Removal control of the highly invasive fish *Gambusia holbrooki* and effects on its population biology: learning by doing

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Abstract

Context. For the success of future conservation and management programs, it is necessary to better understand the resilience mechanisms of invasive species and their invasive potential. In this sense, the study of the effects that management actions have on their biological traits is essential.

Aims. The present study aimed to assess the effects of removal control on the abundance and biology of an isolated population of the top invasive fish *Gambusia holbrooki* (eastern mosquitofish).

Methods. Experimental removal control with traps and handnets was carried out on a population of mosquitofish inhabiting a small semiarid stream in south-eastern Spain. Mosquitofish were periodically captured for more than 3 years. Temporal variations in abundance, fish somatic condition and reproductive investment, percentage of mature females, size at maturity and population recruitment were analysed.

Key results. Individuals of the 1+ age class increased their reproductive investment when population abundance was lower, thus increasing recruitment rate during the first months of the recruitment period. Individuals of the 0+ age class were responsible for expanding the reproductive period in conditions of low fish abundance.

Conclusions. The mosquitofish population showed variations of reproductive parameters that could indicate a compensatory density-dependent phenotypic response under diminished abundance conditions. However, its removal by the constant use of a combination of active and passive capture methods, reinforced by increased extraction effort according to its local biology, has led to an eradication of the population. The target mosquitofish population showed distinct ecological features that may have contributed to the effectiveness of local control, namely, low initial fish density, isolation in a headwater stretch and the prevalence of individuals in sunlit shallow ponds.

Implications. The compensatory mechanisms of this invasive species in low-density conditions should be considered in the design of management programs. Moreover, further research into removal control methods for mosquitofish or similar species is also needed.

Additional keywords: density, eradication, life-history, management, Poeciliidae, population dynamics.

Introduction

Invasion by non-native species is widely considered one of the major global threats to biodiversity, especially in the case of inland aquatic ecosystems (Gherardi 2007; Gozlan *et al.* 2010), and the management of invasive species is a key element for biodiversity conservation (Genovesi 2005). Both the knowledge of the biology and ecology of invasive species within new invaded habitats, and the study of the effects that management actions have on their biological traits, are essential in understanding their resilience mechanisms and invasive potential (Cucherousset *et al.* 2009). Consequently, they must be considered crucial factors for the success of future conservation and management programs (Kopp *et al.* 2009).

Eastern mosquitofish, *Gambusia holbrooki* Girard 1859, is a poeciliid fish that was introduced as a mosquito-control agent into inland aquatic systems worldwide. Together with the closely related western mosquitofish, *G. affinis* (Baird & Girard 1853), it is the most abundant, widespread freshwater fish in circum-Mediterranean systems (Pyke 2005). The negative ecological impacts of the introduced mosquitofish are well known; their presence has been related to numerous reductions and extinctions of native fish species and they also negatively affect amphibians, invertebrates and whole aquatic communities. For these impacts, mosquitofish are regarded among the top invasive species in the world (Pyke 2005, 2008).

