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Managing the environment in a pinch: red swamp crayfish tells a cautionary tale of ecosystem based management in northeastern Italy

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ABSTRACT

Farmlands are globally widespread and their management should consider both human and environmental needs. In fact, these man-made ecosystems provide subsistence to the human population but are also habitats for plant and animal communities. The worldwide increase of exotic species has affected native communities, but also human activities or health. We used an exploited farmland in northern Italy, where many exotics are present, as a test case for identifying restoration measures based on an ecosystem approach. In particular, we focused on red swap crayfish for its ecosystem engineering capabilities, and examined the factors affecting its invasion success in order to attempt the definition of management strategies. We used multivariate and regression analysis to evaluate the relationships between the red swamp crayfish, water quality, macrophytes abundance, watercourse hydraulics and the fish community. All analyses indicated that red swamp crayfish was less likely to establish in large, deeper and fast flowing waterways, especially when these are deprived of vegetation and less eutrophicated. Based on our results, fish predation was also a significant factor in limiting red swamp crayfish abundance. We thus concluded that a different hydraulic management, which leaves more water in irrigation canals throughout the winter, could be possibly used to slow down or even reverse the invasion process.

1. Introduction

The sustainable management of human activities has become one of the most imperative goals for the majority of developed countries (UN General Assembly, 2015). A major challenge to achieve this goal has been the divergence between environment conservation and activity development targets (Margules and Pressey, 2000), creating an exacting management gap (Griggs et al., 2013). The concept of ecosystem approach has been developed trying to bridge this gap: it consists of an integrated management of human activities based on the best available knowledge of ecosystems and their dynamics, in order to identify and solve primary causes of ecosystem degradation (UN General Assembly, 1992; Secretariat of the Convention on Biological Diversity, 2004). The product of the ecosystem approach, ecosystem based management, should therefore ensure that development can occur without preventing the ecosystem to provide its services. Being a relatively new concept, its application is not overly widespread and has been perceived to be overly complex and limited in scope to some human activities or particular environments (e.g. such as with fisheries management, Garcia et al., 2003). Furthermore, several other challenges persist on the development and application of ecosystem based management; namely the difficulties in integrating knowledge from different fields and the incredibly complicated interactions between factors that are at play in human-impacted ecosystems (Long, Charles and Stephenson, 2015; Slocombe, 1998).

The field of agriculture management is a prime example of such difficulties, as it involves complex interactions between soil and water ecology (Altieri, 1995; Kramer, 1969). Farmlands often have a long history and are globally widespread; their modified environment providing sustenance to human populations and, perhaps surprisingly, habitats suitable to some species (Clavero et al., 2015; Freemark et al, 2002; Katayama et al., 2013). Often overlooked as a biodiversity-capable environment, irrigation canals are habitat-simplified watercourses that are connected to natural rivers and constitute an interconnected network within farmlands. Managing irrigation canal environments involves governance at different levels (e.g. on fisheries) but perhaps

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the most relevant is hydraulic regulation (Ricart and Gandolfi, 2017). Hydraulic regulation in canals presents challenges common to other human-impacted watercourses, where conservation and production goals often diverge and a major knowledge gap has been underlined as to the effect of variations in water flow on the freshwater plant and animal communities (Bunn and Arthington, 2002; Poff and Zimmerman, 2009).

Similarly, the fauna living in canals can be influenced by pressures much similar to those of natural aquatic environments; primarily eutrophication derived from field fertilization (Castaldelli et al., 2013a; Huang et al., 2017), habitat degradation (Dudgeon et al., 2006) and the introduction of exotic species (Strayer, 2010).

Exotic species are widely recognized as one of the “big five” causes of biodiversity loss (Sala et al., 2000) and can also become invasive, with adverse consequences extending to human activities as well. Among the most invasive exotic species introduced in temperate freshwaters, crayfishes have recently become increasingly common and have had direct effects on native communities (Gherardi and Lazzara, 2006; Rodríguez-Pérez et al., 2016). One of the most prominent and invasive crayfishes, the red swamp crayfish (*Procambarus clarkii*, Girard, 1852), has been found to affect aquatic macrophytes (Carreira et al., 2014) and even damage watercourse banks due to it burrowing habits (Barbaresi et al., 2004). This species thus presents a veritable threat to ecosystem functioning and hydraulic stability, but also a potential impact on crop production (Anastácio et al., 2000) and restoration practices (Rodrigo et al., 2013) posing a serious question to both conservation and agricultural management.

