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PRIMARY RESEARCH PAPER

Reproductive parameters in native and non-native areas of *Padogobius bonelli* and comparison with *P. nigricans* (Actynopterigii, Gobiidae)

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Abstract The introduced goby *Padogobius bonelli* has established abundant populations in the River Tiber basin (Central Italy) and its expansion coincided with the decrease of the endemic *P. nigricans*. *P. bonelli* exhibits a more aggressive behaviour than *P. nigricans*, but other biological attributes may advance its colonization success. To test this hypothesis, some reproductive parameters (gonado-somatic index, age at maturity, egg size, absolute and relative fecundity) of a long-time established non-native population of *P. bonelli* were analysed and compared to a population from the native area as well as to those of *P. nigricans* inhabiting the same river. As a result, no differences between non-native and native populations of *P. bonelli* were observed. On the contrary, non-native *P. bonelli* showed higher values of gonado-somatic index for both sexes, a more protracted spawning season and produced a greater number of eggs than *P. nigricans*. These results indicated a greater reproductive output of *P. bonelli* that can enhance its invasion process and favour the expansion outside of its native range, causing further decline of *P. nigricans* populations.

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Introduction

Several freshwater fish species of the Mediterranean basin, that is considered one of the world's biodiversity hotspots (Myers et al., 2000), are currently threatened by extinction (Smith & Darwall, 2006; Hermoso & Clavero, 2011) and within the native fauna, endemic fish species are the most vulnerable (Crivelli, 1995). The survival of endemic fishes is threatened by several factors such as pollution, habitat modification, dam construction (Lorenzoni et al., 2006; Cucherousset & Olden, 2011; Ribeiro & Leunda, 2012; Franchi et al., 2014) and introduction of non-native species, that is widely counted as the second severe cause of the worldwide decline of fish fauna (Cambray, 2003; Clavero & Garcìa-Berthou, 2005; Ribeiro & Leunda, 2012). Italian watersheds were intensively affected by introduction of non-native species, especially in the last 30 years (Bianco & Ketmaier, 2001). The translocation of fish species from Northern to Central Italy has dramatically changed the original distribution of native fauna and caused the decline of native populations due to hybridization, predation and competition (Bianco, 1995).

The Padanian goby *Padogobius bonelli* (Bonaparte, 1843) is a small benthic fish endemic to Northern Adriatic basins, from Vomano (Italy) to Krka drainages (Croatia) (Kottelat & Freyof, 2007) (Fig. 1). Since the early 80s, the species has been accidentally introduced in the Tyrrhenian basins of Central Italy (Bianco & Ketmaier, 2001; Zerunian, 2004; Pompei et al., 2014) where the congeneric *P. nigricans* (Canestrini, 1867), is present. *P. nigricans* is endemic to Central Italy (Fig. 1) and it is listed as "vulnerable" according to the IUCN Red List of Threatened Species (Crivelli, 2006) and the Red List of Italian Vertebrates (Rondinini et al., 2013). *P. bonelli* is currently considered as one of the major causes of the decline and/or local extinctions of *P. nigricans* populations (Zerunian, 2004; Crivelli, 2006; Nocita & Zerunian, 2007; Mecatti et al., 2010; Pompei et al., 2016). Both species exhibit complex reproductive behaviour, comprising fights between males for the selection of the best breeding sites and paternal nest guarding (Zerunian, 2002). However, *P. bonelli* is much more aggressive and territorial than *P. nigricans: P. bonelli* may outcompete *P. nigricans* for spawning sites preventing its reproduction, as demonstrated by laboratory studies (Mecatti et al., 2010). Moreover, a high diet overlap has been observed, therefore food competition may occur if resources are limited and a mutual predation was also observed (Pompei et al., 2014). The rapid and wide expansion of *P. bonelli* in Central Italy raises serious concerns regarding the negative impacts on *P. nigricans* and other native species. Although no study on life-history traits of *P. bonelli* out of its native range was reported in the literature, a full understanding of life-history characteristics of alien species is crucial to develop effective management strategies (Yeates et al., 2012; Guo et al., 2013). In the recent years, several studies focused on the ability of newly introduced species to generate life-history traits that substantially differ from those of native populations (Bøhn et al., 2004; Britton et al., 2008; Čápová et al., 2008; Gutowsky & Fox, 2012), providing a valuable insight in the prediction of their invasive potential (Ricciardi & Rasmussen, 1998; Olden et al., 2006; Grabowska et al., 2011; Guo et al., 2013). Usually, this plasticity involves a higher investment in reproduction and an early maturation of the introduced populations compared with the native ones (Bøhn et al., 2004; Britton et al., 2008; Grabowska et al., 2011; Gutowsky & Fox, 2012).

