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Does rainbow trout justify its high rank among alien invasive species? Insights from a nationwide survey in Greece

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Abstract

1. Rainbow trout is ranked as one of the world's worst alien invasive species; in Europe, however, the extent of established populations remains localized and poorly reported. This study aims to assess rainbow trout establishment in Greece and explores the factors affecting the success or failure of establishment.
2. Fish samples and site-specific environmental attributes collected during the past 17 years (2001–2017) were analysed. All available literature on the distribution patterns of rainbow trout were reviewed in parallel to those of the Greek native *Salmo* trout species and demographic criteria were applied to infer potential establishment.
3. Data indicating poor persistence of populations and population structure support the argument that recruitment of rainbow trout is extremely limited in Greece. Lack of suitable environmental conditions is not the main factor leading to the failure of rainbow trout to become established. Genetic factors affecting reproduction, possibly through a combination of outbreeding depression resulting from the admixture of unrelated intraspecific lineages, and maladaptive behaviour resulting from domestication in captivity, remain probable causes of poor establishment for the Greek populations of rainbow trout.
4. Overall, the threat of rainbow trout as a highly invasive species in Greece is lower than suggested by recent risk assessments.

KEYWORDS

established, Europe, Greece, introduced, *Oncorhynchus mykiss*, salmonids

1 | INTRODUCTION

Rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792) is an important species for aquaculture and inland fisheries. It occupies the second place in the list of the most frequently introduced species in the world, having been spread to more than 100 countries for farming and stocking (Crawford & Muir, 2008; Hutchings, 2014; Jönsson, Kaiya, & Björnsson, 2010). In Europe, it ranks as the most frequently introduced species with reported entry to at least 30 countries (Gherardi, Gollasch, Minchin, Olenin, & Panov, 2009). Given the enormous global scale of rainbow trout introductions, concerns have been raised about their adverse impact on local biota. The literature reports many such impacts, especially on other salmonid species through mechanisms such as predation, resource competition, hybridization, behavioural disruption, disease transmission and food web alteration (Kerr & Lasenby, 2000). These impacts have been well documented in countries where rainbow trout is well established and widespread (e.g. US (Hitt, Frissell, Muhlfeld, & Allendorf, 2003), Canada (Van Zyll de Jong, Gibson, & Cowx, 2004), Australasia (Jackson, Raadik, Lintermans, & Hammer, 2004), South Africa (Shelton, Samways, & Day, 2015), Argentina (Pascual et al., 2007), Chile (Arismendi et al., 2014) and Japan (Sahashi & Morita, 2016)). Through such documentation, rainbow trout has gained a reputation as an exceptionally harmful invasive species. It is listed as one of the 100 'worst invasive alien species' identified globally by the IUCN (Lowe, Browne, Boudjelas, & De Poorter, 2000) and ranks high in the list of the top 18 fish species that cause severe ecological impacts, compiled from establishment and impact assessment data contained in FISHBASE (Casal, 2006).

In Europe, the ecological impacts of rainbow trout are less well documented and have often been inferred from indirect evidence. Some of this evidence comes from laboratory and small-scale field experiments that have highlighted potential competition with, and predation on, native fishes (Blanchet, Loot, Grenouillet, & Brosse, 2007; Landergren, 1999; Nellen & Plate, 1997). However, a meta-analysis by Korsu, Huusko, and Muotka (2010) raised the possibility that such experimental results may reflect a laboratory or scale artifact resulting from intensified species interactions under conditions of confinement. Only a few studies have investigated impacts using field data on species distributions and demographic structure. The most substantial evidence of this kind has been produced for the alpine streams of the Rhine and Lake Constance, where large increases in the range and abundance of rainbow trout in recent decades coincided with the decline or collapse of several native brown trout populations (Bassi et al., 2001; Burkhardt-Holm, Peter, & Segner, 2002). There remains a minority of studies that have indicated weak or negligible impacts of rainbow trout on native fishes (Musseau et al., 2016, 2017; Vincenzi, Crivelli, Jesenšek, & De Leo, 2010).

In the absence of sufficient evidence of the ecological effects of rainbow trout introductions from most European regions, impacts are sometimes speculated rather than demonstrated, based on published data on feeding habits and habitat use patterns, pathogen spillover and adverse effects elsewhere (Almeida & Grossman, 2012; Candiotto, Bo, & Fenoglio, 2011; Larios-López, de Figueroa, Galiana-García, Gortázar, & Alonso, 2015; Leunda, 2010; Oscoz et al., 2005). Broader reviews on this subject are dominated by evidence from other regions of the world and cite only a few studies providing evidence from Europe (Cowx, Nunn, Harvey, & Noble, 2012; Fausch, 2007; Korsu, Huusko, & Muotka, 2008; Stanković, Crivelli, & Snoj, 2015). With few exceptions, the studies cited for Europe have been conducted in areas where rainbow trout is not known to have become established. Establishment is a key issue to consider when assessing environmental impacts of biological invasions. Through its control over the recruitment process, establishment exerts a dominant influence on the invader's abundance which, together with the total area occupied and the per capita impact, is a major determinant of the overall impact of the invader (Parker et al., 1999). If a species fails to establish self-sustaining populations, the impacts are localized, variable (depending on stocking densities), temporary and possibly reversible.

So far, risk assessments of rainbow trout introductions in Europe have been based on general considerations about impacts on biodiversity, but with insufficient information on establishment rates. Rainbow trout has been listed among the worst invasive alien species in Europe (van der Veer & Nentwig, 2015) and has been included in the black lists of some countries (Essl et al., 2011; Gederaas, Moen, Skjelseth, & Larsen, 2012; Pergl et al., 2016). Recently it was proposed as a candidate for inclusion in the list of invasive alien species of Union concern (the Union List), according to the EU Regulation 1143/2014 (Nentwig, Bacher, Kumschick, Pyšek, & Vilà, 2018). Risk assessment models developed to identify potential invaders have generated variable but mostly high-risk scores for European countries. In Luxemburg it was assessed to be a species of 'low' invasion risk (Ries, Krippel, Pfeiffenschneider, & Schneider, 2014). 'Medium' risk assessments were made for Finland (Puntila, Vilizzi, Lehtiniemi, & Copp, 2013) and Hungary (Ferincz et al., 2016). For Bosnia and Herzegovina, Croatia and Slovenia, Greece and the Iberian peninsula the risk scores range from 'medium' to 'moderately high' (Almeida, Ribeiro, Leunda, Vilizzi, & Copp, 2013; Glamuzina et al., 2017; Perdikaris et al., 2016; Piria et al., 2016). 'High' or 'very high' risk scores were assigned for the UK (Copp, Garthwaite, & Gozlan, 2005), Belarus (Mastitsky, Karatayev, Burlakova, & Adamovich, 2010) and Serbia (Simonovic et al., 2015).

