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Growth of black bullhead *Ameiurus melas* (Rafinesque, 1820) in Corbara Reservoir (Umbria – Italy)

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ABSTRACT

Key-words:
age, growth, length-weight relationship, Lee's phenomenon, relative weight

The age and growth of the invasive black bullhead *Ameiurus melas* (Rafinesque, 1820) were studied in the Corbara Reservoir, an artificial lake located on the River Tiber in central Italy. The results of the research revealed that the population was made up of eight cohorts, the oldest specimens being spawned in 1999. The sex ratio appears to be balanced, although females predominate in the younger cohorts, while the percentage of males increases among older specimens. The differences between sexes in the slope of the length-weight relationship were not statistically significant; the slope for the whole sample (b = 3.055) was significantly greater than 3, indicating an allometric growth pattern of the black bullhead. There were no significant differences in mean back-calculated lengths at age between the sexes. Analysis of Lee's phenomenon revealed the existence of differential mortality among younger individuals (1 and 2 years old) that favours larger individuals. The Von Bertalanffy growth function was $TL_t = 35.69 \{1 – \exp[–0.18 (t + 0.27)]\}$. The specimens caught displayed mean relative weight (W_r) values distinctly below 100 at all ages, while no significant difference emerged between the sexes with regard to condition.

RÉSUMÉ

Croissance du poisson-chat *Ameiurus melas* (Rafinesque, 1820) dans le Lac Corbara (Ombrie – Italie)

Mots-clés :
âge, croissance, rapport longueur-poids, phénomène de Lee, poids relatif

L'âge et la croissance du poisson-chat invasif *Ameiurus melas* (Rafinesque, 1820) ont été étudiés dans le Lac Corbara, un lac artificiel situé le long du cours du fleuve Tevere, en Italie centrale. Les résultats de la recherche ont révélé que la population était composée de huit classes d'âges, les spécimens les plus âgés provenant de la fraie de 1999. Le sex-ratio semble être équilibré, bien que les femelles prédominent dans les classes d'âges plus jeunes, tandis que le pourcentage de mâles augmente parmi les spécimens plus âgés. Les différences entre les sexes en matière de pente du rapport longueur-poids n'étaient pas significatives ; la pente de tout l'échantillon (b = 3.055) était significativement supérieure à 3, indiquant que le poisson-chat a un modèle de croissance allométrique. Aucune différence significative n'a été constatée entre les longueurs rétromesurées moyennes des différents sexes au même âge. L'analyse du phénomène de Lee a révélé l'existence d'une

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différence de mortalité chez les jeunes individus (âgés de 1 et 2 ans) en faveur des individus les plus grands. La fonction de croissance de Von Bertalanffy est de TL_t = 35.69 {1 – exp[–0.18 (t + 0.27)]}. Les spécimens capturés présentaient des valeurs de poids moyen relatif (W_r) nettement inférieures à 100 à tous les âges, tandis qu'aucune différence n'est apparue entre les sexes en ce qui concerne la condition.

INTRODUCTION

One of the most important and least studied factors in the deterioration of aquatic ecosystems is reported to be the introduction of exotic species (Lodge *et al.*, 2000; Mack *et al.*, 2000). In the last century, non-indigenous fish species were introduced into European freshwater systems, both intentionally and by accident (Copp *et al.*, 2005). When exotic species are introduced, biodiversity generally declines, especially if the new arrival displaces one or more indigenous species. The result is that a few species able to adapt to a broad range of habitats will proliferate, often at the expense of indigenous or less adaptable ones (Rooney *et al.*, 2007). Non-indigenous populations may affect indigenous communities through competition for limited food resources, predation, the introduction of parasites and diseases, and genetic deterioration *via* hybridisation or through structural changes in the habitat (Crivelli, 1995).

Native to North America, the black bullhead *Ameiurus melas* (Rafinesque, 1820) has been recorded in Europe since the nineteenth century (Kottelat and Freyhof, 2007). Although the identity of wild European populations is uncertain, the black bullhead is the most widespread of the ictalurid species introduced into Europe (Wheeler, 1978), and has recently been recorded in Spain (Elvira, 1984) and Portugal (Gante and Santos, 2002). In Italy, the black bullhead first appeared in 1904 (Tortonese, 1970), and has now spread throughout most of the country. While *A. melas* is widespread in the River Tiber, one of its most abundant populations is to be found in Corbara Reservoir (Lorenzoni *et al.*, 2006).

A possible reason for the diffusion of the black bullhead is its ability to tolerate a wide range of environmental conditions (Smith, 1949; Stuber, 1982). Black bullhead populations often reach high biomass levels (Brown *et al.*, 1999). For this reason, it is often considered undesirable and a potential threat to autochthonous fish species, on account of both competition for resources and predation upon small fishes. French legislation classifies it as a "species liable to cause biological disequilibrium" (Cucherousset *et al.*, 2006).

Despite the widespread distribution of the species, little information is currently available on the ecology of the black bullhead in Italy and its impact on indigenous fish communities. Any management strategy that aims to contain invasive species and to safeguard biodiversity can only be successful if it is based on thorough knowledge of the diffusion, ecology and biology of the species introduced and of the impact that they have on native communities (Byers *et al.*, 2002). Quantification of age and growth is a vital component in understanding the ecology and life history of any fish species; this is especially important for an introduced species like the black bullhead. Knowledge of the individual growth rates and age structure of an introduced population is required in order to determine the success and degree of establishment as well as to predict the fish's impact on native fauna. Growth rate information can also be used to compare dynamics among water bodies, years and fish size; to describe trends over time; to examine total mortality rates and to determine the general status of a population (Kwak *et al.*, 2006).

The objectives of our research were to quantify the growth rates, age structure, condition and sex ratio of the black bullhead population in Corbara Reservoir, and to compare our findings with those from rivers and reservoirs in native and introduced ranges in order to elucidate trends among populations.

