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Introduction of exotic fish species and decline of native species in the lower Po basin, north-eastern Italy

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ABSTRACT

1. Freshwater ecosystems worldwide are experiencing native fish losses with severe threats to the conservation of freshwater biodiversity and ecosystem functioning, and the debate on whether the cause is biotic or abiotic disturbance is still open.

2. Temporal variation in fish assemblages was analysed over an 18 year period in 14 waterways of the lowland backwaters of the Po River in north-eastern Italy, which are important feeding, spawning and nursery sites for native fish.

3. In 1991, 14 native and eight exotic species were collected. In less than 20 years 10 native species underwent local extinction, three of which – *Rutilus pigus*, *Rutilus aula*, and *Chondrostoma soetta* – were endemic to the Padano-Veneto District in northern Italy.

4. Ordination of the data (MDS, CLUSTER, ANOSIM, SIMPER) showed a clear temporal gradient in fish community structure. After the establishment of the exotic predator *Silurus glanis*, some native species significantly declined in abundance and biomass (i.e. *Alburnus arborella* and *Scardinius erythrophthalmus*) or disappeared (i.e. *Rutilus aula* and *Tinca tinca*). Moreover, exotic species *Cyprinus carpio*, *Ameiurus melas*, and *Carassius auratus* from previous introductions, underwent significant changes in their abundance and biomass. No correlation was found between fish community structure and water quality parameters (BIOENV).

5. The success of exotic species, particularly *S. glanis* which thrived in this degraded habitat, seems to have led to the decline of native fish fauna in the canals of the lower portion of the Po River basin. Conservation strategies focusing on the containment of exotic species and habitat restoration are recommended.

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KEY WORDS: endangered species; alien species; fish; biodiversity; water quality; catchment

INTRODUCTION

Over the past century the decline in native freshwater fish assemblages has become a global concern. This declining trend is well documented for Mediterranean ecosystems. Among the most serious causes of fish species disappearance are habitat degradation (Meador *et al*., 2003), waterway flow regulation (Gehrke *et al*., 1995), exotic fish invasions (Strayer, 2010; Trumpickas *et al*., 2011), particularly those finding ideal conditions at lower latitudes (Crivelli, 1995), and the interaction of these causes (Dudgeon *et al*., 2006; Light and Marchetti, 2007).

Habitat degradation, including modifications of flow regimes, urban and agricultural pollution, dam construction, river channelization, and destruction of riverine vegetation, seems to promote

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the success of invasive species (Bunn and Arthington, 2002; Cowx and Collares-Pereira, 2002). However, the complexity of interactions necessitates analysis on an appropriate time scale, as exotic species introductions may have effects that can be detected only if an understanding of long-term quantitative changes in the fish community is acquired (Vander Zanden *et al*., 2003; Mercado-Silva *et al*., 2006; Matsuzaki *et al*., 2011).

Fish are among the most widely introduced aquatic animals worldwide and also some of the most threatened (IUCN, 2008; Gozlan *et al*., 2010). While some argue that exotic species are the primary cause of decline in native fish populations, Gozlan (2008, 2009) maintains that exotic species are simply taking advantage of the biodiversity-loss process that is driven principally by habitat degradation and poor management practices. Invasiveness of exotic species may also depend on local community composition and on habitat status. Watercourses lacking native piscivorous fishes, or being highly altered by humans, appear to be the most vulnerable (Copp *et al*., 2009). A facilitating factor seems to be the presence of biogeographic barriers and/or man-made barriers such as dams, weirs, culverts, hydroelectric and pumping stations, and the human-mediated pathways, largely related to sport fishing, aquaculture, and ornamental uses. Frequently, these factors co-occur in space and time, and the strength of their additive or synergetic interactions complicates an accurate identification of the relative role of individual stressors in biodiversity loss.

Italy has experienced the highest number of unintentional fish introductions in Europe (Bianco, 1998), and the major Italian river, the Po, along with its extensive canal network is severely affected by the spread of exotic species (Castaldelli and Rossi, 2008; Lanzoni *et al*., 2010). In view also of the lack of research dealing with the impact of exotic fishes on local populations in northern Italy, the objectives of this study were (1) to assess the extent of the loss of native species in the lower Po River basin, (2) to evaluate the outcome of interactions between exotic and native species, and (3) to highlight implications for conservation and management. Changes in fish community structure recorded over an 18-year monitoring period were analysed for 14 canals in the Po basin, selected for their similarity, stable conditions, and ecological importance as a nursery area for native species.

METHODS

Study area

This study was conducted on 14 canals of the lower Po River basin, within the Po di Volano sub-basin, in north-east Italy (Figure 1). It is a reclaimed alluvial area characterized by flat topography with altitude ranging from –3 to 5 m a.s.l. The canals studied are within the administrative borders of Ferrara Province (2600 km^2), which includes a canal network of more than 4000 km and a mean canal density of 1.53 km km^{-2}. Agriculture is the most important activity, and human population density is low and concentrated in towns served by sewage treatment plants that discharge wastewater into minor canals of this network. The hydrological structure is the result of long-term reclamation that began with the ancient Etruscans and continued to the 1960s, sparing only a few residual brackish coastal embayments and lagoons along the Adriatic coast (Cazzola, 2010). The capillary network of canals currently serves for

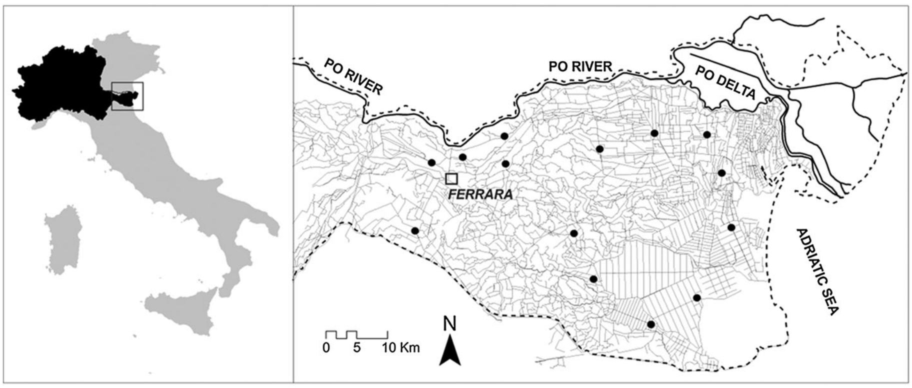

Figure 1. Map of the study area: lower Po River plain (Province of Ferrara, Italy). Black dots represent the location of canal stretches where the fish fauna was assessed.