Is rainbow trout an invasive species in Greece? Does this species justify its generally high rank among the invasive alien species of Europe? An answer to these questions requires an understanding of what is meant by the term 'invasive alien species'. Several definitions have been proposed (reviewed by Heger et al., 2013; Pereyra, 2016), but two groups of definitions prevail in scientific literature: the 'ecological definitions' and the 'policy definitions' (Heink, Van Herzele, Bela, Kalóczkai, & Jax, 2018). Both groups include establishment and spread as necessary criteria of invasiveness but differ over whether ecological or other impacts (e.g. economic, societal) should be included (Lockwood, Hoopes, & Marchetti, 2013; Young & Larson, 2011). Ecological definitions emphasize the ecological aspects of species invasions and do not include any reference to broader impacts (Blackburn et al., 2011; Colautti & Richardson, 2009; Ricciardi & Cohen, 2007). Policy definitions largely follow the definition of an invasive alien species provided by the World Conservation Union (IUCN): '*a species which becomes established in natural or semi-natural ecosystems or habitats, is an agent of change, and threatens native biological diversity*' (IUCN, 2000). This definition, and conceptually similar definitions adopted by the Convention on Biological Diversity (CBD, 2002) and the EU Regulation 1143/2014 on Invasive Alien Species (EU, 2014), implicitly draw a connection between 'invasiveness' and 'impacts' and require an evaluation of harmfulness. Only those alien species that have a demonstrable ecological or economic impact should be considered as invasive, based on a comprehensive risk assessment.

Which definition for invasive species is adopted is largely a matter of research focus and motivation (Heger et al., 2013). Although we lean toward the first (ecological) definition of invasiveness, i.e. based solely on criteria of establishment and spread, for the purpose of the present article we follow the second (policy) definition in order to be consistent with European policy for invasive allien species, as reflected in the EU Regulation 1143/2014. From the perspective of this definition, three criteria must be satisfied for an alien species to be regarded as invasive: (a) transfer and introduction mechanisms to new systems exist, (b) establishment into new systems is successful and an expansion of range is observed, and (c) adverse impacts on the native biota are documented or can reasonably be expected. Owing to the widespread stocking and farming of rainbow trout, the first criterion is readily met. The third criterion is met to various extents in some European regions. Hence, establishment (actual or potential) becomes the decisive criterion of invasion.

The present study was undertaken with two objectives: to describe the degree to which rainbow trout have become established in Greek fresh waters, and to explore possible factors that may account for the success or failure of establishment. The first objective was addressed through an analysis of field survey data from the fresh waters of Greece. So far, no clear and consistent views have emerged as to the extent to which rainbow trout is established in this country. It is referred to as 'established' by IUCN (GISD, 2018), as 'probably established' by FISHBASE (Froese & Pauly, 2017), and as 'not established' by DAISIE, (2018). Scientists within Greece have asserted that this species is not generally established in the country (Economidis, Dimitriou, Pagoni, Michaloudi, & Natsis, 2000; Economou, Giakoumi, et al., 2007). Few breeding populations have been reported by previous studies (Koutsikos et al., 2012; Stoumboudi, Barbieri, & Kalogianni, 2017); however, the establishment status of this species over the entire territory of Greece has not been rigorously surveyed with country-wide distributional and demographic data. The second objective was pursued by analysing data on fish assemblages together with environmental data from the sampling locations.

2 | MATERIALS AND METHODS

2.1 | Sampling procedures

Fish data were obtained from various research surveys conducted over the past 17 years (2001–2017) covering the entire mainland as well as the major islands of Greece. The majority of the field data were derived from two national projects. The first aimed to develop a fish-based index for assessing the ecological status of the upland streams and rivers in Greece (Economou, Zogaris, et al., 2007). The second was the National Monitoring Project for assessing the ecological quality of rivers in Greece (2009, 2012–2015). Fish sampling was typically conducted during spring and summer periods (March–October). In total, 956 samples (665 sites from 76 different drainage basins) collected through electrofishing surveys of the Hellenic Centre for Marine Research (HCMR) were used for the present study.

Fish sampling and environmental data collection was undertaken using standardized procedures developed under the European research project FAME (Schmutz, Cowx, Haidvogl, & Pont, 2007) with some modifications (IMBRIW-HCMR, 2013). A single electrofishing pass was conducted at a stream section about 100 m in length. Although no stop nets were used, crew members sampled river stretches demarcated by physical barriers (e.g. shallow riffles) in order to minimize fish escape in either direction. In small rivers (<10 m wide), the entire river channel was surveyed. When the active channel exceeded 20–30 m width, or when the depth was greater than waist-high, sampling was carried out only from one river bank. Two main types of electrofishing devices were used: a) a Hans-Grassl GmbH battery-powered backpack electrofisher (Model IG200–2, DC pulsed, 1,5 KW output power, 35–100 Hz, max. 850) which was routinely used to sample fish in small streams, and b) a generator-powered unit (EFKO Elektrofischereigeräte GmbH, Model FEG 6000, DC unpulsed, 7,0 KW output power, 150–600 V), which was used in deeper streams and rivers. Fish were identified to species level following Barbieri et al. (2015) as the main taxonomic reference. All fish were measured (total length, TL), grouped in 5-cm length class intervals, and returned alive to the river.

Site characteristics, landscape features and key habitat parameters were recorded in a field protocol modified from FAME (2005; IMBRIW-HCMR., 2013). This protocol contains fields for sampling details, topographic parameters, physicochemical variables, hydrological characteristics, habitat variables, substrate composition and important human pressures affecting the river segment where electrofishing was conducted.

2.2 | Data analysis

A literature review was undertaken in order to document the historical occurrence of rainbow trout at the river basin scale in Greece. By using standardized sampling data, a nationwide distributional database was developed and was used to assess the extent of occurrence of native salmonids and rainbow trout. Native salmonids, which are a part of the ubiquitous brown trout (*Salmo trutta*) complex (Kottelat & Freyhof, 2007), were included in the analyses on the grounds that these are ecologically similar taxa that share similar environmental requirements to rainbow trout (Molony, 2001; Moyle, Crain, Whitener, & Mount, 2003). Examining the spatial distribution and demographic structure of native trout gives an insight into the ecological conditions and processes that influence population persistence and responses to environmental conditions in rainbow trout. Introduced species are typically considered as established when populations in their novel habitats are self-sustaining (Lockwood et al., 2013). The notion of self-sustainability implies that individuals survive and reproduce at sufficient rates, and the population is maintained through time without the need of additional introductions. Demographic criteria (overall abundance, mean abundance at sampling sites, areal densities, length–frequency distribution, and proportions of juveniles) were used to explore evidence of natural reproduction and its contribution to recruitment and to infer demographic viability. Separate analyses were conducted for individuals smaller than 10 cm TL (categories of 'fry', <5 cm and of 'fingerlings' 6–10 cm in total length size-classes) and for larger individuals (all categories >10 cm), roughly corresponding to juveniles and pre-adults/adults respectively. Spatial variability in species densities and size-related parameters were examined for native species and for rainbow trout with the aim of exploring the possible sources of recruitment. Specifically, length–frequency distributions were developed for a) native trout, b) rainbow trout, c) a rainbow trout population in a remote spring-fed stream in S. Peloponnese (Vlisidia stream), which appears to be established (Koutsikos et al., 2012), and d) a rainbow trout population in a stream in Central Greece, Macedonia (Arapitsa stream), where stocking is performed regularly and fishing is forbidden. In addition, rank density diagrams were created to display graphically the site-specific (local) densities of the two species, with the sites ordered in decreasing density.

