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SHORT COMMUNICATION — OPEN ACCESS

Long term patterns in the late summer trophic niche of the invasive pumpkinseed sunfish *Lepomis gibbosus*

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Abstract – Quantifying the trophic dynamics of invasive species in novel habitats is important for predicting the success of potential invaders and evaluating their ecological effects. The North American pumpkinseed sunfish *Lepomis gibbosus* is a successful invader in Europe, where it has caused negative ecological effects primarily through trophic interactions. Here, we quantified variations in the late summer trophic niche of pumpkinseed during establishment and integration in the mainstem of the Guadiana river, using stomach content analyses over a period of 40 years. Pumpkinseed showed a shift from trophic specialization during establishment to trophic generalism during integration. These results were concomitant with an increase in diet breadth that was accompanied by higher individual diet specialization particularly in large individuals. Irrespective of their drivers, these changes in trophic niche suggest that the potential ecological effects of pumpkinseed on recipient ecosystems can vary temporally along the invasion process.

Key-words: invasive species / trophic niche / diet shift / diet breadth / individual diet specialization

Résumé – Tendances à long terme de la niche trophique estivale de la perche soleil *Lepomis gibbosus* invasive. La quantification de la dynamique trophique des espèces envahissantes dans leur aire d'introduction est importante pour prédire leur succès d'invasion et évaluer leurs potentiels effets écologiques. La perche soleil – *Lepomis gibbosus* – est une espèce originaire d'Amérique du Nord qui a été largement introduite en Europe où elle induit des effets écologiques négatifs principalement par des interactions trophiques. Dans cette étude, nous avons quantifié les variations de niche trophique de la perche soleil en fin d'été pendant les phases d'établissement et d'intégration dans le cours principal de la rivière Guadiana (Portugal) en comparant des contenus stomacaux sur une période de 40 ans. Nos résultats ont permis de démontrer que la perche soleil a modifié son régime alimentaire durant cette période en passant d'un régime spécialiste pendant la phase d'établissement à un régime généraliste pendant la phase d'intégration. En parallèle, nous avons également observé une augmentation de la taille de la niche trophique de la population qui était accompagnée d'une augmentation de la spécialisation trophique individuelle, notamment chez les individus les plus grands. Indépendamment des causes induisant ces changements de niche trophique, nos résultats suggèrent donc que les effets écologiques potentiels de la perche soleil sur les écosystèmes aquatiques peuvent varier pendant le processus d'invasion biologique.

Mots-clés : espèce envahissante / niche trophique / régime alimentaire / spécialisation trophique individuelle

Understanding the trophic dynamics of invasive species is crucial, as it can yield insights about the mechanisms of invasion success and the potential impacts of established invaders. The impact of an invasive species does not necessarily remain constant over the course of invasion and changes in competition and resource availability may increase or attenuate the impact of invaders on the recipient ecosystem (Strayer *et al.*, 2006; Strayer, 2012). For instance, increases in trophic niche size may enhance invasion success (Tilberg *et al.*, 2007), as the ability of invaders to exploit larger ranges of food resources may have positive effects on their dispersal and population dynamics (Kolar and Lodge, 2001; Vázquez, 2006). However, this is likely to affect a greater proportion of the native recipient community, either by promoting shifts towards use of unexploited resources (Grey and Jackson, 2012) or by increasing overlap in niche space of individual species (Shea and Chesson, 2002) and thus resulting in increased interspecific competition. Conversely, reductions in trophic niche size of

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invasive species may lead to trophic divergence from natives, which would facilitate the invader's integration into the community and their coexistence with native recipient community (Tran *et al.*, 2015). Therefore, quantifying the temporal patterns in trophic niche of invasive species is critical for understanding whether the consequences of the invasion on recipient communities and ecosystems may change over time.

Here we focused on variations in the trophic niche of pumpkinseed sunfish *Lepomis gibbosus* during its invasion of the mainstem of the Guadiana river (Portugal). Recognized as one of the most invasive fish in Europe (Fox and Copp, 2014), pumpkinseed were introduced about 40 years ago to the Western Iberian Peninsula, becoming a major, ecologically damaging invader (García-Berthou and Moreno-Amich, 2000). Trophic plasticity is common among introduced pumpkinseed populations (Bhagat *et al.*, 2011) and has been associated with its local success and the decline of native fish and prey diversity (Almeida *et al.*, 2009). However, there is scarce evidence of diet variation over the invasion process making it difficult to evaluate whether ecological effects of pumpkinseed may change over time. The specific objectives of this study were (i) to quantify the temporal variations in the trophic niche of pumpkinseed and (ii) to determine whether trophic niche size changed over the invasion process.