drainage or irrigation. Irrigation water is derived from the Po River and distributed by one main canal, the Po di Volano, which feeds the entire network, from the major canals to smaller ditches surrounding fields. Therefore, exotic species have colonized the Po di Volano sub-basin through direct dispersal from the Po River, albeit slowed by the presence of water gates, weirs, and pumping stations. Among the species recently arriving, the only intentional introduction is the grass carp *Ctenopharyngodon idella* (Valenciennes, 1844) which was deliberately stocked in some canals of the network in the mid-1980s for weed control (Melotti *et al*., 1989). Heavy management practices, such as mowing banks and aquatic vegetation and the introduction of the grass carp, led to almost complete disappearance of aquatic vegetation before this study (Piccoli and Gerdol, 1983; Ferrari *et al*., 1985). The emergent vegetation that appears in isolated stretches is mainly represented by the reed *Phragmites australis* Cav Trin. and cattail, *Typha latifolia* L., growing primarily in a narrow strip along the banks.

Surveys and data collection

Surveys were conducted as part of a long-term provincial monitoring programme, and took place in 1991, 1996, 2003, and 2009. To investigate the primary drivers of fish community variation, data were studied from 14 canals of comparable morphology and biological features and characterized by the same degree of catchment and land-use intensity, u-shaped simplified morphology, riparian degradation, and flow regulation (Figure 1). All 14 canal stretches are confined between an upstream weir and a downstream pumping station; thus colonization was possible from upstream, but exit was effectively blocked. During the irrigation season, from the beginning of March to the end of September, the mean waterway width was 14.5 ± 4.2 m, the mean maximum depth was 1.75 ± 0.4 m, the mean water velocity was 5 ± 3 cm s^{-1}, and the mean canal surface was 9.8 ± 4.1 ha. The operational period of the gates and pumps did not change over the 18 year period, because the demands for irrigation remained constant, and the discharge of the Po River is much higher than the inflow of all the gates of this canal network (about 1000 m^3 s^{-1} compared with 30 m^3 s^{-1}). Fish were counted from mid-October to November, about 1 month after the cessation of water capture from the Po at the end of the irrigation season, in mid-September. At that time of year, water depth reaches its annual minimum and most of the canal progressively empties, forcing fish to move to an area of suitable depth (0.6–1.3 m) until the subsequent irrigation season (mid-March). From site to site, these canal stretches have variable length, from one to a few kilometres. Under these hydrological conditions it was possible to capture the major portion of the fish community by using a seine net (Backiel and Welcomme, 1980) 2 m in height with a 25 m mouth and a knot-to-knot mesh size of 8 mm. The cod-end was 3 m long and a knot-to-knot mesh size of 4 mm. In each canal, the fish community was surveyed by fixing a blocking net (4 mm knot-to-knot mesh size) spanning the canal width and depth across one end and dragging the seine towards it. Fish were captured in a single pass at each site and extracted from the cod-end using hand-nets (4 mm knot-to-knot mesh size), mechanical cranes, or manually, when the seine mouth was closed. Extraction lasted from 30 to 60 min. A replicated haul, conducted on some occasions to check the recovery efficacy, always recovered less than 5% of species' abundance and biomass of the original survey.

Fish were identified to species, counted, measured (LT to nearest mm), and weighed (to nearest 0.1 g) before being released. Fish were classified according to Berg (1932), Sterba (1962), and Gandolfi *et al*. (1991). Common and scientific names used in this paper are from FishBase (2009).

Hydrochemical data were taken from the Regional Environmental Protection Agency of Emilia Romagna (ARPA) at monitoring locations coinciding with, or representative of, water quality at each fish sampling site. Water quality monitoring has been performed monthly since 1980, which has enabled the regulation of water quality throughout the 18-year study period.

Data analysis

Data were analysed with univariate statistics, carried out using STATISTICA/w 6.0 (StatSoft Inc., 2001) and multivariate statistics, using the PRIMER-6 software package.

Water temperature (°C), specific conductance (μS cm^{-1}), pH, dissolved oxygen (DO, %), BOD_5 (mg L^{-1}), dissolved inorganic nitrogen (DIN = ammonium + nitrate + nitrite, mg L^{-1}), total phosphorus (TP), and total suspended solids (TSS, mg L^{-1}) were analysed using principal component analysis (PCA) and were presented in a principal component bi-plot.

Environmental data were transformed with log $(x+1)$ where necessary (Clarke, 1993), and then normalized. Since some parameters, such as chlorophyll-*a* and heavy metal concentrations, were gathered less often, they were not included in the analysis.

Abundances of fish species (individuals ha^{-1}) were calculated assuming a surface area equal to the size of the canal stretch at mean water level. Biomass of fish species in catch ($g\,ha^{-1}$) was calculated according to the same assumption. Mean fish abundance and biomass in the catch were compared among years using one-way ANOVA. Community parameters were ln-transformed to meet the assumptions of normality and homoscedasticity. Factors detected as significant by ANOVA were further analysed using a Tukey HSD test set at 5% significance level.

Relative fish abundance and biomass data were transformed by 4th-root to reduce the influence of abundant species (Clarke, 1993), and the Bray–Curtis similarity coefficient was calculated to generate similarity matrices. Non-metric multi-dimensional scaling (nMDS) ordinations were used to graphically display groupings (similarities) and distances (dissimilarities) within and between year-groups based on the Bray–Curtis similarity matrices. These ordinations were iterated several times from at least 50 starting values to ensure that a global optimum was achieved (indicated by no decline in the stress value) (Clarke and Warwick, 2001). In conjunction with ordination, clusters were produced in a dendrogram format using a group average hierarchical sorting strategy. The analysis of similarity (ANOSIM) with year as factor, combined with a randomization test for significance (Hope, 1968), was used to test the significance of observed differences between years in fish assemblage structure. Where appropriate, R-statistic values for pair-wise comparisons, provided by ANOSIM, were used. Similarity of percentage analysis (SIMPER) was used to identify those species most responsible for the dissimilarity between year-groups (Clarke, 1993; Clarke and Warwick, 2001).