Canoco 4.5 (ter Braak & Smilauer, 1998) was used to analyse biotic and environmental data and to assess the differences in environmental features between native trout and rainbow trout sites. The environmental parameters included in the analyses were both physicochemical, i.e. conductivity (μS cm^{-1}), dissolved oxygen (mg L^{-1}) and water temperature (°C), and habitat attributes, i.e. mean active channel width (m), mean wetted width (m), mean depth (cm) and substrate coarseness ('coarse substrate' defined as >63 mm (including cobbles and boulders) and 'fine substrate' defined as substrate <63 mm (pebbles, gravel, sand, etc.). In addition, instream generic habitats were also included: i.e. pools (deep/still), glides (shallow/flowing), runs (deep/flowing), riffles (shallow/turbulent) and rapids (steep gradient/fast flow). Pools and glides were classified as slow-flowing habitats, whereas runs, riffles and rapids were classified as fast-flowing habitats. Wider environmental parameters such as site elevation (m), distance from source (m) and slope were derived from geographical information systems (ESRI - ArcGIS v. 10.4). Before all multivariate analyses, fish densities and abiotic data were log (x + 1) transformed, except those variables (coarse/fine substrate, slow/fast habitat) that were presented as percentages and were arcsine-transformed. Correlations with abiotic variables were calculated for: a) densities of all fish species sampled at native trout and rainbow trout sites, and b) juveniles and pre-adult/adult densities for native and rainbow trout, respectively. A detrended correspondence analysis (DCA) was conducted to test the heterogeneity of trout community data composition. In all cases, the lengths of the gradients for the first axis were < 3, revealing a linear structure of the data and indicating Redundancy Analysis (RDA) as the most appropriate method for multivariate multiple regression analysis (ter Braak & Smilauer, 1998). The Monte Carlo test was further applied with 499 permutations, in order to test the significance of abiotic variables in the ordination model.

Fish abundance data at each site (numbers per single electrofishing run) were converted to areal densities (dividing numbers by the wetted surface area sampled). The surface area sampled at each site was estimated from its geometric characteristics (fished length and cross-sectional width). Owing to a significant positive correlation (r^2 = 0.621, Pearson P < 0.001) between abundance (the number of individuals per site) and fish density (the number of individuals per m^2 per site), both these population indices were used interchangeably, depending on the analyses.

In an attempt to determine the influence of anthropogenic factors on establishment success, information was gathered on past stocking activities. The location of rainbow trout fish farms in the river basins investigated where rainbow trout were caught during this study, were mapped through a survey of accessible sources.

3 | RESULTS

3.1 | Salmonids in Greece: overview of species in freshwater ecoregions and drainage basins

Five salmonid species are native to Greece: *Salmo farioides* (Karaman, 1938); *Salmo lourosensis* Delling, 2011; *Salmo macedonicus* Karaman, 1924; *Salmo pelagonicus* Karaman, 1938 and *Salmo peristericus* Karaman, 1938 (Table 1). All of these species have restricted distributions and have been assessed for their threat status (Table 1). Hereafter, these species are collectively referred to as 'native trout'. Native trout have been reported in total from 20 drainages in Greece.

TABLE 1 Spatial distribution of native and alien salmonid species in river basins within freshwater ecoregions in Greece, based on fish surveys and published sources (Barbieri et al., 2015; Economou, et al., 2007; Koutsikos et al., 2012). Freshwater ecoregions defined by Zogaris and Economou, (2017)

Species	IUCN Red List	Greek Red List	Freshwater Ecoregions: Crete	Ionian	Macedonia – Thessaly	SE Adriatic	Thrace	W Aegean	Total
Native									
Salmo farioides Karaman, 1938	-	VU		7	2 [a]	1	1 [a]	1 [a]	**12**
Salmo lourosensis Delling, 2011	-	EN		1					**1**
Salmo macedonicus (Karaman, 1924)	DD	DD			1 [b]		3		**4**
Salmo pelagonicus Karaman, 1938	VU	VU			2				**2**
Salmo peristericus Karaman, 1938	EN	EN				1			**1**
Alien									
Oncorhynchus kisutch (Walbaum, 1792)	-	-	1	2	1			1	**5**
Oncorhynchus mykiss (Walbaum, 1792)	-	-	4	12	5	2	3	3	**29**
Salmo letnica (Karaman, 1924)	[DD]	-				1			**1**
Salmo salar Linnaeus, 1758	[LC]	-	1					1 [b]	**2**
Salmo trutta Linnaeus, 1758	[LC]	-		1	1				**2**
Salvelinus fontinalis (Mitchill, 1814)	-	-		1	1		1		**3**

IUCN abbreviations: EN, Endangered; VU, Vulnerable; DD, Data Deficient. Abbreviations in brackets indicate species included in IUCN categories, but where populations in Greece are introduced.

[a]indicates translocated population.

[b]indicates a doubtful species presence.

Another six salmonids have been reported as alien (*Oncorhynchus kisutch* (Walbaum, 1792); *Oncorhynchus mykiss*; *Salmo letnica* (Karaman, 1924); *Salmo salar* Linnaeus, 1758; *Salmo trutta* Linnaeus, 1758 and *Salvelinus fontinalis* (Mitchill, 1814). Rainbow trout is by far the most widely introduced of these aliens; the literature review documents its introduction or occurrence in 29 drainage basins (Table 1). From the 16 river basins where rainbow trout individuals were caught during this study, only two (Dafnon and Assopos Pel.) have no rainbow trout fish farms (Figure 1). In addition, based on the only officially available data (Ministry of Agriculture, 2000) over a 13-year period (1988–2000), approximately 2,600,000 rainbow trout fingerlings were stocked in seven river basins (Aliakmon, Acheloos, Alfios, Aracthos, Louros, Axios and Aoos).

From the 956 different samples collected, only 216 samples (163 sites from 17 river basins) contained at least one salmonid species (Figure 1). Native trout were the most frequently recorded taxa of all samples containing salmonids; these were found at 147 sites (57 streams in 12 river basins) (Table 2). Rainbow trout were much less common, recorded at only 25 sites (19 streams in 11 river basins) (Table 2). Both taxa were found together at nine sites (eight streams in five river basins) occupied by salmonids, with co-occurrence in 5.56% of the samples.

The site occupancy map (Figure 1) indicates the known distributions of the native trout and the rainbow trout, providing a large-scale picture of the present distributions and their actual and nominal ranges. With few exceptions, which mostly pertain to spring-fed rivers, native trout sites are located mainly at high altitude (mean 702.66 m ± 21.12) and in streams with steep slopes (mean 3.26 ± 0.25). The spatial range of rainbow trout is narrower than for native trout, with a far lower mean altitude (approx. 408.06 m ± 41.08) and in streams with gentle to moderate slopes (mean 2.28 ± 0.46). Rainbow trout have been reported from drainage basins of different sizes in both mainland and insular Greece (i.e. Crete), whereas native trout occur mainly in upper catchments of large drainage systems of mainland Greece.

