

# INDIRECT EFFECTS OF THE COMMON CARP ON LIFE HISTORY OF THE AMARILLO FISH, *GIRARDINICHTHYS MULTIRADIATUS*, AN ENDEMIC SPECIES TO THE UPPER LERMA BASIN IN CENTRAL MÉXICO

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**Abstract.** The impact of Common carp *Cyprinus carpio* on the environments into which it is introduced, such as most freshwater habitats in Mexico, is largely inferred from correlational data. Here we experimentally quantified the possible indirect effects for local fish of growing up in an environment altered by the presence of introduced Common carp *Cyprinus carpio*. Newborn Amarillo fish *Girardinichthys multiradiatus*, a viviparous fish endemic to central Mexico, were raised in tanks lined with natural substrate. Tanks were partitioned with mesh; the presence of carps (GC) in one of the compartments altered the water quality, whereas adult Amarillo fish of equivalent size were placed in the corresponding compartment of the G treatment tanks holding fish from the same litters. Amarillo fish raised in the GC treatment had lower growth rates and attained lower condition than their counterparts in the G treatment, but fish in both treatments reached the same size at maturity. However, when analysing only the broods represented in both treatments at the end of the experiment, evidence of a trade-off between survival and reproduction was found, with siblings that grew up in the presence of carp reaching sexual maturity earlier than G treatment individuals. Expression of ornaments of males that survived until adulthood was unaffected by the presence of carp. The observed effects of carp on water quality are probably conservative, since small carp were used here to match the size of the adult Amarillo fish in G treatment. It appears that the effect of *C. carpio* on the water quality obliges *G. multiradiatus* to adjust its allocation of resources towards an early maturity,

which is associated with low reproductive output in these viviparous fish.

**Key words:** Viviparous fish, phenotypic plasticity, introduced species, reaction norms.

## Introduction

The deliberate introduction of species is a common and economically important activity around the world, despite the drastic effects on wild populations and natural environments. Once the introduced species is established, this biological pollutant becomes a permanent problem, as it may prey on native species, compete with them for food or space, transmit novel parasites and other infectious organisms -themselves invaders-, or interfere with their reproductive behaviour (EFFORD et al. 1997; HELFMAN et al. 2009; VALERO et al. 2008). Examples of these direct effects include the brown trout *Salmo trutta* L. 1758, a dominant species introduced in every continent, which monopolises in the new environments the areas with best resources (VAN ZWOL et al. 2012), or the Nile perch *Lates niloticus* L. 1758, which through habitat alterations and predation caused the decline/extinction of 70% of native *Haplochromis* cichlids following its introduction in Lake Victoria (WITTE et al. 1992; BALIRWA et al. 2003).

Introduced species can also have indirect effects on local species. Through life, individuals must allocate their total energy to homeostasis, growth and reproduction. The balance between those functions at any given time -the life history strategy- allows them to optimise fitness within the constraints imposed by the environment (WOLTERECK 1909; STEARNS 1989, 1992; ZERA & HARSHMAN 2001; GARDUÑO-PAZ et al. 2010). By modifying the current metabolic demands, environmental changes such as those induced by introduced species may limit the individual's capacity to regulate the energy allocation and may thus lead to a reduction in fitness and population decline. The introduction of fish species, also, can lead to strong modifications of nutrient (e.g., nitrogen and phosphorus) cycles by shifting the relative proportion of each trophic level (SCHINDLER et al. 2001; EBY et al. 2006).

A prime example of an introduced species capable of modifying the habitat is the Asian carp *Cyprinus carpio* L. 1758. This is a widespread invasive species that rarely eliminates native species directly; instead it exerts negative indirect influences on biotic and abiotic components of aquatic ecosystems (WEBER & BROWN 2009; HELFMANN et al. 2009; HUSER et al., 2015). Its feeding behaviour affects the hydrophytes in two ways; directly, by consuming aquatic macrophytes, and indirectly by uprooting or breaking macrophytes while foraging. Once macrophytes are lost, wind increases sediment re-suspension that in turn reduces light availability for phytoplankton and submerged plants. Juvenile *C. carpio* also forage on benthic invertebrates by removing the sediment, thereby increasing the rate at which nutrients such as nitrogen and phosphorus captured in the substrate are brought back into the water columns. Root exposure to suspended sediments and to mechanical damage eventually kills the hydrophytes (ZAMBRANO 2001; MILLER & CROWL 2006; WEBER & BROWN 2009; 2013). These effects promote algal blooming (mostly cyanophyceae) and entail the eutrophication of the system through increased turbidity, nitrogen and phosphorus availability, and loss of refuges for micro-fauna (ZAMBRANO et al. 1999; BADIOU & GOLDSBOROUGH 2010). Several studies have reported negative effects of *C. carpio* on amphibian (ZAMBRANO et al. 2010; KLOSKOWSKI 2011) and on other fish populations (JACK-

SON et al. 2010). The extent of the risk posed by carp on native communities can be inferred from the work of ZAMBRANO et al. (2006), who using ecological niche modelling found that the distributional potential for the invasion of *C. carpio* in the Americas covers most temperate regions and mountain tropical aquatic systems. Additionally, MILLER & CROWL (2006) found that *C. carpio* has a significant impact on species abundance and diversity of macrophytes and invertebrates in wetlands and littoral zones, although the extent of its damage depends on the density of carp and on the types of macrophytes present. Also, USER et al. (2016) reported that in a shallow lake in Michigan, USA, *Cyprinus carpio* have overriding effects on sediment mixing which increases the amount of mobile P, thus likely to have a negative effect on the efficacy of management methods designed to reduce mobile sediment P availability in lakes.

The changes in nutrient cycles may have negative effects on the physiology of native species. For example, phosphates are responsible for a variety of abnormalities and diseases in fishes because at high concentrations they produce hypoxia and inhibit biological and chemical oxidation (MOLINA 1995). For instance, DE LOS SANTOS (2010) reported that a dose of 13.18 mg/l of phosphate caused inefficient oxygen assimilation in the Mexican viviparous topminnow *Skiffia multipunctata*, whose swimming performance became lethargic.

