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Interannual Variability of Fecundity and Egg Size of an Invasive Cyprinid, *Carassius gibelio*: Effects of Density-Dependent and Density-Independent Factors

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ABSTRACT

A population of the invasive Prussian carp (*Carassius gibelio*) was examined over a three-year period in a mesotrophic reservoir to find out interannual variations of fecundity and egg size and the influence of maternal condition (total length, TL, and age class) and environmental factors (water temperature and fish density) on these variables. Prussian carp reproduction was synchronous, with only a single batch, and fecundity ranged from 1,250 to 62,400 eggs per female. Relative fecundities and egg size showed no significant between-year differences. Fecundity increased with age, whereas egg diameter remained unchanged with age and TL. Fecundity was affected positively by TL and negatively by fish density, whereas temperature had no significant effect. Egg size was not affected by fish density or temperature.

INTRODUCTION

Fecundity, combined with survivorship, directly influences population dynamics through its effect on the intrinsic rate of population increase (Roff 1992). Differences in fecundity exist within species, often among geographically isolated populations, and among individuals within the same population depending on size and age (Bagenal 1978) and may represent either phenotypic or genetic causes (Roff 1992, Hendry and Stearns 2004). Accordingly, fecundity and the factors which influence it are of interest to many including evolutionary ecologists, fishery managers, or those attempting to understand the potential effects of large-scale ecosystem changes (e.g., climate change) on a fish species.

The Prussian carp (*Carassius gibelio*) is distributed mainly in the former Soviet Union, Europe, Korea, and northeast China (Zou et al. 2001). It was introduced to Europe from Asia in the 17th century and is now widely distributed in Turkey (Özuluğ et al. 2004, Gaygusuz et al. 2005). This species easily becomes one of the dominant species in stagnant and slow running waters and may change the flow of nutrients in the whole ecosystem (Paulovits et al. 1998). Prussian carp is also well known to have some flexible biological characteristics, including early maturation, a long spawning period, and high individual fecundity (Pipoyan and Rukhkyan 1998, Balık et al. 2004).

Even though few studies have been conducted on fecundity of Prussian carp, to the best of our knowledge there is no study on interannual variability of fecundity and egg

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size of Prussian carp out of its native distribution range. Furthermore, the exact mechanisms and consequences of environmental variation on fecundity and egg size of this species are not well understood.

Thus, we undertook a three-year study on fecundity and egg size of Prussian carp in a temperate Turkish reservoir. We explored interannual variations of fecundity and egg size, relationships between these biological variables and fish size, and how these relationships change between ages of fish and sampling years. We also examined influence of maternal condition (total length, TL, and age class) and environmental factors (water temperature and fish density) on fecundity and egg size.

We hypothesized that there would be positive effect of water temperature and a negative effect of fish density on fecundity and egg size. An increase of fecundity with body size and age was also expected.

METHODS AND MATERIALS

Ömerli Reservoir is a 23.5 km^2 reservoir in İstanbul (41° N, 29° E) that provides approximately 48% of the city's drinking water. It has a maximum depth of 62 m and is mesotrophic (Albay et al. 2003). The most numerous fish species are Prussian carp, rudd (*Scardinius eryhtrophthalmus*), Baltic vimba (*Vimba vimba*), and common carp (*Cyprinus carpio*) (Özuluğ et al. 2005).

A total of 744 Prussian carp individuals was collected with gill nets (8 mesh sizes in the range 10-42 mm) from the spawning area of this species in the reservoir between March and July during three consecutive years (2003-2005). To consider a possible density-dependent effect on egg production, Prussian carp abundance was evaluated using the same fishing effort during each of the three reproductive periods studied. Catch-per-unit-effort (CPUE) was expressed as g m^{-2} gillnet area $night^{-1}$. Total length (TL) and weight (W) were measured to the nearest 1 mm and 0.1 g.

Age was determined from scales, which were taken between the lateral line and dorsal fin (Bagenal and Tesch 1978).

The fecundity of 151 females was estimated gravimetrically. Mature ovaries were subsampled (0.001g) from anterior, middle, and posterior portions of each ovarian lobe. The absolute fecundity (F), which is the number of mature oocytes spawned by a female in a single spawning, was estimated as: $F = GW \times D$ where GW is the weight of the ovary and D is the density of mature oocytes (number of oocytes per g of ovarian tissue). Eggs from the anterior, middle, and posterior parts of ovaries were measured under a stereo-microscope with an ocular micrometer. Samples of 20-30 eggs from each female were collected to measure the egg diameter.

