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Research Article

The diet of the alien channel catfish *Ictalurus punctatus* in the River Arno (Central Italy)

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Received: 1 March 2018 / Accepted: 2 November 2018 / Published online: 12 November 2018

Handling editor: Michal Janáč

Co-Editors' Note:

This study was contributed in relation to the 20th International Conference on Aquatic Invasive Species held in Fort Lauderdale, Florida, USA, October 22–26, 2017 (<http://www.icaais.org/html/previous20.html>). This conference has provided a venue for the exchange of information on various aspects of aquatic invasive species since its inception in 1990. The conference continues to provide an opportunity for dialog between academia, industry and environmental regulators.

Abstract

The North American channel catfish *Ictalurus punctatus* has been widely introduced to Europe, but no in-depth studies on its ecology and potential impacts in the introduced European range have been carried out. In 2016, 248 specimens of *I. punctatus* were collected from the Arno river, Florence (Central Italy), and analysed for their length, weight, size, sex, and stomach contents to assess their diet. Specimens < 30 cm total length (TL) represented the majority of the sampled population. Detritus and phytoplankton dominated the diet, while in larger fish (≥ 30 cm TL) two invasive alien species, the topmouth gudgeon *Pseudorasbora parva* and the red swamp crayfish *Procambarus clarkii*, were dominant prey items. Diet composition of *I. punctatus* significantly varied among size classes, but not between sexes. The results indicate an opportunistic but gape size limited feeding behaviour, suggesting an intra-specific competition avoidance mechanism.

Key words: fisheries, freshwater, impact, feeding habit

Introduction

Europe has been a centre of globalization for the past two centuries making invasive species an increasing concern (Schulz and Della Vedova 2014). Increasing numbers of alien species introductions highlight the need for assessments to determine those that potentially pose invasive threats (Dukes and Mooney 1999; Walther et al. 2009; Vilà et al. 2010; Cucherousset et al. 2017). Managers and policy makers must thus allocate efforts to minimize the threat of more species becoming invasive (Keller et al. 2011). Scientific efforts should therefore focus not only on alien species that have already been classified as invasive,

but also on those that have yet to be assessed. One example in this respect is the multiple cases of alien catfish species negatively impacting recipient European freshwater ecosystems (Benejam et al. 2007; Leunda et al. 2008).

The channel catfish, *Ictalurus punctatus* Rafinesque, 1818 (Siluriformes: Ictaluridae), is native to North America where it is extensively cultured (Appelget and Smith 1951; Etnier and Starnes 2001; Olenin et al. 2008), widely distributed and provides both a major sport and food species (Tucker and Hargreaves 2004; Leonard et al. 2010). It inhabits a wide variety of ecosystem types and is highly tolerant of extreme environmental conditions (Dunham and Masser 2012).

It also shows an opportunistic feeding habit and high fecundity (Appleget and Smith 1951; Toole 1951; McMahon and Terrell 1982). In North America, several studies on its life history, growth, and reproduction as well as on its ecology and behaviour show predictable differences in diet among juveniles and adults (see e.g. Townsend and Winterbourn 1992; Adams 2007). In its native area, it is known for its opportunistic diet, negatively impacting populations of amphibians (Rosen et al. 1995) and threatened endemic fish species (Marsh and Douglas 1997).

Despite introduction and consequent establishment in 22 European countries (Welcomme 1988; Elvira and Almodóvar 2001; Copp et al. 2005), information and data on these introductions are scanty, and no in-depth studies focusing on *I. punctatus*' potential impacts in Europe have been conducted to support the initial literature (Welcomme 1988; Elvira and Almodóvar 2001; Copp et al. 2005; García-Berthou et al. 2005). In Italy, this catfish was first reported in 1986 in the river Oglio in the Northern part of the country (Gandolfi et al. 1991), while in the province of Florence in Central Italy, the area in which this study was conducted, the species was first recorded a decade later in 1998 (Nocita 2001). The species is currently considered established in Italy (Nocita and Zerunian 2007); however, studies until now only report its presence, without any information on population structure and possible impacts (Welcomme 1988; Tyus and Saunders 1996).

This Italian study is the first investigation of *I. punctatus*' diet in a European waterbody and includes size class, fish sex, habitat and seasonality in the assessment of this invasive catfish species.

Materials and methods

Sampling

Specimens of *Ictalurus punctatus* were collected in the inner-city section of the Arno river, Florence, Central Italy. The Arno is characterised by an irregular flow rate, a length of 241 km, a drainage basin of approximately 8,200 km² and a mean annual discharge of about 110 m³/s. It is considered the second most important freshwater river in Central Italy (Bartolomei et al. 2006), and it is inhabited by several alien species such as the European catfish *Silurus glanis* (Linnaeus, 1758), the pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758), the topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1846) and the red swamp crayfish *Procambarus clarkii* (Girard, 1852), while native species are considered rare in the studied ecosystem (see Nocita and Zerunian (2007) and Nocita (2007) for detailed species and fish community

information). Sampling was conducted two to three times per week at the same inner-city site (43°45'49.9"N; 11°18'04.2"E) from March to November 2016, the estimated active period for *Ictalurus*. To catch fish, standard fishing rods (2.20–3.90 m), monofilament line (0.22–0.36 mm) and size 2–26 fishing hooks baited with a variety of baits (maggots, worms, and freshly cut liver or bait-fish) were placed on the river bottom and mid-water. Captured fish were immediately laid on ice, and then transported to the Department of Biology and Natural History Museum's laboratory, "La Specola" in Florence.