Habitat alteration induced by the feeding behaviour of introduced carp can affect the communication and reproductive processes of native fish through its impact on sensory ecology and by distorting the value of signals used in sexual selection. For instance, sediment mixing and bottom stirring promote turbidity, which constrains vision and colour perception. This can interfere with mate choice (MOYAHO et al. 2005; SECONDI et al. 2007; MICHELANGELI et al. 2015; SUNDIN et al. 2016), thus relaxing sexual selection and blocking the mechanism of reproductive isolation in native species, thus promoting a loss of biological diversity (see SEEHAUSEN et al. 1997). Similarly, eutrophication such as that caused by carp feeding behaviour can lead to high productivity and hence an excess of sources of nutrients including carotenoids. These antioxidants are often incorporated into ornaments that signal phenotypic quality, because only organisms in good condition can, normally, afford to divert antioxidants -which must be obtained from the diet- from their role as scavengers of free radicals (see OLSON & OWENS 1989). Consequently, a super abundance of carotenoids means that their role in signalling quality (such as in the male stickleback *Gasterosteus aculeatus*; MILINSKY & BAKKER 1990) is devalued (CANDOLIN et al. 2007; CANDOLIN 2009). More generally, any process that modifies the life histories of sexually-selected organisms is likely to also affect the expression of ornaments and hence the process of sexual selection (e. g. KERVINEN et al. 2015).

*Cyprinus carpio* was originally introduced in ponds and reservoirs in the Estado de Mexico in 1889 to improve the protein intake of peasants and to generate jobs in low-income rural communities. Since then its distribution at national level has increased dramatically invading mostly natural wetlands, shallow lakes, creeks, rivers and swamps (OBREGÓN 1962; WAKIDA-KUSUNOKI & AMADOR-DEL-ANGEL 2001). In addition to the direct effects of carp on water quality and macrophytes, and the inferred indirect effects on invertebrates, there is the suggestion that *C. carpio* may compete for food with some native vertebrates such as the emblematic Axolotl *Ambystoma mexicanum* Shaw & Nodder 1789, judging by the fact that there is some dietary overlap between the two species

(ZAMBRANO et al. 2010). As found by VILA-GISPERT et al. (2005) in Catalonian streams, *C. carpio* in central Mexico has larger size, greater longevity, later maturity, and higher fecundity than native species, which may place this invasive at an advantage in this ecological scenario. The impact of introduced *C. carpio* on native vertebrates is inferred from a very substantial body of field, mostly correlative evidence, but evidence of causality between the carp feeding habits and the wellbeing of native vertebrates is elusive. Here we evaluated experimentally whether carp presence and its foraging behaviour impact indirectly on the life history of the native species Amarillo fish (*Girardinichthys multiradiatus* Meek 1904) when it alters the water quality.

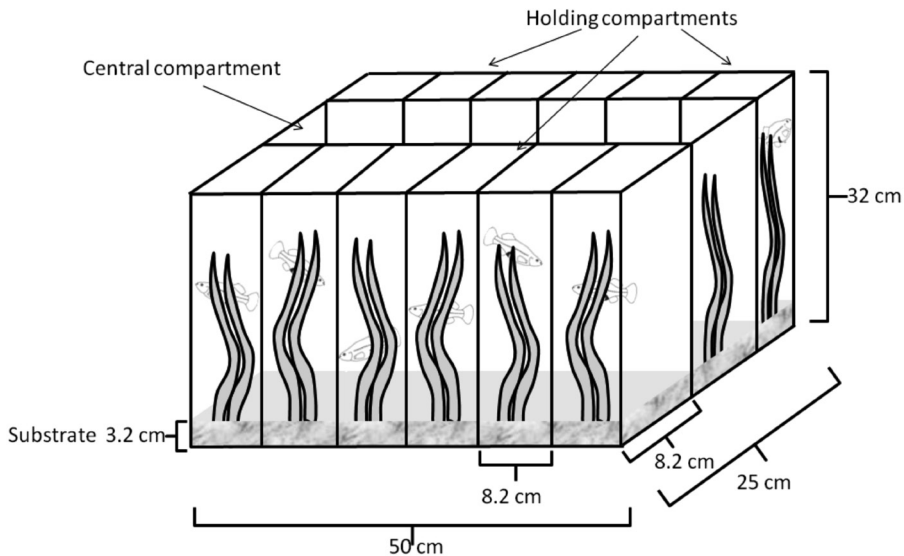
*Girardinichthys multiradiatus*, also known as Amarillo (Spanish for “yellow”), belongs to the Goodeinae, a clade of viviparous fish endemic to central Mexico. It inhabits shallow waters (< 1m deep) of wetlands, ponds, reservoirs and rivers mostly within the upper Lerma River basin (with some populations found in the adjacent Balsas and the Pánuco watersheds; MILLER et al., 2005; GONZÁLEZ-ZUARTH & MACÍAS GARCIA 2006; GESUNDHEIT & MACÍAS GARCIA 2005) where it feeds on small invertebrates (TRUJILLO-JIMÉNEZ & ESPINOSA DE LOS MONTEROS VIVEROS 2006; TRUJILLO-JIMÉNEZ & TOLEDO BETO 2007). Internal fertilization requires consensual mating, which allows the expression of female mate choice based on male complex courtship patterns and large and colourful ornamental dorsal and anal fins (MACÍAS-GARCIA et al. 1994; MACÍAS-GARCIA & BURT DE PERERA 2002; MACÍAS-GARCIA & SABORÍO 2004; MACÍAS-GARCIA & VALERO 2010).

The Lerma basin in Central Mexico is one of the largest watersheds in the Country, but also one of the most polluted. Its headwaters, the upper Lerma basin (ULB), is a densely populated area whose freshwater biota face habitat destruction and degradation through water extraction, urban and industrial pollution and introduction of exotic species (MACÍAS GARCIA 2007), and where substantial habitat degradation following the introduction of *Cyprinus carpio* has been reported (ZAMBRANO et al. 1999). As most of its populations lie within the ULB, *G. multiradiatus* is currently regarded as vulnerable (IUCN 2011). In spite of the above, information on the tolerance of Amarillo fish to environmental stressors is scarce (ARELLANO-AGUILAR & MACÍAS GARCIA 2008; GARCIA-TREJO et al. 2013). Therefore, in the present study *G. multiradiatus* is used to experimentally evaluate the threat that an endemic vulnerable species confronts as a consequence of sharing its habitat with introduced *C. carpio*. Three questions are addressed here to determine the effect of the presence of the common carp on the Amarillo; 1) Does it alters water quality? 2) Does it affect negatively the life history traits of *G. multiradiatus* life history traits? and 3) Does it affect negatively the expression of sexually selected behaviour and traits?