3.2 | Population structure: size distribution, abundance and juveniles

The dominant size class of rainbow trout (21–25 cm) consisted mainly of adults (Figure 2b). On the contrary, the populations of native trout were mainly structured by the dominance of juveniles (6–10 cm) followed by older classes (Figure 2a). Owing to stocking activities, it is not clear whether and to what extent recruitment in rainbow trout arises from natural reproduction, stocking or escapes. This is particularly evident by comparing two sites – one, the Vlisidia population (Figure 2c) where no stocking has been conducted for the last 20 years, and the Arapitsa population (Figure 2d) where stocking is performed regularly.

Differences among taxa were particularly evident in abundance, as native trout substantially exceeded rainbow trout both in the total (overall abundance) and per site (mean local abundance) values (Table 3). The abundance of juveniles was also substantially higher for native trout (Table 3, Figure 3). The two taxa were similar in size range; however, they differed substantially in the proportion of juveniles to older fish, which was much lower in rainbow trout than in native trout. For native trout, juveniles comprised 42% of the total number of individuals captured, whereas for rainbow trout the corresponding value was 21% (Table 3). The juvenile to adult ratio for rainbow trout was 0.19, whereas the ratio for native trout was 0.62.

Rank density diagrams showed that the curves of local density, for both taxa, were strongly concave, indicating that a large proportion of the overall density was contributed by relatively few sites

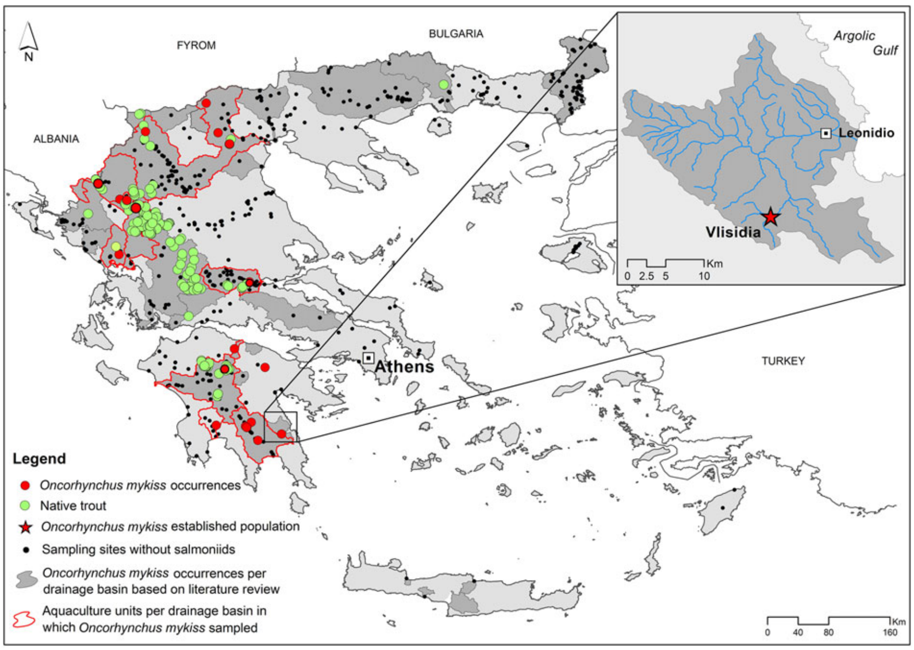

FIGURE 1 Occurrence of trout in the fresh waters of Greece based on sampling surveys (216 samples of 163 sites from 956 different ichthyological samples), the presence of rainbow trout based on literature (in 29 river basins), and the presence of aquaculture units per drainage basin in which rainbow trout individuals were caught

TABLE 2 Spatial occurrence of native trout species and rainbow trout in Greece based on sampling data (216 samples at 163 sites during 2001–2017)

	Native Trout				Rainbow Trout				Co-occurrence			
Basins	Presence	Streams	Sites	Samples	Presence	Streams	Sites	Samples	Presence	Streams	Sites	Samples
Acheloos	●	21	59	87		-	-	-		-	-	-
Alfeios	●	7	22	31	●	2	2	3	●	1	1	1
Aliakmonas	●	6	12	16	●	4	5	7	●	3	4	6
Aoos	●	4	11	14	●	1	1	1	●	1	1	1
Arachthos	●	10	26	29	●	3	3	3	●	1	1	1
Asopos Pel.		-	-	-	●	1	1	1		-	-	-
Dafnonas		-	-	-	●	1	1	4		-	-	-
Evinos	●	1	1	1		-	-	-		-	-	-
Evrotas		-	-	-	●	2	6	7		-	-	-
Kalamas	●	1	1	1		-	-	-		-	-	-
Krathis		-	-	-	●	1	1	1		-	-	-
Louros	●	1	1	1	●	1	2	2		-	-	-
Nestos	●	1	1	1		-	-	-		-	-	-
Pamisos		-	-	-	●	1	1	1		-	-	-
Prespes	●	1	2	3		-	-	-		-	-	-
Pinios The	●	1	1	1								
Sperchios	●	3	10	12	●	2	2	3	●	2	2	3
Total	**12**	**57**	**147**	**197**	**11**	**19**	**25**	**33**	**5**	**8**	**9**	**12**

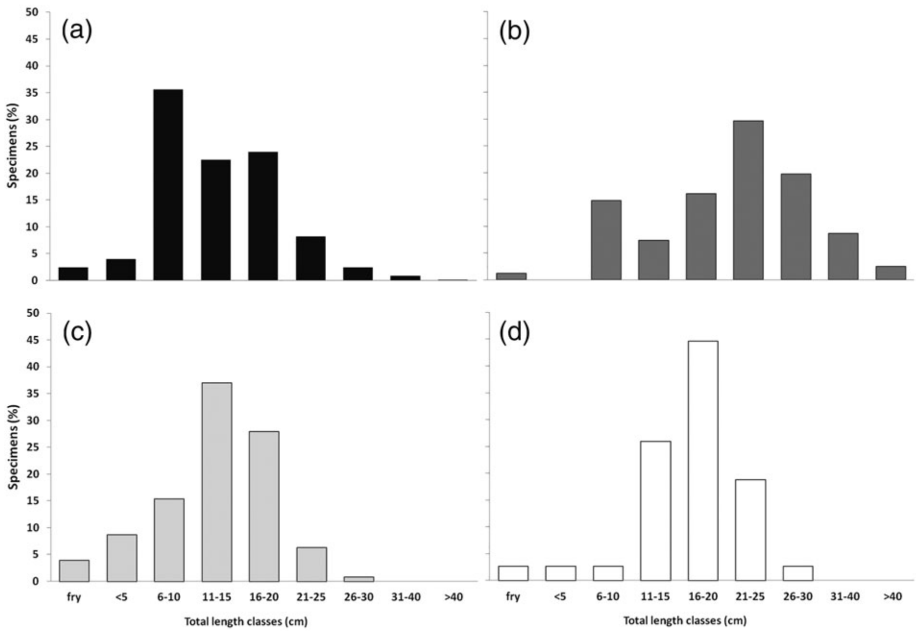

FIGURE 2 Length–frequency distributions of a) native trout and b) rainbow trout, in fresh waters of Greece, c) rainbow trout at a remote spring-fed stream in S. Peloponnese (Vlisidia stream), and d) rainbow trout at a stream where stocking is performed regularly while fishing is forbidden (Arapitsa stream). Data were averaged over all salmonid sites and sampling periods, respectively. (Note that the rainbow trout populations of Vlisidia and Arapitsa streams are excluded from Figure 2b)