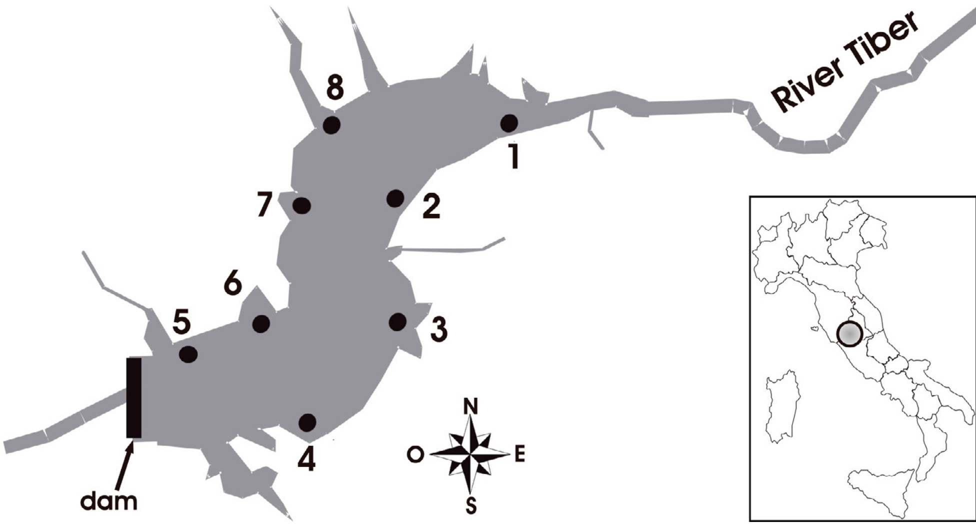

Figure 1
Area investigated. Numbers indicate the sampling stations.

Figure 1
Situation du Lac Corbara. Les nombres indiquent les stations de recueil d'échantillons.

MATERIALS AND METHODS

> *STUDY SITE AND SAMPLING PROCEDURES*

With a capacity of 207 million cubic metres, Lake Corbara is the largest reservoir in Umbria (Italy) (Figure 1). Situated along the course of the River Tiber (42°42'20" N; 0°13'30" W) (Rome meridian), about 185 km from the source, the reservoir was constructed in the 1960s in order to feed the Baschi hydroelectric power station. The fish community in the Corbara Reservoir is dominated by non-indigenous species. Indeed, among the 18 fish species currently present in the reservoir, the most abundant are pike-perch *Sander lucioperca* (L.), black bullhead *A. melas* (Raf.), goldfish *Carassius auratus* (L.) and common carp *Cyprinus carpio* L. Only three native fish species are to be found: European chub *Leuciscus cephalus* (L.), eel *Anguilla anguilla* (L.) and rudd *Scardinius erythrophthalmus* (L.).

Fish sampling was carried out seasonally on the following dates: 14th November 2005 and 27th February, 8th May and 11th September 2006. Black bullheads were caught by means of multi-mesh gillnets and fyke-nets at eight sampling stations along the perimeter of the reservoir. The gillnets were assembled by using panels of different-sized mesh (22, 28, 35, 50, 70, 80 and 100 mm), to allow more efficient and representative sampling (Craig *et al.*, 1986; Degerman *et al.*, 1988). Each gillnet was 2 m high and 250 m long. The fyke-nets had a total length of 8 m and a mesh of 20 mm (mouth width: 1.5 m). One gillnet and one fyke-net were set overnight at each sampling station.

All black bullhead specimens caught (n = 3260) were measured (total length, TL (cm) (± 1 mm)) and weighed (wet body weight, W (g) (± 1 g)).

On each single sampling date, a randomly selected sub-sample made up of about 10% of the specimens caught (n = 313) was brought back to the laboratory for sex determination and back-calculation of growth. Fish were sacrificed by administering an overdose of anaesthetic acetone chloroform (trichloro-ter-butyl alcohol).

> LABORATORY ANALYSIS

Age and sex

Bhattacharya's method (Bhattacharya, 1967) was used to split the age-classes from the length-frequency data of all black bullheads caught (n = 3260), by means of the program FiSAT II (version 1.2.2) (Gayanilo *et al.*, 2006). This was followed by the application of modal class progression analysis, which yields an index that must be greater than 2 to provide meaningful separations.

Specimens were assigned to a given age-class on the basis of the number of winters that they had lived through before being caught. The date conventionally used as a cut-off between one age-class and the next was 31st December (Devries and Frie, 1996). As sampling was carried out in two different calendar years, the same specimen could be assigned to two different age-classes, depending on the period in which it was caught. For this reason, in the analyses of population structure, the cohorts were identified according to the year of spawning of the individual specimens, rather than the age-class.

Sex was determined by means of macroscopic examination of the gonads (Bagenal, 1978). To analyse the sex ratio, the percentages of males and females in each cohort were compared by means of Fisher's exact test.

Back-calculation of total lengths

The right pectoral spine of 82 black bullheads was removed for back-calculated growth analysis. Specimens included in the study were selected at 1-cm length intervals, in order to encompass the whole length range of the sub-sample brought back to the laboratory. The spines removed were cleaned of dry tissue and sectioned. Sections approximately 0.5 mm thick were cut through the dorsal and anterior processes. This location minimises the influence of the central lumen (Buckmeier, 2002).

Photographs were taken of all pectoral spines for image analyses, which were carried out by means of ImageJ software (1.26 version). This software served to accurately measure pectoral spine radius at the time of capture (from the focus to the edge) and the different radii of age-rings (from the focus to the corresponding ring-mark identified as an annulus).

