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Review

Tales of two fish: the dichotomous biology of crucian carp (*Carassius carassius* (L.)) in northern Europe

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Crucian carp, a common Eurasian cyprinid fish, shows striking dichotomies in several aspects of its physiology and ecology, at both the individual and population levels. These dichotomies consistently reflect the communities and ecosystems in which they occur, contrasting crucian carp that occur in "monocultures" (single-species fish assemblages) in ponds with those occurring in multi-species assemblages, primarily in lakes. Dichotomies also occur in the physiological state of individuals between summer and winter. All these dichotomies, involving differences in morphology and population structure, population dynamics and life history, reflect in an integrative way the adaptive strengths and limitations of a unique species. In numerous northern ponds, dense monocultures of crucian carp are sealed in by thick ice and snow to live more than six months in dark, anoxic waters at near freezing temperatures. In summer, these populations experience temperatures of up to 30°C during a relatively brief period of vigorous growth and repeated bouts of reproduction in almost continuous daylight. Crucians in lakes experience a more benign abiotic environment and, with densities that can be orders of magnitude lower than those in ponds, are likely unaffected by intraspecific interactions. However, co-occurring species present a challenging biotic environment. Crucian carp is exceptionally vulnerable to predation and populations persist via three kinds of refugia. Aided by extreme physiological adaptations, crucian carp can be the sole piscine inhabitant of seasonally harsh but productive small ponds, the *refugium habitat*, where they form dense monocultures of stunted individuals. The structural complexity offered by dense beds of macrophytes in productive larger lakes, the other common habitat (*habitat refugium*) of crucian carp, ensures survival of a few offspring, even in the presence of piscivores. The risk of predation still remains high for crucians until a certain length (and/or body depth), the *size refugium*, is attained. Crucian carp's unique anoxia tolerance, accompanied by many exceptional structural and functional features, and the species' suitability for laboratory studies, has recently raised crucian carp to a status of a physiological model species like its relative, the goldfish. Moreover, the dichotomy found in the structure of natural populations has made crucian carp an attractive model for ecological studies in competititon and predation. Crucian carp's resistance to adverse environmental conditions further suggests promising economical use in aquaculture to produce hybrids endowed with higher survival capacity than common carp.

1. Introduction

Perhaps more so than other fields of biology, a number of distinct approaches have been employed in ecological research, often more-or-less faithfully, by different groups of practitioners (Peters 1991). Conceptual ecology is based fundamentally on the search for general, synthetic notions about the way ecological systems operate, e.g., the equilibrium theory of island biogeography and the keystone species concept. Mechanistic ecology proposes that by identifying and quantifying components, one can (often by using a conceptual blueprint) build a functioning model of nature, e.g., individual-based models of populations, optimal foraging models. Predictive ecology operates by developing simple empirical descriptions of nature that relate response variables to one or more preconditions and predictors e.g., phosphorous-loading and chlorophyll-*a* models of eutrophication. However, another approach that has had a long history in ecology is the research program that has as its focus a particular organism or taxon. With such a focus, organism-driven researchers address questions, such as, what are the biological traits of a particular species that contribute to its success in certain habitats, but not in others? What are the biotic and abiotic factors that affect the ecological success of this species? How does its success or failure affect other components of the ecosystem? One can incorporate aspects of each of the previous aproaches into organism-driven ecological research; with a fortuitous choice of species, organism-based studies can make significant contributions to the development of ecological concepts and the understanding of ecological mechanisms. By exploiting well-founded organism-based ecological knowledge, one can develop meaningful biological indicators to use within a predictive ecology framework. Further, as suggested by the aforementioned questions, organism-centered research is not limited to the organismal level of the biological hierarchy and is not relegated to only investigating behaviour and physiology. An understanding of the distribution and abundance of a species requires consideration of the local and regional environment, therefore, organism-based ecology must also be integrated with population, community and ecosystem ecology.

Among the many notable examples of taxa successfully used for organism-based research in ecology and evolutionary biology are *Anolis* lizards (e.g. Spiller & Schoener 1990), European tits (*Parus* spp.; Krebs & Davies 1993, Verhulst *et al.* 1995) and the three-spined stickleback, *Gasterosteus* (Wootton 1984, Bell & Foster 1994). These taxa share at least some of the following attributes: i) they are found in communities or ecosystems that clearly illustrate, or exceptionally facilitate the study of important ecological processes or concepts, ii) they play a key role in their community or ecosystem, and iii) they possess especially interesting (or even unique) biological traits. We believe that Fennoscandian populations of crucian carp, *Carassius carassius* (L.) (Family Cyprinidae, Order Cypriniformes) satisfy many of the criteria listed above.

The littoral fish communities of European freshwaters are dominated by cyprinid species; the family Cyprinidae contains more than 80 indigenous species in Europe, many of which form dense populations (Lelek 1987). Many cyprinid species are eurytopic, shallow-water inhabitants and generally prefer or tolerate warm, nutrient-rich and even turbid waters. They often have effective feeding systems with broad diets (e.g. Junger *et al.* 1989), as well as high reproductive potentials. Because of their preferences and tolerances, cyprinids may be considered survivors, even benefactors, in the face of many anthropogenic threats, like cultural eutrophication and global warming. As a result, the ecological and even economical importance of many cyprinid species is increasing. Despite their general association with warmer water, cyprinids also fill important, often dominant, positions in the fish assemblages of northern Europe. Community analyses of non-salmonid fish assemblages in the lakes of Finland and Sweden identify a continuum from assemblages dominated by perch (*Perca fluviatilis*) in smaller, more oligotrophic lakes to assemblages dominated by roach (*Rutilus rutilus*), and other cyprinids in larger, more-eutrophic lakes (Tonn *et al.* 1990, 1995). These analyses (see also Zhakov 1974) also identify another relatively distinct set of assemblages dominated by (or containing exclusively) crucian carp. Crucian carp-dominated assemblages are found in very small, shallow, but often productive lakes and ponds. Eutrophic con-

ditions, when combined with seasonal stratification or long-lasting ice cover, in shallow water bodies, often lead to hypoxia. Few fish species are able to live in seasonally hypoxic environments. Perhaps the most specialized species for existing under such conditions in Europe is crucian carp.

Relying on its exceptional physiological adaptations to low oxygen conditions, crucian carp is frequently the only fish species in a commonly found habitat, seasonally hypoxic ponds. However, it is also a member of multi-species, roach-dominated fish assemblages in large lakes (Brönmark *et al.* 1995). A clear dichotomy in morphology, population structure, and even life history is found between crucian carp from these communities. The ecological factors operating in small ponds are quite different from those in multi-species, often predator-regulated fish communities. In many Scandinavian forest ponds, the annual cycle for crucian carp, can be divided into three main periods: growth and multiple reproductive episodes in early summer, reserve build-up in late summer, and anoxic overwintering. Each period makes specific functional demands and the shifts from period to period need considerable metabolic rearrangements, particularly adaptation to the period of torpor during anaerobic winter conditions.

In this paper, we review the general biology of crucian carp and examine the two contrasting ecological strategies that arise from its unique biology. Specifically we focus on crucian carp's high tolerance to abiotic, environmental stressors and its contrasting sensitivity to biotic factors, especially predation.

2. Distribution and relatives

The genus *Carassius* Jarocki 1822 contains two closely related species in European freshwaters: *C. carassius* (L.), the common crucian carp, and *C. auratus* (L.), the silver crucian carp or goldfish (Berg 1932, Libosvarsky 1962, Penaz *et al.* 1979). Since some forms of *C. auratus* resemble *C. carassius* morphologically and are often informally called "crucian carp", some confusion may still arise between the two species and among the various subspecies or forms.

Carassius spp. are warm-water species belonging to the boreal fish group (Libosvarsky 1962) and have widespread, continuous distribution in Eurasia. With probable origins in East Asia, both species had a wide distribution in Eurasia before the Wisconsin glaciation. Surviving this colder climatic period in southern and eastern refugia, they effectively redispersed to central and north European waters (Libosvarsky 1962). The present distribution of common crucian carp includes most of Europe, and ranges from the Arctic Circle in Scandinavia to central France and the Black Sea in the south, and from England to the Lena River in Russia (Libosvarsky 1962, Lelek 1987). It is common in the watersheds of the Baltic and the North Seas, including central Fennoscandia. The natural distribution of the species is not certain, however, since the present limits are thought to represent many successful introductions. Nevertheless, Lelek (1987) classifies the current status of common crucian carp as "rare to vulnerable" because of a reduction in suitable habitat and competitive replacement by goldfish in areas of sympatry (e.g., Lusk *et al.* 1977).