Fig. 1 Original distribution of *P. bonelli* (*dark grey*) and *P. nigricans* (*light grey*) in Italy and location of the study areas in the River Aggia (*1*), where native *P. nigricans* (Pn) and non-native *P. bonelli* (PbA) were sampled, and River Burano (*2*), where native *P. bonelli* (PbB) was sampled

The main aim of this study was to provide the first data on reproduction parameters of *P. bonelli* outside its native range by analysing spawning cycles, egg size, fecundity and size at maturity of a long-time established population from the River Aggia, in Umbria, Central Italy. The first report of *P. bonelli* in Umbria Region occurred exactly in the River Aggia in the middle 90s and from there the species has colonized the upper and middle River Tiber basin over the last years (Pompei et al., 2015). From this, two further objectives followed: (1) comparing the data of non-native *P. bonelli* from the River Aggia with those of a native population of *P. bonelli* from the River Burano (Marche Region, Adriatic drainage) so as to gain a preliminary insight of its invasive potential and (2) comparing the reproductive traits of non-native *P. bonelli* from the River Aggia with those of the endemic *P. nigricans* inhabiting the same river, in order to evaluate the hypothesis that other biological characteristics, apart from the aggressive behaviour reported previously by other authors in laboratory observations, may advance *P. bonelli* in its invasion process at the expense of the native *P. nigricans*.

Materials and methods

Study areas, collection and processing of samples

Specimens of the non-native population of *P. bonelli* (PbA) were collected from the middle stretch of the

River Aggia (AGG02: 43°24′15.88″N, 12°12′33.54″E), a tributary of the River Tiber (Tyrrhenian slope of Central Italy) (Fig. 1).

The reproductive parameters of the *P. nigricans* population inhabiting the River Aggia used for comparison with PbA were described in detail in Pompei et al. (2016). The sample of *P. nigricans* (Pn) analysed was collected in a sampling station located 700 m upstream of AGG02 in a river sector not yet colonized by *P. bonelli* due to the presence of a weir (AGG01: 43°24′28.28″N, 12°12′12.67″E) (Fig. 1). In the present work, only the data collected during the reproductive period were used for the comparison with PbA.

Specimens of *P. bonelli* from its native area (PbB) were sampled from the River Burano (BUR: 43°35′4.67″N, 12°40′28.21″E), in the Adriatic slope of Central Italy (Fig. 1).

The river sectors investigated of both River Aggia and River Burano flowed in low hill areas and presented similar characteristics: continuous dense vegetative cover on riverbanks and substrate predominantly compiled of large stones and rocks, interspersed with areas of fine sand. Both areas were characterized by torrential regime typical of the streams in the Central-Southern Apennines (Lorenzoni & Esposito, 2013; Pompei et al., 2016). Moreover, the several physical/chemical parameters (water temperature, oxygen concentration, pH, conductivity, Chemical Oxygen Demand (C.O.D.), ammonium, chloride, nitrate, nitrite, phosphate and sulphate), measured monthly in each sampling site, were found similar in the two locations.

All fish were collected monthly during the pre-spawning and spawning period (March–July) by means of electrofishing. Specimens were caught over a standard area of 4 m wide ×60 m long, with a depth range of 0.2–0.5 m.

After catching, fish were immediately anesthetized and then euthanized with an overdose of 2-phenoxyethanol, and preserved in 4% formaldehyde for laboratory analysis. Fish were weighed (W, nearest 0.1 g) and measured for total length (TL, nearest mm). All specimens were dissected and sex was assessed through macroscopic observation of the gonads; the gonads were removed and weighed to the nearest of 1×10^{-3} g (Wg). Based on macroscopic appearances, gonads of both sexes were classified into six reproductive stages (stage I–VI) following Nikolsky (1963).

