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RESEARCH ARTICLE

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Exotic species, rather than low flow, negatively affect native fish in the Oglio River, Northern Italy

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Abstract

Rivers worldwide are impacted by human activities such as habitat degradation, habitat fragmentation, waterway flow regulation, and introduction of exotic species, which are responsible for the reduction or the disappearance of native species in many parts of the world. The Oglio River, a tributary of the Po River in Northern Italy, is a good example of a river with a long history of human alteration and where exotic invasions are present. We used data on water parameters and fish communities along the watercourse to investigate whether low flow conditions, degraded water quality, abundant exotic species, and the presence of migration barriers could be a disadvantage for native species. We used ordination methods (redundancy analysis), variance partitioning analysis, and the threshold indicator taxa analysis to explore changes in community composition and ecofunctional traits along an altitude gradient. We found that exotic species affected native ones more than water quality and hydromorphological parameters. Native species were most abundant in the upper reach of the Oglio River, despite low flow and shallow depth. Moreover, rheophilic and clear water native fish decreased rapidly in the lower reach of the river, where exotic species increased. This distribution could be explained by the presence of barriers in the middle reach, which block exotic species migrating upstream from the highly invaded Po River, and by a lower suitability of the upper reach for some exotic species. Our results provide a general description of the fish fauna of a strongly regulated river and can contribute to develop more effective fish and water management practices.

KEYWORDS

dam, discharge, habitat fragmentation, hydromorphological alterations, non-native species, water abstraction

1 | INTRODUCTION

Rivers are some of the most human-altered ecosystems worldwide (Dudgeon et al., 2006). Anthropogenic pressures such as impoundment (Haas, Blum, & Heins, 2010), habitat degradation (Meador, Brown, & Short, 2003), longitudinal interruptions and lateral connectivity, riverbed, and flow modifications (Bunn & Arthington, 2002; Nilsson, Reidy, Dynesius, & Revenga, 2005), and exotic species introduction (Ribeiro & Leunda, 2012) are common in all medium and large rivers worldwide (Tharme, 2003; Tockner, Stanford, Tockner, & Stanford, 2002). Although there is evidence that exploitation of rivers increased exponentially in the 20th century (Rosenberg, McCully, & Pringle, 2000), human impact on river ecosystems is an age-old phenomenon in some regions. Large lowland rivers in Europe were influenced by landscape changes in their catchment area because the Stone Age and main alterations on flow regime began already in the Middle Ages (Müller, 1995).

European rivers thus offer good examples of habitats impacted by hydrological and morphological stressors, which, together with exotic species invasions, are the major drivers of native fish loss in this region (Corbacho & Sánchez, 2001; Crivelli, 1995; Hermoso, Clavero, Blanco-Garrido, & Prenda, 2011; Maceda-veiga, Mac, & De Sostoa, 2017).

Despite the undeniable importance and necessity of maintaining a flow suitable for aquatic life (i.e., "minimum flow"; Bunn & Arthington, 2002), humans abstract water for agriculture and power production causing severe disturbance to biotic communities (Gehrke, Gilligan, & Barwick, 2002; Nilsson et al., 2005; Poff & Zimmerman, 2009). However, a unique definition, terminology, or parametrization of minimum flow is still lacking (Tharme, 2003). This is due to the high variability of riverine ecosystems worldwide, the differences in estimation methods, and the fact that minimum flow values could vary for different target species (Murchie et al., 2008).

Traditional studies attempting to investigate minimum flow on target populations included instream habitat models, used to estimate the impact of flow changes (King, Brown, & Sabet, 2003; Lamouroux, Doutriaux, Terrier, & Zylberblat, 1999), or before–after studies on the effects of flow restoration (Lamouroux et al., 2006; Schmutz et al., 2016). Unfortunately, the response of biotic communities to variations in flow resulted largely unpredictable or not assessable, leading to contrasting results (Dudgeon et al., 2006; Poff & Zimmerman, 2009). Furthermore, even if some evidence that flow regulation might favour exotic fish species exists (Bunn & Arthington, 2002), studies on minimum flow that distinguish between native and exotic communities are generally lacking (with few exceptions, see e.g. Marks, Haden, O'Neill, & Pace, 2010, Caiola, Ibáñez, Verdú, & Munné, 2014).

In this study, we used the Oglio River to analyse the interplay between the fish community and environmental factors, such as flow. The Oglio River is a strongly regulated river, which can be representative of medium-sized European rivers with a long history of anthropic modification, where the discussion on minimum flow is currently still ongoing. The water quality (Bartoli et al., 2012; Soana, Racchetti, Laini, Bartoli, & Viaroli, 2011), macroinvertebrate, and plant communities (Bolpagni & Piotti, 2015; Guareschi et al., 2014) of the Oglio River are well known, but no studies have been carried out on the fish fauna and its relations with environmental descriptors, so far. The aim of this study was to investigate how flow conditions, water quality, and the presence of dams affect the balance between native and exotic fish species. We hypothesized that low flow conditions would be detrimental to the native fish community. We also hypothesized that degraded water quality and abundant exotic species would also be, to a lesser extent, disadvantageous for native species. Finally, we hypothesized that migration barriers could disrupt the longitudinal connectivity, further negatively impacting native fishes. We used threshold gradient analysis, ordination methods, variance partitioning, and nonparametric correlations to test which of these factors could play a central role in affecting the native fish community status, among multiple disturbances. Using these results, we also considered whether minimum flow regulations could be effective towards native fish conservation in the currently altered river conditions.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out on the Oglio River, a watercourse of 156 km originating from the subalpine Iseo Lake (185 m a.s.l.) and flowing into the Po River (16 m.a.s.l.), with a watershed total surface of 3,800 km^2 in the Lombardy Region, Northern Italy. The Mella, Strone, and Chiese Rivers are the three major tributaries of the Oglio River, with an extended drainage network dispersed in the agricultural lands. Agricultural lands cover the 58% Oglio River watershed, with intensive maize cultivation and livestock farming practices. Urbanized lands covered around the 12% of the watershed area. The Po River basin is characterized by a Mediterranean continental climate, an annual average precipitation of 1,036 mm, a mean temperature of ~12°C, a variable flow regime, and seasonal drought periods (Montanari, 2012; Turco, Vezzoli, Da Ronco, & Mercogliano, 2013). The Po River is also known as a hot spot of exotic species invasion (Lanzoni, Milardi, Aschonitis, Fano, & Castaldelli, 2018; Milardi, Aschonitis, et al., 2018), and the Po River tributaries, such as the Oglio River, could be good models to study the interactions between exotic and native fish species in the framework of a long-term history of hydraulic interventions.

