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Growth and Life History Traits of a Highly Exploited Population of Non-Native Gibel carp, *Carassius gibelio* from a Large Eutrophic Lake (Lake Uluabat, NW Turkey): is Reproduction the Key Factor for Establishment Success?

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Abstract

To assess establishment success of a heavily exploited population of non-native gibel carp *Carassius gibelio*, biological traits and population structure of the species from a large eutrophic lake (Lake Uluabat, Turkey) were investigated from June 2009 to May 2010 and attributes were compared with the published information from the introduced and native range. Commercial harvesting of gibel carp did not seem to affect population size and viability of gibel carp in Lake Uluabat but it had one of the slowest growth rate represented by twelve age groups, and its life span was one of the longest recorded for the populations both in its natural and introduced areas. The reproductive season lasted from March to early May. Size at maturity was earlier and relative fecundity was higher than those in the introduced range. Higher investment in reproduction displayed by earlier maturation, higher relative fecundity and gonadosomatic index with gynogenetic spawning in Lake Uluabat is likely to be the key factor for establishment success of gibel carp.

Keywords: Invasion, gynogenetic spawning, slow growth, fishing pressure.

Büyük Ötrofik bir Gölden (Uluabat Gölü, Kuzey-Batı Türkiye) Yüksek Oranda Sömürülen Yabancı bir Tür *Carassius gibelio* Populasyonun Hayat Döngüsü Özellikleri ve Büyümesi: Üreme, Yerleşme Başarısı için bir Anahtar Faktör mü?

Özet

Yabancı bir tür olan gümüşi havuz balığı, *Carassius gibelio*'nun aşırı bir avcılık baskısı ile avlandığı Uluabat Gölü'ndeki yerleşme başarısını anlayabilmek amacıyla, bu balığın biyolojik özellikleri ve populasyon yapısı Haziran 2009 ile Mayıs 2010 tarihleri arasında incelenmiştir. Ayrıca, elde edilen bulgular bu balığın doğal olarak ve aşılanmış olarak bulunduğu bölgelerdeki populasyonları ile karşılaştırılmıştır. Gümüşi havuz balığının Uluabat Gölü'ndeki ticari avcılığı bu balığın populasyonunu etkilememiş ancak 12 yaş grubu ile doğal ve aşılanmış alanlardan karşılaştırma yapılan populasyonlar arasında en uzun yaşama ve en ağır büyümeye sahip populasyon olduğu görülmüştür. Üreme mevsimi Mart ile Mayıs ayları arasındadır. Doğal alanı dışındaki bölgeler içinde, bu balığın Uluabat populasyonu cinsi olgunluğa daha erken erişmiş ve nispi fekonditesi daha yüksek olarak bulunmuştur. Yüksek üreme yatırımı, erken cinsi olgunluğa erişme, yüksek nispi fekondite ve gonadosomatik indeks değerleri ile ortaya çıkmış ve ginogenetik üreme stratejisi ile birlikte bu balığın Uluabat Gölü'ndeki yerleşme başarısı için anahtar faktör olabileceği sonucuna varılmıştır.

Anahtar Kelimeler: İstila, ginogenetik üreme, yavaş büyüme, balıkçılık baskısı.

Introduction

Biological invasions are now considered one of the most major issues causing serious threats to the conservation of biodiversity (Gozlan *et al*., 2005; Copp *et al*., 2005). Although the most introduced species fail to establish, establishment success varies across regions (Ross, 1991) and taxa (Lockwood, 1999). However, the introduction of a non-native species into a novel ecosystem is likely to create an ecological impact if the species is able to successfully establish a self-reproducing population (Gozlan and Newton, 2009). The resulting impacts can be both direct with predation, competition, hybridisation, habitat modification, and transmission of novel diseases (Hänfling *et al*., 2005; McDowall, 2006; Gozlan *et al*., 2006; Yonekura *et al*., 2007) and indirect with economic costs and risks posed to public health (Andersen *et al*., 2004; Gozlan *et al*., 2010).

The establishment success of an introduced species highly depends on its intrinsic ecological and life history characteristics (e.g. reproduction guild, fecundity, dietary breadth) and extrinsic features of the environment, which are difficult to predict (García-Berthou, 2007). One such introduced invasive species is gibel carp, *Carassius gibelio* (Bloch, 1782) in which populations introduced to Europe from Asia in the 17th century and is now widely distributed in European (Crivelli, 1995; Vetemaa *et al*., 2005) and Turkish waters (Özcan, 2007). Indeed, rapid increase and spread of this species have been reported in many areas including the Danube River Basin (Holčík, 1980), southern Russia (Abramenko *et al*., 1997), Greece (Paschos *et al*., 2004), Estonia (Vetemaa *et al*., 2005), and Eastern Ukraine (Liasko *et al*., 2011).