The previous growth of black bullhead was determined by back-calculation from the sections of pectoral spine measurements. Back-calculation is based on the assumption that the growth of the fish is proportional to the growth of its bony structures. The relationship between the chosen structure and the body length of the fish can be described by means of various linear or non-linear equations (Francis, 1990; Secor and Dean, 1992). Length at age was back-calculated by means of various models: the direct-proportional method of Dahl-Lea (DPM) (Dahl, 1907; Lea, 1910), the Fraser-Lee method (Devries and Frie, 1996), the linear body proportional hypothesis (LBPH), and the non-linear body proportional hypothesis (NLBPH); detailed descriptions of the formulae and rationale of these methods can be found in Smedstad and Holm (1996). On comparing the various methods by means of the ANOVA test, no significant differences emerged in the back-calculated lengths at the different ages; the relationships between TL and radius of the pectoral spine were substantially homogeneous in terms of the variance justified by the different models. For this reason, in subsequent analyses and figures, the widely used Fraser-Lee method was preferred (Ricker, 1992); the relationship between the TL of specimens at the time of capture (TL_c) and total radius of the pectoral spine (R_s) was described by means of the equation: $TL_c = a + b\,R_s$. The past TL at the time of check formation was back-calculated by means of the formula (Devries and Frie, 1996): $TL_t - a = R_t / R_s\,(TL_c - a)$, where TL_t is total length (in cm) relative to age t and R_t is the radius (in cm) of the annulus t; the parameter a was defined as the intercept of linear regression between TL_c and R_s. The Fraser-Lee method of back-calculation is used when the intercept of the relationship between fish length and hard-part radius is not at the origin (Devries and Frie, 1996).

When back-calculated lengths at age are smaller for older fish than for younger fish in the sample, Lee's phenomenon might be occurring. For example, this could imply that slower-growing members of the year-class escaped fishing-related or natural mortality better than faster-growing members did (Devries and Frie, 1996); Lee's phenomenon may also be due to non-random sampling of the stock; for example, if sampling tends to select the larger members of the younger ages (Bagenal, 1978).

By contrast, a reverse Lee's phenomenon occurs when back-calculated lengths at the various ages are greater for the older fish than for the younger ones in the sample. The presence of Lee's phenomenon was checked by comparing the total lengths back-calculated at the various ages t between the specimens at age t and those of greater age ($t + i$) (Bagenal,1978); statistical comparison was made by means of the Mann-Whitney U test.

The ages attributed by means of Bhattacharya's method were validated on the basis of the results yielded by the analysis of the pectoral spine sections.

Growth models

Theoretical growth in length was assessed by means of the Von Bertalanffy model (1938): $TL_t = L_\infty \{1 - \exp[-k(t - t_0)]\}$, where TL_t is the theoretical total length (in cm) at age t, k is the rate at which the ultimate length L_∞ is approached, and t_0 is the theoretical age (in years) at length zero. The index of growth performance Φ' was estimated by means of the equation $\Phi' = \log(k) + 2\log(L_\infty)$ (Pauly and Munro, 1984), where k and L_∞ are the Von Bertalanffy growth parameters. The analysis was conducted by using the lengths at the various ages of all the specimens caught.

To determine whether or not the growth of the black bullhead undergoes a stasis in the winter, the mean length of the age-class t in the autumn was compared with that of the age-class (t + 1) in the following winter. This comparison was carried out by means of the Mann-Whitney U test only for the age-classes containing a sufficient number of specimens (age-classes 0+, 1+, 2+, 3+ and 4+).

Length-weight relationship

Length and weight data of black bullheads were log-transformed and the resulting linear relationship fitted by the least-square regression, using weight as the dependent variable: $\log(W) = \log(a) + b\log(TL)$ (Bagenal, 1978). This analysis was performed both on the whole sample (all specimens caught) and on the sample subdivided by sex. The relationships between the sexes were compared by analysis of covariance (ANCOVA), and the hypothesis of isometric growth was tested by means of Student's t-test.

Relative weight (W_r)

To represent the nutritional status of *A. melas*, the relative weight (W_r) index was calculated by means of the following equation (Murphy *et al.*, 1991): $W_r = 100\ W/W_s$, where W is the actual weight (g) on sampling, and W_s is the standard weight for fish of the same length. To calculate the standard weight, the following equation was used: $\log(W_s) = -4.974 + 3.085 \log(TL)$ (Bister *et al.*, 2000). The mean values of the relative weight calculated for each sex were compared by means of the Mann-Whitney U test. The ANOVA test was used to compare the mean values of relative weight calculated in the different cohorts. Specimens belonging to the 1999, 2000 and 2006 cohorts were excluded from this analysis because the number of fish was too small to allow valid interpretation. Tukey's *post-hoc* test was used to determine which cohort differed significantly.

Catches per unit effort (CPUEs)

Catches per unit effort (CPUEs) were used as indicators of black bullhead abundance (Hubert, 1996). In the case of fyke-nets, CPUEs were expressed as both biomass (g) and the number of individuals (ind.) caught per night; for gillnets, fishing effort was calculated on the area of nets, and CPUEs were expressed as ind·m^{-2} and g·m^{-2} per night. In order to analyse the trend in black bullhead stocks over time, the CPUEs calculated were compared with those recorded during a similar study conducted in Corbara Reservoir in 2000, which used the same sampling pattern (the same stations, equipment and seasonal periods). The data from the two studies were therefore directly comparable. The basic principle underlying the use of CPUE data is that changes in CPUE accurately reflect changes in the abundance of fish in the stock (King, 1995). Comparison between the mean CPUEs in each of the two sampling years was carried out by means of the Mann-Whitney U test.

RESULTS

> *SEX, AGE AND LENGTH DISTRIBUTIONS*

The black bullheads caught (n = 3260) ranged in size from 8.00 to 29.50 cm TL (mean ± SE = 16.23 ± 0.06 cm) and in weight from 5.50 to 330.84 g (mean ± SE = 60.55 ± 0.59 g). Of the 3260 black bullheads caught, sex was determined in 313 specimens: 163 were identified as females, while 150 were males.

