprocal crosses of grass carp with silver carp and bighead, Mantelman (1973) observed no differences in the hybrid pattern of sperm head transformation into the pronucleus or of the union of male and female pronuclei. The allogenic chromosomes combined normally during metaphase of the first cleavage division.

Chinese workers at the Yangzte Institute of Fisheries investigated pituitary cytology and effects on it by luteinizing releasing hormone (LH-RH) or its nonapeptide analog (Anon., 1978a, 1978b). Basophilic gonadotropins, which had round or oval, rarely polygonal, cross sections, dominated the median lobe during the breeding season. They reacted uniformly to various stain techniques, indicating there was only one cell type which contained three types of secretory mucoprotein granules (Table II). The endoplasmic reticulum was scattered among the granules. Aggregated ribosomes were dispersed in the cytoplasm. Mitochondria and the Golgi body were small. The nucleus occurred near the cell membrane. Cell fusion of gonadotropins took place on administration of LH-RH. The number of smaller granules decreased and the endoplasmic reticulum increased. With a second dose of LH-RH, the gonadotrophs exhibited a further decrease in small granules, an increase in endoplasmic reticulum, enlargement of interconnecting cisternae, increases in size (50 000-100 000 \AA) and number of large granules. The gonadotroph reactions to stains and LH-RH indicated that

Table II

Characteristics of gonadotroph granules (Anon., 1978b)

Granule type	Shape	Diameter (\AA)	Electron density	Abundance
Small	round, pear-shaped or rod-like	1 000-2 000	high	high
Globular	irregular	3 000-10 000	low	low
Huge heterogeneous	irregular	>20 000	low	low

two granule types were involved in the release of luteinizing and follicle-stimulating hormones, resulting in ovulation.

The blood cells of grass carp and its hybrid from common carp crosses have been investigated. Erythrocytes of acclimatized grass carp varied in mean size (μ) and surface area (μ^2) from 10.9 x 7.8 and 199 in 0⁺-year-old fish to 11.8 x 8.5 and 234 in 1⁺-year-old specimens. Amitotic division of erythrocytes was also observed in the blood (Lyakhovich and Leonenko, 1971). In crossing female common carp with male grass carp, Makeeva (1976) obtained diploid matroclinous young which had a mean erythrocyte size of 75.90 μ^2 and triploid hybrids with a mean value of 103.30, as compared to 77.15 for the maternal parent and 55.10 for the grass carp. Investigating the same cross, Stanley (1976b) and Stanley, Biggers and Schultz (1976) measured erythrocyte nuclear area to be 12.4-12.5 μ^2 in grass carp, 18.2 μ^2 in common carp, and 23.5 μ^2 in the hybrid, indicating polyploidy. Kelényi (1972) described the leucocytes found in grass carp blood and hematopoietic tissue. Large, round, electron-dense granules characterized the eosinophil leucocytes. An elongated granule, with fibrillar-tubular structures and occasionally crystalloid inclusions, occurred in neutrophil or azurophil leucocytes.

1.4.4 Proteins and other constituents

In a review of the literature concerning composition of the grass carp, Jähnichen (1971) cited ranges in percent composition for the following: water 73.0-79.4, protein 16.1-19.9, fat 0.4-6.7, and ash 0.8-1.6. Okoniewska and Okoniewski (1968) determined flesh samples to be 76.8 % water, 17.9 % protein, 4.2 % fat, and 1.2 % ash. Kilocalories per kilogram for protein and fat were respectively, 769.7 and 399 for wet mass and 3 319.6 and 1 757.5 for dry mass. Essential amino acids in fillets did not vary significantly from the reference protein (egg white), except for deficiencies in cystine, proline and phenylalanine. Nevertheless, grass carp fillets were considered to be a quality protein source.

Tan (1971) investigated the chemical constituents of eviscerated grass carp which had received different foods. Small fish (80-100 g) had significantly higher water (87.37 % versus 84.97 %), ash and sodium contents than large fish (360-400 g). Mean percent compositions were 74.16 for protein, 21.26 ash, 4.50 fat, 4.34 sodium, 3.42 phosphorus, 2.54 potassium, and 1.12 calcium. The three test diets of hydrilla (*Hydrilla verticillata*), napier grass (*Pennisetum purpureum*) and tapioca leaves (*Manihot utilissims*) had little effect on protein content, but hydrilla-fed specimens had much higher fat (10.12 % versus 6.88 % and 6.95 %) and lower ash (15.60 % versus 18.76 % and 18.08 %) contents.

Dabrowski (1979) reported on the effects of diets with variable amounts of protein on the composition of grass carp fingerlings. A non-protein diet caused a decrease in protein content relative to fat and ash contents. Increases in dietary protein caused increases in both protein and fat constituents, while ash remained constant.

Shimma and Shimma (1969) examined the amount and fatty acid composition of lipids extracted from various tissues of naturalized and cultured grass carp fed different foods. Dorsal flesh had lipid contents ranging from 1.09 % to 1.38 % and 0.545 % to 1.06 % and cholesterol contents from 30 to 59 mg/100 g tissue and 51 to 63 mg/100 g tissue in naturalized and reared fish, respectively. Lipid content was probably related more to size than origin of fish. Major fatty acid components of lipids in dorsal flesh were 16:0, 16:1, 18:0, 18:1, 20:4, 20:5 and 22:6 acids. The depot lipids of ventral flesh and abdominal and skull cavities had high concentrations of 18:1 and 18:3 acids. Over 20 %, 18:3 acid occurred in the oil of skull cavities of three samples. Food plants were almost certainly the major sources of these fatty acids. Diet affected the lipids in reared grass carp. In two samples fed marine fish (*Decapterus lajjang*), 22:6 acid ranged 24.3-32.6 % of the lipids in dorsal flesh, hepatopancreas and milt, while in lipids of five other specimens given commercial feed, 22:6 acid varied 10.4-13.3 % in dorsal flesh and hepatopancreas, 7.2-8.6 % in milt and 14.6 % in eggs.

Workers at the Alabama Department of Conservation (1972) investigated the production of proteolytic digestive enzymes in the liver, intestinal swelling and intestine of grass carp. The hepatopancreas was the primary secretion site of trypsin, chymotrypsin and carboxypeptidase, indicating that protein digestion occurred primarily in this organ. In addition to small amounts of the above enzymes, leucine aminopeptidase was found evenly distributed throughout the intestinal tract. The hepatopancreas lacked this enzyme. Fasting specimens exhibited higher hepatopancreatic trypsin levels with other enzyme production remaining unchanged. Cold water temperatures increased carboxypeptidase in the liver. Seasonal changes did not influence any other enzymes.

Research at the Yangtze Institute of Fisheries (Anon., 1978a) revealed the effects of luteinizing-releasing hormone (LH-RH) on ovarian levels of the enzymes glucose-6-phosphatase (G-6-Pase), alkaline phosphatase (ALP), 3 β -hydroxy steroid dehydrogenase (3 β -OH-SDH), and acid phosphatase (AcP). During the spawning season, the ovaries contained low levels of G-6-Pase and ALP. Stage-IV follicles had evident G-6-Pase activity, indicating steroidogenesis, but AcP was negative. With the first LH-RH treatment, all enzyme levels rose, except AcP, which remained

negative. Following the second dose, AcP became positive in some ripened follicular cells and the other enzymes showed very strong activity. AcP rose sharply just prior to ovulation and all enzyme levels quickly dropped after spawning. By use of Sephadex G-100 filtration, Malaysian researchers demonstrated the presence of three gonadotrophic hormones in grass carp pituitaries (Prowse, 1969, 1970). Only the second fraction induced ovulation, while both the first and second fractions initiated milting. Both whole and fractional injections resulted in the shedding of some immature eggs. All fractions were found in mature and immature fish of both sexes, and the pattern of eluted peaks corresponded closely with that of pituitary chromatograms.

Kirilenko and Ermolaev (1976) found grass carp muscle to have the following (in micromoles of adenine per gram of wet tissue): 0.91 adenosine triphosphate (ATP), 1.05 adenosine diphosphate (ADP), and 1.54 adenosine monophosphate (AMP). The high ratio of AMP to ATP and ADP was typical of fish muscle.

The amounts of milligram percents for the following blood constituents of grass carp are: phosphorus 11, calcium 11, potassium 19, sodium

350, and blood sugar 37 (Molnár, 1969). The mean hemoglobin content is 8.9 % (Molnár and Tamássy, 1970). Sukhomlinov and Matvienko (1974, 1977) investigated the physiochemical characteristics of grass carp hemoglobins and found absorption spectra to have five maxima at 275, 345, 415, 542 and 572 nm, which were similar to those of most animals. Chromatographic separation revealed two heme components in a 1:3 ratio. The two components differed quantitatively in the amounts of cystine, glycine, threonine, alanine and aspartic acids. In conjunction with dactylographic analysis of trypsin hydrolyzates of the globins in total hemoglobin and its components, the data indicated that grass carp hemoglobin consisted of two heterogeneous heme proteins. Pokhil' (1972) demonstrated the presence of species-specific antigens in grass carp blood by comparative erythrocyte agglutination experiments with different breeds of the silver crucian carp (*Carassius auratus gibelio*) and common carp.

Table III gives the presumptive loci and their tissue distribution for 18 enzymes and general proteins, as determined by Utter and Folmar (1978). Three variable protein systems

Table III
Electrophoretic survey of five tissues in the grass carp.
Dashes denote no data (Utter and Folmar, 1978)

Protein system	Presumed number of loci expressed in different tissues					Estimated total number of loci in all tissues
	Serum	Eye	Liver	Heart	Muscle	
acid phosphatase	2	2	2	2	2	2
alcohol dehydrogenase	0	0	1	1	0	1
alkaline phosphatase	no distinct banding					-
α -glycerophosphate dehydrogenase	0	0	2	0	2	2
aspartate aminotransferase	-	1	1	1	1	1
β -glucuronidase	no distinct banding					-
creatine kinase	-	2	0	2	1	2
esterase (Est)	4	3	3	2	3	6
glucose-6-phosphate dehydrogenase	no distinct banding					-
glutamate pyruvate transaminase	no distinct banding					-
glyceraldehyde-3-phosphate dehydrogenase	-	1	2	2	2	2
hexokinase	no distinct banding					-
isocitrate dehydrogenase	-	1	2	1	1	2
lactate dehydrogenase	2	2	2	2	2	2
leucine aminopeptidase	no distinct banding					2
malate dehydrogenase	1	3	3	3	3	3
malic enzyme	0	1	0	1	1	1
nucleoside phosphorylase	no distinct banding					-
phosphoglucomutase	-	3	0	3	3	3
phosphoglucose isomerase (PGI)	2	2	2	2	2	2
6-phosphogluconate dehydrogenase	0	1	1	1	1	1
phosphomannose isomerase	-	1	1	1	1	1
peptidase	-	1	2	2	2	3
peroxidase	no distinct banding					-
sorbitol dehydrogenase	-	0	0	2	2	2
superoxide dismutase	0	1	1	1	1	1
General Protein:						
Muscle	-	-	-	-	5	5
Eye	-	3	-	-	-	3
Serum	4	-	-	-	-	4
Estimated total number of loci overall protein systems						49

were observed that were apparently two-allele systems with codominant expressions: phosphoglucose isomerase (PGI), esterase (Est), and a serum protein, presumably haptoglobin (Hp). With PGI and Est, phenotypic expression was the same for all of a given individual's tissues, indicating a genetic basis for phenotypic variation in the protein system. In the PGI system, the three-banded expression of the common homozygous phenotype was best explained by a two-locus model where the two extreme bands were homodimers and the middle band represented the interlocus heterodimer. The heterozygous phenotype had three additional bands. Heterozygous individuals in the Est system expressed three-banded phenotypes, indicating a dimeric structure for the esterase molecule. The Hp system was best explained on the basis of a one-locus model, where the homozygous phenotypes expressed one band and the heterozygous two. Genotypic and allelic frequencies indicated a recent common ancestry in many of the six populations examined. In the Est phenotypes of one collection, all ten individuals were heterozygous, suggesting that they were progeny of a single cross between parents homozygous for alternate alleles.

Stanley, Biggers and Schultz (1976) investigated the proteins of gynogenetic, androgenetic and hybrid forms of the grass carp and common carp. Hemoglobin electrophoretic phenotypes of the parental types were three-banded with one band common to the two species. Androgenetic (common carp roe x grass carp milt) and gynogenetic (grass carp eggs x

UV-irradiated common carp milt) grass carp had electropherograms identical to their normal analogues. Female common carp x male grass carp hybrids had five-banded phenotypes with the bands corresponding to those of the parentals. The general proteins of gynogenetic and androgenetic grass carp were also present on the hybrid electropherograms. A simulated-hybrid sample, made by mixing plasma from the two species, did not express the intermediate bands, but did have other bands not found in the hybrid. Hybrid isozyme patterns strongly resembled those of common carp in contrast to the intermediacy found in isozyme expression by Burkalov, Makeeva and Rybov (1973). Esterases stained and banded differently in grass and common carp. Androgenetic, gynogenetic and normal grass carp had a single band in most cases. Lactate dehydrogenase electropherograms exhibited five bands for all phenotypic grass carp. The hybrid pattern followed that of common carp with no evidence of grass carp inheritance, even though the simulated hybrid sample had all grass carp bands on its electropherogram. No significant differences were detected between the expressions of alkaline phosphatase and malate dehydrogenase.

2. DISTRIBUTION

2.1 Total area

From its natural range in eastern China and the USSR (Figure 2), the grass carp has been introduced worldwide into over 50 countries (Table IV). The original distribution includes low-gradient rivers, lakes, and ponds

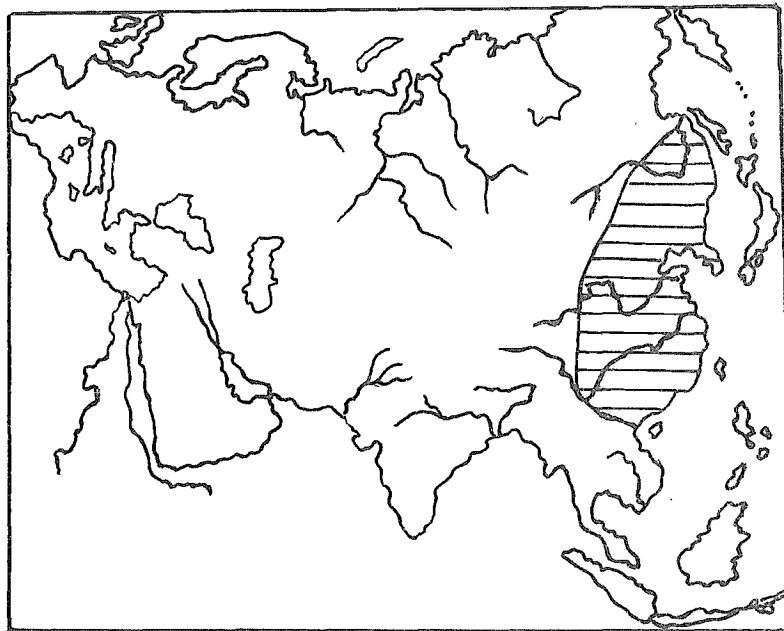


Figure 2 Native range of the grass carp (after Antalfi and Tölg, 1972)

Table IV

Introductions of grass carp

Country	Date	Source	Purpose	Authority
Afganistan	1966-67	China	Culture	El-Zarka (1974)
Argentina	1970	Japan	Experimental weed control	Mastrarrigo (1971)
Austria	1960	Romania	Experimental	Liepolt and Weber (1969)
Bangladesh	1976	?	Culture	Bari (1976)
Bulgaria	1964	USSR	Polyculture	Krupauer (1971)
Burma	1969	India	Culture	Anon. (1969c)
Cambodia	?	?	Culture	Ling (1977)
Canada	?	?	Experimental	Sutton (1977a)
Cuba	1966	USSR	Experimental	Anon. (1970b)
Czechoslovakia	1961-65	USSR	Polyculture	Krupauer (1968, 1971)
Denmark	?	?	Experimental	Blanc <i>et al.</i> (1971)
Egypt, the Arab Republic of	1976	USA	Experimental culture and weed control	Bailey (1977)
England	1964	Hungary	Experimental weed control	Cross (1969)
Ethiopia	1975	Japan	Weed control	Anon. (1975a)
Fiji	1968	Malaysia	Experimental weed control and culture	Wurtz-Arlet (1971) Anon. (1969a)
the German Dem. Republic	1965	USSR	Experimental weed control	Jähnichen (1973)
Germany, Federal Republic of,	1964	Hungary	Weed control	Bohl (1979)
Hong Kong	?	China	Culture and weed control	Chow (1958)
Hungary	1963-66	China and USSR	Polyculture	Krupauer (1971)
India	1959	Hong Kong and Japan	Culture and weed control	Anon. (1968a) Chaudhuri <i>et al.</i> (1976)
Iran	1966	USSR	Experimental	Ivanov (1970)
Iraq	1968	Japan	Culture	Anon. (1969b)
Israel	{ 1952	?	Polyculture	Yashouv (1958)
	{ 1965	Japan	Polyculture	Tal and Ziv (1978a, 1978b)
Italy	1972	Yugoslavia	Experimental culture	Anon. (1972e)
Japan	{ 1878	China	Culture	Kuronuma (1954)
	{ 1943-45	China	Culture	Tsuchiya (1979)
Java	1949	China	Culture	Schuster (1952)
Kenya	1970	?	Culture	Anon. (1970a)
Korea	1967	Taiwan, Prov. of China	Experimental culture	Anon. (1968b)
the Lao, PDR of	1968	Japan	Culture	Chanthepha (1972)
Malaysia	~1930	China	Culture	Gopinath (1950) Anon. (1975b), Gándara, Sánchez and Herrera (1975), Rosas (1976)
Mexico ^{a/}	1960	Taiwan, Prov. of China and China	Weed control and culture	Sánchez and Herrera (1975), Rosas (1976)
Nepal	{ 1966-67	India and Japan	Culture	Shrestha (1973)
	{ 1972	Hungary	Culture	Anon. (1973)
the Netherlands	1968	Taiwan, Prov. of China	Experimental weed control	Anon. (1969a)
New Guinea	1965	Hong Kong	Culture	Anon. (1965)
New Zealand	1966	Malaysia	Experimental weed control	Chapman and Coffey (1971)
Nigeria	1972	?	Culture	Moses (1972)
Pakistan	1964	China	Weed control and culture	Naik (1972)
Panama	{ 1977	?	Culture and weed control	Panama Canal Co. (1977)
	{ 1978	USA	Weed control	Custer <i>et al.</i> (1978)
the Philippines ^{b/}	1966-69	?	Culture	Datingaling (1976)
Poland	1964-66	USSR	Culture	Opuszyński (1968)
Romania	1959	China	Polyculture and weed control	Krupauer (1971)
Sarawak	? Hong Kong, Taiwan, Prov. of	China	Polyculture	Ji (1976)
Singapore	?	?	Culture	Ling (1977)
South Africa	1967	Malaysia	Experimental	Pike (1977)
Sri Lanka	1949	China	Culture	Schuster (1952)
Sudan	1973	?	Culture and weed control	Anon. (1974-75)
Sumatra	1915	China	Culture	Schuster (1952)
Sweden	1970	Poland	Experimental weed control	Thorslund (1971)
Taiwan, Prov. of China ^{c/}	?	China	Polyculture	Lin (1965), Tang (1960a, 1960b)

(continued)

Country	Date	Source	Purpose	Authority
Thailand	?	China	Culture	Schuster (1952)
United Arab Emirates	1968	Hong Kong	Experimental culture and weed control	Anon. (1969c)
Uruguay	?	?	Experimental	Gaevskaya (1969)
USA ^{d/}	1963	Mayalysia and Taiwan, Prov. of China	Experimental weed control	Guillory and Gasaway (1978)
USSRA/ (European and Central Asian)	1937, 1950s 1954-59	?	Culture and weed control	Nikolsky (1971) Ovchynnyk (1963), Vinogradov and Zolotova (1974)
Viet Nam	1969	Taiwan, Prov. of China	Culture	Anon. (1969c)
Yugoslavia	?	?	Culture	Jhingran and Gopalakrishnan (1974)

a/ Have established populations

b/ Reportedly breeding in Pampanga River

c/ Has reportedly bred in reservoirs

d/ Reportedly breeding in Mississippi River (Conner, Gallagher and Chatry, 1980)

below 1 000 m on the Pacific coasts of USSR and China from latitude 50°-23°N. Grass carp occur in the lower and middle reaches of the Amur, Ussuri and Sungari Rivers and in Lake Khanka (Berg, 1964). The southern distribution includes records from the Liao, Hai, Yellow (Hwang Ho), Hwai, Yangtze, Pearl, East (Tung Chiang), Chientang and Min Rivers (Lin, 1935a; Mori, 1936; Dah-Shu, 1957; Chang, 1966). A monsoon climate characterizes the area (Hsieh, 1973). Average annual humidity varies from 70 % to 80 % and average annual temperature varies from 24°C in southern China to 0°C in the north. Annual temperature extremes range from 15°C in January and 30°C in July to -22°C and 22°C in corresponding months farther north. Average yearly rainfall varies from 200 cm in the south to 50 cm in the north. January has the least rain, averaging 5 cm in southern China and 0.5 cm farther north, whereas rainfall in July ranges from 30 cm to 15 cm from south to north. In Manchurian rivers, high water occurs in August with a secondary high level in the spring. In the vicinity of the Yellow River, the highest water levels are achieved in August, but floods occur in the spring due to snowmelt and in summer as a result of sudden showers. The Yangtze, Pearl, Hsi and other rivers of southern China flood during the typhoon season (from July to September).

The grass carp has become established outside its native range in three countries: Japan, the USSR and Mexico (Stanley, 1976d). Japan imported fry from Shanghai as early as 1878, but the major influx came between 1941 and 1945, after which time importation stopped (Kuronuma, 1954). Reports of fry and fingerlings have come from the Tone River drainage since 1947 (Kuronuma, 1954), and spawning and eggs have been documented since 1954 (Kuronuma, 1955; Inaba, Nomura and Nakamura, 1957). In the past, the spawning ground has extended 25 km along the Tone River from Manume-machi, Saitama Prefecture, to Kaki-machi, Ibaragi Prefecture,

but the distance has diminished and shifted downstream due to dam building (Tsuchiya, 1979). Chemical weed control, eutrophication of lakes, and development of swampy rearing areas for domestic purposes have also decreased established populations. If current dam and irrigation plans are carried out, hydrological conditions of the Tone River may become unsuitable for natural reproduction.

As a result of intensive introduction and accidental releases, the European and central Asian areas of the USSR now have naturally reproducing grass carp populations in the Amudar'ya, Syrdar'ya, Ili, Terek, Volga and Kuban Rivers and in the Karakum Canal (Nikol'sky and Aliev, 1974). After collection of eggs and larvae and examination of histology and anatomy in adults, Martino (1974) concluded that grass carp could and did reproduce in the lower Volga under conditions much different from the monsoon flooding which accompanies spawning in their native range. Eggs and larvae were collected from the Ili in 1972-73 (Nezdoliy and Mitrofanov, 1975) and from the Syrdar'ya in 1975-76 (Verigin, Makeeva and Mokhamed, 1978). An established population now occurs throughout the Ili River (Dukravets, 1972). Aliyev (1976) reported successful spawning in the Karakum Canal, which is associated with the Amudar'ya, a river with its own completely naturalized population (Bykov, 1970). Motenkov (1966, 1969) confirmed reproduction and establishment of grass carp in the Kuban River.

Most recently, the grass carp has become established in Mexico after introduction in 1970. Although some fry have been identified from Lago Bodegas, Hidalgo (Anon., 1975b), the grass carp is becoming abundant in the Rio Balsas system of Michoacan Province. Thousands of fry have been taken from 18 different sites, demonstrating that grass carp can spawn naturally at latitudes 5° farther south of its native distribution (Anon., 1976b; Rosas, 1976).

The grass carp has also naturally reproduced in the Philippines, Taiwan, Province of China, Yugoslavia and the USA, but establishment in these countries is still problematical. Reproduction in the Pampanga and Agno Rivers in central Luzon of the Philippines is unverified and the grass carp is rare, relative to other species (Datingaling, 1976; Bailey and Haller, unpubl. MS). Lin (1965) mentioned that spawning had occurred in the Wu-Shan-Tou Reservoir of Taiwan since 1962. Tang (1960a, 1960b) obtained unintroducted fry during 1959 and 1960 from Ah-Kung-Tien Reservoir in Taiwan. Bailey and Haller (unpubl. MS) felt that this instance of natural spawning was unique and possibly due to unusual climatic and hydrologic conditions. At any rate, this population presently appears to be extinct. Stanley, Miley and Sutton (1978) cites Djisalov (1978) as having reported the capture of several thousand juveniles from the flood plain of the Tisa River, a major tributary of the Danube in Yugoslavia. The grass carp has been introduced into many states in the continental USA (Guillory and Gasaway, 1978). Larvae from natural reproduction have only recently been documented for the Atchafalaya and Mississippi Rivers in Louisiana and southern Arkansas (Conner, Gallagher and Chatry, 1980). Specimens were taken from 1975 to 1979 from the northernmost spawning ground in central Arkansas.

2.2 Differential distribution

2.2.1 Spawn, larvae and juveniles

Grass carp spawn in the primary channels of rivers and canals during high water and depending on temperature and current velocity, the semi-buoyant eggs theoretically may drift from 50 km to 180 km before hatching. The pelagic larvae have a characteristic behaviour of alternate sinking and swimming, which allows them to migrate farther downstream. Eventually, they leave the main waterway and enter associated lakes, reservoirs and floodplains, which serve as nursery areas. The young rest and hide in vegetation. Juveniles may move out of nursery areas into the main channel and migrate upstream or downstream as much as 1 000 km from their original spawning grounds. Home ranges do not seem to be important. The young winter in deep holes in the riverbed and do not associate with the adults (Chang, 1966; Stanley, Miley and Sutton, 1978).

2.2.2 Adults

A radiotelemetry study of adults in Lake Conway, Florida, indicates a definite preference for densely vegetated inshore areas 1-3 m in depth (Nall *et al.*, 1979). At Deer Point Lake, Florida, Nixon and Miller (1978) found their radio-tracked specimens frequented shallow areas, except during periods of movement and low water temperature, when flooded creek channels and deep midwater areas were utilized. All but one fish moved in a northerly (upstream) direction. Oxygen content and ephemeral climatic factors did not affect adult distributions. Nitzner (1975a)

demonstrated seasonal influences on movements of radiotagged fish in Red Haw Lake, Iowa. All but one specimen were located within 10 m off shore, most of the time, but they spent varying amounts of time in midwater as well. Ratio of inshore to midwater contacts was 51/49 in June, increased to 1 000/0 by September, then decreased to 20/80 in November. Movement to midwater areas correlated with reductions in temperature and vegetation of littoral habitats. No significant circadian patterns were observed in microhabitat selection or movement. On several occasions, grass carp alternately surfaced and sounded in a midwater area at dusk. Some individuals set up definite activity centres and spent most of their time in them. In closed systems, Buckley and Stott (1977) described the grass carp as a shoaling fish often seen near the surface, and Ellis (1974) observed loose aggregations of up to 7 subadults, of which several would simultaneously break the water surface. In Taiwan fish ponds, the grass carp frequents all water strata (Chen, 1976).

Although studies pertaining to grass carp distributions in rivers have not been conducted, presumably it would be similar to that of reservoirs, with concentrations in abundantly vegetated backwaters and littoral areas. During high water, the grass carp migrates upstream to specific spawning grounds, which are generally associated with rapids, islands, sandbars or tributary junctions, and reproduction occurs in the upper water layer, or sometimes at the surface proper (Lin, 1935a, Dah-Shu, 1957). Nikolsky (1956 [cited by Fischer and Lyakhnoich, 1973]) describes seasonal changes in habitat selection by the Amur River population. The fish leave the river after spawning and enter floodplains, lakes and backwaters, where they feed on both aquatic and flooded terrestrial vegetation. During autumn, the fish return to the river and overwinter in deep holes in the lower reaches without feeding.

2.3 Behavioural and ecological determinants of distribution

The grass carp is generally a highly adaptable species, which accounts for its widespread and successful introduction. Strict spawning requirements, however, are responsible for its relatively restricted native range and its failure to form self-reproducing populations in most countries. Conditions for successful spawning will be discussed in Sections 3.1.6 and 3.1.7, but it will suffice at this point to say that the three primary prerequisites are a waterway of sufficient length, temperatures about 18°C, and current velocities from 0.6 m/s to 1.8 m/s (Stott and Cross, 1973; Stanley, Miley and Sutton, 1978).

Most studies investigating grass carp tolerance of various physico-chemical conditions are performed with eggs, fry and juveniles. The optimal temperature range for incubation is 21-25°C for normal development

of embryos (Anon. 1970c). A drop in temperature to 18°C or below during incubation results in very low survival, but a similar drop with 20-hour-old larvae has little effect (Stott and Cross, 1973). Fry and fingerlings in India tolerated a temperature range of 16-40°C (Singh, Banerjee and Chakrabarti, 1967). In Poland, Opuszyński (1967) found unacclimated fry to have a mean lethal maximum of 40°C and minimum of 0-0.1°C. Acclimated yearlings could not withstand a maximum of 35°C, but could survive at temperatures down to 0°C. In the Amur, Sungari and other Manchurian rivers, an ice cover forms from late October until March (Hsieh, 1973). Singh, Banerjee and Chakrabarti (1967) determined that Indian grass carp fry and fingerlings could survive the following ranges in water conditions: 125-215 ppm turbidity, pH 5.0-9.0, 1-28 ppm dissolved O₂, 88-620 ppm (to 1 500 ppm in soft water) total alkalinity, 7.5-12.0 % salinity, 0-3.8 ppm free ammonia, 0-0.2 ppm free chlorine, and 0-5.0 ppm free sulphide. Mean lethal minima of dissolved oxygen for acclimated fry and yearlings in Poland were 0.41 and 0.22, respectively (Opuszyński, 1967).