Environmental parameters for the whole study period were linked to fish assemblages using the BIO-ENV routine. This measures the amount of agreement between the Euclidean distance similarity matrices of water variables and Bray–Curtis similarity matrices of fish abundance and biomass data.

RESULTS

Environmental characterization

Annual mean and range values of physico-chemical parameters are listed in Table 1. Temperature, conductivity and pH showed relatively constant values over the 18-year monitoring period (Table 1). Mean conductivity was relatively high, as expected for lowland reaches, and showed inter-annual variations owing to the rainfall and hydrological regime. Several transient conductivity peaks were measured during dry winter months in two canals located near the sea coast and occasionally exposed to salt water intrusion. In summer months, oxygen over-saturation caused by extreme photosynthetic activity, and depletion caused by intense respiration and night consumption, were registered on some dates in all sites. Nutrients, particularly dissolved inorganic nitrogen (DIN), showed high concentrations, characterizing all sites as eutrophic (Dodds, 2006). Atrazine and heavy metals (e.g. Ni, Pb, and Cd) remained below the detection limits of methods used, or presented low values in all canals, indicating generally low chemical disturbance.

The first axis of the PCA ordination (Figure 2) explained 28% of the total variance and was negatively correlated with the BOD_5 and TP, loading more than $|0.50|$ and $|0.40|$, respectively. The second axis of the PCA explained 22% of the total variance and was positively correlated with DO, and negatively correlated with DIN, loading greater than $|0.50|$ and $|0.35|$, respectively. The PCA ordination plot did not show any clear temporal and spatial trends across environmental gradients.

Trends of fish assemblage composition

In total, 29 333 individuals belonging to 12 families and 30 species of freshwater fish were collected (Table 2). In all survey years, the number of cyprinid species was higher than that of other families, accounting for 50% in 1991, 1997, and 2003 and 59% in 2009 of the total number of species.

In 1991, the fish fauna of the canal network studied consisted of 22 species, 14 native and eight exotic. Native species accounted for 44% of the total number of individuals and for 18% of the total biomass (Table 2).

In 1997, 18 species were found, eight native and 10 exotic. Six native fishes – the endemic Italian

Table 1. Yearly average of the physico-chemical parameters (minimum–maximum values) measured monthly in 1991, 1997, 2003 and 2009, in the 14 canals of the Po di Volano basin where fish fauna was assessed

Variable (unit)	Year 1991		1997		2003		2009	
Temperature (C°)	15.81	(2.1 - 30.4)	16.74	(2.7 - 31)	15.89	(0.5 - 29.8)	16.17	(1.1 - 30)
Specific conductance (μs cm^{-1})	1308.5	(318 - 5015)	1302.34	(266.5 - 5630)	1110.19	(218 - 5990)	1037.19	(322 - 2930)
pH	8.06	(6.95 - 8.91)	7.69	(7 - 8.4)	7.99	(7.43 - 8.93)	7.89	(7.23 - 8.69)
DO (%)	75.5	(23 - 150)	75.5	(23 - 150)	81.12	(26 - 126)	82.26	(22 - 236)
BOD_5 (mg L^{-1})	5.97	(1.5 - 18.25)	4.15	(1.5 - 16)	4.6	(2 - 18)	4.7	(2 - 26)
DIN (mg L^{-1})	3.47	(0.05 - 17.11)	2.79	(0.07 - 16.39)	3.41	(0.25 - 16.15)	3.87	(0.23 - 13.91)
Total phosphorus (mg L^{-1})	0.23	(0.03 - 0.87)	0.17	(0.04 - 0.91)	0.16	(0.04 - 0.59)	0.17	(0.03 - 0.58)
Total suspended solids (mg L^{-1})	32.19	(3 - 131)	37.83	(2.5 - 256)	41.01	(5 - 197)	41.67	(5 - 149)
Atrazine (μg L^{-1})	<0.05	-	<0.05	-	<0.05	-	<0.05	-
Cd (μg L^{-1})	<1.25	-	<1.25	-	<1.25	-	<1.25	-
Cr TOT (μg L^{-1})	<5	-	<5	-	<5	-	<5	-
Hg (μg L^{-1})	<0.5	-	<0.5	-	<0.5	-	<0.5	-
Ni (μg L^{-1})	7.4	(2.5 - 20)	6.1	(2.5 - 23.5)	9.8	(5 - 33)	3.3	(1 - 30)
Pb (μg L^{-1})	3.7	(2.5 - 12)	3.4	(2.5 - 16)	3.1	(5 - 5)	0.9	(1 - 2)
Cu (μg L^{-1})	5.1	(2.5 - 28)	4.9	(2.5 - 23)	5.2	(5 - 72)	2.27	(2.5 - 7)

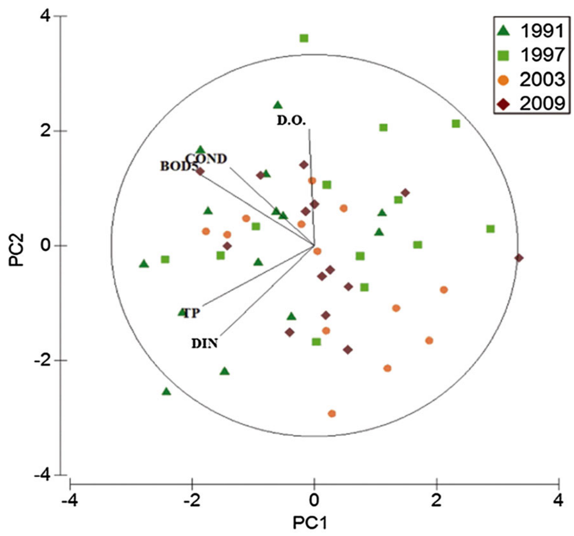

Figure 2. Principal component analysis (PCA) ordination of the principal physico-chemical variables (DO dissolved oxygen %, COND specific conductance μS cm^{-1}, BOD_5 biochemical oxygen demand mg L^{-1}, DIN dissolved inorganic nitrogen mg L^{-1}, TP total phosphorus mg L^{-1}). PC1 accounted for 28% of the variance and PC2 for 22%. Length of the vectors indicates their relative importance in determining station distribution.