In the second half of the 19th century, water abstraction was aimed at two primary uses: agriculture and hydropower production. In the 20th century, other uses have gained importance, namely, the distribution of drinking water and the discharge of polluted water from sewage treatment plants and from different industrial activities. Presently, the Oglio River can be divided into three distinct sections based on patterns of abiotic features (river flow and depth) and water abstractions. In the upper reach, from the Iseo Lake to 25 km downstream, there are six hydropower plants and the largest water abstraction for agriculture. The middle reach, between 25 and 60 km, is characterized by low flow and low depth. The lower reach, from 60 km to the confluence with the Po River, is characterized by the constant increase of flow due to the contribution of the primary tributaries (the Strone River, the Chiese River, and the Mella River) and of the aquifer, seeping directly into the river.

Two main longitudinal connectivity interruptions are also present on the middle and lower reaches of the river, around 70 and 110 km downstream of the Iseo Lake, near the towns of Pontevico and Isola Dovarese, respectively (Figure 1).

2.2 | Surveys and data collection

Water quality and fish data were taken from 44 sampling stations in the Oglio River course. Sampling was conducted during the warm season (from April to September) of the period 2009–2010 as a part of the project "Evaluation of the minimum vital flow of the Oglio River (2009–2015)" supported by the Oglio River Water Authority (in Italian, *Consorzio dell'Oglio, Regione Lombardia*).

Fish sampling was performed by electrofishing along both shorelines of each sampling station, for a variable length according to river width (five times the maximum width of the river at that location, to ensure that all relevant macrohabitats were sampled). Sampling was

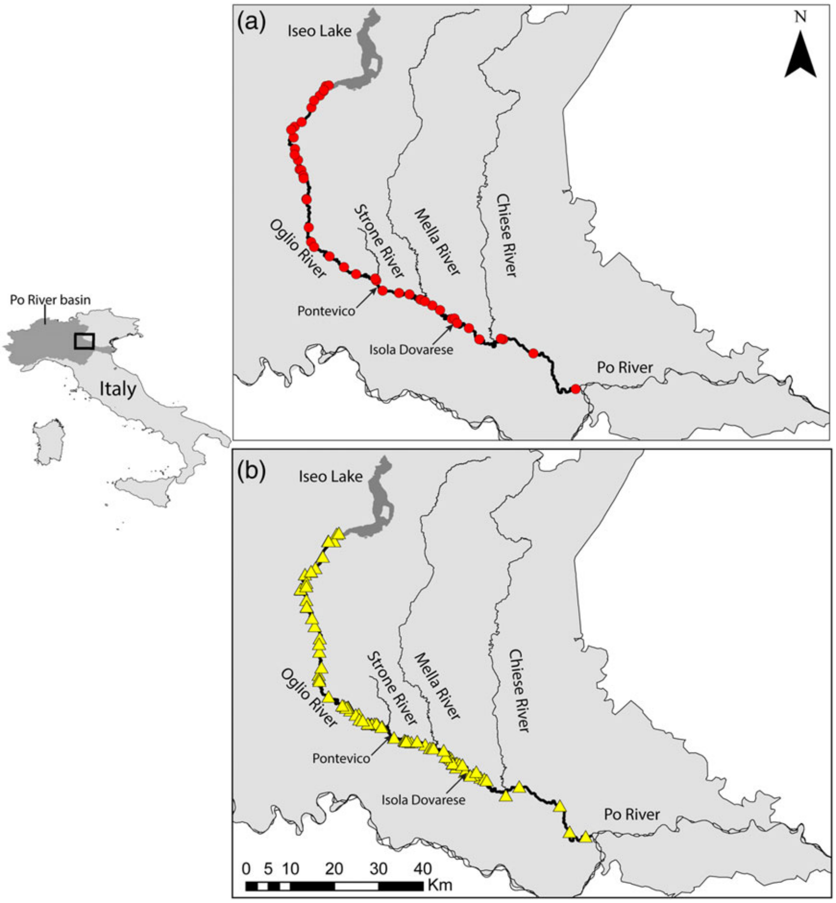

FIGURE 1 Map of Italy and the Po River basin (in darker grey, on the left) and of the study area (right panels) with locations of the fish and abiotic parameters sampling sites (red dots, a) and water abstraction sites (yellow triangles, b) [Colour figure can be viewed at wileyonlinelibrary.com]

conducted by wading, where depth was less than 1 m, and from a boat in deeper waters, keeping operators and gear constant. Captured fish species were classified according to Kottelat and Freyhof (2007), taking into account recent taxonomic determinations and common names listed in FishBase (http://www.fishbase.org; see Table 1). Fish data were expressed as CPUEs (unit of sampled mass [kg] per unit of sampled water surface [ha]).

A total of eight water quality parameters were measured at each sampling site. Water temperature and saturation of oxygen (%) were measured in situ using a handheld sonde (Yellow Spring Instruments Inc.). The ammonia (NH_4^+) and nitrate (NO_3^-) nitrogen, BOD_5 at 20°C, total phosphorus, chlorophyll *a*, and total suspended solids (TSS) were measured in the laboratory according to American Public Health Association (2005) standards. Shading, mean depth of the river, water velocity, and flow were also recorded for each sampling site (see Table 2). Water velocity and flow were also measured daily by the Oglio River Water Authority; for this study, we considered only values corresponding to our sampling dates. Water abstraction data (mean water abstraction for derivations and power plants) was provided by the Oglio River Water Authority.