### Sample

The study was conducted using laboratory-born *G. multiradiatus* offspring of pregnant females collected at Huapango, Pasteje, and San Elías (ULB), and Zempoala (Balsas, adjacent to the divide between Balsas and ULB). Broods were kept in their maternal 40-L home tank for two weeks. Each treatment-tank was partitioned with nylon mesh into three contiguous compartments, each measuring 50 x 8.2 x 32 cm deep. The lateral compartments were in turn divided into six holding compartments each measuring 8.2 x 8.2 x 32 cm deep (Fig 1). When broods reached the age of 15 days, one half of the fish from each brood was transferred to the experimental tank *G. multiradiatus* + *C. carpio* (GC) and one half to the only *G. multiradiatus* (G) treatment-tanks. Twelve young *G. multira-*

**Fig. 1.** Newborn *Girardinichthys multiradiatus* were raised individually in the holding compartments (8.2 x 8.2 x 32 cm), while in the central compartments (50 x 8.2 x 32 cm) we placed either four adult *Amarillo* fish (*G* treatment) or four similar-sized carp (*GC* treatment).



*diatus* were kept in individual holding partitions in the lateral compartments, and either four small carp (GC) or four adult *G. multiradiatus* (G) were held in the central compartment. The size of the carp and the adult *G. multiradiatus* kept in the central compartments was the same (SL= 45 ± 5mm), but the carp were heavier (*G. multiradiatus* weight ≈ 4g; *C. carpio* weight ≈ 9g). We used juvenile carp because it shares microhabitat with *G. multiradiatus*. Density of carp was determined following the standard practice by the Mexican authorities in charge of carp introduction (ZAMBRANO & HINOJOSA 1999). Carps were substituted every 15 days in order to keep carps of the same size range as *Amarillo* adults. Every 15 days we measured 1) standard length (SL; mm) from digital photographs of the left side of each fish, analysed using Image Tool®, and 2) weight (g) using an analytical balance Ohaus® (±0.005).

All treatment tanks were conditioned with a foam filter, light, and aeration in the central compartment, as well as Waterweeds *Elodea canadensis* Michaux 1803 in all compartments. Photoperiod was maintained constant (12/12 h dark/light) throughout the experiments, and temperature was allowed to vary between 26 and 28°C. To reproduce the effects of feeding behaviour of *C. carpio* on water quality, we added to each tank a 3.2 cm deep substrate layer formed by mix of sand and sterilized mud from the bottom of a pond (San Elías pond) in which *C. carpio* populations coexist with *Amarillo* fish (Fig 1).

Every seven days, from the beginning of the experiment, measures were taken, of the following water quality variables: pH (pHydriion Vivid™ paper), concentration (mg/L) of NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, and suspended solids (SS) with a HACH™ dr/2010 spectrophotometer. The effect of carp feeding behaviour on water quality was evident several weeks within the experiment, thus the measures from the second half of the experiment were used

as indicative of this effect, and were entered into a principal components analysis (PCA; see below).

### Life history traits

Five life history traits of *G. multiradiatus* young were compared among treatments: growth rate, condition factor, age and size at maturity and survivorship. The growth curves for each treatment were modelled adjusting SL and age to the von Bertalanffy growth model (1938) using PAST<sup>®</sup>, and parameter differences between treatments were evaluated using the likelihood ratio test (Kimura, 1980). Two indices of weight-length relationship were used to describe fish condition: 1) the coefficient *b* from Huxley's allometric equation, and 2) the condition factor (Kn) from Fulton equation (1911). To remove the effect of random factors, Kn was analysed using an exploratory factor analysis (EFA), and differences among treatments were tested for significance using Mann-Whitney U-test. For experimental reasons, the size and age at sexual maturity (SSM and ASM respectively) were estimated behaviourally, recording the SL and age at which individuals started to express secondary sexual characters (and courtship; see DE GASPERIN & MACÍAS GARCIA 2015). Cumulative survivorship (lx) was estimated in each treatment from the raw data of fish that survived and those who died during the experiment. Finally, survival curves from both treatments were plotted for comparison using the Kaplan-Meier method (1958).

### Reaction norms and trade offs

The traits values of different genotypes (each genotype represented by siblings from the same litter but raised in different conditions) were compared using bivariate correlations between treatment and life history trait to evaluate the possible existence of reaction norms. If the regression line had a slope  $\neq 0$ , the existence of a reaction norm for that trait was assumed (plasticity; STEARNS 1989; HUTCHINGS 2011). Trade-offs were measured and analysed using Pearson bivariate correlations among traits expressed by fish raised in the presence of carp (GC) at the level of 1) genotype, using only siblings, and 2) phenotype, including all the individuals in that treatment (STEARNS 1989; MACKE et al. 2012). To facilitate the interpretation of the life history traits expressed by *G. multiradiatus* in each experimental condition compromises were classified into two types: 1) trade-offs, recognised by a negative slope in any regression between two life history traits (meaning a compromise between them) and 2) trades, which were defined as a difference amongst treatments in the sign of a correlation between traits (e.g. a positive correlation between traits A and B in fish from treatment G, and a negative correlation between the same traits in fish from GC).

### Male attributes

**Ornamentation.** 180 days-old males were anaesthetized with a dilution of 1g benzocaine per 100ml acetone, laid on their right side next to a ruler on a photoGraphic™ board, and photographed with a digital camera. The images were stored on a computer and subsequently measured using Image Tool©. Height and length (mm) of unpaired fins (dorsal, caudal and anal) and total length (attributes associated with female mate choice; GONZÁLEZ ZUARTH & MACÍAS GARCIA 2006) were measured for each fish. The averages of three measurements of each attribute were entered into a principal components analysis (PCA) to reduce the number of variables to one, which was compared using Mann-Whitney U-test. The colour of anaesthetized males was assessed using an Ocean Optics™ Usb4000 spectrophotometer (spectral range  $\lambda=360 - 740$  nm). Reflectance spectra were obtained of



one point in the operculum (known to be reflective in the UV; MACÍAS GARCIA & BURT DE PERERA 2002), one point in the flank, and one in each of the unpaired fins. From the spectral data, it was calculated total chroma saturation, yellow chroma saturation ( $\lambda=500 - 630$  nm), red chroma saturation ( $\lambda=630 - 740$  nm) and UV chroma saturation ( $\lambda=360 - 400$  nm), which were compared among treatments using Mann-Whitney U tests.