(Figure 4 a, b). However, there were few rainbow trout juveniles and these were collected from a limited number of sampling sites (Figure 4b) compared with the frequent presence of native trout juveniles (Figure 4a). This observation is further confirmed by the comparison of the regressions generated for juvenile abundance against total abundance in both taxa (Figure 4 c,d). For native trout, a strong relationship was observed between total and juvenile local abundances ($r^2 = 0.81$; Figure 4c). For rainbow trout, the data show that the samples consisted of relatively few (often one or two) individuals. The proportion of juveniles was generally small and varied considerably among sites. By excluding from the analysis the only established rainbow trout population in mainland Greece (the Vlisidia population), the

TABLE 3 Abundance of salmonid species collected in fresh waters of Greece based on sampling data (2001–2017)

	Sub-samples of native trout					Native trout	*O. mykiss*	*O. mykiss* Vlisidia pop.
	S. farioides	*S. pelagonicus*	*S. peristericus*	*S. macedonicus*	S. lourosensis			
No. of samples	176	17	2	1	1	197	29	4
No. of sites	131	13	1	1	1	147	24	1
No. of specimens	4103	424	6	3	2	4538	193	254
Mean local abundance	23.4	24.9	3.0	3.0	2.0	23.1	6.7	63.5
No. of YOY[a]	1748	153	2	2	0	1905	22	71
YOY %	42.6	36.1	33.3	66.7	0.0	42.0	11.4	28.0

Mean local abundance is the product of no. of specimens divided by no. of samples.

YOY indicates young of the year individuals.

[a]fish <10 cm in length were considered YOY.

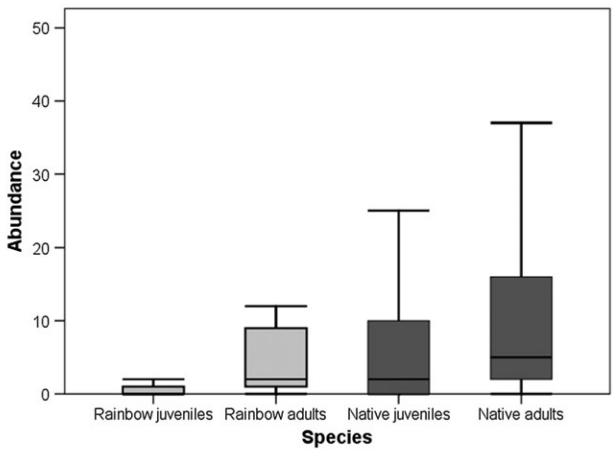

FIGURE 3 Abundances (no. of individuals) of adult and juvenile rainbow and native trout species caught

relationship between total and juvenile abundances was found to be weak and not significant (r^2 = 0.05; Figure 4d), and the slope of the relationship was much lower than the slope for native trout. In fact, juveniles were absent from most sites and the slope was heavily influenced by data from only the few sites where juveniles were relatively abundant.

3.3 | Environmental matching

The Monte Carlo test indicated that dissolved oxygen, coarse substrate and active channel width were the statistically significant environmental variables (P < 0.05). RDA results revealed differences in environmental variables between native trout, rainbow trout and all the other species (Figure 5a; Table S1). Native trout were positively correlated with coarse substrate, slope and altitude, but negatively correlated with conductivity, wetted width, active channel width, depth and distance from source. The densities of rainbow trout showed a positive correlation with dissolved oxygen, and a negative correlation with temperature and with active channel width. The ordination model was significant in all canonical axes, with the second axis explaining 64.3% of the fish densities data variance and the fourth 85.6%.

A similar pattern emerged when the two trout species were separated into juveniles and adults. RDA results indicated differences in environmental variables between native and rainbow trout (Figure 5b).

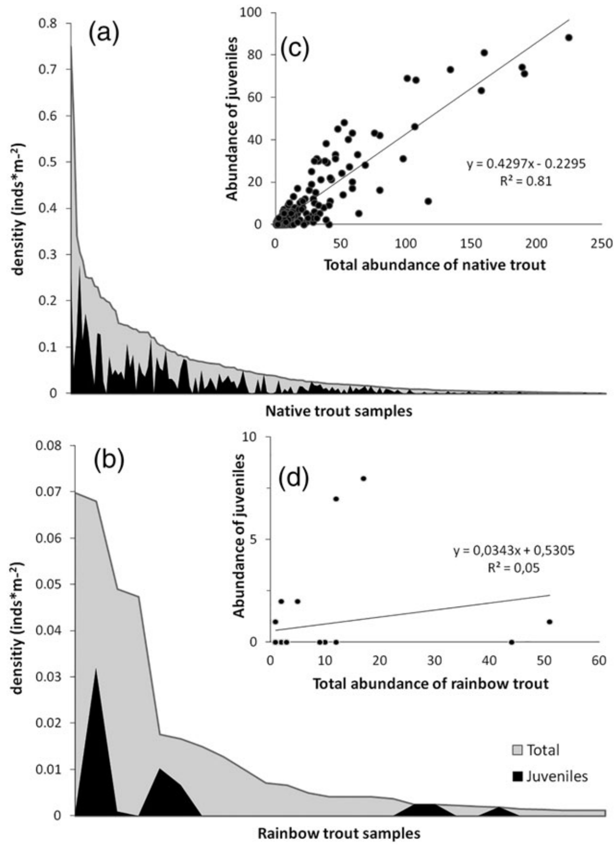

FIGURE 4 Ranked total (grey lines) and juvenile (black lines) densities (inds. m^{-2}) of (a) native trout and (b) rainbow trout in decreasing order for each sample, and regression between total abundance and juvenile abundance in (c) native trout and (d) rainbow trout. (Note that scales vary between figures. In addition, the rainbow trout population of Vlisidia stream is excluded from Figures 4b and 4d)

The ordination model was significant for all axes, with the first axis explaining 97.9% of the variance for fish density data, and the explained variance in the second axis, between fish density and environmental variables, was 98.0%.

The co-occurrence of rainbow and native trout was rare (Table 2). Both species were collected in only five basins (out of the 76 surveyed). Only in four cases (out of 12 samples of co-occurrence) were native trout numerically outnumbered by the rainbow trout (Figure 6; Table S2).