It has long been recognized that crucian carp occurs in two distinct forms, although the status of these forms has changed from time to time. The stunted or pond form of *C. carassius (C. vulgaris* Nilss.) has been called *C. c. gibelio* (Ekström 1838, Nilsson 1855, Ekman 1922) in contrast to the lake form, *C. c. vulgaris* Kroeg (Valle 1934, Kivirikko 1940). More recently, the pond form has been called *C. carassius morpha humilis* Heckel 1840 (Cerny 1971, Mikelsaar 1984, Lelek 1987).

Goldfish (*C. auratus* (L.)) originated in eastern Asia but cultured varieties have repeatedly been introduced in Europe (possibly as early as 1611) to be kept in ornamental ponds and aquaria. At present wild (or feral) forms of *C. a. auratus* are common in European natural waters (Libosvarsky 1962, Lusk *et al.* 1977). Another subspecies, *C. a. gibelio* (Bloch 1783), the silver crucian carp (Berg 1932), is also found in European waters. It is often considered indigenous since it fits a description by Gessner in 1558, well before any known introductions from Asia. This subspecies is thought to be more western in origin, and native from Siberia to eastern Europe (Libosvarsky 1962). As a result of introductions (e.g. Curry-Lindahl 1985), *C. a. gibelio* now lives sympatrically with *C. carassius* in many areas in western Eu-

rope. It appears to be expanding in some regions, such as the Danube River drainage (Holcik 1980). Silver crucian carp occurs in the Baltic countries (Mikelsaar 1984), southern Sweden and southern Norway but is not found in Finland (Koli 1973, 1990, Curry-Lindahl 1985, Lelek 1987).

According to Hensel (1971), *C. a. auratus* and *C. a. gibelio* are morphologically undistinguishable and Lelek (1987) describes gibelio as a geographic variant of the goldfish. However, based on karyological analysis, Penaz *et al.* (1979) recommended recognition of the subspecific classification of the two forms of goldfish.

Several other forms or subspecies of *C. auratus* are reported from Japan (Okada 1960, Hensel 1971, Penaz *et al.* 1979). Both *C. a. auratus* and *C. a. gibelio* (Lieder 1959), as well as some forms from Japan, are reported to have natural gynogenetic populations that produce all-female, triploid (3n = 150) progeny (Hensel 1971, Penaz *et al.* 1979, Sezaki *et al.* 1991). In contrast, crucian carp (*C. carassius*) is reported to have only diploid populations with equal numbers of males and females.

Morphometric data for different developmental stages of crucian carp, in comparison with *C. a. gibelio*, are found in Schaeperclaus (1953) and Dmitrieva (1957), and for the adult stage, along with data for both goldfish subspecies, in Hensel (1971). Very briefly, crucian carp is best distinguished from goldfish by the low number (21–34) of gill rakers on the first pharyngeal arch. In goldfish these gill rakers number 39–50 or more (Berg 1932, Hensel 1971).

3. Seasonality and physiology

3.1. Environmental tolerance and overwintering behaviour

Crucian carp is known for its wide tolerance range for a variety of abiotic factors. It can tolerate temperatures from 0 to 38°C (optimum at 27°C; Lenkiewicz 1964, Horoszewich 1973), low pH down to 4 (Bryukhatova 1937, EIFAC 1969, Holopainen & Oikari 1992) and survive in anoxic waters for several months at low temperatures (Blazhka 1960, Holopainen & Hyvärinen 1985, Piironen & Holopainen 1986).

The biologically unique and ecologically significant adaptation of crucian carp to the long, cold and anoxic winter is ensured by several behavioural and physiological mechanisms. Locomotory activity is seldom required in winter because crucians fast (Penttinen & Holopainen 1992) and predators are absent in anoxic waters. Being inactive, crucian carp do not enter traps during winter but can be caught in large numbers by active fishing methods, e.g. seining (Holopainen unpubl.). In simulated winter conditions in the laboratory (+ 2°C, $O_2 < 1$ mg l^{-1}, darkness, see Holopainen & Hyvärinen 1985), fish voluntarily fasted (i.e., refused to eat, see also Vornanen 1994b) and stayed inactive close to the tank bottom, but maintained a horizontal orientation and were capable of swimming when disturbed. These fish may have employed a mixed aerobic–anaerobic metabolism (Blazhka 1958). Goldfish behave similarly in a closed respirometer (Van den Thillart & van Waarde 1991). Nilsson *et al.* (1993) have quantified the anoxic depression in spontaneous locomotory activity of crucian carp in the laboratory.

In northern Europe, general failure to trap or gill net any crucian carp in winter, even from populations known to be dense, gave rise to the idea that this species overwinters within the bottom sediment. Furthermore, the inshore habitat of lakes and ponds that are frequently used by crucian carp are generally believed to be shallow enough to freeze solid, forcing the fish to burrow into the mud. Although burrowing has not been empirically confirmed (or refuted), indirect evidence from the field and laboratory, suggest that locomotory inactivity is the main reason why crucians are absent from winter catches. Practically no information on the winter behaviour of crucian carp in very shallow waters (< 1-m deep) or in large lakes is available.

3.2. Anaerobiosis

In addition to behavioural adaptations, such as fasting and inactivity, crucian carp has physiological capabilities for overwintering in hypoxic or anoxic water that combine several different elements. Indeed, crucian carp is among the vertebrate species most tolerant of environmental anoxia (Van Waarde *et al.* 1993).

A large body of knowledge on the physiology of hibernation and/or anaerobiosis of ectothermic vertebrates has been reviewed by Hochachka (1980), Hochachka and Guppy (1987), Ultsch (1989) and Hochachka *et al.* (1993). Physiological problems encountered during extended environmental anoxia are related to high substrate requirements for energy production by glycolysis only, and to the toxicity of acidic end-products of glycolytic catabolism.

Blazhka (1958, 1960) was the first to report that crucian carp can survive up to 5–6 months of anoxia in natural ponds. In the pond form of crucian carp, seasonal tolerance of anoxia, in addition to prevailing low temperature with low metabolic demands, is based on the ability to (1) collect carbohydrate reserves large enough to allow fasting and the use of inefficient metabolic routes throughout a prolonged winter (> 6 months), (2) to use alternative metabolic routes, with ethanol, CO_2 and ammonia as end-products, and (3) to depress the metabolic rate down to 20–30 % of the aerobic rate. It is not known to what degree these capabilities are possessed or used by fish in lake populations. In Central Finland (62°N) the shift in the energy allocation from growth and reproduction to the build-up of glycogen stores, for crucian carp in small ponds, occurs in July, when liver size and the glycogen content of both liver and muscles begins to increase. This shift may be controlled by a decrease in day length or water temperature. Swimming and feeding activities end two months later, in late September–early October (Penttinen & Holopainen 1992), which may also be triggered by temperature. In the laboratory, low temperatures (< 5°C) alone will induce fasting, even with a constant light cycle and high oxygen concentrations (see above). By late October, liver size increases from the summer minimum of 2% to 15% of body wet mass and hepatic glygocen content increases from 3% to 35% (Hyvärinen *et al.* 1985). This build-up is accompanied by a simultaneous increase of muscle glygocen to levels up to 4% of wet mass (Fig. 1, Piironen & Holopainen 1986). Vornanen (1994a) demonstrated a clear seasonal cycle in glycogen content for crucian carp heart with massive winter accumulation (8% of wet mass).

In vertebrates, the ethanol pathway was first described as a component of anaerobic metabolism of goldfish (Shoubridge & Hochachka 1980, 1981) and has since been demonstrated from only two other fish (both cyprinids), the crucian carp (Johnson & Bernard 1983, Holopainen *et al.* 1986, Van den Thillart & van Waarde 1991) and the bitterling, *Rhodeus sericeus amarus* (Bloch 1782) (Wissing & Zebe 1988). Lactate produced in anoxic cellular metabolism is transported to myotomal muscles for conversion to ethanol, which is a relatively harmless compound, easily excreted via the gills into the surrounding water. A high activity of alcohol dehydrogenase is found in red and white muscles of crucian carp. The quantitative dynamics and balance between carbohydrate reserves and metabolic products by goldfish and