Historical and contemporary dietary data were combined, covering the establishment (1985) and integration (2003 and 2013) stages of pumpkinseed invasion in the Guadiana river (Western Iberian Peninsula). During establishment, sampling was conducted at two neighboring sites in the mainstem of the Guadiana river (38°1′38"N; 7°38′38"W), and during the integration stage, we sampled at the proximate center between the two first sites. Riverine habitats were similar among sites, with local conditions being described in detail in Domingos (1986) and Ribeiro *et al.* (2007). Although native barbels (*Luciobarbus* spp.) likely dominated the fish assemblages over the study period, pumpkinseed has become increasingly widespread and locally abundant (Godinho *et al.*, 1997a; Ribeiro and Collares-Pereira, 2010).

Each year, sampling was conducted late in summer (September), when prey availability is generally low and dietary plasticity may play a major role in shaping both inter- and intra-specific relationships in Iberian fish assemblages (Magalhães, 1993). At each 200-m site, pumpkinseed were sampled by electrofishing in all available habitats and immediately frozen. In the laboratory, individuals were measured for standard length (SL, mm), and stomach contents were analyzed under a binocular microscope. Prior to analysis, stomachs were screened for fullness, and empty stomachs were excluded from subsequent analyses. Prey items were identified to the lowest possible taxonomic level and counted. Since previous studies have reported marked variation in diet throughout ontogeny (Godinho *et al.*, 1997b), we conducted separate analyses for small (30−60 mm SL) and large (61−90 mm SL) individuals, with the former generally being immature (Ribeiro and Collares-Pereira, 2010). Prey were grouped into categories, based on their taxonomic linkage, percentage of occurrence and relative abundance in the diet, so that each category contributed >1% to the total prey items in at least one year and for one of the size classes.

Interannual variations in prey relative abundance in the diet were analyzed using non-metric multidimensional scaling (NMDS) and the Bray-Curtis dissimilarity index (Clarke and Gorley, 2006). Ordination was interpreted in ecological terms for stress values <0.2. Prior to analysis, data were square-root transformed to reduce the influence of abundant prey and to overcome the unity-sum constraint, and then submitted to Wisconsin double standardization to improve the gradient detection of the Bray-Curtis dissimilarity index (Clarke and Gorley, 2006). Analysis of similarity (ANOSIM) was used to assess differences in diet between years with overall significance level corrected for multiple testing using the Bonferroni sequential correction. Similarity Percentage (SIMPER) analysis was used to identify prey categories with the highest contribution to diet dissimilarity. Prey categories were listed in decreasing order by their mean contribution to the total average dissimilarity, with a cut-off at 50% of cumulative average dissimilarity (Clarke and Gorley, 2006). Population diet breadth was determined for each year using the Shannon-Wiener index (H; Levins, 1968), which is maximized when the population uses more prey more evenly (Colwell and Futuyama, 1971). Likewise, the degree of individual diet specialization was determined using the index of individual specialization (IS; Bolnick *et al.*, 2002), which declines towards zero when individuals use smaller subsets of the population diet and equals 1 when all individuals consume the full set of population diet. Estimates for both indices were obtained using bootstrapped 95% confidence intervals (1000 permutations). All analyses were conducted using R (v3.0.1, R Development Core Team, 2014) and the Primer software v6.

A total of 62 stomachs and 5839 prey items were analyzed. Percentage of occurrence data indicated that chironomids were the most frequent encountered prey, with trichoptera, hemipterans and ephemeropterans also present, though in differing frequencies between them (Table 1). Copepods and cladocerans were also taken frequently by *L. gibbosus*, being highly apparent in 2003 (Table 1). The relative abundance of chironomids was high in the diet of pumpkinseed in 1985 and 2013 (Table 1). However, in 2013, hemipterans were also abundant in the diet of both size classes and ephemeropterans in the diet of large individuals. Copepods dominated the diet of pumpkinseed in 2003 but were seldom consumed in the other years. Cladocerans were important only in the diet of small individuals in 1985 and 2003 (Table 1).

Diet composition varied significantly among years, with 2003 being significantly dissimilar from 1985 and 2013 (Figure 1). Dissimilarity in diet among years for both size classes resulted from variation in the numeric frequency of several prey categories, with chironomids having the most consistent contribution (Table 2). Dissimilarity in the diet of small individuals between 2003 and both 1985 and 2013 reflected increases in the consumption of copepods and cladocerans. Copepods were also important in differentiating the diet of large individuals between 1985 and 2013, with less chironomids and more hemipterans and ephemeropterans being consumed through time. Similar patterns were found for diet dissimilarity between 2003 and 2013 in large individuals with the decrease in the proportions of copepods and chironomids and the increase of ephemeropterans (Table 2).