roach *Rutilus pigus* Lacépède, 1804, the endemic Italian nase *Chondrostoma soetta* Bonaparte, 1840, Italian barbel *Barbus plebejus* Bonaparte, 1839, Italian golden loach *Sabanejewia larvata* De Filippi, 1859, three-spined stickleback *Gasterosteus aculeatus* L., and European perch *Perca fluviatilis* L., found in 1991 – were not recorded in this and the following surveys. Two exotic species, the stone moroko *Pseudorasbora parva* Temminck and Schlegel, 1846 and pikeperch *Sander lucioperca* L., were recorded for the first time.

In 2003, 16 species were recorded, of which four were native. Local extinction was documented for chub *Squalius cephalus* L., the endemic Italian red-eye roach *Rutilus aula* Bonaparte, 1841, and tench *Tinca tinca* L. Two new exotic cyprinids appeared – the freshwater bream *Abramis brama* L. and bitterling *Rhodeus sericeus* Pallas, 1776.

In 2009, the fish assemblage comprised 17 species, four native and 13 exotic. The exotic species accounted for 92% of the total abundance and five species – wels catfish *S. glanis* (58%), grass carp *C. idellus* (17%), common carp *Cyprinus carpio* (15%), freshwater bream *A. brama* (4%), and *Hypopthalmichthys molitrix* (4%) – accounted for 98% of the total biomass. The four remaining native species accounted for 8% of the abundance and for 0.2% of the total biomass.

Temporal variation in fish assemblage composition and structure was pronounced. Mean fish abundance

Table 2. Taxa, status (N = native species; E = exotic species), mean fish abundance (number of individuals ha^{-1}), percentage of the total individuals (%) and biomass ($g\,ha^{-1}$) for fishes collected in 1991, 1997, 2003 and 2009 surveys, in 14 canals of the lower Po River plain

			1991			1997			2003			2009		
Family	**Species**	**Status**	Fish abundance	%	Biomass	Fish abundance	%	Biomass	Fish abundance	%	Biomass	Fish abundance	%	Biomass
Anguillidae	*Anguilla anguilla* (Linnaeus, 1758)	N	36.1	2.9	6568.0	5.9	2.8	1055.7	1.5	0.5	270.0	0.6	0.2	102.9
Clupeidae	*Alosa fallax* (Lacépède, 1803)	N	7.1	0.6	399.6	-	-	-	0.9	0.3	47.1	-	-	-
Cyprinidae	*Rutilus pigus* (Lacépède, 1804)	N	2.1	0.2	333.2	-	-	-	-	-	-	-	-	-
	Rutilus aula (Bonaparte, 1841)	N	55.7	4.4	1598.5	4.4	2.1	127.0	-	-	-	-	-	-
	Squalius cephalus (Linnaeus, 1758)	N	10.1	0.8	1927.1	0.4	0.2	67.9	-	-	-	-	-	-
	Tinca tinca (Linnaeus, 1758)	N	27.4	2.2	5371.1	2.5	1.2	501.1	-	-	-	-	-	-
	Scardinius erythrophthalmus (Linnaeus, 1758)	N	172.9	13.7	23335.7	14.8	7.1	1996.1	5.0	1.8	1350.0	1.1	0.3	308.6
	Alburnus arborella (Bonaparte, 1841)	N	185.0	14.6	1387.5	25.4	12.2	190.2	41.9	14.7	313.9	25.9	7.7	193.9
	Chondrostoma soetta (Bonaparte, 1840)	N	30.0	2.4	1650.0	-	-	-	-	-	-	-	-	-
	Barbus plebejus (Bonaparte, 1839)	N	4.6	0.4	618.1	-	-	-	-	-	-	-	-	-
	Carassius auratus (Linnaeus, 1758)	E	266.4	21.1	23978.6	40.5	19.5	3645.0	29.0	10.2	3915.0	25.8	7.6	4254.6
	Cyprinus carpio (Linnaeus, 1758)	E	18.8	1.5	4132.9	9.1	4.4	2148.6	17.9	6.3	10714.3	36.6	10.8	52900.0
	Abramis brama (Linnaeus, 1758)	E	-	-	-	-	-	-	11.4	4.0	1419.6	86.3	25.6	14237.1
	Rhodeus sericeus (Pallas, 1776)	E	-	-	-	-	-	-	27.6	9.7	96.8	35.6	10.5	124.5
	Pseudorasbora parva (Temminck and Schlegel, 1846)	E	-	-	-	4.0	1.9	30.0	44.6	15.7	334.3	36.1	10.7	270.5
	Ctenopharyngodon idellus (Valenciennes, 1844)	E	1.9	0.2	3471.4	0.8	0.4	1846.4	2.2	0.8	19817.9	6.8	2.0	60732.1
	Hypopthalmichthys molitrix (Valenciennes, 1844)	E	-	-	-	-	-	-	-	-	-	1.6	0.5	13592.9
	Aspius aspius (Linnaeus, 1758)	E	-	-	-	-	-	-	-	-	-	7.1	2.1	1591.1
Cobitidae	*Sabanejewia larvata* (De Filippi, 1859)	N	15.7	1.2	149.3	-	-	-	-	-	-	-	-	-
Siluridae	*Silurus glanis* (Linnaeus, 1758)	E	2.3	0.2	6514.3	28.6	13.7	120000.0	14.6	5.1	99085.7	26.1	7.7	208571.4
Ictaluridae	*Ameiurus melas* (Rafinesque, 1820)	E	213.6	16.9	17085.7	31.3	15.0	2502.9	15.9	5.6	1110.0	20.7	6.1	1139.3
	Ictalurus punctatus (Rafinesque, 1820)	E	-	-	-	0.5	0.2	72.5	0.6	0.2	82.9	1.6	0.5	238.2
Esocidae	*Esox lucius* (Linnaeus, 1758)	N	13.1	1.0	3006.4	0.8	0.4	180.7	-	-	-	0.1	0.0	46.4
Poeciliidae	*Gambusia holbrooki* (Girard, 1859)	E	18.6	1.5	46.4	-	-	-	60.7	21.3	157.9	-	-	-
Gasterosteidae	*Gasterosteus aculeatus* (Linnaeus, 1758)	N	2.9	0.2	15.7	-	-	-	-	-	-	-	-	-
Centrarchidae	*Micropterus salmoides* (Lacépède, 1803)	E	29.6	2.3	3705.4	1.6	0.8	205.4	-	-	-	-	-	-
	Lepomis gibbosus (Linnaeus, 1758)	E	16.2	1.3	154.0	28.9	13.9	2452.9	3.9	1.4	255.4	11.4	3.4	640.0
Percidae	*Perca fluviatilis* (Linnaeus, 1758)	N	135.0	10.7	22275.0	-	-	-	-	-	-	-	-	-
	Sander lucioperca (Linnaeus, 1758)	E	-	-	-	8.4	4.0	1378.9	7.1	2.5	1071.4	14.0	4.2	2618.0
Mugilidae	*Liza ramada* (Risso, 1827)	N	-	-	-	0.4	0.2	53.6	-	-	-	-	-	-