A LIFE-Nature project was developed between 2005 and 2008, to contribute to the conservation of the endangered cyprinodontid Iberian toothcarp, *Aphanius iberus* (Valenciennes 1846). Among its general objectives, the project focussed on the habitat restoration of a headwater stretch of the Chicamo stream (south-eastern Iberian Peninsula), which is the home of one of the most imperiled Iberian toothcarp populations (Oliva-Paterna 2006). According to the recommendation of Britton *et al.* (2011), after assessing the risk that the occurrence of eastern mosquitofish at this locality posed to the toothcarp population and considering the spatial constraints of the invasive population, a mosquitofish removal control program was developed. In this context, the present study aimed to assess the effects of the removal of individuals on the mosquitofish population. Specifically, a 3-year removal experiment was carried out, and the phenotypic response on the population biology was registered. It is known that mosquitofish presents an opportunistic life-history strategy (Vila-Gispert and Moreno-Amich 2002), with features that allow a high reproductive potential, such as ovoviviparity, early maturity, a long reproductive season, several spawning bouts and a high rate of generational turnover. It is also adaptable and considerably variable in its biology, at both individual and population level, frequently influenced by changes in environmental conditions (Pyke 2005, 2008). On the basis of previous studies with poeciliids (e.g. Lutnesky and Adkins 2003; Borg *et al.* 2006) and commercially harvested fish (e.g. Johnston and Post 2009; Sharpe and Hendry 2009), it can be predicted that mosquitofish should be able to modify its population biology as a compensatory response to the removal of individuals and, consequently, to alter the expected pattern of abundance diminution result of extractions. To test this, the main objectives of the present study were (1) to analyse the removal effects on population abundance and (2) to compare the biological traits of mosquitofish between the years included in the removal program. As hypotheses, a higher reproductive investment, smaller size at maturity and a higher percentage of mature females were expected with decreased population abundance. Consequently, a higher recruitment intensity was also expected in such conditions.

Materials and methods

Control area and removal program

The study was performed in the Chicamo stream (30XSH7029, UTM), a 59.4-km-long semiarid stream located in the Segura River basin (south-eastern Iberian Peninsula) that drains a watershed of $502\,km^2$. Mean annual temperature in the study area is 18°C and mean annual precipitation is ~250 mm, mainly concentrated in spring and autumn. Average flow in the stream is usually lower than $15\,L\,s^{-1}$. The environmental features of the Chicamo stream are described in detail by Vidal-Abarca *et al.* (2001). A prospective sampling to locate mosquitofish along the stream was carried out in May, June and November 2005. The selected area for the removal control of this species was established in a 150-m-long sector close to the source, with permanent water flow, where mosquitofish has been encountered since 1995. There, mosquitofish cohabited with two other fish species, namely, the endangered Iberian

toothcarp and the cyprinid southern Iberian barbel, *Luciobarbus sclateri* (Günther 1868). The Iberian toothcarp population inhabiting the Chicamo stream is particularly important because it is one of the species' most imperiled populations (Oliva-Paterna 2006). In this stretch, shallow pools (<70 cm deep) and short runs (<20 cm deep) constitute the principal aquatic habitats. Aquatic primary producers include the macrophyte *Chara vulgaris* Linnaeus 1753, an extensive diatom assemblage on fine sediments, and epilithic periphyton, although filamentous green algae tend to predominate in spring. This sector is located upstream from a small canyon (1.5 km long) where runs and waterfalls predominate, so it can be considered to be isolated from other populations of mosquitofish inhabiting downstream waters. This area was selected for the removal control principally because of such isolation of mosquitofish population and its small size and accessibility.

Mosquitofish were captured with traps and hand nets (40 × 40-cm long-handled dipnets; 1-mm mesh size). These two techniques have a low impact on the aquatic environment and its biota, and are suitable methods for small systems with low initial densities of small-sized target species (8–13 individuals m^{-2} were estimated at the study site during summer 2005) (Clavero *et al.* 2006). Two types of traps (1-mm mesh size) were used, including minnow-traps (Harrison *et al.* 1986) and polyethylene traps made with water bottles (Fouilland and Fossati 1996).

Samplings were performed from November 2005 to December 2008, using two removal strategies. In Type-1 samplings, the effort was standardised by uniformly distributing 20 minnow-traps and 20 polyethylene traps for roughly 24 h, together with 20–30 min of hand-netting. Type-1 samplings were performed twice per season (eight times per year). Type-2 samplings consisted of handnetting for 30–40 min weekly and fortnightly during the reproductive period (April–October), and monthly during the rest of the year. The fish captured in Type-1 samplings by minnow-traps and hand nets were identified and counted, and catch per unit of effort (CPUE) was calculated as a measure of abundance, 1 unit of effort being 20 minnow-traps in place for 24 h together with 20 min of hand-netting. To ensure that mosquitofish had been eradicated and to monitor the native fish community, Type-1 samplings extended up to April 2010, although with reduced frequency (once per season) from January 2009 onwards.