**Sexual behaviour:** Courtship performance was quantified starting when males were 90 days old. Males were individually transferred to a 40 L observation tank and allowed to habituate for 1 hour. Then a female was placed in a plastic bag and introduced into the tank, and the behaviour of the male was recorded for 20 min by an observer acquainted with the behaviour of the species, but who was kept ignorant of the identity of the fish/treatment. Behaviours registered were the duration and frequency of male displays (lateral fin display, frontal fin display, courtship fin folding, flagging and figure-of-eight dance; MACÍAS GARCIA 1991; MACÍAS GARCIA & VALERO 2010). To quantify female preference, each female was transferred to a 40 L observation tank. After 1 hr of habituation, two males (one from each treatment) were individually introduced into plastic bags at opposite sides of the tank. Then it was recorded the frequency of visits (to within ca. 3 cm of a male) and of copulation attempts (mutual embraces of male and female through the plastic bag) directed to each male. This procedure was repeated with all adult females, each exposed to a different pair of males which, due to asynchrony in the births, were always their siblings. The position of the males of each treatment within the tank was alternated between replicates. Frequencies and the durations of courtship displays were analysed separately, first by reducing the number of variables through a PCA following standardisation of each variable, and then comparing the individual scores for PC1 between treatments using a one-way ANOVA.

## Results

Information on broods is detailed in Table 1. In both treatments, there was substantial mortality of fish before reaching adulthood. This resulted in a reduced sample size for assessing ornament magnitude and behavioural trials, thus results related to male secondary sexual characters must be regarded as preliminary.

### Water quality

The two principal components explained 47% of the variance in water chemistry (CP1= 33%; CP2= 24%). The second component is the most informative, separating the sample by treatment based on the concentration of the nutrients in a way that is consistent with greater eutrophication in the GC treatment (higher loadings in four of the five measured parameters;  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{PO}_4^{3-}$  and suspended solids; Fig 2), the difference being significant ( $t = -5.87$ , d.f. = 1,45,  $P < 0.05$ ).

### Fish performance

The growth curves for the fish in the G ( $L_\infty = 27.4$ ,  $k = 0.624$ ,  $t_0 = -0.18$ ) and GC ( $L_\infty = 29.4$ ,  $k = 0.59$ ,  $t_0 = 0.11$ ) treatments were similar (Fig 3a). They show no difference in asymptotic standard length ( $\chi^2 = 1.08$ , d.f. = 1,  $P > 0.05$ ), yet because G fish grew somewhat faster, they reached the  $L_\infty$  at earlier age than the fish living in a tank with carp ( $\chi^2 = 7.83$ , d.f. = 1,  $P < 0.05$ ).

Individual weight and SL were highly and significantly correlated, and showed negative allometry in both treatments ( $b < 3$ ,  $P < 0.05$ ; Table 2), but fish in the G treatment had

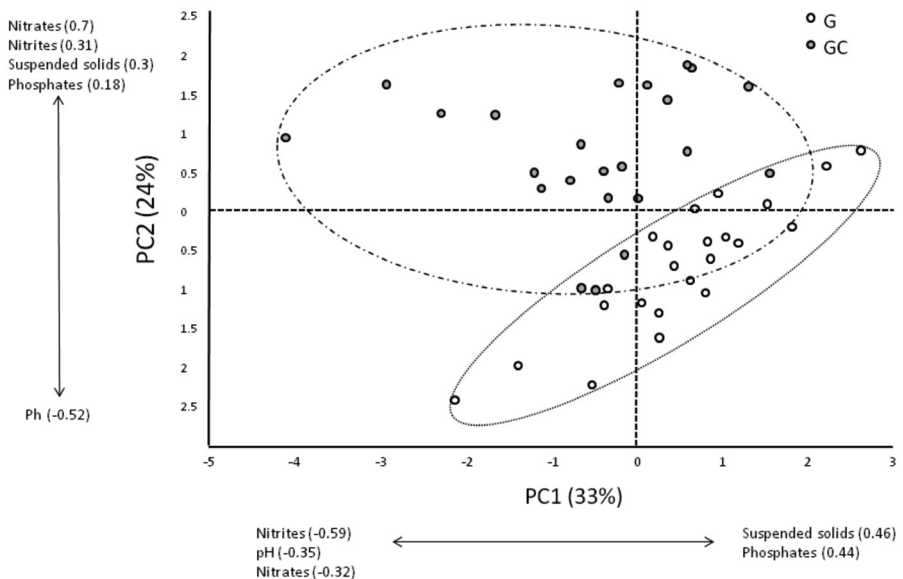
**Table 1.** We obtained eight broods from wild-caught female *Girardinichthys multiradiatus*, totalling 70 offspring, half of which were allocated to each treatment. Sample size was reduced at the end of the experiment due to mortality, leaving only a few fish to measure adult male ornamentation/behaviour and female mate preferences.

Treatment	Broods		Individuals per brood ( $\pm$ SD)	
	Initial sample	Final sample	Initial sample	Final sample
<i>G. multiradiatus</i> (G)	8	6	4.25 $\pm$ 2.81	1.5 $\pm$ 0.83
<i>Cyprinus carpio</i> (GC)	8	6	4.5 $\pm$ 2.39	1.3 $\pm$ 0.81

a higher  $b$ , and closer to isometry, than fish in the GC treatment ( $t = 2.19$ , d.f. = 1,23,  $P < 0.05$ ). Allometry changed non-linearly with age, but whereas  $b$  was rather constant for fish in the G treatment, in the case of fish raised next to carp it was low at the beginning of the experiment, and increased at the end (Fig. 3b).

Fish in the GC treatment also had lower  $K_n$  than fish growing next to conspecifics ( $t = 2.31$ , d.f. = 1,29,  $P < 0.05$ ; Fig 3c). The condition of fish was high at birth -and similar in both treatments as they were siblings-. It decreased steadily until they were 90 days old -approximately 20 days after the average age at which they became sexually mature- but the reduction was steeper for GC individuals. Fish in both treatments became sexually

**Fig. 2.** Water quality differed between treatments (G = only *Girardinichthys multiradiatus*; GC = *Girardinichthys multiradiatus* and carp). The first PC gave high loadings to suspended solids and phosphates concentrations, and low loadings to pH and nitrogen compounds; PC1 scores were similar for readings from both treatments. The second PC, which was positively loaded by variables associated to eutrophication, separated the data according the treatment, giving higher scores to readings from the GC treatment.