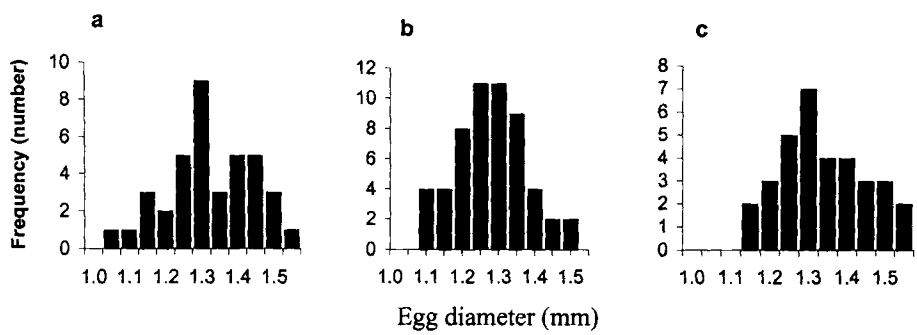

Figure 1. Egg-diamater frequency distributions of ripening Prussian carp in 2003 (a), 2004 (b), and 2005 (c).

Change in ovarian content is linked both to the direct accumulation of proteins and lipids within the ovary and to their transfer from the somatic body during previous growth periods (Kamler 1992). Hence, the environmental condition associated with a reproductive period at the study site was defined as being the mean value of each environmental variable recorded at the site during the 10 months before the spawning time.

Relationships between fecundity, egg diameter and female TL were tested using simple linear regressions. The equations were calculated for each sampling year and age class separately, and the slopes were compared using analysis of covariance (ANCOVA) (Zar 1999). Analysis of variance (ANOVA) was used to test the null hypothesis of significant differences in fecundity and egg diameter among age classes (Zar 1999). Fecundity and egg diameter were correlated with TL, fish density, and water temperature using Spearman correlation analysis. The individuals of age classes 4 and 5 years were grouped to have a number of individuals of at least equal to 30.

RESULTS

Water temperature during the three years ranged between 5.2 °C and 27.1 °C. Mean annual fish density increased considerably in the three consecutive years and ranged from 4.2 to 32.6.

Largest yolky oocytes were found in May or early June, and gonad maturation followed a similar pattern at all sampling sites. Frequency histograms of ripe oocyte sizes showed a single spawning mode from April to June. Just before spawning, the egg size distribution of all sampled gravid females showed a single mode (Fig. 1) indicating that females laid their eggs during the same period.

Among actively reproducing Prussian carp females, maximum age, TL, and mass were respectively five years, 322 mm, and 587.7 g; whereas the minima for these parameters were one year, 112 mm, and 26.3 g. Fecundity ranged from 1,250 to 62,400 eggs per female and was significantly correlated with TL ($r=0.804$, $P<0.0001$) and W ($r=0.909$, $P<0.0001$) (Fig. 2). Egg diameter ranged from 1.04 to 1.94 mm, it was however not significantly correlated to TL ($r=0.057$, $P>0.05$).

Mean fecundity mainly increased from age classes 1 to 3 years (from 6,624 to 26,576) and remained almost constant among older females (Table 1). Between-year variability of relative fecundities was examined with one-way ANOVA separately for each year classes. No significant between-year differences were found ($P=0.179$). For egg size, a similar approach also showed no significant ($P=0.058$) between-year differences. Mean egg diameter did not change between age classes.

Fecundity-length and fecundity-weight relationships of Prussian carp were best described by following equations: $F = 1.2832(TL)^{2.9988}$ ($r^2=0.81$), $F = 369.26(W)^{0.6948}$ ($r^2=0.46$), respectively. The slopes of the equations for these relationships differed statistically between age groups and years (ANCOVA, $P<0.001$).

Spearman correlation analysis indicated that fecundity was affected positively by TL ($r_s = 0.86$, $P<0.0001$) and negatively by density ($r_s = -0.50$, $P = 0.014$), whereas temperature had no significant effect on fecundity ($r_s = -0.24$, $P>0.05$). On the other hand, egg size was not affected by TL ($r_s = 0.20$), density ($r_s = 0.01$), or temperature ($r_s = 0.04$) ($P>0.05$).