and biomass of native species recorded in all survey sites varied significantly among years ($F = 27.15$, $P < 0.001$; $F = 22.45$, $P < 0.001$, respectively) (Table 3(a)). Post-hoc tests showed that mean annual abundance and mean annual biomass of native fish in 1991 (Figure 3(a), (b)) were always significantly different compared with the other years (Table 3(a)). No significant differences between 1997 and 2003 were detected for both the community parameters (Table 3(a)). Mean fish abundance and biomass of exotic species recorded in all sampling sites varied significantly among years ($F = 21.32$, $P < 0.001$; $F = 10.88$, $P < 0.001$, respectively), (Table 3(b)).

Post-hoc tests showed that mean annual abundance of exotic fish in 1991 (Figure 3(a)) was always significantly different from the other years (Table 3(a)), and no significant differences between 2003 and 2009 were detected (Table 3(b)). The highest annual mean biomass of exotic species was measured in 2009 (Figure 3(b)) and was significantly different from the other years (Table 3(b)). No significant difference was found in the mean annual biomass of exotic species in 1991 from that recorded in 1997 and 2003 (Table 3(b)).

The MDS ordinations of the 56 fish samples (Figure 4(a), (b)), based on 4th-root transformed abundance and biomass data, showed 2-D stress values below 0.2, which were sufficiently low to provide a useful representation of the distribution of the large number of samples in two dimensions. A clear spatial segregation of the sample points revealed a temporal gradient in fish community structure. The cluster analysis showed that the greatest difference in fish assemblages occurred between 1991 and 1997, with a separation at 42%

Table 3. Analysis of variance of fish abundance (number of individuals ha^{-1}) and total biomass (g ha^{-1}) of native (a) and exotic (b) species between years. HSD Tukey test: $P < 0.05$. SS = sums of squares; DF = degrees of freedom; MS = mean square

		SS	DF	MS	F	p	HSD Tukey test
(a)	**Native species**						
	Abundance	25.28	3	8.427	27.15	0.001	1991 > 1997 = 2003 > 2009
	Biomass	54.94	3	18.31	22.45	0.001	1991 > 1997 = 2003 > 2009
(b)	**Exotic species**						
	Abundance	4.70	3	1.57	21.32	0.001	1991 > 1997 > 2003 = 2009
	Biomass	5.67	3	1.89	10.88	0.001	1991 = 1997 = 2003 < 2009

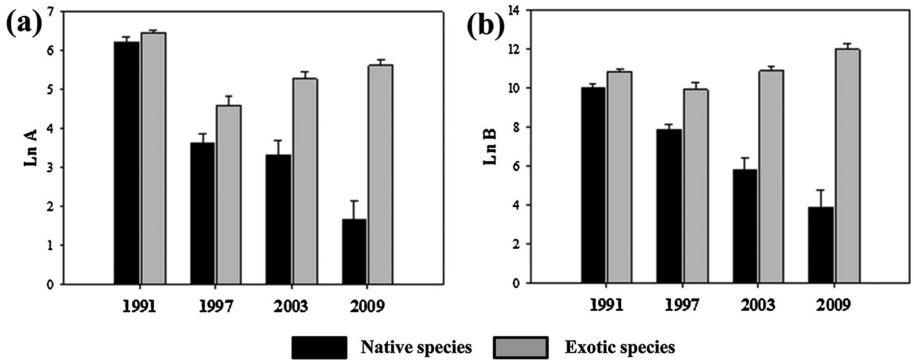

Figure 3. (a) Mean fish abundance (ln-transformed data of the number of individuals ha^{-1}, ln N), and (b) biomass (ln-transformed data of the fish biomass, g ha^{-1}, ln B), belonging to native and exotic fish assemblages collected in 1991, 1997, 2003, and 2009 surveys in 14 canals of the lower River Po plain. Bars indicate standard errors.

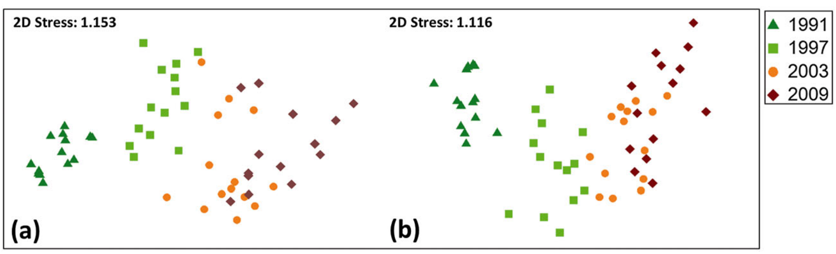

Figure 4. Non-metric multi-dimensional scaling (nMDS) plots of fish community structure based on 4th-root transformed relative abundance (a) and relative biomass (b) data recorded in 14 canals of lower River Po plain for each survey.

similarity relating to fish abundance (Figure 5(a)), and at 43% relating to fish biomass (Figure 5(b)).