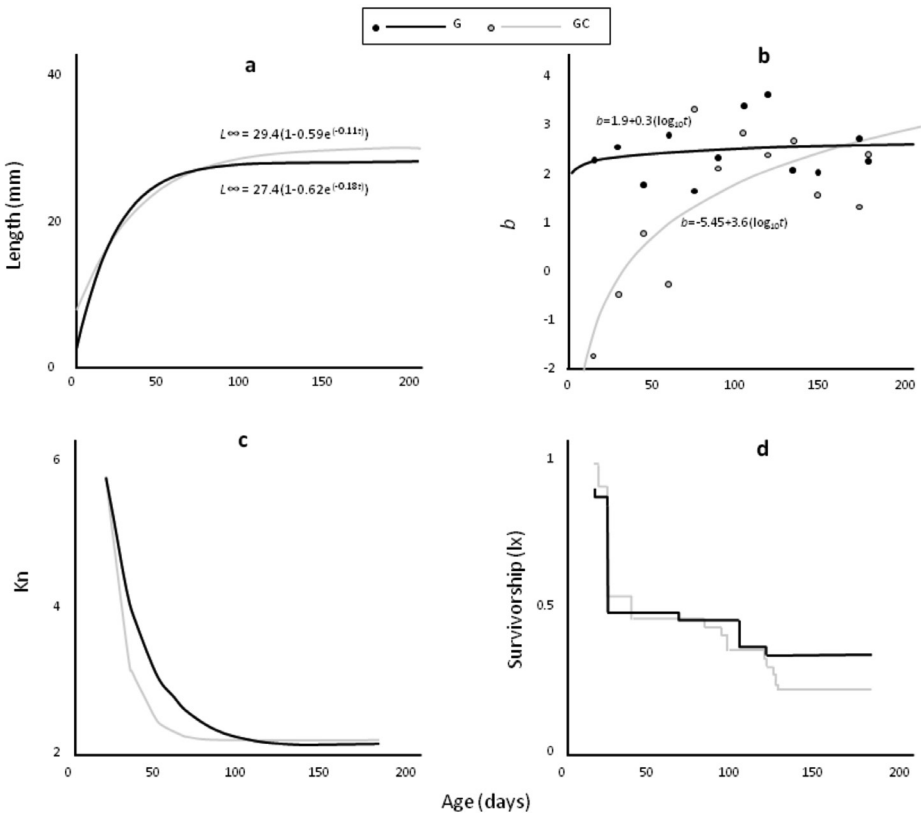




**Table 2.** Parameters of the regression analysis between size and weight of *Girardinichthys multiradiatus* raised in the absence (G) or in the presence of carp (GC).

Treatment	N	Standard length (cm) range	Weight (g) range	Intercept (a)	Slope (b)±SE	r <sup>2</sup> (percent)	Hypothesis test (t)
G	12	0.02-0.3855	1.12-2.71	0.0004	2.45±0.37	81%	b<3
GC	12	0.0249-0.45	1.27-2.93	0.0017	1.41±0.96	76%	b<3

**Fig. 3.** Fish in the G treatment reached asymptotic size earlier than GC fish, but final size was not different between the two groups (a). For fish growing in the absence of carp, the allometry coefficient (b) of the weight-SL regression remained constant and closer to the isometric value throughout the experiment, whereas that of GC fish was very low initially, and only towards the end of the experiment matched that of G fish (b). The condition factor (Kn) decrease through life in both treatments, the decrease is faster in fish exposed to carp (c). Survivorship curves show very similar patterns of mortality in both treatments (d).

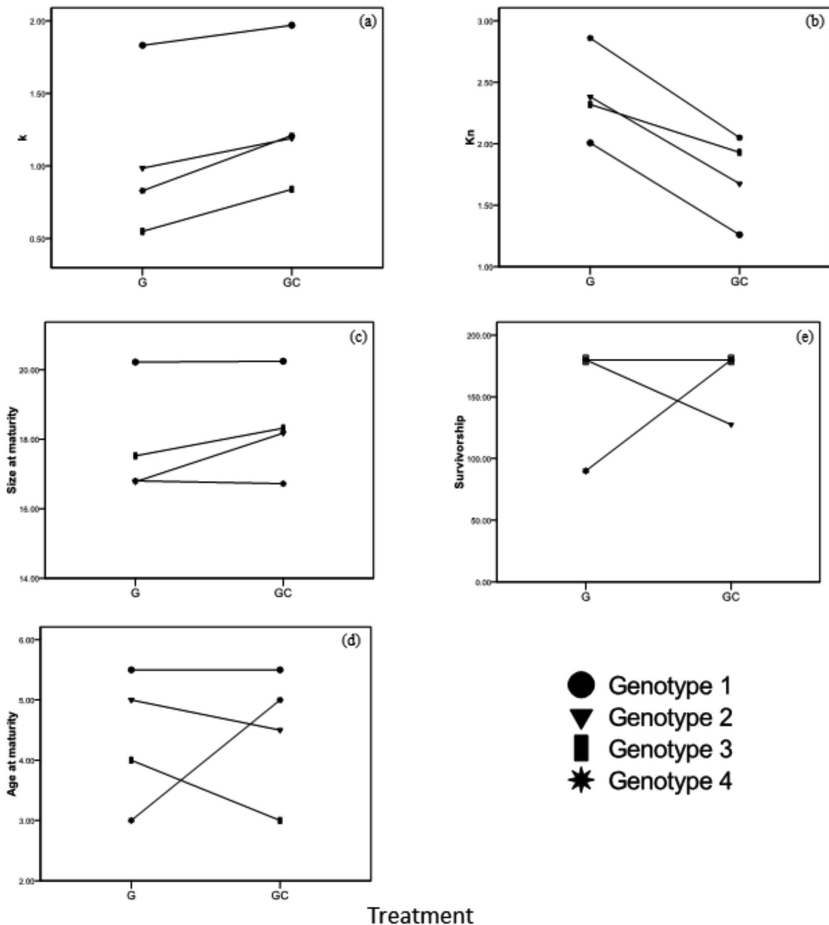


mature at a similar size (SSM;  $t = -1.25$ , d.f. = 1,28,  $P > 0.05$ ) and age (ASM;  $t = 0.43$ , d.f. = 1,28,  $P > 0.05$ ). The accumulated survivorship did not differ between treatments ( $\chi^2 = 0.546$ ; d.f. = 1,  $P > 0.05$ ; Fig 3d). There was a high mortality rate at early ages in both treatments, followed by a period of constant loss; a pattern consistent with type III survivorship model.