Recognition of gibel carp in Turkey was relatively late compared to European countries. This species entered Turkish waters from Thrace region via River Meriç (Baran and Ongan, 1988). After its first introduction, it was transported to numerous inland water bodies throughout Turkey intentionally by fishermen and accidentally by stocking practices, which are very common in Turkish waters with the aim of increasing fish production and sport fishing (Aydın *et al*., 2011; Önsoy *et al*., 2011). Once introduced into a novel system, gibel carp may easily become one of the dominant fish species in especially stagnant and slow-running waters (Aydın *et al*., 2011; Tarkan *et al*., 2012a). In Turkey, the first wild recording of gibel carp was in 1988 (Baran and Ongan, 1988) and it was reported in 46 water bodies in 2007 (Özcan, 2007), the majority being reservoir established for irrigation and drinking water supply. This number, however, should be much more now indicated by recent confirmed reports of the species (i.e. Aydın *et al*., 2011; Tarkan *et al*., 2012a). Negative ecological impacts of gibel carp to native fish communities through reproductive interference and habitat degradation have been reported from Turkish waters (Gaygusuz *et al*., 2007; Tarkan *et al*., 2012b) as well as from introduced range in Europe (Paulovits *et al*., 1998; Hänfling *et al*., 2005). Although it is considered a pest species out of native distribution range, it has been utilized by local fishermen in some big reservoirs and lakes in Turkey. One such water body is Lake Uluabat, which is located in north-west Turkey. Recently, this fish species has been caught over 10 tons per day and 400 tons per year since 2005 in the lake. However, such high fishing pressure has evidently no negative impact on the population size of the species, as it is still known to be collected abundantly, which is high enough to export to Iraq since beginning of 2011. Despite increased number of studies on biological features of gibel carp, factors behind its establishment success in its newly introduced areas is still poorly known. Also, to the best knowledge of authors, no information existed on this species in a highly exploited site in its introduced range. The aim of this study was, therefore, to determine the age structure, growth rate and life history traits (age and length at maturity, fecundity, gonadosomatic index, duration of spawning season, mode of spawning) of gibel carp population from Lake Uluabat, Turkey and compare these attributes with published information from similar sites in its introduced and native range to better understand the underlying mechanisms responsible for the species ecological plasticity and consequent invasive character. In the introduced range, all comparable sites were selected according to their geographic proximity (i.e. latitude) and similarity of physical structure of the site (shallow and large lakes), because significant differences in life history and growth in introduced gibel carp populations have recently been shown resulting from type of the water body in which they live (Tarkan *et al*., 2012a). Given that gibel carp has become important component of European freshwater ichthyofauna in terms of rapid spread with invasive character, such knowledge is crucial when assessing the potential impacts and risk assessment tools of this species in its introduced range.

Materials and Methods

Fish were collected from Lake Uluabat located in Marmara Region, north-western of Turkey (40°10' N, 28°35' E). It is a shallow and eutrophic lake at an altitude of 9 m above sea level with a surface area of 156 km^2 (Magnin and Yarar, 1997). Lake Uluabat and its surrounding area were included in the Ramsar List that was established in response to Article 2.1 of the Convention on Wetlands held in Ramsar, Iran in 1971. The lake is currently considered to show a typical eutrophication character. Domestic and industrial waste discharges affect water quality (Arslan *et al*., 2010). Deposits of incoming silt from a big river (Mustafakemalpasa River), which flow into the lake, have formed an inland delta covering an area of 3,747.6 ha that is under agricultural use (Salihoğlu and Karaer, 2004). The lake is one of the most important fish breeding areas of Turkey. However, recently the productivity of this breeding site is threatened by over contamination of agricultural fertilizers and non-native gibel carp. Based on the data obtained from Gölyazı Fishbreeding Cooperative Records, 412 tons of gibel carp, 93.5 tons of pike, *Esox lucius* Linnaeus 1758, 61 tons of roach, *Rutilus rutilus* (Linnaeus 1758), 31.5 tons of common carp, *Cyprinius carpio* Linnaeus 1758, and 18.5 tons of rudd, *Scardinius erythophthalmus* (Linnaeus 1758) were caught from Lake Uluabat in 2006. Gibel carp having entered to the lake in early 2000s adapted to the ecological nature of the lake and became the dominant species in the lake in a short period.

Gibel carp were monthly collected in the littoral zone at a depth 0.6 to 2.1 m by gillnetting with various mesh sizes (18, 20, 24, 28, 38, and 40 mm) from June 2009 to May 2010. Immediately after capture, gibel carp were killed with an overdose of 2-phenoxyethanol, immersed in a slurry of iced water and chilled to freezing. In the laboratory, the specimens were defrosted and each specimen was measured for standard length (SL) to the nearest mm and total weight (TW) to the nearest 0.1 g. To examine age and growth parameters, scales of specimens were taken from between the lateral line and dorsal fin. Age determination was made by counting true annuli (as per Steinmetz and Müller, 1991) using scale impressions on acetate strips, read on a micro-projector. Two independent age determinations were made by two different researchers. When the results were different, an additional determination was made; if there was still disagreement, the sample was rejected. Samples with ambiguous age readings (less than 5%) were not used in age and growth analysis. Age readings were validated by examination of the opercula of 10% of the sample under a binocular microscope (20×). Linear and non-linear models were fitted to determine what equations best describe the relationship between body length and scale radius. The body–scale relationships were best described by a linear equation, and SL at previous ages was back-calculated according to the Fraser–Lee equation (Francis, 1990): Lt = c + (SLc – c)(St/R), where Lt is SL when growth mark t was formed, SLc is SL at the time of capture, St is the distance from scale focus to the growth mark t, R is scale radius, and c is the intercept on the length axis from linear regression between SL and scale radius (Bagenal and Tesch, 1978).

