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ORIGINAL ARTICLE

Eurasian otter *Lutra lutra* diet mirrors the decline of native fish assemblages in a semi-arid catchment (River Segura, SE Spain)

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Abstract
In semi-arid environments, the effects of irregularly distributed rainfall, flow regulation and water inter-basin transfer enhance the spread of non-native fish to the detriment of native communities. In the River Segura, since the 1980s the number of non-native fish species has progressively increased, also because of the building of water transfer facility connecting the rivers Segura and Tajo. With the aim of highlighting how man-driven changes in the diversity of fish communities affect the diet of top-predators, we compared Eurasian otter *Lutra lutra* diet in the span of 20 years, i.e. 1997–98 vs. 2016–19. As habitat quality affects the condition of Andalusian barbel *Luciobarbus sclateri*, the most widespread native fish, we also compared the size of preyed barbels to point out whether human activities may have lowered their profitability to otters. Fish and introduced red swamp crayfish *Procambarus clarkii* formed the bulk of otter diet in both study periods. In 2016–19 the contribution of non-native species to otter diet increased significantly, both for crayfish and fish, which included ten non-native species. Otter feeding habits faithfully mirrored the variation in the composition of the fish community and confirmed the importance of crayfish as alternative-to-fish prey in the Iberian Peninsula. The average length of preyed barbels was significantly lower in the second study period, consistently with a decline in barbel profitability for otters.

Keywords Environmental stress · Non-native fish · *Procambarus clarkii* · Inter-basin water transfer · Invasive species

Introduction

Throughout arid lands, water demand is increasing with human population density and climate warming, resulting in the alteration of flow regimes and freshwater communities (Miller et al. 1989; Kingsford 2000; Olden and Poff 2005). Since the second half of the nineteenth century, inter-basin water transfer (IBT) projects have been considered as an effective solution to solve water resource deficits and management problems (Shiklomanov 1999), and, currently, there are over 170 active IBTs globally (Schmidt et al. 2019). Connecting different biogeographic regions, water diversions can act as invasion corridors, facilitating the spread of non-native invasive species (Galil et al. 2007; Gallardo and Aldridge 2018), as demonstrated in all continents (e.g., River Rhine, NW Europe, Leuven et al. 2009; River Huai, China, Qin et al. 2019; Tasmania, rivers Gordon and Pedder, Sanger 2001; rivers Great Fish and Sundays, South Africa, Kadye and Booth 2013; coastal drainages of southern California, Swift et al. 2015). Chronic colonization by non-native fishes, coupled with the buffering of seasonal variability due to damming and flow regulation, can drive the decline of native fish assemblages, especially in water-limited catchments (Propst et al. 2008; Clavero et al. 2015).

Flowing in south-eastern Spain, the River Segura is one of the driest and most regulated (24 dams higher than 10 m and 121 weirs > 2 m; CHS 2007; Grindlay et al. 2011) European watersheds. Agricultural and urban water is mainly supplied from saltwater desalination plants and, since 1978, through

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the Tajo-Segura IBT, a 286-km-long water transfer facility connecting the Entrepeñas and Buendia dams in the upper River Tajo to the Talave Dam in the catchment of the River Segura (Pittock et al. 2009). Fish dispersion through the Tajo-Segura IBT system has been imputed as the cause of the spread of several non-native fish species in the recipient basin (e.g., Andreu-Soler et al. 2004; Oliva-Paterna et al. 2005).

As in many European countries, in SE Spain, otter populations declined throughout the 1970s and 1980s due to water pollution, man-driven alteration of freshwaters habitats, and hunting (Delibes 1990; Yelo and Calvo 2004). Following improvement in water quality (mainly through water treatment plants) and habitat restoration (Jiménez et al. 2008), in the last three decades, the species has progressively recovered and is currently reported on a ca. 230-km-long stretch of the main river (Dettori et al. 2019). Fish availability is considered a major factor affecting the diet of this semi-aquatic top-predator of freshwater habitats (Kruuk 2006).

Interactions between introduced species and native predators are highly complex, being exacerbated by environmental factors (Mack and D'Antonio 1998). As other native semi-aquatic predators (e.g., kingfisher *Alcedo atthis*; Nessi et al. 2021), otters usually prey on non-native fish less than expected based on their relative abundance (Balestrieri et al. 2013). Nonetheless, few studies have been carried out in arid and semi-arid freshwater habitats, where anthropogenic impacts add to strong natural environmental stress (Ormerod et al. 2010). In arid rivers of Morocco, otters mainly prey on widespread, native barbels *Luciobarbus* spp. (Libois et al. 2015; Riesco et al. 2020), despite about 60% of recorded species are non-natives (Clavero et al. 2015, 2017).