Considerable work has been directed toward the salinity tolerance of grass carp. Fry withstand salinity contents from 7 % to 12 % depending on the acclimation period for fish and ionic composition of the water (Doroshev, 1963; Chervinski, 1977). Using 2+-year-old specimens, Cross (1970) obtained similar results with maximum survival times ranging from 24 days in 10.5 % salinity (30 % seawater) to 5 hours in 17.5 % (50 % seawater). He cites Pavlov and Nelovkin (1963) as reporting the migration of grass carp from the Volga to the Ural River, through the brackish Caspian Sea. Maceina and Shireman (1979, 1980) found decreasing survival, weight, muscle tissue water content, feeding rate, and growth in fingerlings exposed to salinities increasing to 15.7 %. They predicted that grass carp could inhabit brackishwater bodies up to 9 % salinity.

Since the adult grass carp is a voracious and efficient feeder on vascular plants (Hickling, 1966), it follows that an extensive aquatic flora must be present in its environment. Reduction of macrophytes due to chemical control or to reduced light transmission as a result of phytoplankton blooms, has apparently caused a substantial decrease in a naturalized population of the Tone River and its associated water bodies in Japan (Tsuchiya, 1979). A discussion of nutrition and growth will be deferred until Section 3.5.

3. BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

The grass carp is typically heterosexual, although artificial andro- and gynogenesis have been reported (Sections 1.4, 3.1.4 and 3.1.6). Stanley (1976a) demonstrated that surviving gynogenetic fish were female, and provided indirect evidence for sex determination by female homogamety. External sexual dimorphism appears in adults with the onset of maturity. Many authors have reported the presence of deciduous tubercles (pearl organs) on the dorsal and medial surfaces of the pectoral fins of male grass carp during the breeding season. Courtenay and Miley (1973) also found pearl organs on the dorsal fin and dorsum of the caudal peduncle. Chang (1966) reports that females also have pearl organs, although they are not as highly developed as in males. When fully ripe, females exhibit soft bulging abdomens and swollen pinkish vents. Table V summarizes the literature on secondary sexual characters. Hong *et al.* (1974) investigated methods for accurate and economical determination of sex, particularly in immature fish, without damage to specimens. They used scanning electron microscope procedures to identify incipient pearl organs. This evaluation, however, was time-consuming, subjective and required high levels of expertise.

Table V

Secondary sex characters and seasonal occurrence of ripe grass carp

Location	Sex	Character	Time of year	Authority
India (Cuttack)	Male	Roughness on pectoral fins	March-September	Alikunhi and Sukumaran (1964), Alikunhi, Sukumaran and Parameswaran (1962, 1963a, 1963b, 1973)
	Female	Soft distended abdomen, swollen pinkish vent	June-July	Chaudhuri, Singh, Sukumaran (1966)
India (Tamilnadu)	Male	Rough pectoral surfaces, serrated ridges on pectoral fin rays, thickened first pectoral ray, nuptial tubercles on head	March-August	Prabhavathy and Sreenivasan (1977)
	Female	Soft bulging abdomen, pinkish vent	May-August	Prabhavathy and Sreenivasan (1977)

(to be continued)

(continued)

Location	Sex	Character	Time of year	Authority
Japan	Male	Pearl organs on pectoral, dorsal and caudal fins	April-August	Kawamoto (1950)
Malaysia (Malacca)	Male	Roughness on pectoral fins, thickened first pectoral fin ray, pectoral fin longer than in female	All months	Hickling (1967b)
	Female	Soft distended abdomen, vent sometimes swollen and pinkish	All months	Hickling (1967b)
Malaysia (Malacca)	Male	Roughness on pectoral fins	All months	Chen, Chow and Sim (1969)
	Female	Soft bulging abdomen, swollen pinkish cloaca	All months	Chen, Chow and Sim (1969)
Nepal (Kathmandu)	Male	Roughness on pectoral fins	May-June	Shrestha (1973)
	Female	Distended belly, swollen pinkish vent	May-June	Shrestha (1973)
Taiwan, Province of China	Male	Deciduous serrations on pectoral fins	April-September	Lin (1965)
	Female	Distended belly, swollen pinkish vent	April-September	Lin (1965)
Taiwan, Province of China	Male	Roughness on inner sides of pectoral fins	March-July	Chen (1976)
	Female	Soft distended belly, swollen pinkish vent	March-July	Chen (1976)
USA (Arkansas)	Male	Pearl organs on dorsal sides of pectoral fins	May	Bailey and Boyd (1972, 1973)
	Female	Distended abdomen	May	Bailey and Boyd (1972, 1973)
USA (Florida)	Male	Deciduous tubercles on pectoral fins, first dorsal fin ray and dorsum of caudal peduncle	May-June	Courtenay and Miley (1973)
USSR (Ukraine)	Male	Thickened first pectoral fin ray	June	Prikhod'ko and Nosal' (1963)
USSR	Male	Rough inner surface on pectoral fins	May-June	Anon. (1970c)
	Female	Soft sagging abdomen, occasional swelling of vent	May-June	Anon. (1970c)

The identification of sex-chromatin structures (analogous to Barr bodies in humans) or sex-specific chromosomes was unsuccessful. Preliminary research on the production of a rabbit serum antibody to grass carp sperm indicated the possibility exists for sexing grass carp by the differential antigenic reactions to this antibody. Anatomical differentiation of the gonads occurs at a mean total length of 58 mm (50-60 days old) in the USA (Shelton and

Jensen, 1979) and precedes cytomorphological differentiation (Bobrova, 1972) (Section 1.4). Shelton and Jensen (1979) found that gonads differentiated histologically at 94-125 days in females and 150-300 days in males. In the central USSR, oocytes began protoplasmic development in three-year-old females and spermatogenic waves first appeared in two-year-old males (Bobrova 1972).

3.1.2 Maturity and maturation

Maturity occurs at ages from 1 to 11 years and standard lengths from 58 to 67 cm in females (Table VI). Males mature an average of one year earlier at standard lengths from 51 to 60 cm. One-year-old milting males at Cuttack,

India, ranged from 43.9 to 49.3 cm total length and 0.95 to 1.40 kg (Alikunhi and Sukumaran, 1964; Alikunhi, Sukumaran and Parameswaran, 1965). Grass carp mature at earlier ages and smaller sizes in tropical climates and climate and nutrition act synergistically on the attainment of maturity (Bobrova, 1972; Anon., 1970c; Opuszyński, 1972).

Table VI

Initial and average age and size of grass carp at maturity in different countries

Location	Sex	Age	Length (cm)	Weight (kg)	Authority
China:					
Sunchow, Kwangsi Prov.	-	3(4)	-	3.5(4.1-5.9)	Lin (1935a)
Southern Yangtze River	-	3-4	-	-	Konradt (1968)
	-	5-6	-	-	Konradt (1968)
	-	4-5	-	-	Opuszyński (1972)
	-	3-4	-	-	Brown (1977)
Central and Southern	-	4	-	5	Dah-Shu (1957)
Hungary:	-	6-7	-	-	Opuszyński (1972)
India:					
Cuttack	male ^{a/}	2(3)	75.2-86.0 ^{b/}	4.54-6.61	Alikunhi, Sukumaran and Parameswaran (1962, 1963a, 1963b, 1973)
	female ^{a/}	3	73.8-79.2 ^{b/}	4.76-7.03	Alikunhi, Sukumaran and Parameswaran (1962, 1963a, 1963b, 1973)
	male	1	43.9-49.3 ^{b/}	0.95-1.40	Alikunhi and Sukumaran (1964)
	female	2	-	-	Alikunhi and Sukumaran (1964), Alikunhi, Sukumaran and Parameswaran (1965)
Tamilnadu	male	1	-	-	Prabhavathy and Sreenivasan (1977)
	female	2	-	-	Prabhavathy and Sreenivasan (1977)
Israel:					
Dor	male	2	-	4.0	Yashouv (1958)
	female	4-5	-	5.0	Yashouv (1958)
Malaysia:					
Malacca	-	2	-	6.0	Slack (1962)
	male	1-2	51-60 ^{b/}	1.2-2.0(2-3)	Hickling (1967b)
	female	1-2	58-63 ^{b/}	2.3-3.2	Hickling (1967b)
Nepal:	-	2	-	-	Chen, Chow and Sim (1969)
	-	4	-	-	Shrestha, (1973)
Poland:	female	6	-	3.0-3.5	Wolny (1971)
Romania:	-	6-7	-	-	Opuszyński (1972)
Taiwan, Province of China:	male	3-4	-	-	Lin (1965), Chen (1976)
	female	4-5	-	3+	Lin (1965), Chen (1976)

(to be continued)

(continued)

Location	Sex	Age	Length (cm)	Weight (kg)	Authority
USA:					
Alabama	male	2	-	-	Alabama Department of Conservation (1968)
	female	3	-	-	Alabama Department of Conservation (1968)
Arkansas	female	4	-	-	Bailey and Boyd (1971, 1973)
	-	3	-	-	Sneed (1971)
USSR:					
Amur River (middle)	-	6-8(9-10)	54-55(68-75) ^{c/}	-	Gorbach (1961)
	female	7-8(9-10)	60(68-75) ^{c/}	-	Makeeva (1963)
	male	6-7(9-10)	60-65(68-75) ^{c/}	-	Gorbach (1966)
	female	6-7(9-10)	60-68(70-75) ^{c/}	-	Gorbach (1966)
	-	8-9	70-75 ^{c/}	-	K'o-lei-hei-chin (1966)
Amur River (lower)	-	8-9	-	-	Ma-k'ai-yeh-wa, Su-yin and Po-t'a-po-wa (1966)
Amur River (upper)	-	9-10	-	-	Ma-k'ai-yeh-wa, Su-yin and Po-t'a-po-wa (1966)
Turkmen	male	2-3	-	-	Vinogradov (1968)
	female	3-4	-	-	Vinogradov (1968)
Kiev	male	7-8	-	-	Vinogradov (1968)
	female	8-9	-	-	Vinogradov (1968)
Krasnodar	male	4	-	-	Vinogradov (1968)
	female	5	-	-	Vinogradov (1968)
	male	3-4	-	-	Anon. (1970c)
	female	4-5	-	-	Anon. (1970c)
Moscow	male	9	-	-	Vinogradov (1968)
	female	10	-	-	Vinogradov (1968)
	-	10	-	-	Opuszyński (1972)
Central	male	7-8	-	-	Bobrova (1972)
	female	8-9	-	-	Bobrova (1972)
South Central	male	2-3	-	-	Anon. (1970c)
	female	3-4	-	-	Anon. (1970c)
Lower Volga River	-	5(6+)	60 ^{c/}	-	Martino (1974)

- a/ Brood stock
b/ Total length
c/ Standard length

Although long growing seasons and plentiful food supply can speed maturity, overfeeding on certain foods may actually retard maturation. Chen, Chow and Sim (1969) suggested that exclusive feeding on hydrilla could cause extensive mesenteric fat accumulation (to >6 % of body weight), which might effectively inhibit gonad development. Maturation might also be cued to season and physical environment. A pond or other still water environment is inadequate for final maturation of females. In Malaysian ponds, Slack (1962) determined that ovarian development proceeded to the secondary-yolk stage and then regressed. The gonadosomatic ratio was 0.0006 in a mature-but-unripe 5.0 kg female, rose to 0.04 in a 7.3-kg ripe individual, dropped to 0.03 in a 6.3-kg regressing female, and decreased to 0.014 in a fully regressed 5.9-kg fish. Hickling (1967b) found testes weight to be highly variable in Malaysian fish and independent of fish size or season (Table VII). Seasonal cycles in the histological maturation of the gonads have been documented in the temperate Amur region of USSR (Makeeva, 1963; Gorbach, 1966, 1972). The gonads pass the winter in early maturity stages, develop to an intermediate level during spring, and quickly reach final maturation just prior to spawning in June and July. Some females begin resorption of unspawned eggs in late July. Both temperature and photoperiod may influence maturation. Experiments by Shireman, Colle and Rottmann (1978b) indicate the possibility for manipulation of the reproductive season by varying regimes of these two factors and by varying these factors they have spawned grass carp throughout the year. In the Netherlands, Huisman (1979) successfully induced spawning in grass carp during January by raising water temperature 1°C/day from 3-5°C to 23°C and by holding fish at 23°C for 25-30 days. Induced spawning by this method is now done regularly in December and January in Holland and Poland (Sutton, Miley and Stanley, 1977).

3.1.3 Mating

Mating is promiscuous and has been observed in the West River of China (Lin, 1935a; Dah-Shu, 1957) and the Tone River, Japan

(Inaba, Nomura and Nakamura, 1957). Two to three males ($\bar{x} = 2.3$) follow the female, which swim at or near the water surface in the centre of the river channel. Spawners sometimes swim against the current and at other times do not orient themselves with the current. Water depth seems unimportant. The fish roll and rub their bodies together and often jump out of the water. After a time, the male prods the female's belly with his head and leans closely to one side. Intermittent splashing generally accompanies spawning, which frequently occurs at the surface.

3.1.4 Fertilization

Fertilization is external. Bobrova (1972) described the cytology of syngamy which took one hour from the first premeiotic division to first cleavage division (Section 1.4.3). Mantelman [(1969) cited by Stanley (1976b)] and Boev (1970) examined fertilized eggs and found that 5 % had three or more pronuclei, probably as a result of polyspermy. Androgenetic and gynogenetic grass carp can be obtained by using common carp roe or irradiated milt, respectively (Stanley, 1975, 1976a, 1976b, 1976c, 1976d; Stanley, Biggers and Schultz, 1976; Stanley and Jones, 1976). The diploid androgenetic individuals presumably arose through polyspermous fertilization of common carp roe with grass carp milt and subsequent exclusion of the maternal genomes. By using irradiated carp milt, development of grass carp eggs began without incorporation of paternal DNA. Retention of the second polar body, equivalent to secondary nondisjunction, was the probable mechanism whereby diploid gynogenetic progeny resulted. In reciprocal crosses of grass carp with silver or bighead carp, the cytological events of syngamy take place similarly to those in homo-genetic crosses (Mantelman, 1973).

3.1.5 Reproductivity

3.1.5.1 Coefficient of maturation

The most-used measure of maturation is the percentage of total body weight comprised by

Table VII

Testes weight in various sizes (total length) of grass carp (Hickling, 1967b)

Length (cm)	Weight (kg)	Testes weight (g)
63	3.0	13
65	3.3	22
75 (5 fish)	4.5-5.9	12-30
76	4.8	65
79	5.4	18
79	5.9	46
79	6.1	8
81	6.5	16

Table VIII

Relative gonad size and factors influencing size in grass carp

% Body weight in gonad	Body weight (kg)	Age (years)	Month of examination	Characteristics of specimens/	Location	Authority
0.5-1.0b/ 16-20b/	5.0+	4+	March-April	developing ♀s	China	Dah-Shu (1957)
15	5.0+	4+	May	gravid ♀s		
11	4.7	3	June		India (Cuttack)	Alikunhi, Sukumaran and Parameswaran (1963a)
15	4.8	3	June			
12	4.9	3	June			
20	5.5	3	June	♀ brood stock after injection		
15	5.7	3	June			
11	5.8	3	June			
8	6.2	3	June			
4.2	7.0	3	June			
4.2	7.1	-	Late July	gravid ♀	Japan (Waterase R.)	Inaba, Nomura and Nakamura (1957)
0.6	7.1	2.4	May	stage I ♀	Malaysia (Malacca)	Slack (1962)
4	7.3	2.5	July	stage IV ♀		
3	6.3	2.7	August	stage III ♀ (regressing)		
1.4	5.9	3.3	March	stage I ♀		
0.13-1.4	3.0-6.5	-	-	♂s		Hickling (1967b)
0.1-13.4, \bar{x} = 4.6	-	-	July-August	uninjected ♀s		
1.8-20.5, \bar{x} = 6.0	-	-	June-September	injected ♀s		
5.3	5.2	-	-	stage IV ♀s		
17	2.2	-	-	-		Chen, Chow and Sim (1969)
20	2.3	-	-	-		
0.03-0.2, \bar{x} = 0.09	-	4-10 (most 5-7)	June-July	stage II ♂s	USSR (middle Amur R.)	Gorbach (1966)
0.09-0.4, \bar{x} = 0.2	-	-	June-July	stage II-III ♂s		
0.9	-	-	June-July	stage III ♂s		
0.9-2.5, \bar{x} = 1.7	-	-	June-July	stage IV ♂s		

(to be continued)

Table VIII continued

% Body weight in gonad	Body weight (kg)	Age (years)	Month of examination	Characteristics of specimens ^{a/}	Location	Authority
1.0	-	-	June-July	stage V-VI ♂s		
0.1-1.2, $\bar{x} = 0.4$	-	4-10 (most 5-7)	June-July	stage II ♀s		
0.3-2.5, $\bar{x} = 1.0$	-	-	June-July	stage II-III ♀s		
0.5-3.7, $\bar{x} = 1.3$	-	-	June-July	stage III ♀s		
0.7-3.8, $\bar{x} = 1.9$	-	-	June-July	stage III-IV ♀s		
4.3-11, $\bar{x} = 0.4$	-	-	June-July	stage IV ♀s		
2.0-2.7, $\bar{x} = 2.4$	-	-	June-July	stage V-VI ♀s		
1.5	-	-	June-July	stage VI-VII ♀s		
4.2-5.6	-	$\bar{x} = 9-10$	June-July	stage III-IV ♀s		Makeeva (1963)
5.1-7.5 ²	-	-	-	pre-spawning ♀s		
0.6	-	$\bar{x} = 9-10$	late June	stage II post-spawning ♀s		
$\bar{x} = 0.05$	$\bar{x} = 1.7$	5	all months	stage I ♀s		Gorbach (1966)
0.2-0.8, $\bar{x} = 0.4$	2.0-6.5, 10.3	4.5-8, 9	all months	stage I-II ♀s		
0.6-3.7	5.1-13.3	8-13	May-September	stage II-III ♀s		
11-12	-	9-10 (few 6-8)	June	stage IV ♀s		
5.0-7.2	10.8-15.6	10-15	June	stage IV-V ♀s		
$\bar{x} = 3.8$	8.9-10.6	10-11	late June-July	stage II regressing ♀s		
1.6-2.1, 1.2	8.0-13, 5.5	9-14, 7	August-September	stage VI post-spawning ♀s		
4.1-4.3	8.0-11.9	9-14	late August-early October	stage II regressing ♀s		

a/ Maturation stages for ova are as follows: I, perinucleolus; II, yolk vesicle; III, primary yolk; IV, secondary yolk; V, tertiary yolk; VI, prematuration. For testes: I, spermatogenic cells (stem spermatogonia); II, spermatogonia; III, spermatocytes; IV, spermatid; V, spermatozoan; VI, prematuration.

b/ Calculated on basis of body weight without internal organs.

the gonads. The various gonadosomatic ratios and coefficients reported in the literature are converted to this value in Table VIII. The only naturally-reproducing grass carp populations which have been studied to any extent are those populations of the Amur and Assuri Rivers in the Soviet Union. The relative gonad weights of mature males and females increase during spring, reach maxima just prior to spawning in June and July, then decrease progressively from August to October (Gorbach 1966). In tropical countries, seasonal changes in gonad size are not nearly so marked, and some individuals are continuously ripe (Hickling 1967b). Chen, Chow and Sim (1969) found that relative ovarian weight ranged up to 20 % and was not necessarily correlated with size or maturation stage of cultured Malaysian fish. He also determined that females fed napier grass (*Pennisetum purpureum*) produced larger ovaries than those fed hydrilla (*Hydrilla verticillata*), which subsequently accumulated over 6 % by weight of mesenteric fat.

3.1.5.2 Relation of fecundity to biotic and environmental factors

Absolute fecundity ranges from tens of thousands to two million eggs with an average of 500 000 for 5 kg to 7 kg brood stock (Anon. 1970c). Geographical location does not appear to affect fecundity (Table IX). Larger amounts of hormone injections can increase the number of ovulated eggs (Konradt 1968). Using three-year-old injected fish in the United States, Shireman (1975) determined the mean numbers of ovarian and ovulated eggs to be 740 000 and 367 000 with standard deviations of 276 000 and 209 000 respectively. Neither measure correlated significantly with weight nor length. He suggested the high variability might be due to limited sample size and to selection of brood stock. Alikunhi, Sukumaran and Parameswaran (1963a) found relative fecundity of cultured Indian specimens to average 82 eggs/g total weight and 610 eggs/g ovary. Malaysian farm fish had 2 to 138 eggs/g ($\bar{x} = 41$) after injection (Hickling 1967b). Hypophysation increased the number of yolked ovarian eggs but did not always induce ovulation.

Table IX

Absolute fecundity of grass carp

Number of eggs ($\times 10^3$)	Weight (kg)	Total length (cm)	Age (years)	Characteristics of specimens	Locality	Authority
100*	7.3	-	-	wild-caught	China (West R., Kwangsi Prov.)	Lin (1935a)
960*	14.6	-	-	wild-caught	China (Yangtze R.)	Chang (1966)
373	4.8	73.8	3		India (Cuttack)	Alikunhi, Sukumaran and Parameswaran (1963a)
564	4.9	75.8	3			
396	5.5	78.6	3	brood stock		
618	5.7	78.9	3	after injection		
442	5.8	75.0	3			
309	7.0	79.2	3			
200-300	4-6	-	-	injected	India (Tamilnadu)	Prabhavathy and Sreenivasan (1957)
485*	7.1	88	-	wild-caught	Japan (Waterase R.)	Inaba, Nomura and Nakamura (1957)
816*	7.4	76 ^a /	7	wild-caught	USSR (Amur River)	Berg (1964)
$\bar{x} = 470$	$\bar{x} = 7.5$	-	-	8 mg injection	USSR (Leningrad)	Konradt (1968)
$\bar{x} = 785$	$\bar{x} = 7.5$	-	-	24 mg injection		
237-1637 $\bar{x} = 820^*$	5.1-16.4	66-96 ^a /	7-15	wild-caught	USSR (middle Amur R.)	Gorbach (1972)
10-700 $\bar{x} = 367$	3.7-7.4	-	3	injected	USA (Florida)	Shireman (1975)
$\bar{x} = 740^*$	3.7-7.4	-	3	injected		

*Values with asterisks denote number of ovarian eggs and those without are the number of ovulated eggs.

^aStandard lengths

Gorbach (1972) investigated fecundity and its associated parameters of an indigenous grass carp population in the middle Amur River, USSR (Table X). Number of ovarian eggs ranged from 237×10^3 eggs in a 7-year-old, 67.5 cm (SL) female to $1\,687 \times 10^3$ in a 15-year-old, 96 cm

(SL) specimen. About 90 % of the fish had from 600 000 to 1 150 000 eggs. Relative fecundity varied from 48 to 177 with an average of 110 eggs per gram weight of the body less viscera. Absolute and relative fecundity increased with length weight and age (Tables XI and XII, Figure 3).

Table X

Mean indicators of grass carp investigated for fecundity (Gorbach, 1972)

Year	Standard length (cm)	Total weight (kg)	Weight without viscera (kg)	Age (years)	Absolute fecundity ($\times 10^3$)
1963	87.5	12.0	9.5	13	1167
1964	84.5	10.7	8.8	11.6	1211
1965	81.9	10.3	8.7	10.7	891
1966	81.6	10.3	8.4	11	902
1967	77.6	9.4	7.7	9.9	857
1968	76.2	8.7	7.2	9.7	788
1969	73.2	7.5	6.4	8.4	600
MEAN	77.1	9.2	7.6	9.9	820.

Table XI

Mean absolute fecundity in '000s of eggs for grass carp of different ages and lengths (Gorbach, 1972)

Standard length (cm)	Age (years)						n
	7	8	9	10	11	12	
65-66	-	540	-	-	-	-	1
69-70	475	426	519	-	-	-	5
71-72	-	598	663	650	-	-	5
73-74	-	664	777	-	-	-	10
75-76	-	-	798	813	1002	-	16
77-78	-	-	752	788	844	-	19
79-80	-	-	870	1104	1141	-	13
81-82	-	-	-	-	972	-	8
83-84	-	-	-	-	1276	1271	8
85-86	-	-	-	1169	-	1083	2
87-88	-	-	-	-	-	967	2
91-92	-	-	-	-	-	1176	1
n	1	9	33	20	18	9	90

Table XII

Fecundity, condition and fat content in grass carp of different weight (Gorbach, 1972)

Weight of body without viscera (kg)	Absolute fecundity (x 10 ³)	Relative fecundity (No. eggs/g body wt.)	Condition factor		Fat content index	Tester's fat content factor	n
			Fulton's	Clark's			
4	476	115	1.78	1.46	5.9	11.4	3
5	551	120	1.84	1.51	3.2	13.0	5
6	738	110	1.93	1.59	3.9	13.8	18
7	843	107	1.97	1.63	5.1	14.5	24
8	892	109	2.08	1.73	6.1	15.7	22
9	1159	123	1.97	1.53	5.6	15.8	12
10	1252	120	2.10	1.70	6.1	16.4	4
11	1067	91	1.91	1.65	4.0	18.3	2
MEAN	860	112	1.97	1.64	5.1	14.4	
					TOTAL	n	90

A four-fold increase from 600 000 to 1 635 000 eggs accompanied a length change from 66 cm to 96 cm. Egg number increased by 40 - 50 % in fish heavier than those of the same length. Older specimens were generally, but not invariably more fecund than young fish of the same size. Absolute fecundity varied by a factor from two to three within groups of fish with the same length, weight and age.

Both absolute and relative fecundity correlated positively with length, weight and age, but to different extents (Tables, VI and VI, Figure 3). In samples from 1967 and 1963-1969, respectively, egg number had the highest correlation coefficients with weight ($r = + 0.73$, $+ 0.73$ for total weight and $+ 0.66$, $+ 0.82$ for weight of eviscerated fish) and increased by 105.2 or 96.3 thousand per kg total weight and 114.7 or 167.1 thousand per kg weight of fish without internal organs. Length had intermediate values ($r = + 0.68$, $+ 0.71$) and one cm of growth caused an average increase of 134.3 or 1212.1 thousand eggs. Relative fecundity increased only slightly in old or large fish. Weak positive correlations occurred with length ($r = + 0.10$, $+ 0.24$), total weight ($r = + 0.12$, $+ 0.10$), and age ($r = + 0.04$, $+ 0.02$).

Condition, fat content, prespawning nutrition, and fishing pressure also influenced grass carp fecundity. Egg number correlated weakly with Fulton's ($r = - 0.25$) and Clark's ($r = + 0.20$) condition factors. Absolute fecundity corresponded slightly with Tester's fat content factor ($r = + 0.32$) but not with the fat content index ($r = - 0.04$). Scarcely any correlation was observed between relative fecundity and Fulton's ($r = + 0.05$) or Clark's ($r = - 0.13$) condition factors, but weak negative corre-

lations were determined for Tester's fat content factor ($r = - 0.18$) and the fat content index ($r = - 0.17$). Absolute fecundity and fat content were interdependent in females the same size with stage IV gonads during the breeding season (Table XIII). Fat content was usually lowest in mid-June, just prior to spawning, and was associated with fat expenditure for gonad maturation and consequently with increased fecundity. Fat content generally increased somewhat during late June and early July when intensive feeding began. Absolute fecundity decreased irregularly at the end of the reproductive season due to intermittent spawning. Two distinct sizes of yolked oocytes occurred in the ovaries of 91 % of stage IV females. The first group of eggs ranged from 55 to 91.5 % and averaged 67 % of absolute fecundity. Fecundity, condition, and fat content were all dependent on prior feeding conditions, which were determined by the amount of time in the previous year that the vegetatively rich floodplain was inundated and available to grass carp. This area was flooded for 120 to 130 days during the summer of 1966 and for only 35 to 40 days in 1968. All biological indicators, including fecundity, consequently fell in 1969 compared to those in 1967 for fish of the same size. Intensive fishing pressure reduced the population fecundity four-fold from 2 344 million eggs in 1967 to 547 million in 1969. The spawning population decreased especially with regard to older, more fecund fish (Table X).

3.1.6 Spawning

3.1.6.1 Spawning seasons

A well-marked and limited season characterizes grass carp spawning in temperate climates. The breeding season expands and becomes less distinct in tropical areas.