Table 1. Variation in the numeric frequency (%) and percentage of occurrence (%, in parentheses) of prey categories consumed by small (30−60 mm SL) and large (61−90 mm SL) pumpkinseed *Lepomis gibbosus* during the establishment (1985) and integration (2003 and 2013) stages of the invasion in the mainstem of the Guadiana river (Portugal). Prey categories with numeric frequencies >20% are highlighted in bold.

	1985		2003		2013		Overall
Size range (SL, mm)	Small fish (30−60)	Large fish (61−90)	Small fish (30−60)	Large fish (61−90)	Small fish (30−60)	Large fish (61−90)	
Chironomidae	**51.0** (95.7)	**93.9** (100.0)	4.4 (50.0)	12.4 (57.1)	**54.5** (100.0)	**41.7** (100.0)	**38.7** (83.1)
Cladocera	**29.7** (26.1)	0.1 (20.0)	**38.3** (100.0)	12.6 (100.0)	2.7 (33.3)		**20.0** (44.1)
Trichoptera	6.6 (73.9)	1.3 (80.0)		1.6 (57.1)	1.8 (16.7)	0.4 (14.3)	2.9 (45.8)
Hemiptera	4.8 (30.4)	1.4 (80.0)	9.4 (30.0)	7.0 (71.4)	**23.2** (100.0)	**26.8** (100.0)	7.7 (54.2)
Copepoda	4.1 (21.7)		**45.2** (100.0)	**64.8** (100.0)	8.9 (50.0)	0.2 (14.3)	**25.6** (44.1)
Ostracoda	1.4 (34.8)	0.8 (80.0)	0.1 (10.0)	0.1 (14.3)			0.6 (23.7)
Hydracarina	1.0 (8.7)				1.0 (16.7)		0.3 (5.1)
Ephemeroptera	0.6 (34.8)	0.2 (20.0)		0.4 (28.6)	4.5 (33.3)	**30.6** (100.0)	2.8 (33.9)
Mollusca	0.4 (21.7)	1.3 (40.0)	1.6 (60.0)				0.6 (22.0)
Other prey	0.3 (26.1)	0.9 (80.0)	0.9 (50.0)	1.1 (85.7)	3.4 (50.0)	0.3 (14.3)	0.8 (42.4)
Total fish	21	7	10	9	7	8	62

Table 2. Results of ANOSIM and SIMPER analyses showing prey categories with the highest contribution (%) to between-year average dissimilarity (AvD) in the diet of small (30−60 mm SL) and large (61−90 mm SL) pumpkinseed during the establishment (1985) and integration stages (2003 and 2013) of the invasion in the mainstem of the Guadiana river (Portugal). Rank order of contribution is represented in parentheses.

	AvD	Copepoda	Chironomidae	Cladocera	Hemiptera	Ephemeroptera	Trichoptera
Between years							
Small fish (R = 0.578; P < 0.001)							
1985 *vs.* 2003 (R = 0.665; P < 0.001)	77.40	24.14 (1)	19.86 (3)	22.03 (2)			
1985 *vs.* 2013 (R = 0.348; P = 0.005)	61.18		21.75 (1)		18.09 (2)		16.12 (3)
2003 *vs.* 2013 (R = 0.843; P = 0.002)	72.86	26.44 (2)		27.31 (1)			
Large fish (R = 0.779; P < 0.001)							
1985 *vs.* 2003 (R = 0.687; P = 0.003)	66.24	25.42 (1)	25.36 (2)				
1985 *vs.* 2013 (R = 0.995; P < 0.001)	53.60		20.57 (2)		15.83 (3)	28.62 (1)	
2003 *vs.* 2013 (R = 0.796; P = 0.002)	68.13	25.06 (1)	14.77 (3)			20.76 (2)	

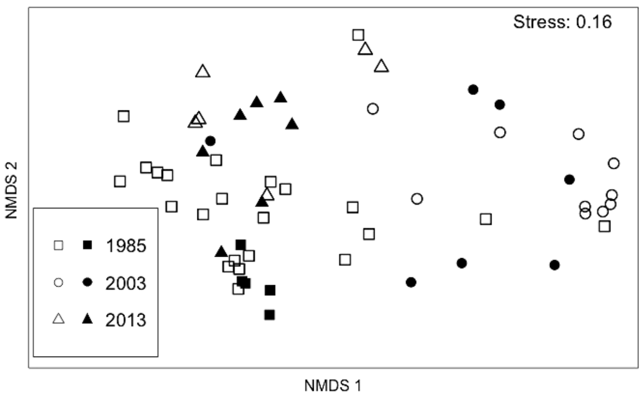

Fig. 1. Non-metric multidimensional scaling (NMDS) ordination comparing the diet of small (open symbols) and large (black symbols) pumpkinseed *Lepomis gibbosus* during the establishment (1985) and integration stages (2003 and 2013) of the invasion in the mainstem of the Guadiana river (Portugal).