DISCUSSION

Reproduction in Prussian carp appeared to be synchronous, occurring over a period of two months and producing only single batch of eggs per year. Peňáz and Dulmaa (1987) and Balık et al. (2004) also found that the Prussian carp lays only one batch of eggs annually; however some authors (Pipoyan and Rukhkyan 1998 and references therein) reported that Prussian carp had asynchronous ovogenesis and shed the eggs over several months. These differences could be related to environmental conditions such as water temperature, flow regime, and abundance of food (e.g., Smyly 1957).

There is a widespread trend for fecundity in fishes to be positively correlated with length and age (Peters 1983). For Prussian carp in Ömerli Reservoir, this trend remained consistent even when considering fecundity and TL relationships separately for each age class. Similar patterns have been described for several cyprinds (Pihu 1961) and for Prussian carp from different regions (Peňáz and Dulmaa 1987, Pipoyan and Rukhkyan 1998, Balık et al. 2004).

Comparison absolute fecundity values of Prussian carp between Ömerli Reservoir and other localities could give biased results since absolute fecundity is strongly size-dependent. We therefore compared relative fecundities to see location variations in fecundity of Prussian carp. Relative fecundity values of the Prussian carp population in

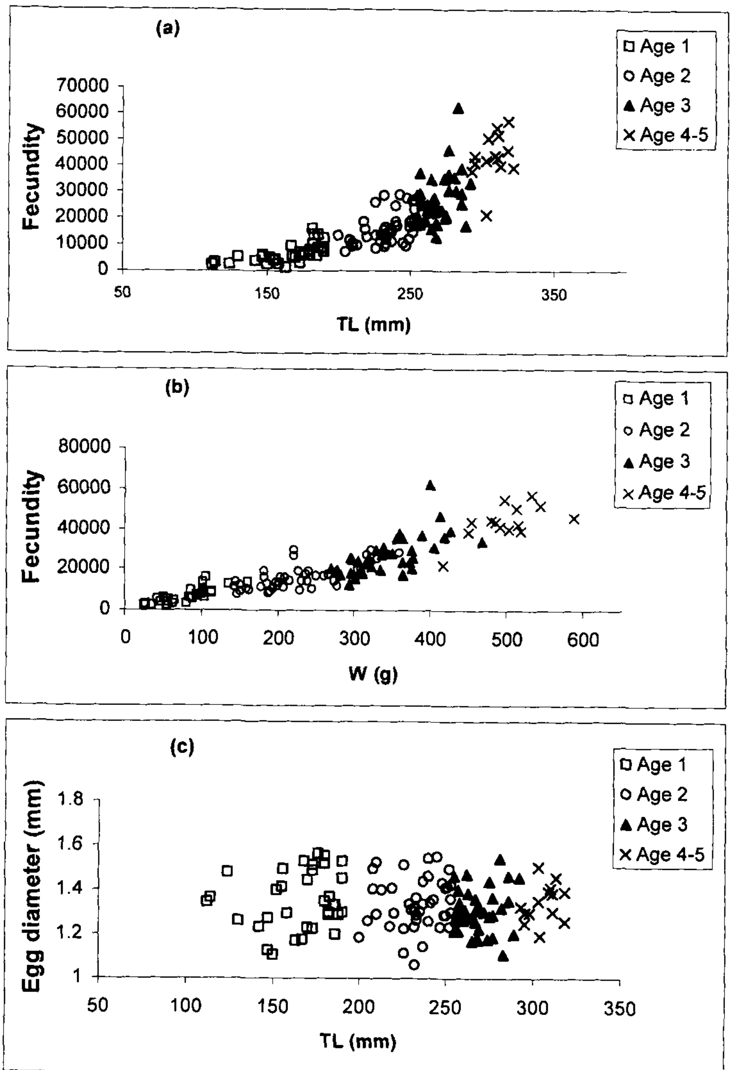

Figure 2. Relationships between fecundity and total length (a), fecundity and total weight (b), and egg diameter and total length (c).

the present study were similar to those of other localities, especially from more northern regions. However, the values are much lower than those reported from some localities at approximately the same latitude with Ömerli Reservoir (Lake Eğirdir and Ararat Valley waters). Although comparisons may be biased by differences in time (stock composition possibly influencing potential fecundity) and also by differences in methods used in the fecundity analysis, Balık et al. (2004) estimated a fecundity-length relationship for prussian carp sampled in Lake Eğirdir (southern Turkey) using the same method as in the present study, and the exponent '*b*' of this relationship was higher (3.694) than ours (2.999), resulting in a more curved relationship and higher predicted fecundity. Bagenal (1978) stated that the exponent often ranges from 2.3 to 5.3, and frequently exceeds 3.