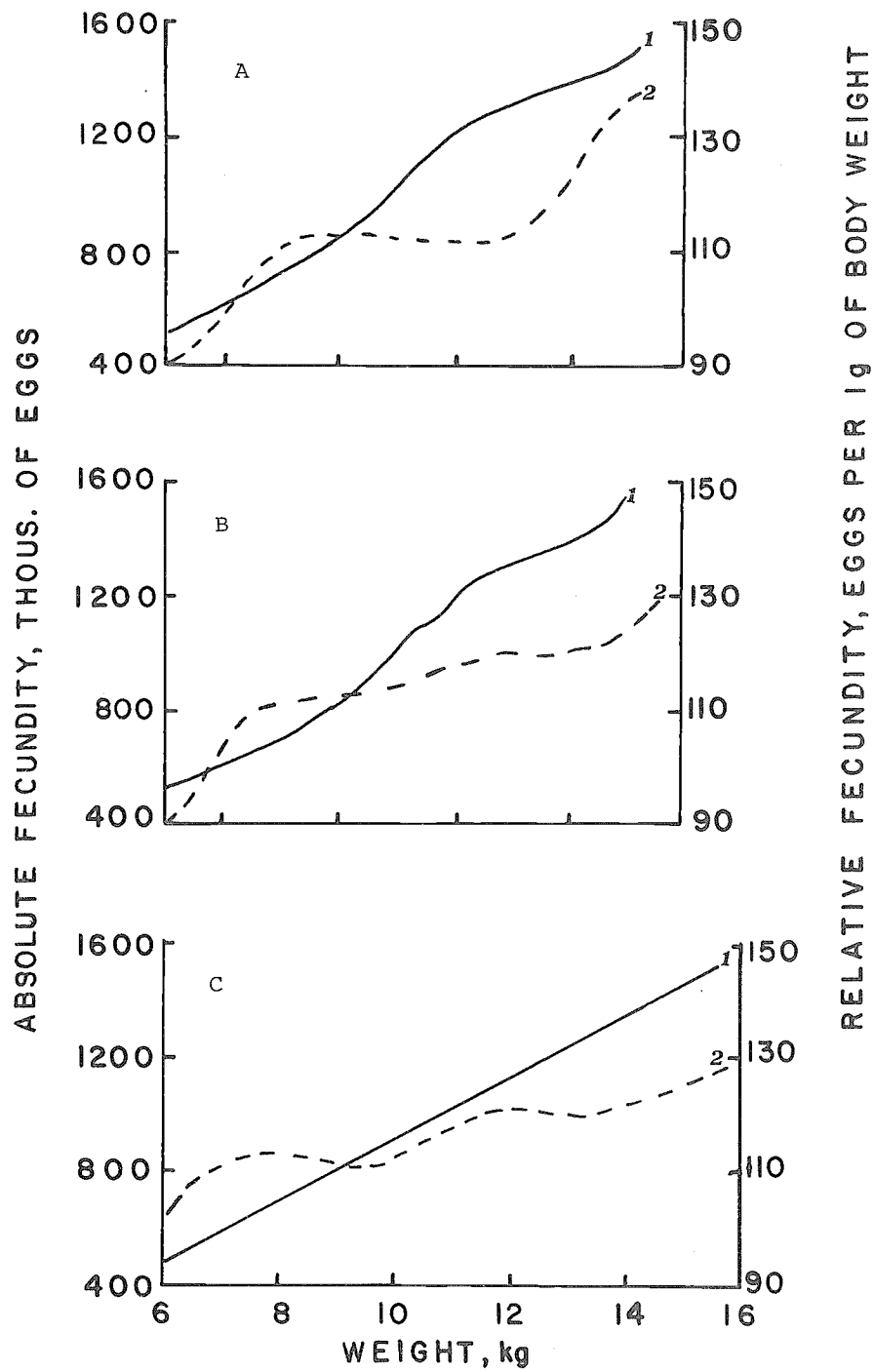


Figure 3 Absolute (1) and relative (2) fecundity of grass carp as a function of age (A), and of weight of body without viscera (B), and of a total weight (C) (after Gorbach, 1972)

Table XIII

Seasonal variation of fecundity and fat content in grass carp (Gorbach, 1972)

Standard length (cm)	Indicator	May		June		July		August
		late	early	mid	late	early	late	early
71-75	Absolute Fecundity ($\times 10^3$)	714	820	608	562	374	301	185
	Fat Content Index	4.1	3.2	1.7	4.8	3.0	2.7	6.0
76-80	Absolute Fecundity ($\times 10^3$)	865	790	740	569	482	719	-
	Fat Content Index	6.1	5.6	4.9	6.3	5.9	5.4	-
81-85	Absolute Fecundity ($\times 10^3$)	1209	808	1014	472	892	459	-
	Fat Content Index	5.6	7.9	8.5	2.4	4.2	5.1	-

Mature females occur in the middle Amur River of the USSR from late May to early August (Gorbach 1972) with breeding peaks during late June and early July (Ma-k'ai-yeh-wa, Su-yin, and Po-t'a-po-wa 1966). The indigenous Chinese populations spawn from late April to June in the Yangtze River and from April to September in the Pearl and West Rivers further south (Dah-Shu 1957). Most fish in the West River breed from the end of May to the middle of June (Lin 1935a). The naturalized population of the Tone River, Japan reproduces from June to August with peak activity from late June to mid-July (Kuronuma 1955, Inaba, Nomura, and Nakamura 1957, Tsuchiya 1979). The spawning season, however, might be shifting to July and August as a result of construction of weirs which delay migration (Bailey and Haller unpubl. MS). In Malaysia, ripe specimens occur year-round, but are more common from March to October, indicating retention of a vestigial breeding cycle (Hickling 1967b). Spawning can occur in all months of the year in naturalized and cultured grass carp, depending upon climate and artificial conditions (Table XIV). Reproductive seasons of naturalized and cultured populations can be found in Table XIV.

3.1.6.2 Number of frequency of spawnings per year

Hickling (1967b) presents the only evidence for multiple-spawning by individual grass carp in one year. Two of his Malaysian specimens ovulated in May and were ripe again in July and September, respectively. Many authors have noted asynchronous development of oocytes in females from China (Lin 1935a, Gorbach 1966), the Tone River (Inaba, Nomura, and Nakamura 1957), Malaysia (Chen, Chow, and Sim 1969), the Amur River (Makeeva 1963, K'o-lei-hei-chin 1966, Ma-k'ai-yeh-wa, Su-yin, and Po-t'a-po-wa 1966, Gorbach 1972), and the lower Volga River (Martino 1974). Gorbach (1972) found that 91% of his mature Amur River specimens had two size-classes of oocytes. K'o-lei-hei-chin (1966) reports that intervals between spawns increase with age of the fish and Makeeva (1963) suggests that some individuals may not spawn every year.

3.1.6.3 Spawning time of day

The sole reference on this subject states that spawning of the established Tone River population occurs from early morning to early evening with peaks at dawn and twilight (Inaba, Nomura, and Nakamura 1957). In induced breedings of cultured fish, Tsuchiya (1979) observed spawning at all times of day with peak activity taking place at night. While daytime hormone injections must have influenced time of ovulation, his observation still demonstrates the possibility of nocturnal spawning in nature. Rottman and Shireman (1979) found that spawning occurred 9 to 11 hours after pituitary injection, when fish were allowed to spawn freely in tanks, indicating that the time of hormone injection determined spawning time.

3.1.6.4 Artificial reproduction, hybridization and sex reversal

There exists an immense body of literature dealing with the managed reproduction of grass carp. Lin (1935a, 1949) captured spawners from the West River in China and stripped their eggs and milt by hand. Fertilized eggs hatched successfully in boxes anchored in a river or stream. This method of fry production did not develop beyond a supplemental source of collection of wild eggs and fry. Induction of spawning by pituitary injection was first achieved in 1960 in China (Kuronuma 1968) and during 1961 in the USSR (Verigin 1963, Vinogradov 1968). A large number of injection procedures for successful ovulation have been determined and the methods for artificial fertilization also have great variety (Table XV).

The method used in the USSR is probably the most widespread (Anon 1970c). Depending on their size and productivity, one to three males are used for each female. Brood fish are selected when in appropriate physiological condition. Aside from secondary sexual characters (Table XV) males are selected which eject milt with little or no pressure and females which exhibit flaccid abdomens. Ripe females may also be identified by

Table XIV

Seasonality of maturation in naturalized and cultured grass carp populations

Location	Maturation season	Authority
Austria	June	Brown (1977)
India (Cuttack)	May-July June-August	Alikunhi, Sukumaran, and Parameswaran (1963a)
(Tamilnadu)	May-August	Chaudhuri, Singh, and Sukumaran (1966)
Japan (Tone River*)	June-July June-early August	Kuronuma (1955) Inaba, Nomura and Nakamura (1957)
(Shiga Prefecture)	June-August (peaks late June--mid-July) April-July	Tsuchiya (1979) Kawamoto (1950)
Korea	July-August	Kim (1970)
Malaysia (Malacca)	May-August ^{a/} all months all months	Slack (1962) Hickling (1967a) Chen, Chow and Sim (1969)
Nepal	mid-May--June	Shrestha (1973)
Netherlands	July	Huisman (1978)
Taiwan, Prov. of China	May-early July March-July	Lin (1965) Chen (1976)
USA (Arkansas)	May-July May-June	Bailey and Boyd (1970, 1973) Addor and Theriot (1977)
USSR		
Astrakhan Ili River*	latter June peaks mid/late May	Anon. (1970c) Nezdoliy and Mitrofanov (1975)
Kara Kum Canal*	May-June	Aliyev (1976)
Krasnodar	latter May	Anon. (1970c)
Moldavia	early June	Anon. (1970c)
Syrdar'ya River*	latter May	Verigin, Makeeva and Zaki Mokhamed (1978)
Turkmen	early May	Anon. (1970c)
Ukraine, southern	late May-late June	Hao (1973)
Uzbek	early May	Anon. (1970c)
Volga R. (lower)	May--mid-August	Martino (1974)
Volgograd	latter June	Anon. (1970c)

* Indicate self-reproducing populations. All other localities relate to induced spawning

^{a/} Imported as fingerlings

catheterization and examination of eggs, but this procedure can damage the fish and frequently causes an egg plug or egg resorption (Chen, Chow and Sim 1969). Anaesthesia with quinaldine mixed in water or sprayed directly on the gills, reduces the risk of injury during handling (Alabama Department of Conservation 1968; Bailey and Boyd 1970, 1973; Jeffrey 1970). In the USSR, spawning is induced when the average daily water temperature reaches 19° to 20°C. The entire year's production is completed in 25 to 30 days. Acetonated and dried cyprinid pituitaries are pulverized and suspended in

saline solution. Common carp glands are most readily available, but the non-specificity of the hypophyseal hormones permits successful use of many cyprinid species as donors (Alikunhi, Sukumaran and Parameswaran 1962, 1963a, 1963b, 1973; Chaudhuri, Singh and Sukumaran 1966, 1967; Hickling 1967a; Bardach, Ryther and McLarney 1972). Bacteriostatic or distilled water serves as a solvent (Alabama Department of Conservation 1966, 1967; Boyd and Bailey 1972). Females receive two injections, with the second dose 8 to 10 times greater than the first. The initial stimulating injection usually amounts to 3 mg

Table XV

Injection procedures and yields in induced ovulation of grass carp

Locality	No. of females	Weight (kg)	Injections ^{1/}	Internal between injections (hours)	No. ^{2/} of eggs (x 10 ³)	No. ^{2/} of fry obtained (x 10 ³)	Authority
China	-	-	0.5 LH-RH ^{3/} , 6.5 LH-RH ^{3/}	8	yes*	yes**	Anon. (1978a)
Germany, Fed. Rep. of	-	-	0.4, 3.2—3.4	24	yes	yes	Bohl (1979)
India (Cuttack)	1	6.8	3.0, 6.0	7	428	5	Alikunhi, Sukumaran and Parameswaran (1962, 1963a, 1963b, 1973)
	1	2.3	4.0, 6.0	7	-	80	Chaudhuri, Singh and Sukumaran, (1966)
	1	1.6	4.0, 7.0	7	-	50	
	1	2.6	1.0, 3.0, 6.0	3	-	35	
	1	3.2	1.0, 3.0, 7.0	3	-	2	
	1	3.0	1.5, 3.0, 6.0	3	-	3	
	1	3.4	4.0, 7.0	4	-	30	
	1	2.8	4.0, 8.0	4	-	40	
(Tamilnadu)	-	-	2.0-3.0, 5.0; 8.0	4	yes*	yes*	Prabhavathy and Sreenivasan (1977)
Japan	-	-	5.0—10.0	-	yes*	yes*	Tsuchiya (1979)
	-	-	2.5—5.0, 2.5—5.0	6	yes*	yes*	
Malaysia (Malacca)	-	-	5.0—7.0, 5.0—7.0	5	yes	yes	Chen, Chow and Sim (1969)
Nepal	1	4.0	5.3, 2.7	6	-	0.1	Shrestha (1973)
	1	4.0	3.0, 2.3, 2.3	3	-	0.2	
	1	6.0	3.0, 3.0	6	-	3	
	1	6.0	1.0, 3.5	11	-	18	
	1	6.0	0.5, 3.5	14	-	9	
	1	5.0	1.6, 3.3	6	-	35	
	1	4.0	1.5, 3.0	6	-	30	
	1	3.5	1.7, 2.6	6	-	50	
	1	5.0	1.8, 3.6	7	-	55	
Taiwan. Prov. of China	-	-	1.5—2.0 +5**, 1.5—2.0+10**	6	yes	yes	Lin (1965)
USA							
(Alabama)	1	4.1	0.85, 2.9 + 500*	21	300-500	2	Alabama Dept. of Conservation (1966)
	1	3.4	1.0, 3.5 + 500, 3.5 + 500*	21, 7	2-3	0.01	
	1	3.9	0.5, 2.1 + 130*	24	yes	yes	Alabama Dept. of Conservation (1967)
	1	3.0	0.7, 2.7 + 170*, 3.0 + 170*	24, 12	yes	yes	
	1	2.7	0.7, 3.3 + 180*, 3.3 + 180*	24, 22	yes	yes	
	1	3.0	0.7, 3.0 + 170*	24	yes	yes	
	1	5.7	0.4, 2.6 + 180*, 2.6 + 180*	24, 12	yes	yes	
	1	3.6	0.6, 2.5 + 280*, 2.5 + 280*	24, 12	yes	yes	
	1	3.0	0.7, 3.0 + 340*	24	yes	yes	
	-	3.7—6.8	0.3—0.5, 2.2—4.0 + 1000*	24, 12	yes	yes	Alabama Dept. of Conservation (1968)
	1	4.4	2.2—4.0 + 1000*(optional)	-	yes	yes	Ventura (1973)
	1	4.7	6.6, 6.6	-	yes	yes	
(Arkansas)	4	5.0	4.4	-	yes	yes	
	1	6.4	220*, 1870*, 2.2	24	7185	270	Bailey and Boyd (1971, 1973)
	3	-	220*, 1870*, 0.2, 2.2	24	2500	600	Bailey and Boyd (1971a)
	2	-	220*, 1870*, 0.2, 1.3	24	600	60	
	1	-	220*, 1870*, 0.2, 0.2, 0.2	24, 12	710	500	
	1	-	220*, 2200*, 0.2, 2.2	24	350	227	
	1	-	220*, 2200*, 0.2, 4.4	24	630	358	
	1	-	0.2, 4.4	24	72	0.7	
	8	5.7, 9.8	220*, 1870*, 2.2	24	6850	3000	Boyd and Bailey (1972)
	5	6.1—8.4	220*, 1870*, 2.2	24	7000	2250	
	2	6.8—7.3	220*, 1870*, 2.2	24, 48	2700	1300	
	-	-	440*, 1760*, 11.0	24	yes	yes	Stanley (1975)
	-	-	100*, 400*, 2.0—3.0	24	yes	yes	Stanley (1976b)
	-	-	400*, 1600*, 10.0	24	yes	yes	Stanley (1976d)
(Florida)	88	-	440*, 1760*, 3.0—5.0	12, 24	46900	yes	Thomas (1977)
	3	-	440*, 1879*, 9.0	16, 15	1950*	yes*	Rottmann and Shireman (1979)
USSR							
(Leningrad)	-	5—7	0.5, 3—6	24	500	200	Anon. (1970c)
	3	7.5	3.7	-	156	yes	Konradt (1968)
	14	7.5	0.5, 3.7	24	11000	yes	
	14	7.5	0.5, 3.7	6	6600	yes	

1/* Denote I.U./kg of human chorionic gonadotropin

** Denote rabbit units/kg of Synahorin

2/ Values without asterisks indicate eggs or fry obtained by hand stripping and dry fertilization.

* Denote cases where eggs were collected from spawning ponds or tanks, but numbers not reported

** Indicate fry obtained, but numbers not included

3/ Luteinizing-releasing hormone

Table XVI

Results of grass carp hybridization with other Cyprinids

Cross	Result	Life stage or age reported	Authority
<u>Abramis brama orientalis</u> (eastern bream) male	intermediate to matroclinous hybrids	8 days	Ryabov (1973)
<u>Carassius auratus</u> (goldfish) male	intermediate hybrids	larva	Stanley (1973a, 1974c),
(goldfish) female	intermediate hybrids	larva	Stanley and Sneed (1973a, 1973b)
<u>Catla catla</u> (catla) male	not described	1 day*	Alikunhi, Sukumaran and Parameswaran (1962, 1963a, 1963b, 1973)
<u>Cirrhina mrigala</u> (mrigala) female	not described	3 days*	Hickling (1968)
<u>Cyprinus carpio</u> (common carp) male	gynogenetic progeny	yearling	Aliev (1967)
	inviable diploid or gynogenetic progeny	?	Vasil'ev, Makeeva and Ryabov (1975)
	not described	larvae	Stanley (1974c, 1975)
	not described	fry	Avault and Merkowsky (1978)
<u>Cyprinus carpio</u> (common carp) female	intermediate hybrids	fry	Makeeva (1972, 1976)
	intermediate hybrids and androgenetic progeny	fingerling	Stanley (1973a, 1974c)
	intermediate and matro- clinous hybrids	yearling	Makeeva and Verigin (1974)
	intermediate fertile hybrids	maturity	Stanley (1975) Avault and Merkowsky (1978)
	intermediate hybrids	yearling	Theriot and Sanders (1975)
	intermediate triploid hybrids	?	Vasil'ev, Makeeva and Ryabov (1975, 1978)
	Matroclinous hybrids	yearling	Makeeva (1976)
<u>Cyprinus carpio</u> (common carp) female	intermediate hybrids and androgenetic progeny	3 months	Stanley (1976b, 1976c) Stanley and Jones (1976)
	not described	larvae	Bakos, Krasznai and Marian (1978)
<u>Hypophthalmichthys molitrix</u> (silver carp) male	not described	larvae	Andriasheva (1968)
female	patroclinous hybrids	yearling	Aliev (1967)
	not described	larvae	Andriasheva (1968)
<u>Hypophthalmichthys nobilis</u> (bighead carp) male	matroclinous hybrids	yearling	Aliev (1967)
	intermediate hybrids	fingerling	Andriasheva (1968)
	intermediate hybrids	fry	Makeeva (1972)
	intermediate triploid hybrids	fingerling & yearling	Krasznai and Máriań (1977), Máriań and Krasznai (1978, 1979)
	not described	larvae	Bakos, Krasznai and Marian (1978)
	intermediate triploid hybrids	?	Lynch (1979)
<u>Hypophthalmichthys nobilis</u> female	not described	larvae	Andriasheva (1968), Bakos, Krasznai and Marian (1978)
	intermediate hybrids	fry	Makeeva (1972)
	intermediate hybrids	fingerling	Berry and Low (1970), Verigin et al. (1975)
<u>Labeo ariza</u>	not described	?	Prabhavathy and Sreenivasan (1977)
<u>Labeo rohita</u> (rohu carp) male	not described	1 day*	Alikunhi, Sukumaran and Parameswaran (1962, 1963a, 1963b, 1973)
female	not described	2 weeks*	
<u>Megalobrama terminalis</u> (black bream) male	intermediate hybrids	yearling	Aliev (1967)
<u>Mylopharyngodon piceus</u> (snail carp) female	not described	fry (26 days)	Chen (1969)
<u>Parabramis pekinensis</u> (white bream) male	not described	?	Hickling (1968)
<u>Puntius (=Barbus) gonionotus</u> (puntius carp, tawes, or pla-tapien) male	not described	larvae	Boonbrahm, Tarnchalanukit and Chuapoehek, (1970)
female	not described	40 hours*	

* All specimens died by this age.

for 5-7 kg spawners and 5-6 mg for larger fish. Resolving doses are determined by weight and girth of the female and are administered one day later. Males also receive 4-6 mg of pituitary at this time; larger specimens may be injected with 10-15 mg to produce greater amounts of milt. Males however, often do not require artificial stimulation (Shrestha 1973). Fish are injected in the anterior dorsal muscles, below the dorsal fin. They are held at 20-28°C in ponds until ovulation, which occurs in 7-12 hours depending on temperature. Holding brood stock at higher temperatures adversely affects spawn quality.

Hand stripping spawn from brood fish initiates the process of artificial fertilization. Sperm can be kept on ice for 10-12 hours. Stripped eggs are combined immediately with milt and a small amount of water in shallow bowls or pans. The time-honoured tool for mixing them is a bird feather, but gentle swirling serves as an alternative. After one or two minutes, the delicate eggs are washed a few times with fresh water and transferred to Weis/Zoug jars or similar apparatus for incubation. Oxygenated water at 21-25°C is pumped into the hatching vessel to keep the eggs in gentle motion.

Many culturists are investigating wet-fertilization or spawning of injected fish in ponds or tanks. Reduced damage to breeders, less labour investment, better spawn quality, and high fertilization rates constitute the potential advantages. Disadvantages include difficulties in controlling environmental factors and in collecting eggs. Breeding activity usually requires an artificial current as stimulation. Successful reproduction without hand stripping has been achieved in ponds (Lin 1965, Kuronuma 1968, Ling 1977, Tsuchiya 1979), net-enclosed pond sections (Chaudhuri, Singh, and Sukumaran, 1966, 1967), pools (Tapiador *et al.* 1977), and circular tanks 1.8 m in diameter (Rottman and Shireman 1979). Eggs are incubated in a variety of ways, but procedures include protection from predators and diseases, moving oxygenated water, and temperatures from 21-25°C. Treatment with tannin or formalin can prevent fungal and bacterial infection (Shrestha 1973; Anon. 1972c, 1972g; Bohl 1979). Hatching containers range from pools (Tang 1965, Tapiador *et al.* 1977) to net or cloth vessels set in streams and raceways (Lin 1949, 1965; Shrestha 1973; Ling 1977) to circular fish tanks (Rottman and Shireman 1979) to jars or troughs (Konradt 1968, Kuronuma 1968, Chen, Chow and Sim 1969) and many others).

Luteinizing hormone (LH) and mammalian chorionic gonadotropins have also been used to induce ovulation in grass carp (Table XVI). Chinese researchers first obtained success with natural and synthetic LH in 1975 (Anon. 1978a). The hormone is administered intraperitoneally as an initial stimulating dose

with natural and synthetic LH in 1975 (Anon. 1978a). The hormone is administered intraperitoneally as an initial stimulating dose of 0.5 mg/kg followed in eight hours by a resolving injection of 6.5 mg/kg. The gonadotropins include Puberogen, Gonagen, Synahorin (Synorhorin) and human chorionic gonadotropin. They do not work reliably by themselves, but are used to reinforce hypophysial injections. Because of variable breeder conditions and injection procedures, conflicting reports exist as to their effectiveness. Tang (1965) increased the percentage of ovulating females from 33 to 78 by adding Synahorin, while Chen, Chow, and Sim (1969) found no significant effect with the same hormone. The number of injections used ranges from one to five with two or three used most commonly. Pituitary is usually given intraperitoneally at the base of a pelvic or pectoral fin, but Chen, Chow and Sim (1969) have found dorsal intramuscular sites to be as effective. Gonadotropins are usually injected intramuscularly just below the dorsal fin or on the dorsal surface of the caudal peduncle.

Artificial reproduction has allowed for crossing grass carp with many cyprinids (Table XVI), as well as production of gynogenetic and androgenetic progeny. Polyploidy occurs when grass carp are hybridized with male bighead (Krasznai and Mária 1977; Mária and Krasznai 1978, 1979) and female common carp (Vasil'ev, Makeeva, and Ryabov 1975, 1978). Morphological descriptions of hybrids are given in Section 1.4. Stanley (1973a, 1973b, 1974c, 1975, 1976a, 1976c, 1976e, 1979), Stanley and Sneed (1973a, 1973b), Stanley, Martin, and Jones (1975), and Stanley and Jones (1976) studied gynogenesis and androgenesis in grass carp. Gynogenetic fish were obtained by use of irradiated milt from goldfish or common carp. Grass carp roe was fertilized with a mixture of one-part sperm to four-parts Hank's balanced salt solution. The small yields of gynogenetic diploids could not be increased by cold shocks, pressure, high incubation temperatures nor colchicine. Androgenetic specimens arose spontaneously at a very low rate when common carp roe was fertilized with grass carp milt. Morphological, biochemical and cytological analysis indicated that gynogenetic and androgenetic progeny had pure grass carp inheritance. Shelton and Jensen (1979) obtained sex-reversed males (genotypic females), intersexes, females with undeveloped gonads, and potential neuters by treating normal stocks and gynogenetic females with methyltestosterone administered orally or via silastic implants (Table XVII). Sex reversal, indicated by morphological and histological examination, was successful only with implants, and did not necessarily require treatment during the period of gonadal differentiation.

Table XVII

Results of methyltestosterone treatment (MT) of grass carp (Shelton and Jensen, 1979)

Treatment	Initial age in days	Number of				Sex ratio ^{1/}
		Females	Males	Inter-sexes	Unknown sex	
275 days	110					
Control		15	27	0	0	1:1.8
60 mg MT/kg food		13	34	0	0	1:2.62
120 mg MT/kg food		26	22	0	0	1.18:1
410 days	110					
Control		16	17	0	0	1:1.05
60 mg MT/kg food		22	19	0	2	1.16:1
120 mg MT/kg food		24	14	0	2	1.71:1
189 days	309					
Control		5	5	0	0	1:1
MT implant		0	5	4	0	0.5
202 days	309					
Control		36	21	0	0	1.7:1
MT implant		13	21	6	1	1:1.62
461 days	309					
Control		7	5	0	0	1.4:1
MT implant		0	7	2	0	0:7*
500 days	319 ^{2/}					
Control		33	37	0	0	1:1.2
Sham implant		29	42	0	0	1:1.4
MT implant		26	27	12	4	1:1.14
460 days	55 ^{3/}					
Control		21	0	0	4	21:0*
MT implant		5	5	9	8	1:1
Normal		42	0	0	13	42:0*

^{1/} Sex ratios with asterisks differ significantly ($P < 0.01$) and those without asterisks do not differ ($P < 0.05$) from 1:1 by chi-square test with Yate's correction

^{2/} Stunted specimens averaging 14.7 g in weight and 123 mm in total length

^{3/} Gynogenetically produced females

3.1.7 Spawning conditions and grounds

The grass carp is a pelagophilic spawner in relatively-large rivers. Breeding migrations commence when water temperature reaches 15-17°C (Aliev 1976). In the native range, reproduction occurs during the monsoon season, when water levels rise quickly, temperatures range between 20° and 30°C and current velocities vary from 0.7 and 1.8 m/sec (Lin 1935a, Dah-Shu 1957, Chang 1966). A minimum water temperature of 18°C has been reported for successful spawning in most acclimatized populations (Inaba, Nomura and Nakamura 1957, Aliev 1976). Eggs can develop at current speeds as low as 0.24 m/sec, but flow rates greater than 0.6 m/sec may be necessary for initiation of breeding behaviour (Leslie *et al.* unpubl. MS). Verigin (1961) states that grass carp spawn after water level increases of only 10-15 cm. In the USSR, Aliev (1976) found reproduction in the Kara Kum Canal, where water levels remain constant. He writes that breeding may require a minimum discharge rate

of 170-200 m³/sec. Increased turbidity may or may not be a factor in initiating spawning, but it probably does lessen predation on the vulnerable eggs and larvae (Stanley, Miley, and Sutton 1978). Chemical contents decrease during flood conditions and this may influence reproductive activity (Inaba, Nomura, and Nakamura 1957). During spawning periods in the Tone River of Japan, pH ranged from 6.9 to 7.2 (Inaba, Nomura, and Nakamura 1957, Tsuchiya 1979).

River physiography has considerable impact on spawning success. Length of the waterway may be important; both for physiological preparation of adults, and for proper spawn development. Aliev (1976) observed reproduction in fish which swam up to 80 km while others did not spawn when flood control gates limited their migration to 1.5-2.0 km. Calculating on the basis of incubation times and current velocity, Stanley, Miley, and Sutton (1978) determined that egg development could take place in waterways with minimum lengths of 50-180 km. Leslie *et al.*

(unpubl. MS) demonstrated that egg development could occur at much slower current velocities, which would permit a minimum length of 16 km for incubation at 27°C. Turbulent areas immediately below islands, tributary junctions, sandbars or stone beds serve as breeding grounds (Lin 1935a, Dah-Shu 1957, Chang 1966, Anon. 1970c). Grass carp also spawn downstream from bridge pilings (Bailey and Haller unpubl. MS) and sluice gates (Aliev 1976). Rock, gravel or sand comprise the substrate and vegetation is scarce in these areas (Lin 1935a, Kuronuma 1955, Dah-Shu 1957, Inaba, Nomura, and Nakamura 1957, Chang 1966, K'o-lei-hei-chin 1966). The larvae must be able to find water nursery areas with vegetation at a proper distance downstream from the spawning site (Miley, Sutton and Stanley 1979).

3.1.8 Milt and spawn

Lin (1935b) describes milt as a creamy, white, somewhat sticky fluid which coagulates in water. Most spermatozoa live for 15-30 seconds in water (Anon. 1970c).