Bhattacharya's method was useful in validating age (Table I) when using length-frequency largest samples and several normal components were clearly necessary to explain the length-frequency distribution. The sex and age distribution of black bullhead in Corbara Reservoir are shown in Table II. The population structure of the overall sample (n = 3260) revealed the presence of eight cohorts. The oldest specimens were spawned in 1999. The older specimens (cohorts: 1999, 2000, 2001) were fewer, while the most abundant specimens were those belonging to the 2002, 2003, 2004 and 2005 cohorts. Specimens spawned in 2006 proved to be very scarce; this finding might have been partly due to the selectivity of the nets used, which may not have been able to entrap the smallest specimens.

The sex ratio was 1.09 females to 1 male. This ratio was not significantly different from 1:1 in the sample observed. In the younger cohorts, females predominated, while the percentage of males increased among older specimens. Only among specimens spawned in 2005 did the differences in the percentage frequencies between the two sexes prove to be significant.

> *GROWTH*

The parameters of theoretical growth in length (± SE), according to the Von Bertalanffy model, were calculated for both sexes (Figure 2). In the females, they were: L_∞ = 32.06 ± 7.77, k = 0.22 ± 0.11, t_0 = –0.60 ± 0.38; in the males, they were: L_∞ = 32.27 ± 8.24, k = 0.22 ± 0.13, t_0 = –0.83 ± 0.66. No significant difference emerged between the sexes with regard to each parameter (t-test, $P > 0.05$). The values of the Von Bertalanffy parameters calculated for the overall sample of specimens caught, without distinction between the sexes, were: L_∞ = 31.78 ± 1.21, k = 0.21 ± 0.02, t_0 = –0.78 ± 0.07. The value of Φ' was 2.82.

Comparison between the mean lengths recorded in each age-class in autumn and those recorded in the following winter revealed that growth in length does not present a stasis during the winter period (Figure 3). Indeed, the mean winter values were higher than those of the previous autumn for all age-classes, with statistically significant differences emerging for all ages (Table III).

> *LENGTH-WEIGHT RELATIONSHIP*

The relationship between body weight and total length proved to be log(W) = –2.021 + 3.091 log(LT) (r^2 = 0.98, r = 0.99, $P < 0.01$) for females and log(W) = –2.073 + 3.129 log(LT) (r^2 = 0.97, r = 0.98, $P < 0.01$) for males (Figure 4). In both sexes, the value of the parameter b was significantly greater than 3 (females: t-test, $P < 0.05$; males: t-test, $P < 0.01$). Comparison between the regressions did not reveal any statistically significant differences between

Table I

Breakdown of length-frequency data of total length of black bullhead in the Corbara Reservoir population by means of Batthacharya's method followed by modal class progression analysis. To provide a meaningful separation, the value of the separation index (S.I.) must be greater than 2. The dates indicate when fish were captured.

Tableau I

Décomposition des données longueur-fréquence de la longueur totale des poissons-chats de la population du Lac Corbara en utilisant la méthode de Batthacharya, suivie d'une analyse de la progression de la classe modale. Pour fournir un groupe séparé pertinent, la valeur de l'indice de séparation (S.I.) doit être supérieure à 2. Les dates indiquent les dates auxquelles les poissons ont été capturés.

Sample	Group	Mean ± SE TL (cm)	*n*	S.I.	Estimated age	Estimated cohort
14 November 2005		8.94 ± 0.17	8		0+*	2005
	1	10.78 ± 0.08	84	-	1+	2004
	2	15.10 ± 0.12	83	4.46	2+	2003
	3	18.76 ± 0.05	383	2.42	3+	2002
	4	23.44 ± 0.34	14	3.47	4+	2001
		29.25 ± 0.25	2		6+*	1999
27 February 2006	1	9.56 ± 0.13	38	-	1+	2005
	2	12.23 ± 0.16	34	3.29	2+	2004
	3	17.09 ± 0.05	503	3.33	3+	2003
	4	19.05 ± 0.03	304	2.31	4+	2002
	5	23.63 ± 0.24	4	5.10	5+	2001
		27.00	1		6+*	2000
8 May 2006	1	10.62 ± 0.09	21	-	1+	2005
	2	14.92 ± 0.09	270	3.69	2+	2004
	3	17.95 ± 0.04	450	3.69	3+	2003
	4	19.94 ± 0.04	339	2.35	4+	2002
		26.20	1		5+*	2001
11 September 2006		8.07 ± 0.07	7		0+*	2006
	1	10.60 ± 0.03	440	-	1+	2005
	2	12.99 ± 0.09	211	4.35	2+	2004
	3	18.28 ± 0.16	28	4.19	3+	2003
	4	21.33 ± 0.24	35	2.05	4+	2002

* Age determination was carried out only by articulating process sections of pectoral spines.

Table II
Sex and age compositions of black bullhead in Corbara Reservoir. Statistical comparisons between the sexes are given (Fisher's exact test).

Tableau II
Compositions en sexe et âge du poisson-chat dans le Lac Corbara. Les comparaisons statistiques entre les sexes sont indiquées (test exact de Fisher).

Cohort	Overall sample			Female sample			Male sample			Fisher's exact test
	n	%		*n*	%		*n*	%		
1999	2	0.06								
2000	1	0.03								
2001	19	0.58		-	-		1	100		$P > 0.05$
2002	1061	32.55		35	46.67		40	53.33		$P > 0.05$
2003	1064	32.64		50	53.19		44	46.81		$P > 0.05$
2004	599	18.37		68	51.91		63	48.09		$P > 0.05$
2005	507	15.55		10	83.33		2	16.67		$P < 0.05$
2006	7	0.21								
Total	3260	100		163	52.08		150	47.92		$P > 0.05$

the sexes with regard to either the parameter *b* (ANCOVA, $P > 0.05$) or the intercept (*t*-test, $P > 0.05$). The relationship between body weight and total length calculated on the entire sample of specimens caught ($n = 3260$), without distinction between the sexes, is described by the equation $\log(W) = -1.974 + 3.055 \log(LT)$ ($r^2 = 0.99$, $r = 0.99$, $P < 0.01$). The value of the parameter *b* calculated on the entire sample proved to be significantly greater than 3 (*t*-test, $P < 0.01$).