The somatic condition was expressed using as CF = (TW x SL $^{-3}$) x 10^5 (Fulton, 1911). The length-weight relationship was described separately for males and females by the equation:

$$TW = a\ SL^b,$$

where a and b are constants (Le Cren, 1951). Comparisons of the growth trajectories of gibel carp populations in different locations were made by calculating the relative growth based on the back-calculated SLs at age data. Firstly, parameters (L_∞, k and t_0) of the von Bertalanffy growth equation were estimated using the non-linear least squares method. Secondly, SLs at age were obtained from $l_i = SL_\infty (1 - k^i)$ where $SL_\infty = l_t/(1\text{-}k)$; l_t is the interception on the y axis; l_n the SL at age i; k the slope of the non-linear algorithm. Finally, the mean SLs at age for each year classes were expressed as a proportion (%) of these SLs. The proportions are then summed, and the resulting mean was used to determine relative growth in different years (Hickley and Dexter, 1979).

Gonads of each individual were inspected to determine the sex and sex ratio variation over the year. The gonads of 419 females and 153 males were dissected out and weighted to nearest 0.001 g (GW). The gonadosomatic index (GSI) was defined as GSI = GW x TW $^{-1}$ x 10^2. Age at maturity was calculated from the percentage of mature females in each age-class using the formula of DeMaster (1978), as adapted by Fox (1994):

$$a = \sum_{x=0}^{\omega} (x)\ [f(x) - f(x\text{-}1)]$$

where a is the mean age of maturity, x is the age in years, f(x) is the proportion of fish mature at age x, and w is the maximum age in the sample. A modified version of this formula (10 mm SL intervals in place of age-classes; Trippel and Harvey, 1987) was used to calculate mean SL at maturity.

Females with ovaries containing non-yolked or indistinguishable eggs were classified as immature, and those with ovaries containing yolked eggs (even if spent) were classified as mature. To test whether the ovaries were homogenous with respect to follicle diameter and density (number of follicles per gram of ovary), samples were taken from anterior, middle, and posterior pieces. The fecundity of females was estimated gravimetrically (Bagenal, 1978): F = GW x D where; F is the number of mature oocytes spawned by a female in a single spawning, GW is the weight of the ovary and D is the density of mature oocytes (number of oocytes per g of ovarian tissue). The diameters of about 50 randomly sampled oocytes from each of females were measured on a binocular microscope and then pooled data were used to determine the size frequency for consecutive months over the year.

Statistical Analyses

Variation in sex ratio (number of males divided by the number of females) was tested by χ^2 (Zar, 1999). Conversions among total length, fork length and standard length were calculated according to Gaygusuz *et al*. (2006). Linear and non-linear regressions were used to test the relationships among GSI, fecundity, egg diameter, female SL, TW and GW. The seasonal differences in condition (CF) of sex and age were tested using analysis of covariance (ANCOVA) with SL as a covariate. Condition values were log-transformed ($\log_{10}$(x+1)) prior to analyses in order to meet the parametric assumptions of homogeneity and normality of variances. The results of these analyses were subsequently back-transformed for ease of interpretation. ANCOVA was also used to compare seasonal differences in slope of the length-weight relationships (Zar, 1999). Factorial analysis of variance (ANOVA) was used to test the null hypothesis of significant differences in fecundity, egg diameter and in condition values among age classes. Differences between mean back-calculated SLs and observed lengths of the same age groups were tested the Mann–Whitney 'U' test. Differences in growth index between populations in introduced and native range were undertaken with Student t-test. All analyses were conducted using Statistica 9.0 for Windows (www.statsoft.com).

Results

A total of 572 gibel carp individuals was collected. In total, 153 were male and 419 were females, a ratio (1.0:2.7) that deviated statistically from parity (χ^2 = 78.05, P<0.001). Female biased sex ratio remained the same throughout the sampling period (χ^2 test, P<0.05) except than November and December 2009 and April 2010 (χ^2 test, P>0.05, Figure 1). The mean sex ratio of males to females during the reproductive season was 1:1.5 (χ^2 = 4.23, P<0.05).

Age and Growth

Gibel carp population in Lake Uluabat was represented by twelve age groups (Table 1). Age 8 individuals dominated in the population, representing 33% of all individuals sampled. As the nested ANOVA did not show any differences in SL between sexes (d.f = 1, 668, P>0.05), data on female and male SLs were pooled. The average annual increment of SL varied but the highest increments were noted between the first and second year. Nevertheless, the growth slightly decreased as the age increased, although this was not so apparent because of small number of individuals in older ages (Table 1). The mean back-calculated SLs of older age groups were significantly smaller than observed length of the same age group when captured (Mann–Whitney, *P* < 0.01, Table 1), which may be attributed to Lee's phenomenon (Bagenal and Tesch, 1978). As gibel carp population in Lake Uluabat is highly exploited especially in older ages, one of the principal causes of Lee's phenomenon (Lee, 1920) is expected due to earlier exposing of faster growth fish of a year class to the fishing nets.