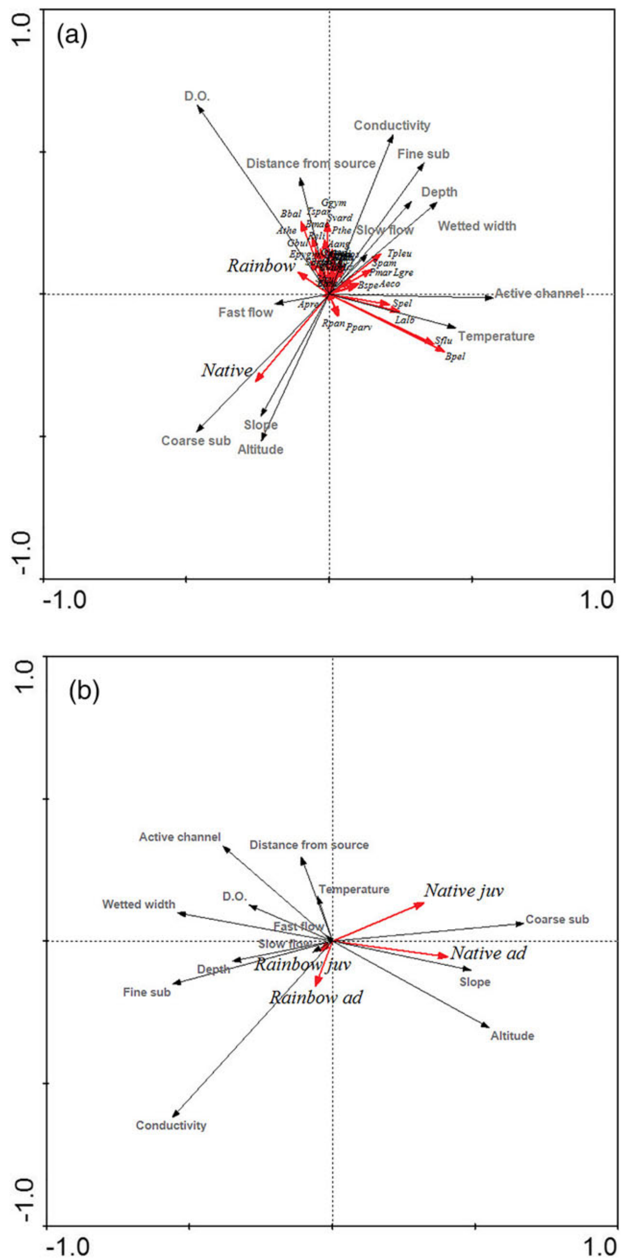

FIGURE 5 Ordination analyses (Canoco) among various environmental parameters: a) all fish species sampled (for species abbreviations see Table S1); b) adult native (*Native ad*) and adult rainbow trout (*Rainbow ad*) and native (*Native juv*) and rainbow trout (*Rainbow juv*) juveniles

4 | DISCUSSION

4.1 | Status of rainbow trout populations in Greece

Rainbow trout has been intensively farmed and stocked in Greece for almost six decades, following an initial importation of fertilized eggs from Switzerland in 1951 for aquaculture production (Economidis et al., 2000). In the following years, more (but not well-documented) imports took place from Denmark, Poland, Spain and the USA, particularly by private trout farms, and several new mainly small in-farm hatcheries were established. Around 80 small-to-medium scale trout farms have been established in rivers, streams and springs, mostly in the north-western part of Greece (Piria et al., 2018), and these have been key introduction vectors of rainbow trout into natural systems (Liasko, Anastasiadou, Ntakis, Gkenas, & Leonardos, 2012). In addition, intensive stocking programmes have been put in place (and continue to date) by government agencies, and there is no doubt that many unrecorded introductions of rainbow trout in natural waters have taken place by local authorities and anglers. However, the vast majority of stocking activities are undocumented (Ministry of Agriculture, 2000).

Recent compilations of the Greek fish fauna based on published sources and survey results, rank rainbow trout as the second most widespread alien species in Greek fresh waters, occurring in 29 river basins (Economou, et al., 2007; Koutsikos et al., 2012). Despite its widespread occurrence throughout the country (Economou, et al., 2007), no documented evidence of establishment in the wild had been provided until recently. Koutsikos et al., (2012) and Stoumboudi et al., (2017) reported evidence of natural reproduction of the species in the south-eastern Peloponnese and on the island of Crete.

Historical information on drainage-specific native species occurrences and alien species introductions indicates a much wider spatial distribution of rainbow trout (29 drainage basins) than of native trout (20 drainage basins). According to the site-specific catch data presented here, rainbow trout were absent from many of the basins in which it was historically recorded, and appeared to be far less common than native trout, both spatially and numerically. Indeed, rainbow trout was sampled in only 25 sites (compared with the 147 sites where native trout were sampled) and the catches consisted of relatively few specimens, often single individuals. Moreover, juveniles were either absent or comprised a very small portion of the catch at most sites. From this demographic profile, it can be inferred that the contribution of wild spawning to recruitment is small and probably insignificant in most of the locations examined. Natural recruitment appears to be spatially restricted and there are insufficient numbers to support viable populations; we speculate, therefore, that most populations would not persist in the absence of stocking. The picture emerging from this study is that rainbow trout is not currently established in the greater part of Greece, and the reason for this appears to be a failure of natural reproduction.

The comparisons of the distributional, demographic and habitat data for rainbow trout and those for native trout indicated broadly overlapping distributions, occupying sites with similar environmental conditions as both species did not differ appreciably in the range of most environmental variables. Other studies involving comparisons of rainbow trout with brown trout (*S. trutta*) have indicated similar habitat preferences and tolerance ranges to a variety of environmental factors (Kerr & Lasenby, 2001; Moyle et al., 2003; Shirvell & Dungey, 1983). The only difference noticed by Molony, (2001) is that rainbow trout can tolerate a slightly higher temperature than brown trout (see also Beitinger, Bennett, & McCauley, 2000). These ecological similarities between rainbow trout and European trout species indicate considerable niche overlap and imply that the amount and quality of habitat available to native trout species may provide at least aminimum estimate of the extent and suitability of habitat available to rainbow trout.