Reproduction parameters

The gonado-somatic index (GSI) of females and males was calculated for all individuals by the formula GSI = 100 Wg/W. Spawning period of PbA, PbB and Pn was determined by identifying monthly changes in GSI for all females and males. The differences among the three populations in mean GSI values were tested for both sexes and considering only the specimens with mature gonads (IV and V stage) (Table 1), by means of Analysis of Variance (ANOVA) after an arcsine transformation of GSI data. Tukey's HSD post hoc test was then used for pair-wise comparisons between groups.

Mean size at maturity was calculated for PbA and PbB from the percentage of mature individuals in each size class (in 1 cm TL intervals; Trippel & Harvey, 1987) using the formula:

$$\alpha = \sum_{x=0}^{w} (x)[f(x) - f(x-1)] \text{ DeMaster (1978)},$$

where α is the mean size at maturity, x is size in cm, $f(x)$ is the proportion of fish mature at size x and w is the maximum size in the sample.

For females showing gonads at stages IV and V, eggs were counted to obtain absolute fecundity (F) and relative fecundity ($RF = F \times W^{-1}$); the diameters of 25 randomly sampled oocytes from each female were measured by means of the software Image J. The mean values (δ in mm) of the 25 diameters measured for each female were used in the subsequent analyses. Data of F, FR and δ were log-transformed and the ANOVA test was used to compare PbB, PbA and Pn; Tukey post hoc test was then used for pair-wise comparison between groups.

In order to analyse whether F, RF and δ varied with the increase of length of the females, the following regressions were calculated for PbA and PbB samples: $\log_{10}F = a + b\log_{10}TL$, $RF = a + bTL$, $\delta = a + bTL$. The regressions for Pn were already reported in Pompei et al. (2016).

Differences between PbA and PbB, and between PbA and Pn in F, RF and δ were tested using the Analysis of Covariance (ANCOVA), with TL as covariate variable.

Results

In total, 164 PbA specimens (58 females, 102 males) were collected from the River Aggia during the study

Table 1 Number of individuals (N), mean lengths (TL in cm), minimum and maximum lengths (min–max) in brackets of total samples of males and females and of the males (Males IV–V) and females (Females IV–V) with gonads at IV–V stage of non-native *P. bonelli* from the River Aggia (PbA), native *P. bonelli* from the River Burano (PbB) and native *P. nigricans* from the River Aggia (Pn) collected in consecutive months

	Males		Males IV–V		Females		Females IV–V	
	N	Mean TL cm (min–max)	N	Mean TL cm (min–max)	N	Mean TL cm (min–max)	N	Mean TL cm (min–max)
March								
PbA	22	5.4 (2.9–7.3)	11	6.1 (4.2–7.3)	12	4.7 (3.0–6.3)		
PbB	17	5 (3.3–7.6)			12	5.2 (3.3–6.8)	3	6.6 (6.5–6.8)
Pn	25	4.6 (3.2–7.3)	3	6.3 (4.3–7.3)	15	4.6 (3.7–6.7)	3	5.3 (4.2–6.7)
April								
PbA	22	5.5 (3.2–7.3)	19	5.8 (3.7–7.3)	13	4.8 (3.3–6.2)	11	5.1 (4.3–6.2)
PbB	35	5.4 (3.0–8.0)	33	5.5 (3.3–8.0)	16	5.1 (3.6–7.0)	13	5.3 (3.3–7.0)
Pn	60	4.9 (3.1–9.2)	11	6.3 (4.2–9.2)	27	4.6 (2.9–7s.5)	15	5.7 (4.0–7.5)
May								
PbA	19	5.6 (3.3–7.5)	19	5.6 (3.3–7.5)	14	4.6 (3.0–7.3)	12	5 (3.7–7.3)
PbB	23	5.5 (3.3–8.0)	23	5.7 (3.3–8.0)	15	5 (3.5–6.5)	13	5.2 (3.6–6.5)
Pn	34	5.4 (3.1–8.9)	18	5.9 (3.7–8.9)	25	5 (3.4–6.7)	21	5.3 (4.2–6.7)
June								
PbA	18	5.6 (3.4–7.4)	18	5.6 (3.4–7.4)	10	4.9 (3.3–5.7)	8	5.4 (4.2–5.7)
PbB	21	5.9 (3.6–8.1)	21	5.9 (3.6–8.1)	18	5.1 (3.7–6.7)	13	4.9 (3.7–6.7)
Pn	38	5.4 (3.8–8.2)	16	6.1 (4.1–8.2)	24	5.2 (4.1–6.5)	14	5.5 (4.1–6.5)
July								
PbA	21	5.9 (3.6–7.4)	10	6.3 (3.8–7.4)	9	5.4 (4.7–6.0)	1	5.9 (5.9)
PbB	14	5 (4.2–6.7)			17	5.3 (4.7–7.7)		
Pn	36	5.7 (4.5–7.8)	11	6.1 (5.0–7.8)	24	5.2 (4.3–7.8)		
Total								
PbA	102	5.7 (2.8–7.5)	77	5.9 (3.3–7.5)	58	4.9 (2.9–7.3)	32	5.2 (3.7–7.3)
PbB	110	5.5 (3.0–8.1)	77	5.6 (3.3–8.1)	78	5.0 (3.3–7.0)	42	5.1 (3.3–7.0)
Pn	193	5.2 (3.1–9.2)	59	6.1 (3.7–9.2)	115	5.0 (2.9–7.5)	53	5.5 (4.0–7.5)