Fecundity is a highly variable trait, which can differ among populations and also within one population between consecutive years. Even though evidence of increased fecundity with increased temperature has been given by various authors (Wootton 1979), the fecundity differences in Prussian carp from Ömerli Reservoir and other localities could not be due to solely to temperature because the relative fecundity values differed greatly between locations of almost the same latitude-areas having similar photoperiods and temperatures. According to energetic cost of gamete production, food is probably one of the most important environmental factors involved in fecundity (Wootton and Evans 1976, Wootton 1979). Food quality, and particularly the effect of dietary proteins on reproduction, may be responsible for differences in fecundity. In other fish species, a decrease in fecundity is generally observed with a reduction of feeding levels (Bagenal 1969, Wootton 1973, Springate et al. 1985, Tarkan 2006). However, as fecundity is generally linearly related to fish body weight, effect of feeding of fecundity may be difficult to discriminate from the effect of resulting of weight gain (Wootton 1982).

Holopainen et al. (1997) compared two lakes with different fish density and predation pressure and suggested that fecundity of crucian carp (*Carassius carassius*) was high when its density was high and predators were present. Indeed, no predator fish species inhabits in Ömerli Reservoir and relative fecundity of Prussian carp in the reservoir is lower than Lake Eğirdir, which has an introduced top predator *Sander lucioperca*. This may be ascribed to phenotypic adaptation to the environment with an increase in egg numbers with increasing predation pressure.

Another explanation for lower fecundity of Prussian carp in Ömerli Reservoir could be stress factor which was caused by unstable environment of the reservoir. As the reservoir is used as a source of drinking water for the Istanbul metropolitan area, an average of 872,000 m^3 per day water is discharged from the reservoir which leads very unstable water level stabilization, and this certainly can affect the population dynamics of fish as shown by several studies before (Cushman 1985, Sloman et al. 2002, Pegg et al.2006, Balcombe and Humphries 2006). Furthermore, algicide (copper sulphate)

Table 1. ANOVA results for the test of significant differences in fecundity and egg diameter among age classes of Prussian carp from the Ömerli Reservoir. Mean values with same superscript (a-e) do not differ significantly (P<0.005)

Age group (years) (n)	Mean $\pm_{S.E.}$ fecundity	Mean $\pm_{S.E.}$ egg diameter (mm)
1 (34)	$6,624 \pm 604^a$	1.35 ± 0.02^a
2 (48)	$15,993 \pm 923^b$	1.34 ± 0.02^a
3 (39)	$26,576 \pm 1525^c$	1.30 ± 0.02^a
4 (16)	$35,029 \pm 5816^{c,d}$	1.30 ± 0.03^a
5 (14)	$47,379 \pm 2707^d$	1.40 ± 0.09^a

treatments are applied in the reservoir to the decrease cyanobacterial blooms, which influence water quality negatively and cause severe fish kills. Acting together, these stress factors could reduce the fecundity of Prussian carp in Ömerli Reservoir.

A positive parental effect (TL and age in the present study) on egg size has been observed in many studies on various groups of animals (Peters 1983), and especially for fishes (Kamler 1992). Kamler (1992) stated that females with the largest mean egg diameters were intermediate in age for many fish species. This study showed that female fish spawning for the first time produce the smallest eggs. Egg diameter increases clearly between the first and second spawnings, and more moderately with further spawning, giving a curvilinear increase in egg mass. However, egg diameter values were not different by age and TL of fish in the Ömerli Reservoir Prussian carp population. Pipoyan and Rukhkyan (1998) found a similar pattern for Prussian carp in Ararat Valley waters. Moreover, egg diameters of Prussian carp are quite similar between Ömerli Reservoir and other contrasting populations of this species from different water bodies.

It is generally true that under poor feeding conditions fecundity decreases, and the results of the present study tend to highlight a possible density-dependent effect in relation to increasing interindividual competition. Significant between-year variability of TL and fecundity was related to fish density.

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