These differences were confirmed by one-way ANOSIM analyses, which showed that, for fish abundance and biomass estimates, the time-period data were significantly different ($P < 0.001$ for all comparisons) (Table 4).

The average dissimilarities in fish abundance and biomass, determined for all possible year pairs by the SIMPER routine, showed that dissimilarity increased progressively from 1991 to 1997 (51% and 51% for abundance and biomass, respectively) to 2003 (64% and 63% for abundance and biomass, respectively) and reached the highest values in the most recent survey of 2009 (72% and 71% for abundance and biomass, respectively).

To assess whether environmental parameters influenced the observed fish assemblages in the study period, fish abundance and biomass data were tested against water quality (BIO-ENV routine). A weak correlation between both fish abundance and water variables (best result was a correlation of 0.092 using water temperature and DIN, $P = 0.29$) and fish biomass and water variables (best result was a correlation of 0.1 using water temperature and DIN, $P = 0.23$) indicated that the fish communities observed were probably little affected by physico-chemical parameters.

Trends of abundance and biomass for the most representative species are plotted in Figure 6. In 1991, wels catfish had low abundance and biomass, and pikeperch was not present in the canals studied; they both increased steeply to 1997 and at lower rates until 2009 (Figure 6(a)). Relative abundance and biomass of the native species preyed upon by wels catfish and pikeperch consistently dropped until 2009 (Figure 6(b)). Tench and Italian red-eye roach decreased dramatically from 1991 to 1997 until local extinction in 2003. Rudd, *Scardinius erythrophthalmus* L., and bleak, *Alburnus arborella* Bonaparte, 1841, exhibited very low abundance and biomass from 1997 to 2009 (Figure 6(b)). An exotic species introduced more than a century ago, largemouth bass, *Micropterus salmoides* Lacépède, 1803, declined from 1991 to 2003 and was not found in 2009 (Figure 6(c)). Black bullhead, *Ameiurus melas* Rafinesque, 1820, and goldfish, *Carassius auratus* L., decreased at differing rates before and after 1997. Abundance and biomass for pumpkinseed, *Lepomis gibbosus* L., showed a less pronounced reduction throughout the monitoring period (Figure 6(c)). A different trend was recorded for common carp, which increased in biomass from 1997, becoming, together with wels catfish, the most represented species in 2009 (Figure 6(c)). Two exotic species of recent appearance, stone moroko and freshwater bream, showed a rapid expansion soon after their establishment (Figure 6(d)). From 2003 to 2009, numbers of stone moroko decreased, while those of freshwater bream expanded (Figure 6(d)).

Table 4. Results of one-way ANOSIMs based on similarity matrices derived from 4th-root transformed fish abundance and biomass data. Global R statistic for testing for differences between all years and pairwise comparisons of years, with significance level from 999 permutations given

	Fish abundance		**Fish biomass**	
	R statistic	p (%)	R statistic	p (%)
Among years	(Global R = 0.757)		(Global R = 0.724)	
1991 vs 1997	0.791	0.1	0.759	0.1
1991 vs 2003	0.990	0.1	0.999	0.1
1991 vs 2009	0.993	0.1	0.99	0.1
1997 vs 2003	0.578	0.1	0.53	0.1
1997 vs 2009	0.798	0.1	0.711	0.1
2003 vs 2009	0.236	0.3	0.204	0.8

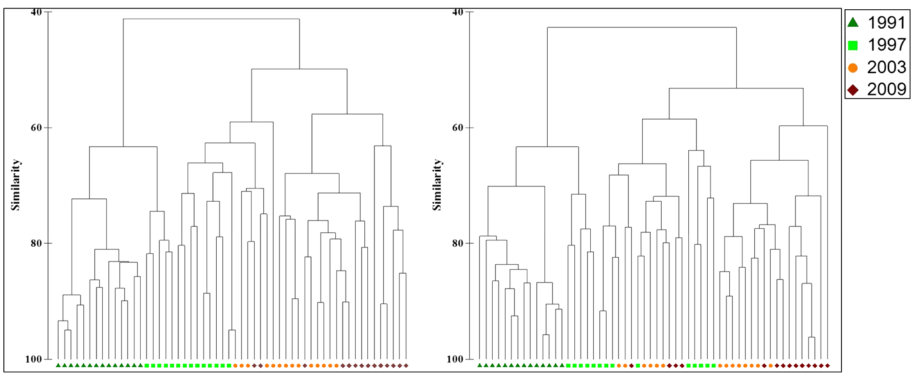

Figure 5. Dendrograms for hierarchical clustering (using group-average linking) based on the Bray–Curtis similarity matrix of 4th-root transformed relative abundance (a) and relative biomass (b) data recorded in 14 canals of lower River Po plain for each survey.