period; the TL range was 2.90–7.30 cm (mean ± SE = 4.86 ± 0.13) for females and 2.80–7.50 cm (5.68 ± 0.11) for males (Table 1). The total sample of PbB from the River Burano was composed by 204 fish (78 females, 110 males) and TL ranged from 3.30 to 7.00 cm (5.01 ± 0.13) in females and from 3.00 to 8.10 cm (5.52 ± 0.13) in males (Table 1). No differences in size were found comparing the two samples at Mann–Whitney U test (females: $Z = 0.29$, $P = 0.78$; males: $Z = 2.52$, $P = 0.06$).

Data of Pn analysed refer to 115 females and 193 males, ranging in size from 2.90 to 7.5 cm (4.97 ± 0.09) and from 3.1 to 9.2 cm (5.21 ± 0.09), respectively (Table 1).

PbA versus PbB

The mean size at maturity were similar between the samples of *P. bonelli* from different locations: regarding females, maturity was attained at 3.76 cm in PbA and 3.88 cm in PbB, while for males it was 3.73 and 3.93 cm for PbA and PbB, respectively.

From the beginning of the spawning period (March), a rapid increase in ovary weight took place in both samples, coinciding with rising of water temperatures (Fig. 2). In PbA, GSI reached the highest mean value in June (13.08 ± 2.70), whereas in PbB no striking peak in the GSI occurred, and the spawning cycle showed much flatter pattern (Fig. 3a). The mean

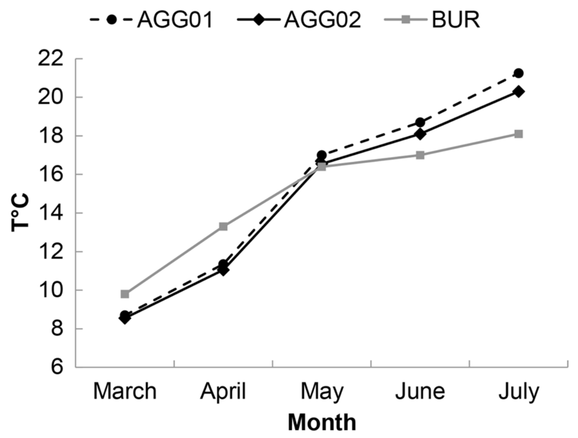

Fig. 2 Monthly water temperatures of the sampling stations located in the River Aggia, where native *P. nigricans* (AGG01) and non-native *P. bonelli* (AGG02) were sampled and in the River Burano, where native *P. bonelli* was sampled (BUR)

GSI (±SE) measured on mature females was 12.60 ± 0.97 in PbA and 11.22 ± 0.95 in PbB (Table 2); although ANOVA revealed differences among all three groups, in particular, no significant differences emerged between PbA and PbB females at Tukey's HSD test (Table 2). No differences emerged in the mean values of GSI even in mature males (Table 2). Analysing the mean monthly GSI for all males, the highest value was reached in May for PbA (2.37 ± 0.24) and in June for PbB (2.01 ± 0.26) (Fig. 3b).