Females had higher condition than males (ANCOVA on $\log_{10}$ TW with SL as covariate; d.f.=1, n=668, P<0.001). The seasonal dynamics of condition did not differ between males and females for reproduction season (spring) (ANCOVA, F = 1.238, d.f. = 1, n=141, P>0.05) and summer (ANCOVA, F = 1.889, d.f = 1, n=229, P>0.05) while it was higher for females in fall (ANCOVA, F = 55.892, d.f. = 1, n = 165, P<0.01) and winter (ANCOVA, F = 9.882, d.f = 1, n = 99, P<0.05) (Figure 2). Condition was highest during spawning season (mean ± S.E., 3.56±0.15 in males and 3.67±0.14 in females) and it decreased significantly after reproduction (ANCOVA, F = 6.669, d.f = 12, n=668, P<0.05). According to age structure, condition showed a fluctuated pattern over the sampling period, being high in mid-ages (5-8) (ANCOVA, F = 18.986, d.f = 12, n=668, P<0.01). Females conditions were significantly higher than males in older ages (ANCOVA, F = 8.521, d.f = 1, n = 668, P<0.05). Length–weight relationships of all individuals showed that growth of gibel carp was isometric (*b* = 3) throughout sampling (*a* = 0.0349, *b* = 3.0039, *r* = 0.99, SE of *b* = 0.213) and did not differ seasonally (ANCOVA, F = 0.893, d.f = 12, n = 668, P>0.05). However, similar to the condition dynamics, females had higher b values than males (ANCOVA, F = 88.742, d.f = 1, n = 668, P<0.01) (Table 2).

Reproduction

Assessment of the main spawning period of gibel carp in Lake Uluabat was based on gonadosomatic index (GSI) analysis (Figure 3), and analysis of seasonal development in mean egg diameter (Figure 4), and direct observation of the gonads. GSI varied from 0.26 to 14.09 for the females and from 0.37 to 5.58 for the males. Female mean GSI in March and April was correlated with fish size (log GSI = 0.7489 x log SL – 0.6458, r^2 = 0.56, *P* < 0.01). Male GSI in the same period was not significantly correlated with SL (log GSI = –0.4563 x log SL –1.6427, r^2 = 0.09, P>0.05). Apart of the reproductive period, GSI seemed to be size-dependent

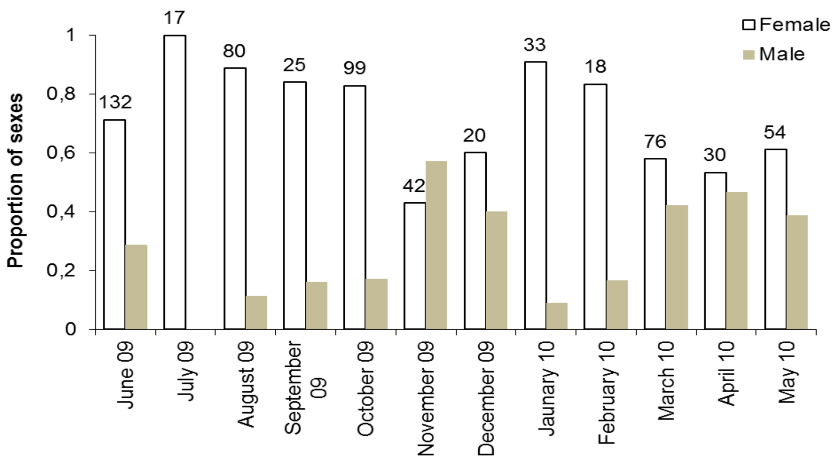

Figure 1. Seasonal dynamics in proportion of female and male gibel carp individuals. The number of fish used for the sex ratio estimate is shown above individual bar.

Table 1. Year of hatching, number of specimens (n), mean standard length (SL) in mm at capture, mean back-calculated lengths-at age, standard error (SE) and mean annual growth increments for gibel carp in Lake Uluabat.