Water temperature (°C), salinity, pH and vegetation cover (%) were periodically registered to assess their possible influence on the population abundance of mosquitofish. Possible relationships between CPUE and these environmental variables were assessed by Spearman's correlation coefficients.

Analysis of population biology

All captured mosquitofish were anesthetised with benzocaine, fixed in buffered formaldehyde (10%), sexed and measured for total length (L_T, ± 1 mm). A sample of 1371 individuals was dissected (each individual within 30 days of capture), and total mass (M_T, ± 1 mg), eviscerated mass (M_E, ± 1 mg) and gonadal mass (M_G, ± 1 mg) were recorded. Eggs found in ovaries were classified into six developmental stages as described by Reznick (1981). In each ovary, there was only one litter of developing

embryos at the same time, so that most of the embryos were in the same developmental stage (Pyke 2005). From a total of 106 females, a sample of 20 eggs female^{-1} (or all eggs if n <20) in the same developmental stage was dried (55°C, 24 h) and weighed, to calculate the mean dry mass per egg (M_S, ± 0.1 mg). The number of non-fertilised eggs (Stage I) present in each gonad was used to calculate potential fecundity (F_P) and the number of fertilised eggs (Stages II–VI) was used to calculate real fecundity (F_R) (Fernández-Delgado and Rossomanno 1997).

Size and age structure of the mosquitofish population was assessed from scales, together with monthly and seasonal length–frequency distributions (as described in Ruiz-Navarro *et al.* 2011). The life-history of the species was undertaken by studying somatic condition, reproductive investment (gonadal mass, fecundity and egg size), percentage of mature females, size at maturity and population recruitment. Life-history was analysed separately for the two main age classes found in the population (0+ and 1+), because it is well known that they display different strategies (Fernández-Delgado and Rossomanno 1997). Monthly mean values of M_E, M_G, F_P, F_R and M_S were calculated, and interannual comparisons of these parameters were performed selecting, respectively, the most representative time periods depending on the species biology (e.g. the months of maximum somatic condition or the months just before reproduction). Particularly, the M_E of 1+ individuals was compared between the end of February and May and the M_E of 0+ individuals was compared for the period August–October; M_G, F_P, F_R and M_S were compared for April–May in the case of 1+ individuals and for July–September in the case of 0+ individuals. Changes in somatic condition (M_E), gonadal mass, fecundity and egg size following removal were analysed by using analyses of covariance (ANCOVA), with L_T as the covariate (as described in Ruiz-Navarro *et al.* 2011) and year as the main effect. Females with yolked oocytes or embryos were classified as mature. Size at maturity, defined as the size at which 50% of the females were mature, was estimated by logistic regression and was contrasted between years by generalised estimating equations (GEE), with binomial errors and the logit-link function. Length of the reproductive season was determined by

calculating the time interval between the presence of the first yolked oocytes and the last embryos in the ovaries of the females from the population. The recruitment period was characterised by a significant presence of young-of-the-year (YOY) with L_T <20 mm. Recruitment intensity was assessed by comparing the ratio YOY : mature individuals by using the chi-square method, and separately analysed for the reproduction of 1+ individuals (recruitment in May–July) and the reproduction of 0+ individuals (August–November). All the analyses were performed using the SPSS v. 15.0 (SPSS Inc., Chicago, IL, USA) statistical package.

Results

In total, 2236 mosquitofish were captured in the headwaters of the Chicamo stream. This species control program led to a progressive diminution of abundance during the removal period (ANOVA, year as a factor: $F_{(5,27)} = 24.15$, $P < 0.001$) (Fig. 1); for instance, mosquitofish abundance in 2007 was only a 38% of that in 2006, and no individuals have been captured from February 2008 onwards.