2.3 | Fish ecofunctional traits

To investigate ecological changes in community composition along altitude and distance from Iseo Lake gradients, we took into account the ecofunctional traits of fish species. The habitat ecological function was chosen due to its power to inform on habitat choice; within this ecological function, there are two broad guilds based on current speed and water transparency preference. The first one identified the flow preference of species: rheophilic species that prefer fast flowing water, limnophilic species that prefer slow or no current, and eurytopic species that no have flow preference. The second guild identified water preference: species preferring clear water, species preferring turbid water, and species with a broad range of conditions (Table 1). Every species was assigned to a single category within each of the two ecofunctional guilds: ecological functions, guilds, and traits of each species follow the work of Milardi and Castaldelli (2018).

2.4 | Statistical analysis

To assess the relationship between different variables and fish species, the data were used to form four groups of variables: native fish species (Native species), exotic fish species (Exotic species), morphological descriptors (Morpho), and water quality parameters (WQ; Tables 1 and 2). Fish CPUE were log transformed, whereas abiotic parameters were log and arcsin transformed (see Table 2). The data transformation was made in order to reduce normality departures for achieving simpler and more linear responses and for reducing the influence of descriptors' extreme values and the influence of highly variable abundances of fish species as suggested by Lepš and Šmilauer (2003) and Baker and King (2010).

Detrended correspondence analysis was initially performed in order to select the most appropriate response model, between linear or unimodal, for gradient analysis (Lepš & Šmilauer, 2003). Taking into

TABLE 1 Fish species sampled in the 44 sampling sites of the Oglio River

Family	Species	Common name	S[a]	NP[b]	Mean (g ha^{-1})[c]	Abbrev	Flow preference guild	Water clarity preference guild
Anguillidae	*Anguilla* (Linnaeus, 1758)	European eel	N	19	2025.08	Aang	R	W
Cyprinidae	*Leucos aula* (Bonaparte, 1841)	Italian red-eye roach	N	32	410.87	Laul	L	W
	Squalius squalus (Bonaparte, 1837)	Cavedano chub	N	44	10487.13	Ssqu	E	W
	Telestes muticellus (Bonaparte, 1837)	Italian riffle dace	N	27	1167.36	Tmut	E	W
	Phoxinus phoxinus (Linnaeus, 1758)	Eurasian minnow	N	15	119.17	Ppho	E	C
	Tinca tinca (Linnaeus, 1758)	Tench	N	15	1371.16	Ttin	L	C
	Scardinius hesperidicus Bonaparte, 1845	Italian Rudd	N	33	1078.64	Shes	E	W
	Alburnus arborella (Bonaparte, 1841)	Italian bleak	N	42	385.73	Aaal	E	W
	Chondrostoma soetta Bonaparte, 1840	Italian nase	N	11	13.22	Csoe	L	C
	Protochondrostoma genei (Bonaparte, 1839)	South European Nase	N	11	75.53	Pgen	R	C
	Gobio benacensis (Pollini, 1816)	Italian gudgeon	N	19	20.25	Gben	R	C
	Barbus plebejus Bonaparte, 1839	Italian barbel	N	41	7270.77	Bple	R	C
	Carassius spp.	Goldfish/Crucian carp	E	25	1903.69	Ccar	E	T
	Cyprinus carpio Linnaeus, 1758	Common carp	E	22	20836.67	Ccarp	E	T
	Abramis brama (Linnaeus, 1758)	Common bream	E	6	754.92	Abra	E	T
	Blicca bjoerkna (Linnaeus, 1758)	White bream	E	1	42.95	Bbjo[d]	E	T
	Rutilus rutilus Linnaeus, 1758	Roach	E	5	35.37	Rrut	E	W
	Rutilus pigus (Lacépède, 1803)	Pigo	N	3	249.80	Rpig	E	W
	Rhodeus sericeus (Pallas, 1776)	Bitterling	E	31	143.13	Rser	L	W
	Pseudorasbora parva (Temminck and Schlegel, 1846)	Stone moroko	E	23	28.27	Ppar	E	W
	Leuciscus aspius (Linnaeus, 1758)	Asp	E	7	469.08	Lasp	R	T
Cobitidae	*Misgurnus anguillicaudatus* (Cantor, 1846)	Pond loach	E	6	11.33	Mang	R	W
	Cobitis bilineata Canestrini, 1856	Italian spined loach	N	17	29.95	Cbi	R	C
Siluridae	*Silurus glanis* Linnaeus, 1758	Wels catfish	E	32	23399.16	Sgla	E	T
Ictaluridae	*Ameiurus melas* (Rafinesque, 1820)	Black bullhead	E	1	10.98	Amel[d]	L	T
Esocidae	*Esox cisalpinus* (Bianco & Delmastro, 2011)	Southern pike	N	10	1370.47	Ecis	L	C
Poeciliidae	*Gambusia holbrooki* Girard, 1859	Eastern mosquitofish	E	2	0.40	Ghol[d]	E	T
Cottidae	*Cottus gobio* Linnaeus, 1758	Bullhead	N	1	2.60	Cgob[d]	R	C
Centrarchidae	*Micropterus salmoides* (Lacépède, 1803)	Largemouth black bass	E	4	23.98	Msal	L	C
	Lepomis gibbosus (Linnaeus, 1758)	Pumpkinseed	E	12	110.98	Lgib	L	C
Percidae	*Perca fluviatilis* Linnaeus, 1758	European perch	N	21	532.19	Pflu	E	C
	Sander lucioperca (Linnaeus, 1758)	Zander or Pike-perch	E	6	514.58	Sluc	L	T
Mugilidae	*Mugil cephalus* Linnaeus, 1758	Flathead grey mullet	N	5	456.49	Mcep	E	W
Gobiidae	*Padogobius bonelli* (Bonaparte, 1846)	Padanian goby	N	39	134.00	Pbon	R	C

Note. Abbrev: fish name abbreviation. Flow preference guild: rheophilic species (R), limnophilic species (L), and eurytopic species (E). Water clarity preference guild: clear water species (C), turbid water species (T), and species in wide range of water clarity conditions (W).