Morphometry and population structure

Total lengths (TL, mm) were taken, wet weights (g) were measured, and sex of all specimens were determined using pelvic fin morphology, as female *I. punctatus* have two openings, whereas male fish develop just one (the anus) in addition to a small protruding fleshy flap (genital papillae) (Norton et al. 1976). We attempted to assess the maturity of each individual by conventional methods. For males, maturity was confirmed by the presence of white milt within the gonads. In the case of females, ovary maturity was determined based on i) one or more eggs containing yolk and ii) red capillary arteries as part on the circulatory system around the outside of the ovaries (De Silva 1973; Infa et al. 2015) as well as oocyte development, i.e. analysing if gonads demonstrate the capacity to ripen (Gordon Copp, *pers. comm.*).

During this assessment, however, maturity could not be determined for every specimen in our study due to the absence of gonads in some large (> 50 cm TL) specimens. For this reason, we instead chose size classes as a proxy for maturity. We set the "maturity" threshold at 30 cm (corresponding to maturity thresholds set in Appleget and Smith 1951; DeRoth 1965; Perry and Carver 1973). This threshold was chosen because in this survey we found no mature gonads [as defined by De Silva (1973) and Infa et al. (2015)] in fish < 30 cm total length. Size ranges of 7–29.9 cm TL were therefore designated as "immature" (n = 175) and 30–52 cm as "mature" individuals (n = 73).

To initially characterise the population, the length-weight relationship was plotted on a graph. As the data were not normally distributed, the distribution of length and weight of sampled specimens was compared between males and females using a non-parametric Mann-Whitney U-test to characterise population and enable comparisons with other populations. For the same purpose, frequencies of males/females and "maturity" stage ("mature"/"immature") were

compared using a chi-squared test to estimate if they significantly differ in numbers. The Fulton condition factor (K), generally used to compare populations, was applied using the formula $K = 100 * W / L^3$ (Nash et al. 2006) to better visualize length-weight relationship of this species outside its native region and to be available as a reference for future studies on *I. punctatus* outside its native area.

Dietary analysis

In the laboratory, stomachs were removed from the fish, and their content analysed (Zacharia and Abdurahiman 1974). Prey items were identified to the lowest possible taxa with a standard stereomicroscope and standard fish and invertebrate identification keys. Fragmented prey items were considered part of a whole organism and counted as such. Only number of occurrences of prey items was recorded. A comparison of prey composition was made for fish sex, maturity and sampling season. The nine months of sampling in 2016 were merged into three groups (spring: March–May; summer: June–August; autumn: September–November), resulting in a distribution of individuals among spring (n = 42), summer (n = 131) and autumn (n = 75; note no fish were caught in November). Diet was analysed as frequency of occurrence ($F\% = 100 * A_i / N$) where A_i was the number of fish containing prey item i and N the total number of fish analysed (excluding those with empty stomachs; Zacharia and Abdurahiman 2004). The diet breadth of the “mature” and “immature” sub-population was estimated, also for all seasons, based on Levin’s index formula (Whittaker et al. 1973): $B_i = \frac{1}{\sum p_i^2}$ where B_i is the standardized index of diet breadth for subpopulation i and $\sum p_i^2$ the sum of all squared proportions of individuals found with prey item i in their stomach, estimated by dividing the number of individuals containing prey item i by the total number of individuals sampled (Krebs 1998). To determine whether sample size was sufficient to describe the diet of non-native channel catfish in the Arno river, the cumulative number of prey taxa was plotted against the cumulative number of examined stomachs while analysed stomachs were randomized ten times (Ferry and Cailliet 1996; Ferry et al. 1997). Cumulative curves were considered to be asymptotic if ten previous values of the total number of prey taxa were within ± 0.5 of the range of the asymptotic number of prey, indicating the minimum sample size required to describe the diet (Cailliet et al. 1986; Cortés 1997; Huvencers et al. 2007). Because specimens yielded multiple prey taxa, prey composition was analysed using multivariate statistical methods. Fish without any stomach content (n = 16) were

excluded from the dataset and the analysis, resulting in 166 stomach contents (spring = 32; summer = 76; autumn = 58) from “immature” and 66 (spring = 7; summer = 48; autumn = 11) from “mature” specimens. A bivariate non-parametric Spearman-correlation was conducted between the total sum of different prey items found in the stomach and the total length of individual fish.