				Back-calculated at lengths at																							
Year		SL at capture		Age 1		Age 2		Age 3		Age 4		Age 5		Age 6		Age 7		Age 8		Age 9		Age 10		Age 11		Age 12	
class	n	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE	SL	SE
2009																											
2008	35	81.0	2.8	49.0	3.3	72.1	4.7																				
2007	54	92.0	1.9	44.8	1.7	64.7	1.7	80.9	1.8																		
2006	58	113.3	3.6	39.1	2.9	59.5	3.4	78.9	3.7	97.1	3.3																
2005	47	153.4	5.1	45.5	2.6	71.7	2.6	93.2	3.7	117.6	3.6	136.4	3.7														
2004	42	175.8	4.5	46.3	1.8	69.7	2.8	94.6	3.7	121.2	3.9	148.6	3.3	168.1	4.0												
2003	51	184.5	3.9	45.9	1.4	69.0	1.7	94.5	2.2	114.9	2.6	137.6	2.6	156.1	3.2	172.0	3.5										
2002	135	208.3	5.8	51.9	2.5	72.1	3.1	93.4	3.1	114.1	2.9	133.8	2.9	155.2	3.8	175.9	4.1	193.4	4.8								
2001	108	220.6	5.7	50.3	1.0	70.0	1.3	90.9	2.1	112.5	2.2	133.9	2.7	155.1	3.4	173.6	3.5	194.1	3.9	209.8	3.9						
2000	26	260.0	6.5	57.9		80.4		95.9		114.5		125.6		151.7		174.4		196.8		224.4		248.7					
1999	9	265.5	8.4	49.2		74.0		90.9		108.3		123.3		139.7		162.2		179.6		198.9		214.7		230.4			
1998	7	273.0	9.5	43.0	1.5	63.3	0.2	84.7	3.0	104.3	2.0	122.7	2.3	146.4	5.2	173.3	11.1	193.2	11.5	219.6	6.6	239.1	13.7	255.4	14.5	273.0	18.0
Means length at age				47.5	1.5	69.7	1.7	89.7	1.9	111.6	2.4	132.7	3.1	153.2	3.3	171.9	2.0	191.4	3.0	213.2	5.6	234.2	10.1	242.9	12.5		

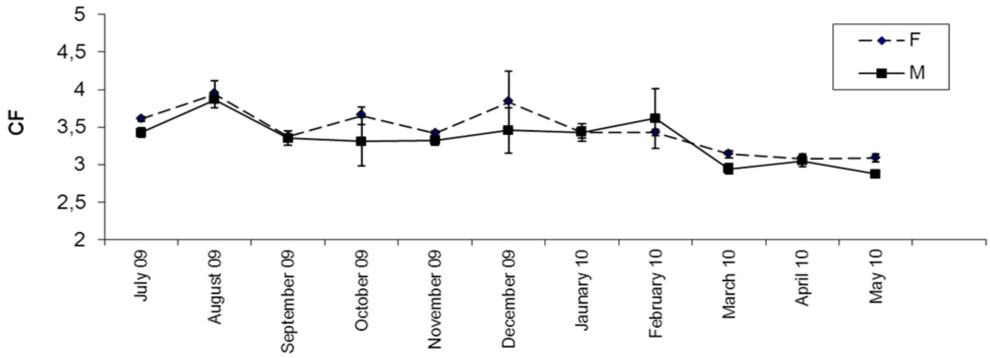

Figure 2. Seasonal dynamics of mean ± S.E. Fulton's condition factor (CF) in male and female gibel carp from Lake Uluabat.

Table 2. Seasonal variation in weight-length relationship of gibel carp males and females in Lake Uluabat

	Length range (mm)	Weight range (g)	Parameters of the length-weight relationship			
			a	*b*	95%CI for *b*	R^2
Spring (female)	89–253	21–577	0.026	3.068	2.959–3.176	0.979
Spring (male)	87–210	19–294	0.030	3.011	2.866–3.156	0.962
Summer (female)	71–291	14–768	0.035	3.004	2.949–3.059	0.985
Summer (male)	24–79	17–403	0.040	2.946	2.812–3.080	0.977
Autumn (female)	90–324	23–1111	0.045	2.914	3.795–3.034	0.952
Autumn (male)	83–227	16–335	0.068	2.754	2.460–3.047	0.893
Winter (female)	86–249	20–497	0.041	2.933	2.817–3.048	0.980
Winter (male)	84–236	19–411	0.043	2.910	2.612–3.208	0.974