[a]S: status where N is for native and E is for exotic species.

[b]NP: number of sampling sites where the species is present.

[c]Mean (g ha^{-1}): Mean CPUE of each species collected in 44 sampling sites.

[d]Rare species occurring in less than three sampling sites was removed.

account the results of detrended correspondence analysis, the linear gradient method (redundancy analysis [RDA]) was ultimately selected (Lepš & Šmilauer, 2003). Full and partial RDAs were performed using native species as dependent variables and the remaining groups as descriptor variables, similarly as Aschonitis et al. (2016). Species sampled in less than three sites were considered rare and excluded from the RDA (Table 1; Aschonitis et al., 2016); this affected one native species (*Cottus gobio*) and three exotic species (*Blicca bjoerkna*, *Gambusia holbrooki*, and *Ameiurus melas*). Collinear variables, with a variance inflation factor higher than 8 were excluded before the RDA (Zuur, Ieno, & Smith, 2007).

A variance partitioning scheme (Borcard, Legendre, & Drapeau, 1992) was applied for each group of variables on the basis of the overall variance explained by the partial RDAs. This procedure allowed the distinction between unique effects (i.e., the variance explained by a single group of variables), joint effects (i.e., the variance jointly explained by variables of two or three groups), and unexplained variance. Variance partitioning was also run with all variables to identify the marginal effects (λ-1) and the conditional effects (λ-A) of each descriptor variable.

To investigate the changes in the fish community along the river and to assess possible correlations between water abstractions, flow, depth, TSS, and fish assemblages, a Spearman rank correlation was performed using untransformed data, except for fish assemblages. For this step, fish assemblages were expressed as the ratio between the total native CPUE and the total exotic CPUE, both log transformed, for each sampling site (Nat/Exo).

The threshold indicator taxa analysis (TITAN; Baker & King, 2010) was used to investigate changes in the fish community composition in terms of ecofunctional guilds, along the correlated gradients of altitude and distance from the Iseo Lake. This analysis identifies at which point of the environmental gradients the decline/increase in CPUEs of

TABLE 2 Average and range of abiotic parameters in the 44 sampling sites

Parameter	Abbrev.	Unit	Transformation	Minimum	Maximum	Average	*SD*	Group[a]
Longitude	Long	Dec. degrees	log(x + 1)	9.84	10.65	10.06	0.22	-
Latitude	Lat	Dec. degrees	log(x + 1)	45.04	45.66	45.36	0.18	-
Altitude	Alt	m a.s.l.	log(x + 1)	17	183	80	54.59	-
Shading	Shading	%	$arcsen(x/100)^{0.5}$	0.00	45.00	12.50	13.32	Morpho
Depth	Depth	m	log(x + 1)	0.40	2.90	0.61	1.46	Morpho
Water velocity	WaterV	$m\ s^{-1}$	log(x + 1)	0.11	1.16	0.40	0.22	-
Flow	Flow	$m^3\ s^{-1}$	log(x + 1)	4.54	65.80	28.23	17.55	Morpho
Ammonia nitrogen	N_NH4	$N\ mg\ l^{-1}$	log(x + 1)	0.02	0.15	0.06	0.03	WQ
Nitrate nitrogen	N_NO3	$N\ mg\ l^{-1}$	log(x + 1)	0.17	7.72	4.07	2.65	WQ
BOD_5	BOD5	$O_2\ mg\ l^{-1}$	log(x + 1)	0.40	4.45	1.84	1.00	WQ
Total phosphorus	TP	$P\ mg\ l^{-1}$	log(x + 1)	15.50	222.50	55.91	43.58	-
Chlorophyll *a*	Chla	$\mu g\ l^{-1}$	log(x + 1)	0.50	33.25	3.46	4.76	WQ
Total suspended solids	TSS	$mg\ l^{-1}$	log(x + 1)	0.80	103.35	11.93	16.40	WQ
Saturation of oxygen	O%	%	log(x + 1)	88.50	114.00	101.52	6.79	WQ
Water temperature	WT	°C	log(x + 1)	20.2	25.8	23.0	1.3	-

Note. TSS: total suspended solids; RDA: redundancy analysis.

[a]Variable coded "-" not used for RDA due to collinearity (variance inflation factor > 8).

fish belonging to each guild was most prominent. TITAN was performed with 500 replicates for the bootstrap resampling on "TITAN2" R package (Matthew, Baker, & King, 2015).

3 | RESULTS

The Oglio River fish fauna consisted of 34 species, 19 native, and 15 exotic, belonging to 12 families. The *Cyprinidae* was the most represented family, accounting for almost 60% of the total number of species (Table 1).

Among native species, the most abundant was *Squalius squalus* (mean density: 10487.13 g ha^{-1}), which was also the only ubiquitous species. The least represented native species sampled was *Cottus gobio*, present only in one site and with a low density (2.60 g ha^{-1}). Among exotic species, *Cyprinus carpio* and *Silurus glanis* had the highest average densities (20836.67 and 23399.16 g ha^{-1}, respectively). The least represented were *A. melas*, *G. holbrooki*, and *B. bjoerkna*, sampled in only few sites.