Reproductive parameters F, RF and δ were estimated in 31 PbA females ranging in size between 3.7 and 7.3 cm TL and in 35 PbB females from 3.6 to 7 cm TL. In PbA, the value of F varied from 121 to 316 eggs (209.58 ± 10.49); PbB showed a higher average F (228.17 ± 18.28) and a wider variation of values (min = 61, max = 341) (Table 2). Mean RF was higher in PbA (106.35 ± 5.54) than PbB (98.32 ± 4.79), while egg size was quite similar in the two samples (PbA: mean ± SE = 1.03 ± 0.04 mm; PbB: mean ± SE = 0.97 ± 0.03 mm) (Table 2). Highly significant differences were found among all the groups at ANOVA (Table 2), but no differences between the samples of PbA and PbB in any of the above parameters were found at Tukey's HSD test (Table 2).

The correlation between F, RF and δ with size of females was comparable in the two samples of *P. bonelli*: the total number of eggs was positively correlated with length of females in both samples (Table 3; Fig. 4a) and the same relationship was found

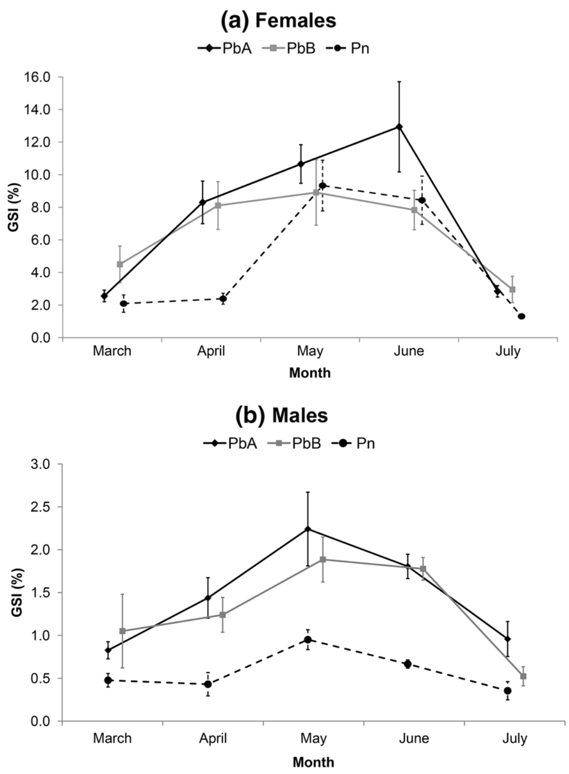

Fig. 3 Monthly variations in mean gonado-somatic index (GSI) values for females **a** and males **b** of non-native *P. bonelli* from the River Aggia (PbA: *black, solid line*), native *P. bonelli* from the River Burano (PbB: *grey*) and native *P. nigricans* from the River Aggia (Pn: *black, dotted line*). *Vertical bars* indicate Standard Error

between eggs diameter and females size (Table 3; Fig. 4c). Conversely, RF decreased as a function of size in both PbA and PbB (Table 3; Fig. 4b). No significant differences between the samples of PbA and PbB females in F, FR and δ were found at ANCOVA (F: $F = 0.47$, $P = 0.49$; RF: $F = 2.08$, $P = 0.13$; δ: $F = 1.52$, $P = 0.22$; Covariate TL = 5.21 cm).

PbA versus Pn

P. nigricans and *P. bonelli* showed different onsets of spawning: regarding females, the increase of GSI in Pn occurred from April with a spawning peak during May (9.68 ± 1.05); GSI remained still high in June (8.88 ± 1.59), when PbA reached the highest mean value of 13.07% (Fig. 3a). In males, the trend of GSI during pre-spawning and spawning period was similar, but the mean values reached each month were clearly higher in PbA (Fig. 3b).