With the aim of highlighting if otter feeding behavior in the catchment of the River Segura may be affected by man-driven changes in the diversity and richness of the fish community and the ongoing recovery of this semi-aquatic mustelid hindered by food availability, we compared its diet, as assessed by the analysis of fecal samples, in 1997–1998 and 2016–2019.

Andalusian barbel *Luciobarbus sclateri* was the most abundant and widespread fish in both study periods (Miñano et al. 2003; Oliva-Paterna et al. 2014). As habitat quality (Vila-Gispert and Moreno-Amich, 2001; Oliva-Paterna et al. 2003) and the spread of introduced species (Castejón Bueno 2010) may affect barbel condition, we expected otters to prey on smaller fishes in the second study period. To test for this hypothesis, the length of preyed barbels was assessed using diagnostic bones and available regression equations.

Study area

The catchment of the River Segura (352 km) covers 14,432 km^2 and hosts a stable population of about 1,850,000 inhabitants (Uche et al. 2015). The climate ranges from sub-humid to semi-arid Mediterranean, with mean annual temperature of 17 °C. Annual rainfall is ca. 400 mm, with large fluctuations in both seasonal and yearly values and pronounced summer droughts (Machado et al. 2011; Belmar et al. 2013). As in arid and semiarid areas of Australia and South Africa, intermittent and ephemeral streams are the predominant watercourse classes in the river catchment (Belmar et al. 2011).

Land use includes shrubland and woodland (45%), crops (52%), urban areas (2%), pastures, and sparsely vegetated areas (Bruno et al. 2014a). Riparian vegetation consists of both European and Ibero-African species (*Salix* spp., *Fraxinus angustifolia*, *Populus* spp., *Tamarix* spp., *Nerium oleander*) (Bruno et al. 2014b). From the first half of the 1980s traditional rain-fed crops have been progressively replaced by irrigated ones, and urban areas have largely grown (Alonso-Sarría et al. 2009). River longitudinal connectivity has been recently improved through restoration projects aimed at eliminating or permeabilizing barriers (e.g., LIFE12 ENV/ES/1140 SEGURA RIVERLINK; Sanz-Ronda et al. 2019), and controlling the invasive giant reed *Arundo donax* using soft engineering techniques (e.g., LIFE13 BIO/ES/001407 RIPISILVANATURA; Bruno et al. 2019).

The catchment of the River Segura currently hosts 18 fish species, of which 13 (72%) are non-natives (Oliva-Paterna et al. 2014). Native *Luciobarbus sclateri* and introduced *Gobio lozanoi*, *Alburnus alburnus*, *Lepomis gibbosus*, and *Pseudochondrostoma polylepis* form the bulk of the fish community (Oliva-Paterna et al. 2014).

Methods

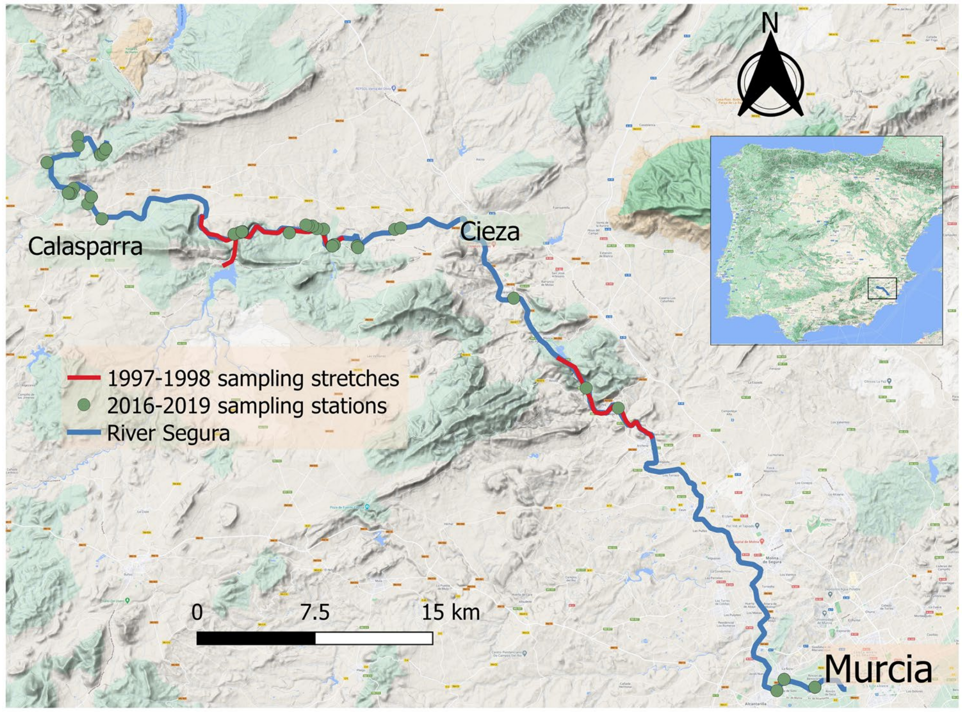
In 1997–1998 and 2016–2019, undisputable spraints were searched for on a 110-km-long stretch of the River Segura (Fig. 1), by surveying typical otter marking sites (e.g., large stones, bridges, pool banks, confluences) on both banks.