Among abiotic parameters, temperature showed relatively constant values over the sampling period with a mean of 23.0 ± 1.3°C (Table 2). Along the river, hypoxic conditions were never found and the oxygen values ranged from 88.50% to 114.00%. Both chlorophyll *a* and TSS were generally low, with mean values of 3.46 μg l^{-1} and 11.93 mg l^{-1}, respectively. The most downstream sampling site, however, had the highest values (33.25 μg l^{-1} of chlorophyll *a* and 103.35 mg l^{-1} of TSS). Ammonia, BOD_5, and total phosphorus showed a large variability that reflected the heterogeneity of the sampling sites and the diverse contributions of the tributaries. Nitrates ranged from 0.17 to 7.72 mg l^{-1}. The percentage of shading due to riparian vegetation was generally low, with a mean value of less than 13% and a maximum of 45% (recorded only in two sampling stations).

Mean river depth showed a high variability in the first 30 km (0.40–2.90 m; Figure 2a). Further downstream depth and flow increased until the Isola Dovarese dam, after which flow increased and depth decreased, due to a substantial widening of the river bed in the last stretch before the confluence with the Po River. TSS were low in the first 50 km and increased progressively downstream until the confluence with the Po River (Figure 2b).

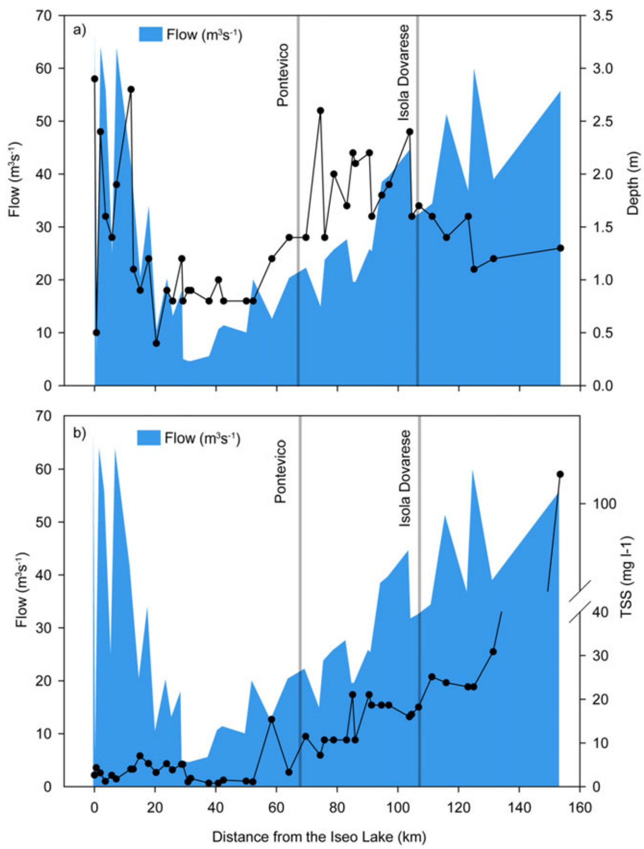

FIGURE 2 (a) Depth and (b) total suspended solids along the Oglio River watercourse. The most important longitudinal connectivity interruptions are indicated with vertical grey lines [Colour figure can be viewed at wileyonlinelibrary.com]

3.1 | Weights of native species descriptors in RDA

Longitude, latitude, altitude, distance from the Iseo Lake, water velocity, total phosphorus, water temperature, *Pseudorasbora parva*, and *Abramis brama* were all excluded from the RDA due to their high collinearity (variance inflation factor > 8).

The proportion of native species variance explained by exotic species group was higher (16.60%) than the variances explained by morphological (5.70%) and water quality (12.90%) groups (Figure 3a,b). The partial joint effects were 10.50%, 26.20%, and 27.90% for morphological, water quality, and exotic species groups, respectively (Figure 3a). Overall, the total joint effect was 28.70% (Figure 3b). Among abiotic parameters, the marginal (λ-1) and conditional (λ-A) effects of each covariate (Figure 3c) showed a high contribution of TSS, nitrogen nitrates, flow, and depth in affecting the native fish community. Among exotic species, the most important were *Lepomis gibbosus*, *Leuciscus aspius*, *C. carpio*, and *S. glanis*.

The direction and magnitude of the descriptors effects on the native fish community is shown in Figure 4. High TSS negatively affected native species, such as *S. squalus* and *Protochondrostoma genei*, but showed a positive effect on exotic species such as *L. aspius* and *C. carpio* and the native *Mugil cephalus*. High values of flow and depth were positively related to *S. glanis*; conversely, many native species were negatively affected by these factors. Among native species, only *M. cephalus* showed a positive relationship with the exotics *L. aspius*, *C. carpio*, and *S. glanis* (Figure 4).

3.2 | Relationship between river conditions and fish species

Flow, depth, and TSS were positively correlated among each other but negatively correlated with the ratio between native and exotic species (Table 3). Water abstraction was not correlated with any of the other parameters. Water flow ranged from 4.54 to 65.8 $m^3 s^{-1}$, with a mean of 28.23 $m^3 s^{-1}$. The highest flow was measured in the upper reach, 20 km from the Iseo Lake (Figure 5a,b).

Native species were most abundant in the middle reach of the river, from 30 to 50 km downstream of the Iseo Lake (Figure 5a). In this reach, the mean native species CPUE was 58.96 kg ha^{-1}, with a maximum of 174.69 kg ha^{-1} and a minimum of 5.59 kg ha^{-1}. Contrarily, exotic species had the lowest CPUEs (mean of 2.85 kg ha^{-1}). Exotic CPUEs increased in the lower reach of the river, especially downstream of the Isola Dovarese dam up to the confluence with the Po River, where the fish community was composed by almost entirely by exotic species (Figure 5a,b). A corresponding change in the fish community ecofunctional composition was evident 60 to 80 km downstream of the Iseo Lake, at an altitude of 45–40 m a.s.l., corresponding with the location of the Pontevico dam (Figures 5 and 6). Upper- and middle-reach communities of the Oglio River were generally dominated by rheophilic and clear water species, whereas lower-reach communities were dominated by turbid water species. Species adapted to a wide range of flow and water clarity conditions were distributed rather evenly across the river course, whereas limnophilic species did not have a distribution predictable according to the gradients analysed (Figure 6).