A presence/absence matrix was built including stomach content records from each sampled specimen and a Permutational Analysis of Variance (PERMANOVA; 3 orthogonal fixed factors: “maturity” [“immature”, “mature”] (threshold TL = 29.9 cm), “sex” [male, female] and “season” [spring, summer, autumn]); sums of squares: type III, partial; permutation of residuals under a reduced model) was used to test if the diet of the studied population differed according to the total length of specimens, the sex of individuals, the season or a combination of factors. A post-hoc test (pair-wise test) was included to identify differences between pairs of levels for each factor/factor interaction found significant by the PERMANOVA main test. Additionally, a Canonical Analysis of Principal Coordinates (CAP) for factors whose levels were found to be significantly different was applied, thus identifying the variables (i.e. prey items) contributing more consistently in differentiating the levels. Spearman correlations for each variable with CAP1 axis, the only one found informative in differentiating “mature”/“immature” specimens and the three seasons considered, are reported. PERMANOVA and CAP were performed using PRIMER v. 6 (Clarke 1993). For all tests, the level of significance under which the null hypothesis was rejected is $\alpha = 0.05$ and values are reported as median and interquartiles (i.e. the first and third quartile).

Results

Morphometry and population structure

Overall, 248 specimens of *I. punctatus* (females = 135, males = 113) ranging from 7 to 52 cm TL (Md = 23 cm, Q1–Q3 = 17–31 cm) were analysed (Figure 1). Males and females differed in TL (Mann-Whitney U-test, $U = 4.395$; $n = 248$; $p < 0.001$; females: Md = 27 cm, Q1–Q3 = 19–35 cm; males: Md = 20.8 cm, Q1–Q3 = 16–26.5 cm) and weight (Mann-Whitney U-test, $U = 4.607$; $n = 248$; $p < 0.001$; females: Md = 198 g, Q1–Q3 = 89–420 g; males: Md = 91 g, Q1–Q3 = 59–181.5 g) with females being longer and heavier. No significant difference for the overall number of sampled males and females was found (males = 45.5%; females = 54.5%; chi-square test, $\chi^2 = 0.9777$; $n = 248$; $p > 0.5$). The size of captured specimens was strongly

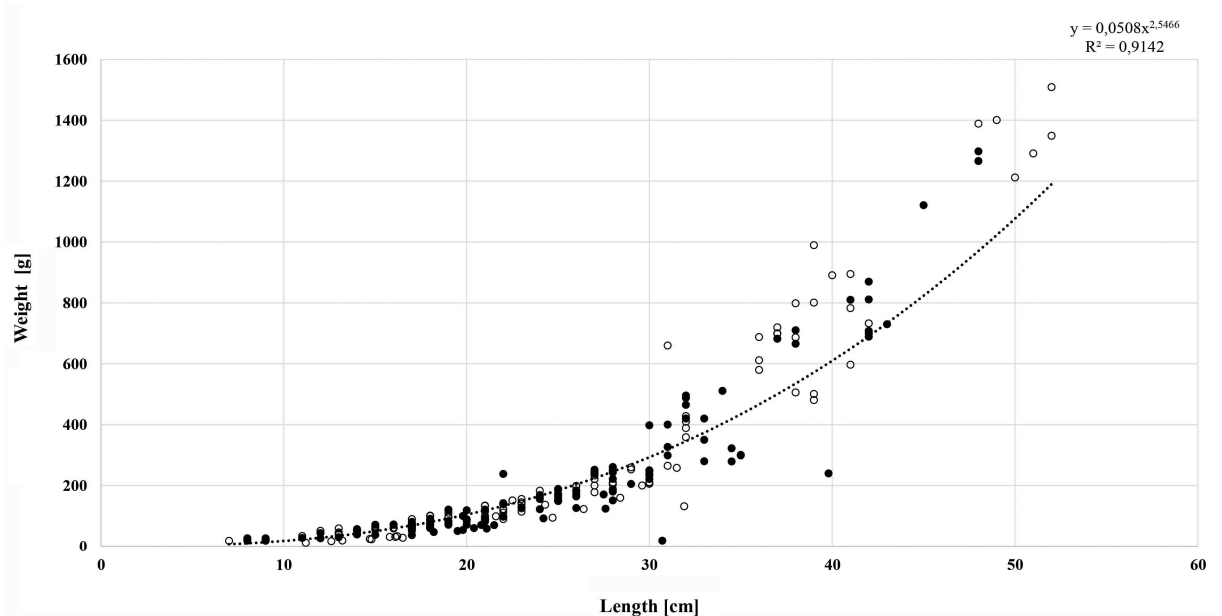


Figure 1. Growth curve for the overall sampled population of channel catfish, differentiating female ($n = 135$, open circles) and male ($n = 113$, filled circles) specimens.