Ripe spawn varies from grayish-blue to bright orange with little ovarian fluid. Overripe spawn is watery and contains some cloudy white eggs. On ovulation, the egg is 1.2-1.3 mm in diameter with a two-layer membrane immediately adjacent to the yolk. The outer layer has adhesive properties which disappear during fertilization. The membrane separates from the yolk within 10 minutes and the perivitelline space absorbs water and swells the egg to 3.8-4.0 mm in 40 minutes after fertilization. The egg attains a maximum diameter of 4.32-5.32 mm in 1.5-2.0 hours and is bathypelagic or buoyant in flowing water. Egg mortality by suffocation increases greatly in oxygen-deficient, slowly-moving, or silt-laden water. (Anon. 1970c). Because the egg membranes are delicate, eggs are very prone to bacterial and fungal infections (Anon. 1972c, 1972g; Shrestha 1973; Bohl 1979). In an experimental release of eggs in the USA divers observed voracious predation by *Notropis venustus*, *Percina nigrofasciata*, and *Lepomis auritus* (Leslie et al. unpubl. MS). The 2.33 million released eggs were reduced by 99.9 % over 3.2 km. Analogous predatory species probably occur anywhere grass carp might spawn. Predaceous invertebrates, especially copepods, also attack eggs (Anon. 1970c).

3.2 Embryonic to juvenile life history: development and survival

3.2.1. Embryonic stage

Bobrova (1972) and others describe cellular events from fertilization to the first cleavage division (Sections 1.4.3 and 3.1.4). Incubation lasts from 16 to 60 h at temperatures ranging from 30°C to 17°C (Lin 1965, Anon. 1970c). The optimal temperature range for greatest yields of viable larvae

is 21-25°C, which results in hatching from 23 to 33 h after fertilization. At 22-26°C, embryogenesis proceeds in the following stages, with age measured from fertilization (Anon. 1970c).

Stage I (0-0.7 hours): During the first few minutes, the unhydrated fertilized egg measures 1.2-1.3 mm, with the chorion abutting the yolk (Figure 4-a). At 10 minutes, the membrane separates from the yolk and the cytoplasm concentrates at the animal pole (Figure 4-b). At 40 minutes the cytoplasm tuberculates into a blastodisc and hydration of the perivitelline space swells the egg to 3.8-4.0 mm (Figure 4-c).

Stage II (1-7 hours): The blastodisc divides into two blastomeres at 60 minutes (Figure 4-d), four blastomeres at 80 minutes (Figure 4-e), and 8 blastomeres at 100 minutes. Early (large-cell) morula begins at 2.5 h (Figure 4-f). Late (small-cell) morula occurs at about 5 h when the egg has swollen to its maximum diameter of 4.32-5.32 mm. Blastula starts at 6 h (Figure 4-g).

Stage III (7-13 hours): Gastrulation begins at 7 hours with the blastoderm growing over the yolk toward the vegetative pole (Figure 4-h). A node arises in a section of the blastomere fringe zone, rapidly divides and turns inward and under, and differentiates into the three germ layers of the rudimentary embryonic body, which lengthens and thickens (Figure 4-i). Gastrulation concludes at approximately 12 hours and the embryo assumes the shape of a thickened spindle and extends from a broadened head section at the animal pole to a narrow tail area at the vegetable pole (Figure 4-j).

Stage IV (13-24 hours): At 15 hours, the optic vesicles form, the notochord forms, mesodermal segmentation begins, and the cerebral vesicles differentiate (Figure 4-k). At 21 hours, crystalline lenses appear in the eye, auditory vesicles develop, segmentation is extensive, the notochord is distinct, and the embryo occasionally bends (Figure 4-l).

Stage VI (24-29 hours): The tail detaches from the yolk sac and the body straightens. Small vesicles appear in the head and cardiac regions representing the hatching glands. The embryo moves energetically (Figure 4-m).

Incubation at 28-31°C considerably speeds embryonic development (Alikunhi, Sukumaran, and Parameswaran 1962, 1963a, 1963b, 1973). First cleavage occurs at 0.7 hours, 8-16 cell stages at 1.5 hours, morula at 3.5 hours, and gastrula at 4.0 hours. The yolk-plug stage is reached 6.0 hours after fertilization and a rudimentary embryo appears. At 10.3 hours the 2.4 mm embryo is well differentiated and possesses a 1.7 mm elongated yolk sac. Myotomes number 23, auditory and Klüppfer's vesicles appear, and the

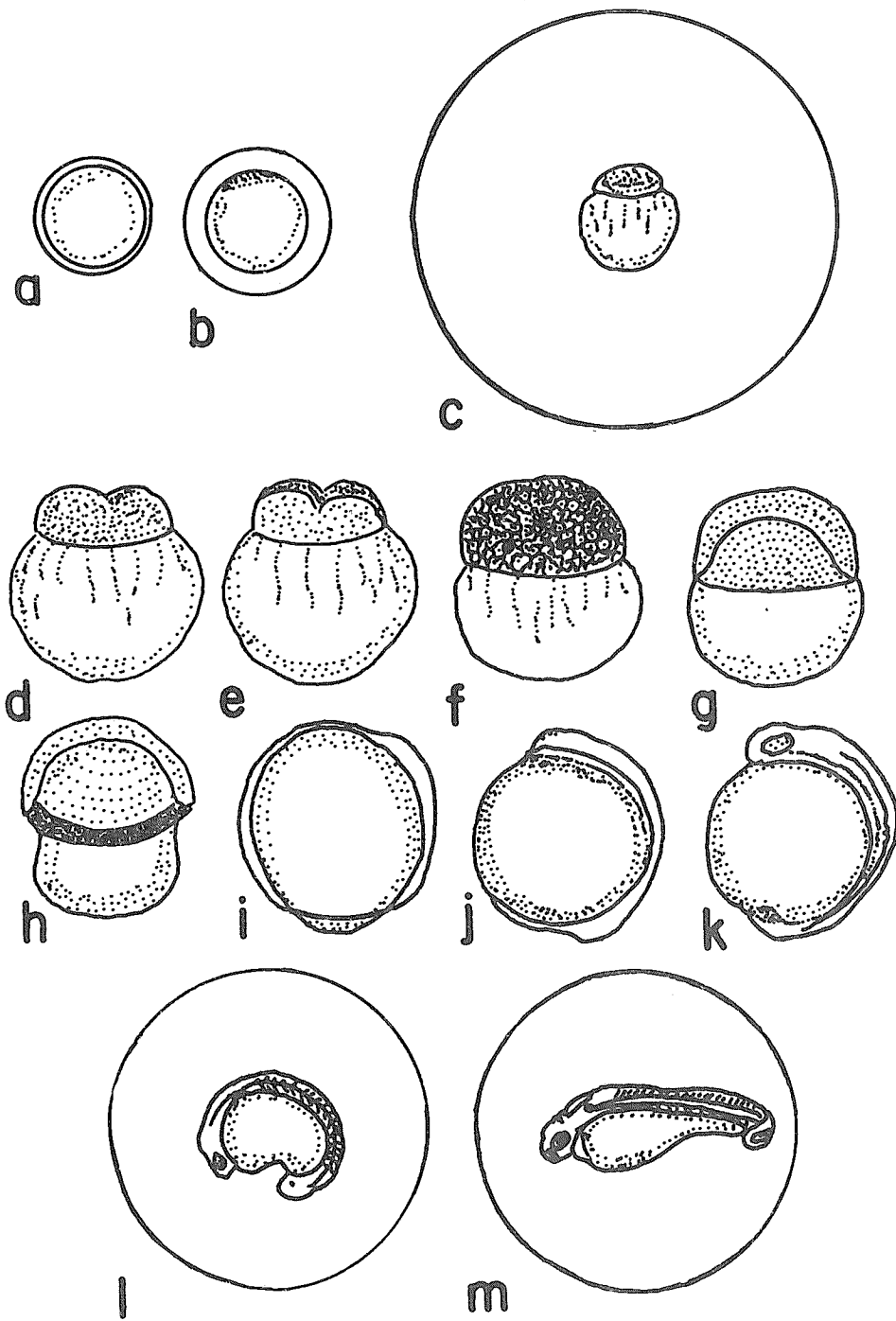


Figure 4 Embryonic development of grass carp, description in text
 (after Aliev in Antalji and Tölg 1972)

and the optic cups become distinct. Embryonic movement begins at 12.5 hours and is vigorous by 18.5 hours. Hatching occurs 19-23 hours after fertilization.

In Soviet fry production, mass hatching generally lasts from 1-3 hours (Anon. 1970c). High temperatures and low oxygen content encourage synchronous hatching by increasing activity by both embryos and their hatching glands.

Inadequate fertilization and various incubation conditions may result in embryonic or larval mortality (Anon. 1970c). Unfertilized spawn undergoes false development through gastrulation when the eggs disintegrate. Overripe spawn has large heterogeneous yolk granules which interfere with development by causing the blastomeres to break away from the yolks. Dropsy is usually characterized by enlargement and hydration of the pericardial cavity, with consequent deformation of the heart. It may also occur behind the cavity or beneath the intestines. Dropsy and other deformities are caused by overmature eggs, extreme water temperatures, sudden drops in temperature and low oxygen. Spawn develops normally in salinities less than 0.15 ‰. Stott and Cross (1973) observed 6-7°C falls from 24.4°C during incubation to result in developmental deformities and inviable larvae.

3.2.2 Protolarval stage

Protolarval development, during the first three days after hatching, proceeds as outlined below (Inaba, Nomura, and Nakamura 1957, Anon. 1970c, Soin and Sukhanova 1972).

Stage VI (0-1 day): Hatchlings measure 5.0-5.5 mm and possess 28-31 trunk and 12-16 tail myotomes. The transparent eye has a few melanophores in the lower part of the optic-cup symphysis. No other pigment is present. The protolarva has rudimentary otoliths in the auditory capsules and a visible pulsating heart with ventricle and auricle. It lies on the bottom and occasionally swims vertically to the surface, then drifts back to the bottom (Figure 5-a).

Stage VII (1-2 days): Length ranges from 6.5 to 6.7 mm. Myotomes generally number 30 in the trunk and 14 in the tail. A pectoral bud develops. Circulatory vessels fill with blood and become visible. Broad ducts of Cuvier are present in the anterior section of the yolk sac. An enlarged caudal vein occurs in the hollow of

the anal fin fold. Swimming is more pronounced (Figure 5-b).

Stage VIII (3 days): The advanced protolarva is 7.4-7.5 mm and has 30 trunk and 14 tail myotomes. The mouth moves from a subterminal to semiterminal position. Moveable mouthparts develop, but the lower jaw remains incomplete. The operculum covers most of the gills. The pectoral fins become membranous. The eyes are completely pigmented and have gold irises. Ground colour of head and dorsum is greenish-yellow. Star-shaped melanophores occur on the back of the head, in the sub-orbital area, on the trunk dorsum, at the pectoral base, around the heart, on the anterior yolk sac on the margin between the yolk and lateral myotomes, at the ventral edge of the postanal myotomes, and on the posterior edge of the future hypural bone. The gills have branched blood vessels and begin to function. A rudimentary swim bladder forms. The protolarvae swim sporadically to the surface and swallow air (Figure 5-c).

With high temperatures (30°C), protolarvae quickly attain development stages, but as smaller sizes (Alikunhi, Sukumaran, and Parameswaran 1962). Hatchlings measure 4.5 mm in length and 2.9 mm in height. The 0.78 x 2.84 mm yolk sac is a pale yellowish-brown. Myotomes number 45 with 19 posterior to the anus. At one day of age, body dimensions are 0.8 to 0.9 x 5.9 to 6.1 mm and the yolk sac measures 0.35-0.50 x 2.47-2.75 mm. Fully-pigmented eyes and functional pectorals are present. Two days after hatching, the protolarva is 0.9-1.0 x 6.3-6.5 mm with a 0.33 x 2.66-2.84 mm yolk sac. The mouth forms and the eyes are fully-developed. The notochord tip is straight. The top of the head has a light-yellow ground color with 8-10 melanophores. A continuous line of chromatophores extends dorsally from the swim bladder to beyond the anal fin. At three days the fish measure 0.99 x 6.98 mm.

Conner *et al.* (1980) report the meristics of protolarval grass carp. Total lengths varied from 6.6 to 8.4 with a mean of 7.5 mm. Ranges and means of the following dimensions as a percentage of total length are given: pre-anal length 67.6 to 73.5, \bar{x} = 70.0; predorsal length 36.6 to 45.4, \bar{x} = 41.2; head length 14.3 to 23.1, \bar{x} = 20.0; eye diameter 4.3 to 7.2, \bar{x} = 6.2; body depth 12.0 to 17.5, \bar{x} = 14.3 and depth behind vent 4.8 to 7.2, \bar{x} = 5.8. Myotomes number 41 to 44 in all, 9-14 predorsally, 30 to 33 pre-anally, and 9-13 postanally. Protolarvae have 42 to 43 vertebrae, round eyes, vestigial yolk sacs at 7.5 mm and no midventral pigment.

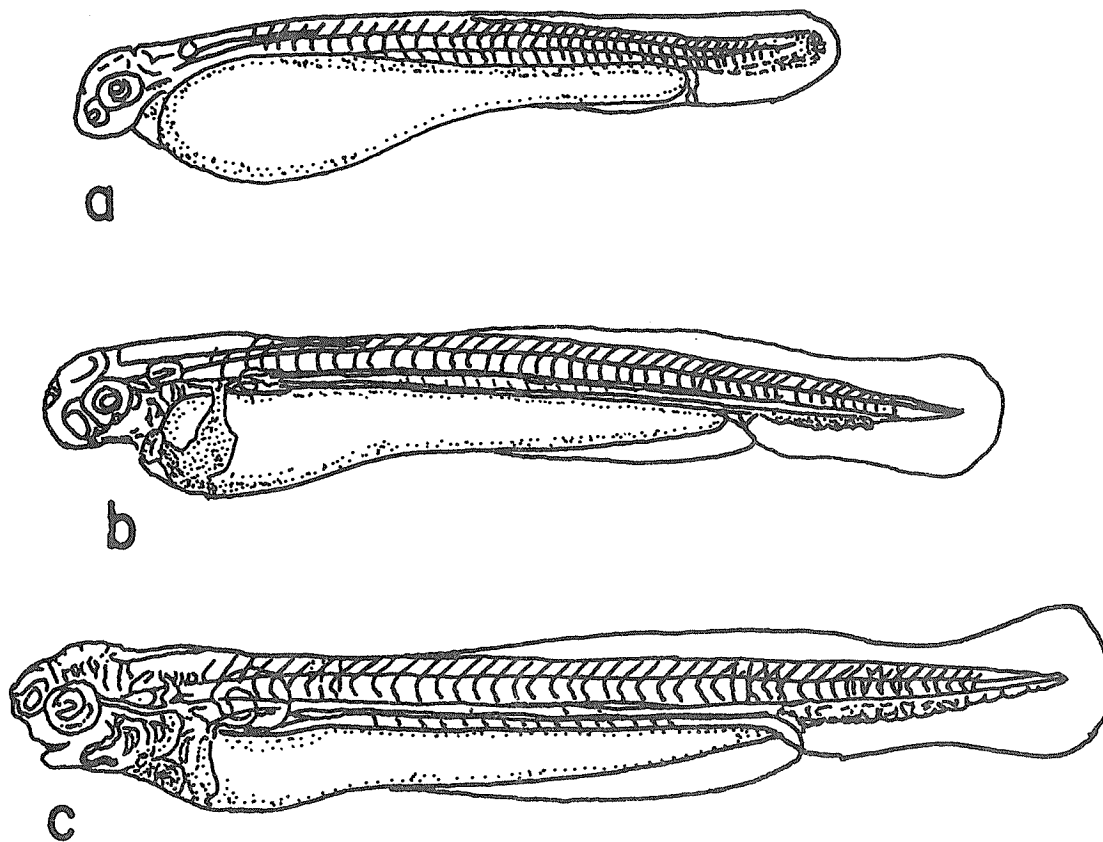


Figure 5 Protolarval development of grass carp, description in text (after Aliev in Antalji and Tšig 1972)

Because of their limited mobility, proto-larvae are prone to suffocation in silt (Bailey 1972). Hatchlings 20 hours of age seem to be fairly resistant to temperature drops from 24.4° to 17°C (Stott and Cross 1973). Mortality rates in the wild are undoubtedly high at this stage (Vladimirov 1975), but survival from hatching to exogenous feeding is generally greater than 50 % for fish under Soviet culture (Anon. 1970c).

3.2.3 Mesolarval stage

The mesolarval period extends from the fourth to thirtieth day after hatching. Morphological changes progress as set forth below (Dah-Shu 1957, Inaba, Nomura and Nakamura 1957, Anon. 1970c).

Stage I (4.5 days): The larva is 7.5 to 8.0 mm in length. The swim bladder is inflated and respiration proceeds by means of gills. Feeding is mixed, with a much reduced yolk sac remaining. Pigmentation and mobility increase (Figure 6-a).

Stage II (7 days): The mesolarva measures 7.5 to 8.1 mm, has absorbed its yolk sac

and feed exogenously. The lower jaw is slightly inferior to the upper jaw. The mouthparts are terminal and moveable. The head is relatively large and slightly square with a large interorbital distance. Lobes of the unpaired fins differentiate from the common fin fold. The caudal lobe is rounded with lighter colouration below and caudal fin rays begin to form. Melanophores occur on the head and trunk except on the venter. The notochord tip is straight. Blood vessels under the vertebrae have reddish-orange cells. The first gill arch has 8 to 9 cylindrical rakers. Sharp pharyngeal teeth are embedded in the buccal epidermis. At this time, the larvae swim continuously (Figure 6-b).

Stage III (9-18 days): Distinct fin rays appear in the lower part of the caudal lobe. Lengths range 8.0 to 12.4 mm during this stage. At 12 days of age, the dorsal fin differentiates and calcification takes place in the caudal fin. Gill rakers are 32 to 49 μ long and

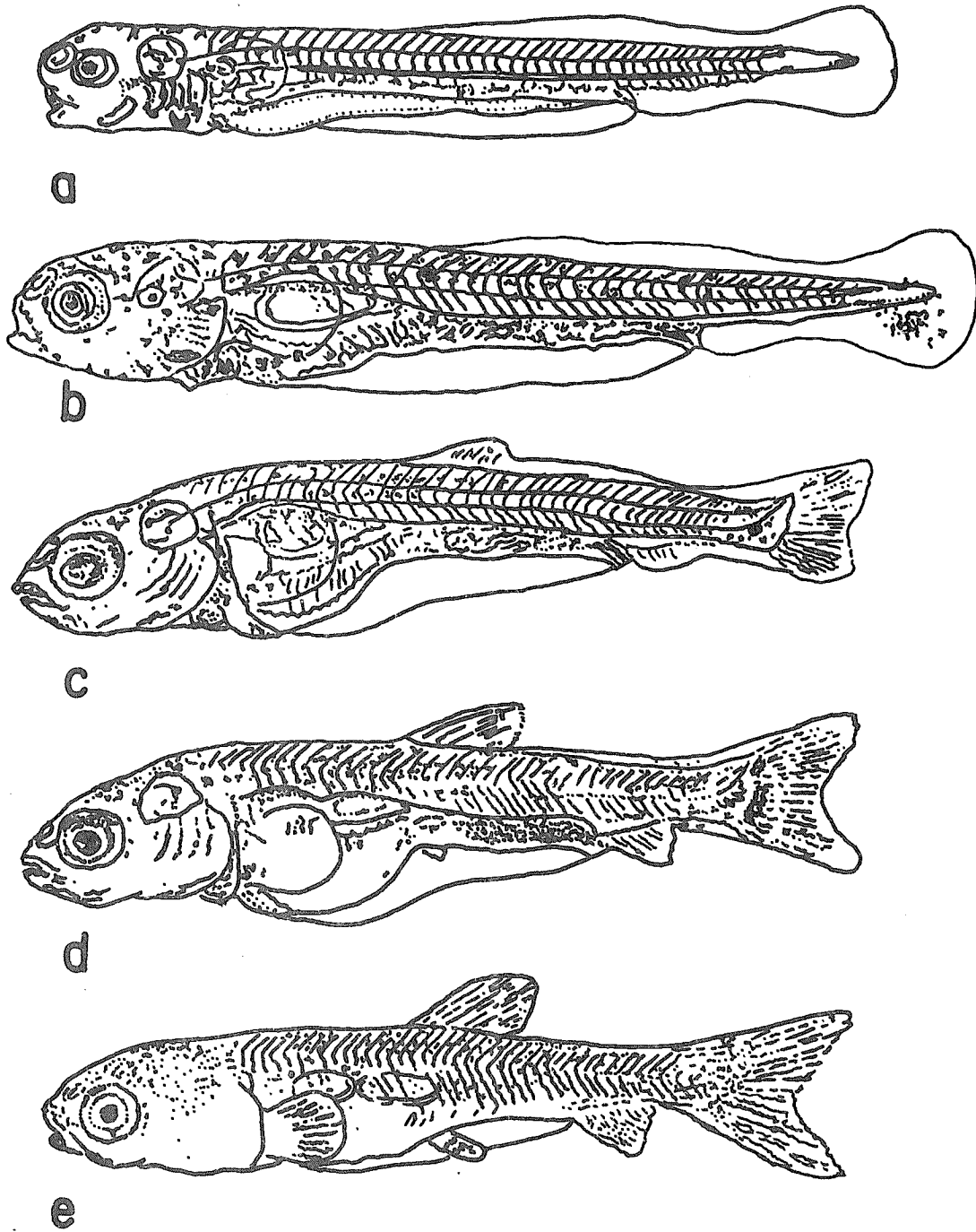


Figure 6 Mesolarval development of grass carp, description in text
(after Aliev in Antalji and Tšlg 1972)

73-106 μ apart. Four large claw-shaped pharyngeal teeth and two small ones are embedded in the buccal skin. The swim bladder has one chamber. From 14 to 18 days after hatching, many developmental changes occur. The dorsal, caudal and anal fins become distinct and possess fin rays (Figure 6-c). Fin formulae are 5-8 primitive rays in the dorsal and 4-7 in the anal fin. The caudal fin divides into two lobes with about 8-10 + 7-9 bony rays. The end of the notochord bends upward and the hypural bone develops. Iridocytes appear. The pelvic fins begin development and a rudimentary anterior section of the swim bladder forms (Figure 6-d). Four large and two small pharyngeal teeth are well developed. The first gill arch possesses 11 rakers 81.7 μ high and 102 μ apart.

Stage IV (20 days): Larvae measure 11.5-18.6 mm. Fin formulae are 4 + 8 rays in the dorsal, 2 + 8 for the anal, 1 + 6 for the pelvic, and 8 rays in the fan-shaped pectoral fin. The caudal fin is deeply indented. A vestigial median fin fold remains between the pectoral fins and anus and on top of the caudal peduncle. The dorsum is brownish-yellow with a greenish tinge, fading toward the belly. Iridocyte layers occur on the opercle, pre-opercle, branchiostegals and peritoneum. The swim bladder has two well developed lobes (Figure 6-e).

Conner, Gallagher, and Chatry (1980) describe the morphology of grass carp meso-larvae as follows:- total lengths ranged 7.6-8.9 mm with a mean of 8.0 mm. They give ranges and means of the following dimensions as a percent of total length: pre-anal length 69.0-71.6, \bar{x} = 70.3; pre-dorsal length 36.6-45.5, \bar{x} = 43.3; head length 21.4-23.2, \bar{x} = 22.4; eye diameter 6.4-7.4, \bar{x} = 7.0; body depth 12.3-16.1, \bar{x} = 13.8; and depth behind vent 4.8-6.3, \bar{x} = 5.7. Myotomes and vertebrae number the same as in proto-larvae. Mesolarvae have no yolk sac, round eyes, and no midventral pigment.

Environmental tolerances of mesolarvae are discussed in Section 2.3. They are less resistant to adverse water conditions than are post-larval stages and great mortality presumably occurs, especially if inadequate vegetation exists to provide cover from predators (Stanley, Miley, and Sutton 1978). Growth and survival through the larval period seems to be enhanced by high levels of zinc sulphate, which appear important in the metabolic processes leading to calcification of bony tissue (Sabodash 1974). In fish culture in the USSR (Anon. 1970c), survival through the larval period is usually 30-40 %.

3.2.4 Post-larval (fry and fingerling) stage

The two developmental periods correspond with the transitions to fry and fingerlings (Dah-Shu 1957, Inaba, Nomura, and Nakamura 1957, Anon. 1970c).

Stage I (20 days to 1 month): The post-larva measures 15-23.4 mm. A remnant of the median fin fold remains in the pelvic region. Fin rays number 21-27 in the caudal, 7-11 in the anal, and 7 in the pelvic fin. Fins are well-developed with adult formulae. The caudal is forked. Scales form dorsally and laterally. Lateral line scales number 38. Iridocyte layers occur on the post-orbital, opercle, subsurface of the midlateral trunk area, and peritoneum. The jaws interlock in one plane. The first gill arch has 11-13 rakers 114-180 μ long and 123-220 μ apart. The rakers form branched protruding tops. The well-developed pharyngeal teeth have the adult formula. Reserve teeth are embedded in the jaw. The swim bladder attains the adult shape. The intestine lengthens and approaches the coil pattern found in adults (Figure 7-a).

Stage II (1.5-2.0 months): Young fingerlings vary 3.7-6.7 cm in length during this period. At 50 days, scalation is complete and the vestigial median fin fold is absent (Figure 7-b). Openings of the lateral line canal are visible. At 55 days and 67.3 mm, the fingerling appears identical to the adult.

Morphological changes occur in the blood and gonads during the fingerling period. The amount of hemoglobin per weight of fish increases from 2.87 g/kg in 0+ specimens to 3.39 g/kg in 1+ fish, due primarily to an increase in erythrocyte size (Lyakhovich and Leonenko 1970). Grass carp 1-1.5 months of age show respiratory distress at 0.59 mg O₂/l, with a lethal minimum at 0.44 mg O₂/l (Negonovskaya and Rudenko 1974). Individuals larger than fingerlings are less sensitive to low-oxygen contents. Shelton and Jensen (1979) investigated gonadal development in grass carp (Sections 1.4 and 3.1). Anatomical differentiation begins at 50-60 days of age in 58 mm fish and is complete by 75 days and 69 mm. The appearance of oogonia in 130 mm fish 94-125 days old marks the start of histological differentiation. In males, spermatogenic waves form at 90-125 days of age and 135 mm in length. Spermatogonia develop in fish 150-300 days old and 130-185 mm in length. Size, rather than age, is more important to sexual differentiation, which may be delayed by stunting.

The tolerance of fry and fingerlings to various physicochemical characteristics of

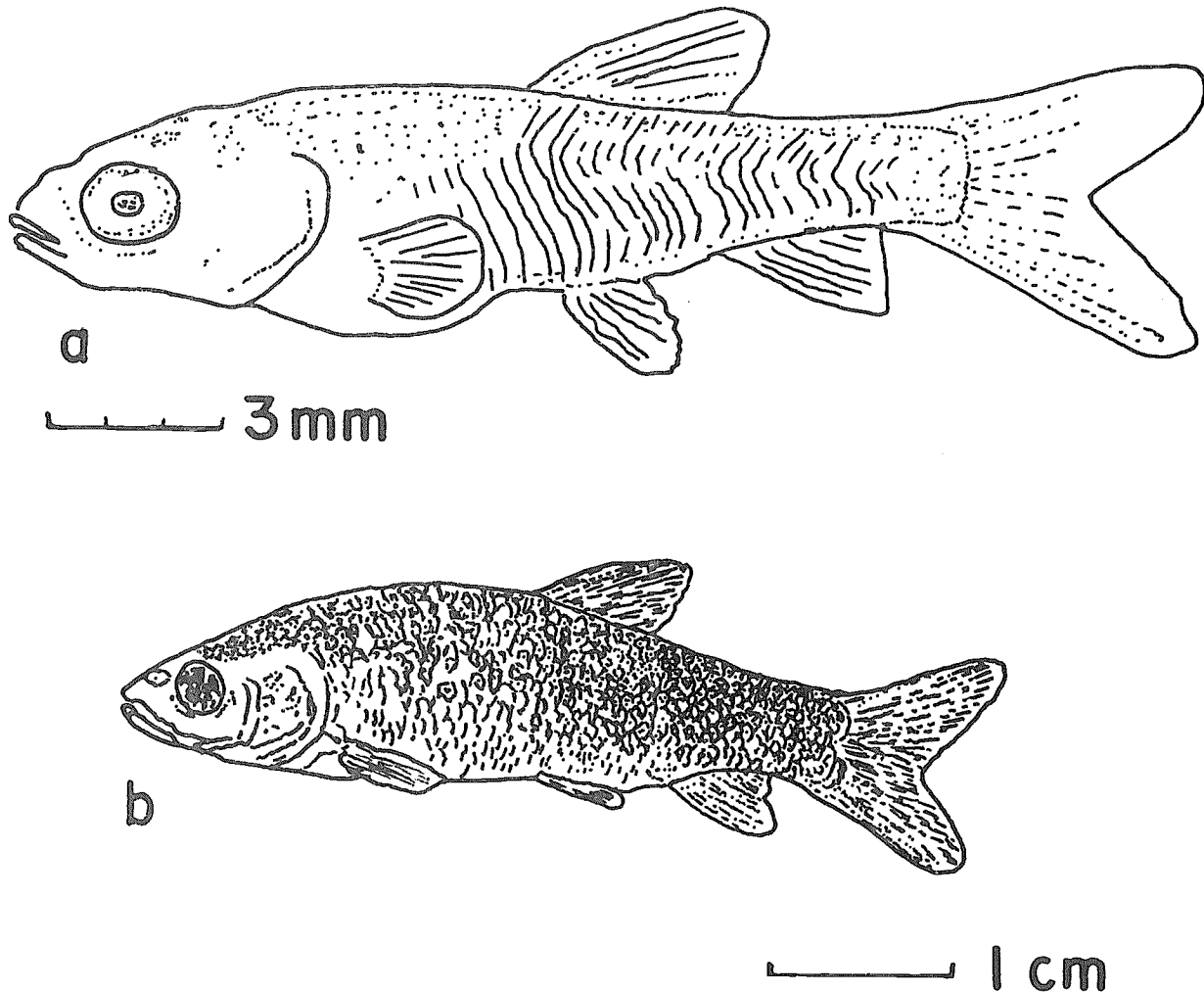


Figure 7 Fry (a, after Soin 1963 in Fischer and Lyakhnovich 1973) and fingerling (b, after Soin and Sukhanova 1972) stages of the grass carp

water is discussed in Section 2.3. Dorsal lordiosis (upward curvature) of the spine has been noted in 1-2 % of artificially spawned fry and probably would cause increased mortality (Shireman 1975). Survival from fry to 15-30 g fingerlings in Soviet fish culture averages 50-70 % (Anon. 1970c).