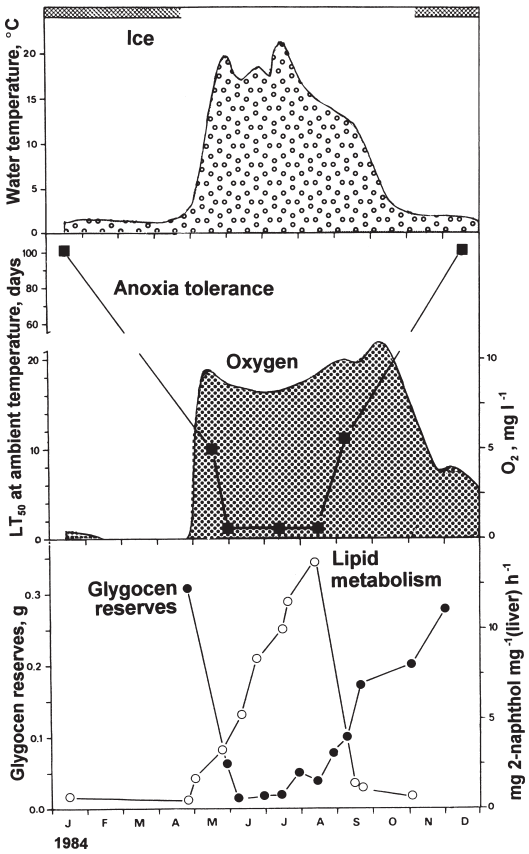

Fig. 1. Seasonality in the environment and in the life of crucian carp in Lake Hermanninlampi in eastern Finland (Piironen & Holopainen 1986). The absolute amount of glycogen reserves refer to a 10-g fish in October. The activity of lipid metabolism is described by activity of the lipase esterase enzyme in the liver (Hyvärinen *et al.* 1985).

crucian carp under anoxic conditions are reviewed by Van Waarde *et al.* (1993).

Metabolic arrest (Hochachka & Guppy 1987), a dramatic drop in metabolic rate, is a common characteristic of anaerobiosis and an important factor for maintenance of pH and ion homeostasis. Metabolic heat production of goldfish during anoxia decreased to 28% of the normoxic rate (Van Waversveld *et al.* 1989). Comparable responses are probable for crucian carp, although not as yet documented. The anoxia tolerance of juvenile bitterling was reported to be 2–3 hours at 12°C (Wissing & Zebe 1988). The anoxic metabolism and capacities of goldfish have been studied for a long time (e.g., Egashira 1935). Anoxic survival times are 6–8 days at 4°C for laboratory acclimated goldfish (Walker & Johansen 1977). Van den Thillart *et al.* (1983) reported LT_{50} values of 22 h (at 20°C) to 45 h (5°C) and 65 h (10°C) in anoxia for goldfish after 4 months of temperature acclimation in the laboratory. Piironen and Holopainen (1986) demonstrated a clear seasonality in the anoxia tolerance of crucian carp; in the laboratory 6–10-cm fish from a natural pond survived ca. 20 hours of anoxia in summer (at 18°C) but > 160 days in winter (at 2°C) (Fig. 1). The performance of winter fish also displayed a temperature dependency; at 9°C the LT_{50} value was only 25 days.

3.3. Winter torpor in brain and heart

The cessation of activity during winter is a behavioural response that contributes to the ability of crucian carp to withstand anoxia but also constrains a fish's ability to feed, search for profitable habitats, etc. Crucian carp experience a number of other physiological and biochemical changes during anoxia/anaerobiosis that can also be viewed as trade-offs. For vertebrates, maintaining functions of the brain and heart are among the most important requirements for achieving homeostasis in the face of changing environmental conditions. However, several studies suggest that considerable adaptive changes occur in various enzymatic functions within the brain and heart of crucian carp in response to hypoxia (Nilsson *et al.* 1993, Vornanen 1994a).

Schmidt and Wegener (1988) detected significant stores of glycogen in the brain of crucian carp and demonstrated hypoxia-induced changes in the relative proportions of three forms of glycogen phosphorylase. In goldfish, O'Connor *et al.* (1988) and Crawshaw *et al.* (1989) demonstrated thermoregulatory changes as a result of anoxia exposure and/or experimental injection of ethanol in the brain. These treatments caused fish to select lower environmental temperatures, an adaptive response that would contribute to energy conservation. Such behaviour is especially effective if organ systems show inverse compensation, as discussed below for the circulatory system of crucian carp.

Pronounced changes also occur in levels of many neurotransmitters in the brain of crucian carp following exposure to anoxia (Nilsson 1990, 1991). Generally, inhibitory compounds increase and excitatory ones decrease. These changes are probably largely responsible for the lowered physical activity and metabolic arrest in crucian carp in anoxic waters (Nilsson 1992, 1993, Nilsson *et al.* 1993, 1994, Johansson & Nilsson 1995). The typical vertebrate heart is a strictly aerobic organ that normally displays increased activity to compensate for low temperatures. Studies of the heart function of crucian carp (Vornanen 1989, Matikainen & Vornanen 1992, Vornanen 1994a), however, have demonstrated inverse thermal compensation, an important mechanism for minimizing energy consumption during winter. Indeed, inverse temperature compensation is a common reaction in ectotherms capable of cold torpor (Hochachka & Guppy 1987). Vornanen (1994a) suggests that the crucian carp heart tolerates the long hypoxic winter by suppressing energy consumption, through a strong bradycardic reflex, and by using the massive glycogen stores in its tissues for anaerobic metabolism. Ample lactate dehydrogenase activity facilitates a steady glycolytic flux in the heart. Other changes in the structure and function of the crucian carp heart induced by low temperature and anoxia have been investigated by Vornanen (1994b, 1996) and Pelouch and Vornanen (1996).

4. Food and feeding

Both the high frequency of empty guts and low enzymatic activity, from late autumn to spring, among crucian carp from ponds facing winter anoxia, indicate that the main period of active feed-

ing is restricted to the summer (Penttinen & Holopainen 1992). Like other cyprinids, crucian carp lack oral teeth and a stomach, but they do have strong pharyngeal teeth for food processing (Sibbing 1988) and a long coiled gut (Junger *et al.* 1989). Planktonic and benthic invertebrates form dominant part of the diet in all size-classes (Szlauer 1971, Andersson *et al.* 1978, Penttinen & Holopainen 1992, Paszkowski *et al.* 1996); plant material (Prejs 1973, 1984), phytoplankton (Hyvärinen 1964) and detritus (Penttinen 1990, Paszkowski *et al.* 1996) are commonly found in the gut, but their nutritional value for crucian carp is not known. Among five lakes studied by Uspenskaja (1953), molluscs dominated the diet of crucian carp (13–16 cm) in three lakes, chironomid larvae in one lake, and cladocera dominated in the final lake. Together these three groups of invertebrates accounted for 70% of the prey consumed within the five lakes. Penttinen and Holopainen (1992) studied the diet of crucian carp across the size range (1 to 15 cm total length) typically found in monospecific forest ponds. No strong ontogenetic diet shift was observed, but the dominance of food items gradually changed from planktonic microcrustaceans to benthic cladocerans and chironomids. Only fish > 13 cm complemented their diet with large odonate larvae. Paszkowski *et al.* (1996) found that the guts of crucian carp captured inshore contained a predominance of benthic cladocerans, whereas larger individuals captured offshore contained more chironomids.

According to Nikolsky (1963) and Szlauer (1971), feeding in crucian carp is not dependent on light intensity and the species forages successfully at night. Siegmund and Wolff (1972) reported nocturnal ativity for crucian carp during winter at 20°C in a constant L:D 12:12-rhythm in the laboratory. In March, however, the fish became active diurnally and their body colouration turned lighter. Further, both goldfish (Spieler & Noeske 1984) and crucian carp (Rosenfeld *et al.* 1985) are reported to show diurnal peaks in locomotory activity, although this cycle can be altered by feeding patterns, etc. The days are long during the northern European summer: in Joensuu, Finland, the period of daylight is 16, > 20 and 14 hours in early May, late June and late August, respectively. Based on successive 3-hour catches of crucian carp in mid-August in the presence of perch and pike in a small natural pond, Holopainen *et al.* (1988) reported a diurnal activity peak for larger fish in the offshore habitat (> 5 m from the shoreline), whereas most of the smaller fish were caught inshore at night. In this system, daily activity patterns (as well as habitat selection) appeared to be governed by food availability and predator threat, in addition to photoperiod (see Section 7.2).

5. Reproduction, growth and longevity

Temperature, rather than photoperiod, is generally reported to control the timing of ovulation and spawning in cyprinids, e.g., goldfish (Bye 1984) and crucian carp (Seymour 1981). Like most European cyprinids, the spawning season for crucian carp is from late spring through mid-summer, after water temperatures in the littoral zone warm; water temperatures of 17–20°C are needed for spawning (Hakala 1915, Schäperclaus 1953, Astanin & Podgorny 1968, Seymour 1981). Crucian carp is a phytophilous, open substrate spawner with eggs that adhere to submerged twigs and macrophytes. During the spawning season, the head and scales of both males and females develop tubercles in the epithelium.