4 | DISCUSSION

Contrarily to our initial hypothesis, in the Oglio River, low flow conditions did not seem to be detrimental to the native fish community. Conversely, according to our initial hypothesis, degraded water quality and the abundance of exotic species had a clear negative effect on native fish, with a greater influence than flow conditions. Migration

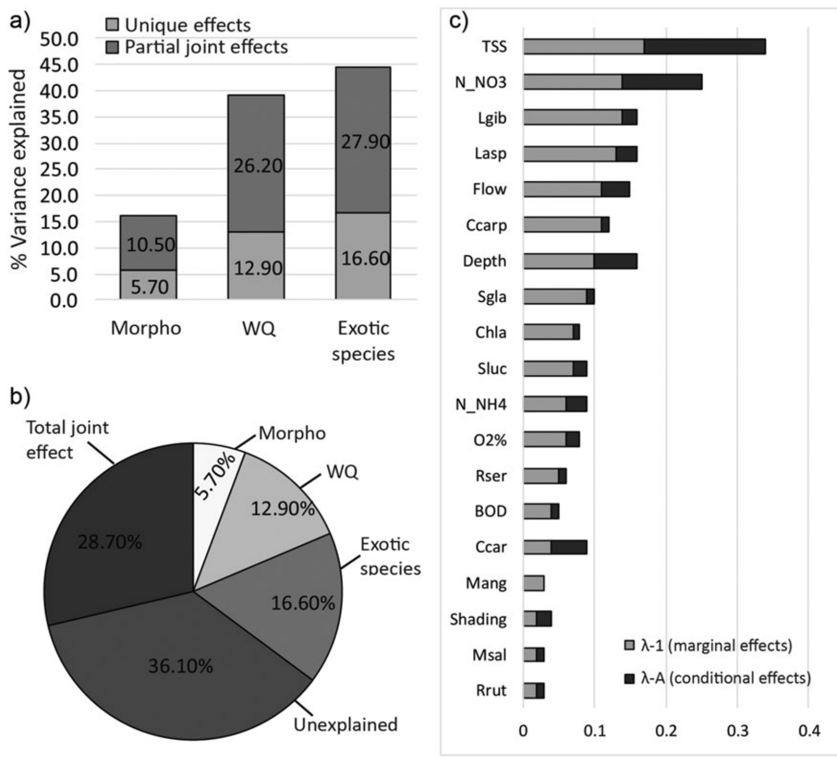

FIGURE 3 Unique and partial joint effects for each one of the three groups of variables (a), unique and total joint effects (b), marginal λ-1 and conditional λ-A effects of each parameter affecting native species from the full redundancy analysis (c)

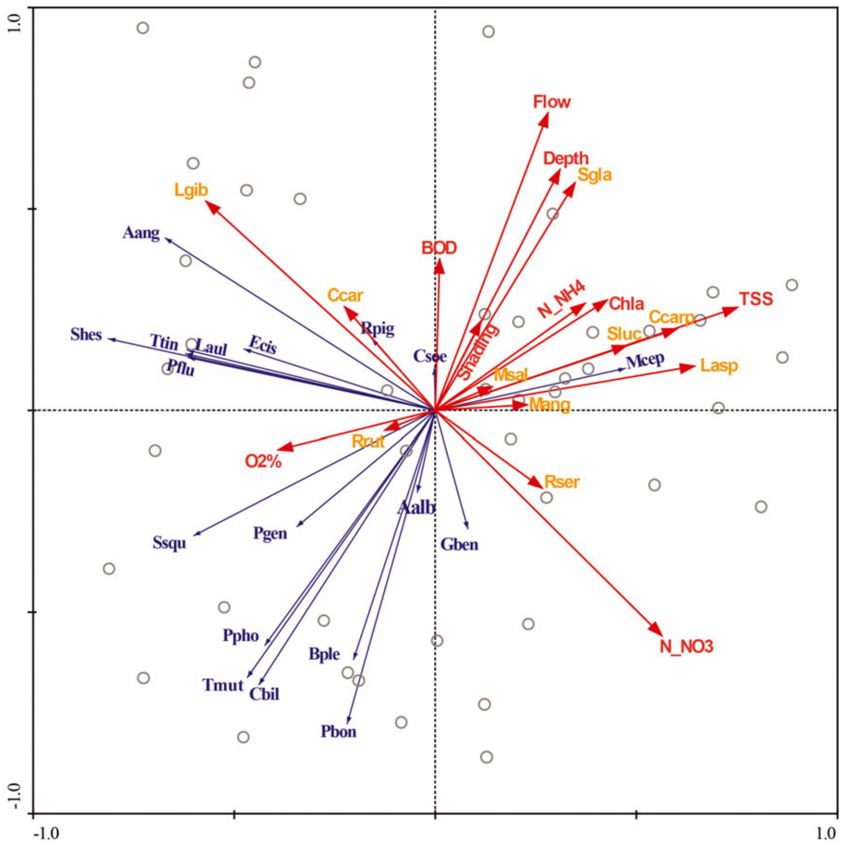

FIGURE 4 Triplot of redundancy analysis of native species as dependent variables (blue arrows) and morphological and water quality descriptors (red label) and exotic species (orange label) as descriptor variables (red arrows) in the 44 sampling sites (grey circles). Abbreviations are given in Tables 1 and 2 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Spearman rank correlations for abstraction, flow, depth, and TSS and the ratio between native and exotic species

	Nat/Exo	Abstraction ($m^3\ s^{-1}$)	Flow ($m^3\ s^{-1}$)	Depth (m)	TSS ($mg\ l^{-1}$)
Nat/Exo	1				
Abstraction ($m^3\ s^{-1}$)	0.2201	1			
Flow ($m^3\ s^{-1}$)	−0.5828**	−0.0237	1		
Depth (m)	−0.5489**	−0.1755	0.6294**	1	
TSS ($mg\ l^{-1}$)	−0.8316**	−0.1212	0.4259*	0.3848*	1

Note. TSS: total suspended solids.