In the lowest portion of the Po River basin, by far the largest and one of the most exploited farmlands in Italy, the presence of red swamp crayfish was reported in 1996 (for a general view, see Gherardi et al., 1999) but its effects or its potential management have been scarcely investigated. This area is also heavily invaded by exotic fish species, which are crayfish predators (e.g. wels catfish *Silurus glanis* L. (Carol et al., 2009) or common carp *Cyprinus carpio* L. (Britton et al., 2007)), but in turn also pose a question of exotic species management. To examine the factors affecting the invasion success of red swap crayfish and to attempt the definition of management strategies, we selected both natural and artificial waterways and worked under the hypothesis that low water levels outside of the growing season could favor crayfish invasion by preventing effective fish predation. We used multivariate analysis to evaluate the relationships between the red swamp crayfish, water quality, macrophytes, watercourse hydraulics and the fish community. Using our results, we identify factors that could be accounted for in hydraulic management, which could be possibly used to slow down or even reverse the invasion process. This test case study could be used as a stepping stone to reduce complexity, achieve sustainable management and be transferred to other regulated watercourses where multiple environmental stressors are present.

2. Materials and methods

2.1. Study area

The waterways investigated in this study are located in the lower stretch of the Po River, within the administrative boundaries of the Province of Ferrara (Emilia-Romagna Region, northeastern Italy). In this area, the natural swamp of the delta has been reclaimed over nearly two centuries and was turned into an heavily exploited farmland, extending over 2200 km^2, half of which is below sea level. To provide water for irrigation, a capillary network of canals was built, which accounts for more than 4000 km in linear extension in the Province of Ferrara. Other waterways include the Po River, a constricted river with a relatively natural flow regime, and the Reno River, a constricted and flow-regulated river.

A total of 34 sampling sites, along 27 different waterways, were sampled to assess presence and abundance of both crayfish and fish (Fig. 1). Moreover, hydrological and environmental variables were also measured. These waterways had variable widths (2–100 m), depths (0.5–4 m) and water current (0–0.3 $m\,s^{-1}$; but peak values up to 1 $m\,s^{-1}$ were registered in the Po and Reno rivers). All water courses presented a muddy-silty layer of variable thickness, covering the clayey sediment of the canal bed, except the Po River, where a prevalence of sandy sediment could be found in the sites sampled. These waterways are also affected by severe microhabitat simplification due to management practices, such as frequent vegetation mowing (Castaldelli et al., 2013a). Irrigation canals are flooded during the growing season (typically April to October) to provide water for irrigation; but water levels are significantly lower outside of this time, further limiting the habitat available to aquatic species.

In the lowest portion of the Po River basin, native white-clawed crayfish *Austropotamobius italicus* (Lereboullet, 1858), belonging to the *A. pallipes* complex, was historically present (Morpurgo et al., 2010), but its abundance and distribution sharply declined in the ‘70s, with numerous local extinctions in rivers and canals. Afterwards, two exotic crayfish species accidentally escaped from aquaculture ponds, took advantage of the empty niche: the red swamp crayfish was first reported in 1996, and the spinycheek crayfish, *Orconectes limosus* (Rafinesque, 1817), was reported in 2006 about 60 km downstream of the waterways sampled in this study (see Gherardi et al., 1999 for a general overview). It is unclear whether exotic crayfish presence in this area is due to local introductions or dispersal from nearby invaded areas.

In this area, several species of native fish were historically present but exotic fish species introductions date as far back as the XVII century, with most species being introduced around 1970 from Asia or East Europe (Lanzoni et al., 2018; Milardi et al., 2018a). This is one of the most heavily invaded areas in the country, where severe impacts on the native fish communities have been detected (Castaldelli et al., 2013b; Milardi et al., 2018a) and sites with fully exotic fish communities have been found (Lanzoni et al., 2018).

2.2. Crayfish and fish sampling

Sampling of crayfish was conducted between May and June 2009, a period when crayfish were active and environmental stressors, such as flow variations, were not present. In each waterway, crayfish presence was investigated in stretches with homogenous morphology, hydrology and with no tributaries or discharges using plastic traps baited with a can of fish-flavored cat food (see e.g. Lappalainen and Pursiainen, 1995). No professional or sport fishing targeted the crayfish populations in these waterways.