Concordance with the geographic distributions of native trout and rainbow trout in Greek fresh waters, as well as their similar demographic responses to environmental conditions, suggests that the availability of suitable habitat is not a limiting factor for rainbow trout

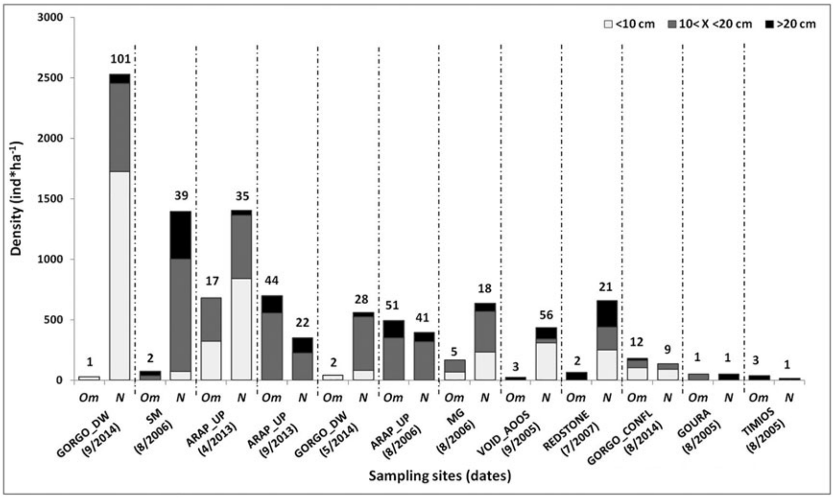

FIGURE 6 Ranked densities of the total recorded where there is co-occurrence of both rainbow trout (*Om*) and native trout species (*N*). Numbers above bars denote the total species abundances for each site

survival and reproduction. Although the ordination analyses depict some differences in environmental matching of the two species, this is to be expected owing to the much lower number of rainbow trout samples and the fact that all are stocked, often released at heterogeneous river sites at lower elevations.On the assumption that conditions that are favourable for the reproduction of native trout species are also appropriate for the reproduction of rainbow trout, these data provide another piece of evidence that a lack of suitable breeding habitat is not the reason why rainbow trout fail to become established in Greece. The rainbow trout population in the remote spring-fed stream of Vlisidia (Dafnon river basin) on Mount Parnon in the south-eastern Peloponnese, stands out as a notable exception to this pattern of the demographic dynamics. This population has a robust structure consisting of multiple year-classes and appears to be successfully reproducing in the absence of stocking. Moreover, there are no trout farms in the area and the nearest farm is located in a different river basin. Apparently, the small-sized individuals recorded during the surveys were the product of recent natural spawning activity. In addition, the overall proportion of juveniles was well above the average country-wide percentage for the species. These demographic characteristics provide evidence of successful reproduction and sufficient natural recruitment. We therefore assert that this population is established and persists without any apparent human intervention.

4.2 | Factors influencing establishment success

Recently evaluated literature shows that the low establishment success of rainbow trout is a general phenomenon across Europe. Rainbow trout appears to be firmly established and widespread in the alpine streams of Austria (Füreder & Pöckl, 2007), Liechtenstein (Peter, Staub, Ruhlé, & Kindle, 1998), Slovenia (Povž, 2017) and Switzerland (Wittenberg, 2005). Instances of localized establishment (single or only a few isolated populations) have been reported from a number of other countries: Greece (Koutsikos et al., 2012; Stoumboudi et al., 2017), Italy (Candiotto et al., 2011), Norway (Hesthagen & Sandlund, 2007), Slovakia (Koščo, Košuthová, Košuth, & Pekárik, 2010), UK (ICES, 2013), France (Pascal, Lorvelec, Vigne, Keith, & Clergeau, 2003), and possibly in Cyprus (Zogaris et al., 2012) and the Czech Republic (Musil, Jurajda, Adámek, Horký, & Slavík, 2010).

The reasons preventing the establishment of rainbow trout in Europe have been debated for many years and are still not fully understood (Fausch, 2007; Fausch, Taniguchi, Nakano, Grossman, & Townsend, 2001; Hindar, Fleming, Jonsson, Breistein, & Sægrov, 1996; Korsu & Huusko, 2010). In the search for explanations, various hypotheses have been developed. Most link establishment success with three sets of causative agents: ecological constraints, propagule pressure, and the genetic effects of hatchery propagation.

4.2.1 | Ecological constraints

The following factors, or combinations of them, have been considered widely as key ecological constraints on the establishment of rainbow trout: unsuitable thermal regimes, low levels of oxygen saturation, adverse water flows, lack of appropriate reproductive substrate, barriers preventing access to spawning grounds, angling pressure, and competition from native salmonids (reviewed by Fausch, 2007; Fausch et al., 2001; Fausch, Rieman, Dunham, Young, & Peterson, 2009; Kerr & Lasenby, 2000; Korsu & Huusko, 2010).

In other parts of the world, ecological hypotheses have been successful in explaining patterns and rates of rainbow trout establishment (Fausch et al., 2001; Lapointe & Light, 2012). In Europe, ecologically-based hypotheses have fared poorly in explaining why establishment has succeeded or failed. Each explanation can account for particular cases of establishment success or failure, but none has sufficient generality and predictive power. Hindar et al., (1996) remarked that rainbow trout is a highly flexible and adaptable species having overlapping habitat requirements with brown trout and salmon. He asserted that there is plenty of good habitat for this species in Norway and implied that there is no obvious environmental constraint on establishment. Other researchers have similarly asserted that lack of suitable environmental or habitat conditions is not the main limiting factor for rainbow trout reproduction and establishment in Europe (Fausch, 2007; Korsu & Huusko, 2010; Landergren, 1999; Welton, Ibbotson, Ladle, & Brookes, 1997). In the present study, rainbow trout was typically encountered in a broad range of altitudes (from lowlands close to sea level up to 825 m in mountain tributaries) with water temperature above 10°C, fast-moving water, hard bottom substrate and high levels of dissolved oxygen. The values measured for these variables were within the limits reported as favourable for this species in other works (Fausch, 2007; Montgomery, Beamer, Pess, & Quinn, 1999; Moyle et al., 2003; Raleigh, 1984; Shelton et al., 2015). Although not all variables were found at optimal values in all sites, at least those variables considered as being critical for successful ovulation and spawning – namely temperature, flow regime, oxygen saturation levels and availability of gravel substrate (Montgomery et al., 1999) – were within appropriate ranges at most sites and broadly match those in the native habitats of rainbow trout.

A highly speculative hypothesis links reproductive failure of rainbow trout in Europe with high susceptibility to whirling disease caused by the myxozoan parasite *Myxobolus cerebralis*. Hindar et al., (1996) have put forward the hypothesis that the high susceptibility of rainbow trout to whirling disease can potentially account for the difficulty of this species to become established in Europe. Some authors have partly accepted this hypothesis (Fausch, 2007; Jönsson et al., 2010; Jonsson, Jonsson, Hansen, & Aass, 1993; Landergren, 1999) while others are sceptical (Walker, 2003). To our knowledge, whirling disease has not yet been reported from Greek fresh waters, probably owing to a lack of research targeting this issue. However, the fact that the disease has not been yet reported from the rainbow trout farming sector (Savvidis G., pers. comm.) leads to the suggestion that it may also be at least uncommon in the wild. Nevertheless, the presence and prevalence of this and other diseases need verification in Greece and its possible impact on recruitment must be evaluated against other probable causes.