Crucian carp is an intermittent spawner; females deposit eggs in temporally discrete batches (Kryzhanovskii 1949, Pihu 1961, Astanin & Podgorny 1968). In Estonia (Pihu 1961) and Central Finland (Moisander 1991) three periods of spawning have been commonly observed from late May to mid-July, with females producing similar numbers of eggs during each bout (Pihu 1961). This intermittant spawning pattern may result in separate size-classes among young-of-the-year fish (Piironen & Holopainen 1988).

The gonadosomatic index of female crucian carp (GSI, gonad weight as a percentage of fish weight) decreases from May to mid-July. Moisander (1991) compared two Finnish water bodies, one containing a "lake" population (piscivores present, low density of crucian carp) and the other a "pond" population (no piscivores, high density) and found GSI values to be significantly higher in the lake-type population (Table 1). Similarly, the relative fecundity (numbers of mature eggs per gram of fish) was higher in large-bodied fish

from the "lake" population (Moisander 1991). This appears to be due to the size difference so that at the same weight (which the pond fish reach at larger length and higher age) the fecundities are equal. These results are in agreement with those of Pihu (1961), who stated that both the absolute and relative fecundity of crucian carp increases with increasing body size. Published data on the size of eggs are variable; usually a diameter between 1 and 2 mm is given for fertilized eggs. A sample of eggs from a pair of ovaries may contain several size classes and the diameter of eggs depend on sampling time and the preservation methods used. When in contact with water and at fertilization the eggs swell. In general, larger females from multi-species communities with better food availability and higher overall growth rate, seem to have larger reproductive efforts, with higher absolute and relative fecundity and larger eggs (Table 1).

In the laboratory the fertilized eggs of crucian carp develop normally at 15–28°C but die at 5, 10 and 30°C. Incubation time from fertilization to the free embryo stage was shortest (< 3 days) at 24–28°C. In two natural ponds in eastern Finland, eggs hatched in 6 days (at 18–19°C; Laurila *et al.* 1987). The length of free embryos was 4.5–5.5 mm at hatching and they started to feed in 2–4 days (Laurila & Holopainen 1990). Highest larval growth rate (0.32 mm day^{-1}) was achieved at 28.5°C in the laboratory (Laurila *et al.* 1987).

The size attained by young crucian carp during their first summer of life is highly variable because spawning and hatching encompasses a period > 2 months. In a manipulated forest pond in eastern Finland containing low densities of crucian carp, Piironen and Holopainen (1988) found that the length of 0+ crucian carp ranged from 2.5 to 10.5 cm in April–May 1984. Three peaks within the size distribution, at 3.5, 6 and 9 cm, were interpreted to represent the respective average length of young from three successive spawning periods during the previous summer. Growth conditions were considered optimal because of the very low densities of crucians present (population density of 1+ and older fish was 0.02 m^{-2}) in summer 1983 after an experimental removal of the natural, high-density population. The respective peaks in the 0+ length distribution in spring 1987 were at 2.2, 3.3 and 4.2 cm, when the population density of 1+ and older fish was 0.77 m^{-2}. According to Schäperclaus (1953), crucian carp grew to a maximum length of 9.5 cm in their first summer in German ponds and the fastest growing individuals also displayed the deepest bodies. Skóra (1982) reported lengths ranging from 4.2 to 10.9 cm for F_2 carp–crucian carp hybrids after one growing season in fish ponds in Poland. The growth of crucian carp is highly density-dependent as discussed below (see also Tonn *et al.* 1992, 1994). Direct measurement of growth rates of crucian carp in multi-species assemblages in lakes is rare, but the available

Table 1. Reproductive statistics of crucian carp in two contrasting populations in 1989 (Moisander 1991). GSI is gonadosomatic index or 100(Wo/Wf) where Wo is ovarian mass and Wf is fish total mass. Gonad stage IV refer to maximum size, non-flowing ovarium (Nikolsky 1963). "Formalin" or "Gilson" refer to egg or gonad preservation method.

	Lake Varaslampi	Lake Hermanninlampi
Lake size, ha	4.5	1.5
Max. depth, m	4	1.6
Fish species present	7	1
Crucian carp density	low	high
Catch size	37	133
Female size range, cm	15–40	11–19
Average length, cm	32.4	14.1
Average wet mass, g	942.9	43.6
Egg diameter (mm) in ovarium (ripe with yolk; formalin)	1.0 (0.85–1.34)	0.74 (0.62–0.91)
Egg dry mass, mg (Gilson)	0.215	0.144
GSI (at gonad stage IV)	11.8 (*S.D.* = 6.7)	6.7 (*S.D.* = 2.1)
Relative fecundity (eggs g^{-1} fish)	129.2 (*S.D.* = 68.7)	83.2 (*S.D.* = 28.8)

evidence (e.g., Holopainen *et al.* 1997) suggest rapid growth because of low densities and ample food availability.

6. Dichotomy in the habitats and morphology of crucian carp populations

The retreat of the ice after the last glaciation left Scandinavia with thousands of small lakes. In Finland alone there are 56 000 lakes > 1 ha, and > 130 000 ponds 0.05–1 ha (Raatikainen 1987). About half of the freshwater fishes occurring in Fennoscandia are able to live in small forest lakes (Tonn *et al.* 1990, 1995), but most of the species are concentrated in the larger, less isolated and less acidic of these water bodies. Small ponds are often characterized by brown water, low pH, shallow depth and hypoxia during the long northern winter, making them uninhabitable for most other fishes, but suitable habitats for crucian carp. Because it can tolerate a wide range of abiotic conditions, crucian carp is a consistent exception to the ordered distribution pattern. The distribution of crucian carp tends to be bimodal, occurring regularly in both small ponds (often as the only fish species present; likely introduced into many as a source of bait fish) and in larger, species-rich lakes (Zhakov 1974, Tonn *et al.*1990, Brönmark *et al.* 1995). This bimodality, or dichotomy, in the distribution of crucian carp is also seen in many other aspects of the species' ecology as well as in morphology and physiology.

The dichotomy, which is reflected in differences in population density, fish size and other morphological characteristics, has led to the recognition of two different kinds of populations — the pond crucian carp and the lake crucian carp. Although these forms have been given taxonomic status by some (see above), they cannot be considered ecotypes since there is no evidence of genetic differentiation. On the contrary, transplants strongly suggest that dichotomies in population characteristics and body morphology are environmentally induced (Ekström 1838, Holopainen & Pitkänen 1985, Holopainen *et al.* 1997). Despite references to "pond" and "lake" forms, a number of comparative studies have indicated that the dichotomies are more strongly related to the presence or absence of piscivores than to the size of the native water body or to other abiotic characteristics (Holopainen & Pitkänen 1985, Piironen & Holopainen 1988, Brönmark *et al.* 1995, Poléo *et al.* 1995).

In the largest of such surveys, covering over 600 Swedish lakes and ponds over a wide geographical area, populations of crucians in both lakes and ponds lacking piscivores were dominated by small-bodied fish (mean 9.2 cm, 20 g), with few individuals > 17–20 cm (Brönmark *et al.* 1995). In lakes and ponds where piscivorous fish were present, populations were composed almost exclusively of fish > 20 cm (mean 31.3 cm, 735 g; the size record for crucian carp, 4.7 kg, is from a small eutrophic lake in southern Finland, but fish up to 2 kg are commonly found). Densities of crucian carp (based on catch-per-unit-effort) were some 40 × higher in waterbodies without piscivores (Brönmark *et al.*1995). Other studies indicate that absolute densities are < 100 individuals ha^{-1} in multispecies fish communities (Hamrin 1979) but several thousands or tens of thousands per hectare in monospecific ponds; 29 000 crucians ha^{-1} (87 kg ha^{-1}) were removed with rotenone from Hermanninlampi in eastern Finland (Holopainen & Pitkänen 1985, Piironen & Holopainen 1988). Even higher densities have been reported from Central Europe and Russia (e.g. Cerny 1971, Nikolskiy & Shubnikova 1974). Experimental studies have confirmed the role of piscivory in producing these population level dichotomies (see below).

In addition to divergence in population structure, the body shape of the "pond" and "lake" forms differ. Although the data of Oissar (1965), for crucian carp of both the pond and lake forms in Estonia, revealed differences in 3 meristic and 21 plastic characters, the most important differences seem to be in relative body depth and head size. The height index (100 height/length) for seven populations of crucian carp from small ponds and larger lakes in eastern Finland (four from one-species and three from multispecies fish communities) ranged from 26 to 43 (Holopainen & Pitkänen 1985). The index increased with size up to the length of ca. 16 cm, but tended to decrease after that. Poléo *et al.* (1995) studied 21 lakes or ponds in Norway and reported a larger size and deeper body depth for crucian carp in lakes with predators. A comparison of crucian populations

Fig. 2. Two specimens of crucian carp representing contrasting populations in eastern Finland. Both are of the same length (19.8 cm) but differ mainly in body depth and relative head size. The upper is from a multi-species fish community (Lake Varaslampi, the smallest specimen caught) and the lower from a one-species assemblage (Lake Hermanninlampi, ca. 12 km from Lake Varaslampi; the second largest fish caught; see also Fig. 3).