Plastic traps had proved to be the most reliable survey measure in preliminary tests and previous sampling campaigns in the area (2004–2006), due to the high turbidity and the presence of emergent vegetation along the bank (Lanzoni, unpublished data). The traps (40 × 25 × 25 cm, 0.3 cm mesh size) had two openings at opposite ends, plus a central opening for extraction (Fjälling, 1995). A set of 15 traps was used at each sampling event, placed along the waterway banks at depths between 0.5 and 1 m, and left overnight (12 h, from 19.00 to 7.00). 3 replicate sampling events were performed at each site, and catches were expressed as average CPUE, defined as the mean number of crayfish caught per trap, per sampling event. Carapace and total length of all crayfish were measured to the nearest 0.1 mm using calipers. Crayfish wet weight was measured in the field, after removing excess water, to the nearest 0.1 g using an electronic scale.

A temporally and spatially overlapping sampling of the fish fauna was also performed using a combination of electrofishing and netting, adapting the national standard guidelines to the unique conditions of these waterways (Lanzoni et al., 2018). Fish were identified to the species level and individuals of each species counted. Species abundances were expressed in Moyle classes (Moyle and Nichols, 1973), which range from 1 (low abundance, 1–2 individuals per site) to 5 (high abundance, > 50 individuals per site).

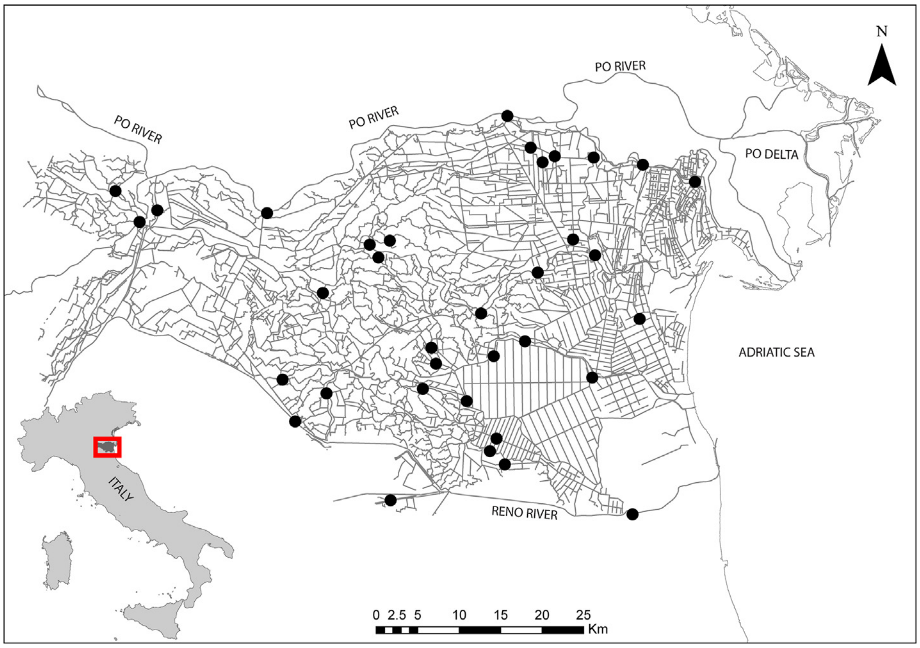

Fig. 1. Map of the study area: the lower Po River plain and the complex hydrological network of the Province of Ferrara (Italy). The 34 black dots represent the location of sampling sites, distributed along 27 different waterways, used in this study.

2.3. Environmental variables

At each of the 34 sampling stations, a number of different environmental variables were measured. Over the span of a year, maximum current velocity (Vmax) and minimum depth (Depth) were measured respectively during flood events by means of a current meter (Open Stream CurrentMeter 2100) and during drought using a dipping metric tape or, in the largest canals and rivers, a probe (Ocean Seven 316, Idronaut, Brugherio, MI, Italy). The waterway width (Width) was measured with a binocular laser rangefinder (Leica 10x42 Geovid BRF) with metric resolution or with a metric tape, depending on the site characteristics. The span of aquatic vegetation (mostly reeds) along the waterway banks (Veg) was measured with a floating metric pole with centimetric resolution. Oxygen concentration (Oxy) was measured with a multiparametric probe (Ocean Seven, 316). Levels of chlorophyll *a* (Chl-*a*, indicative of phytoplankton biomass and eutrophication levels), total suspended solids (TSS, indicative of turbidity), and of Biochemical Oxygen Demand (BOD_5, indicative of nutrient load) were determined according to APHA (2005).