> BACK-CALCULATED GROWTH

The relationship between the TL of specimens at the time of capture and total radius of the pectoral spine was described by the equation: $TL_c = -0.088 + 76.484\ R_S$. Pectoral spine radius and TL_c showed a positive linear correlation ($r^2 = 0.750$, $r = 0.866$, $P < 0.01$), indicating that TL was proportional to spine radius. Comparison of the back-calculated mean TL values did not reveal any statistically significant differences between the sexes at any of the ages considered (Mann-Whitney U test: $P > 0.05$) (Figure 5). The subsequent analyses were therefore conducted without taking sex into account.

Comparison of the mean back-calculated lengths between specimens of age *t* and those of age ($t + i$) revealed the existence of a reverse Lee's phenomenon: the back-calculated lengths reached at the various ages showed significant differences for the ages of 1 year (Mann-Whitney U test: $z = -2.13$, $P < 0.05$) and 2 years (Mann-Whitney U test: $z = -3.50$, $P < 0.01$) in favour of the older specimens (Table IV).

> RELATIVE WEIGHT (W_r)

The mean value (± SE) of the relative weight calculated on the total sample of specimens caught was 75.88 ± 0.09. No difference emerged between the sexes on comparing the mean values of relative weight, which were 75.33 ± 0.55 for females and 74.63 ± 0.52 for males (Mann-Whitney U test: $z = 0.31$, $P > 0.05$). For this reason, in order to analyse variations

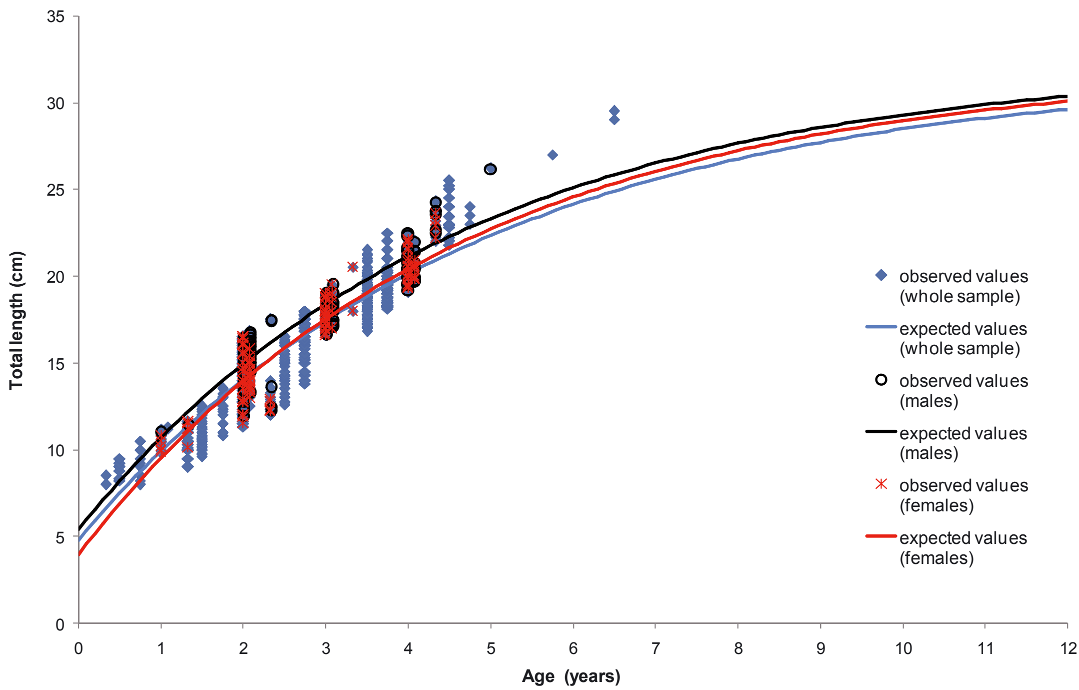

Figure 2
Von Bertalanffy growth curves.

Figure 2
Courbes de croissance de von Bertalanffy.