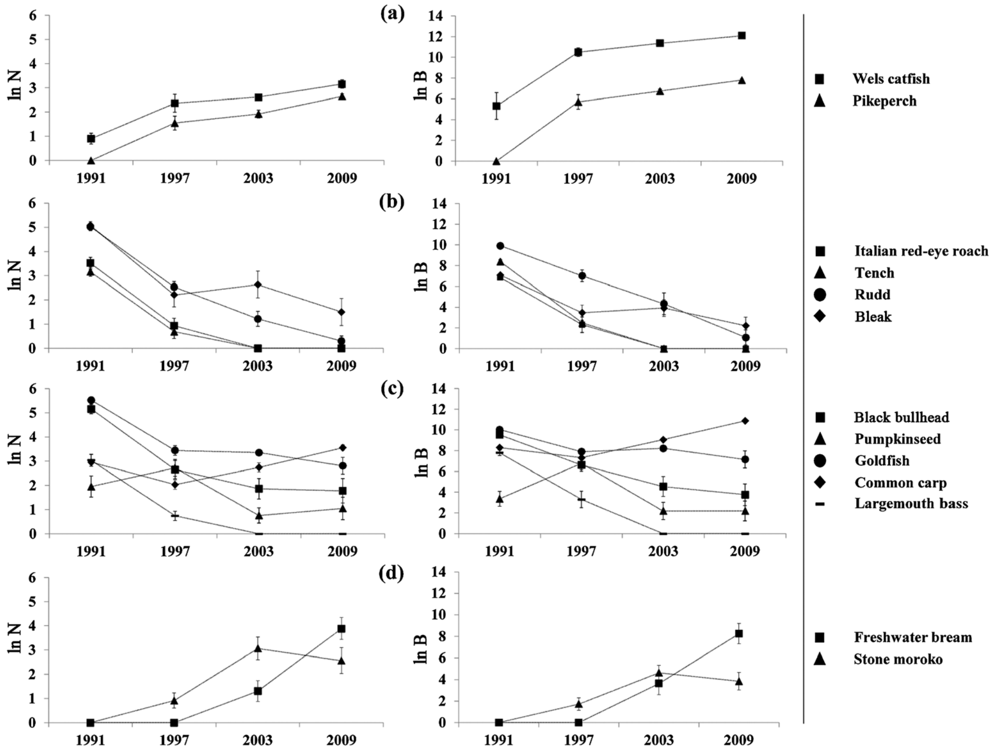

Figure 6. Temporal variation in fish abundance (ln number of individuals ha^{-1}, left) and biomass (ln g ha^{-1}, right) of the most representative species collected in the 14 canal stretches of the lower Po River plain. The graphs refer to (a) exotic predators of recent introduction, (b) native species, (c) exotic species of ancient introduction, (d) exotic species of recent introduction.

DISCUSSION

Understanding which ecological traits of a species make it a successful invader and which features of an ecosystem make it vulnerable to invasion is increasing but is not yet predictive (Clavero and García-Berthou, 2005; Didham *et al.*, 2007).

Habitat degradation

Habitat degradation occurred before this study began, and conditions remained at a steady state throughout the 18-year period. All canals were eutrophic and turbid, without morphological complexity, and with sparse vegetation. The occurrence of aquatic vegetation, generally absent or present in a few stretches in a narrow strip along the banks, remained constant throughout the study period (Piccoli and Gerdol, 1983; Ferrari *et al.*, 1985).

Water quality is unlikely to have affected fish communities in the study area during the period monitored. Environmental parameters remained stable, as no new canals were added, their morphology was unchanged, and they were managed in the same manner, both in the timing of opening and closing of sluice gates and the water level and velocity maintained (personal communication by the local water authority, the Consorzio di Bonifica Pianura di Ferrara). Pollution, such as episodic discharge, or critical events such as winter or summer fish kills can also be excluded, as no mass mortality was reported during the study period. Although some water quality parameters, such as reduced oxygen during hot summers, could be a potential source of stress for fish, none reached lethal levels. While oxygen levels lower than 3.5 mg L^{-1} have been reported to kill most species (Moore, 1942), and high mortality at oxygen below 1.75 mg L^{-1} at 28°C has been reported for northern pike (Casselman, 1978; Casselman and Lewis, 1996), such low values were not recorded during the study period. Dissolved oxygen fluctuations coupled with temperature gradients may have been a source of stress in the system studied, but their effect was not severe. Aluminium levels are not considered critical for fish at pH above 5.6 (Sparling *et al.*, 1997), while nickel levels are safe at the microgram level (Meyer *et al.*, 1999; Pane *et al.*, 2003). Both these conditions were met during the period monitored. Lead was within the global average of about 2 μg L^{-1} (Eisler, 1988), but the form of lead in water can be crucial, as fish larva survival is inhibited at 3.5 μg L^{-1} of tetraethyl lead. However, no information on the form of lead in the waters studied was available. Copper LC50 for minnows is reported at 116 $\mu g\,L^{-1}$ (Meyer *et al.*, 1999), well above that recorded during this study.

In 1991, northern pike and European perch were the only native predators. Other predators were the exotic largemouth bass and black bullhead catfish, introduced into these waters at the beginning of the 1900s (Gandolfi *et al.*, 1991). These fish were scarce in 1991, probably due to a synergetic effect of habitat conditions and fishing pressure, and to high turbidity, which is not favourable for predators that rely on sight, such as the northern pike, European perch, and largemouth bass. Water turbidity could have also favoured the increase in the populations of exotic species such as pikeperch and wels catfish, that are adapted to low light and transparency. Small cyprinids are not intensively fished and were relatively abundant in 1991 when wels catfish entered from the Po. The absence of refugia, water level fluctuations during the year, and obstacles (weirs, sluice gates, pumps) which limit escape may have further exposed these species to predation.

Exotic species introduction

The introduction of exotic fishes into fresh waters can have detrimental effects, disrupting the food web from its apex or centre (Strayer, 2010). Several cases have been reported of disastrous consequences of the introduction of predators such as that of pikeperch in Lake Egridir (Campbell, 1992) or northern pike in Spain (Rincon *et al.*, 1990). Scarce and contrasting information is available on the effects of wels catfish introduction. It has been described as an ‘opportunistic forager’, and it has been hypothesized that serious consequences of its introduction may occur only in environments where ‘other human impacts are already in force’ (Copp *et al.*, 2009), as in the present case.

The first record of wels catfish in Italy dates from 1956 in the River Adda, a mid-course left tributary of the Po, when it was reported as accidentally escaped from angling ponds (Manfredi, 1957; Gandolfi and Giannini, 1979). After an initial phase of expansion, in the 1980s it became established in the Po drainage, colonizing tributaries and related sub-basins at the beginning of the 1990s (Gandolfi *et al.*, 1991; FAO, 1997; Bianco, 1998). A suitable thermal regime could explain the extremely rapid invasion by *S. glanis* into the lower reaches of the Po, bordering the monitored Po di Volano sub-basin, where the growth rate, calculated according to the von Bertalanffy model, was found to be highest when compared with populations of Eastern European basins (Rossi *et al.*, 1991).