2.4. Statistical analysis

In order to explore the relationship between crayfish, fish and environmental parameters multivariate statistics were employed. A Detrended Correspondence Analysis (DCA) was initially performed to select the most appropriate response model for gradient analysis (Lepš and Šmilauer, 2003). The dominant gradient length in DCA was always lower than 3 so the Redundancy Analysis (RDA) was finally chosen (Lepš and Šmilauer, 2003). RDA is a linear gradient analysis that allows to quantify the variation of a multivariate data set explained by independent variables (ter Braak and Šmilauer, 2002). The environmental variables were considered as independent parameters, whereas the faunal community (red swamp crayfish and fish species) was considered as dependent. Fish species sampled in less than 3 sites, were excluded from the RDA analysis (Aschonitis et al., 2015; Feld and Hering, 2007; Godinho and Ferreira, 2000). Variables with a Variance Inflation Factor (VIF) higher than 8 should excluded before the RDA analysis in order to exclude collinear (redundant) ones (Zuur et al., 2007), but all variables were below the limit.

The relationship between the environmental parameters and the abundance of red swamp crayfish was assessed using a multiple regression analysis. Spearman's correlation coefficient ($|r| > 0.7$) was used to remove redundant variables in environmental data (Dormann et al., 2013). A forward stepwise selection of variables based on an F-toenter test was performed: at each step, the algorithm adds to the multiple regression the variable that will be the most statistically significant if entered (F-value > 4.0). Variance analysis was performed to test the statistical significance of the fitted model and to check the relationship between crayfish abundance and independent variables.

A hierarchical partitioning was performed to evaluate how much of the explained variation of crayfish abundance can be independently and jointly attributed to each environmental variable (Chevan and Sutherland, 1991; Mac Nally and Walsh, 2004). This approach allows to break up the variation explained by a set of independent variables into independent components (I), which reflect the relative importance of individual variables, and joint contributions (J), which are cumulative effects of each variable with all other variables. The distribution of joint effects shows the relative contribution of each variable to shared variability in the full model. Negative joint effects are also possible for variables that act as suppressors of other variables (Chevan and Sutherland, 1991). To avoid minor rounding errors, only the five most important factors previously identified with forward selection procedures were chosen for hierarchical partitioning (Mac Nally and Walsh, 2004; Walsh and Nally, 2013). The significance of the hierarchical model was assessed using a randomization test with 100 permutations (Walsh and Nally, 2013).

Environmental and crayfish abundance data, were log-transformed with $X' = \log_{10}(X + 1)$ to reduce the departure from normality. The DCA and RDA analyses were performed using CAONOCO 4.5 *for Windows* (Lepš and Šmilauer, 2003). The multiple regression analysis was performed using StatGraphics Centurion XV software (Statpoint Technologies, Warrenton, VA, USA) and the hierarchical partitioning was performed using R software (R Core Team, 2017) and the "hier.-part" package 1.0–4 (Walsh and Nally, 2013).

Table 1
Observed fish species in the 34 sampling sites, status of species (N is for native and E is for exotic species) and number of sampling sites where each species was present (S). Rare species "*" occurring in less than 3 sampling sites were excluded from statistical analyses.

Family	Species	Common Name	Status	S
Anguillidae	*Anguilla anguilla* (Linnaeus, 1758)	European eel	N	5
Clupeidae	*Alosa fallax* (Lacépède, 1803)	Twaite shad	N	5
Cyprinidae	*Squalius squalus* (Bonaparte, 1837)	Italian Chub	N	2*
	Scardinius hesperidicus Bonaparte, 1845	Italian rudd	N	10
	Alburnus arborella (Bonaparte, 1841)	Italian bleak	N	26
	Chondrostoma soetta Bonaparte, 1840	Italian nase	N	1*
	Barbus plebejus Bonaparte, 1839	Barbel	N	1*
	Barbus barbus (Linnaeus, 1758)	European barbel	E	1*
	Carassius spp.	Crucian carp/Goldfish	E	31
	Cyprinus carpio Linnaeus, 1758	Common carp	E	33
	Abramis brama (Linnaeus, 1758)	Common bream	E	16
	Blicca bjoerkna (Linnaeus, 1758)	White bream	E	1*
	Rhodeus sericeus (Pallas, 1776)	Bitterling	E	14
	Pseudorasbora parva (Temminck & Schlegel, 1846)	Stone moroko	E	25
	Ctenopharyngodon idella (Valenciennes, 1844)	Grass carp	E	5
	Leuciscus aspius (Linnaeus, 1758)	Asp	E	6
Siluridae	*Silurus glanis* Linnaeus, 1758	Wels catfish	E	30
Ictaluridae	*Ameiurus melas* (Rafinesque, 1820)	Black bullhead	E	10
	Ictalurus punctatus (Rafinesque, 1820)	Channel catfish	E	2*
Poeciliidae	*Gambusia holbrooki* (Girard, 1859)	Eastern mosquito fish	E	4
Centrarchidae	*Micropterus salmoides* (Lacépède, 1803)	Largemouth black bass	E	1*
	Lepomis gibbosus (Linnaeus, 1758)	Pumpkinseed	E	13
Percidae	*Perca fluviatilis* Linnaeus, 1758	European perch	N	1*
	Gymnocephalus cernuus (Linnaeus, 1758)	Ruffe	E	1*
	Sander lucioperca (Linnaeus, 1758)	Pike-perch	E	20
Mugilidae	*Liza ramada* (Risso, 1827)	Thinlip grey mullet	N	2*