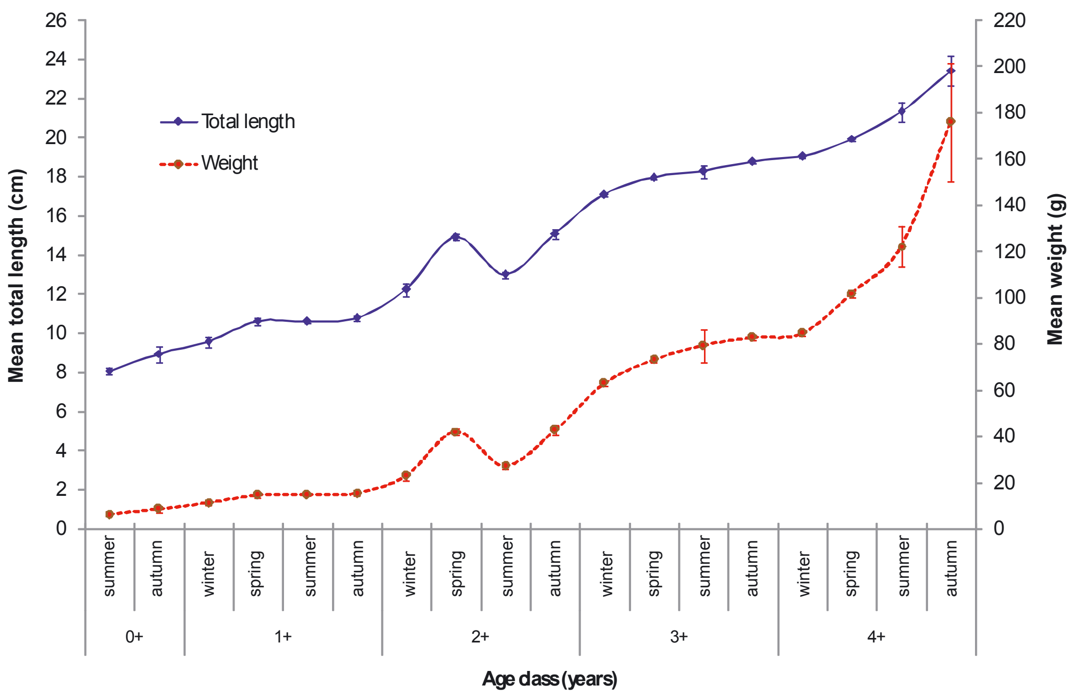

Figure 3
Seasonal mean total length and weight at the various ages. Vertical bars indicate 95% confidence intervals.

Figure 3
Moyenne saisonnière de la longueur et du poids à différents âges. Les barres verticales indiquent les intervalles de confiance à 95 %.

Table III
Comparison between the mean total length (TL) at age t in autumn (November 2005) and at age (t + 1) in winter (February 2006).

Tableau III
Comparaison entre la longueur moyenne totale (TL) à l'âge *t* en automne (novembre 2005) et à l'âge (*t* + 1) en hiver (février 2006).

November 2005			February 2006			Mann-Whitney U test	
Age-class	*n*	Mean ± SE TL (cm)	Age-class	*n*	Mean ± SE TL (cm)	*z*	*P*
0+	8	8.94 ± 0.17	1+	38	9.56 ± 0.13	–2.29	< 0.05
1+	84	10.78 ± 0.08	2+	34	12.23 ± 0.16	–6.71	< 0.01
2+	83	15.10 ± 0.12	3+	503	17.09 ± 0.05	–11.52	< 0.01
3+	383	18.76 ± 0.05	4+	304	19.05 ± 0.03	–4.57	< 0.01

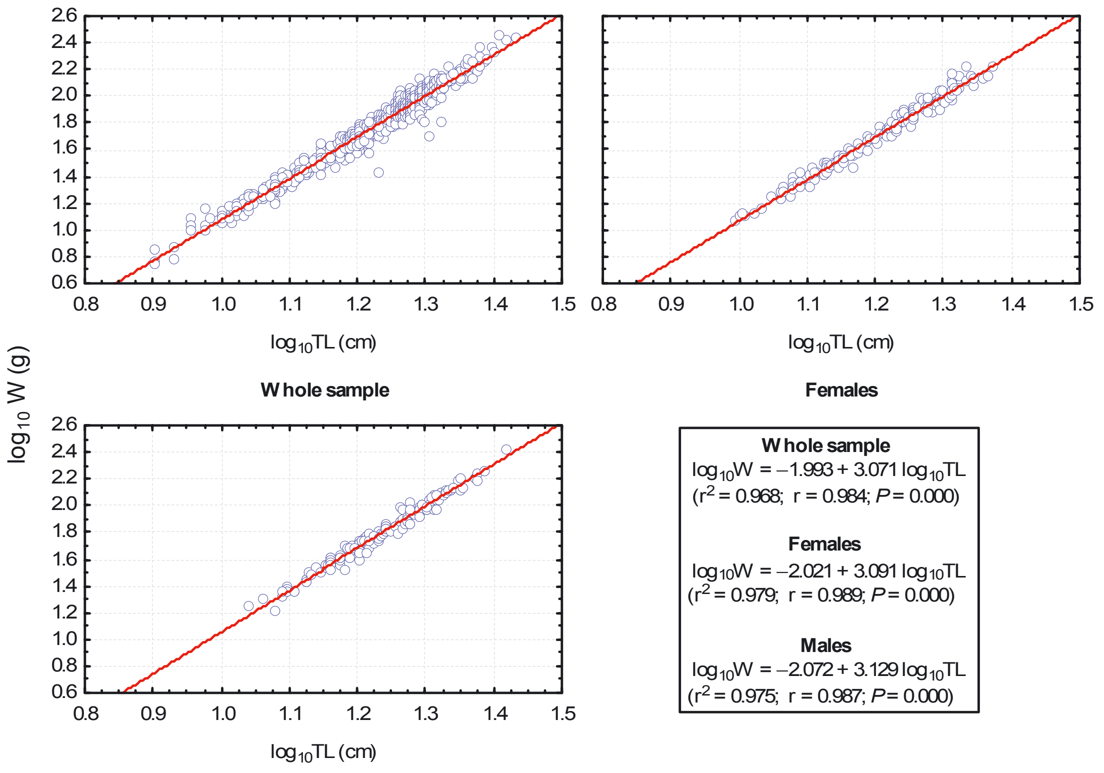

Figure 4
Total length-weight relationships.