4.2.2 | Propagule pressure

The propagule pressure for rainbow trout is undoubtedly among the highest for alien vertebrate taxa (Fausch, 2007). A positive relationship between propagule pressure and the success of rainbow trout establishment has been reported from some environments (Consuegra, Philllips, Gajardo, & Garcia de Leaniz, 2011; Monzón-Argüello et al., 2014). In Europe high and constantly increasing stocking rates over the past 100 years (MacCrimmon, 1971) have resulted in a very small number of established populations (Stanković et al., 2015), and there is evidence suggesting that this number is declining through time (e.g. in Britain and Ireland (Frost, 1974; Welton et al., 1997), and in Norway (Hindar et al., 1996; Sandlund & Hesthagen, 2011). This evidence runs contrary to the expectations from the propagule pressure invasion hypothesis, which posits that the probability of establishment increases with introduction events and the number of individuals introduced (Lockwood, Cassey, & Blackburn, 2005). We do not mean to imply that propagule pressure per se impedes establishment; rather, we explore below the probable influence of propagule-driven genetic influences, which may be responsible for both poor establishment success and for the loss of previously established populations.

4.2.3 | Genetic effects of hatchery propagation

Although there is substantial evidence that genetic change is occurring during hatchery propagation in salmonid species, the nature of this change and the impact of hatchery effects, both on wild trout conspecific populations and on establishment success, have long been debated (Naish et al., 2008; Scott & Gill, 2008). Three major and not mutually exclusive mechanisms for adverse hatchery effects have been postulated:

- Domestication selection and artificial selection imposed by breeders with the intention of enhancing desired traits, but which are possibly maladaptive in the wild (e.g. Araki, Berejikian, Ford, & Blouin, 2008).
- Inbreeding depression, which leads to a decrease in heterozygosity with a concomitant reduction of fitness through either or both of two mechanisms: increased expression (unmasking) of deleterious recessive alleles that otherwise would remain at low frequency, and the reduced frequency of beneficial allelic combinations (Keller & Waller, 2002; Naish, Seamons, Dauer, Hauser, & Quinn, 2013).
- Outbreeding depression by the mingling of previously allopatric lineages which can result in harmful hybridizations with detrimental effects on offspring fitness and particularly an ability to spawn in natural conditions, mainly through the loss of adaptive capacity to local conditions (Allendorf, Hohenlohe, & Luikart, 2010; McClelland & Naish, 2007; Tymchuk, Biagi, Withler, & Devlin, 2006).

Inbreeding depression and outbreeding depression are widely accepted as explanations for the reduction of fitness in introduced fish, but their relative importance and contribution to the dynamics of the invasion process are not clearly understood (Blanchet, 2012; Roman & Darling, 2007; Salmenkova, 2008). By far, the risk of inbreeding depression has received most research attention (Edmands, 2007). However, successfully established populations of rainbow trout in the southern hemisphere (e.g. New Zealand: Scott, Hewitson, & Fraser, 1978; Argentina: Riva Rossi, Lessa, & Pascual, 2004) and in some European locations (Italy, Lemme Creek in the River Orba: Candiotto et al., 2011; Slovenia, Idrijca stream in River Soca: Vincenzi et al., 2010) originated from small founding populations and persist to date, despite their probably reduced genetic diversity. The established rainbow trout population of the Vlisidia stream (in the present study) also originated from a single introduction event and has persisted with no further stocking. On such evidence it is reasonable to speculate that reduced genetic variability caused by founder effects and low introduction effort, and the resulting inbreeding depression, is not the reason of most establishment failures of rainbow trout in Europe (see Valiente, Juanes, Nuñez, & Garcia-Vazquez, 2007 for a further discussion on this topic). It is therefore tempting to suggest that outbreeding depression is a possible cause of the poor establishment success of rainbow trout in Europe. Outbreeding depression also has the capacity to explain the decline of established populations in several European countries, which occurred because of (rather than despite of) increasing propagule pressure. This speculation leads to the hypothesis that rainbow trout stocking may impede, rather than facilitate establishment, and fits in with the findings of Miller, Close, and Kapuscinski, (2004), who showed that the viability of naturalized rainbow trout populations in streams in Minnesota can be compromised by continued stocking of hatchery propagated fish from unrelated sources. We conclude that genetic factors affecting the reproductive process, possibly through a combination of outbreeding depression resulting from the admixture of unrelated intraspecific lineages and maladaptive behaviour resulting from domestication selection acting in captivity, remain probable causes of poor establishment in the Greek populations of rainbow trout.

4.3 | Conservation implications

Rainbow trout stocking in Greece is often undocumented and, more crucially, occurs without any scientific supervision or any justification that stocking is needed to enhance salmonid populations for particular targets. Increased stocking of rainbow trout may have adverse impacts through agonistic behaviour on native salmonids owing to predation, competition for space and food, and (rarely) by redd superimposition (Scott & Irvine, 2000; Seiler & Keeley, 2009; Van Zwol, Neff, & Wilson, 2012). These impacts could be severe at a local scale such as in certain enclosed aquatic habitat types (e.g. cold-water springs) which may be inhabited by locally endemic aquatic species. Based on the current knowledge gained by this study, however, the potential for widespread establishment or future spread of rainbow trout in Greece seems to be highly unlikely. Even changing conditions, such as climate change impacts, should affect all cold-water salmonid species negatively (Papadaki et al., 2016). Although some aquacultural strains or populations of rainbow trout could survive in slightly warmer conditions than those described for the *S. trutta* complex, there is no evidence that rainbow trout would benefit over native trout by climate-change warming in Greece.

Similarly, Greek native salmonids are often translocated and stocked in areas outside their historical native range, in order to increase recreational fishery potential. We assert that the impact of native salmonid translocations on genetic diversity may create irreversible deleterious impacts on native trout because of the likelihood of introgressive hybridization between populations or closely related *Salmo* species (Berrebi, Jesenšek, & Crivelli, 2017; Jug, Berrebi, & Snoj, 2005). Evidence for this hybridization among translocated trout species and native forms has already been documented in Greece (Apostolidis, Madeira, Hansen, & Machordom, 2008) and it has been seen in many other Mediterranean catchments (Vincenzi et al., 2010). The widespread threat of this kind of indiscriminate stocking leads to intraspecific and intrageneric negative impacts on native *Salmo* species has also been widely voiced (Buoro, Olden, & Cucherousset, 2016) but not widely referred to as a conservation problem in Greece. Thus, conservation efforts in Greek trout streams should concentrate on controlling translocations of native or related 'brown trout' clones and monitoring stocking practices and outbreaks of disease from fish farms.

This study has provided evidence that the establishment of rainbow trout is geographically limited in Greek streams and rivers mainly due to spawning failure in the wild, possibly attributed to genetic factors, which is also supported from observational evidence in other European countries. Rainbow trout stands out as an example where the risk assessment tools may promote an artificially increased risk status as they cannot appreciate the idiosyncrasies of the problem (i.e. genetic issues and limitations of establishment). Hence, rainbow trout should not at present be considered as a primary conservation threat in Greece, while emphasizing that stocking actions must be properly managed. The perceived problem with rainbow trout as an invasive species may actually mask other serious conservation issues that plague cold-water lotic habitats – a prominent one being other fish-farming pressures and hatchery-based stocking translocations on native trout streams. It is widely acknowledged that the management rationale and implications of stocking activities have not received the attention they require (Cowx, 1999), and in the case of Greece this issue may produce multiple adverse effects on trout streams.

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