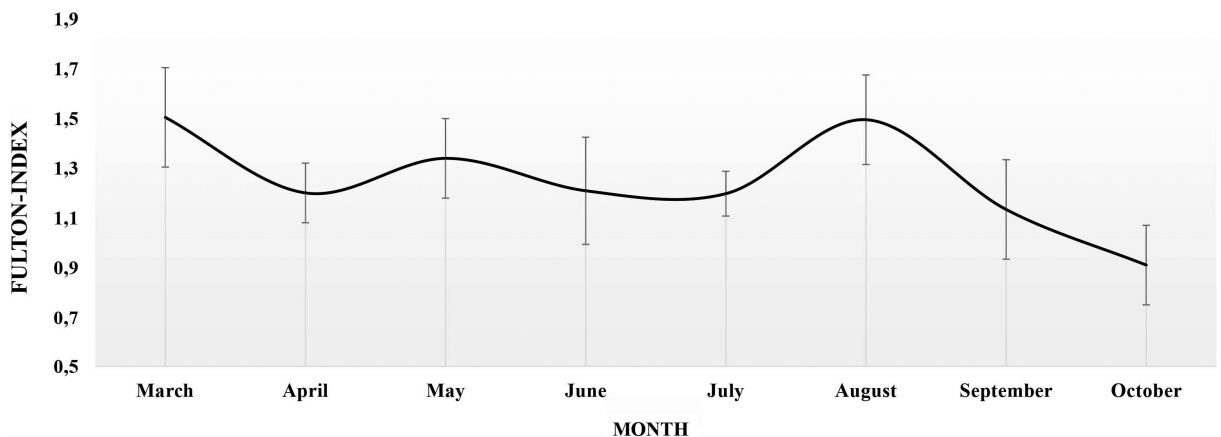


Figure 2. Development of the length-weight relationship in form of the estimated monthly Fulton-Index (mean \pm SD) over the activity period of caught specimens.

biased towards “immature” specimens under 30 cm, (“immature” = 70.6%; “mature” = 29.4%; chi-square test, $\chi^2 = 21.9$; $n = 248$; $p < 0.05$). The Fulton condition factor for the entire population was estimated between 0.07 and 5.27 (overall: Md = 1.174, Q1–Q3 = 0.936–1.424; females: Md = 1.123, Q1–Q3 = 0.904–1.326; males: Md = 1.256, Q1–Q3 = 0.981–1.640) and showed the highest values in March (Md = 1.526, Q1–Q3 = 1.157–1.814) and the lowest in in September (Md = 0.887, Q1–Q3 = 0.717–1.370) (Figure 2).

Dietary analysis

Overall, 16 invertebrate and fish prey taxa were identified (Table 1). The plotted cumulative prey curve for total number of prey taxa reached the asymptote after 74 stomachs (Figure 3). A significant correlation was found between the total number of individual prey items in catfish stomachs and fish size (TL) ($r_s = -0.129$; $n = 232$; $p < 0.043$), showing that larger fish generally had fewer prey items in their stomach. On the other hand, the diet breadth for “immature” ($B_{\text{immature}} = 10.8$) and for “mature” fishes

Table 1. Frequency of occurrence (%) for observed prey items according to season in “immature” specimens (n = 166), “mature” specimens (n = 66) and overall sampled specimens (n = 232).

Prey	Total	“Immature”			“Mature”				
	n=232	Overall n=166	spring n=32	summer n=76	autumn n=58	Overall n=66	spring n=7	summer n = 48	autumn n = 11
Fish									
<i>Pseudorasbora parva</i>	29.7	19.0	56.3	11.8	8.6	56.0	14.3	58.3	81.8
Unid. fish larvae	8.2	8.4	6.3	9.2	8.6	7.5	28.6	6.3	0.0
<i>Cyprinus carpio</i>	6.0	1.8	3.1	1.3	3.4	16.4	28.6	6.3	27.3
<i>Lepomis gibbosus</i>	4.7	1.8	6.3	0.0	1.7	11.9	0.0	14.6	0.0
<i>Gobio gobio</i>	0.4	0.0	0.0	0.0	0.0	1.5	0.0	2.1	0.0
Crustacean									
<i>Procambarus clarkii</i>	17.6	10.2	15.6	11.8	5.2	35.8	28.6	39.6	9.1
<i>Paleomonetes</i>	10.3	12.0	21.9	10.5	10.3	6.0	0.0	4.2	9.1
<i>Dikerogammarus villosus</i>	6.9	8.4	12.5	3.9	10.3	3.0	0.0	2.1	0.0
Amphibian									
<i>Tadpoles</i>	1.7	0.6	0.0	1.3	0.0	4.5	0.0	6.3	0.0
Molluscs									
<i>Sinanodonta woodiana</i>	0.4	0.6	0.0	0.0	1.7	0.0	0.0	0.0	0.0
<i>Radix auricularia</i>	0.4	0.6	0.0	0.0	1.7	0.0	0.0	0.0	0.0
Insects									
<i>Coleoptera</i>	18.5	22.9	15.6	17.1	34.5	7.5	14.3	6.3	0.0
Unid. insect larvae	10.3	13.9	3.1	14.5	19.0	1.5	0.0	2.1	0.0
<i>Heteroptera</i>	8.6	10.8	15.6	10.5	8.6	3.0	0.0	2.1	9.1
<i>Diptera</i>	5.6	6.6	0.0	3.9	13.8	1.5	14.3	0.0	0.0
<i>Hymenoptera</i>	5.6	6.0	6.3	6.6	5.2	4.5	0.0	6.3	0.0
Fragments of insects	3.9	5.4	3.1	9.2	1.7	0.0	0.0	0.0	0.0
<i>Odonata</i>	3.4	3.0	6.3	3.9	0.0	4.5	0.0	4.2	9.1
<i>Dermoptera</i>	0.9	0.6	0.0	0.0	1.7	1.5	0.0	2.1	0.0
Other									
<i>Detritus</i>	55.8	66.9	59.4	63.2	75.9	28.4	42.9	22.9	36.4
<i>Algae</i>	48.5	58.4	53.1	75.0	37.9	23.9	42.9	18.8	36.4
<i>Phytoplankton and terrestrial plants</i>	28.8	32.5	50.0	22.4	37.9	19.4	14.3	20.8	9.1
<i>Detergent</i>	25.3	31.3	6.3	7.9	6.9	10.4	14.3	10.4	9.1
<i>Plantseeds</i>	7.3	9.0	18.8	22.4	50.0	3.0	0.0	4.2	0.0