3. Results

3.1. Crayfish and fish

Neither the native white-clawed crayfish nor the exotic spinycheek crayfish were found in traps, so the red swamp crayfish was the only crayfish captured. In six sampling sites, no crayfish were found.

A total of 830 red swamp crayfish specimens were caught and measured. Their average density was 1.6 CPUE (± 2.1 SD); with a maximum average density of 8.4 CPUE (± 4.8 SD). Average total length, carapace length and weight were respectively 57.1 mm (± 35.4 SD), 27.0 mm (± 16.0 SD) and 12.6 g (± 8.7 SD).

The fish fauna consisted of 26 species, 17 exotic and 9 native, belonging to 9 families. Cyprinids were the most represented family, accounting for almost 50% of the total number of species. Gradient analysis was performed on 16 fish species (12 exotic and 4 native) since species present in less than 3 sites were not included in the analysis (Table 1). In almost all waterways, the most abundant species were exotic.

3.2. Environmental variables

Environmental parameters (Table 2) were highly variable among sites. Maximum values of water velocity were measured in a canalized river (130 $cm\,s^{-1}$), whereas minimum values were sampled in drainage canals. Minimum water depth ranged from 0.3 m, measured in a small drainage canal, to 3 m measured in a canal used both for irrigation and drainage. Emergent vegetation was mainly represented by *Phragmites australis*, *Typha latifolia* and *Glyceria maxima* and its extension was generally limited (mean 2.3 ± 3.7 SD m). Oxygen showed a high variability from hypoxic condition (2.4 $mg\,l^{-1}$) to high concentrations (17.2 $mg\,l^{-1}$). Also chlorophyll *a* showed a wide range of values, from 3.0 to 92.6 $\mu g\,l^{-1}$, but with generally high levels (mean 31.2 ± 26.7 SD $\mu g\,l^{-1}$).

3.3. Relationship between crayfish, fish and environmental variables

Red swamp crayfish thrived in smaller waterways rather than larger ones, as defined by Depth and Vmax and Width, and its abundance was

Table 2
Average and range of environmental variables measured at the 34 sampling sites during May/June 2009.

Parameter	Abbrev.	Unit	Minimum	Maximum	Average	SD
Maximum water velocity	Vmax	($cm\,s^{-1}$)	5.0	130.0	33.1	32.4
Minimum depth	Depth	(m)	0.3	3.0	1.4	0.7
Width	Width	(m)	4.0	329.0	34.2	60.9
Emergent vegetation	Veg	(m)	0.2	20.0	2.3	3.7
Oxygen concentration	Oxy	($O_2\,mg\,l^{-1}$)	2.4	17.2	7.0	2.9
BOD_5	BOD_5	($mg\,O_2\,l^{-1}$)	1.2	11.2	4.5	2.6
Chlorophyll *a*	Chl-*a*	($\mu g\,l^{-1}$)	3.0	92.6	31.2	26.7
Total suspended solids	TSS	($mg\,l^{-1}$)	28.7	205.0	75.3	41.2