No significant correlation between the fish abundance and environmental parameters was found (Table 1). Water temperature showed an annual pattern of variation, with maxima (24.6°C) in summer and minima (13.4°C) in winter. Mean salinity was 1.3 and remained quite stable throughout the study period (s.e. = 3.18×10^{-3}). pH presented small variations in a range from 8.05 to 8.49, except for five occasions when its values reached up to one unit further away from this range. Vegetation cover presented a mean value of 21.6%, ranging from 13.0% to 36.3%. None of the environmental parameters showed significant differences between the years 2006 and 2007, even considering seasonal variation (Table 2).

Monitoring the fish community also showed a clear increase in the abundance of the southern Iberian barbel that coincided with the decline of mosquitofish (Fig. 1). The population of Iberian toothcarp presented low densities until 2010, when a considerable increase was detected (Fig. 1).

Because of the substantial reduction in abundance of the targeted mosquitofish, the biological effects of removal could
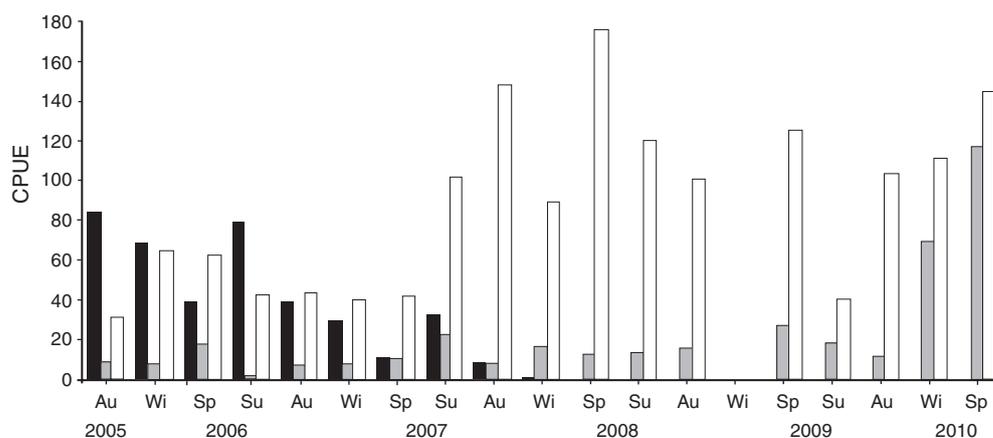

Fig. 1. Abundance (seasonal means) of *Gambusia holbrooki* (black bars), *Luciobarbus sclateri* (white bars) and *Aphanius iberus* (striped bars) over the study period. CPUE, catch per unit of effort; Au, autumn; Wi, winter; Sp, spring; Su, summer.

Table 1. Results of Spearman's correlation analyses between the abundance of *Gambusia holbrooki* and environmental parameters

Environmental parameter	r_S	P
Water temperature	0.16	0.156
Salinity	−0.13	0.233
pH	-1×10^{-3}	0.991
Vegetation cover	−0.26	0.065

Table 2. Results of the statistical analyses comparing the annual mean values of environmental parameters between the years 2006 and 2007

Environmental parameter	ANOVA		
	F	d.f.	P
Water temperature	0.44	1, 142	0.508
Salinity	0.08	1, 130	0.776
pH	2.64	1, 127	0.106
Vegetation cover	0.02	1, 275	0.897

be analysed only by comparing all of the parameters between the first removal year (2006) and the second removal year (2007). Periodic extractions of individuals altered the population size structure, mainly by removing the largest and oldest individuals from the population, and diminishing the annual mean size of individuals (2006: $L_T = 25.36 \pm 0.23$ mm; 2007: $L_T = 23.20 \pm 0.34$ mm; ANOVA: $F_{(1,513)} = 58.58$, $P < 0.001$). This pattern was particularly patent in males because, in 2007, their 1+ cohort disappeared from population in May, whereas it remained until July in 2006. The sex ratio of the population was significantly different from 1 : 1 in the whole study period, with females being more abundant in almost every month. Nevertheless, accordingly with the previously mentioned loss of population structure, both studied years contrasted in the temporal variation of sex ratio. In 2006, the male : female ratio gradually increased up to May

(1.31 : 1.00), when it started decreasing again until December (1.00 : 9.67). In 2007, contrarily, sex ratio was more variable along the year, with three maximums of male proportion in April (1.00 : 1.04), July (1.23 : 1.00) and November (1 : 1), respectively.