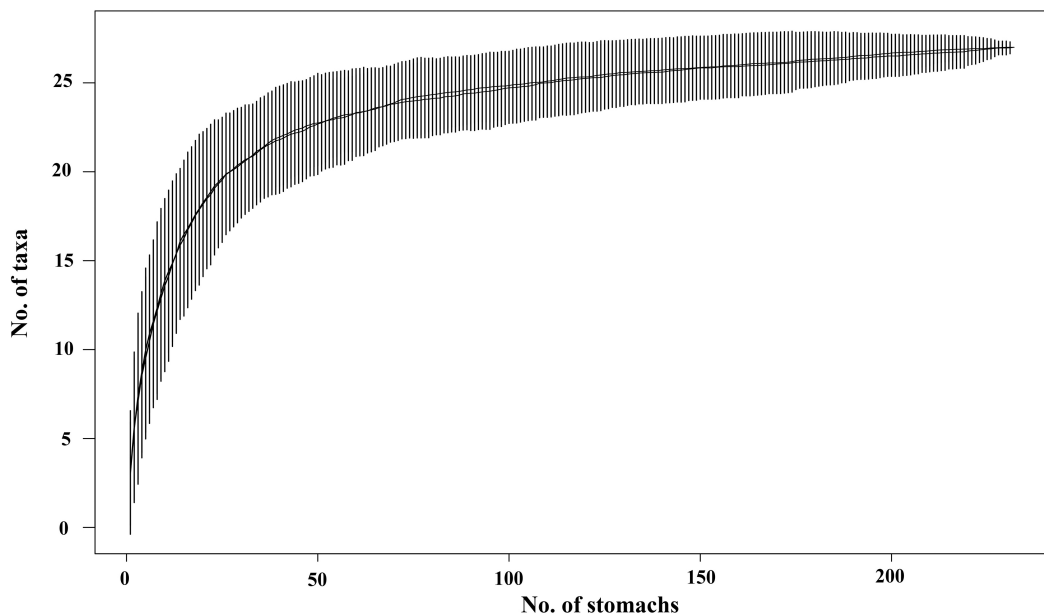


Figure 3. Cumulative prey curve displaying prey taxa per stomach for *Ictalurus punctatus* collected in Arno river in Florence, Central Italy (n = 232). Error bars represent standard deviations.

($B_{\text{mature}} = 10.7$) was almost identical. Seasonally, the diet breadth for “mature” and “immature” catfish was similar in spring ($B_{\text{mature} \times \text{spring}} = 9.4$; $B_{\text{immature} \times \text{spring}} = 9.0$) and summer ($B_{\text{mature} \times \text{summer}} = 8.6$; $B_{\text{immature} \times \text{summer}} = 8.1$), while immature fish expressed a higher diet breadth in autumn ($B_{\text{mature} \times \text{autumn}} = 5.3$; $B_{\text{immature} \times \text{autumn}} = 9.7$). The most common prey items found in stomachs was detritus, followed by algae and plants. Generally, detritus, algae and plants were found to occur in higher percentages in “immature” rather than in “mature” specimens (Table 1). The most common animal prey found in “immature” fish were the topmouth gudgeon *Pseudorasbora parva* and Coleoptera, while in “mature” fish *P. parva* and the red swamp crayfish *Procambarus clarkii* were most common. Also, a high frequency of white “crumbs” with the consistency of soap products, visually and gustatorily detected as detergent (P. Haubrock, *pers. obs.*), occurred in the stomach contents of “immature” fish. Overall, *P. parva*, Coleoptera and *P. clarkii* were major contributors to the diet of *I. punctatus* (Table 1).