3.2.5 Juvenile stage

The juvenile stage is a period of feeding, growth, and dispersal which may last one to nine years, that is, until sexual maturity is reached (Section 3.1.2). Temperature and food conditions determine the duration. Juveniles migrate long distances upstream and downstream with home ranges assuming little or no importance (Stanley *et al.* 1978). In Soviet ponds, over-wintering losses of yearlings amount to 10-20 % (Anon. 1970c). After fingerlings are stocked in Chinese culture, mortality ranges from 40 to 50 % for first-year fish and from 20 to 30 % for second- or third-year fish (Dah-Shu 1957). Under natural conditions, mortality rates are presumably lower for juveniles than for younger stages and pro-

bably decrease as young grass carp grow larger.

3.3 Adult life history

3.3.1 Longevity

Based on examination of scale annuli, grass carp 13+ to 15+ years of age have been taken sporadically in the Amur River, USSR (Gorbach 1966, 1972). A 21+ year-old specimen was captured in 1958 (Gorbach 1961). Ages typically ranged from 5 to 11 years in Amur catches of grass carp (Berg 1949).

3.3.2 Greatest size

Chen (1933 cited by Lin 1935a) reported that grass carp could reach weights over 200-300 catties (120-180 kg). Dah-Shu (1957) states the species grows to 50 kg in the Yangtze River of China. Nikolsky (1954) writes that grass carp attain lengths over 1 m and weights to 32 kg. The largest Amur specimen examined by Berg (1949) was 110 cm in length and 15 kg in weight. Gorbach (1961, 1972) measured the following maximum lengths

and weights from samples involving hundreds of Amur grass carp captured by fishermen: 105 cm, 11.9 kg; 95 cm, 14.9 kg; and 96 cm, 16.4 kg.

3.3.3 Hardiness

That the grass carp is very tolerant of extreme environmental conditions is not surprising in view of its native distribution and behaviour. Long seasonal ice cover occurs in the northern part of its range while a subtropical climate prevails in the southern extreme. Spawning usually takes place in rivers of very high turbidity. Since its stillwater feeding grounds typically have extensive macrophyte beds, the grass carp must encounter wide circadian fluctuations in oxygen content and associated chemical parameters. Section 2.3 describes tolerance ranges for various physicochemical properties of water. The grass carp is sensitive to rotenone and other fish toxicants (Marking 1972, Henderson 1974, Colle *et al.* 1978a, Hardin 1980) (Sections 4.3 and 5.4.3).

Custer *et al.* (1978) investigated the effects of temperature changes on 5-7 cm fingerlings. They withstood an increase from 4-22°C in 2-3 hours with little problem. Stress appeared at 23-24°C if the transition from 4°C occurred in 6-8 hours. Dissolved oxygen levels below 3 mg/l caused stress, from 3 to 7 mg/l had little effect, and above 7 mg/l encouraged recovery during temperature changes. Successful acclimation from 4 to 7°C required at least 24 hours and a 12-hour stabilization period at 18-22°C helped greatly. After the recovery period, highly-stressed fish recuperated if the temperature was decreased to 2-4°C.

3.4 Feeding phases

The grass carp initially feeds on plankton but quickly changes to a diet entirely composed of macrophytes (Chang 1966). Little detailed information is available on food preferences under natural conditions. The observations reviewed below deal with cultured and introduced populations, usually under atypical conditions, but they probably reflect grass carp food habits in the native habitat.

Rozmanova (1966) investigated the early feeding phases of cage-reared fish. Mixed feeding began at two days when the protolarvae were 4.0-6.15 mm TL and 1.0-1.5 mg in weight. Guts contained a combination of yolk and green algae (e.g., *Scenedesmus quadricaudata*, *Ankistrodesmus acicularis*). At the start of exogenous feeding when the 4-day-old larvae measured 6.5-7.0 mm and 1.6-2.0 mg, the algal food items diversified to include *Pediastrum boryanum*, *Coelastrum acicularis*, *Cryptomonas marssonii*, and *Nitzschia spp.* in addition to the aforementioned species. Occasional zooplankton also appeared. By five days of age, zooplankton (e.g., *Keratella vulga*, *Moina rectirostris*) predominated. Tamas and Horvath (1976) found four 5-day-old, 6-8 mm larvae took zooplankton 50-150 μ in size, especially Rotatoria (*Brachionus*, etc.). Advanced larvae ate cladocerans such as *Moina rectirostris* and

Daphnia magna. Appelbaum and Uland (1979) determined appropriate particle sizes of the initial food items. Particles should be less than 200 μ during the first and second days of feeding, 150-200 μ for the third through fifth days, 250-400 μ on the sixth and seventh days, and up to 0.75-1.00 mm at the tenth through twelfth days when the larvae measure 12 mm. Food must be suspended in the water and included yeast, *Artemia salina nauplii*, commercial flakes, Rotatoria (mostly *Brachionus*) and Ciliata. In general, grass carp eat protozoa, rotifers and nauplii at 7-9 mm, include small cladocerans (*Moina*, *Daphnia*, *Chydorus*) and *Cyclops* at 10-12 mm, and concentrate on cladocerans, copepods, and small benthic animals at 13-17 mm (Dah-Shu 1957, Ling 1967, Bardach, Ryther, and McLarney 1972). Sobolev (1970) determined the zooplankton species preferred by 14-day-old, 12-17 mm larvae to be *Daphnia longispinna*, *Polyphemus pediculus*, *Scapholeberis mucronata*, and in some ponds *Bosmina longirostris*. Zooplankton, which were rarely eaten, included *Bosmina longirostris*, *Ceriodaphnia quadrangula*, *Chydorus sphaericus*, *Cyclops strenuus* and *Diaptomus*. Chironomid (tendipedid) larvae become important constituents in the diet of 17-18 mm and longer fry (Opuszyński 1972, 1979).

At about 2 cm the grass carp begins to feed on macrophytes but retains some potential to utilize animal food throughout life. Plant material comprises 5.4 % by weight of gut contents in 0.5 g fry with standard lengths of 19 mm and ages of 20 days, 50 % at 26-30 mm and 26 days, 79 % in 1.3 g fish at 37.5 mm and 30 days, 85 % at 35-40 mm and 36 days, and 100 % in 45-52 mm fish 36-46 days old (Sobolev 1970). Watkins *et al.* (unpubl. MS) reported that periphyton dominated the food habits of 36-86 mm fish comprising 56 % of the diet. Aquatic macrophytes became a regular constituent of the diet when fish reached 55 mm TL. Hydrilla and pond bank grasses (*Graminaceae*) were the major items after fish reached 87 mm TL, comprising 86 % of their total diet. Initially preferred vegetative food encompasses small tender varieties such as filamentous algae, the moss *Fontinalis*, Charales (*Chara*, *Nitella*), and the anthophytans *Lemna*, *Spirodella*, *Potamogeton*, *Elodea*, *Callitriche*, *Paspalum* and *Najas* (Lin 1935a; Opuszyński 1972, 1979; Edwards 1974, 1975; Sutton 1977b). Fischer (1968) also found 22-38 g fingerlings to choose soft plants such as *Lactuca sativa*, *Lemna minor* and *Glyceria fluitans* over others offered (*Juncus*, *Hottonia*, *Potamogeton*, *Carex* and *Typha*).

Fingerlings also eat animal food under certain conditions. In aquaria with vegetative food available, 10.5-14 cm, 18-40 g fingerlings preyed on ephemeropteran nymphs (*Deleatidium spp.*, etc.), plecopteran nymphs, oligochaetes, chironomid larvae, the gastropods *Potamophyrus antipodum* and *P. corolla*, trichopteran larvae (*Hydropsyche spp.*), amphipods, and neuropteran larvae (*Archichauliodes spp.*) (Edwards 1973). Invertebrate survival increased greatly with the

addition of stones which the foraging fish never disturbed. Grass carp measuring 12.5-15 cm and 33-53 g did not accept trout eggs, but did prey on hatchlings and fry. Singh, Dey, and Reddy (1976) observed that 7-13 cm fingerlings ingested common carp eggs while browsing on vegetation. The grass carp rejected the eggs but apparently damaged them and prevented further development. These same fish fed avidly on 5-7 mm common carp hatchlings. Larger 20-25 cm specimens refused hatchlings even in the absence of other food. Willey, Doskocil, and Lembi (1974) investigated the carnivorous potential of 15-cm fingerlings with vegetation available as alternative food. The grass carp accepted mayflies (*Ephemera* spp.), odonatan nymphs (*Anax* spp.), 13-mm minnows (*Notropis* spp.), and toad tadpoles only when all other food was depleted. In a 0.04-ha pond containing hydrilla, small grass carp (17-31 mm TL) consumed benthic invertebrates (primarily chironomid larvae) and continued to eat benthos up to 90 mm TL (Watkins *et al.* unpubl. MS). In a larger pond (0.8 ha) Colle, Shireman, and Rottman (1978b) found only trace amounts of invertebrates in 63-220 mm grass carp. Plant contents of the gut, in order of importance, were *Eleocharis* spp., *Sagittaria graminea*, *Potamogeton illinoensis* leaves, and *Najas flexilis*, filamentous algae. Kilgen and Smitherman (1973) determined that juveniles in small ponds resorted to insects when vegetation became unavailable. In another study, 190-g grass carp fed primarily on invertebrates, especially cladocerans, in small devegetated ponds (Forester and Avault 1978). In samples of large introduced grass carp (\bar{x} length 59-70 cm) taken from a 29-ha lake, food items consisted mostly of the vascular plants *Potamogeton*, *Elodea*, *Najas* and *Ceratophyllum*, with trace amounts of animal material such as cladocerans and dipterans and of the filamentous algae *Oedogonium* and *Spirogyra* (Mitzner 1978). In the Amur basin, adult grass carp fed to a small extent on animals, primarily epifauna (Nikolsky and Aliev 1974). Gaevskaya (1969) suggests that the insignificant aggregates of animals found in the gut represent mostly epiphytic organisms ingested along with plants. However, he points out that grass carp do feed on animals in sparsely-vegetated water bodies.

Most investigations of grass carp plant selectivity have been carried out with fingerlings and juveniles. Hundreds of species are documented in the literature (Table XVIII). Young fish prefer soft plants such as filamentous algae and duckweeds, until they reach a weight of about 1.4 kg when algae decrease in importance (Bailey 1972). Increased body size and higher water temperature broaden the species range of plant selection (Edwards 1973, 1974). Highly-preferred plants are succulent, with little fibre, and include genera such as *Hydrilla*, *Anacharis*, *Elodea*, and *Lagorasiphon*, while fibrous or woody reeds, sedges, and rushes have low selectability (Prowse 1971). Fish of 2+ age eat the young tender parts and

3+-to 4+-year-olds take whole plants of *Potamogeton lucens*, *P. natans*, *Typha angustifolia*, *Ranunculus fluitans*, and *Polygonum amphibium* (Krupauer 1971). Larger grass carp consume not only more species, but tougher ones, than do smaller specimens. The proportion of plant foods in the diet increases with age throughout juvenile life. In Polish culture ponds, percent composition by weight of gut contents was 75 % vegetative matter, 20 % zooplankton, and 5 % benthos in yearlings; 75 % plants and 25 % commercial pellets in 2+-year-olds; and 90 % plants and 10 % pellets in 3+-year-old fish (Sutton, Miley, and Stanley 1977, citing Opuszyński). Zolotova (1966) states that the different results on grass carp selectivity reported by various authors arise from different rearing and feeding conditions and from the high trophic plasticity of the species and that in fact little if any difference exists between food habits of the late juvenile and adult stages.

3.5 Nutrition and growth

3.5.1 Feeding behaviour, conditions and grounds

The only reports pertaining to grass carp feeding under natural conditions come from the temperature Amur basin of the USSR, where a marked seasonality in the feeding pattern exists. During periods of low water (spring and autumn), adults feed on the limited macrophytes available in the primary waterways. After spawning (during May), both adults and fry move into the richly-vegetated floodplains and feed intensively in still-water areas until the water level drops in August or September. In winter, adult fish overwinter in deeper strata of the main river channels without eating (Nikolsky 1963). Condition and fat content correspond both with food conditions and the amount of time the floodplain was available for intensive feeding during the previous year (Gorbach 1971, 1972).

Fry ignore inanimate food particles, unless they are suspended in the water column (Stevenson 1965, Appelbaum and Uland 1979) and generally eat zooplankton in the lower and middle water layers (Inaba, Nomura, and Nakamura 1957). Even though fingerlings eat benthic animals, they never disturb the bottom while foraging (Edwards 1973). Adults masticate plants into 1-3 mm pieces (Stroganov 1963, Hickling 1966). As grass carp grow larger, they take a wider variety of food plants (Edwards 1974, 1975) (Section 3.4) although young grass carp often have difficulty in tearing suitably sized pieces of vegetation from growing plants, thus lessening their effectiveness as herbivores (Alabaster and Stott, 1967). Chapman and Coffey (1971) found that consumption relative to body weight decreased in 10.2 kg compared to 3.3 kg fish. Authorities differ on preferred feeding time of day with daytime

Table XVIII

Representative food plants of fingerling and juvenile grass carp

Species	Ref. No. ^{a/}	Species	Ref. No. ^{a/}
<i>Alternanthera philoxeroides</i>	1	<i>Nasturtium officinale</i>	3
<i>Anacharis</i> spp.	10	<i>Nitella hookeri</i>	3
<i>Azolla</i> spp.	15	<i>Paspalum notatum</i>	10
<i>A. rubra</i>	3	<i>Phalarus arundinacea</i>	6
<i>Callitriche</i> spp.	13	<i>Phragmites communis</i>	6,7
<i>C. stagnalis</i>	3	<i>Pithophora</i> spp.	1,15
<i>Ceratophyllum demersum</i>	15	<i>Polygonum</i> spp.	10
<i>Chara</i> spp.	1,5,9,10,11,12,15	<i>P. amphibium</i>	6
<i>Eichhornia crassipes</i>	1,4	<i>Potamogeton</i> spp.	9
<i>Eleocharis</i> spp.	2,10	<i>P. crispus</i>	3,15
<i>E. acicularis</i>	1	<i>P. diversifolius</i>	1,5
<i>Elodea canadensis</i>	1	<i>P. foliosus</i>	15
<i>E. densa</i>	3,6,7,8,15	<i>P. illinoensis</i>	2,12
<i>Eremochlea ophiuroides</i>	5	<i>P. lucens</i>	6
<i>Fontinalis</i> spp.	7	<i>P. natans</i>	6
<i>Glyceria aquatica</i>	6	<i>P. pectinatus</i>	7,13
<i>G. maxima</i>	7	<i>P. pusillus</i>	15
<i>Hydrilla</i> spp.	9	<i>Ranunculus circinatus</i>	13
<i>H. verticillata</i>	12	<i>R. fluitans</i>	6
<i>Lagarosiphon major</i>	3	<i>Sagittaria graminea</i>	2
<i>Lemna</i> spp.	7	<i>S. sagittifolia</i>	7
<i>L. gibba</i>	11	<i>Schoenoplectus lacustris</i>	7
<i>L. minor</i>	3,4,11,15	<i>Sirogonium</i> spp.	15
<i>Lynghya</i> spp.	15	<i>Spirodella polyrhiza</i>	1
<i>Myriophyllum</i> spp.	15	<i>Trapa natans</i>	6
<i>M. brasiliense</i>	1	<i>Typha angustifolia</i>	6
<i>M. propinquum</i>	3	<i>T. latifolia</i>	6
<i>M. spicatum</i>	1,5,12	<i>Vallisneria</i> spp.	9
<i>Najas</i> spp.	10	<i>V. americana</i>	1,12
<i>N. flexis</i>	2,15	<i>Wolffia columbiana</i>	15
<i>N. guadalupensis</i>	1,11,12		

a/ Reference No. key below

Ref. No.	Authority	Experimental environment	Size/age specimens	Ref. No.	Authority	Experimental environment	Size/age specimens
1	Avault (1965)	small pools	30-40 cm	9	Prabhavathy and Sreenivasan (1977)	ponds	30 cm
2	Colle <i>et al.</i> (1978a)	small lakes	6.3-22 cm	10	Stevenson (1965)	ponds	0.9-1.3 kg
3	Edwards (1974, 1975)	small ponds	0+-1+	11	Sutton (1977a)	small pools	fingerling
4	Johnson and Laurence (1973)	ponds	160-190 g			370-1 tanks	3+, 1.1-3.5 kg
5	Kilgen and Smitherman (1971, 1973)	ponds	yearlings	12	Sutton and Blackburn (1973)	small pools	40-400 g
6	Krupauer (1971)	ponds	2+-4+	13	Sutton, Miley and Stanley (1977)	ponds	200-300 g
7	Opuszyński (1972, 1979)	ponds	250 g	14	Van Dyke (1973)	55-1 aquaria	225-589 g
8	Pentelow and Stott (1965)	ponds	19 cm, 140 g	15	Willey, Diskocil and Lembi (1974)	57-1 aquaria	15 cm
						64-1 barrels	15 cm

(Anon. 1970c), morning and evening (Stroganov 1963), afternoon and evening (Hickling 1962), and night (Woynarovich 1968) activity periods.

Weather and disturbance can influence grass carp feeding. They eat irregularly with breaks of five to seven days at water temperatures of 3-6°C (Stroganov 1963). Steady consumption starts at 10-16°C with optimal feeding rates at 21-26°C (Stroganov 1963, Woynarovich 1968, Anon. 1970c, Vietmeyer 1976, Colle *et al.* 1978b). As water temperature rises, selectivity of food plants decreases (Edwards 1974, 1975) (Section 3.4). Sudden temperature drops or windy weather may disrupt feeding (Stroganov 1963, Hickling 1966). Disturbance through fishing or transplantation can cause grass carp to cease eating for one or more days (Hickling 1962).

3.5.2 Consumption rate

Body size and food type are important determinants of consumption rate. When reared in tanks at 21-26°C, fingerlings from 6-15 cm in total length eat 6-10 % of their body weight per day of vegetation such as duckweed (*Lemna* spp.) (Shireman 1975; Shireman, Colle, and Rottman 1977, 1978a; Maceina and Shireman 1980). In addition, 6.3 cm, 2.8 g fish consume food at a significantly higher rate than 15 cm, 35 g specimens on diets such as duckweed (*Lemna minima*) or catfish pellets (Shireman, Colle and Rottman 1978a). Because food passes through the gut of 0.8-2.5 kg fish in less than eight hours at 27-30°C (Hickling 1966), intermediate-size fish to 1.2 kg may eat several times their body weight daily in vegetation, and larger individuals may consume a daily ration equal to their own weight, under optimal conditions (Vietmeyer 1976). Woynarovich (1968) reports that a 1 kg grass carp can eat 0.8-1.5 kg of vegetation per day. Relative consumption apparently decreases in large specimens.

Shireman and Maceina (1980) estimated that 6+ kg grass carp in a United States lake ate 26-28 % of their body weight per day in hydrilla (*Hydrilla verticillata*), a highly preferred food and dominant plant in the lake. Chapman and Coffey (1971) found daily consumption rate to drop from 63 % of body weight in 313 kg fish to 32 % in those weighing 10.2 kg.

Food type, including the proportion of animal food, affects grass carp consumption rates. Fischer (1973) determined that 0.5- to 3-year-old, 20-450 g specimens at 22°C achieved the highest consumption and growth rates in kcal/individual with a diet of 75 % tubificid worms and 25 % lettuce (*Lactuca sativa*). Shireman, Colle and Rottman (1978a) found 6.3 cm, 27 g and 15 cm, 35 g fingerlings at 25.4°C to have lowest consumption rates when fed catfish chow followed by duckweed (*Lemna minima*), catfish chow-ryegrass, and ryegrass (*Lolium terenne*). Best growth occurred with duckweed diet. In India, Mehta, Sharma and Tuank (1976) observed daily relative consumption rates ranging up to 168 %, depending on fish size and plant species offered (Table XIX). Verigin, Viet and Dong (1963) reported that 170-260 g grass carp kept in cages at 30-34°C, ate daily the following amounts of preferred plants as a percentage of their body weight: *Potamogeton pectinatus* (135 %), *Hydrocharis morusranae* (145 %), *Ceratophyllum demersum* (114 %), *Elodea canadensis* (109 %), and *Lemna triscula* (102 %).

Chapman and Coffey (1971) observed a reduction in consumption by 8.3 kg fish during winter. Edwards (1974) found grass carp to eat very little at 8-9°C, but to consume up to their body weight in vegetation per day at 20-23°C. Relative gut content weights of fingerlings in a United States pond fell from 9.42 % at 23°C to 1.42-4.01 % at 18-22°C and ranged from 0.19-1.23 % at 10.5-14°C (Colle, *et al.* 1978b). In concrete-tank experiments, the amount of hydrilla consumed by fish with average initial weight of 176 g had an

Table XIX

Daily consumption as a percentage of body weight by different size grass carp of various plant species (Mehta, Sharma and Tuank, 1976)

PLANT SPECIES	WEIGHT OF FISH (g)	DAILY CONSUMPTION AS A PERCENTAGE OF BODY WT.
<i>Chara</i> spp.	165	168
	96	146
	930	131
<i>Najas foveolata</i>	1837	99
	76	27
	1208	140
<i>Potamogeton perfoliatus</i>	205	15
	2800	18
<i>Typha angustata</i>	200	3
	4000	14

estimated correlation with water temperature of 0.7916 ($P < 0.01$) (Sutton and Blackburn 1973, Sutton 1974). The regression equation relating consumption to water temperature explained 62 % of the variation in the amount of hydrilla eaten. Maceina and Shireman (1980) demonstrated the 9-13 cm fingerlings reduced their feeding on duckweed (*Lemna minor*) as salinity increased. Consumption rate ranged from 5.8-6.4 % of body weight at 3-6 ‰ salinity, declined significantly to 1.3-9 ‰, and was nil at 12 ‰. Fingerling consumption of duckweed was also significantly correlated ($r = 0.775$, $P < 0.01$) with oxygen level (Shireman 1975, Shireman, Colle, and Rottman 1977). Feeding decreased approximately 45 % when oxygen content fell below 4 mg/l. Von Zon (1977, citing van Sarkenburg and van der Zweerde 1976) reported that sudden changes in water depth or disturbances by strong draughts affected feeding rate for only a few days after which time the fish quickly adapted themselves to the new conditions. Salinity effects were much more persistent, decreasing food intake by one-third at levels of 500-2 000 mg Cl⁻/l, all far below lethal concentration. Tooby *et al.* (1980) showed that the food intake of the fish decreased in the presence of sublethal concentrations of many herbicides, and feeding was inhibited in concentrations 4-5 times lower than the 96h LC₅₀ value.

3.5.3 Growth rates and patterns

Compared to fish of similar size, the grass carp, under optimal conditions, exhibits an intrinsic growth rate perhaps greater than any other species. Vietmeyer (1976) reports that it regularly grows to 1 kg in the first year and at 2-3 kg per year thereafter in temperate latitudes or up to 4.5 kg per year in the tropics. He quotes L.C. Lui as documenting growth in Malaysia from 20 g fingerling to 2-2.5 kg in six months and to 8-8.5 kg in one year with weight increases averaging 1 kg per month. Rates of 10-22 g per day during the growing season appear frequently in the literature (Hickling 1960, 1967b; Alinkunhi and Sukumaran 1964; Crowder and Snow 1969; Sinha 1973; Mitzner 1975c; Shireman 1975; Sinha and Gupta 1975; Mehta, Sharma and Tuank

1976; Miley, Van Dyke and Riley 1976; Shireman, Colle and Maceina 1980; Shireman and Maceina 1980). Gorbach (1961) provides the only data on growth rates in a naturally-occurring population (Table XX). Grass carp in the Amur basin grow slowly, with annual increments of 9-10 cm in the first four or five years, 6-7 cm during the sixth and seventh years, and 2.5 cm after the eighth year. Growth in weight increases with age, especially in the fifth to seventh years, and decreases in older fish only during adverse years. Data from one year's commercial catch indicated average weight increments of 480, 674, 680, 1 250, 2 700, 1 012 and 1 180 g in the fourth through tenth years of age, respectively. No differences in male and female growth rates were apparent.

Growth of grass carp can be highly variable due to different culture conditions. Under intensive cage culture with high densities, 30-55 mg fry attain 1 180-1 652 mg in seven weeks (Table XXI), with a relative gain over initial weight of 60-100 % (Huisman 1978). They reach 10 g in eight weeks more, 60 g in another six weeks, and 25-300 g in the last ten weeks or so after which time they are stocked in ponds. In United States ponds, 46-day-old fingerlings averaging 77 g grew to a mean weight of 286 g in 78 days (Table XXII) (Alabama Department of Conservation 1966). Under Indian culture conditions, grass carp attained average weights of 5, 750, and 4 500 g at 30, 362 and 645 days of age, respectively (Table XXIII) (Mehta, Sharma, and Tuank 1976). Six-month-old fingerlings stocked into Arkansas, United States, ponds at a mean weight of 4 g, grew to 372 g in six months and to 1 816 g in one year (Table XXIV) (Stevenson 1965). Mean daily weight increments ranged from 1.9-9.9 g in the ponds. Ninety-gram grass carp placed in a Florida lake had average weights of 3.8, 7.5, 11.2 and 15.0 kg after one to four years, respectively (Table XXV) (Shireman, Colle, and Maceina 1980). Growth rates ranged 10.1-10.4 g per day. In another Florida lake, 0.79-kg specimens attained mean weights of 5.24 kg and 9.17 kg in their first and second years after stocking, respectively (Table XXV) (Shireman and Maceina 1980). Daily growth rates in this lake ranged from 10.4-12.3 g.

Table XX

Grass carp growth (cm) in the Amur Basin, USSR (Gorbach 1961)

LOCALITY	AGE: 1+	2+	3+	4+	5+	6+	7+	8+	9+	10+
Amur R. at Leninskoe (1958)	9.8	20.0	29.6	38.2	45.2	50.3	57.1	64.5	67.5	-
Amur R. at Leninskoe (1959)	9.9	20.9	30.7	40.0	47.9	54.4	60.6	65.8	70.0	74.4
Lower Ussuri R. (1957)	10.1	19.2	27.9	34.6	43.0	51.4	58.1	67.2	69.5	76.6
Lake Bolon' and canals (1957)	9.5	17.3	25.6	34.7	42.9	49.8	56.3	63.0	66.5	71.0
Lake Bolon' and canals (1958)	9.5	18.3	27.5	37.9	46.1	52.6	57.3	66.8	69.3	73.5

Table XXI

Intensive rearing of grass carp fry in cages at high density and 23-25°C with zooplankton and trout starter as feed (Huisman 1978)

DAYS IN CULTURE	\bar{x} weight (mg)
7-14	30-55
14-21	65-137
21-28	127-270
29-35	234-484
35-42	425-764
42-49	722-1 168
49-56	1 180-1 652

Table XXII

Growth of fingerlings stocked in Alabama ponds, USA, and given supplementary pelleted food (Alabama Department of Conservation (1966)

AGE IN DAYS	\bar{x} weight (g)	\bar{x} length (mm)
46	77	167
60	115	166
73	166	230
89	263	259
102	271	280
124	286	284

Table XXIII

Growth of grass carp in Indian culture (Mehta, Sharma and Tuank, 1976)

AGE IN DAYS	\bar{x} weight (g)
30	5
46	20
156	55
226	130
261	165
274	205
293	256
310	422
362	750
380	828
402	930
419	1 250
447	2 083
493	2 500
536	2 800
645	4 500

Table XXIV

Grass carp growth in Arkansas ponds, USA (Stevenson 1965)

Age (month)	6	9	12	15	18
\bar{x} Weight (g)	4	21	372	1 271	1 816
\bar{x} Length (cm)	8	12	28	45	50
\bar{x} Growth (g/d)	0.02	1.9	3.9	9.9	6.0

Table XXV

Grass carp growth in two Florida lakes, USA (Shireman, Colle and Maceina 1980; Shireman and Maceina 1980)

Lake Wales, Florida: Years after Stocking	\bar{x} Weight (kg)	\bar{x} Total Length (mm)	\bar{x} Growth (g/d)
0	0.09	200	-
0.5	-	-	-
1	3.8	661	10.2
1.5	-	-	-
2	7.5	812	10.1
3	11.2	900	10.1
4	15.0	962	10.4

Lake Baldwin, Florida: Years after Stocking	\bar{x} Weight (kg)	\bar{x} Total Length (mm)	\bar{x} Growth (g/d)
0	0.79	408	-
0.5	3.00	592	12.1
1	5.24	720	12.3
1.5	7.27	807	11.1
2	9.17	876	10.4

In Indian pond culture, Prabhavathy and Sreenivasan (1977) observed monthly-length increments to increase to a maximum of 50-55 mm at 10-12 months of age and then to decline to 10 mm in four-year-old grass carp (Table XXVI). Monthly growth rates by weight increased steadily from 20 g at three months and levelled to 175-200 g at two to four years of age. Gasaway (1978) discovered that 20 cm specimens stocked into a southern United States lake had linear growth to 13-14 kg over 31 months. The equation, $y = -875.3 + 452.4x$, related weight in grams (y) with the time in months (x). Hickling (1967b) observed that female grass carp grew considerably faster than males in Malaysia culture (Table XXVII). Table XXVIII summarizes growth data from the literature.