Table 2 Descriptive statistics of gonado-somatic index (GSI, %) in females and males with gonads at IV–V stage and descriptive statistics of number of eggs (F), relative fecundity (RF *n* eggs g^{-1}) and diameter of eggs (δ in mm) in non-native *P. bonelli* from the River Aggia (PbA), native *P. bonelli* from the River Burano and native *P. nigricans* from the River Aggia (Pn) including the results of comparisons among groups by means of ANOVA (*F* = Fisher's *F*-distribution; *P* = level of significance) and pair-wise comparisons by means of Tukey's HSD test (*P* = level of significance)

	N	Mean	Min	Max	SE	ANOVA		Tuckey's HSD (*P*)		
						F	*P*	PbA	PbB	Pn
Males										
GSI										
PbA	77	1.78	0.4	6.81	0.13	16.85	<0.01		0.22	<0.01
PbB	77	1.59	0.31	4.75	0.11			0.22		<0.01
Pn	59	0.93	0.25	3.57	0.08			<0.01	<0.01	
Females										
GSI										
PbA	29	12.59	4.94	26.32	0.97	3.06	<0.05		0.15	<0.05
PbB	42	11.22	1.6	23.59	0.95			0.15		0.84
Pn	53	9.68	1.79	27.89	1.05			<0.05	0.84	
F										
PbA	31	209.59	121	316	10.49	52.5	<0.01		0.99	<0.01
PbB	35	228.8	61	341	16.65			0.99		<0.01
Pn	49	128.69	41	355	8.13			<0.01	<0.01	
RF										
PbA	31	106.35	45.09	185.71	5.55	20.48	<0.01		0.44	<0.01
PbB	35	96.65	54.13	192.22	4.92			0.44		<0.01
Pn	49	70.87	25.56	218	2.78			<0.01	<0.01	
δ										
PbA	31	1.03	0.62	1.59	0.05	5.01	<0.01		0.75	0.1
PbB	35	0.97	0.51	1.44	0.04			0.75		<0.01
Pn	49	1.23	0.45	2.07	0.06			0.1	<0.01	

GSI of Pn mature females averaged 9.68 ± 0.95, significantly lower than that found in PbA at Tukey's HSD test ($P < 0.05$) (Table 2). Also for males, the difference in the reproductive allocation between the two species was significant (Tukey's HSD test: $P < 0.01$), being the value of GSI recorded for Pn (0.92 ± 0.08) lower than that found in PbA (Table 2). The difference in reproductive allocation between the two species is also reflected in the higher F and FR of PbA resulted both at Tukey's HSD test ($P < 0.01$) (Table 2) and ANCOVA (F: $F = 113.61$; $P < 0.01$; RF: $F = 80.030$, $P < 0.01$; Covariate TL = 5.43). Pn laid generally bigger eggs than PbA, but no significant differences were observed in the mean diameter of eggs between Pn and PbA in the ANCOVA ($F = 2.60$; $P = 0.11$; TL covariate = 5.43) and in the Tukey's HSD test ($P = 0.10$) (Table 2).

Discussion

Padogobius bonelli is considered a major pest species outside its natural range (Freyhof, 2006). It possesses some of the features typical of a successful invader that make an alien species an invasive species, such as a fairly wide tolerance to environmental disturbance (Zerunian, 2004), aggressive behaviour (Mecatti et al., 2010) and parental care (Grabowska et al., 2011). It is widely assumed that the success of an invasive species can largely depend on the plasticity of its life-history traits, i.e. a shift in some biological characteristics towards a more generalist strategy in order to maximize the chance to establish in a new environment (Vila-Gispert et al., 2005; Olden et al., 2006; Fox et al., 2007; Hôrková & Kováč, 2013). From the results of the present research, the population of non-native *P.*

Table 3 Estimated parameters and regression coefficient a and b (±SE) for the relationships of fecundity (F), relative fecundity (RF) and diameter of eggs (δ) with total length (TL) calculated for non-native *P. bonelli* from the River Aggia (PbA), native *P. bonelli* from the River Burano (PbB) and native *P. nigricans* from the River Aggia (Pn)