The PERMANOVA main test confirmed differences for the interaction between the factors “maturity” and “season” (Table 2), with no inter-sex differences (i.e. no differences in item composition between males and females). In particular, post-hoc tests revealed that in “immature” fish, the diet differed significantly according to season, while a significant difference for “mature” fish occurred only between summer and autumn (Table 3). Moreover, focusing on each season level, significant differences in diet (i.e. item composition) of “immature” and “mature” fish were found in summer and autumn, but not in spring (Table 3). The CAP1 and 2 axes (squared canonical correlation of $\delta_1^2 = 0.484$ and $\delta_2^2 = 0.183$, respectively), with an overall mis-classification error of 48.28% (i.e. reallocation of each sample to the right level of the factor), only partially separated the groups of specimens identified by the combination of factor “maturity” and “season” (Figure 4). Correlation of variables’ scores on the CAP1 axis revealed detritus ($r_s = -0.63$), detergent ($r_s = -0.56$) and Coleoptera ($r_s = -0.39$) as major variables in characterizing “immature” specimen diet (negative sector of CAP1 axis), especially in summer and autumn, while *P. parva* ($r_s = 0.66$) and *P. clarkii* ($r_s = 0.40$) highly characterized “mature” specimen diet in summer and spring (positive sector of CAP1 axis). Correlations with CAP1 and the other variables ranged from -0.23 to 0.14 , therefore cannot clearly characterize identified groups, and are thus not reported in the text (Supplementary material Table S1). CAP2 axis was not considered for further analysis, due to its low power in discriminating groups and inconsistent correlations

Table 2. Results of PERMANOVA on stomach content of collected specimens. The value of F statistic and its probability values P (after Monte Carlo correction) are shown together with degrees of freedom (df) and mean squares (MS). Significant differences are marked with (*).

Source	df	MS	Pseudo-F	P(perm)
Season	2	13001	5.1548	0.001*
Sex	1	3595.4	1.4255	0.221
Maturity	1	19933	7.9032	0.001*
Season x sex	2	3326.5	1.3189	0.211
Season x Maturity	2	5423.1	2.1502	0.012*
Sex x Maturity	1	5399.2	2.1407	0.068
Season x sex x Maturity	2	1992.9	0.79017	0.647
Res	220	2522.2		
Total	231			

Table 3. Results of pairwise comparison (PERMANOVA) after significant differences founded in the interaction between TL and season on stomach content of collected specimens. The value of t and its probability values P (after Monte Carlo correction) are shown. Significant differences are marked with (*).

Source	t	P(perm)
Within level “immature” of factor “TL”		
spring, summer	2.4849	0.001*
spring, autumn	2.9868	0.001*
summer, autumn	2.7633	0.001*
Within level “mature” of factor “TL”		
spring, summer	0.66594	0.751
spring, autumn	1.2633	0.171
summer, autumn	2.1626	0.001*
Within level “spring” of factor “season”		
“immature vs. mature”	0.68573	0.439
Within level “summer” of factor “season”		
“immature vs. mature”	4.388	0.001*
Within level “autumn” of factor “season”		
“immature vs. mature”	1.634	0.031*

with variables, despite a unique high inverse correlation with algae ($r_s = -0.86$), that characterised specimens from the negative sector of the CAP2 axis (Figure 4).

Discussion

This study showed an imbalanced *I. punctatus* population structure in the inner-city section of the Arno river in Florence, with more “immature” individuals representing a young population present, suggesting stable reproduction and a well-established population, similar to observations from native populations in North America (Holland and Peters 1992). Also, females were significantly longer and heavier than males, matching the sexual dimorphism described in native populations (Wang 1986). The Fulton conditional index for both sexes was higher compared to specimens analysed in other North American studies