The oldest sample consisted of 951 scats collected between February 1997 and March 1998. All fecal samples collected in a same sampling station/date were pooled together.

Between April 2016 and June 2019, 600 fecal samples were collected along 37 sampling stations, consisting of a 0.5 ± 0.05-km-long stretch of the river, stored in test tubes containing ethanol, labeled, and frozen at −20 °C.

For the analysis, each spraint was soaked for 24 h in a solution of hydrogen peroxide 30% w/v (100vol) stabilized pure. Each spraint was then washed by a strong water jet into a sieve with 0.5-mm-wide meshes. Undigested remains were carefully examined using a microscope. Fish remains were identified from their vertebrae, pharyngeal teeth, and scales, using personal collections and the keys

Fig. 1 Stretch of the River Segura (110 km; Murcia, SE Spain) surveyed for otter spraints in 1997–1998 and 2016–2019



of different authors (Prigioni 1997; Oliva-Paterna et al. 2014, 2019). Feathers and chelae and thoracopods were the main diagnostic features for birds and crustaceans, respectively. The diagnostic remains of amphibians and reptiles were identified by the keys of Prigioni (1997) and Smiroldo et al. (2019a).

For both study periods, data were split into two seasons (warm: IV–IX; cold: X–III), and, to allow comparison, results were expressed as percent relative frequency of occurrence [FR% = (number of occurrences of an item/total number of items) × 100]. Raw frequency data were compared by the chi-squared (χ^2) test, using Bonferroni's sequential method as a conservative correction for multiple testing (Rice 1989). Trophic niche breadth was estimated by standardized Levins' index $B = 1/(R\ \Sigma p_i^2)$ (Feinsinger et al. 1981), with p_i = RF and $R = 20$.

The length of preyed barbels was assessed based on key diagnostic bones (maximum length/width of pharyngeal teeth, length of cephalic, thoracic, and caudal vertebrae), using the methods and equations proposed by Ruiz-Olmo (1995). Average total body lengths were compared between the two study periods by Mann–Whitney's *U* test.

Results

Fish and introduced red swamp crayfish *Procambarus clarkii* formed the bulk of otter diet in both study periods (Table 1), with the minor contribution of birds, frogs, and small mammals (< 5% each). In 1997–1998, fish (%RF = 76.8), particularly native Andalusian barbel (59.9), was the main otter prey, while in the second study period crayfish dominated (47.9). In the late 1990s, preyed fish included only four species, of which two (Eastern mosquitofish *Gambusia holbrooki* and Iberian nase *Pseudochondrostoma polylepis*) were non-natives. In 2016–2019, otter diet was more diverse than in 1997–1998 ($B = 0.2$ vs. 0.1), including twelve fish species, of which ten were non-natives (Table 1). The contribution of introduced species to otter diet increased significantly, both for crayfish (47.9 vs. 17.5, $\chi^2 = 255.6$, $P < 0.001$) and fish, particularly Iberian nase (3.4 vs. 0.1, $\chi^2 = 93.3$, $P < 0.001$) and mosquitofish (2.3 vs. 0.3, $\chi^2 = 65.6$, $P < 0.001$), while the relative frequency of Andalusian barbel declined (15.5 vs. 59.9, $\chi^2 = 234.4$, $P < 0.001$). The frequency of non-fish prey, frogs (2.9 vs. 0.3, $\chi^2 = 72.6$, $P < 0.001$), and small mammals (4.5 vs. 0.9, $\chi^2 = 76.4$, $P < 0.001$) also increased.