Figure 4
Relations longueur-poids.

in the condition of the black bullhead as a function of age, we utilised the total sample of specimens caught, broken down by cohort. Specimens belonging to the 1999, 2000 and 2006 cohorts were excluded from this analysis on the grounds of insufficient numbers. In the Corbara Reservoir, specimens spawned in 2001 displayed the highest mean value of W_r

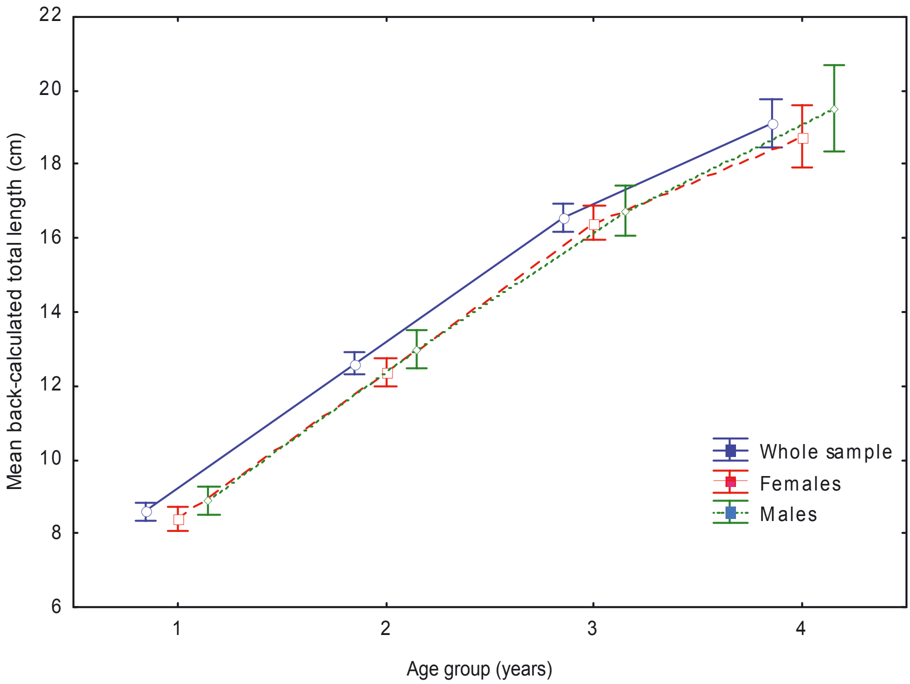

Figure 5
Mean back-calculated total length at age. Vertical bars indicate 95% confidence intervals.

Figure 5
Longueurs rétromesurées aux différents âges. Les barres verticales indiquent les intervalles de confiance à 95 %.

Table IV
Lee's phenomenon in the overall sub-sample (sexes combined): comparison of back-calculated total lengths between the specimens at age t and (t + i).

Tableau IV
Le phénomène de Lee dans le sous-échantillon général (sexes combinés) : comparaison entre les spécimens des longueurs totales moyennes rétromesurées à l'âge *t* et (*t* + *i*).

	age *t*		age (*t* + *i*)		Mann-Whitney U test	
Age group	*n*	Mean ± SE TL (cm)	*n*	Mean ± SE TL (cm)	*z*	*P*
1	7	7.76 ± 0.34	75	8.67 ± 0.12	–2.13	< 0.05
2	23	11.70 ± 0.26	52	13.00 ± 0.16	–3.85	< 0.01
3	31	16.31 ± 0.23	21	16.92 ± 0.30	–1.54	> 0.05

(81.56 ± 2.24); the worst conditions were recorded in specimens spawned in 2002 (W_r = 75.24 ± 0.15), 2003 (W_r = 75.83 ± 0.17) and 2004 (W_r = 75.46 ± 0.22), while those spawned in 2005 presented an intermediate condition (W_r = 77.44 ± 0.24). The differences in the mean values of the relative weight in the various cohorts proved to be significant (ANOVA, $P < 0.01$). A *post-hoc* test revealed that the mean value of W_r recorded in the 2001 and 2005 cohorts differed significantly from the values recorded in all the other cohorts, while the mean condition of the specimens spawned in 2004 did not differ from that of those spawned in 2002 or 2003. The seasonal pattern of the mean values (± SE) of W_r shows that the condition of the specimens examined worsened during the colder seasons (spring: 76.21 ± 0.19; summer: 76.47 ± 0.21; autumn: 75.36 ± 0.10; winter: 75.32 ± 0.17), the differences being statistically significant (ANOVA, $P < 0.01$).

> *CATCHES PER UNIT EFFORT (CPUEs)*

In Corbara Reservoir, no data on CPUEs are available for the years prior to 2000. In 2000 the mean CPUEs were clearly lower than in 2006, both for gillnets (2000: 0.0002 ± 0.0001 ind·m^{-2}, 0.04 ± 2.77 g·m^{-2}; 2006: 0.27 ± 0.06 ind·m^{-2}, 14.26 ± 2.77 g·m^{-2}) and for fyke-nets (2000: 0.59 ± 0.33 ind, 31.35 ± 39.51 g; 2006: 45.84 ± 7.85 ind, 2416.31 ± 450.60 g). Statistical comparison between the mean CPUEs by means of the Mann-Whitney U test revealed significant differences with regard to both gillnets (number of individuals: $z = 8.20$, $P < 0.01$; biomass: $z = 8.15$, $P < 0.01$) and fyke-nets (number of individuals: $z = 6.39$, $P < 0.01$; biomass: $z = 6.23$, $P < 0.01$).

DISCUSSION

Among-population comparisons of growth in fish are a common and useful means of assessing the adaptation of a species to different environmental conditions (Živcov *et al*., 1999). The potential of an animal species to colonise new ecosystems, or to re-colonise those previously occupied, is influenced by its ability to modify its allocation of energy resources to somatic and gonadal growth in response to different environments (Copp *et al*., 2004). The fact that the populations introduced into Europe display lower adult growth rates and lower ultimate lengths (L_∞) than native North American populations may be the result of the greater reproductive effort needed to colonise new ecosystems (Copp *et al*., 2004).

The slope *b* values of the length-weight relationship (Figure 4) showed that weight increases allometrically with length (Ricker, 1975); growth in length takes second place to growth in the other spatial dimensions, so that weight increases more than proportionately with length. *A. melas* in Corbara Reservoir display a higher regression coefficient than other European and North American populations ($n = 11$), for which the mean value of *b* is 2.99, ranging from a minimum of 2.89 to a maximum of 3.41 (Froese and Pauly, 2006). With regard to comparison with other populations in northern Italy, Ceccuzzi (2004) reported *b* values of 2.61 for females and 2.80 for males in a population of black bullhead in Lake Varese, while in Lake Ghirla *b* is reported to be 3.02 (Graia, 2001). In five waterways in the Province of Padua, *b* varies from 2.68 to 3.17, with a mean value of 2.85 (Turin *et al.*, 1995).