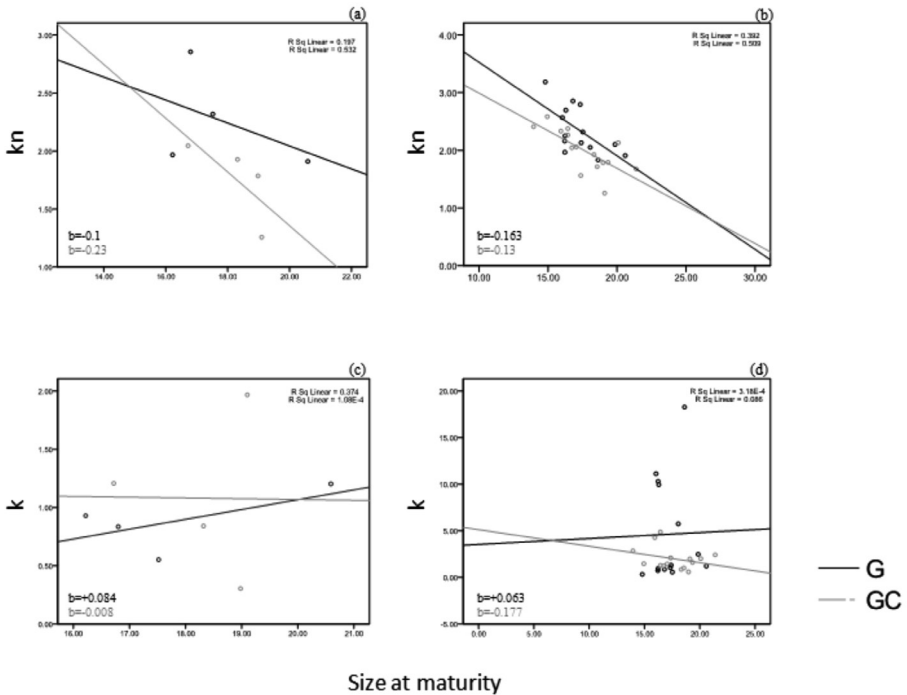
*Reaction norms and trade-offs.* Marked slopes between treatments, both positive and negative, in every genotype (brood) suggest the existence of reaction norms. In a few cases these reaction norms differ between phenotypes, indicating genotype by environment interactions ( $G \times E$ ). These are evident in Kn, age and size at maturity, and  $k$  (Fig 4; genotypes 2, 3 and 4) where the lines of phenotypic trajectories are crossed among genotypes.

Four phenotypic trade-offs were identified by the presence of negative slopes, in both treatments, in the regressions lines of  $k$  vs ASM,  $k$  vs  $l_x$ , Kn vs SSM and Kn vs  $l_x$ . Geno-

**Fig. 4.** Reaction norms of four different genotypes of *Girardinichthys multiradiatus* raised in two different conditions. Life history traits are: (a) growth rate ( $k$ ); (b) Fulton (Kn) condition factor; (c) size at sexual maturity (SSM); (d) age at sexual maturity age (ASM).



**Fig. 5.** (a) Genetic and (b) phenotypic correlations between size at sexual maturity and physiological condition factor ( $Kn$ ) for fish from both treatments. Genetic (c) and phenotypic (d) correlations between size at sexual maturity and growth rate ( $k$ ) for both from treatments.



typic compromises were also detected in both treatment between  $k$  and  $Kn$ ,  $kn$  and SSM,  $Kn$  and ASM and  $Kn$  and  $l_x$ . However, no trade-offs were detected between  $k$  and SSM, SSM and ASM, SSM and  $l_x$ , or ASM and  $l_x$  (see Table 3). Examples of this trade-offs are illustrated in Figure 5a and b.

Genotypic trade-offs induced by the presence of carp were evident in three regressions;  $k$  vs SSM, SSM vs ASM and SSM vs  $l_x$  (Figures 5c, d). Additionally, phenotypic trades between  $Kn$  and:  $k$ , SSM and ASM were detected.

**Male ornaments and behaviour.** Expression of male ornamental fins, assessed from the first principal component (mPC1; 87.4% variance in fin morphology explained), was not different between treatments ( $W = 11.0$ , d.f. = 1,7,  $P > 0.05$ ), nor was the chromatic saturation of flank, operculum, or the sexually-dimorphic median fins (Table 4). Growing in the presence of carp had no effect on either the frequency (fPC1; 75.5% variance in display frequency explained,  $F_{(1,7)} = 0.22$ ,  $P = 0.65$ ) or the duration of the courtship displays (dPC1; 72.6% variance in duration of courtship displays explained) when measured in standardised conditions (i.e. not in the experimental tanks/water;  $F_{(1,7)} = 0.34$ ,  $P = 0.58$ ). Similarly, females exposed in standardised conditions to males from both treatments showed no preference for either (Repeated-measures ANOVA,  $F_{(1,3)} = 2.46$ ,  $P = 0.22$ ).

## Discussion

We experimentally demonstrated a causal link between the presence of *Cyprinus carpio* and a change in water quality towards eutrophic conditions -high concentrations of  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{PO}_4^{3-}$  & SS. Given that biomass and the input of nutrients to the system were the same in both treatments, this effect can be attributed solely to the presence of carp due to its behaviour, which, as reported by HUSER et al. (2015) provokes sediment mixing which increases de amount of mobile P. The pattern resembles the descriptive findings of ZAMBRANO et al. (1999), although the relative increase in phosphorus – whose concentration was higher in the field study, whereas that of nitrogen compounds was the greatest effect in this study-. This contrast may be due to the absorption of phosphorus by the plants in the holding compartments -a species which thrives even if uprooted-. Also, most sources of phosphorous compounds in the field (effluents, irrigation, manure and detergent; MARTÍNEZ-CORDOVA 1998; ZAMBRANO 2001) were absent in the aquaria, where phosphates (and indeed nitrogen) beyond those found originally in the sediment, were only available as waste products of fish metabolism (PACHECO et al., 2002). The lack of information on water quality tolerance by *Girardinichthys multiradiatus* do not allow us to determine how elevated the values of  $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{PO}_4^{3-}$  & SS are for this species. However, it is important to understand the differences found among our treatments. Indeed, ZAMBRANO et al. (1999) reported increases in  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$  & SS associated to the presence of common carp (*i.e.* without carp, 0.03mg/l of  $\text{PO}_4^{3-}$ , 0.03 mg/l  $\text{NO}_3^-$  and 14.8 for SS; with carp, 0.10 mg/l, 0.02mg/l and 55.9 mg/l respectively). These authors also found negative effects on free floating and rooted macrophytes and reported a coverage of 89% without carp and 31% with carp, although here, we did not measure impact on vegetation we could notice that uprooting of plants was higher in the carp division of the GC treatment.