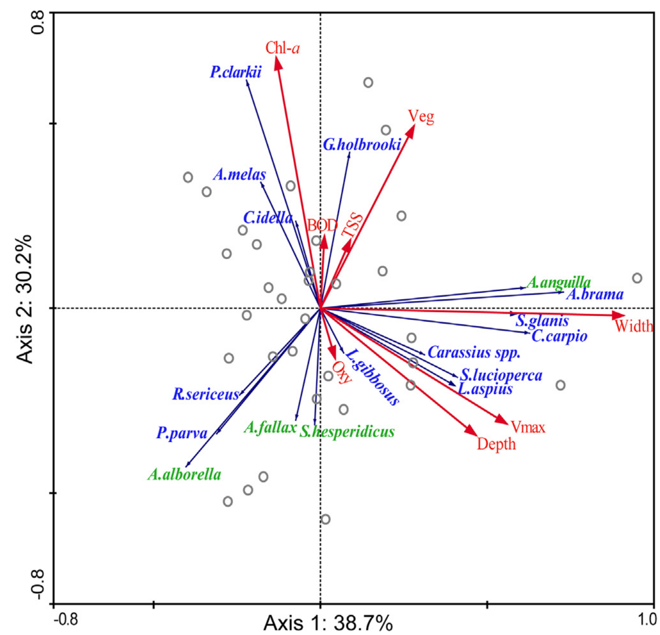

Fig. 2. Redundancy analysis (RDA) triplot showing the relationships between red swamp crayfish, fish fauna (blue arrows, native species with green labels, exotic ones with blue ones) and environmental parameters (red arrows). Empty dots represent sampling sites. Fish species abbreviations are given in Table 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Regression analysis results; standard error, *t*-test and p values are reported for each retained variable.

Variable	Estimate coefficient	Standard Error	T Statistic	P-Value
Intercept	0.922	0.083	11.051	< 0.001
Vmax	−0.260	0.035	−7.518	< 0.001
Depth	−0.730	0.080	−9.090	< 0.001
Chl-a	0.216	0.037	5.808	< 0.001
Veg	0.185	0.022	8.411	< 0.001
Oxy	−0.340	0.064	−5.343	< 0.001

also positively influenced by high values of Chl-*a* and Veg (Fig. 2). Crayfish predators such as wels catfish, European eel (*Anguilla anguilla*, L.), common carp and other fish species were also found in large waterways and negatively influenced red swamp crayfish abundance (Fig. 2). BOD, TSS and Oxy did not appear to be as strong descriptors of red swamp crayfish distribution (Fig. 2).

The Spearman rank test showed a high correlation between Width and Depth ($P < 0.01$, Correlation Coefficient = 0.7439). In order to avoid redundant variables, only Depth, as better descriptor of watercourse hydraulics, was retained in the multiple regression analysis. The forward selection procedure included Vmax, Depth, Chl-*a*, Veg and Oxy as significant for red swamp crayfish abundance (Table 3). The fitted multiple regression model explained 41.25% (adjusted R-squared) of the variability in crayfish abundance. Analysis of variance of this model showed a statistically significant relationship between environmental variables and crayfish abundance ($F_{5,579} = 83.01$; $P < 0.001$). Chl-*a* and Veg positively influenced red swamp crayfish abundance, while Depth, Vmax and Oxy negatively affected it.

The hierarchical partitioning showed that Vmax explained the highest percentage of total variance (29.79%) of red swamp crayfish abundance (Fig. 3a and b), with an independent contribution of 0.13)