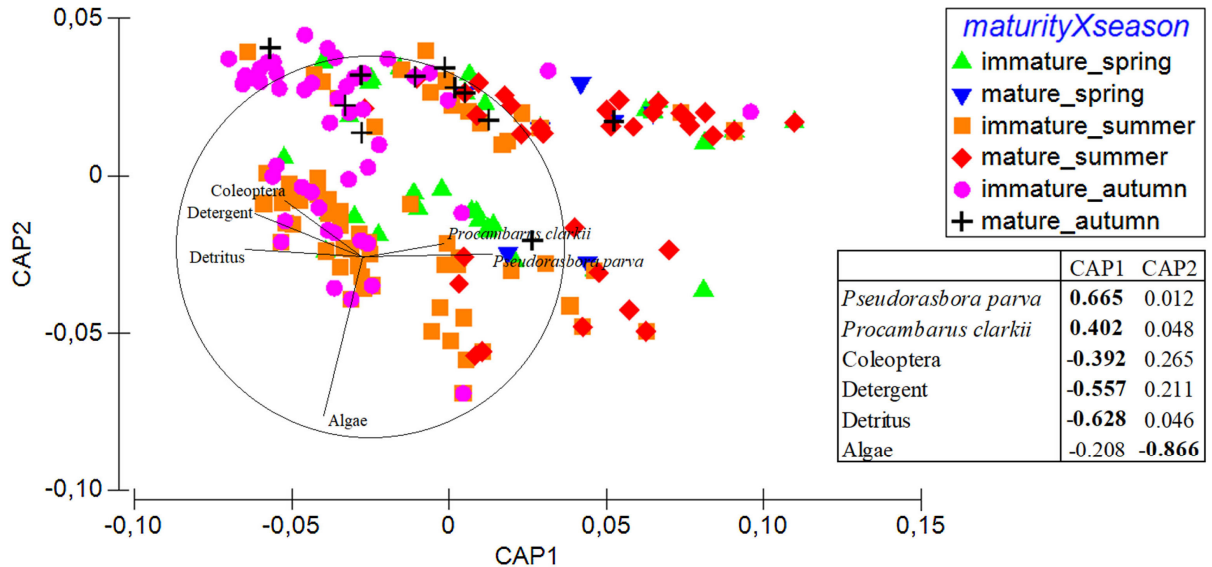


Figure 4. Two-dimensional scatter plot of the first and second principal coordinates axis (after resemblance matrix with Sørensen distance on presence/absence matrix of data, n samples = 232, n variables = 26) for “maturityXseason”, a combination of factor “maturity” (“immature”, “mature”) and “season” (spring, summer, autumn). Vectors of the linear correlations between individual variables are superimposed on the graph (only those with Spearman correlation index >0.4 are shown) and are listed in the lower right of the figure.

(see e.g. 0.62–0.73, Holland and Peters 1992; 0.77, Mesa and Rose 2015). This could be due to increased linear growth (without a simultaneous rapid weight growth) or a fundamentally different growth pattern in the Arno, an introduced habitat, possibly due to environmental factors (availability of prey, longer activity time, temperature, etc.). A link between growth and water temperature has been also suggested for *I. punctatus* in Japan (Endo et al. 2017) and was observed in non-native populations of the black bullhead *Ameiurus melas* (Copp et al. 2016). Nonetheless, the Fulton index has also been identified as an indicator for migratory behaviour (Gillanders et al. 2015). Because channel catfish are known to reduce their feeding activity in relation to falling ambient temperatures, the observed low Fulton index values in September may indicate a potential fall migration for adult and sub-adult catfish (Pellett et al. 1998), while low values between April and July but also in September could relate to periods of breeding (Peters et al. 1992). An adaptation towards secondary reproductive phases has been described for several alien fish species (Copp and Fox 2007), but never from North American Siluriformes in Europe.

The stomach content analysis showed a wide and opportunistic feeding habit of channel catfish, without any differences between sexes, but did reveal a difference between lifestages. With increasing size, the total sum of stomach contents decreased, likely due to changing prey composition. “Mature” fish expressed

a more piscivorous diet typical for this species (Hubert 1999). Detritus with algae and Coleoptera represented the most frequent non-animal and animal portion of the diet respectively in “immature” fish, confirming that they forage close to the river bank in reed areas, where algae are present (Endo et al. 2015). In “mature” fish, detritus and algae were less frequent, while the invasive species, *P. clarkii* and *P. parva*, were major dietary contributors. As the crayfish *P. clarkii* is benthic, whereas *P. parva* is found occupying the middle and upper water layers (Gozlan et al. 2010; Čech and Čech 2011), the mature catfish in the Arno site are likely to be predators both on the benthos and throughout the water column as previously recorded for *I. punctatus* in other areas (Heard 1958; Poe and Rieman 1988; Townsend and Winterbourn 1992; Matsuzaki et al. 2011).

Dietary variation according to age and size classes are commonly related to idealized energy intake, especially as the diets of fish are partitioned by life history to lower potential intra-specific competition (Flecker 1999; Couture and Pyle 2015). This may be especially true for opportunistic channel catfish (Busbee 1968), which exhibit varying predation according to predator size, higher mobility, and predation in open water by adult specimens and also by availability of prey (Robinette and Knight 1981; Boersma et al. 2006; Matsuzaki et al. 2011). In our case, dietary differences and proposed implications for the frequented habitat are indeed potentially

linked to gape-limited predation (Nowlin et al. 2006; Johnson et al. 2008; Slaughter and Jacobson 2008). *Pseudorasbora parva* occurred in both mature and “immature” specimens, although with low frequency in the smaller catfish. This could be explained both by optimal foraging behaviour in *I. punctatus* with their capacity to predate small sized or ailing fish (~ 3 cm), and by the developmental threshold for gape size to consume *P. parva*, suggesting an intra-specific competition avoidance mechanism.

It is likely that the observed diet change in “mature” specimens would not be observable without the presence of *P. clarkii* and *P. parva*, both being highly invasive and frequently abundant species (Gherardi and Acquistapace 2007; Nocita and Zerunian 2007; Britton et al. 2010). The applied CAP analysis underlines the importance of *P. clarkii* and *P. parva* in the diet of *I. punctatus*, as both these prey items characterize the diet of “mature” specimens while also contributing to the diet of “immature” catfish. The significance of *P. clarkii* and *P. parva* for “mature” specimens was apparent especially in spring and summer, the activity peak of these two species, although they were less frequent in the diet of “immature” individuals during summer and autumn. Especially in summer, populations of *P. parva* and *P. clarkii* can reach high densities in the Arno river, although considerably lower than observed in standing water bodies (Correia and Ferreira 1995; Gozlan et al. 2010; Gherardi and Acquistapace 2007). Therefore, it is no surprise that both prey items were frequently consumed by “mature” catfish in summer, and in the case of *P. parva* also in autumn. These results are furthermore consistent with studies from Lake Kitaura, Japan, where it was shown that invasive channel catfish exerted heavy predation on *P. clarkii* and *P. parva* opposed to available native prey (Endo et al. 2015). The highest frequency of *P. parva* in “immature” *I. punctatus* was observed in spring, coinciding with the lowest frequency of this prey items in the diet of “mature” fish. This can possibly be explained by spring habitat use shift in *P. parva*, which at this time typically searches for suitable spawning substrate such as plants or structure close to the river banks, i.e. the parts of the river, where most of the other prey items of “immature” *I. punctatus* occur. *Procambarus clarkii* was less frequently found in the diet of both “mature” and “immature” catfish caught in autumn, which is possibly linked to a changing habitat use of *P. clarkii* in autumn due to rising water levels (Correia and Ferreira 1995).