The oldest specimens caught in Corbara Reservoir were more than 6 years old (Table I); this finding is in line with reports in the literature. Indeed, the mean lifespan of the species in Italy is 4–5 years, though a few specimens may live as long as 8–9 years (Gandolfi *et al.*, 1991).

According to Taylor (1962), the Von Bertalanffy equation provides a good description of the growth pattern if the maximum observed length is approximately 95% of the asymptotic length; in Corbara Reservoir the maximum theoretical length that can be reached by specimens of the population examined is 31.78 cm (Figure 2), while the maximum length of the specimens caught was 29.50 cm; this would suggest a good description of the growth pattern for the overall population without taking sex into account (93%).

Very few published data on the growth rates of black bullhead in other Italian waterways are available for comparison with those recorded in Corbara Reservoir. Our study shows that black bullhead in Corbara Reservoir reach a mean length of 8.53 cm during their first year of life, 10.56 cm in the second year, 14.11 cm in the third, 17.87 in the fourth and 19.69 in the fifth. The growth of *A. melas* in Corbara Reservoir is lower than has been reported in the literature with regard to acclimatised populations in Italy; according to Gandolfi *et al.* (1991), the black bullhead reaches a length of 18–25 cm by the age of three years. In Lake Varese, specimens reach a length of 17 cm within the first year, 22 cm within the second, 26 cm in the third and 30 cm in the fourth (Ceccuzzi, 2004). The values reported by Turin *et al.* (1995)

are lower: 11.2 cm in the first year, 13.9 in the second, 15.8 in the third, 17.7 in the fourth and 24.5 in the sixth. Moreover, black bullhead growth in Corbara Reservoir is markedly lower than that recorded in the original North American populations (Carlander, 1950; Houser and Collins, 1962; Shelley, 1981; Morris, 1985; Hanchin *et al.*, 2002a; Froese and Pauly, 2006).

Our analysis revealed that growth in length is not constant throughout the year; rather, it takes place mainly in autumn and spring, without suffering any stasis in the winter period (Figure 3). This might not, however, be due to a real increase in length; it might be the result of differential mortality, to the detriment of smaller individuals. Indeed, winter is a particularly critical period for many fish species (Lorenzoni *et al*., 2002); temperatures fall and food supplies dwindle, which may increase mortality among smaller or more malnourished specimens as a result of tougher intra- and interspecific competition (Bujise and Houthuijzen, 1992; Ludsin and Devries, 1997). Our analysis of relative weight revealed that winter is the season in which the black bullhead in Corbara Reservoir display their worst condition. The finding of a reverse Lee's phenomenon in the younger age-classes (1- and 2-year-olds) (Table IV) suggests that predation or intra- and interspecific competition takes place among younger individuals and that this favours the larger specimens (Bagenal, 1978).

The relative weight of the Corbara specimens is distinctly below 100. When W_r values are well below 100 for an individual or size-group, problems may exist with regard to food supply or feeding conditions (Anderson and Neumann, 1996). That the food supply is inadequate for the black bullhead population in Corbara Reservoir seems clear if the mean W_r values calculated in the different cohorts are compared with those reported by Morris (1985) with regard to some South Dakota populations. It seems likely that this situation is the consequence of intense intraspecific competition, due to the recent numerical expansion of the population, as is evidenced by the increase in CPUEs in recent years. Indeed, the current CPUE values calculated in the Corbara Reservoir are high and, according to what has been reported by Brown *et al.* (1999), typical of high-density populations.

Our analysis also revealed a possible relationship between the relative abundance of the various cohorts and the pattern of relative weight. Indeed, the lack of young of the year may be partly explained by the size-selectivity of the gillnets used. However, we also used fyke-nets (20-mm mesh). These capture gears have proved to be particularly efficient in capturing benthonic species (Krueger *et al.*, 1998), such as the black bullhead; moreover, Hanchin *et al.* (2002b) claim that fyke-nets (19-mm mesh) appear to more effectively capture smaller black bullheads. The age structure showed that the number of newly-spawned specimens in the population underwent a marked increase in 2002 and 2003, and declined in subsequent years (Table II). With regard to the relative weight, by contrast, it emerged that those specimens spawned in 2002, 2003 and 2004 were most heavily penalised. Several studies have found that black bullhead growth is highly correlated with relative abundance and size-structure (Moen, 1959; Houser and Collins, 1962; Hanchin *et al.*, 2002a).

Black bullhead growth has generally been correlated with the population characteristics of some potential competitors (Brown *et al.*, 1999). Competition for food resources would most likely occur between black bullhead and common carp (Rose and Moen, 1951; Hanchin *et al.*, 2002a). In Corbara Reservoir, common carp and goldfish are the most abundant species, accounting for 41.40% and 30.78%, respectively, of the total biomass (unpublished data); moreover, the abundance of these two species showed an increase from 2000 to 2006 (goldfish: CPUE 2000 = 0.0086 $ind \cdot m^{-2}$, CPUE 2006 = 0.023 $ind \cdot m^{-2}$; common carp: CPUE 2000 = 0.0028 $ind \cdot m^{-2}$, CPUE 2006 = 0.01 $ind \cdot m^{-2}$), which proved significant on the Mann-Whitney U test (goldfish: $z = 2.71$, $P < 0.01$; common carp: $z = 4.36$, $P < 0.01$). However, this issue deserves further study.

The information yielded by this research increases our knowledge of the biological characteristics of *A. melas* and provides a frame of reference for further analyses, with a view to monitoring trends in the black bullhead population of Corbara Reservoir. It seems particularly important to investigate the internal dynamics of the population and the intra- and interspecific interactions that characterise this population.

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