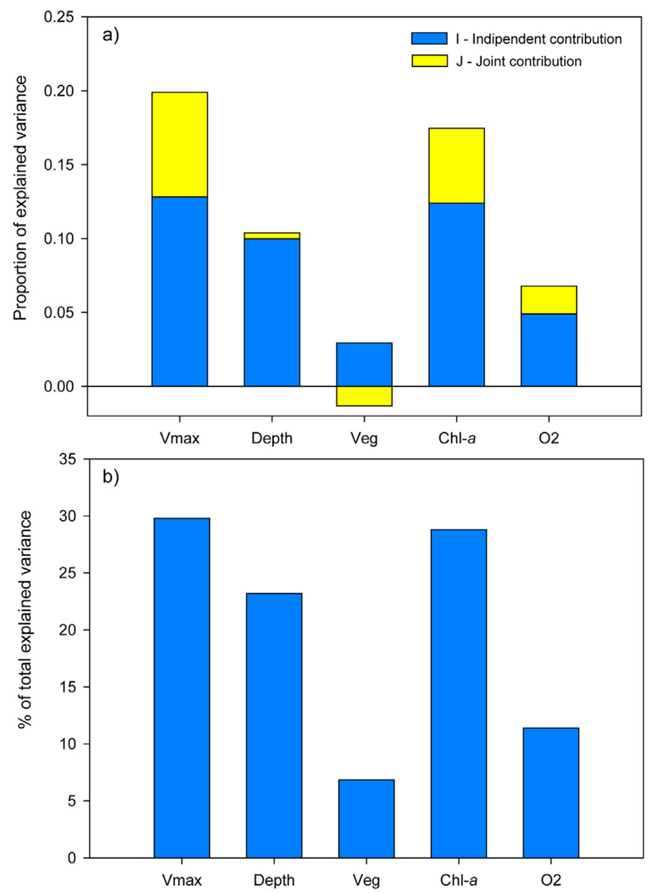

Fig. 3. Hierarchical partitioning of the environmental variables retained in the multiple regression analysis ($P < 0.001$). Proportion of red swamp crayfish abundance variance explained independently and jointly by the variables (a) and percentage of total red swamp crayfish abundance variance explained by each variable (b).

closely followed by Chl-*a* (23.19% of total variance). Veg and Oxy had the lowest values: 6.84% and 11.28% of total explained variance, respectively (Fig. 3b). Veg was the only variable with a negative joint effect (−0.01). The randomization test retained all variable included in hierarchical partitioning as significant.

4. Discussion

Our results show, for the first time, that the abundance of red swamp crayfish in the lower Po plain is affected by complex interactions between the environment and the fish community, with predation playing a central role. All analyses indicated that red swamp crayfish was less likely to establish in large, deeper and fast flowing waterways, especially when these are deprived of vegetation and less eutrophicated. Larger waterways also host more fish species that prey upon red swamp crayfish, adding to that effect. Unfortunately, it was not possible to clearly disentangle the effect of these factors, but it was clear from all analyses that managing the invasion would require to take into account multiple and often contrasting factors.

Although some authors suggest that hypoxia conditions can affect abundance of red swamp crayfish (Bonvillain et al., 2015), dissolved oxygen did not have a strong influence on red swamp crayfish in our study. Although retained in the forward selection procedure and in the multiple linear regression, dissolved oxygen had the lowest independent contribution to explain the crayfish abundance, probably due to the low variation among sites. However, an indirect effect of low dissolved oxygen values cannot be excluded; an anoxic zone could limit the presence of fish and consequently decrease predation pressure on the red swamp crayfish. High flow rates and highly variable flow regimes have been previously shown to negatively affect the dispersion of red swamp crayfish (Kerby et al., 2005). An increase of mortality in high flow conditions was also shown in other crayfish species such as the signal crayfish (*Pacifastacus leniusculus,* Dana, 1852) (Light, 2003) and the white-clawed crayfish (Robinson et al., 2000). However, in the studied area, water velocity possibly affected red swamp crayfish density indirectly, acting through other environmental factors. In fact, while maximum water velocity was higher in the rivers of the Province of Ferrara, it was generally low in the canals and presumably even lower among the vegetation of the banks, where red swamp crayfish were found. Water velocity could have a significant effect on the sedimentation of fine detritus: higher flows would cause lower sedimentation rates. Fine detritus is mostly derived from phytoplankton, which is the dominant primary producer in this system (Mantovani et al., 2004). Lower sedimentation could mean less food resources available to the crayfish as phytoplanktonic detritus is a primary food source for the red swamp crayfish in this area (Lanzoni, unpublished data), contrarily to what previously found by Gherardi and Lazzara (2006). Therefore, this could also explain the positive influence of Chl-*a* levels on red swamp crayfish abundance underlined by our data. In turn, the bioturbation activity of red swamp crayfish can release nutrients trapped in sediments and thus favor phytoplankton blooming (Angeler et al., 2001; Rodríguez et al., 2003). Thus, there could be a complex positive feedback mechanism between red swamp crayfish and eutrophication, which could be further reinforced by other species.