The somatic condition of mosquitofish significantly differed between the first and the second removal years, although the pattern varied by age class. Individuals of the 1+ age class showed better somatic conditions in 2007 (Table 3), whereas the somatic conditions of 0+ individuals diminished (Table 3, Fig. 2).

During the period just before reproduction, 1+ males and females showed higher gonadal mass in 2007 and, in accordance with this, 1+ females also had higher potential fecundity and real fecundity in 2007 (Table 3, Fig. 2). In contrast, 0+ individuals did not display significant changes in this parameter during their first reproductive event (Table 3). Females of age class 0+ increased potential fecundity in 2007, although no significant difference was found in their real fecundity (Table 3, Fig. 2). No significant differences in oocyte and embryo mass appeared between the two years, neither in 1+ females nor in 0+ females (Table 3, Fig. 2). However, the relatively low number of eggs analysed, particularly in the case of oocytes, should be considered.

The reproductive season began at approximately the same time in 2006 and 2007, although it lasted about 1 month longer in the second year. In 2006, the first yolked oocytes were detected on 3 March, and the last embryos were detected on 14 September. Because these were Stage III–V embryos, the expected birth date was ~1 October (Tavolga 1949; Haynes 1995). In 2007, females with yolked oocytes were detected, beginning on 27 February, and females with embryos in the last stage of development were detected up to 5 November. The percentage of mature 1+ females at the beginning of the reproductive season was not significantly different between the years (2006: 95.61%, 2007: 96.23%, $\chi^2 = 0.12$, $P = 0.732$), although mature 0+ females experiencing

Table 3. Results of ANCOVA analyses of the life-history traits in *Gambusia holbrooki*
Total length (L_T) is the covariate, and year is the fixed factor