The length [(L) in mm] to weight [(W) in g] relationship for grass carp usually does not differ significantly from the standard cubic

growth equation. Chow (1958) determined the weight-length relationship of grass carp 27-66 cm TL from Hong Kong culture ponds to be:

$$W = -0.566 \times 10^{-5} L^{3.108}$$

(or converted to a logarithmic regression, $\log_{10}W = -5.247 + 3.108 \log_{10}L$).

Condition coefficients (K) ranged from 1.09-1.13. Shireman (1975) found the weight-length relationship of specimens 29-252 mm TL to be closely described by the equation,

$$\log_{10}W = -4.916 + 3.002 \log_{10}L,$$

with a correlation coefficient, $r = 0.99$.

For fish stocked in a United States lake for two years, Shireman and Maceina (1980) determined the weight-length relationship of individuals 450-700 mm TL to be,

$$\log_{10}W = -4.821 + 3.005 \log_{10}L$$

and for 700-1 111 mm TL specimens to be

$$\log_{10}W = -5.239 + 3.127 \log_{10}L.$$

For grass carp over 650 mm, they found significant differences in the weight-length

relationships of males,
 $(\log_{10}W = -4.367 + 2.823 \log_{10}L)$
 and females,
 $(\log_{10}W = -5.157 + 3.101 \log_{10}L)$.
 Females were heavier than males of the same
 length and had significantly higher condition
 coefficients (K) than males
 $(\bar{x} K = 1.392 \text{ vs. } 1.311)$
 Mitzner (1975c) calculated a weight-length

relationship of
 $\log_{10}W = -3.484 + 2.477 \log_{10}L$
 for 60-75 cm (TL) fish stocked in a northern
 United States lake. The low exponent indi-
 cated the larger grass carp were atypically
 light for their size, which was undoubtedly
 due to the measurements being taken during the
 winter. Condition factor (K) was 1.16 in
 January and February compared to 1.22 in July,
 August, and September.

Table XXVI

Growth rates of grass carp at different ages in Tamilnadu, India
 (Prabhavathy and Sreenivasan 1977)

Age	Monthly Increase	
	Length (mm)	Weight (g)
30 days	60	-
60 days	30	-
90 days	20	20
120 days	20	25
150 days	45	35
180 days	45	65
210 days	45	75
240 days	35	80
270 days	45	85
300 days	55	90
330 days	50	100
380 days	50	100
2 years	20	200
3 years	20	200
4 years	10	175

Table XXVII

Growth of male and female grass carp in Malaysian ponds at 28° to 32°C (Hickling 1960)

Number per ha	Initial \bar{x} weight (kg)		Final \bar{x} weight		Days in culture	Growth (g/day)	
	Male	Female	Male	Female		Male	Female
140	0.002	0.002	4.5	5.9	515	8.6	11.4
150	3.8	4.0	4.4	6.1	348	4.3	7.3
150	2.7	2.5	4.8	6.1	306	6.6	11.7
Tagged specimens:							
	Initial weight (kg)		Days in culture			\bar{x} = weight gain (kg)	\bar{x} = growth (g/day)
Male (n = 6)	2.1-4.2		1 699			12.7	7.5
Female (n = 6)	2.0-4.0		1 455			13.2	9.1

Table XXVIII
Growth of grass carp in different countries under varying conditions

Country and Culture Conditions	Size	Age or Time Period	Authority
China, High Density Polyculture	30-100 g	1 y	Dah-Shu (1957)
	280-300 g	2 y	
	1.8-2.4 kg	3 y	
China, Pond Culture	25.5 cm, 0.68 kg	1 y	Gidumal (1958)
	1.8-2.3 kg	2 y	
	4.5 kg	4 y	
Fiji, Pond Culture	6.5 g	- *	Adams and Titeko (1970)
	1341 g	243 d	
	2174	365 d	
	3069	486 d	
India (Cuttack) Pond Culture	17.2-20.5 cm	4.5 months	Alikunhi and Sukumaran (1964)
	280 g	9.5 "	
	60 cm, 2.7 kg	19 "	
India (Cuttack) Polyculture	16-37 g	- *	Chaudhuri <i>et al.</i> (1975)
	1.3-2.6 kg	1 y	
India (Kalyani) Pond Culture	31 g	- *	Sinha (1973)
India (Kalyani) Intensive Polyculture	2.53 kg	6 months	Sinha and Gupta (1975)
	45 g	- *	
	1.59 kg	4 Months	
	45 g	- *	
	2.03 kg	5 months	
	82 g	- *	
	5.04 kg	1 y	
India (Karnal) Pond Culture	2.00-2.13 kg	1 y	Prabhavathy and Sreenivasan (1977)
India (Tamilnadu) Pond Culture	50-55 cm, 1.5 kg	1 y	
	66.5-70 cm, 4.0 kg	2 y	
	85-88 cm, 7.0 kg	3 y	
	90 cm, 8.0 kg	4 y	
India (Uttar Pradesh) Pond Culture	1.67-1.95 kg	6 months	Sinha and Gupta (1975)
Israel, Pond Culture	113 g	- *	Yashouv (1958)
	2.86 kg	180 d	
Malaysia (Malacca) Pond Culture	3.3 kg	267 d	Hickling (1960)
	4.24 kg	413 d	

(to be continued)

Table XXVIII continued

Country and Culture Conditions	Size	Age or Time Period	Authority
South Africa, Pond Culture	0.96 kg 3.1 kg 6.4 kg 9.8 kg	1 y 2 y 3 y 4 y	Pike (1977)
USA - (Alabama) Culture Ponds	13-14 cm, 33-46 g 0.8 kg 5.3 kg	80-90 d - * 2.4 y	Alabama Department of Conservation (1967)
USA - (Alabama) Polyculture	6.0 g 1.35 kg	- * 6 months	Crowder and Snow (1969)
USA - (Florida) Vegetated Ponds	40.5 g 531.5 g 55 g 195 g 304 g 740 g 410 g 593 g	- * 112 d - * 112 d - * 56 d - * 56 d	Sutton and Blackburn (1973), Sutton (1974)
USA - (Florida) Vegetated Ponds	48 mm 186 mm	- * 5.5 months	Colle, Shireman, and Rottman (1978b)
USA - (Iowa) Vegetated Lake	1.82 kg, 47.2 cm 4.26 kg, 70.2 cm	- * 5 months	Mitzner (1975c)
USSR - Vegetated Lake	20.0 cm, 148 g 38.5 cm, 975 g	- * 122 d	Aliev (1963)
USSR - Sown Rice Fields	29 g 460 g	- * 80 d	Bizyaev and Chesnokova (1966)
USSR - Fallow Rice Fields	250 g	80 d	
USSR - Drainage Ditch	230 g	80 d	

* Age not reported but initializes time period for values following.

3.5.4 Relation of growth of consumption, food type, and environment

The grass carp has a notable low conversion rate of food into fish biomass. It is apparently unable to digest cellulose, so every plant cell wall must be broken mechanically by mastication before the cell contents can be assimilated (Hickling 1965). The gut is usually packed tightly with vegetation and only the outside layer may be exposed to the intestinal wall for absorption (Gaevskaya 1969). Estimates of digestion of plant material by adults range from 50-70 % (Stroganov 1963, Hickling 1966, Vietmeyer 1976). Food coefficients reported in the literature include 14-54 (\bar{x} = 18) in a Soviet pond (Stroganov 1963), 30 for Soviet fish culture in general (Anon. 1970c), 48 for napier grass (*Pennisetum purpureum*) consumed in Malaysian pond culture (Hickling 1960), about 30 for fish kept in cages at 30-34°C (Verigin, Viet, and Dong 1963), and 16-79 for grass carp fed duckweed (*Lemna spp.*) (Sutton and Blackburn 1973, Sutton 1977b). Conversion rates can be high in young fish and decrease with size, as Huisman (1978) reports for specimens reared on trout starter pellets at 20-30°C. Food coefficients were 1.1-1.4 for 0.2-10.0 g, 1.3-1.5 for 10-60 g, and 1.5-2.4 for 60-300 g fish.

Diet affects the growth rate in a variety of ways. Young fish seem to grow best when given supplemental animal food in some form. In Soviet pond culture, the optimal diet for 7-10 cm fingerlings contains approximately 30 % animal food (Anon. 1970c). Fischer (1970, 1972a, 1972b, 1973) investigated the growth parameters of grass carp fed variable combinations of lettuce (*Lactuca sativa*) and tubificid worms. The best diet for 20-450 g specimens at 22°C included 75.76 ± 0.27 % animal food. Assimilation efficiency was 40 cal% for animal food and 20 cal% for lettuce. Conversion rates with lettuce were poor. The cal% values of consumption used for growth were 0.5, 2.2, and 3.0, and those of assimilation were 8.4, 16, and 18 for hypothetical fish weights of 1, 50 and 100 g, respectively. Conversion values for protein were 27.94 cal%, for lipids 12.20 cal%, and for carbohydrate 59.86 cal%. The cal% values of consumption and assimilation devoted to growth were 12.5 and 40.4, with the tubificid diet and 2.2 and 14.5 with lettuce, respectively. Fish on the plant diet used lipids (23.8 cal% of consumption and 39.2 cal% of assimilation) rather than protein (6.5 cal% of consumption and 15.9 cal% of assimilation) for growth. Those on animal food used protein more than lipid, with 15.2 cal% of protein consumption and 60.1 cal% of assimilation devoted to growth. The functions relating growth (G in cal per day) to weight (W in g) were $G = 11.51 W^{0.46}$ for the plant diet and $G = 1.92 W^{1.18}$ for animal food. A certain proportion of plant material in the diet apparently plays an important role in facili-

tating ingestion and digestion of food, and in supplying vitamins and carbohydrates necessary for respiration and proper growth.

I-kuei, Chin-hsia, and Hsi-t'ao (1966, 1973) also investigated the effects of plant and animal diets on grass carp. For 3.0- to 3.3-cm fish at 29°C, conversion coefficients were 6.49, 11.3, and 14.1, and daily percent weight increases were 11.5-14.3, 7.3-8.2, and 4.9 for diets of the cladoceran *Moina sp.*; duckweed (*Wolffia arrhiza*), and soybean cake, respectively. With chironomid larvae (*Chryomyia megacephala*) as food, conversion coefficients and daily percent weight increases, respectively, were 11.8 and 0.78 for 10- to 12-cm fish at 20°C, 7.54 and 19.7 for 7- to 10-cm fish at 22°C, and 6.03 and 4.17 for 10- to 12-cm fish at 29°C. The respective values for duckweed (*Spirodella polyrrhiza*) under the same experimental conditions amounted to 40.63 and 0.19, 25.48 and 1.29, and 15.63 and 2.2. For 10- to 12-cm fish at 29°C, water hyacinth (*Eichhornia crassipes*) yielded a food coefficient of 44.93 and daily weight increase of 0.62 %, while soybean cake permitted a daily weight increase of 1.91 %. A diet with 30 % animal food, given simultaneously or in rotation with the plant material, provided similar results to those obtained with 100 % animal matter.

Appelbaum and Uland (1979) observed significantly better larval growth by using Alkan yeast supplemented with vitamins and protein, as compared to other diets. In their first 7 days of feeding, larvae attained 10.3 ± 0.20 mm TL with yeast, 9.2 ± 0.14 mm with *Artemia salina* nauplii, and 8.8 ± 0.11 mm with commercial flake food. Dabrowski (1979) determined that the theoretically-best protein content of a diet for optimal growth in 0.14-0.21 g fry, should be 52.6 ± 1.93 %, which would produce a relative weight increase of 200.3 ± 4.0 % in 40 days. The protein efficiency ratio (PER) and net protein utilization (NPU) decreased with increasing protein content (x) according to the functions, $y = 1.66 - 0.18x$ and $y = 40.8 - 0.327x + 302.6/x$, respectively. Sharma and Kulshrestha (1974) found yeast with vitamin B-complex superior to ground nut oil cake, rice bran hydrilla (*Hydrilla verticillata*), or pondweed (*Potamogeton perfoliatus*) diets for rearing fry and fingerling grass carp. Dabrowski and Kozak (1979) found the best diet for optimum growth of 0.4 g fry to contain 40 % fish meal, which yielded a relative weight increase of 209 % in 70 days. The PER was 1.26 % and NPU was 20.3 %. The equation, $y = 14.75 + 0.49 x$ (y = total yield in g of aquarium, x = time in days), described the linear growth obtained during the experiment. Meske and Pfeffer (1978) tested the effects of different combinations of green algae (*Scenedesmus obliquus*), trout feed and whey powder soybean diets on the growth and food conversion of fry and fingerling grass carp. A mixture of 80 % algae and 20 % whey powder soybean yielded the highest growth rate (0.78 g/day) and lowest conversion coefficient (1.34) of any diet over a four-month period. Higher

algal concentrations and the pure trout feed diet caused malformation, especially dorsal lordiosis.

Because of its high-protein content and softness, duckweed (*Lemna sp.*) proves to be a highly-nutritious vegetative food for grass carp. In one study, 225-589 g fish assimilated an average of 65-67 % of the duckweed consumed, including 80 % of the crude protein and 61 % of the available energy (Van Dyke 1973, Van Dyke and Sutton 1977). Growth rates ranged from -6.74-4.93 g/d. The functions relating weight increase in g (y) to duckweed consumption in g wet weight (x) were $y = -45.27 + 0.0704x$ ($r = 81.42$) for all fish and $y = -22.13 + 0.0501x$ ($r = 0.7620$) for growing individuals only. Maintenance nutrition for each g of fish biomass was calculated as 2.45×10^{-3} g of crude protein and 27.4 cal/day. A 1-g weight increase required 0.285 g of crude protein and 3194 cal. The conversion coefficient amounted to 42.5 based on wet weight or 2.46 dry weight of duckweed. Michewicz *et al.* (1972a) observed that grass carp averaging 364 g grew from 1.3-5.7 g/d in outdoor concrete tanks and that 224 g specimens at higher density in indoor aquaria grew from 0.8-2.7 g/d. Conversion coefficients based on weight of fresh duckweed ranged from 12.1-49.6 in the tanks and from 21.2-80.6 in the aquaria. Duckweed consumed in decagrams fresh weight (y) was related to weight increase in g (x) by the equation $y = 222.26 + 6.79x$ ($r = 0.5518$) in the tanks and by $y = 870.37 + 26.45x$ ($r = 0.6657$) in the aquaria. Water quality changes, temperature fluctuation, variable nutrient composition of duckweed, and stress induced by crowding could have caused the low correlations of growth with consumption.

Grass carp growth was significantly higher with duckweed than with southern naiad (*Najas guadalupensis*) or chara (*Chara spp.*) (Table XXIX) (Sutton 1977b).

Proximate analysis revealed that duckweed had 22.8 % crude protein compared to 9.2-13.1 % in the other two plants. Fingerlings 35 g in weight grew from 0.8-2.1, with a mean rate of 1.1 g/d and converted 22 g wet or 1.5 g dry weight of duckweed into 1 g of biomass. Smaller 16-g fingerlings converted 2.86 g dry weight of duckweed into 1-g fish and consumed 50-100 % of their body weight per day for a wet weight food coefficient of 38.8-43.6 and growth rate from 0.32-0.46 g/d. For three-year-old, 1.1-3.3 kg ($\bar{x} = 1.6$ kg) grass carp, the equation relating weight in g/d of fresh duckweed consumed (x) to growth in g/d (y) was $y = -1.3864 + 0.0201x$ ($r = 0.9167$, $p < 0.01$) which explained 84 % of the variation in growth. The wet weight conversion coefficient was 68.9 and maintenance ratio for these fish averaged 69 g/d. The highest growth rates of 20 to 22 g/d occurred from April through June when consumption was about 50 % of body weight per day. Kept in cages, 320-g fish grew 3-5 g/d with a conversion coefficient of 57-79 when fed to excess, while underfed fish grew 1.8 g/d but converted more efficiently, as indicated by a coefficient of 16.

Shireman, Colle, and Rottman (1978a) investigated the effects of duckweed, catfish chow, catfish chow-ryegrass pellet, and ryegrass (*Lolium terenne*) pellet diets on grass carp growth. For the first 10 days, the 15 cm, 35-g fish had similar growth on all diets except ryegrass which caused weight loss during the first 10 days and slow growth thereafter. From day 10 to day 68, fingerlings fed duckweed grew significantly faster at 1.15 g/d than those on all other diets. Another group of fish given catfish cage-culture pellets from day 18 to day 48, grew as fast as those receiving duckweed. After 28 days, 6.3-cm, 2.8-g fingerlings also exhibited higher growth rates to one another until day 58 when growth of those fed ryegrass fell behind. The small fish given duckweed in tanks grew 0.54 g/d while

Table XXIX

Fingerling growth on three different food plants (Sutton 1977b)

Days in Culture:	0	28	56
Duckweed (<i>Lemna gibba</i> , <i>L. minor</i>)			
\bar{x} Weight (g)	3.2	16.1	15.7
\bar{x} Growth (g/d)	-	0.5	0.6
Southern naiad (<i>Najas guadalupensis</i>)			
\bar{x} Weight (g)	3.2	7.9	12.1
\bar{x} Growth (g/d)	-	0.2	0.2
Chara (<i>Chara spp.</i>)			
\bar{x} Weight (g)	3.2	8.4	18.9
\bar{x} Growth (g/d)	-	0.2	0.4

pond-cultured fish of similar size gained 0.45 g/d. The conversion coefficient based on dry weight of duckweed was 2.7 for large and 1.6 for small fish. Percentage of crude protein was highest in cage-culture pellets (36 %) followed by catfish chow (32 %), duckweed (31 %), catfish chow-ryegrass pellets (22 %), and ryegrass pellets (12 %). Except in the case of ryegrass diets, the results suggested that the presence or absence of essential nutrients determined growth rates. Tal and Ziv (1978a, 1978b) reported growth rates of 380-g fish to be 1.9 g/d with pelleted food and 6.1 g/d with duckweed. Fingerlings given duckweed grew 3.4 g/d with a conversion coefficient of 37 in the second year.

Other food plants investigated, with regard to grass carp include hydrilla (*Hydrilla verticillata*), water hyacinth (*Eichhornia crassipes*), napier grass (*Pennisetum purpureum*), a hybrid grass (*P. purpureum* x *typhoideum*), egeria (*Egeria densa*), southern naiad (*Najas guadalupensis*), coontail (*Ceratophyllum demersum*), chara (*Chara* spp.), and tapioca leaves (*Manihot utilissimus*). Growth (y) in g of grass carp averaging 176 g was related to hydrilla consumption (x) in g x 10³ by $y = 8.8447 + 0.0137x$ (Sutton and Blackburn 1973, Sutton 1974). This regression had a correlation coefficient of $r = 0.6264$ significant at $P < 0.01$ but explained only 39.2 % of the variation in growth. Dry weight conversion coefficients were 4.61, 6.14, and 2.41 for November, December, and April, respectively, and indicated that utilization efficiency of hydrilla by grass carp varied during the year and might account for the unexplained variation in growth. Tan (1970) found that grass carp grew considerably faster when fed hydrilla rather than napier grass or tapioca leaves (Table XXX). Hydrilla's superiority apparently was due to its relative softness and to the minerals present, as indicated by a high ash content. Blackburn and Sutton (1971) determined that both hydrilla and southern naiad permitted higher growth

rates than commercial feed. Fingerlings fed hybrid napier grass grew three times faster than those fed hydrilla and five times faster than those given coontail (Venkatesh and Shetty 1978). Food conversion values were 27.0, 94.0 and 128.4, respectively. Grass carp of 1 kg or more eat whole plants of water hyacinth, but small individuals can only utilize the roots. Growth rates of 1.0-1.2 kg fish range from 1.4-8.8 g/d and for 0.1 kg specimens vary from 4.7-1.7 g/d (Blackburn and Sutton 1971, Sutton and Blackburn 1973, Baker, Sutton, and Blackburn 1974).

Stanley (1974a, 1974b) investigated the utilization of egeria by grass carp. A 1-kg fish consumed daily an average of 24 g dry or 265 g wet weight of egeria, assimilated 50 % of it, and converted 33 % to biomass. Of 96 kcal ingested, 58 % was assimilated, 8 % (8 kcal) was used in respiration, and 50 % (48 kcal) was devoted to growth. Fish lost more nitrogen than they took in but retained more than 50 % of the phosphorus. They assimilated 57 % of carbohydrate consumed, metabolized 6 %, and presumably deposited the rest as fat.

The environmental factors which influence grass carp growth include temperature, density, oxygen level, and salinity. Low temperatures reduce growth rate indirectly by decreasing consumption (Section 3.5.2) and directly by slowing the metabolic processes leading to synthesis of new biomass. In New Zealand, 6-g fingerlings increased little in size from April to October, when water temperature was below 14°C, but they grew to 0.2-0.5 kg from October to February, and increased at rates up to 4 g/d (Edwards 1974). Colle, Shireman, and Rottman (1978b) recorded growth of 48- to 186-mm fingerlings in a United States pond to be 0.59 g/d and 1.29 mm/d before November and to drop to 0.17 g/d and 0.17 mm/d from November through February, a period when the temperature was below 14°C. Chapman and Coffey (1971) documented growth rates of 8.1 and 26 g/d for 3.3- and 10.2-kg fish, respectively,

Table XXX

Growth of three-month-old grass carp on three food plants over six months (Tan 1970)

		Hydrilla <i>Hydrilla verticillata</i>	Napier Grass <i>Pennisetum purpureum</i>	Tapioca Leaves <i>Manihot utilissimus</i>
Initial size	Length (cm)	28.8	27.2	25.0
	Weight (g)	336.6	290.6	311.3
Final size	Length (cm)	49.4	46.4	37.7
	Weight (g)	2 000	1 562.3	708.9
Absolute increase	Length (cm)	20.6	19.2	12.7
	Weight (g)	1 663.4	1 271.7	397.6
Percentage increase	Length (cm)	71.52	70.58	50.80
	Weight (g)	494.1	437.6	127.7

during the New Zealand summer, and a rate of 4.8 g/d for 8.3-kg individuals during the winter. Sutton (1974) found the growth rates of small fish to be more sensitive to changes in temperature than those of large ones. A water temperature increase from 23-29°C correlated with increased growth in 0.1-kg fish but not in 1-kg specimens.

Density and oxygen levels are often interrelated since the grass carp not only decreases oxygen by direct use for respiration but also indirectly by encouraging eutrophication through large releases of nutrients as fecal wastes. Feeding stops at an oxygen level of 2.5 ppm (Stanley 1975). With 61-mm, 2.7-g fingerlings fed duckweed (*Lemna minima*) under intensive culture conditions, stocking density had no effect on growth rates until oxygen content fell below 4 mg/l, causing consumption to decrease 45 % (Shireman 1975, Shireman, Colle, and Rottman 1977). The four densities were 0.53, 1.06, 1.59 and 2.11 fish/l and density did not significantly affect growth until day 35. In 88 days, fingerlings at the lowest density grew to an average of 72.7 g, almost double the gain of fish at the two highest concentrations. A plot of total g of fish per l against stocking density indicated that the two highest densities were approaching the system's carrying capacity. In plastic pool experiments, 154- to 159-g grass carp had growth rates of 13.5 g/d at a density of 950/ha, 10.9 g/d at 1 900/ha, and 3.6 g/d at 3 800/ha. (Blackburn and Sutton 1971). Fry to 205-g fingerling grass carp has exhibited depressed growth when stocked densely in polyculture with other carps and *Tilapia* (Moav *et al.* 1977, Murty, Day, and Reddy 1978). Kilgen and Smitherman (1971) observed significantly different growth rates in grass carp stocked from 49-395 fish per ha in vegetated ponds (Table XXXI).

Maceina and Shireman (1980) investigated the effects of salinity on growth and related factors in 9- to 13-cm grass carp fed duckweed (*Lemna minor*). Dry weight conversion coefficients varied significantly from 1.95 at 0.1 ‰ (freshwater) to 2.38-2.26 at 3-6 ‰ salinity to 1.34 at 9 ‰. Feeding ceased

at 12 ‰. Significantly different values of percent weight gain corresponded to the following salinities: 56.3 % at 0.1 ‰; 46.2-23.7 % at 3-6 ‰; 14.6 % at 9 ‰; and 0.6 % at 12 ‰. Fingerlings at 12 ‰ salinity exhibited behavioural stress at day 8 and two died in 14 days.

3.6 Interspecific interactions

3.6.1 Disease and parasitism

Disease and parasitism are not nearly as prevalent in wild populations as in fish culture, where high densities and enriched waters are the rule. Most of the parasites listed in Table XXXII are reported from pond-raised grass carp and more important afflictions are described below.

Viruses, fungi, and bacteria cause considerable debilitation and mortality in grass carp culture. Spring viremia or acute dropsy is a highly infectious and deadly viral disease caused by *Rhabdovirus carpio* and affects other cyprinids as well as grass carp (Bohl 1979). Ahne (1975) isolated an additional undescribed serotype of *Rhabdovirus* from grass carp. Symptoms of acute dropsy include abdominal swelling, ventral hemorrhagic inflammation, necrotic fins, and petechial lesions on the swim bladder. In Taiwan, Province of China, Wu (1971) implicated an infectious bacterium, *Aeromonas punctata*, in a similar form of dropsy, which caused high grass carp mortality. Another contagious bacterium, *Aeromonas salmonicida*, is the etiological agent in chronic dropsy which is characterized by erythrodermatitis (Bohl 1979). The bacterium, *Myxococcus piscicola*, causes gill rot and high mortality, especially in young grass carp (Laboratory of Fish Disease, date unknown). Columnaris disease may be chronic in ponds and may cause death quickly when the fish are crowded or handled (Shireman 1975, Shireman, Colle, and Rottman 1976). The most prevalent fungus is *Saprolegnia* spp. which occurs on the epidermis and usually plays a secondary role in mortalities (Edwards and Hine 1974). Both bacteria and fungi attack the eggs and fry of grass carp (Bailey and Boyd 1971; Anon. 1972c, 1972g).