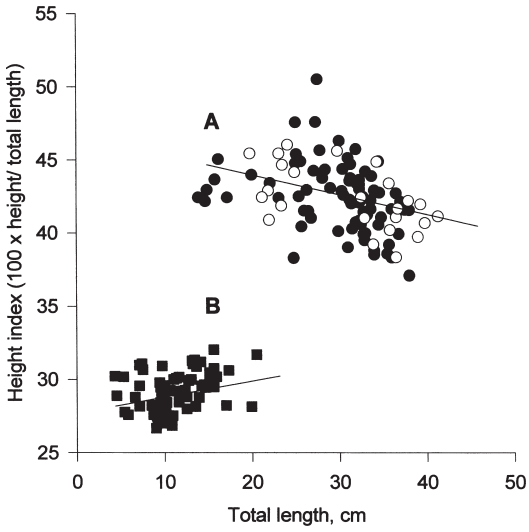

Fig. 3. Morphometry of crucian carp from contrasting populations. — A: Fish from the multispecies Lake Varaslampi; the dots are fish caught by Moisander (1991) and the circles refer to material by Holopainen *et al.* (1996). — B: Fish from Lake Hermanninlampi with crucian carp as the only fish present.

from two ponds near Joensuu, Finland (Figs. 2 and 3), showed that the height index from the pond lacking piscivores (crucian carp only) was smaller (26–33) than the values for fish from the pond with piscivores (37–47; Holopainen *et al.* 1997). Equally, an introduction of small, low-bodied crucian carp to a fishless, but productive pond, resulted in rapid growth and dramatic change in shape towards "lake type" crucian carp in three months time (Holopainen *et al.* 1997).

We now recognize that body shape is not a genetically determined trait in crucian carp but a plastic morphological feature that can change with environmental conditions. Growth patterns of crucian carp alter so as to produce a deeper body under two conditions: 1) the presence of piscivorous fish and 2) increased availability of food in the absence of piscivores. Recently, the greater relative body depth of crucian carp from multi-species communities has been proposed to be an induced defense against gape-limited predation (Brönmark & Miner 1992). Brönmark and Miner (1992) first noted that crucian carp of a given length developed deeper bodies in the presence of piscivores during experiments in small Swedish ponds (0.1 ha) that had been halved with curtains to create a section with crucians alone and a section with crucians plus pike (*Esox lucius*). This result paralleled the occurrence of deep bodied crucians in larger lakes, where piscivores are typically present, versus shallow bodied crucians in ponds where piscivores are typically absent.

Several subsequent laboratory experiments (Brönmark & Miner 1992, Brönmark & Pettersson 1994, Holopainen *et al.* 1997) verified that these phenotypic differences were growth responses linked to the presence of predators. Increased body size has repeatedly been demonstrated to protect fishes from gape-limited predators (Tonn & Paszkowski 1986, Hambright 1991, Tonn *et al.* 1991, Paszkowski & Tonn 1994) either by offering an absolute refuge or by making larger individuals less profitable, less attractive prey. Of course, an increase in body length is usually accompanied by an absolute increase in body depth. Experiments by Nilsson *et al.* (1995) showed that, when length differences were corrected for, pike displayed increased handling times for deep-bodied versus shallow-bodied crucian carp. Consistent with handling costs, pike preferred shallow-bodied over deep-bodied crucians in choice trials.

A deep body does appear to offer crucian carp protection from piscivores and to develop in the presence of these predators, but what processes and cues are responsible for the change in body

form? Laboratory experiments by Brönmark and Pettersson (1994) showed that chemical cues from pike or perch feeding on crucian carp could trigger deepening of the body. Exposure to perch-fed chironomids or crucian carp alarm substances alone did not trigger growth changes. Nilsson *et al.* (1995) and Holopainen *et al.* (1996) noted that exposure to piscivores resulted in reduced activity in crucian carp. Holopainen *et al.* (1996) also recorded reduced heart beat and respiration rates in the presence of predators and proposed that energy savings could be shunted to growth, specifically to deepening of the body (cf. Koch & Wieser 1983, Nilsson *et al.* 1993). Holopainen *et al.* (1996) found that when a variety of morphological features were compared between lake (with predators) and pond (without predators) populations, the deeper body was achieved through growth of the epaxial musculature and associated bony supports. Relatively deeper bodies are also seen in crucian carp in the absence of piscivores, when population densities are low and/or food is abundant. This has been documented in a number of whole-pond manipulations when either a low number of "stunted" crucians were introduced into an empty (food-rich) pond (Holopainen & Pitkänen 1985, Holopainen *et al.* 1997) or comparisons were made between low- and high-density populations inhabiting different sections of the same pond (Tonn *et al.* 1992).

Brönmark and Miner (1992) proposed that crucian carp develop a deep body only when actually threatened by predators because of the increased cost of swimming with a gibbous shape (due to drag). We may ask that if this body shape is such a handicap, why would crucians ever become deeper-bodied in the absence of predators? On the other hand, if this body shape is so advantageous in protecting them from predators, why don't all crucians grow rapidly in the presence of predators (e.g., Tonn *et al.* 1991)?

In any case, a 20-cm crucian from the predator-free pond near Joensuu would have a body depth of 6 cm whereas a fish of the same length from a pond with piscivores would have an average depth of 9 cm (Moisander 1991, Holopainen *et al.* 1997). Although not examined directly in crucian carp, results of studies with other species would suggest that such a difference in body shape could significantly reduce vulnerability to gape-limited predators (Hambright 1991), especially the perch and small pike that are the typical piscivorous fishes in Fennoscandian ponds (Piironen & Holopainen 1988). In lakes with larger piscivores, the morphological refuge may be attained via an overall larger size rather than a greater body depth. Interestingly, at lengths greater than 15–20 cm, the height index decreases (Holopainen & Pitkänen 1985, Holopainen *et al.* 1997) as if a greater body depth is no longer a necessary morphological refuge. We would argue that a deep body can only be attained if food is adequate. If crucians become inactive in the presence of predators and the local food supply is low (e.g., due to high densities of fish seeking refuge in littoral vegetation), growth in body length and depth may be retarded (Holopainen *et al.* 1991, Tonn *et al.* 1991, Paszkowski *et al.* 1996). In the absence of predators, crucian densities are constantly high so that food is universally scarce, growth is low, and crucians can not lay down or maintain normal masses of muscle tissue.

7. Population regulation

As noted earlier, comparative studies and transplant experiments have indicated that the dichotomous structure of "lake" and "pond" crucian carp populations is caused by biotic interactions rather than their being the result of abiotic environmental differences between these two types of habitats. Furthermore, the structural differences themselves reflect the operation of different ecological processes that regulate these populations. We have integrated laboratory and field studies to understand the dynamics of these two types of crucian carp populations in northern Europe. Using patterns observed in natural populations in eastern Finland as our starting point (Holopainen & Pitkänen 1985, Piironen & Holopainen 1988), we conducted a series of laboratory experiments (Paszkowski *et al.* 1989, 1990) to examine the mechanistic basis through which biotic interactions contribute to population regulation and the production and maintenance of the two population types. These experiments were complemented by whole-pond manipulations of predators (Tonn *et al.* 1989, 1991, 1992, Holopainen *et al.* 1991) and the density of crucians (Holopainen *et al.* 1992,

Tonn *et al.* 1994) to examine the direct and indirect effects of predation and intra-specific competition on population-level processes at realistic spatial and temporal scales.

7.1. Intraspecific competition

Laboratory experiments offer an effective approach for documenting feeding patterns in fishes that are often difficult to observe under natural conditions (e.g. Werner & Hall 1974). Because they adapt well to tank environments, crucian carp are excellent subjects for such controlled behavioural observations. At the high densities typical of crucian carp populations occurring in monospecific ponds, food limitation leading to strong intraspecific competition is assumed to be responsible for stunting and perhaps for abbreviated life spans. The largely overlapping diet (see above) tends to enhance intraspecific competition, e.g., chironomids are a prominent part of the diet of all sizes of fish.