*Cyprinus carpio* induced habitat modification which led to changes in life history traits of the *Girardinichthys multiradiatus*, characterised by a decrease in condition factor and growth rate. These traits depend on the allocation of energy, known to be sensitive to environmental conditions (STEARNS 1989; CHARNOV & GILLOOLY 2004; BRUNEL et al., 2013). For instance, exposure to high concentrations of ammonium and other nitrogen compounds inhibits growth rate early on life (LEWIS & MORRIS 1986; REINBOLD & PESCIPELLI 1990; MCGURK et al. 2006). Fish and other aquatic animals are particularly susceptible to intoxication by  $\text{NO}_2$  because it can enter the body through the gill epithelium, reaching large concentrations that lead to the formation of methemoglobin, causing physiological alterations in several organs (REICHENBACH-KLINKE 1982; MARGIOCCO et al. 1983; RODRIGUEZ-MORENO & TARAZONA 1994; KROUPOVA et al. 2005) and impairing the immune system and the electrolytic balance (CAMARGO & ALONSO 2006; DOLOMATOV et al., 2013). Exposure to high concentrations of phosphates causes alterations to the liver and nervous system, reducing swimming ability, and also affect the production of mucus in the gills, which impairs oxygen intake (RONDÓN-BARRAGÁN et al., 2007).

This study revealed the existence of reaction norms in five life histories traits of *G. multiradiatus*, whereas the observed G×E interactions suggest that carp-induced habitat degradation impact, in particular, the traits associated with reproduction. This may influence the phenotype of subsequent generations, since genetic correlations are particularly sensitive to changes in the frequency of genes with different paths of pleiotropic effects when there are G×E interactions (STEARNS 1989), thus a punctual environment change may generate trades in the Life History traits.

**Table 3.** Compromises or positive associations between growth rate (*k*) physiological condition factor (*Kn*), size at sexual maturity (*SSM*) age at sexual maturity (*ASM*) and survivorship (*lx*) of *Girardinichthys multiradiatus* raised in the presence (*CG*) or in the absence (*G*) of *Cyprinus carpio*. A tick (✓) indicates the existence, and a cross (✗) indicates the absence, of trade-off, a trade, or a positive correlation between traits. Values in bold indicate significant differences between slopes (b).

Trait on y	x	b		Trade-off				Trade				Positive correlation				p	
		Phenotypic	Genotypic	Genotypic	Phenotypic	Genotypic	Phenotypic	Genotypic	Phenotypic	Genotypic	Phenotypic	Genotypic	Phenotypic	Genotypic	Phenotypic		Genotypic
k	Kn	G=+0.95	C=-0.31	✓	✗	✗	✗	✓	✗	✗	✗	✗	✗	✗	✗	✗	>0.05
		GC=-3.11	E=-1.29														
k	SSM	G=+0.063	C=+0.084	✗	✗	✓	✓	✓	✗	✗	✗	✗	✗	✗	✗	✗	>0.05
		GC=-0.177	E=-0.008														
k	ASM	G=-0.86	C=+0.053	✗	✓	✗	✗	✗	✗	✗	✗	✗	✓	✗	✗	✗	>0.05
		GC=-0.09	E=+0.46														
k	lx	G=-0.021	C=+0.0007	✗	✓	✗	✗	✗	✗	✗	✗	✗	✓	✗	✗	✗	>0.05
		GC=-0.002	E=+0.01														
kn	SSM	G=-0.23	C=-0.1	✓	✓	✗	✗	✗	✗	✗	✗	✗	✗	✗	✗	✗	>0.05
		GC=-0.13	E=-0.163														
kn	ASM	G=+0.035	C=-0.072	✓	✗	✗	✗	✗	✗	✗	✓	✗	✗	✗	✗	✗	>0.05
		GC=-0.135	E=-0.14														
kn	lx	G=-0.006	C=-0.009	✓	✓	✗	✗	✗	✗	✗	✗	✗	✗	✗	✗	✗	>0.05
		GC=-0.004	E=-0.0004														
TMS	EMS	G=+0.28	C=+1.38	✗	✗	✓	✓	✓	✗	✗	✗	✗	✗	✗	✓	✗	>0.05
		GC=-0.39	E=-0.28														
SSM	lx	G=+0.019	C=+0.015	✗	✗	✗	✓	✓	✗	✗	✗	✗	✗	✗	✓	✗	>0.05
		GC=+0.009	E=-0.009														
ASM	lx	G=+0.022	C=+0.007	✗	✗	✗	✗	✗	✗	✗	✗	✗	✓	✗	✓	✗	>0.05
		GC=+0.028	E=+0.003														

**Table 4.** Expression of ornamental colour in the fins, flank and operculum of male *Girardinichthys multiradiatus* raised in the absence (G) or in the presence of carp (GC) (Mann-Whitney U-test). Yellow (CY), Red (CR), UV ( $C_{UV}$ ) and Total spectral saturation Ch) did not differ between treatments (Mann-Whitney U-test). Chromatic variables were calculated as follows:  $Ch = (R_{max} - R_{min})/B_M$ ;  $CY = R_{(500-630)}/R_{(360-740)}$ ;  $C_R = R_{(630-740)}/R_{(360-740)}$ ;  $C_{UV} = R_{(360-400)}/R_{(360-740)}$ .  $R =$  reflectance (%) in the specified wavelength ( $\lambda$ ) and  $B_M$  (medium brightness) =  $R_{(360-740)}/n_w$ , where  $n_w$  is the number of wavelengths measured. Chr = Chroma, Tr = Treatment.

Structure	Chroma	Treatment	Chroma Saturation (mean)	W	P d.f.=1,7
Caudal fin	Ch	G	0.775089	12.0	>0.05
		GC	0.646561		
	Cy	G	0.35817	8.0	>0.05
		GC	0.36148		
	Cr	G	0.310463	5.0	>0.05
		GC	0.305459		
	Cuv	G	0.0915171	5.0	>0.05
		GC	0.0885697		
Anal fin	Ch	G	0.763841	10.0	>0.05
		GC	0.872729		
	Cy	G	0.348372	10.0	>0.05
		GC	0.376097		
	Cr	G	0.309169	6.0	>0.05
		GC	0.300708		
	Cuv	G	0.0955868	4.0	>0.05
		GC	0.0840934		
Dorsal fin	Ch	G	0.805809	10.0	>0.05
		GC	0.748577		
	Cy	G	0.350157	8.0	>0.05
		GC	0.375499		
	Cr	G	0.314382	4.0	>0.05
		GC	0.298842		
	Cuv	G	0.0936112	6.0	>0.05
		GC	0.0849121		