Regressions	Sample	N	Regression coefficients		r^2	r	P
			a ± SE	b ± SE			
$\log_{10}F = a + b\log_{10}TL$	PbA	31	1.270 ± 0.173	1.454 ± 0.243	0.571	0.756	<0.01
	PbB	35	0.615 ± 0.124	2.388 ± 0.174	0.921	0.845	<0.01
	Pn	49	0.074 ± 0.280	2.688 ± 0.377	0.52	0.721	<0.01
RF = a + bTL	PbA	31	274.742 ± 22.409	−32.384 ± 4.266	0.681	−0.825	<0.01
	PbB	35	194.756 ± 18.297	−18.815 ± 3.440	0.394	−0.628	<0.01
	Pn	49	102.226 ± 22.727	−8.256 ± 4.055	0.081	−0.285	<0.05
δ = a + bTL	PbA	31	0.024 ± 0.033	0.015 ± 0.006	0.169	0.412	<0.05
	PbB	35	0.033 ± 0.016	0.012 ± 0.003	0.294	0.542	<0.01
	Pn	49	0.005 ± 0.051	0.021 ± 0.009	0.071	0.298	<0.05

bonelli from the River Aggia did not show significant differences in biological traits from the native population from the River Burano. The mean size at maturity were similar between the samples of *P. bonelli* from different locations and the specimens attained sexual maturity at around 3.7–3.9 cm TL. As reflected by the monthly averages of GSI in females, the onset and duration of reproductive season is entirely comparable: in both samples reproductive period began in April, in correspondence with the sharp increase of ovary mass and ended in July. The reproductive investment resulted similar, since there were no differences, nor for males or for females, in the GSI values. Again, as to the number of eggs produced, no significant differences between the samples were found in terms of absolute and relative fecundity.

Some generalist traits such as early maturation and high reproductive effort would be favoured during the early invasion of a new environment since they promote population growth enhancing the colonization process. However, once the species is spread and established, these traits are not necessarily convenient (Britton et al., 2008) and might otherwise be unfavourable. The population of non-native *P. bonelli* is present in the River Aggia for twenty years and then we can consider that it has concluded this colonization process and it is now fully established. Thus, we can expect that the population have redirected its energy towards a more specialized strategy (Grul'a et al., 2012).

Nevertheless, *P. bonelli* from the River Aggia exhibited some differences in life-history traits if compared with the information available on populations from the native range in North of Italy (Cinquetti & Rinaldi, 1987; Bisazza et al., 1989; Marconato et al., 1989; Lugli et al., 1992). Population of native *P. bonelli* from the North of Italy seems to mature at bigger sizes: Lugli et al. (1992) reported that no males in parental care were found under 5 cm TL, nor mature females smaller than 4.5 cm TL in the River Stirone; Marconato et al. (1989) found that the majority of mature specimens were 2 years old, and very few individuals reached sexual maturity at sizes smaller than 4 cm TL in the River Timonchio. The spawning period of the species in the Northern part of its native range is reported to be May–July (Cinquetti & Rinaldi, 1987; Lugli et al., 1992); in the present study, high values of GSI were already found in April, suggesting a more extended breeding season. Moreover, a higher reproductive allocation emerged for *P. bonelli* from the River Aggia if compared with data available for a native northern population (Cinquetti & Rinaldi, 1987). Analysing the monthly mean values of GSI for females from North Italy, the highest value recorded was equal to 6.5% (in May) (Cinquetti & Rinaldi, 1987), while for *P. bonelli* females from the River Aggia, the maximum GSI was double (13% in June). A similar pattern occurred in males: in the native range the highest mean value was 1.1% (June) (Cinquetti & Rinaldi, 1987), while in the present research the males showed a mean value of 2.9%, reached in May.