The only season, in which PERMANOVA detected similar diet for “mature” and “immature” *I. punctatus* was spring, which is likely based on the high occurrences of detritus and algae in both subpopulations as

revealed by the post-hoc PERMANOVA. Although fish generally tend to prey on the most available and easy to obtain as well as energetically valuable prey (Vanni 1987; Gill 2003), it is unlikely that these similar diets of “immature” and “mature” fish during spring can be based solely on the availability of prey items. More likely, it can be assumed that higher levels of water and oxygen (respectively increasing water temperature) in spring lead to higher activities of all catfish and, thus, lower selectivity in all catfish. Additionally, “mature” catfish are likely to increase their energy intake after decreased rates of physiological processes due to colder temperatures during the winter and in preparation for the reproductive season (Kim and Lovell 1995), potentially explaining the high occurrences of algae and detritus, as both items are present in high quantities and are easily accessible. Although regular consumption of algae with potentially positive physiological effects on weight gain has been observed in other studies of this species (Lilyestrom et al. 1987; Tyus and Nikirk 1990; Guerry et al. 2009; Li et al. 2009), it is possible that catfish consume algae and detritus because of the lack of other, more energetically valuable prey, or in their search for any potential energy source prior to spawning. Seasonally, the flow regime changes from high water level and strong current in winter towards low water level and almost stagnation in summer, between river weirs; while increased water temperature leads to increasing catfish activity and the abundance of potential prey.

Our study furthermore shows an unusual high frequency of detergent in summer and autumn, likely remains of water pollution or filter attempts by sewage disposal facilities (Annamaria Nocita, *pers. comm.*) undermining the dominant benthic feeding. Detergent in stomach contents could generally be described as “accidental ingestion” that could potentially also occur in other fish species feeding on the river bottom (e.g. the common carp *Cyprinus carpio*). Nonetheless, the ingestion of detergent, as observed by Mahajan and Singh (1973), leads to pronounced “spitting” and decreasing appetite, resulting in fish starving rather than feeding on detergent treated prey items (Gupta et al. 1983). However, commercially available soap has been successfully used to catch *I. punctatus* in its native range and in the Arno river (P. Haubrock, *pers. comm.*) but has not been described for any species so far, raising the question of whether *I. punctatus* willingly ingests detergents found on the river bottom and how it might be affected by it. The occurrence of detergent in the diet of catfish clearly needs further investigation.

In conclusion, channel catfish and especially the “mature” fish in this study frequently feed on invasive

alien species during summer and autumn in this highly-invaded environment, which is seemingly a common behaviour in alien fish species (Copp et al. 2009). Interestingly, these prey species are also major prey items of other predators such as the Wels catfish *Silurus glanis* (Carol-Bruguera 2007; Copp et al. 2009). The wide-ranging feeding habit, with “immature” specimens feeding on algae and detritus and “mature” specimens feeding on higher invertebrates (and to some degree on highly abundant *P. clarkii* and *P. parva*), potentially lowers intra- and inter-specific competition between co-occurring species and other life stages (Tyus and Nikirk 1990; Townsend and Winterbourn 1992; Copp et al. 2004; Simberloff and Von Holle 1999). Therefore, it would be interesting to investigate the relationship between *I. punctatus* and competitors such as *S. glanis* in respect to possible overlaps in feeding niches, especially considering observed declines in *S. glanis* populations after introductions of *I. punctatus* (Annamaria Nocita, pers. comm.). Additional studies including more data from different European ecosystems and a more detailed assessment of reproduction are needed. Finally, potential relationships with other alien species and thus varying feeding dynamics and the occupied ecological role in invaded communities should be analysed, to gain a better understanding of this species potential impacts on recipient ecosystems.

Acknowledgements

We would like to thank Dr. Kit Magellan for initial improving comments on an earlier version of the manuscript and Dr. Michal Janáč for his time and dedication to improve the quality of this work. Lastly, we thank Prof. Frances Lucy for proofreading. Funding was provided by the Aquainvad-ED project (2020 Marie Skłodowska-Curie ITN-2014-ETN-642197).

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Supplementary material

The following supplementary material is available for this article:

Table S1. List of variables (n=26) used for PERMANOVA tests, along with the correlation (Spearman rank correlation r_s) with CAP1 and CAP2 axis of the Canonical Analysis of Principal Coordinates performed.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Haubrock_etal_Table_S1.pdf