|		Log L_T			Among years		
		F	d.f.	P	F	d.f.	P
(a) Fish condition							
Males 0+	Eviscerated mass	3264.24	1, 121	<0.001	9.34	1, 121	0.003
Males 1+	Eviscerated mass	1988.67	1, 120	<0.001	6.75	1, 120	0.011
Females 0+	Eviscerated mass	15008.35	1, 180	<0.001	9.71	1, 180	0.002
Females 1+	Eviscerated mass	9120.84	1, 142	<0.001	8.85	1, 142	0.003
(b) Reproductive traits							
Males 0+	Gonadal mass	19.76	1, 128	<0.001	0.12	1, 128	0.724
Males 1+	Gonadal mass	151.91	1, 120	<0.001	9.20	1, 120	0.003
Females 0+	Gonadal mass	121.62	1, 89	<0.001	0.10	1, 89	0.747
	Potential fecundity	5.38	1, 89	0.023	16.04	1, 91	<0.001
	Real fecundity	24.37	1, 33	<0.001	2.20	1, 34	0.148
	Oocyte dry mass	5.58	1, 5	0.065	0.63	1, 6	0.459
	Embryo dry mass	1.33	1, 17	0.266	0.01	1, 18	0.914
Females 1+	Gonadal mass	365.51	1, 130	<0.001	11.82	1, 130	0.001
	Potential fecundity	57.92	1, 74	<0.001	39.45	1, 75	<0.001
	Real fecundity	98.70	1, 86	<0.001	5.42	1, 87	0.022
	Oocyte dry mass	0.56	1, 5	0.489	1.19	1, 6	0.317
	Embryo dry mass	0.90	1, 15	0.357	0.46	1, 16	0.506
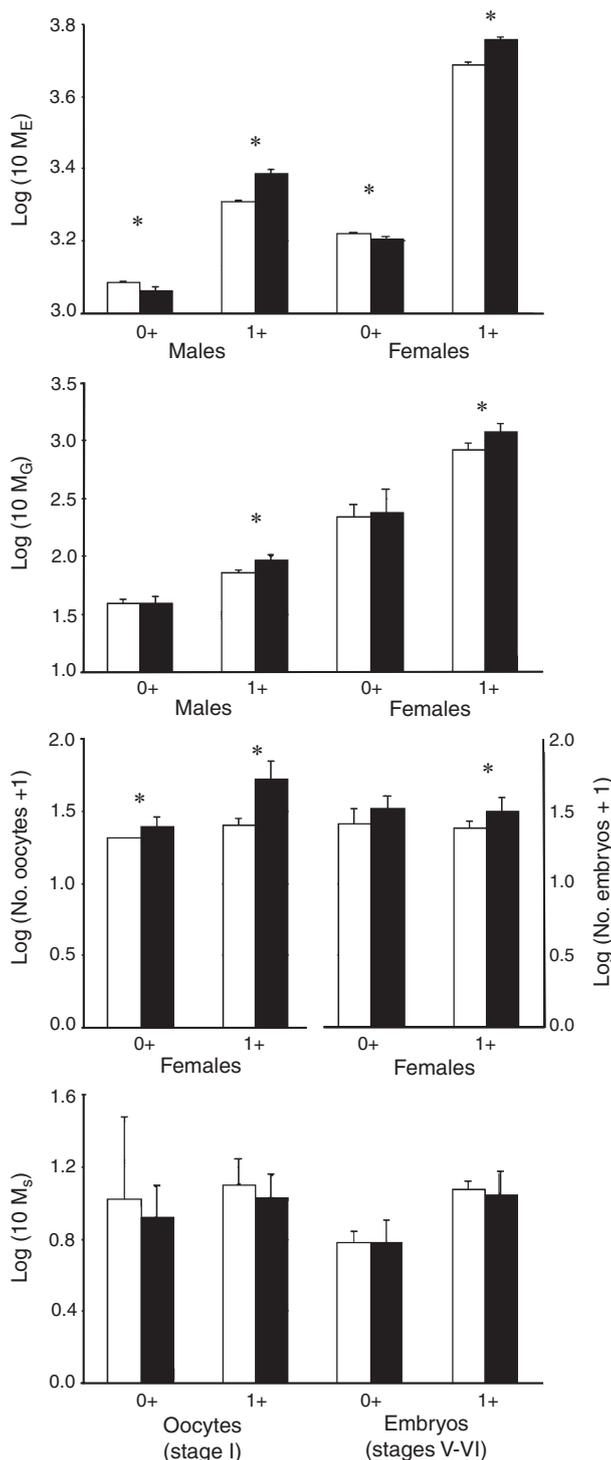
Fig. 2. Comparison of somatic condition and reproductive parameters (mean ± s.e.) of *Gambusia holbrooki* between years. White bars represent the year 2006 and black bars represent the year 2007. Statistically significant ($P < 0.05$) differences are indicated with an asterisk. M_E, eviscerated mass; M_G, gonadal mass; M_S, dry mass.

their first reproductive event were less abundant in 2007 (2006: 53.10%, 2007: 39.58%, $\chi^2 = 8.63$, $P = 0.003$). Although estimated size at maturity for 0+ females was slightly larger in

2007 ($L_T = 29.6$ mm) than in 2006 ($L_T = 27.0$ mm), differences were not statistically significant (GEE: Wald-$\chi^2 = 0.538$, $P = 0.463$). All 1+ females were mature in 2007.