Handling times and return rates (mass of prey ingested per time invested in handling) for different sizes of crucian carp eating different sizes of prey was used to infer competitive abilities, especially to examine the premise that small individuals are at a competitive disadvantage (Paszkowski *et al.* 1989). Handling times were recorded for crucians of 5–14 cm (total length) eating artificial prey (pieces of cooked spaghetti) 1–16 mm long. Results suggested that the two smallest size-classes, 5-cm and 7-cm fish, were "inferior" competitors compared with larger crucians. Return rates for all sizes of prey were lower for 5-cm and 7-cm crucians than for larger fish and "diet breadth" was limited as return rates declined dramatically for larger prey items. These results suggest that under conditions of food limitation small crucians might experience bottlenecks to growth, delimited by morphological constraints, and leading to stunting.

Because crucian carp is able to process food extensively with their pharyngeal apparatus before it is swallowed (Sibbing 1988), they often handle and then swallow several prey items simultaneously. This potential for mixing of prey types during handling might influence foraging patterns by reducing a crucian's ability to assess the rewards associated with a specific prey type. Indeed, our experiments showed that, although return rate differed with prey size, crucian carp were relatively insensitive to differences in prey size when selecting items during choice trials.

To measure intraspecific competition directly (Paszkowski *et al.* 1990), we recorded consumption of pelleted food by small (6-cm) crucians competing with: 1) one other small crucian, 2) one large (10-cm) crucian, or 3) four small crucians whose combined biomass equalled that of the large fish. Not surprisingly, the small focal crucian consumed the most pellets when confronted with a single, similarly sized competitor. Of more interest was the fact that a single large competitor or four small competitors depressed food intake by the focal fish comparably. The impact of large crucians was through exploitation competition as they consumed food more rapidly than small crucians. In contrast, aggression and interference characterized competitive interactions among groups of small crucians.

Month-long growth experiments in which marked small crucians were held with groups of competitors, consisting of small crucians or of large crucians of equal biomass, yielded results consistent with the foraging trials. Marked fish grew comparably under the two competitive regimes (Paszkowski *et al.* 1990). The results of our feeding experiments suggest that in a simple environment, with a single small-sized prey, numbers of competitors can compensate for body size, and biomass of fish is a good indicator of the competitive regime. However, in a more complex setting in which a range of prey sizes exist, the size distribution of competing crucians may play a more important role in shaping the outcome of intraspecific competition.

7.2. Predation

Under laboratory conditions, we found predation on crucian carp by perch to be strongly size dependent. Perch significantly altered the size distributions of crucians from populations dominated by small individuals to ones dominated by the large, i.e., a change that parallels the differences in size structure between "pond" and "lake" populations (Tonn *et al.* 1991). Perch consistently

preyed most heavily on the smallest crucians that were available, but the mechanism was not one of simple gape limitation. Perch are capable of successfully handling crucian carp up to 50% of their body length, but typically select crucians smaller than that; crucians > 80 mm in length are relatively safe, even with perch up to 210 mm.

In trials with a combination of crucian carp and roach as prey (using individuals of equal biomass), perch consistently selected crucians over roach (Tonn *et al.* 1991). Interestingly, this was true even though a crucian carp has a deeper body than a roach of the same biomass; body depth *per se* had no effect on the vulnerability of the prey. Similar results, indicating a "preference" of piscivores for crucian carp, were obtained in pond enclosures using rudd (*Scardinius erythrophthalmus*) as the alternate prey (Greenberg *et al.* 1995) and pike and zander (*Stizostedion lucioperca*) as predators.

Our laboratory experiments established that (i) perch, as size-limited piscivores, alter the size structure of crucian carp populations in a way that is consistent with the pattern observed for crucian populations co-occurring with predators, (ii) crucian carp is exceptionally vulnerable as a prey fish, compared with other cyprinids with which it co-occurs, and (iii) crucian carp can achieve a size refuge from predation by perch, with the safe size dependent on both the size of the predaceous perch and on the relative sizes of crucians available as prey. Laboratory results suggest that the direct effects of predation play important roles in shaping "lake" populations of crucian carp. Short-term, small-scale experiments with other species have demonstrated that predators can also affect prey indirectly, e.g., via altered habitat use and reduced foraging (e.g., Gilliam & Fraser 1987, Helfman 1989). Ecologists recognize that thorough examination of the full consequences of predation on populations requires experiments that are performed at spatial and temporal scales that are relevant to population-level processes. However, the number of such appropriately-scaled experiments, especially with vertebrates, remains limited. Studies with crucian carp provide several interesting examples.

The basic experiment, examining the responses of crucian populations in the presence and absence of a predator, was conducted in 1986–87 in Hermanninlampi, a small (1.5-ha), shallow (1.6-m) isolated pond in eastern Finland (Fig. 4, Holopainen *et al.* 1991, Tonn *et al.* 1992). This pond had been the site of several earlier studies on the ecology and ecophysiology of "pond" crucians (e.g., Holopainen & Hyvärinen 1985, Holopainen & Pitkänen 1985, Piironen & Holopainen 1986, 1988). The pond was extensively trapped to remove the existing population of crucians, rotenoned and divided into four sections by plastic curtains that extended from the substrate to well above the water surface; the pond then remained empty of fish for one year. The following spring, all sections were stocked with crucian populations whose size distributions were comparable among sections and patterned after natural populations from ponds lacking predators (average length 7.6 cm, range 4.0–12.6 cm). Four size-classes were given distinct marks to monitor their growth. Three weeks later, 26 perch, 16–26 cm in length, were added to two of the sections. The four populations of crucians were monitored throughout the summer, pre-winter liver sizes and liver glycogen were measured in October, and in the following spring populations were sampled quantitatively by mark–recapture and removal methods. Any surviving perch were removed at that time; although the surviving stocked fish were subsequently moved among sections for another experiment, young fish produced during the first year were left in their natal section for a second summer before being sampled quantitatively following another rotenone treatment in the fall of the second year (1987). The young-of-year crucians from the second year, all of which were produced in the absence of perch, were also monitored.

As expected, after one year, mortality among the stocked crucian carp was twice as high in sections with perch (55%) versus sections lacking perch (24%). Contrary to initial expectations, however, this did not produce a shift in the population structure in sections with predators to a dominance of large-bodied individuals via an elimination of the smaller crucians. Indeed, although size distributions between the treatments differed one month after perch were added, results were the opposite of predictions, i.e., there were fewer small crucian carp in the predator-free sections than in sections with predators. The laboratory experiments clearly showed that perch are size-selective and size-limited predators, therefore the greater mortality of crucians in sections with predators was not to-

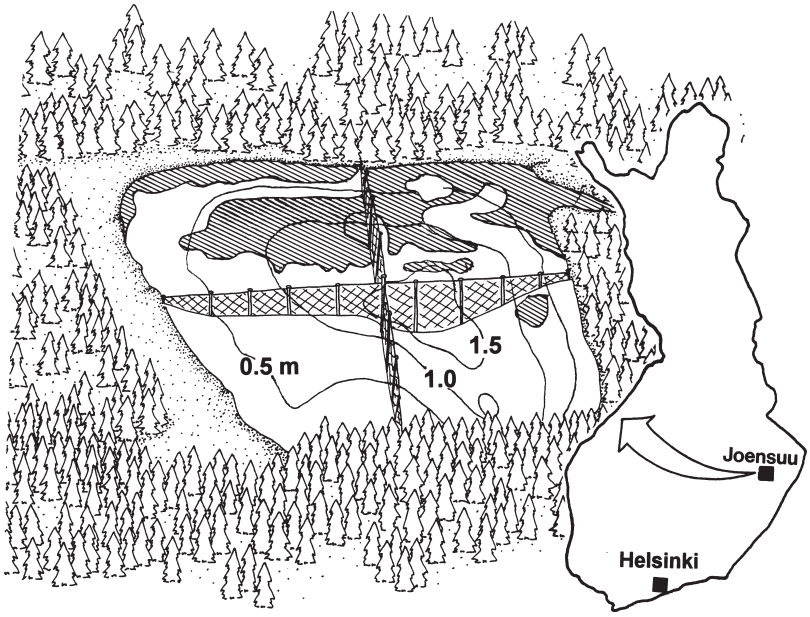

Fig. 4. The natural forest pond, Lake Hermanninlampi in eastern Finland (62°41´N, 29°41´E), was subdivided with plastic curtains for whole-pond experiments in 1985. The figures give the depth contours and the shading describes floating macrophyte cover. This 1.5-hectare lake was formed in 1859 from a large lake with a water level drop of 9.5 m. Crucian carp was introduced into the lake in 1948, and consisted of 44 000 fish (29 000 ha^{-1}) with an average mass of 3 g (6-cm total length) when rotenoned in July 1982.

tally caused by predation but also by the indirect effects of the presence of added predators.