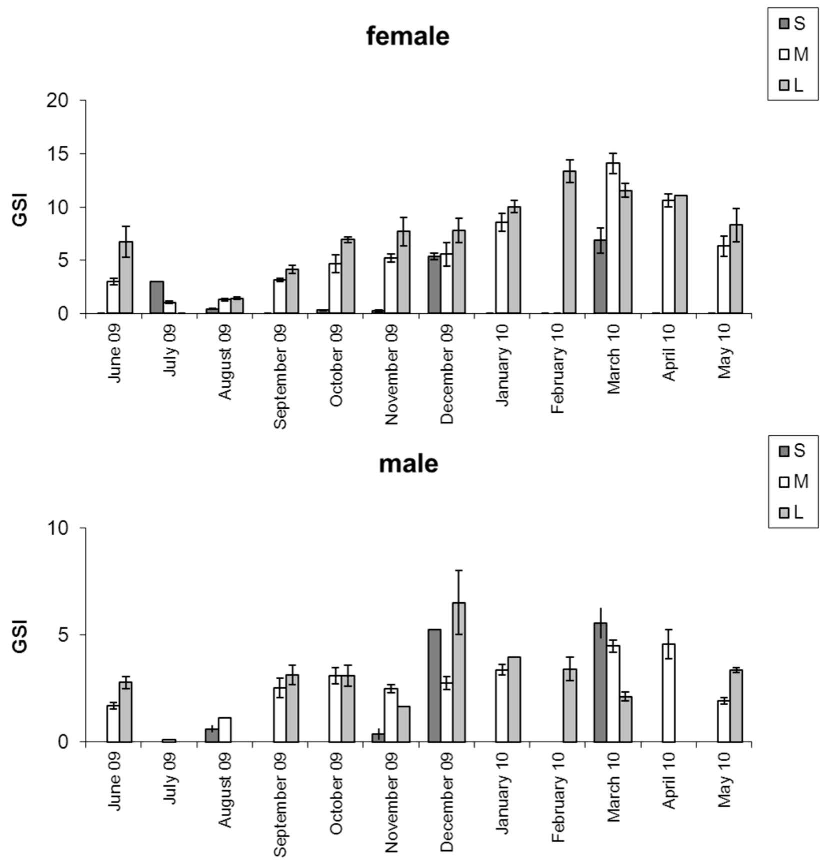

Figure 3. Mean gonadosomatic index (GSI) ± S.E. and maximum and minimum values over the year for female and male in different length classes corresponding with age groups. S, small (ages 2-4), M, medium (ages 5-8), L, large (ages 9-12).

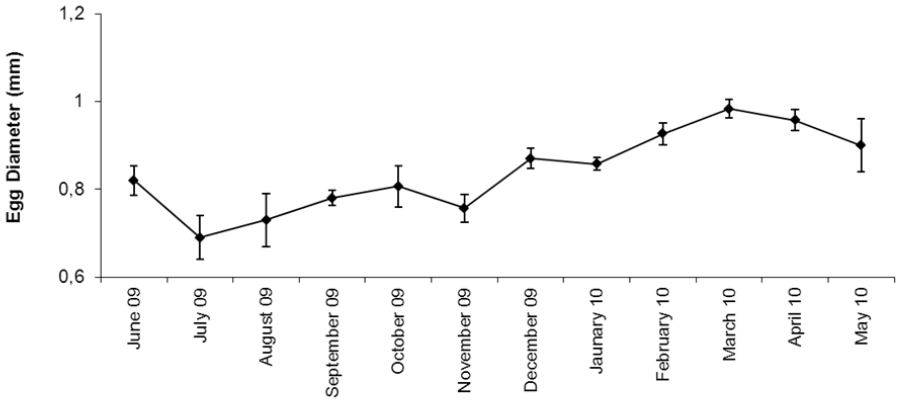

Figure 4. Seasonal dynamics of mean ± S.E. egg diameter of gibel carp from Lake Uluabat.

in females as correlation coefficients varied between 0.45–0.55. However, it was not the case for the males (r^2 varied between 0.001 and 0.05). The highest values for both sexes were in March and April (Figure 3) and there was a decrease in June when spawning took place in the most individuals. Mean egg diameter was highest in March (0.98±0.06 mm) while it was minimum in July (0.69±0.05 mm) (Figure 4). Thus, the spawning period occurred from March to early of May. After spawning there is a relatively 4–months quiescent period, during October–February rapid growth of the gonads occurred.

Egg diameter was not significantly correlated (Spearman's Rank correlation test, r<0.01, P>0.05) to SL or TW for gibel carp in Lake Uluabat. Mean absolute fecundity in mature female gibel carp was 112,409 eggs (SE = 53,65 eggs), ranging from 12864 eggs (a female of age 7) to 298,650 eggs (a female of age 10). Absolute fecundity and egg diameter increased with age classes (ANOVA, P<0.001). Absolute fecundity (AF) was significantly related to SL ($AF = 0.0636(SL)^{2.6648}$, r^2=0.47, P<0.05, F=35.17), to weight ($AF = 402.67(TW)^{0.9593}$, r^2=0.49, P<0.05, F = 35.17) and to gonad weight ($AF = 10623(GW)^{0.6554}$, r^2=0.60, P<0.001, F = 61.19). Mean relative fecundity was 355.6±15.3 eggs g^{-1}.

The youngest mature fish were age 2 and the oldest mature male and female were age 10 and 12, respectively. No fish of <71 mm SL (i.e. 0^+ and 1^+) were captured and therefore the mean lengths and ages at maturity given for Lake Uluabat was approximation (Table 3).

Differences Between Introduced and Native Populations

Highest growth index was in Lake Chimaditis (Greece) while lowest one was in Lake Uluabat, which both was from the introduced range (Table 3). Relative fecundity was highest in Lake Uluabat, while it was lowest in Lake İznik (Table 3). Length at maturity and egg diameter of gibel carp were lowest in the present study (Table 3). Mean growth index in introduced populations was significantly higher than that in native populations (*t*-test, P<0.05) while the both groups had mean higher growth index than gibel carp population in the present study (Figure 5). Comparison of reproduction characteristics between introduced and native gibel carp populations was not possible, as the reproductive data from native area was not available.