Mechanisms of potential invasional meltdown have been previously hypothesized to be at play in the area, favoring the invasion of exotic fish (Lanzoni et al., 2018) through e.g. an increase of eutrophication effects. These mechanisms could further magnify the action of red swamp crayfish, creating a positive synergy among habitat engineering species. For example, bighead and silver carp (*Hypophtalmychthys* spp., L.) have been introduced in this area and found to be able to naturally recruit (Milardi et al., 2017). These fish are plankton feeders, with bighead carp feeding mainly on zooplankton (Dong and Li, 1994), and thus are potentially able to decrease zooplankton grazing pressure and increase phytoplankton blooms, ultimately favoring the red swamp crayfish. However, several exotic fish species are also active crayfish predators, so that the net outcome of these interaction is less than predictable. Common carp was one of the most abundant and widespread fish species in the canals (Castaldelli et al., 2013b; Milardi et al., 2017, 2018b; Lanzoni et al., 2018) and is well-known for its ability to resuspend nutrients from the sediment while feeding (Badiou and Goldsborough, 2015) but can also prey on smaller red swamp crayfish (Britton et al 2007, Lanzoni, unpublished data). Our data seems to suggest that the latter mechanism is predominant, as the presence in deeper watercourses of fish that prey upon crayfish (such as wels catfish or common carp) seemed to correlate negatively with crayfish abundance.

Besides mechanical mowing, also fish presence can influence the presence of aquatic vegetation. Resuspension of sediments by benthivorous fish can increases water turbidity, limiting the amount of light available to submerged vegetation (de Backer et al., 2010). Moreover, some fish can feed directly on aquatic macrophytes: grass carp (*Ctenopharyngodon idella,* Valenciennes 1844), an herbivorous fish capable of overgrazing aquatic plants (Cudmore and Mandrak, 2004), has been massively introduced in the area and found to naturally recruit (Milardi et al., 2015). In all waterways of the study area, submerged vegetation was indeed absent, while emergent vegetation was dominantly represented by reed *Phragmites australis* (Cav. Trin. ex Steud). Except for the early vegetative phase (in this area from early to mid-May), reed is a poor food item for fish or crayfish. Thus, vegetation positively influences red swamp crayfish density by providing habitat and shelter from fish (Carol et al., 2009; Musseau et al., 2015) and water birds (Huner, 2000) predation, rather than a food resource. In northern Italy, the grey and white herons and the little egret have become very abundant in the last decades, and are active predators of red swamp crayfish (Fasola et al., 2010; Fasola and Cardarelli, 2015) In the western portion of the Po River basin, red swamp crayfish has become an increasingly predominant food item in heron diet (Fasola and Cardarelli, 2015). Predation by water birds could be increased by the total absence of submerged vegetation, but higher water depths in winter should in turn decrease predation, by making crayfish less accessible to birds. However, our results show that minimum water depth seemed to favour, rather than limit, red swamp crayfish presence. Perhaps this indicates that fish predation is a stronger pressure than bird predation on the red swamp crayfish population.

5. Conclusions

Given the tight interplay between invasive red swamp crayfish, other exotic fish species, native bird predators and the environmental management of irrigation canals, it is clear that managing the crayfish invasion is a complex task. The invasion of red swamp crayfish is widespread in all Continental Europe, measures of containment have been proposed, but ultimately eradication appears unfeasible (Gherardi et al., 2011). Solving the red swamp crayfish conundrum would require extensive conservation measures, which are sadly not affordable due to current management budget constraints. Similarly, the use of pyrethroid substances to control the invasive crayfish population would have too high social and environmental costs. Thus finding alternative and low-cost management alternatives is of primary importance. However, the understanding of factors favoring the invasion may help to promote dedicated management to control the population in invaded areas and limit the colonization of new areas.

Our results clearly indicate that, in irrigation canals, hydraulic features and hydraulic management play a central role in favouring the presence of red swamp crayfish. If the canals could be excavated to increase depth and width, hydraulic transport would be enhanced and red swamp crayfish presence could be limited. Furthermore, agricultural management practices (i.e. hydraulic management) could also directly affect red swamp crayfish abundance. Fish predation could be enhanced by keeping higher water levels through the winter season, allowing a cost-effective control of red swamp crayfish density. However, fish predation pressure is now mostly given by exotic fish and managing exotic fish has been a generally troublesome undertaking, where several management and conservation issues have arisen (Milardi et al., 2018a,b).

Limiting the presence of some of the exotic ecosystem engineering fish species (e.g. common and grass carp) could favour native fish species conservation by increasing aquatic macrophytes that are used as a spawning substrate (Milardi and Castaldelli, 2018). Unfortunately this could also increase red swamp crayfish predation shelter, so that the ultimate outcome of such management is uncertain and would need to be field-tested.

Ultimately, a reasonable management for red swamp crayfish invasion would have to be ecosystem-based, taking into account all components of the aquatic and terrestrial environment and the socio-economic factors to delineate an optimal strategy.

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