Table XXXI

Grass carp growths over 99 days at various stocking densities in vegetated ponds (Kilgen and Smitherman 1971)

Number Fish per ha	Initial size		Final size		
	Weight (g)	Total Length (cm)	Weight (g)	Total Length (cm)	Growth (g/d)
49	64	175	552	356	4.9
99	64	176	283	281	2.2
196	76	184	297	290	2.2
395	78	186	154	238	0.8

Table XXXII

Parasites of grass carp

VIRUSES			
<i>Rhabdovirus</i> spp.	3,8	<i>Spiroucleus</i> spp.	21(e)
<i>R. carpio</i>	8	<i>Tetrahymena pyriformis</i>	21(a)
BACTERIA		<i>Thelohanelleus oculi-leucisci</i>	26
<i>Achromabacter</i> spp.	24	<i>Trichodina</i> spp.	10,19,21(g)
<i>Aeromonas</i> spp.	24	<i>T. bulbosa</i>	21(b,d)
<i>A. punctata</i>	25	<i>T. carasii</i>	21(d)
<i>A. salmonicida</i>		<i>T. domerguei</i>	21(c,d)
var. <i>achromogenes</i>	8	<i>T. meridionalis</i>	21(d)
<i>Flexibacter columnaris</i>	5	<i>T. nigra</i>	21(d,f)
<i>Mycococcus piscicola</i>	18	<i>T. nobilis</i>	21(d),25
<i>Pseudomonas</i> spp.	24	<i>T. ovaliformis</i>	21(a,b)
FUNGI		<i>T. pediculus</i>	21(a,b,c,f)
<i>Branchiomyces sanguinis</i>	8	<i>T. reticulata</i>	16,21(f)
<i>Saproglenia</i> spp.	11,12,15,20	<i>Trichodinella epizootica</i>	21(c,e)
PROTOZOA		<i>Trichophrya</i> spp.	21(g)
<i>Apiosoma</i>		<i>T. sinensis</i>	10,16,21(a,b,e)
<i>cylindriciformis</i>	16,21(a,b,e)	<i>Tripartiella</i> spp.	12,21(e)
<i>A. magna</i>	21(f)	<i>T. bulbosa</i>	21(a,c)
<i>A. minimicro nucleata</i>	21(f)	<i>T. lata</i>	16
<i>A. piscicola</i>	16,21(f)	<i>Zschokkella nova</i>	21(a)
<i>Balantidium ctenopharyngodontis</i>	5,7,20,21(a,b,e)	TREMATODA	
<i>Chilodonella</i> spp.	8	<i>Amurotrema dombrowskajae</i>	5,21(a)
<i>C. cyprini</i>	10,16,17,19,20,21(d,e)	<i>Ancyrocephalus subaequalis</i>	21(a)
<i>Chloromyxum</i> spp.	17	<i>Apharyngostrigea curru</i>	8
<i>C. cyprini</i>	21(a,e)	<i>Aspidogaster amurensis</i>	21(a)
<i>C. nanum</i>	21(a,e)	<i>Cotylurus communis</i>	21(g)
<i>Costia necatrix</i>	10,21(b)	<i>C. pileatus</i>	21(f)
<i>Cryptobia</i> spp.	8	<i>Dactylogyrus</i> spp.	10
<i>C. brancialis</i>	10,16,21(a,b,e)	<i>D. ctenopharyngodontis</i>	12,16,19,21(a,g)
<i>C. cyprini</i>	1	<i>D. lamellatus</i>	5,16,17,19,21(a,d)
<i>Eimeria carpelli</i>	21(f)	<i>D. magnihamatus</i>	21(a)
<i>Eimeria mylopharyngodontis</i>	16	<i>Diplostomum</i> spp.	21(d)
<i>E. sinensis</i>	16	<i>D. indistinctum</i>	21(d)
<i>Entamoeba</i>		<i>D. macrostomum</i>	21(f)
<i>ctenopharyngodontis</i>	21(a,b)	<i>D. mergi</i>	21(f)
<i>Epistylis</i> spp.	21(f)	<i>D. paraspathaceum</i>	21(d)
<i>E. lwoffii</i>	21(d)	<i>D. spathaceum</i>	8,16,19,21(a,d)
<i>Euglenosoma caudata</i>	21(b)	<i>Diplozoon paradoxum</i>	21(a,f)
<i>Glaucoma pyriformis</i>	21(b)	<i>Gyrodactylus</i> spp.	10
<i>Hemiohrysa macrostoma</i>	21(a,b)	<i>G. ctenopharyngodontis</i>	12,19,21(a)
<i>Hexamita</i> spp.	21(b,g)	<i>G. kathariner</i>	21(f)
<i>Icthyophthyrus</i> spp.	8	<i>Metagonimus yokogawai</i>	19,21(a)
<i>I. multifiliis</i>	9,10,12,16,17,18,21(b,d,e),22	<i>Opisthorchis (=Chlonorchis) sinensis</i>	13
<i>Myxidium</i> spp.	21(e)	<i>Posthodiplostomum cuticola</i>	19
<i>M. ctenopharyngodontis</i>	21(a)	<i>Tetracotyle</i> spp.	19
<i>Myxobolus dispar</i>	21(e)	<i>T. percae fluviatilis</i>	8
<i>M. ellipsoides</i>	21(a)	<i>T. variegata</i>	16
<i>Sphaerospora carassii</i>	21(e,f)	CESTODA	
		<i>Biacetabulum appendiculatum</i>	16

Table XXXII (continued)

<i>Bothriocephalus acheilognathi</i> 2,6,7, (= <i>gowkongensis</i>) 8,10,12,16,19, 21(a,d,g),23	CRUSTACEA	
<i>Khawia sinensis</i> 8,16,19,21(d)	<i>Argulus</i> spp.	10,16,20
<i>Ligula intestinalis</i> 16	<i>Lernaea</i> spp.	4,6,10,16
<i>Triaenophorus nodulosus</i> 21(a)	<i>L. stenopharyngodontis</i>	19,21(a)
	<i>L. cyprinacea</i>	12,19,22
	<i>L. elegans</i>	14,23
	<i>L. quadrincuiifera</i>	21(a)
NEMATODA	<i>Neoergasilus longispinosus</i>	21(a)
<i>Capillaria</i> spp.	<i>Paraergasilus medius</i>	21(a)
<i>Philometra</i> spp.	<i>Sinergasilus lieni</i>	23
<i>P. lusiana</i>	<i>S. major</i>	5,10,19,21(a),23
<i>Rhabdochona denudata</i>		
<i>Spirocoys</i> spp.	PENTASTOMIDA	
	<i>Sebekia oxycephala</i>	21
Key to reference numbers:		
1) Anon. 1972b	17) Konradt and Faktorovich 1970	
2) Anon. 1976a	18) Laboratory of Fish Disease (date unknown)	
3) Ahne 1975	19) Musselius and Strelkov 1968	
4) Alikunhi and Sukumaran 1964	20) Prabhavathy and Sreenivasan 1977	
5) Astakhova and Stepanova 1972	21) Riley 1978 citing;	
6) Bardach, Ryther and McLarney 1972	(a) Bykovskaya-Pavlovskaya <i>et al.</i> 1964	
7) Bauer 1968	(b) Chen 1955 (c) Ivanova 1966	
8) Bohl 1979	(d) Kashkovskii 1974	
9) Cross 1969	(e) Molnar 1971 (f) Stepanova 1971	
10) Dah-Shu 1957	(g) Sullivan and Rogers, pers.comm.	
11) Doroshev 1963	22) Stevenson 1965	
12) Edwards and Hine 1974	23) Sutton, Miley, and Stanley 1977	
13) Faust and Khaw 1927	24) Szokolczai and Molnar 1966	
14) Gidumal 1958	25) Wu 1971	
15) Huisman 1978	26) Yukhimenko 1972	
16) Ivasik, Kulakovskaya, and Vorona 1969		

Over forty species of parasitic protozoa are reported from grass carp. *Cryptobia* spp. occurs in the blood and causes death through respiratory failure and/or anaemia. Symptoms include scale protrusion, abdominal hemorrhagics, and slimy skin (Bohl 1979). A leech, *Piscicola geometrica*, acts as a vector for *C. cyprini* which causes high mortality among 1+ to 3+-year old fish in Polish pond culture (Anon. 1972b). *Trichodina* spp. [at least nine species (Riley 1978)] infects the gills and skin, and is responsible for some losses in Soviet pisciculture (Musselius and Strelkov 1968). *Trichodina nobilis* and *Thelohanellus oculi-leucisci* are protozoan parasites native to the Amur River (Yukhimenko 1972). *Trichodina* spp., the gill parasite *Trichophrya sinensis*, and the skin parasites, *Costia necatrix* and *Chilodonella cyprini*, occur in Chinese fish culture (Dah-Shu 1957). *Tripartiella* spp. infests the scales and fins, and the cosmopolitan *Ichthyophthirius multifiliis* lives on the body surface, fins, gills and pharynx (Edwards and Hine 1974). *I. multifiliis* can be the primary or contributing factor causing mortality (Musselius and Strelkov 1968).

Over twenty trematodes, about five cestodes, and a few nematodes have been found in grass carp. Of the trematodes, *Dactylogyrus* spp. occurs in the gills and *Gyrodactylus* spp. affects the scales and fins (Edwards and Hine 1974). *Gyrodactylus* spp. infestations have killed grass carp on Soviet fish farms (Musselius and Strelkov 1968). *D. stenopharyngodontis* and *G. stenopharyngodontis* are host specific (Riley 1978). They and *D. lemellatus* occur in the grass carp's native range (Musselius and Strelkov 1968). *Diplostomum spathaceum* attacks the eyes, causing cataracts and sometimes death (Ivasik, Kulakovskaya, and Vorona 1969, Bohl 1979). Molluscs serve as the intermediate host for this parasite. The grass carp is an intermediate host for *Posthodiplostomum cuticola*, which begins development in molluscs and ends in piscivorous birds (Musselius and Strelkov 1968). *Opisthorchis* (= *Clonorchis*) *sinensis*, the Chinese liver fluke, encysts in the grass carp and completes its life cycle in man and other mammals (Faust and Khaw 1927). Infestation by *Tetracotyle* spp. causes scale bristling, erthrodermatitis, and dropsy (Musselius and Strelkov 1968). The cestode, *Bothriocephalus acheilognathi* (= *gowkongensis*), inhabits the

gut in grass carp of all ages and represents the major parasitic introduction from the Far East to have serious effects on other fish (Ivasik, Kulakovskaya, and Vorona 1969). It is relatively benign in older phytophagous grass carp but has caused extensive losses in European common carp culture. Copepods, especially *Cyclops* spp., are intermediate hosts. Catarrhalic or catarrhalic-hemorrhagic enteritis is symptomatic of heavy infestation (Bohl 1979).

Crustacean parasites are important debilitating pests in fish culture and may cause losses when present in large numbers. The copepod, *Lernaea* spp., and branchiurans, *Argulus* spp. are particularly deleterious ectoparasites on young grass carp and attach to the body surface, musculature, and gills (Dah-Shu 1957, Edwards and Hine 1974). *Sinergasilus major*, a copepod native to the Far East, inhabits the gills of fish older than two years and has been transferred to other countries (Musselius and Strelkov 1968).

3.6.2 Predators

Like most other cyprinids, the grass carp has few defenses and consequently is prone to predation by a variety of animals. Invertebrates such as copepods (especially *Cyclops* spp.), hemipterans (Belastomidea and Notonectidae), Coleoptera (*Cybister* spp. larvae), and odonatan nymphs attack the early life stages (Lin 1949, Anon. 1970c, Wurtz-Arlet 1971, Bailey 1972).

Predaceous fishes in the grass carp's native range include *Luciobrama typus*, *Parasilurus asotus*, and *Siniperca chuatsi* (Dah-Shu 1957). *Channa* (= *Ophicephalus*), *Gobius*, and *Elopichthys bambusa* create problems in Taiwan fish culture (Lin 1949) and *Channa*, *Clarias*, and *Anabas* cause losses in Malaysia (Birtwistle 1931a). Pike (*Esox lucius*) and pike perch (*Lucioperca lucioperca*) prey on grass carp in Russia (Sutton, Miley, and Stanley 1977).

Several investigations of largemouth bass (*Micropterus salmoides*) predation on grass carp have been conducted in the United States. Gasaway (1977d) found 29- to 56-cm bass to shift their feeding habits and to take 10- to 16-cm grass carp which were introduced into a Florida lake. In aquarium studies, Hatton (1977) observed bass to prey on grass carp up to 60 % of the bass's standard length. Compared to bluegill (*Lepomis macrochirus*) and golden shiners (*Notemigonus crysoleucas*), grass carp took less time to capture and had fewer successful escapes. By analyzing bass mouth dimensions and grass carp body size, Shireman, Colle, and Rottman (1978c) determined that a total length range for bass of 50-600 mm theoretically corresponded to a maximum total length range of 21-416 mm for the prey grass carp. An experimental stocking of fingerling grass carp in a pond with an established bass population resulted in almost

total mortality, presumably due to predation. The 48.2 mm, 1.4 g fingerlings were seen to swim near the surface in compact schools and to make no escape attempts as bass slowly approached and captured them head first.

Other reported vertebrate predators of grass carp include frogs (*Rana* spp.), water snakes (*Sinonatrix* (= *Natrix*) *piscator* and *Enhydria chinensis*), herons (*Ardeola schistaceus*), storks, hawks (*Accipiter gularis*), and otters (Birtwistle 1931a, Gidumal 1958, Sutton, Miley, and Stanley 1977). Any piscivorous animal would find the grass carp to be vulnerable and acceptable fare.

3.6.3 Competition and other indirect interactions

The effects of grass carp introduction on a water body are complex and apparently depend on the stocking rate, macrophyte abundance (for adults) and community structure of the ecosystem. Because of the many factors involved, numerous contradictory results are reported in the literature concerning grass carp interaction with other species. The dendrogram (Table XXXVI) may help to clarify the impacts of grass carp stocked at different rates in biocenoses with varying macrophyte abundance.

Much research has been directed toward interspecific competition for food. Fry have been implicated as competitors with other species for zooplankton under polyculture conditions (Opuszynski 1968, 1979; Grygierek 1973). Sobolev (1970) found this competition to be slight at densities of 30- to 50- thousand grass carp per ha, 20- to 30-thousand silver carp per ha, and 60-thousand common carp per ha. In view of the usual superabundance of zooplankton and of the short planktophagic phase of grass carp, it would probably not be a serious competitor in wild situations. In water bodies with limited vegetation, older grass carp may revert to carnivory and compete with local benthophages, including common carp and gamefish (Gaevskaya 1969, Vinogradov and Zolotova 1974, Lewis 1978). However, Kilgen and Smitherman (1971, 1973) found little competition with game fish for animal food in sparsely-vegetated ponds. Grass carp resorted to terrestrial vegetation in other devegetated ponds and only trace amounts of animal matter were identified in their stomach contents (Terrell and Fox 1974, 1975; Terrell 1975a; Terrell and Terrell 1975). Zolotova (1966) points out that grass carp selectivity depends on rearing and feeding conditions and on the species' inherent trophic plasticity.

Macrophytes themselves may provide a source of competition. Forester and Avault (1978) determined that grass carp stocking reduced crayfish (*Procambarus clarkii*) production in small ponds. The interference seemed to arise from competition for plant food.

Crayfish recruitment remained constant, though grass carp did eat small individuals in the absence of vegetation. Overwintering waterfowl such as ducks and coots also feed on aquatic macrophytes like hydrilla (*Hydrilla verticillata*) and Illinois pondweed (*Potamogeton illinoensis*) (Gasaway 1977b, Gasaway and Drda 1977, Gasaway *et al.* 1977, Land 1980).

Vegetation plays an important role in aquatic ecosystems. Its removal can have little effect or drastic impacts on other species. The grass carp partially digests its food and the faeces provide a large influx of nutrients which may be used by other organisms. Because of food selectivity, the grass carp occasionally increases some populations of plant species by preferential feeding on their competitors (Vinogradov and Zolotova 1974). In this manner, grass carp introduction has been noted to benefit eelgrass (*Vallisneria* spp.) (Sutton 1975b, Nall and Shardt 1980) and Eurasian milfoil (*Myriophyllum spicatum*) (Fowler and Robson 1978, Kobylinski *et al.* 1980). This situation may continue until the preferred food supply is exhausted, and then control usually extends to the less palatable species. The concurrent large influx of nutrients via grass carp faeces and quick elimination of macrophytes which might utilize the nutrients, can result in phytoplankton blooms, particularly of blue-green algae (Opuszyński 1972, 1979; Nikolsky and Aliev 1974; Vinogradov and Zolotova 1974). After grass carp were stocked in a lake, Crisman and Kooijman (1980) documented a doubling of algal concentration, with blue-greens increasing their dominance at the expense of diatoms, cryptophytes, and chlorophytes. Similarly Cure (1974) found great increases in phytoplankton densities in the Frăsonet pond in Romania following the introduction of grass carp. At the same time higher vegetation was reduced to about one thirtieth of pre-stocking level. Introduction of grass carp into a Yugoslavian lake resulted in a large decrease of macrophytes and apparently caused extreme fluctuation in planktonic populations, indicating an imbalanced system (Mestrov *et al.* 1973). In Indian culture ponds, Alikunhi and Sukumaran (1964) determined that stocking grass carp in numbers great enough to quickly eliminate hydrilla, almost invariably resulted in algal blooms. Overstocking of grass carp apparently is responsible for algal blooms.

The impacts of grass carp introduction on other animals are more complex and consequently less understood. Cure (1974) and Lembi and Ritenour (1977) found ponds with grass carp to have higher zooplankton and benthos populations than those without. Increases in macroinvertebrate standing crops have been noted in other studies and are generally ascribed to increased nutrient input (Aliyev 1976, Kobylinski *et al.* 1980, Haller and Sutton 1977). At high stocking rates, (45-69 kg/ha) grass carp eliminate the vegetative refugia and

cause reductions in invertebrate numbers and diversity (Vinogradov and Zolotova 1974, Beach *et al.* 1976, Gasaway 1977a). In the USSR they have controlled ectoparasitic dipterans such as mosquitos (*Anopholes* and *Culex*) by removing the vegetation used for larval development (Aliyev and Bessmertnaya 1965, Aliyev 1976, Verigin 1979). Grass carp can cause lower shrimp yields when used in polyculture (Kuronuma and Nakamura 1957). In some cases, a balance is apparently achieved between plant removal and nutrient input, and zooplankton and invertebrate populations remain unaffected (Rottmann 1976, Rottmann and Anderson 1976, Crisman and Kooijman 1980).

The grass carp affects other fish through interference with their reproduction, broadening or narrowing their food base, and decreasing refugia. Reduction of vegetative hiding places makes small fish such as *Gambusia* spp. and fry vulnerable to piscivores (Aliyev and Bessmertnaya 1965, Vinogradov and Zolotova 1974, Beach *et al.* 1976, Baur, Buck, and Rose 1979). With greater availability of prey, gamefish frequently increase their production even though grass carp may interfere with recruitment. Macrophyte removal reduces spawning sites for other fish (Opuszyński 1968, 1979; Krupauer 1971). Grass carp, especially in high densities, wander into spawning beds while foraging and physically disturb species such as largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*). In small ponds stocked with grass carp, bluegill production dropped 52 % and bass failed to spawn in two of three ponds (Forester 1975, Forester and Lawrence 1978). In small Russian lakes, intensively-stocked grass carp eliminated vegetation and prevented spawning by pike (*Esox lucius*) and perch (*Lucioperca fluviatilis*) (Sutton, Miley, and Stanley 1977).

Stocking of grass carp at 67-69 kg/ha (56-305 fish/ha) created unbalanced systems in four American lakes (Gasaway 1977a, 1977c). Diversity and number of fish species decreased and forage fish increased proportionately. Game fish in some lakes exhibited decreased populations, size reductions, and overcrowding, depending on species. The macroinvertebrate food base decreased and became less diverse. Ware and Gasaway (1976) reported the following results in two of the lakes where a 69 kg/ha stocking rate caused total elimination of submerged vegetation; seven fish species disappeared; the bass population was reduced or negatively altered; bluegill increased in number but decreased in size and condition; the warmouth *Lepomis gulosus* population decreased and coarse fish became more abundant. These effects on other fish species might very well have been caused by initial rotenone and blocknet sampling methods, which evidently reduced populations and altered their structures (Beach *et al.* 1976, 1977; Miley, Leslie, and Van Dyke 1979). In the USSR grass carp introductions have adversely affected pike, perch, Crucian carp (*Carassius*

carassius), and roach (*Rutilus rutilus*) (Vinogradov and Zolotova 1974). In the United States, Newton *et al.* (1976) stocked fifty grass carp per ha (45 kg/ha) into a reservoir. The subsequent elimination of vegetation probably disrupted the macroinvertebrate food base and resulted in a 50 % reduction of centrarchid biomass. In a comparison study using ponds, production of companion species increased, apparently due to the addition of nutrients via grass carp faeces. Polyculture with grass carp has been reported to enhance production of cyprinids and centrarchids (Stanely 1973a, Buck, Baur, and Rose 1975, Chaudhuri *et al.*, Rottmann 1976, Rottmann and Anderson 1976, Haller and Sutton 1977, von Zon 1977). In Arkansas, United States lakes managed for fishing, grass carp controlled submerged vegetation but had little or no effect on shad (*Dorosoma* spp.), largemouth bass, sunfish (*Lepomis* and *Chaenobryttus* spp.) and crappie (*Pomoxis* spp.) (Bailey 1978). Overall stocking rate ranged from 2-140 fish per hectare over one to three years, with 25 0.2-kg fish per hectare representing a typical rate. Plant removal by grass carp did seem to improve condition factor in some bass and bluegill populations. Similarly Stott *et al.* (1971) showed that common bream (*Abramis brama*) grew better in ponds stocked with grass carp compared with ponds without the herbivore, and Cure (1974) attributed to the introduction an increase in the productivity of the Frasinet pond on which she worked.

4. POPULATION (stock)

4.1 Structure

4.1.1 Sex ratio

Grass carp sex ratios of catches from the

Amur basin of the USSR (Table XXXIII) show a preponderance of females, which outnumber males nearly three to one for pooled data (Gorbach 1961). In the Tone River of Japan, a catch of sixty spawning grass carp was also dominated by females (Inaba, Nomura, and Nakamura 1957). Females comprise only 20-25 % of the catch from spawning populations in Chinese rivers (Chang 1966). From one to three ($\bar{x} = 2.3$) males follow each female when spawning (Lin 1935a, Dah-Shu 1957, Inaba, Nomura, and Nakamura 1957). Shelton and Jensen (1979) determined the sex ratio of 770 cultured juveniles to be 1 male to 1.03 females, not significantly different ($p > 0.05$) from the expected 1:1 ratio typical for most bisexual animals. Different rates of mortality or migration for male and female grass carp have not been investigated.

4.1.2 Age composition

Gorbach (1961) reported the age composition of grass carp taken at various locations in the Amur basin from 1957 to 1959 (Table XXXIV). Compared to data from the thirties, the proportion of young fish increased markedly. He cited Nikolsky (1956) as reporting that ages of Lake Udy1' fish taken in 1937 ranged from 6+ to 14+, with 10+ to 13+ dominating and that ages of fish caught at Novo-Il'inovka in 1939 varied from 9+ to 12+, with 9+ being most common. The age data for Lake Udy1' catches from Konstantinova (1958), reported by Gorbach (1961), gave a range in age of 4+ to 11+, with 6+, 9+, and 10+ dominating in 1933 and with 7+ and 9+ to 11+ becoming most common from 1936 to 1937. In 1957, grass carp from Lake Udy1' were mostly 4+ to 6+, with none older than 9+ years, and 5+-year-old fish

Table XXXIII

Sex ratios of grass carp catches from the Amur Basin, USSR (Gorbach 1961)

Locality	Date	Ratio	n
Amur River at Leninskoe	6-7/1957	21.8:78.2	55
	6-10/1958	22.8:77.2	136
	5-10/1959	24.4:75.6	131
Lower Ussuri River at Kazakevichevo and Argunskoe	7-9/1957	9.1:90.9	22
Lake Bolon' and the Sii and Serebryanaya Canals	5-8/1957	54.8:45.2	31
	5-8/1958	46.6:53.4	24
Lake Udy1'	7-8/1958	33.3:66.7	9
	5-8/1958	33.3:66.7	3
Total all localities		26.5:73.5	411

Table XXXIV

Age composition of grass carp catches from the Amur Basin, USSR (Gorbach 1961)

Year	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	21+	n
Amur River at Leninskoe													
1957	8.7	29.3	6.5	15.2	15.2	8.7	4.4	4.4	7.6	-	-	-	92
1958	3.2	11.1	33.7	33.7	12.6	4.2	0.5	-	-	-	0.5	0.5	190
1959	0.6	4.5	28.2	32.7	14.1	6.4	5.2	4.5	0.6	3.2	-	-	156
Lower Ussuri River at Kazakevichevo and Argunskoe													
1957	9.0	38.6	20.8	18.0	6.8	2.3	4.5	-	-	-	-	-	44
Lake Bolon' and Sii and Serebryanaya Canals													
1957	-	5.0	40.0	45.0	-	5.0	5.0	-	-	-	-	-	20
1958	-	-	26.3	42.1	21.0	10.5	-	-	-	-	-	-	19
Lake Udyl'													
1957	-	16.7	66.6	16.7	-	-	-	-	-	-	-	-	18

dominated. In the middle reaches of the Amur River, where over half of the annual catch occurred, ages ranged 3+ - 21+ and 5+ - 7+-year-old fish were most common. From 1957-1959, immature fish composed 20-100 % of the grass carp catches, with a mean of 77.5 %.

4.1.3 Size composition

Along with age, the average size of grass carp taken in the Amur basin decreased considerably from the thirties to the fifties (Gorbach 1961) (Table XXXV). Large fish, 80-100 cm in standard length, were found primarily in the lower part of the middle Amur River and rarely in the lower reaches during 1957-1959. Specific data on the percent composition of population by weight or length categories were not reported.

4.2 Natality and recruitment

Natality rates and recruitment in self-reproducing grass carp populations are unknown, but are undoubtedly low. Predation and adverse hydrological conditions must certainly prevent the development of a large proportion of spawned eggs (Sections 3.1.7, 3.1.8, 3.2.1, 3.6.1, and 3.6.2). Survival is low during the period from larva to fingerling, particularly in the first week after hatching (Vladimirov 1975; Sections 3.2.2, 3.2.3, 3.2.4, 3.6.1, 3.6.2, and 4.3). The characteristics which permit grass carp populations to maintain themselves are their wide environmental tolerance (Section 2.3), long lifespan (Section 3.3.1) and high fecundity (Section 3.1.5).

4.3 Mortality, morbidity, and condition

Mortality rates of grass carp in naturalized and indigenous populations are unknown. Available information deals with introduced stocks in closed systems over relatively short periods of time. Thomas and Carter (1977) grew 10-18 mm larvae to 8-25 cm fingerlings over 287-309 days in six small ponds which had been poisoned to remove predators. Survival ranged 22.9-60.2 %, with an average of 34.0 % and monthly mortality rate of 3.2 %. Densities varying from 32 780 to 100 000 fish/ha and oxygen levels approaching 0 mg/l had little effect on mortality. Survival was significantly greater in ponds with vegetative cover. The 8-25 cm yearlings had a survival rate of 91 % and attrition of 2.3 % per month during four months of pond culture (Thomas, Carter, and Greeland 1979). Survival of 1+ - 2+-year-old fish over thirteen months was 76 %, with monthly attrition of 1.9 %. The higher attrition rate for yearling, compared to older fish, probably reflected greater susceptibility to predation by birds and water snakes [*Nerodia* (= *Natrix*) spp.]. Colle, Shireman, and Rottmann (1978b) observed 94.8 % (1.9 % due to electrofishing) mortality over six months for 48-186 mm fingerlings placed in a pond which had been poisoned to remove predators. Piscivorous birds were common and probably caused most of the reduction. Mortality rates of 0.13-1.9 % grass carp ranged from 4-99 % in four ponds over two years (Beach *et al.* 1976, Gasaway 1978). Largemouth bass (*Micropterus salmoides*) predation and macrophyte food base reduction apparently influenced survival the most. Colle *et al.* (1978a) estimated that a 94.6 %

Table XXXV

Standard length and weight of grass carp in catches from the Amur Basin, USSR (Gorbach 1961, citing Nikolsky and Konstantinova 1958)

Locality	Date	Length Range	(cm) \bar{x}	Weight (g) Range	\bar{x}	n
Amur River at Leninskoe	6-8/1957	30-85	50.0	550-10,700	2860	101
	6-10/1958	35-105	55.2	950-11,850	3520	323
	5-10/1959	30-90	59.2	1490-13,600	4230	195
Lower Ussuri River at Kazakevichevo and Argunskoe	7-9/1957	30-95	46.0	850-14,900	2300	47
Pryamoi Canal	5-6/1930	75-90	81.4	-	-	5
Lake Bolon' and the Sii and Serebryanaya Canals	5-8/1957	45-75	56.6	2250-8750	4120	32
	5-8/1958	45-80	58.0	2750-9450	4220	24
Novo-Il'inovka	8-9/1939	60-85	72.1	-	-	22
	6-8/1940	40-85	71.0	-	-	29
Lake Udyl'	1933	40-75	60.8	-	-	12
	5-9/1937	45-80	72.2	-	-	50
	7-8/1957	40-55	47.8	1250-2700	2025	21
	5-8/1958	40-55	48.0	1350-3150	2400	-

decrease in grass carp occurred in a lake two-and-one-half years after stocking. Almost total mortality of 48.2 mm, 1.4 g fingerlings resulted in a pond with an established bass population (Shireman, Colle, and Rottmann 1978c, Shireman and Maceina 1980). The grass carp were observed to swim in a compact school near the surface and to exhibit no escape behaviour when bass attacked them. Stocking fish over 0.5 kg would theoretically result in negligible mortality since predation would be minimized. Birds, pike perch (*Lucioperca lucioperca*), snakehead (*Channa* spp.), and pike (*Esox lucius*) are credited with causing high mortalities and with limiting the abundance of naturalized grass carp in the USSR (Stanley 1977, Sutton, Miley, and Stanley 1977, Stanley, Miley, and Sutton 1978).

Morbidity may be caused by disease (Section 3.6.1), starvation, pollution, or hydrological conditions (Section 2.3). Macrophyte abundance possibly influenced grass carp survival in four ponds (Beach *et al.* 1976, Gasaway 1978). The sensitivity of grass carp to rotenone and other fish toxicants has been investigated by Marking (1972), Henderson (1974), Cumming, Burrell, and Gilerhus (1975), and Miley, Van Dyke, and Riley (1976). LD₅₀s of rotenone in mg/litre range from 0.063-0.083. Colle *et al.* (1978a)

determined LD₅₀ at 24 hours to be 0.075 mg/l rotenone, and LD₁₀₀s to be 0.200 mg/l at 7 hours, 0.150 mg/l at 24 hours and 0.075 mg/l at 36 hours. Grass carp kills or morbidity due to pollution have never been reported.

The tolerance of hydrological conditions is discussed in Section 2.3. Opuszyński (1967) described the symptoms of grass carp as they reached morbidity induced by the temperature characteristics of the water. With rising temperature, fish behaviour is anxious and momentary balance loss, permanent loss of equilibrium, and lack of respiratory movements in that order. Progressively-lower temperatures initially cause apathy and then momentary disturbances of balance. Grass carp then assume a vertical position with their heads touching the bottom and with spasmodic movement of the caudal fin, or they swim in a sideways position. Finally, the fish turns belly-up with barely perceptible respiration, then lies on the bottom with no gill movements.