The growth rate of the smaller size-classes of crucian carp (< 8 cm) was consistently slower in the sections with perch; an increase in the length of crucians with perch averaged 72% of crucians without perch (Holopainen *et al.* 1991). However, the opposite pattern was observed for the larger size-classes; growth was higher in the sections with predators. Smaller, more vulnerable crucians responded to the presence of perch with reduced activity, altered habitat use and diel activity patterns, and reduced feeding, which led not only to slower growth, but also to poorer condition and fewer overwintering reserves (Holopainen *et al.* 1991, Paszkowski *et al.* 1996). Given the overwintering strategy of crucian carp in small, shallow ponds, reduced glycogen stores was likely an important factor contributing to the overall higher mortality of crucians that co-occurred with predators. These results are consistent with the concept of resource depression induced by predation risk (Charnov *et al.* 1976, Holbrook & Schmitt 1988), and involved a shift to a habitat with structural refuge (the vegetated inshore area) and a limitation of activities to times when predators are ineffective. Overall catch rates were reduced significantly in the two sections containing perch, yet were higher in those same two sections in 1987 in the absence of any predators. Stocked crucians in predator sections were also much more concentrated inshore (92% of catches) than were the fish in predator-free sections (52%), and inshore fish were significantly smaller (and thus more vulnerable) than fish caught offshore. In the predator-free sections, offshore activity peaked during the day, with inshore activity highest at night. The same basic diel pattern was observed for larger (< 10-cm) crucians in the sections with perch, but the smaller, more vulnerable fish displayed just the opposite; the few fish that ventured offshore did so at night, when the visually foraging perch were less active.

During the 1986 experiment in Hermanninlampi, predation on the stocked crucians by the size-limited perch was probably substantially reduced by the presence of smaller (and thus more vulnerable) prey, young-of-year crucians that hatched in the pond and were first observed inshore on 1 July. Although qualitative surveys suggested that similar numbers of YOY were initially present in all four sections, catches in subsequent quantitative trappings were significantly lower in the sections with perch through spring 1987 (Fig. 5; Tonn *et al.* 1992). Although young-of-year were generally concentrated inshore even in the predator-free treatment, they were never caught offshore in the sections with perch, yet YOY were caught offshore in those same sections in 1987, when perch were absent.

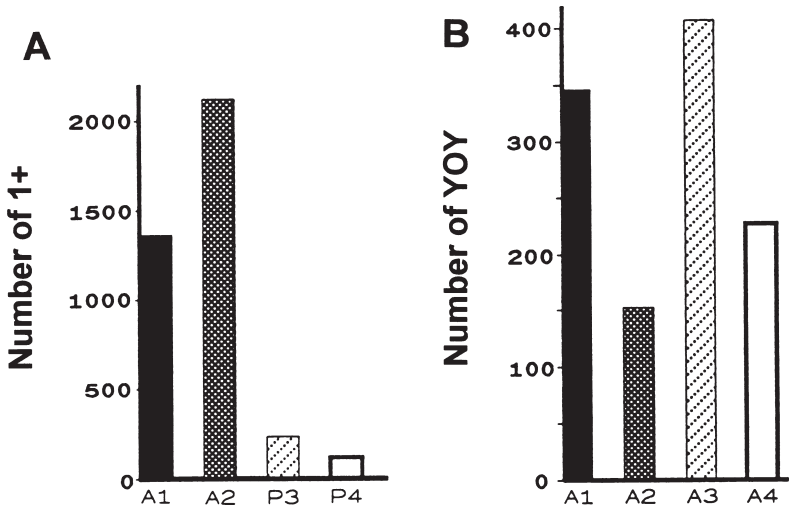

Fig. 5. Numbers of two successive year-classes of crucian carp in a subdivided pond (Lake Hermanninlampi; see Fig. 4) as revealed by a rotenone treatment in September 1987. The 1+ (A) refer to year-class 1986 when two sectors (P1 and P2) contained piscivores (A1 and A2 refer to sections where piscivores were absent in 1986). The young-of-year (YOY) in B refer to year-class 1987 when all sections were piscivore-free (Tonn *et al.* 1992).

The major, direct effect of perch in the experiment was the severe reduction of young fish that survived to recruit into the population. This effect is consistent with field observations of "lake" populations, in which young, small fish are virtually absent from catches year in and year out. That a few young somehow survive is apparent from the persistence of crucian carp in multispecies assemblages; aging of a typical "lake" population coexisting with predators (Lake Tåkern, Sweden; A. Hargeby, pers. comm.) revealed no evidence of dominant year-classes that would suggest pulsed recruitment of the kind one might expect when predator populations were periodically reduced, e.g., by winterkill (Tonn & Paszkowski 1986). Instead, it appears that fish in "lake" populations produce a tiny trickle of recruits each year.

Survival of these recruits is facilitated by the fact that crucian carp can respond to the presence of piscivorous fish in ways that reduce the direct effects of predation. However, these responses come with costs, including reduced foraging (Paszkowski *et al.* 1996), slower growth and reduced overwintering reserves, which likely contribute to increased total mortality in the presence of predators. Given these costs, it is expected that the magnitude of the responses is dependent on the level of hazard faced by the prey. Although this expectation has been met in several small-scale experiments (e.g., Dill & Fraser 1984, Gilliam & Fraser 1987), it has not often been clearly documented in the field at realistic scales.

In the Hermanninlampi field experiment, hazard varied as a function of the size-related vulnerability of the prey, and crucian carp responded accordingly. In a second field manipulation, crucian carp populations also displayed differential responses, in this case to differences in predator densities (Tonn *et al.* 1989). Higher proportions of crucians occurred offshore, and were active during the day, in a section of a divided pond that contained fewer predators (perch and pike) than in two other sections that had higher densities of predators. Survival, growth, and accumulation of glycogen also differed among the sections; although the responses were consistent with differential predation pressure among sections (and differential vulnerability among crucian size-classes), they did not always parallel predation pressure in a linear fashion. More frequently, a step function was observed; among the three sections of the pond, either the section with the highest, or the lowest, density of predators differed from the other two sections, which did not differ from each other.

In a laboratory study, Pettersson and Brönmark (1993) also found that crucian carp generally avoided open areas in tanks. In the absence of a predator, hungry crucians were more likely to be found in the open area than fed crucians, since food was available only in the open area. However, when a pike was present in a chamber adjacent to the open area, crucians spent even less time in the open area, whether they were fed or hungry.

Unlike many European cyprinids which are mobile, schooling species of open water, crucian carp is an inactive fish of the littoral zone. Greenberg *et al.* (1995) were able to directly observe crucian behaviour in ponds during enclosure ex-

periments and to compare activity levels and habitat use of crucian carp and rudd in the presence versus absence of predatory pike and zander. Habitat structure was either absent (bare enclosures) or consisted of artificial vegetation in the form of polypropylene strings anchored to PVC plates resting on the pond bottom. In the presence of a piscivore, the percentage of crucians located in the "vegetation" was > 85%. During observations, these fish rarely left the vegetation and rarely changed position within the patch. In contrast, < 55% of rudd were in the vegetation and schools of these fish rapidly moved in and out of the patch and circled the enclosure. In the absence of pike or zander, crucians were somewhat more mobile and significantly more crucians were located outside the vegetation, but this still involved < 60% of individuals on average. Rudd behaviour was essentially unchanged by piscivores. The enclosure trials were conducted with either a single species of prey fish, crucian carp or rudd, or with both species together. The crucians became more active in the presence of rudd and would form loose, multi-species groups, especially when vegetation was absent. The slow-swimming crucians tended to comprise the trailing edge of these groups which may have made them more vulnerable to predation.

7.3. Cannibalism

Laboratory observations suggest that crucian carp have a significant capacity for cannibalism. In pond populations this must considerably raise the mortality of young-of-the-year in a density-dependent fashion (Tonn *et al.* 1994). In the laboratory (I. J. Holopainen, unpublished data) small crucian carp, < 2 cm in length, consumed recently emerged larvae (0.8 cm), even in the presence of planktonic microcrustaceans. Crucian carp as large as 2 cm were attacked by fish of 7–8 cm, but at the length of 3.5–4 cm a size refuge from conspecific predation was achieved.