Structure	Chroma	Treatment	Chroma Saturation (mean)	W	P d.f.=1,7
Flank	Ch	G	0.855565	10.0	>0.05
		GC	0.802426		
	Cy	G	0.348127	9.0	>0.05
		GC	0.35422		
	Cr	G	0.314804	3.0	>0.05
		GC	0.306849		
	Cuv	G	0.313753	8.0	>0.05
		GC	0.30655		
Operculum	Ch	G	0.773447	11.0	>0.05
		GC	0.871607		
	Cy	G	0.349259	5.0	>0.05
		GC	0.347042		
	Cr	G	0.313753	3.0	>0.05
		GC	0.30655		
	Cuv	G	0.0938143	11.0	>0.05
		GC	0.0974562		

In the absence of carp - i.e. in what would be regarded its natural condition - *Girardinichthys multiradiatus* gave priority to survival and delayed maturity (higher values of  $k$ ,  $Kn$ ,  $SSM$  and  $ASM$ ). This  $k$  strategy (WINEMILLER & ROSE 1992) promotes survival, especially under predation, because fast growing organisms can rapidly attain a size where they are no longer vulnerable (MILLER 1988; MEEKAN & FORTIER 1996, WILSON & MEEKAN 2002), whereas organisms with high physiological condition may be good at escaping incoming attacks (FISHER & BELLWOOD 2001) and produce high-quality offspring (STEARNS 2000). The more  $r$  strategy seen in fish raised in carp-degraded environments (favouring early maturity; low  $k$ ,  $Kn$ ,  $ASM$  and  $SSM$  values), is often favoured in unpredictable environments, where there is a premium on breeding early - especially if mortality risk is high before the first mating (STEARNS 1989, WINEMILLER & ROSE 1992, WINEMILLER 2005). Indeed, early mortality was high in our experiment, but did not differ between treatments.

No evidence was found that either the size or the colour of the ornaments of *G. multiradiatus* are affected by growing in a degraded environment. Besides being used to embrace the female during the copula (MACÍAS GARCIA & VALERO 2010), male dorsal and anal fins are hampering (MACÍAS GARCIA et al. 1994), condition-dependent ornaments (ARELLANO-AGUILAR & MACÍAS GARCIA 2008) on which *Girardinichthys multiradiatus* female mate choice depends. Their expression is compromised by exposure to pesticides during development (ARELLANO-AGUILAR & MACÍAS GARCIA 2008), but it seems that whatever toxicants might have been present in the experimental aquaria (e.g. ammonia) they were not so to the extent of impairing ornament development.



Yellow-red colouration in animals often depends on carotenoids, which are antioxidants and cannot be synthesised by most animals (OLSON & OWENS 1998). Carotenoid-based ornamental colour is only expected to be reduced if 1) the organism is under oxidative stress (e.g. when fighting pathogens or toxicants; e.g. MILINSKI & BAKKER 1990; ARELLANO-AGUILAR & MACÍAS GARCIA 2008), or 2) there is a shortage of carotenoids in the diet. It seems that the toxic effects of ammonia were not too severe to oxidise skin carotenoids in the fish exposed to *C. carpio*, which also were not attacked by pathogens (even if the environment in which they grew up made them more vulnerable). In nature, habitat degradation can in fact lead to an over-expression of male ornaments through an increase in signalling effort (terminal investment) in eutrophic habitats, by devaluating the cost of ornaments (CANDOLIN et al. 2007), or through the effect of polluting hormonal precursors that promote the expression of male epigamic traits (e.g. MARKMAN et al. 2008). Amarillo fish also use UV colour as a criterion for mate choice (MACÍAS GARCIA & BURT DE PERERA 2002), but it is not evident that it signals condition and thus there was no reason to expect differences in UV-chroma between treatments.

The last measured epigamic trait was male courtship performance. This has been shown to be affected by early exposure to pesticides (see above) and it seemed plausible that growing up in eutrophic conditions may also impair its expression. This was not supported by the data, however, although this may be a consequence of small sample size -particularly because it is a very variable trait in *Girardinichthys multiradiatus* (e.g. GONZÁLEZ ZUARTH et al. 2011). A further reason for not finding differences between treatments in courtship performance may be the fact that fish grew up in social isolation. This is known to impair adult courtship behaviour in another viviparous fish, the guppy *Poecilia reticulata* Peters 1859 (Guevara-Fiore, 2012), and there is evidence that social environment during development has an influence in the expression of male courtship in the *Girardinichthys multiradiatus* (DE GASPERIN & MACÍAS GARCIA 2015).

Given the lack of differences in ornaments or behaviour it is not surprising that female *Girardinichthys multiradiatus* were not more attracted to males from one treatment or the other. Since seven of the eight females were from the same population (Huapango), the lack of systematic preferences for, say, G males cannot be due to different population-specific female preferences (see MACÍAS GARCIA et al. 2012) cancelling-out each other. It is uncertain how males would have been perceived if female preferences had been assessed in turbid, eutrophicated water. However, inasmuch as within population female mating preferences are based on male attributes that reflect condition (e.g. ARELLANO-AGUILAR & MACÍAS GARCIA 2008) the direction of the preferences should have been the same in turbid as in clear waters.

This study provides evidence of phenotypic plasticity in *Girardinichthys multiradiatus* expressed in response to the exposure to habitat degradation caused by an exotic invasive species; the common carp *Cyprinus carpio*. It is shown that *C. carpio*-induced changes in the environment prompt a shift in the life-history strategy of the *G. multiradiatus*, from a *k* strategy to a more *r* strategy characterised by low physiological condition and early reproduction. These results are likely to underestimate the impact of carp on *G. multiradiatus* in the field, since small aquarium *C. carpio* were used, rather than large wild specimens. This was decided following a pilot test where the energetic foraging behaviour of wild-caught carp was linked to the death of one brood of *G. multiradiatus* (unpublished data).

Halting the introduction of *Cyprinus carpio* in Mexico would be impossible; it is found in every significant freshwater body, where it is constantly re-introduced by the Mexican Fisheries authority. The problem is in fact global, as *C. carpio* is the most cultivated species worldwide (FAO 2013). *Cyprinus carpio* negative effects on local biota have been reported in the past based largely on field studies where the direct link between *C. carpio* introduction and native biota decline is only inferred, but this study provides experimental evidence causally linking its foraging behaviour with a change in the life history trajectories of native fish. It is to be hoped that this type of evidence may help shifting the practice in inland fisheries from farming *C. carpio* to developing ways of raising/harvesting local species.

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