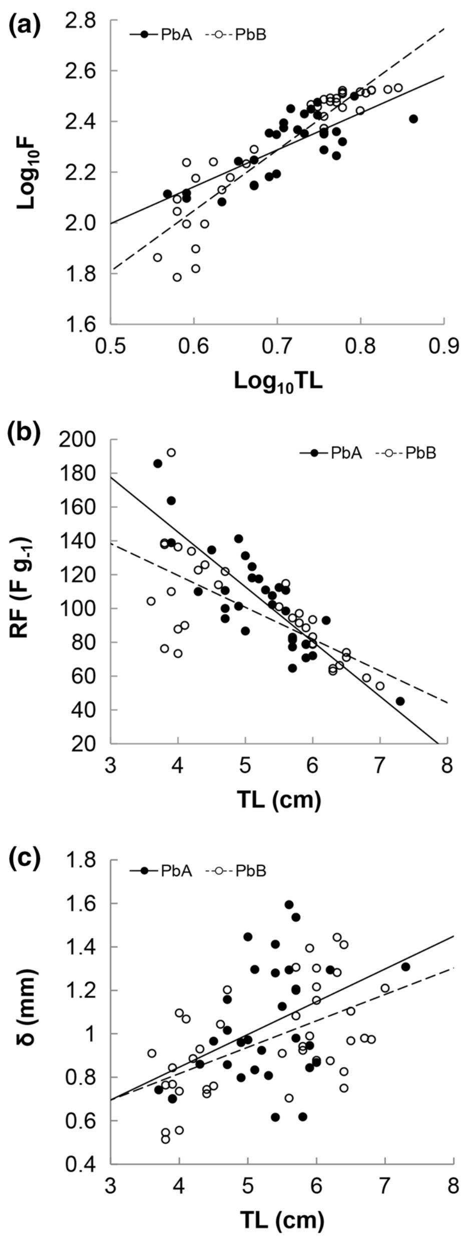

Fig. 4 Correlation between total length (TL) and **a** fecundity (F), **b** relative fecundity (RF) and **c** eggs diameter (δ) in non-native *P. bonelli* from the River Aggia (PbA: *black circles* and *solid line*) and native *P. bonelli* from the River Burano (PbB: *empty circles* and *dotted line*)

The similarity in the life-history traits examined between *P. bonelli* from the River Aggia and from the River Burano, located approximately at the same latitude and with comparable environmental characteristic, led to hypothesize that the differences with the native populations from North Italy could be attributed more to the influence of environmental conditions, and especially to the high unpredictability of the river bodies of Central-South Apennines (Lorenzoni et al., 2014). The water courses of this region are generally characterized by irregular hydrological regimes, high water temperatures and particularly long dry period in the summer due to the climate and geological nature of the area, mainly composed of low permeability substrates (Lorenzoni et al., 2014). The river bodies of Central-South Apennines can be considered as quite unstable and variable ecosystems and this is probably the main factor that affects the life-history traits of the two populations of *P. bonelli* analysed in the present study. As many authors have pointed out, indeed, the high variability influences most of the life-history parameters of fish inhabiting these environments (Bruton, 1989; Fernandez-Delgado & Herrera, 1995; Encina & Granado-Lorencio, 1997). Then the analogies in the reproductive parameters and, at the same time, the differences with those of northern populations are probably an expression of the high phenotypic plasticity of the species as it adapts to habitats with different environmental conditions.

A further remarkable result of this study showed that the non-native *P. bonelli* in the River Aggia has a higher reproductive investment than the population of *P. nigricans* from the same river. The average number of eggs produced by each female is significantly higher in PbA (210 eggs) than Pn (140 eggs) and also the relative fecundity was found to be significantly higher (FR: PbA = 106 eggs g^{-1}; Pn = 71 eggs g^{-1}). Even *P. bonelli* males seem to allocate more energy in reproduction than *P. nigricans* as shown by the average values of GSI (GSI: PbA = 1.78%; Pn = 0.96%). The prevailing of *P. bonelli* on *P. nigricans*, therefore, could not be only due to a more aggressive behaviour or to a wider tolerance to environmental disturbance, but also to a greater allocation of resources in reproduction. Previous researches had suggested that competition for breeding areas is most likely the reason of *P. nigricans* reproductive failure (Mecatti et al., 2010; Pompei et al., 2016) leading, ultimately, to *P. nigricans* reduction or local extinction (Pompei et al., 2015). The results of the present study add a further alarming concern for endemic populations of *P. nigricans* in Central Italy. *P. bonelli*, in addition to prevent in many cases the reproduction of the native goby, would also be favoured in the population dynamics: a greater reproductive investment and the production of a higher number of eggs compared to *P. nigricans* has probably enhanced *P. bonelli* in its invasion process, allowing the populations to rapidly increase the abundances in the several rivers of Central Italy in which it was introduced damaging the endemic *P. nigricans*.

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