Recruitment intensity (YOY : mature) was higher in May–July of 2007 (106 : 66) than during the same months in 2006 (55 : 168) ($\chi^2 = 128.85$, $P < 0.001$). In the second part of the recruitment period (from August to November), no difference was found in recruitment intensity between 2006 (238 : 322) and 2007 (98 : 125) ($\chi^2 = 0.47$, $P = 0.490$).

Discussion

Species with high intrinsic population growth rates, such as mosquitofish, are expected to have a high capacity to recover from progressive removal or environmental shocks that reduce the population (Goodwin *et al.* 2006). The removal control of the mosquitofish population from the headwaters of the Chicamo stream and the consequent significant diminution of its density are probably the main factors explaining the differences found in life-history traits between the two removal years (2006 and 2007). Although the present study is limited in scope to a snapshot in both space and time, the results may show a response in the mosquitofish's reproductive strategy to the diminished densities achieved by removal. Moreover, environmental factors such as temperature, salinity, pH or vegetation cover seem not to be responsible for these changes because no differences among years were detected. It is possible that other environmental factors (e.g. water flow, biological interactions) were involved in the observed phenotypic response in mosquitofish biology, although the reduction in population density must have been a determining factor.

The alteration of population size structure and sex ratio, a direct consequence of the periodic extractions of individuals, would result in a diminished reproductive potential for the population after 1 year of extractive control (e.g. Fernández-Delgado and Rossomanno 1997; Smith 2007). However, the population showed temporal variations of reproductive parameters that could indicate a response in the mosquitofish's reproductive strategy, thus acting for population stability when density was lower. Females of the 1+ age class, which were responsible for the first reproductive event of the population (Fernández-Delgado and Rossomanno 1997), had higher fecundity, with no reduction of embryo size, under the diminished abundance conditions of the second year of removals. Accordingly, their gonads were bigger, as previously shown in experiments carried out by Lutnesky and Adkins (2003). The reproductive investment of 1+ males (assessed by their gonadal mass) was also greater during the second year of removals. As a consequence, higher recruitment intensity was achieved during the first months of the recruitment period, mainly as a result of the reproduction of 1+ individuals. Higher fecundity and recruitment during periods of low population density have been previously reported in poeciliids (e.g. Dahlgren 1979; Borg *et al.* 2006) and other invasive fish (e.g. Britton *et al.* 2008). Contrarily to what was expected, during the second part of the reproductive season, mainly as a result of the reproduction of individuals born at the beginning of the same reproductive season (Fernández-Delgado and Rossomanno 1997), an increase of fecundity was not clear (nor was recruitment

intensity). However, the reproductive season was about 1 month longer in 2007, lasting from March until November (October in 2006). Despite the fact that the length of the reproductive season is closely related to photoperiod and temperature (Pyke 2005), Horn and Stewart (1990) experimentally demonstrated that mosquitofish populations drastically reduced in density elongated the recruitment period by presenting a pulse of recruitment in late autumn that was not present in reference conditions.

Although a smaller size at maturity was expected when population abundance decreased (Fox and Keast 1991; Britton *et al.* 2008), this pattern did not occur, and, in relation to this, a lower percentage of mature 0+ females occurred in 2007. This may be related to the lower density of female mosquitofish in 2007 resulting in reduced stimulation of maturation, because it is well known that in other poeciliids, the presence of other females stimulates maturation (Meffe and Snelson 1989).

Despite the observed response in mosquitofish's life-history, the parameters developed to control the target population have resulted in no individuals of the species being captured since February 2008. The combined use of traps and hand nets, together with increased efforts before and during reproduction, seem to have successfully controlled the mosquitofish population. Nevertheless, the target population presented distinct ecological features that probably favoured the success of the local application of this methodology. First, the initial low density of the target species. Although mosquitofish have dominated the managed headwater stretch of the Chicamo stream since their introduction, they have never shown high densities, which could reflect the non-optimal status of the population in this habitat. For instance, mosquitofish populations are uncommon in lotic systems with high environmental variability (Pritchard *et al.* 2004), and the unpredictability occurring in Chicamo stream (Vidal-Abarca *et al.* 2001) could have contributed to the initial low densities. Second, the mosquitofish population was isolated by the presence of a canyon downstream. It is very unlikely that individuals from other stocks located downstream could migrate upriver through the runs and waterfalls of the canyon (Congdon 1994; Chapman and Warburton 2006). And third, mosquitofish tend to occupy the shallow ponds with direct sunlight (Meffe and Snelson 1989). This fact, together with the small size and accessibility of the control area, must have increased the effectiveness of the removal methodology and were probably additional factors contributing to the successful control of the mosquitofish population.