Discussion

Growth variability in gibel carp populations was apparent in the present study (Table 3, Figure 5), which is quite common phenomenon in also widely distributed fish species (*i.e.* Mann, 1991). This variability is observed even within the same country, such as İznik vs. Uluabat lakes in Turkey or at similar latitudes, such as Lake Chimaditis (Greece) vs. Lake Beyşehir (Turkey) (Table 3). First-year growth of gibel carp was characterized by two clusters of back-calculated values, with short SL values at age 1 from native populations (Table 3). However, couple of gibel carp populations (Chimaditis and İznik lakes) demonstrated exceptionally larger growth increments between ages 1 and 2 (Table 3). Relative growth index clearly indicated that gibel carp population in Lake Uluabat grew considerably slower than other locations although native populations had relatively slower growth compared to those introduced ones (Figure 5). These discrepancies are likely due to differences in population density, local water temperatures and food availability among regions (Tarkan *et al.*, 2012a). However, given all comparable sites had very similar temperature regimes due to their close proximity (i.e. very similar latitudes) and ecological commonality, growth variations among the study sites are probably not only because of differences in water temperature or food availability and quality.

Remarkably lower growth and extended life span of gibel carp in Lake Uluabat can be explained by high and constant fishing pressure on this species in the lake. It was previously shown that exploited

Table 3. Location, mean back-calculated SLs at ages, growth index (GI), mean at age at maturity (AM), mean SL at maturity (SLM), relative fecundity (RF) and mean egg diameter (ED) of gibel carp populations from various water bodies in its native and introduced ranges

Location	Lat.	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	GI	SLM	AM	RF	ED	Source
Introduced range																			
Lake Uluabat (Turkey)	40	48	70	90	112	133	153	172	191	213	234	243	273	73	71	2.0	356	0.91	Present study
Lake İznik (Turkey)	40	111	159	204	242									131	106	1.0	150	1.20	Tarkan *et al*., 2012a
Lake Chimaditis (Greece)	40	166	191	210	237	246	247							141	–	–	158	1.07	Leonardos *et al*., 2008
Lake Eğirdir (Turkey)	38	106	161	204	228	245	264							124	92	1.0	204	–	Balık *et al*., 2004
Lake Marmara (Turkey)	38	110	165	199	237	253								128	–	–	–	–	Tarkan *et al*., 2012a
Lake Beyşehir (Turkey)	37	82	107	174	197	219	238							101	105	2.0	–	–	Çınar *et al*., 2007
Native Range																			
Lake Los (MN)	47	58	109	160	196	213	237	251						96	–	–			Peňáz and Dulmaa (1987)
Lake Orohon Saamar (MN)	47	51	98	139	172	211	239	256	275	292				95	–	–			Peňáz and Dulmaa (1987)
Lake Gun nuur (MN)	47	60	102	140	182	246	273							96	–	–			Peňáz and Dulmaa (1987)
Lake Chock nuur (MN)	48	53	99	148	192	238	285	307	324					104	–	–			Peňáz and Dulmaa (1987)
Lake Hanka (RU)	53	52	109	148	181	217	234	239						92	–	–			Nikoloski, 1956
Lake Dzalunskoe (RU)	53	57	112	155	187	213	229	247	267	274				97	–	–			Nikoloski, 1956

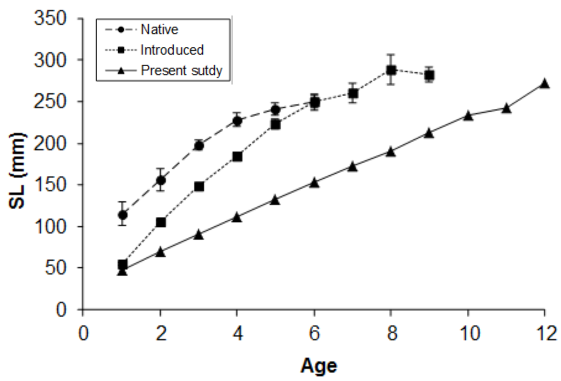

Figure 5. Mean back-calculated standard lengths (SL) ± S.E. at age for gibel carp populations from native and introduced area (see Table 3).

populations are characterized by decreased age at maturity (Rochet, 1988). Negative relationship between fishing pressure and age at maturity was evident by both field (Patriquin, 1967) and experimental studies (Alm, 1959) at small (Reznick, 1993) and large scales (Rijnsdorp, 1989). Indirect effect of high exploitation on age at maturity can also be observed when stock biomass decreases (Hempel, 1978). Earlier maturation, in turn, would cause declined growth rate in later years and longer life span (i.e. Lappalainen *et al*., 2008) as it seemed to be the case in the present study (Table 3). Reaching sexual maturity earlier makes an individual allocate more energy into gonad production leading reduced somatic growth rates (Roff, 1984). Whilst growth rate of gibel carp in Lake Uluabat was the lowest, its life span was the longest one in both in natural and introduced areas (Table 3). Similarly, relatively reduced growth rates have also been observed for some native fishes of Lake Uluabat such as pike (Emiroğlu, 2008), rudd (Emiroğlu *et al*., 2010) and white bream *Blicca bjoerkna* (Şaşı and Berber, 2012) within the period of high exploitation. Although it is contrary to life history theory (Roff, 1984; Metcalfe and Monaghan, 2003), maturing early did not show reduced lifespan for gibel carp population in Lake Uluabat as similarly indicated by another freshwater fish species, white crappie *Pomaxis annularis* from a similar environment in terms of trophic level and water depth (Michaletz, 2012). Growth of Lake Uluabat gibel carp population can also be influenced by pressure of predator fish species of the lake (e.g. pike). A recent work on the dietary content of pike in Lake Uluabat (Yılmaz *et al*., 2010) has demonstrated that gibel carp successfully avoided from pike by possibly exerting greater effort, which might adversely affect its growth rate.