**p < 0.001. *p < 0.05.

barriers limited the upstream migration of exotic species from the highly invaded Po River and thus offered a counterintuitive protection to native fish. Ordination methods showed that the effect of exotic fish species was stronger than all other environmental variables together and that, among abiotic parameters, flow was not the main variable affecting native fish. In light of these results, the concept of minimum flow for the conservation of the native fish community appears to be less than effective, if not even misleading. Minimum flow should therefore reconsidered in a more integrated way, accounting for multiple disturbances affecting the native communities, including hydromorphological disruptions.

Perhaps counterintuitively, flow was not retained by RDA as a strong descriptor of the native community and higher flow values seem to have favoured exotic species over native ones (Figures 4 and 5). An increase in flow does not always result in a positive change for native fish, as the new flow conditions might alter wetted habitats and potentially result in lower habitat suitability for some species (Bradford, Higgins, Korman, & Sneep, 2011). Indeed, our results indicated that native fish were caught more frequently in the upper and middle stretches of the Oglio River, characterized by highest water abstraction and low flow. Large exotic predators such as *S. glanis* were abundant in deep sections with high flow, whereas small native species such as *A. arborella* and *P. bonelli* were more abundant in the middle reach, in shallow sections with low flow. The peculiar hydromorphological conditions of the middle reach, with low flow and low depth, are unsuitable for big predators such as *S. glanis* (which was never caught in this area) and thus effectively provided “refuge areas” for the residual native community. Despite substantial water abstraction, water was never completely absent due to the continuous supply from the aquifer and the numerous tributaries. Furthermore, contrarily to other rivers characterized by higher slopes, the Oglio River was never steep enough to cause the complete absence of water downstream of the abstraction. Further downstream, water from the tributaries and the aquifer progressively increases the flow again until

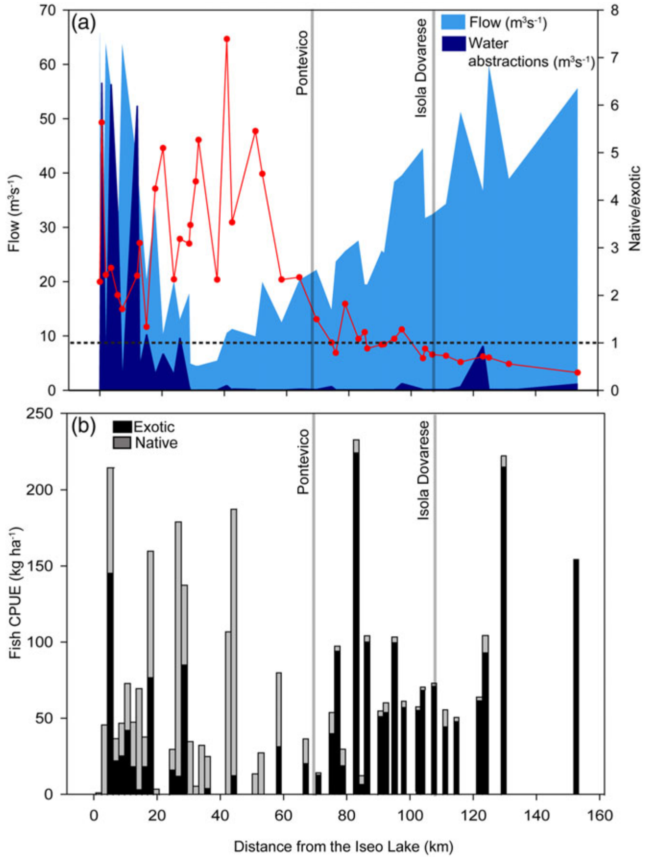

FIGURE 5 Water flow, water abstraction, and the ratio between native and exotic CPUEs; values of the ratio below one (dashed line) indicate the prevalence of exotic fish (a). Sampled fish CPUEs, with a representation of the share of exotics and natives at each sampling sites (b). The most important longitudinal connectivity interruptions are indicated with vertical grey lines [Colour figure can be viewed at wileyonlinelibrary.com]

values prior to abstraction are reached and even surpassed; this is the area where fish communities were mostly composed by rheophilic species. However, this increase in flow did not correspond to an increase in native species abundance but rather to a steep decrease. Although we investigated the relationship between environmental parameters and fish communities through ordination methods, which can only explore the relationships between variables rather than explain them, similar results were reported in field studies that artificially manipulated the flow or the fish community (Arthington, Naiman, McClain, & Nilsson, 2010; Coggins, Yard, & Pine, 2011; Marks et al., 2010). Previous studies have underlined how flow and other environmental parameters could potentially influence the effectiveness of fish sampling (i.e., the catchability of fish) (Gwinn, Beesley, Close, Gawne, & Davies, 2016). However, the information currently available based on other species and other environments (see,e.g., Speas, Walters, Ward, & Rogers, 2004 or Lyon et al., 2014) is insufficient to infer that this could be a relevant issue in our data, and we recommend that future studies investigate this aspect specifically. Although there is mounting evidence that minimum flow restoration could be ineffective on the native community status if water quality improvement and exotic species control are not fully addressed, we advise that future work should further explore the key factors identified in our study to assess their explanatory potential experimentally.