Physiological changes caused by salinity include decreases in weight and muscle tissue water content (Maceina and Shireman 1979). Mortality at salinities over 14 ‰ was attributed to failure of cellular processes to adjust to dehydration. Electrolytes (Na⁺ and

Cl⁻) and total ionic concentrations of the plasma increased significantly in fingerlings exposed to salinities greater than 195 mOsm/kg (616 ‰) with the fish apparently unable to balance electrolyte concentrations at 317 mOsm/kg (10.9 ‰) (Maceina, and Shireman 1980). As the osmotic gradient between the fish and water declined, maintenance of osmotic equilibrium might have been achieved by reduction of blood circulation to the gills, imposing a lower metabolic rate. Oxygen consumption decreased significantly from 0.16 mg O₂/g-h in freshwater to 0.11 mg O₂/g-h at 317 mOsm/kg salinity.

Condition factor (K), fat content, and weight-length variability are indicative of health or lack of it in fish. Gorbach (1971) observed that condition and fat content of grass carp native to the Amur basin, USSR decreased in June and July because of maturation and spawning, increased from July to a maximum in September while fish fed intensively on the floodplain, and declined again during the winter (when they stopped feeding). Mitzner (1978) documented a decrease in condition factor of 2⁺-year-old fish in a temperate lake from 1.22 in July, August, and September to 1.16 in January and February. Hoa (1973) found that increases in weight-length variability, and in positive skewness of fish distributions by weight-length classes, corresponded with poor growth conditions of under-yearlings in ponds. He also noted that the relative length of intestine might decrease.

4.4 Population dynamics

The annual changes in quantitative demographic parameters of self-reproducing grass carp populations have never been investigated. Relative to other species, it has always been uncommon in the Amur basin with average annual catches of 30 metric tons during pre-war years (Nikolsky and Aliev 1974). Fishing pressure has caused marked declines in the average age, length and weight of grass carp taken since the thirties (Gorbach 1961) (Tables XXXIV and XXXV). Variable growth rates in fish from different localities indicate the presence of several local stocks. Annual catches declined steadily in the latter half of the sixties and were reduced by a factor of fifteen by 1970, in spite of constant fishing effort (Gorbach 1972). Large-scale decreases in population fecundity were responsible for the declines. From 1963 to 1969, the mean indicators of spawning females dropped from 87.5-73.2 cm standard length, 11.95-7.53 kg in weight, 13-8.4 years of age, and 1.2-million to 0.6-million eggs in absolute fecundity (Table X, Section 3.1.5). Since maturity occurs at 8-10 years of age in the Amur region (Table VI), it may be concluded that most breeding females were caught during their first spawning migration in 1969. Immature fish also comprise much larger proportions of the catch in more recent years (Section 4.1.2). The annual catch dropped from 6 408 in 1967 to 2 482 in 1969. Estimated population fecundity decreased from

2 344- to 547-million eggs, respectively, due to contraction of the spawning population, reduction in percent representation by older age groups, and adverse feeding condition in 1968.

The grass carp has been introduced, usually along with silver (*Hypophthalmichthys molitrix*) and bighead (*H. nobilis*) carp, into numerous waterways of the USSR reproducing populations occur in the Syrdar'ya, Ili and Kuban Rivers, but establishment is questionable since the areas are stocked with supplemental fish (Stanley 1977, Sutton, Miley, and Stanley 1977, Stanley, Miley, and Sutton 1978). Spawning took place, but recruitment was negligible in the Volga River, where the population density amounted to only 0.1 fish/ha after twenty years of intensive stocking (Sutton, Miley, and Stanley 1977, Miley, Sutton, and Stanley 1979b).

Grass carp catches from the inland waters of Turkmenistan ranged from 1.9-6.4 metric tons (MT) (0.4-1.3 % of total fisheries production) during the years 1967-1969, increased to 76.0 MT (1.7 %) in 1970, when the ban on taking phytophagous fish was lifted, and ranged from 29.7 MT (0.3 %) in 1971 to 23.0 MT (0.2 %) in 1974 (Aliev 1976). Population changes resulted from the interplay of stocking rates, fishing effort, establishment of self-reproduction, and alteration in the macrophyte food base. Similar data is available for the Khauz Khan Reservoir, which is associated with the Kara Kum Canal, where massive successful reproduction has occurred. Catches amounted to 0.2 MT (0.2 %) in 1970, 27.4 MT (10.0 %) in 1971, and 12.4 MT (1.8 %) in 1974. Grass carp have always been relatively uncommon in the reservoir, and reductions since 1970 have been concurrent with decreases in macrophyte abundance (Nikolsky and Aliev 1974). Stanley (1977) and Stanley, Miley, and Sutton (1978) stated that the population decline to half of the 1970 peak in the Kara Kum Canal may have been due to exhaustion of the food supply (citing Kogan 1974) or to a parasitic disease (D.D. Aliev pers. comm.). He also reported that large grass carp populations formed in lakes around the Aral Sea over 1 000 km from the spawning grounds in the Kara Kum Canal and that they dominated one lake, with over 150 kg/ha harvested in a year (citing Bykov 1970).

Absolute and relative abundance of naturalized grass carp in the Tone River, Japan decreased due to declines in macrophytes (used as food by adults and used as cover by juveniles) and to reduced spawning success as a result of dam and weir construction (Section 2.1) (Tsuchiya 1979; Bailey and Haller, unpubl. ms). The percentages of grass carp larvae hatched from phytophagous fish eggs collected in the river was: 39.5 in 1958; 26.2 in 1959; 9.4 in 1960; 12.9 in 1961; 34.3 in 1964; and approximately 3 % since 1964. The catch from Lakes Kasumi and Kita ranged from 7 to 47 t/year during 1956-59 and from 0 to 9 t/year from 1960 to 1975. The ratio of

grass to silver carp decreased from 0.37-1.00 during 1956-1960 to 0-0.07 during 1961-1975.

4.5 Relationships of populations to ecosystem

Section 3.6 reviews the effects of grass carp populations on plants and animals. Changes in water quality frequently occur with relatively high densities of approximately 70 kg/ha. Nitrate-nitrite levels increased significantly after grass carp were stocked in four ponds in Florida, United States (Beach *et al.* 1976, 1977; Gasaway 1977c). Decomposition of fecal plant material from the fish probably caused the increases. Increases of chlorophyll a, b, and c levels indicated heightened phytoplankton, all of which reflected enrichment of the water (Gasaway, no date, 1977b, 1977c). In Indiana ponds, dissolved oxygen decreased when grass carp eliminated all vegetation, including filamentous algae (Lembi and Ritenour 1977, Lembi *et al.* 1978). Significant increases occurred in turbidity, probably due to suspended organic particles, and in potassium levels, which reflected feeding rates of the fish. In a Yugoslavian lake, grass carp drastically reduced the macrophytes, which resulted in lower dissolved oxygen and higher CO₂ levels (Mestrov *et al.* 1973). Kjeldahl nitrogen increased and pH decreased significantly after grass carp were introduced into a Florida lake with considerable flow-through (Kobylinski *et al.* 1980). Decomposition of grass carp faeces and reduction of macrophytes which utilized nutrient and fixed CO₂ probably caused the water quality changes. After a temperate Iowa lake was stocked with grass carp, nitrate-nitrite, biological oxygen demand, and turbidity decreased significantly from 132-115 mg/l (Mitzner 1978). The indicated gradual reduction in fertility may have been due to reduced watershed loading or to chemical binding of nutrients from grass carp excreta in the bottom sediments. Terrell (1975b) demonstrated that orthophosphate, iron, and magnesium introduced into small ponds via grass carp faeces, were bound in bottom sediments and were not available to the plankton community. In Missouri, grass carp ponds had significantly lower pH, higher total alkalinity, and greater dissolved oxygen concentrations than control ponds (Rottmann 1976, Rottmann and Anderson 1976). No significant differences were noted between ponds for algal concentration or turbidity. The presence of grass carp in the Kara Kum Canal and Khauz Khan Reservoir of the USSR improved the oxygen level regime (Aliev 1976, Stanley 1977, Stanley, Miley, and Sutton 1978). They drastically reduced the macrophytes, preventing seasonal die-offs and decomposition which lowered oxygen content prior to introduction. While the influx of nutrients via grass carp faeces might lead to phytoplankton blooms and die-offs which could lower the oxygen levels, the simultaneous stocking of planktonphagic silver

and bighead carp with grass carp in these water bodies apparently prevented this situation from developing.

Because of their high rates of macrophyte consumption, grass carp have great potential for the disruption of their own food supply (Vinogradov and Zolotova 1974). The decreases of their numbers in Khauz Khan Reservoir since 1970 occurred concurrently with reductions of aquatic plant beds (Nikolsky and Aliev 1974). The construction of dams and weirs, which reduced spawning success, as well as a decline in macrophytes used as adult food and juvenile cover, apparently led to a decreased grass carp population in the Tone River, Japan (Section 2.1) (Tsuchiya 1979, Bailey and Haller, unpubl. ms).

5. EXPLOITATION AND OTHER INTERVENTION

5.1 Fisheries

5.1.1 Fishing equipment and techniques

All life stages of the grass carp are harvested. Prior to the advent of induced spawning by hypophysation, all larval or fingerling stock material was captured from Chinese rivers during the reproductive season. The most prevalent devices used for collection were long conical nets of closely-woven materials such as bamboo or linen (Dah-Shu 1957, Bardach, Ryther, and McLarney 1972). Dipnets, pushnets, and seines were also used (Brown 1977). Most effort was directed toward fry rather than eggs, which were collected only in certain regions (Dah-Shu 1957).

Adult grass carp are important commercial fish in many areas but rarely comprise a large proportion of the catch. They are commercially harvested with gillnets, trammel nets, seines, hoop nets, trotlines (rarely), and with hook and line, fish traps and rotenone in other applications (Vietmeyer 1976, Pflieger 1978). The Chinese also use otters and cormorants to capture fish (Chang 1966). Fishing vessels apparently range from small sampans (Lin 1935a) to large motor craft used for setting nets in rivers, lakes, and reservoirs. Conflicting reports exist on the grass carp as a sport fish. Bailey (1972) and Wilson and Cottrell (1979) reported that capture by rod and reel was difficult. Other authors report hook and line fishing is highly effective in a devegetated pond (Terrell and Fox 1974, 1975; Terrell 1975a; Terrell and Terrell 1975). In a sport fishery pond, English anglers frequently took grass carp by rod and reel with maggots, bread paste or flake as bait (Buckley and Stott 1977). Fishermen in the Netherlands successfully use doughballs and willow leaves (Sutton, Miley and Sutton 1977).

5.1.2 Fishing areas

Within the native distribution, fishing for grass carp occurs primarily in the lower sections of river basins and in their associated lakes and reservoirs. 70 % of the total Amur basin catch is taken in the lower part of the middle reaches (Gorbach 1961, 1966).

The Chinese collect fry and sometimes eggs from the lower Yangtze River, especially from Hupei to Kiang-Su Provinces, and from the Pearl River complex, upstream on the West River as far as Poseh (Lin 1935a, Dah-Shu 1957).

Fisheries have also developed in a few areas of introduction. In Japan, an established population breeds in the Tone River (Tsuchiya 1979). The primary fishing areas are in Lakes Kasumi and Kita on the lower end of the river. Eggs are collected from the Edo River, which is too short to permit their development before reaching the sea. In the USSR, fishing of introduced grass carp takes place primarily in the Sydar'ya and Amudar'ya basins, Kara Kum Canal, and Khauz Khan Reservoir (Nikolsky and Aliev 1974, Aliev 1976, Verigin, Makeeva, and Zaki Mokhamed 1978). Stanley, Miley, and Sutton (1978 citing Bykov 1970) stated that the grass carp populations developed in lakes around the Aral Sea and that they dominated the fisheries in at least one lake. In the Philippines, the grass carp is rarely captured from the Pampanga River, where they have been introduced by the United Nations Food and Agriculture Organization (Datingaling 1976, Bailey and Haller unpubl. ms). Though no fishery exists at present in the Rio Balsas system of Michoacan, Mexico, the discovery of thousands of fry from natural spawning indicates great potential (Anon. 1976b, Rosas 1976). Sport-fishing and culture of grass carp occur in many countries of introduction (Table IV) and are discussed further in Section 5.3.

5.1.3 Fishing seasons

Large grass carp are taken primarily during the spawning season and, to a lesser extent, during migrations associated with feeding or overwintering. They are not usually fished during the winter. The season lasts from May to September in the Amur basin, USSR (Gorbach 1971). In China, where eggs, fry and fingerlings are collected and then cultured, the season extends from early May to July on the Yangtze River and from early April to late September in the Pearl River complex (Lin 1935a, Dah-Shu 1957). During various dynasties, fishing activity has been restricted during the breeding season (Chang 1966).

5.1.4 Fishing operations and results

Though widely introduced and commercially exploited, the grass carp rarely comprises a large proportion of a fishery, probably because few areas can produce the macrophyte biomass necessary to support a large population. They are generally taken incidentally in operations directed primarily toward fish such as common carp (*Cyprinus carpio*) or silver carp (*Hypophthalmichthys molitrix*). Catches of the relatively uncommon grass carp averaged 30 MT annually in the Amur basin during prewar years (Nikolsky and Aliev 1974), reach 110 MT/year in the major fishery section of the river from 1957-1966 (Gorbach 1966), and subsequently decreased drastically due to overfishing (Gorbach 1972). In the Khauz Khan Reservoir of the USSR, the highest annual catch was 36.4 MT (21.2 % of total fisheries production) in 1970, but grass carp never became as abundant as common or silver carp (Nikolsky and Aliev 1974). Grass carp never contributed more than 2 % of fisheries production in the inland waters of Turkmenistan (Aliev 1976). In some lakes around the Aral Sea, however, grass carp dominated catches, at least temporarily (Stanley, Miley, and Sutton 1978, citing Bykov 1970).

Most grass carp in Japan are fished out of Lakes Kasumi and Kita. Their numbers have approached 80 % of the phytophagous fish catch in earlier years, but currently make up less than 10 %. Annual production ranged from 7-47 MT from 1956-1959 and from 0-9 MT from 1960-1975 (Tsuchiya 1979). Little information is available on Chinese fisheries. Lin (1949) estimated that 11-billion fry of cultured cyprinid species, including grass carp, were collected annually from the Yangtze and West Rivers. Today, induced spawning techniques have decreased the demand for wild fry and depressed the activity of this fishery.

5.1.5 Fisheries management and regulations

With regard to the Amur basin, much concern has been expressed about the depauperate stocks of grass carp. Regulations such as size limits, seasons, and catch quotas have been proposed (Gorbach 1961, Makeeva 1963, K'o-lei-hei-chin 1966, Ma-k'ai-yeh-wa, Su-yin, and Po-t'a-po-wa 1966). Gorbach (1972) finally recommended that fishing should be suspended for 10 years, beginning in 1971. Ma-k'ai-yeh-wa, Su-yin, Po-t'a-po-wa (1966) pointed out that cooperation between the USSR and China was needed on reservoir construction if deleterious effects on spawning were to be avoided in the Amur region. At various times in China's history, conservation methods have included regulations setting

size limits and restricting fishery activity with regard to spawning fish, their reproductive season, and their breeding grounds (Chang 1966). In Japan, collection of phytophagous fish eggs from the Tone River is prohibited (Tsuchiya 1979).

Other regulations have to do with introductions of grass carp. Nikolsky and Aliev (1974) state that stocking of grass carp must be carefully evaluated in order to avoid problems such as destruction of the spawning sites of other species. Generally, the Russians consider their massive introductions of grass carp to provide positive weed control and enhancement of existing fisheries. Fishing for phytophagous species is usually not allowed until several years after stocking (Aliyev 1976). Other countries range the entire spectrum of liberal to conservative distribution policies. Austria permits purchase and stocking of grass carp by anyone so inclined (Sutton, Miley, and Stanley 1977, Miley, Sutton, and Stanley 1979b). In the United States, 35 states banned importation by 1976 (Anon. 1977b). Arkansas represents the primary state with a relatively liberal distribution policy (Anon, 1972a, 1972d, 1972f). An importer must obtain a health license in England, and further distribution is controlled by local laws (Stott 1979).

5.2 Transplantation

The advent of induced spawning techniques (Section 3.1.6) and rapid transport systems permitted the cosmopolitan transplantation of grass carp, whereas it had previously been restricted to eastern China and adjacent areas. Table IV lists the countries where grass carp have been imported, as well as the major purposes for introduction. The attractive biological properties of this species are rapid growth, high organoleptic quality, and voracious consumption of macrophytes, all of which make it valuable for aquaculture and weed control.

Methods of transportation range from waterproof baskets carried on foot (Lin 1949) to tank trucks carried by airplane (Custer *et al.* 1978). Whatever the method, the water must not become oxygen-deficient or change temperature sharply. Flow-through barges were used on China's freshwater rivers and canals (Brown 1977). Wooden tubs, which had to be mechanically aerated, have been used as containers in both air and sea transport (Birtwistle 1931b, Gidumal 1958). Oxygen under pressure in sealed tins (Lin 1949) and plastic bags (Brown 1977) greatly facilitated transportation. Fish may be starved beforehand and placed in water of relatively low temperature to reduce their metabolism and to prevent deterioration of water conditions (Chang 1966). The development of relatively uncomplicated induced spawning techniques eliminated most transportation needs.

5.3 Fish farming

5.3.1. General role in fish culture

According to archaeological data, grass carp were used for food and their skull bones for ornaments from 15 000-50 000 years ago, but polyculture of Chinese cyprinids, including this species, as opposed to common carp (*Cyprinus carpio*) monoculture, was not recorded until the T'ang Dynasty (618-917 AD) (Chang 1966, Brown 1977). In most fish culture systems, grass carp are stocked in small quantities with other species to control macrophytes, a function which few other fish can perform. Only in China (especially southern China), Southeast Asia, and Malaysia are grass carp used as the major or only species which requires supplementary food, usually terrestrial grasses or silkworm cocoons (Lin 1954, Ji 1976, Anon 1977a, Tapiador *et al.* 1977).

They have been used successfully in fish-cum-duck polyculture (Ling 1971, Pekh 1971, Cheng 1976, Sin and Cheng 1976) and in operations where livestock wastes are used to fertilize ponds (LeMare 1952; Ling 1977; Buck, Baur, and Rose 1978a, 1979b, 1979). Grass carp tolerate high stocking densities from 8 400-27 000 fish/ha without detriment to either themselves or other species (Opuszyński 1968). Sen *et al.* (1978) determined that their presence enhanced the growth of Indian carp to the same extent as fertilization with manure. If lacking vegetative food, grass carp will take pelleted food, which they convert inefficiently, compared to other cultured species (Vinogradov and Zolotova 1974; Tal and Ziv 1978a, 1979b).

5.3.2 Artificial reproduction and rearing

Induced reproduction by injection of pituitary extracts (Section 3.1.6) became commercially applicable during the early sixties, in both China and the USSR (Lin 1965, Vinogradov 1968). This process led to other manipulations such as light intensity and temperature regimes to induce maturation at all times of year (Huisman 1979, Shireman *et al.* 1978b), intergeneric hybridization, production of gynogenetic all-female stocks (numerous papers by Stanley), and sex reversal by administration of methyltestosterone through silastic implants (Jensen, Shelton, and Wilken 1978, Shelton and Jensen 1979).

Sections 3.1.6 and 3.2.1 discuss the handling, incubation and development of eggs. Diets and controlled environments for intensive rearing of larvae, fry, and fingerlings (Section 3.5) have been investigated by Sharma and Kulshrestha (1974), Tamas and Horvath (1976), Shireman, Colle, and Rottmann (1977, 1978a), Huisman (1979), Meske and Pfeffer (1978), Murty, Dey, and Reddy (1978),

Venkatesh and Shetty (1978), Appelbaum and Uland (1979), Dabrowski (1979), Dabrowski and Kozak (1979), and Rottmann and Shireman (1979). Otherwise, fry and fingerlings are reared in small ponds. The preparation of culture ponds usually involves draining and/or curing as a measure to control predators and disease.

5.3.3 Disease control

The grass carp is susceptible to numerous diseases (Table XXXII) and treatments of the more important are described below. Bothriocephalosis, a nonspecific endoparasitic disease, was introduced along with grass carp into Europe and is treated by draining and/or curing infected ponds to kill cestode eggs and the intermediate host (*Cyclops* spp.) and by orally administering Kamala, Mansonil, or phenothiazine to infected fish (Musselius and Strelkov 1968, Ivasik, Kulakovskaya, and Vorona 1969, Bohl 1979). Kwahiosis, caused by another introduced cestode, has oligochaetes as the intermediate host and is controlled by the same methods (Bohl 1979). Antibiotics (administered in the feed, by injection, or with baths) are used to combat the infections and acute dropsies caused by various viral and bacterial pathogens (Dah-Shu 1957, Wu 1971, Bohl 1979). Prophylaxis with Furanace (Kim 1970, Huisman 1979) or copper sulphate (Shireman 1975, Shireman, Colle, and Rottmann 1976) has been successful against columnaris disease. Cryptobiasis can be prevented by eradicating the hirudinean vectors (Anon. 1972b) and can be treated with copper sulphate, saline and ammonia baths (Dah-Shu 1957, Ivasik, Kulakovskaya, Vorona 1969). With regard to ectoparasites, other useful chemicals which are administered through prophylaxis of fish or treatment of ponds, include malachite green, chloramine-T, hexachlorobenzene, formalin, quinine hydrochloride, lindane, Gammexane (Sathanur Dan), and potassium manganese (Dah-Shu 1957, Cross 1969, Edwards and Hine 1974, Prabhavathy and Sreenivasan 1977, Bohl 1979).

5.3.4 Yields

Some truly remarkable yields have been obtained in both monoculture and polyculture of grass carp. Annual production to 18 MT/ha has been claimed for Chinese polyculture operations in the Pearl River delta, though the national average falls in the 1.5-318 MT/ha range (Anon. 1977a). Bardach, Ryther, and McLarney (1972) estimates an average annual yield of 3-8 MT/ha in Far East polyculture. Dah-Shu (1957) described an instance of monoculture with grass carp stocked at 27 000 fish/ha in a blocked-off river channel and given supplementary plant food, that produced 13-19 MT/ha yearly. In Indian polyculture, with supplemental feeding, net annual production ranges up to 9.1 MT/ha with grass carp contributing 19 % by weight (Chaudhuri *et al.* 1975).

Since grass carp are usually a minor constituent in fish culture, gross national production figures are rarely available. In Malaysia, however, grass carp market sales are second only to bighead carp (*Hypophthalmichthys nobilis*) (Ji 1976). Austria cultured 20 MT annually and Korea produced 0.13-1.8 MT per year during 1971-1974 when only a few pilot scale farms were operating (Brown 1977).

5.4 Weed control

5.4.1 The problem of aquatic weeds and the applicability of grass carp

The potential of grass carp as a weed control agent has probably provided more impetus for its rapid spread than has its suitability as an aquaculture species. Eutrophication as a consequence of thermal and chemical pollution has greatly increased the aquatic macrophyte problems in many water bodies in recent years (Krupauer 1968, Liepolt and Weber 1969, Verigin 1979). Introduction of highly-competitive exotics such as hydrilla (*Hydrilla verticillata*) has also aggravated the situation (Miley, Van Dyke, and Riley 1979c). Bailey (1972), Nikolsky and Aliev (1974), Aliev (1976), Beach *et al.* 1976, 1977), Rottmann (1977), and many others reviewed the detrimental effects of macrophyte overabundance on navigation, drainage, water transport, recreation, ecosystem-protein production, parasitic insect control, and other properties of water bodies.

In many situations, the grass carp offers a very attractive alternative weed control in comparison to mechanical removal, chemical applications, water level manipulation, or other biological agents. Weed control with grass carp usually is less expensive and lasts considerably longer than other methods (Aliev 1963, Decell 1975, Aliev 1976, Rottmann 1977, Miley, Van Dyke, and Riley 1979c, von Zon 1979). Herbicides kill macrophytes quickly, effectively returning all nutrients to the water for later vegetative growth, and may have nonspecific or long-term toxic effects (Opuszyński 1972, 1979; Provine 1975; Guillory 1979; von Zon 1979). In experimental pools, Hestand and Carter (1978, observed that phytoplankton blooms occurred with the use of chemicals, but not with grass carp as a weed control. The relatively slow removable of macrophytes by grass carp not only prevents abrupt influxes of nutrients, but also converts some into highly-edible protein (Bailey 1972, Miley, Van Dyke, and Riley 1979c). Dewatering can be carried out in very few water bodies, but is often not desirable even if physically possible. The only other fish macrophyte biocontrols, other phytophagous fish such as tilapia (*Tilapia* spp.), do not have the low-temperature tolerance of grass carp

(Michewicz, Sutton, and Blackburn 1972a, von Zon 1974, Sutton 1977a). The possible effects of grass carp on the ecosystem are summarized in Table XXXVI.

5.4.2 Applications

Grass carp have been used successfully for weed control in a wide variety of situations and Jähnichen (1973) has attempted to quantify the use and cost effectiveness of the fish as a weed control agents. Their dual role in aquaculture has been mentioned in Section 5.3.1. Management of macrophyte overabundance has been achieved in many Soviet lakes, reservoirs, and canals, in particular the Kara Kum Canal and Khauz Khan Reservoir (Aliiev 1963, 1976; Nikolsky and Aliiev 1974; Aliyev 1976). Use of grass carp is being investigated with regard to the Panama Canal and its associated lakes (Panama Canal Company 1977, Custer *et al.* 1978). Many lake and pond studies have had positive results in the United States (Bailey 1978; Mitzner 1975b, 1978, 1979; many others). Glagolev (1963) and Verigin (1963, 1979) have pointed out the utility of grass carp for weed control in cooling reservoirs of electric generating stations and it is used for this purpose in Poland and other countries (Krupauer 1968). Grass carp may provide the only practical control method for water bodies which are used as drinking supplies and where herbicides cannot be used (Kobylinski *et al.* 1980). Fry can be reared in sown rice fields where they selectively remove unwanted plants and improve harvests. Yearlings are cultured in fallow fields, resulting in improved fertility (Bizyaev and Chesnakova 1966, Vinogradov and Zolotova 1974). Sutton (1974, 1975a) and others have suggested first removing the bulk of the macrophytes by chemical or mechanical methods and then using small stockings of grass carp to check regrowth. Shireman and Maceina (in press) discussed the management implications of using grass carp alone and with chemical treatments. Perhaps the most sophisticated

plan for utilization of the grass carp's phytophagous nature is growing duckweed (*Lemna* spp.) or a similar plant in eutrophic water such as secondarily-treated sewage effluent, and then feeding it to the fish to produce protein (Sutton 1977b).

5.4.3 Control of introduced grass carp populations

Though grass carp seldom compete with gamefish for natural or artificial food in polyculture ponds (Kilgen and Smitherman 1971, Kilgen 1973), their sometimes deleterious effects on ecosystems, under certain conditions (Sections 3.6.3 and 4.5), have encouraged research into ways of controlling introduced populations. Standard fish toxicants such as rotenone, antimycin, and thanite, as well as electrofishing, can be used to retrieve introduced stocks (Cumming, Burrell, and Gilderhus 1975), but these methods are not successful for removing large numbers (Shireman and Maceina 1980). Under some conditions (such as high oxygen content), rotenone may exhibit marked selectivity toward grass carp as opposed to other species such as largemouth bass (*Micropterus salmoides*) (Henderson 1974, Colle *et al.* 1978a, Hardin 1980).

The primary control on introduced populations is their usual inability to reproduce in confined water bodies (Vietmeyer 1976). The grass carp, however, has spawned outside its native range. Stocking therefore, should proceed with caution and environmental impacts should be conducted prior to release of the fish. Some countries have regulated the introduction of the grass carp, and in the United States, many states have banned its use (see Section 5.1.5). The use of sterile or monosex fish seems to offer a desirable margin of safety. Intergeneric hybridization may result in sterile phytophagous fish suitable as weed control agents (see Section 3.1.6).

Table XXXVI
Potential effects of stocking grass carp in an ecosystem

GRASS CARP	
MODERATE STOCKING	INTENSIVE STOCKING
<p>LOW MACROPHYTE DENSITY</p> <p>Macrophyte control and moderate nutrient increase in sediments, increase in emergent plants, possible reduction in recruitment of phytophilous spawners, potential plankton and benthos increases, exposure of plant-inhabiting animals to predation, possible production increases of predators (gamefish, etc.).</p>	<p>HIGH MACROPHYTE DENSITY</p> <p>Partial and/or temporary control and moderate nutrient increase in sediments, increase in emergent plants, changes the same, but not as extreme as with complete macrophyte control.</p>
<p>HIGH MACROPHYTE DENSITY</p> <p>Macrophyte elimination (overcontrol), initial nutrient increase in water and sediments.</p> <p>Phytoplankton bloom, reduction in recruitment of phytophilous spawners, possible changes in benthos population, exposure of plant-inhabiting animals to predation and elimination, shift from littoral to pelagic species.</p> <p>Possible increase in detritivores, decreased oxygen levels and pulses, slight reduction in pH.</p>	<p>LOW MACROPHYTE DENSITY</p> <p>Macrophyte control, nutrient release to water and sediments and temporary increase in emergent plants.</p> <p>Possible reduction in recruitment of phytophilous spawners, probable increased predation on plant inhabiting animals, probable production increases of predators (gamefish, etc.)</p> <p>Possible increase in detritivores.</p> <p>Decreased oxygen levels and pulses and a reduction in pH.</p> <p>Increased alkalinity.</p>

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