Reproduction, which usually indicated as principal factor of invasion success of gibel carp (Leonardos *et al*., 2008; Tarkan *et al*., 2012a and b) could be reason for its strong establishment and may contribute reduced growth of the fish in Lake Uluabat. Gynogenetically reproducing populations of gibel carp, including one that in Lake Uluabat (Emiroğlu *et al*., 2011) showed significantly higher gonad production (e.g. relative fecundity) and smaller size at maturities (Tarkan *et al*., 2012a). The female length at maturity 71 mm SL found for gibel carp in Lake

Uluabat is earlier than that in other locations (Table 3), where fish matured after 92 mm SL. Even smaller maturation would be possible in Lake Uluabat since smaller individuals were not available in the sampling and size at maturity estimates were approximation. In addition, relative fecundity of gibel carp in Lake Uluabat achieved considerably higher values than those found in literature (Table 3). It was also remarkably higher than that in River Amur, Russia (Nikolsky, 1956), which was only available reproductive data from the native area of gibel carp. It has been argued in many cases that reproduction strategy shows different patterns among populations and usually populations invaded a new environment represent grater reproductive effort than those being established for a longer time (Copp and Fox, 2007). Gibel carp in Lake Uluabat appears to be such species having elevated reproductive effort with higher egg production. Literature reviews also supported that gynogenetic populations of gibel carp had an increased reproductive effort (Tarkan *et al*. 2012a and b). However, higher reproductive effort can lead decreasing in the growth rate as a result of the energetic trade off between reproduction and growth (e.g. Grabowska *et al*., 2011) as also may be the case in the present study. Invasive species face with novel or unpredictable environments often exhibit high reproductive investment at an early age (Stearns, 1976). Increased reproductive effort of gynogenetic gibel carp in Lake Uluabat seemed to fit this concept and would be one of the main reasons for the species' establishment success. Gynogenetic populations as in Lake Uluabat should have some potential advantages to invade new environments. As females composed of the majority of the population, it allows enhance recruitment in early life stages and all ecological resources can be used mostly for egg production (e.g. Tarkan *et al*., 2012a).

Given profitable catching of gibel carp, fishing pressure is likely to continue in Lake Uluabat. This can be viewed as an effective control of this species, as it may keep its abundance at certain levels, which can limit its impact on native fauna and flora where eradication techniques such as rotenone is rather unlikely at large spatial scales due to reproductive strategy of gibel carp (i.e. *r*-strategy) as highly fecund species maturing smaller sizes (Tarkan *et al*., 2012a). Nevertheless, fish removal by commercial fishermen does not necessarily have any appreciable impact on gibel carp population in the lake. Koehn (2003) reported that 10-year period commercial harvest of non-native common carp did not show any significant catch declines in Gippsland lakes, Australia. It was suggested that populations should be shrunk to less than 10% of virgin biomass before removal is likely to be effective (Thresher, 1997). Commercial fishing in Lake Uluabat, however, targets larger sizes of gibel carp using usually gillnetting with 22 mesh sizes as smallest one, which obviously cannot catch immature individuals. Additionally, prohibited fishing during spawning season in Lake Uluabat would aid recovery of the populations. In this case, consistent cropping gibel carp population, which has already reproduced and recruited, would not have any effect on the population. However, this would not be true for native fish species in the lake. Indeed, sharp decline of native fishes while faster increase of gibel carp was observed despite intense fishing pressure on all fish species in the lake (unpublished data). Moreover, environmental degradation in Lake Uluabat may strengthen successful establishment of gibel carp, which has been proved in other sites that increase of gibel carp was coincided with ecosystem disturbance (Tarkan *et al*., 2012b). Also, reproductive interference of gibel carp with native fish species has recently been demonstrated with a long term monitoring in an environmentally disturbed reservoir (Tarkan *et al*., 2012b), which would be the case for indigenous species in Lake Uluabat, requiring further studies.

In summary, population of gibel carp did not seem to be affected by fishing pressure exposed over 5 years in the lake however this caused reduced growth rates in gibel carp because of reaching smaller age at maturity. Reproduction features of gibel carp are likely responsible for establishment success and viability of the population in the lake, like other gibel carp populations in Turkish waters, which reproduce gynogenetically (Tarkan *et al*., 2012a). Although there has been increasing concern over gibel carp distribution and impacts in Turkey (Tarkan *et al*., 2012b) and Europe (Vetemaa, 2005; Liasko *et al*., 2011), control methods and risk management tools are poorly applied. Once introduced, in order to control of established populations of highly robust and productive non-native fish species such as gibel carp, their invasive populations should be suppressed to prevent detrimental impacts on native species and ecosystem functioning (Britton *et al*., 2011). This work includes control techniques such as fishing, commercial harvesting and habitat rehabilitation for native fishes (Koehn, 2003) and is required the information on behavior, life history traits and population dynamics of the invader (Britton *et al*., 2011).

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