During the first survey, in 1991, wels catfish accounted for 6.1% of the total biomass. With optimal foraging conditions, abundant prey, and few competitors, it reached 77%, 71%, and 62% of the overall biomass in 1997, 2003, and 2009, respectively. In the study area, commercial fishing was no longer practised and anglers were not interested in wels catfish, so fishing mortality was probably low. Conversely, pikeperch, present in the catch of 1997, was immediately targeted by anglers, becoming a substitute for the declining black bullhead population. This may explain why pikeperch did not expand above 1% of total biomass.

It is well documented that wels catfish takes advantage of its diet plasticity and ability to prey upon the most abundant available species of a suitable size within its habitat (Carol *et al.*, 2009; Syväranta *et al.*, 2010; Martino *et al.*, 2011). This may have contributed to the sequence of the decline in species. Among the most abundant native species in 1991, tench and Italian red-eye roach were the first to disappear, with none captured in 2003. These are small fish with a marked benthic lifestyle. The population of Italian bleak and rudd, which differ from the above-mentioned species in having fewer marked benthic traits, decreased more slowly, and they were still present in 2009, although greatly reduced.

Exotic species introduced more than a century ago followed different trends, possibly due to their lifestyle, size, and origin. The number of goldfish, which has a benthic lifestyle, relatively small size, and a different native range from wels catfish, decreased steeply from 1991 to 1997 while the population of wels catfish markedly increased. Common carp, much larger than goldfish, increased throughout the monitored period after an initial phase of slight decrease from 1991 to 1997. This increase, more in biomass than in abundance (also found for grass carp and silver carp) can be related to the attainment of a refuge size. Large-bodied species such as these will be protected by their mass and body shape, avoiding capture by gape-limited predators.

Among cyprinids that entered the Po di Volano sub-basin from the Po River during the study period, freshwater bream was the only species to increase. This success might be explained by increased availability of food resources associated with the reduction and disappearance of competitors, and possibly by a co-evolved capacity to escape wels catfish predation (Wysujack and Mehner, 2005).

The ecological pressures of the large-bodied exotic predator, wels catfish, and of exotic competitor species, common carp and freshwater bream, facilitated by habitat simplification, explain the temporal dynamics of fish populations in this study. Previously an important nursery area for native species, the ecology of this canal network has become homogenized with that of the main river, with fish fauna comprising abundant exotic species and few, declining, native species.

The results of this study, suggesting that biotic interactions played a central role in the decline of native fish assemblages, are in agreement with those reported by Hermoso and Clavero (2011) and Light and Marchetti (2007). These authors found that the abundance of invasive species was the primary driver of native biodiversity loss in the Guadiana River basin in the south-western Iberian Peninsula and in California streams with a similar Mediterranean-type climate. Many examples of catastrophic ecological effects of freshwater fish introduction are documented, involving numerous countries and species such as Nile perch, common carp, and catfishes (Vitule *et al*., 2009).

Implications for conservation and management

The present results have several implications for the expansion of exotic species and the recovery of native fish biodiversity. In general, they indicate that some species might reach high abundance levels several years after their introduction, as in the case of wels catfish, first reported in the Po middle course in 1972. This suggests instituting preventive measures to minimize the risk in those basins where wels catfish does not yet occur or is present at low density.

It is essential that management action be taken to stimulate the recovery of native fish biodiversity. Programmes for eradication of exotic predators and invasive cyprinid species have recently been put into practice with success in closed waters, such as small lakes and ponds (Britton *et al*., 2008; Tsunoda *et al*., 2010). However, in this study, characterized by a wide geographic area, a large overall biomass (about 1500 t), and continual recolonization from the Po mainstream, eradication appears unfeasible. As recently observed by Britton *et al.* (2010), in such conditions typical of large spatial areas where eradication is not practicable, a removal programme appears to be the most promising strategy to manage invasions, as reported for common carp in Australia.

The results of this study highlight the need to operate continuing containment of the most invasive species, accompanied by habitat restoration, to facilitate the recovery of native fish. With regard to habitat, the most effective short-term action is the restoration of aquatic vegetation, which may be achieved through the containment of grass carp and common carp. In the longer term, modification of canal morphology to decrease the embankment slope would allow the recovery of emergent vegetation. Maintaining a constant water level in all branches of the canal network is recommended, including the months outside of the irrigation season, from mid-September to mid-March, when, at present, the water intake from the Po is interrupted and depth reaches the annual minimum with the drying-up of some upstream sections.

Containment should focus on wels catfish. In the study area, a plan for containment through fishing began several years ago with the application of legislative Acts (Regional Low N. 11 of 22 February 1993, Directive N. 1574 of the Regional Council of 3 July 1996) but was insufficient. The main deficiency appeared to be the spatial and temporal discontinuity of intervention in the extensive canal network and the large stock of wels catfish which always recovered rapidly (Castaldelli *et al*., 2008). On the other hand, the increase of fishing effort on such a large scale is economically unsustainable for public institutions. An alternative strategy would be a controlled programme of commercial fishing. This strategy has recently been reinforced by the increase in wels catfish demand and wholesale price on the eastern European markets.

In the hydrological network studied, the stretches of canal confined between two hydraulic works are resistant to immediate re-invasion and represent suitable conditions for containment. The proximity to a town is advantageous, because the results of intervention are evident to a higher number of anglers and citizens who care about the recovery of biodiversity. Other criteria for the site choice, such as the presence of refuges or other habitats with suitable characteristics for native species, are not applicable in this case because all the canals have similar physical and biological features and are managed in the same way. A strategy of containment and habitat restoration has been put into practice in 2011–2012 in the stretch of the Fossa Lavezzola bordering the Berra town centre

(Province of Ferrara), and so far the results are promising (Lanzoni, personal observations).

To facilitate this process of recovery it is crucial to promote the involvement of recreational fishing associations and other stakeholders to increase their awareness of the consequences of exotic fish introductions. It is also important to explain the biological and ecological basis for management actions taken, and to be taken, and the expected beneficial outcomes, so that stakeholders acknowledge their importance and do not hamper them.

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