8. Role in ecosystems

The low density populations of large fish in multispecies fish communities (large lakes) are not considered to have any prominent role in their biotic community. Smaller eutrophic lakes or nutrient-rich, vegetated bays of large lakes may, however, have considerable numbers of crucian carp (Hamrin 1979). Here, the benthic feeding and disturbance of surface sediment may have an important effect on the nutrient cycling and trophic dynamics (Holopainen *et al.* 1992). In numerous small seasonally hypoxic water bodies, crucian carp has a key role in being the sole piscine inhabitant and the most important vertebrate predator. The fish biomass may be high (> 80 kg ha^{-1}, Holopainen & Pitkänen 1985) and by far exceed that of any other trophic level and consequently shape the structure and functioning of the whole ecosystem. In the subdivided natural forest pond, Hermanninlampi in Finland, crucian carp density and macrophyte cover both had considerable impact on planktonic communities and water quality (Holopainen *et al.* 1992). The zooplankton biomass was lower and the phytoplankton biomass higher, at high fish density. During summer, the water transparency was correlated negatively with chlorophyll-*a* at low fish density, but fish-mediated turbidity reduced transparency at high fish density. The composition and dynamics of the planktonic communities differed at different crucian carp densities (Holopainen *et al.* 1992).

9. Scientific and economic value

A large number of recent physiological and ecological studies on crucian carp have been cited in this article. Most of them are based on an experimental approach either in the laboratory or in nature. Obviously, the many peculiar features of this species, like its capacity to survive in anoxic waters and its sensitivity to predators, have promoted these studies. In addition, crucian carp is readily available throughout most of Europe from ponds with high density populations. It is well suited to experimental studies because of its tolerance of a wide range of abiotic conditions and intensive handling. Its metabolic machinery is probably very similar to the goldfish's, a model fish used in many physiological studies. The great potentials for laboratory culture and wide range of feeding habits make crucian carp a suitable fish species for routine ecotoxicological assays to com-

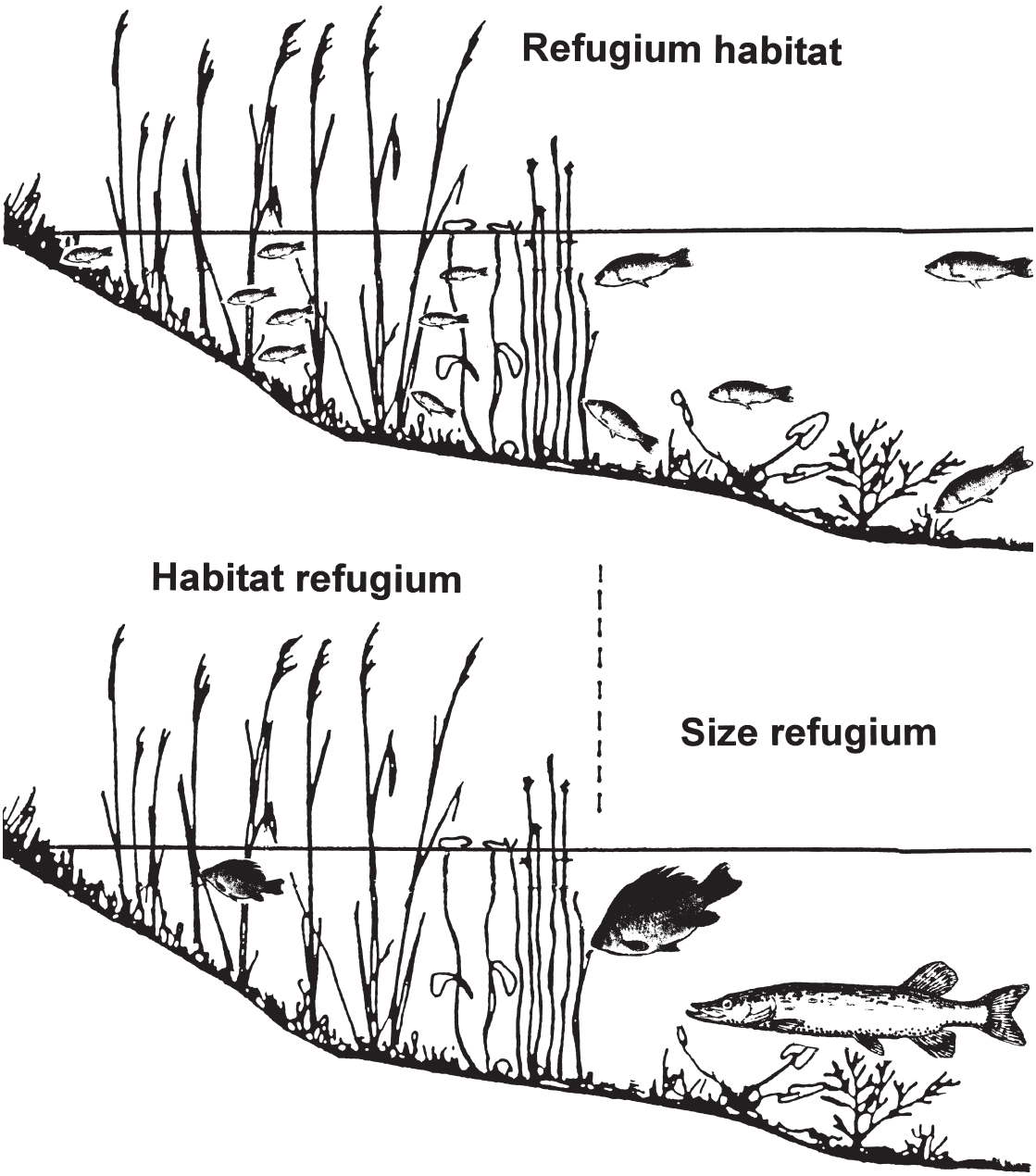

Fig. 6. Seasonally anoxic small ponds typically contain monospecific fish communities (A, *refugium habitat*) where the dense and stunted (small-sized and low-bodied individuals) crucian carp population is regulated by intraspecific competition and cannibalism. In multispecies fish communities of larger lakes (B), the very sparse crucian carp population is strongly regulated by predation: only a few young are able to survive in productive and highly structured littoral habitats (*habitat refugium*). The survivors grow fast and gain *size refugium*, a high body large enough to provide long life, safe from gape-limited piscivores (perch, pike).

plement data obtained from other fish species such as rainbow trout (*Oncorhynchus mykiss*).

Historically, the direct economic value of crucian carp has been low in Europe. Fishermen greatly appreciate it as a superb bait fish but crucians are seldom used as food. However, the species' low demands on water quality and very high growth rate in nutrient rich waters make them

Table 2. Comparison of the environment and the ecology of crucian carp in the two contrasting habitats at the different abiotic and biotic environments of lake and pond populations. YOY = young-of-year.

	Large lakes (normoxic[1)]) Piscivores present	Ponds (hypoxic/anoxic[1)]) Piscivores absent
Crucian carp density	Low	High
Body size	Large	Small
Body shape	Deep	Slender
Head	Small	Large
Food resources	High	Low
Intraspecific competition	Low	High
Growth rate	High	Low
Fecundity	High	Low
YOY mortality	High	Low

[1)] Winter oxygen condition

potential producers of high quality animal protein for fodder or human food by aquaculture. Crucian carp hybridizes with common carp (*Cyprinus carpio*) and the hybrids (Lieder 1957) are considered valuable for industrial aquaculture in central Europe (Skóra 1982, Skóra & Erdmański 1985). These hybrids, especially the F_2 generation, are very promising, with rapid growth, high resistance to polluted hypoxic waters, and high production of fry with excellent survival qualities (Skóra & Erdmański 1985). The behaviour of hybrids (*Cyprinus carpio* × *Carassius carassius auratus*) are reported to be intermediate (Suzuki 1962) and consequent changes in the diet are of high potential interest: the hybrids browse much less on macrophytes than the common carp.

10. Conclusions

The ecology of crucian carp is governed by its ability to withstand hypoxia/anoxia and other abiotic environmental factors on one hand, and its inability to withstand predation pressure on the other. These abilities form the basis for the dichotomous nature of populations (Fig. 6; Table 2). Phenotypic plasticity in many features results in different looking fish, with different physiologies and life-history parameters, occurring at different densities in the two contrasting habitats. In multispecies fish communities, crucian carp may be considered a "loser" with low population density and high mortality of young. In contrast, in numerous monospecific ponds it occupies a key role with high densities and biomass. The ecological and evolutionary significance of phenotypic plasticity or the ability of a single genotype to produce several alternative forms of behaviour, physiology and morphology, has recently aroused increasing theoretical and empirical interest (e.g., West-Eberhard 1989; Moran 1992). Recent evidence from various organisms suggests the ability for phenotypic variation to be selectively advantageous (e.g., Scheiner, 1993). The wide distribution of crucian carp from small ponds with harsh abiotic conditions (extended seasonal anoxia) to large lakes with severe biotic challenges from predators could be a product of the species' phenotypic plasticity. The cost of this flexibility lies in maintaining the genetic and cellular machinery (regulatory genes and enzymes) needed to be plastic.

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