Almost 5 years have passed with no individuals being detected in the control area of the Chicamo stream (occasional samplings have been performed up to now). The authors consider that the control program has resulted in an eradication of the mosquitofish population at the site level. Nevertheless, although eradication has been achieved, ongoing samplings are necessary to monitor the presence of new mosquitofish individuals or reintroductions at the site (IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species, February 2000; www.iucn.org, verified 15 October 2012). Because of the isolation of the reach from other mosquitofish populations located in the same stream, any reintroduction would likely be caused by humans. To prevent this, several educational programs have been developed in the region. Although a big quantity of previous experiences of

mosquitofish control or eradication have been performed, their results are not so well extended. Among the published results, the most successful ones are those using drainage of the aquatic habitat, the piscicide rotenone or a combination of both methods. However, the use of other chemicals (such as calcium hydroxide), electrofishing or the indirect method of habitat restoration have been also proved as successful under favouring conditions (e.g. Chadderton *et al.* 2003; Kroon *et al.* 2004; Scoppettone *et al.* 2005; Ayres and Clunie 2010). The experience presented here seems to be the first published of a successful mosquitofish eradication achieved by capturing individuals using simple traps and hand nets, thus minimising the negative effects on the ecosystem.

The reduced abundance of the mosquitofish population obtained by removal control has been followed by important changes in the larger fish community. The juvenile and small-sized southern Iberian barbel showed clear increases in abundance that coincided with the decline of the mosquitofish, whereas the Iberian toothcarp maintained initial densities until 2009, and began a significant recovery in 2010. Together with the diminished interaction with mosquitofish (Caiola and de Sostoa 2005), the increased abundances were probably also favoured by other conservation actions included in the LIFE-Nature project carried out at the site. In short, the present fish community in the headwaters of Chicamo stream is now mainly constituted by the two species with historical presence in the system.

Considering the results obtained in the headwater stretch of the Chicamo stream, a higher-scale management program could be designed for the Chicamo stream as a whole. The characteristics of the stream (Vidal-Abarca *et al.* 2001) would probably allow a mosquitofish-eradication goal, with a relatively low effort. Although a similar methodology (traps and hand-netting) could be used, it is obvious that the sampling design should be adapted to the higher dimension of the system.

Plasticity that permits fish species to present compensatory mechanisms in low-density conditions, by switching to more opportunistic life-history strategies, facilitates their establishment in new recipient habitats (Britton *et al.* 2008) and thereby increases their invasive potential (Fox *et al.* 2007). It is important to recognise the limitations of the short-time monitoring of the mosquitofish population carried out in the present study, following its prompt extirpation at the control site. However, the present study has provided very interesting life-history data on mosquitofish from the perspective of population control. It has highlighted the compensatory density-dependent phenotypic response of mosquitofish's life-history that should be considered for more effective management programs. In this sense, the compensatory mechanisms of the invasive species' biology that react against the management actions cannot be overlooked, and should be studied for an in-depth knowledge of the species' resilience ability. Despite that response, the present study has also shown how, with a high capture effort and several favourable conditioning factors, the population has been eradicated. In presenting the results of the current local survey, the authors hope to stimulate further research into removal control methods for mosquitofish or similar species, and provide information for those currently engaged in fish control, as discussed by Brookhouse and Coughran (2010).

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