Population diet breadth was similar between 2003 and 2013 for small and large individuals (Figure 2a), but was much narrower in 1985 particularly in large individuals. Individual diet specialization of large individuals was lower in 1985 than in 2003 and 2013 (Figure 2b). Conversely, individual diet specialization showed no changes over time in small individuals.

Our results highlighted that the late summer trophic niche of pumpkinseed varied over the invasion of our study site in the maistem of the Guadiana river. Besides shifts in staple prey, trophic niche size increased during the integration stage. These long-term changes in trophic niche suggest the ecological impacts of pumpkinseed on recipient biota may be temporally dynamic. The patterns perceived in this study are unlikely to be driven only by methodological bias. Although sample-sizes were generally small, this appears unlikely to have affected the results. For instance, population diet breadth was broader in 2003 and 2013 when sampling effort was lower. The lack of data on fish abundance and prey availability may also be considered a potential shortcoming. Fish abundance and prey availability could influence the trophic relations between pumpkinseed and co-occurring species and should thus be addressed in future studies.

Trophic patterns of both small and large pumpkinseed through time reflected a shift from specialization on chironomids during establishment to more generalized feeding during integration, with the inclusion in the diet of copepods followed by hemipterans and also ephemeropterans for large fish. This increase in the array of prey consumed by pumpkinseed

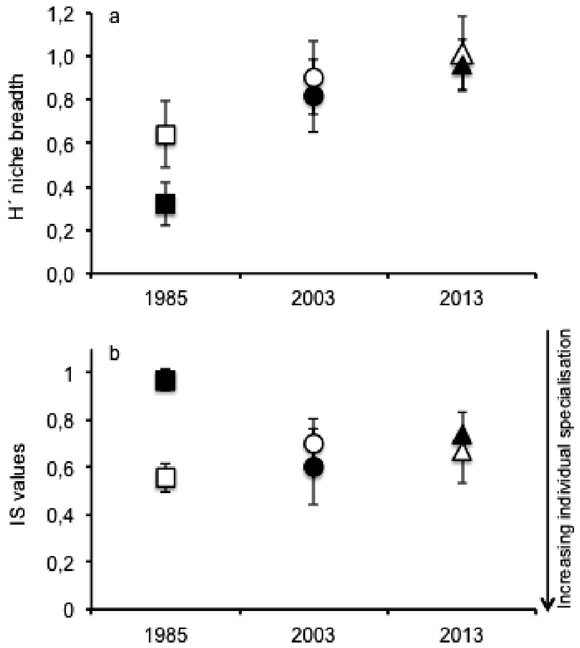

Fig. 2. Variation in (a) population diet breadth (Shannon-Wiener H' index) and (b) individual diet specialization (IS index) for small (open symbols) and large (black symbols) pumpkinseed *Lepomis gibbosus* during the establishment (1985) and integration stages (2003 and 2013) of the invasion in the mainstem of the Guadiana river (Portugal). Error bars represent boot-strapped 95% confidence intervals for each index.

may reflect an adaptive response to the recipient ecosystem (Strayer *et al.*, 2006), with diet varying according to local prey availability and shifting to less exploited preys as it has been pointed for other introduced populations (Godinho *et al.*, 1997b; Almeida *et al.*, 2009). Some changes in the prey availability are likely to have occurred after 2001, following the construction of a large reservoir located about 35 km upstream (Ribeiro and Collares-Pereira, 2010). Nevertheless, trophic patterns reflected the consumption of a higher diversity of preys confirming that plasticity may persist along the invasion process.

The increase in trophic niche size of pumpkinseed was associated with an increase in individual diet specialization in large fish which may result in reduced intra-specific competition (see Svanbäck and Persson, 2004) and thus facilitate the spread and integration of this invasive species. In the case of small fish, the degree of individual specialization remained similar over time although population diet breadth has also expanded across the invasion process.

Variation in biological traits may provide an important advantage to invasive species, allowing successful transitions throughout the invasion process and favoring integration into the recipient ecosystem (Bøhn *et al.*, 2004; Feiner *et al.*, 2012). Especially, high morphological change has been attributed to pumpkinseed (Yavno *et al.*, 2014), which together with variability in trophic niche composition and size recorded herein may enable this species to cope with the novel environments. Pumpkinseed seemed to be able to increasingly use resources at different levels in the food web throughout the invasion process, suggesting that its impacts in recipient native communities may be temporally variable. Further research on long-term feeding of native species in relation to its abundance and prey availability is needed to clarify mechanisms behind resource use and the extent to which invasive species may affect the ecosystem structure and function.

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