Among exotic species potentially affecting native ones, *L. gibbosus* had the highest conditional and marginal effects and was positively related with the density of *Anguilla anguilla*. This is likely due to the preference of *L. gibbosus* for similar habitat and water quality of the native species, that is, low turbidity, low depth, low flow, and mesotrophic conditions with a higher availability of diversified microhabitats (Top, Tarkan, Vilizzi, & Karakuş, 2016). Conversely, the high ranking of *L. aspius* in the ordination graph is likely driven by its capture in only seven sites of the lower reach, where the native community was not significantly represented and other exotic species were also present. *S. glanis* and *C. carpio*, two species with a high rank in the ordination graph, are known to severely affect the native community. *S. glanis* is a generalist predator and a successful invader thanks to adaptability to a wide range of prey and habitat conditions (Copp et al., 2009). Adverse effects on native fish populations in artificial or highly modified environments have been reported in the literature (Castaldelli et al., 2013), although these do not necessarily extend to all waters (Guillerault et al., 2015). It is widely documented that *C. carpio* can alter habitat conditions, increasing turbidity and reducing aquatic vegetation, and thus indirectly affecting native fish communities (Crivelli, 1995).

Among water quality parameters, TSS and nitrates were the two most important factors negatively affecting native fish distribution. Phytoplankton blooms due to nitrates availability were not at the origin of turbidity, as chlorophyll *a* was not retained in the analysis as a strong descriptor. Most likely, a combined effect of the inorganic

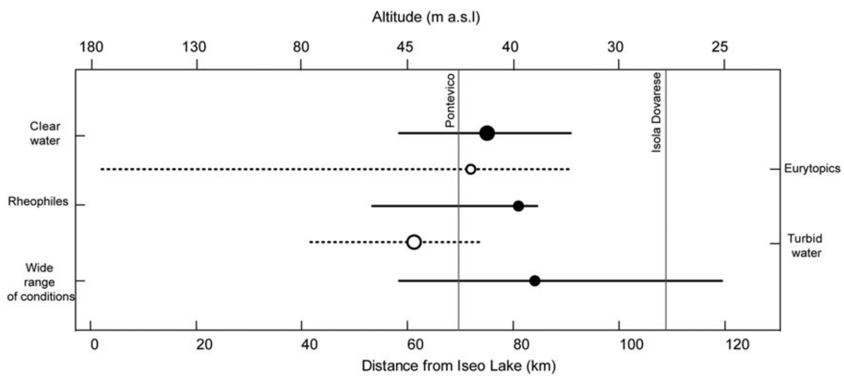

FIGURE 6 Significant thresholds for different ecofunctional guilds related to habitat choice along gradients of altitude and distance from the Iseo Lake (horizontal axes). Lines represent guilds distribution across the gradients, with circles identifying the distribution peak. Solid lines and circles represent guilds that decline along the gradient (grouped on the left), whereas dashed lines and empty circles represent species, which distribution increases along the gradient (grouped on the right). The most important longitudinal connectivity interruptions are indicated with vertical grey lines

fraction of the TSS and phytoplankton blooms is at the root of this effect (Bartoli et al., 2012; Delconte et al., 2014; Soana et al., 2011). Watershed uses, in particular agriculture, are the likely causes of the increase of nitrates and TSS, particularly in the middle reach of the Oglio River. This area was affected by extensive manure spreading and irrigation by submersion, a traditional practice still made possible by high water availability. Through this practice, surface run-off brings inorganic fine materials to the river, which increase TSS (Bartoli et al., 2012). Furthermore, due to the coarse texture and consequent high permeability, water percolates from fields directly to aquifer and then back to the river, transporting a significant nitrates load. This is not uncommon in Mediterranean rivers where TSS and nutrient load typically increase towards the lower areas due to a more intense agricultural land use. The high turbidity could also be partly due to the resuspension of fine sediments operated by *C. carpio* and *Carassius* spp., which dominated the turbid-adapted lower-reach fish communities. Both species are known to thrive in turbid, eutrophic waters and to positively feedback eutrophication by resuspension of sediments of sedimentary phosphates through their feeding (Huser, Bajer, Chizinski, & Sorensen, 2016). In turn, the high turbidity in the lower reach may have further favoured exotic species accustomed to it and disadvantaged native ones, adapted to clearer water conditions and more abundant in the upper and middle reaches.

Ultimately, our results downplay the significance of minimum flow for native fish conservation and highlight the importance of other parameters such as the degree of interruption of longitudinal connectivity and the effects of exotic species. Although longitudinal connectivity is an undeniable necessity for the fish community (Bunn & Arthington, 2002), its interruption can have counterintuitive effects. In the Oglio River, interrupted longitudinal connectivity paradoxically favoured some native species by blocking the invasion of exotics migrating upstream from the highly invaded Po River (Castaldelli et al., 2013). This is most evident in Figure 4, where the exotic community overtakes the native one downstream of the Isola Dovarese dam (the first impassable barrier, the second being a few km upstream, in Pontevico). Our results also suggested that low flow in the Oglio River may have favoured some native species over exotic ones by altering depth, velocity, and sediment features. Consequently, the native community was counterintuitively more nested in the upper and middle reaches of the river, where water abstraction was most intense. In the future, because of climate change, flow in the Po River basin is expected to be further diminished due to a substantial decrease of seasonal precipitation and an accelerated snow melt in spring (Ravazzani, Barbero, Salandin, Senatore, & Mancini, 2014) but net losses and gains of habitats suitable for native species have not yet been modelled. Furthermore, higher temperatures could favour exotic species invasions (Vitousek, D'Antonio, Loope, Rejmánek, & Westbrooks, 1997) even though this might not be a relevant factor in this area (Milardi, Lanzoni, Gavioli, Fano, & Castaldelli, 2018).

5 | CONCLUSIONS

Our study analysed for the first time the interplay between the fish community and environmental factors in the Oglio River. Our results underlined how anthropogenic impacts on river morphology and flow, occurred centuries to decades ago, affected the fish community, favouring some native rheophilic species despite reductions in flow, and blocking the invasion of exotics from invaded downstream areas. Although modified flow regimes in regulated rivers can negatively affect fish communities, there is a wider range of community responses to flow alterations (Murchie et al., 2008). Therefore, we suggest that additional attention should be given to restoring natural hydromorphology when exotic species invasions are ongoing. Management and conservation plans should model the changes in habitat suitability and consider the effect of exotic species before further altering the river hydromorphology.

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