In both study periods, crayfish were preyed on more frequently in the warm season (1997–1998: 20.9 vs. 15.5, $\chi^2 = 7.2$, $P < 0.05$; 2016–2019: 64.8 vs. 40.2, $\chi^2 = 18.7$, $P < 0.01$), while barbels prevailed in autumn–winter (1997–1998: 63.0 vs. 54.8, $\chi^2 = 9.7$, $P < 0.05$; 2016–2019: 20.3 vs. 11.5, $\chi^2 = 8.9$, $P < 0.05$) (Fig. 2). In 1997–1998, insects were used only in the warm season, while birds were preyed on in the cold season of 2016–2019.

The average (± SD) length of preyed barbels was significantly lower in the second study period (18.9 ± 5.6 cm vs. 16.1 ± 5.1 cm; $U = 2936$, $P < 0.001$, $N = 200$ and 46, respectively; Fig. 3).

Table 1 Percent relative frequency %RF of food items in the diet of Eurasian otter *Lutra lutra* on the River Segura (SE Spain) in 2016–2019 ($N=600$) and 1997–1998 ($N=951$). Raw frequency data were compared by the χ^2 test with sequential Bonferroni's correction (n.s. non-significant)

Food items	2016–2019 %RF	1997–1998	*P*	Status
Procambarus clarkii	47.9	17.5	< 0.001	Introduced
Fish	37.0	76.8	< 0.001	
Cyprinus carpio	1.7	0.4	< 0.05	Introduced
Luciobarbus sclateri	15.5	59.9	< 0.001	Native
Pseudochondrostoma polylepis	3.4	0.1	< 0.001	Introduced
Alburnus alburnus	0.1	-	n.s	Introduced
Gobio lozanoi	0.6	-	n.s	Introduced
Tinca tinca	0.2	-	n.s	Introduced
Unidentified Cyprinids	3.1	2.5	n.s	
Sander lucioperca	1.1	-	n.s	Introduced
Micropterus salmoides	0.4	-	n.s	Introduced
Lepomis gibbosus	0.5	-	n.s	Introduced
Esox lucius	0.1	-	n.s	Introduced
Gambusia holbrooki	2.3	0.3	< 0.001	Introduced
Salmo trutta	-	0.3	n.s	Native
Unidentified fish	7.9	13.4	< 0.01	
Birds	1.7	2.8	n.s	
Turdus merula	-	0.1	n.s	
Gallinula chloropus	1.0	-	n.s	
Anas platyrhynchos	0.1	-	n.s	
Unidentified birds	0.6	2.7	n.s	
Ranidae	2.9	0.3	< 0.001	
Natrix maura	0.5	1.2	n.s	
Muridae	4.5	0.9	< 0.001	
Coleoptera	0.6	0.4	n.s	
Orthoptera	0.2	0.1	n.s	
Gastropoda	0.6	-	n.s	
Vegetal matter	3.7	-	n.s	
Garbage	0.2	-	n.s	

Discussion

Since the 1980s, the number of non-native fish species in the River Segura has progressively increased, with some species – bleak *Alburnus alburnus*, Iberian gudgeon *Gobio lozanoi*, pumpkinseed *Lepomis gibbosus* and Iberian nase – currently occurring as frequently as native barbels (Oliva-Paterna et al. 2014). The initial spread of non-native species coincided with the completion of the Tajo-Segura IBT, which probably promoted the invasion by Iberian gudgeon (Mas 1986), golden carp *Carassius auratus* (García de Jalon et al. 1992), Iberian nase (Torralva and Oliva-Paterna 1997), and zander *Sander lucioperca* (Miñano et al. 2002), but also with a phase of exponential increase in the cumulative number of alien fish acclimatized in Spain, suggesting that the "improvement" of fish resources for sport fishing and aquaculture also played a major role in fish introductions (Elvira and Almodóvar 2001).

These deep changes in the composition of the river's fish community were mirrored by the feeding habits of the otter, which shifted from a native barbel-based diet in the late 1990s to a non-native prey-based diet 20 years later. Although the frequency of occurrence of non-native fish in otter diet in 2016–2019 was still rather low, consistently with its disinclination to prey on introduced fish (Balestrieri et al. 2013), their contribution was by far higher than in the late 1990s, both in terms of relative frequency and species diversity. Moreover, most preyed non-native fishes were also the most widespread, except for bleak, which, as recorded for southern Italy (Remonti et al. 2010), was rarely preyed despite being as spread as Andalusian barbel (Oliva-Paterna et al. 2014).

While non-native fish usually represent a minor component of otter diet (Balestrieri et al. 2013), throughout the Iberian Peninsula red swamp crayfish are often preyed by otters (Delibes and Adrián 1987; Beja 1996). North American

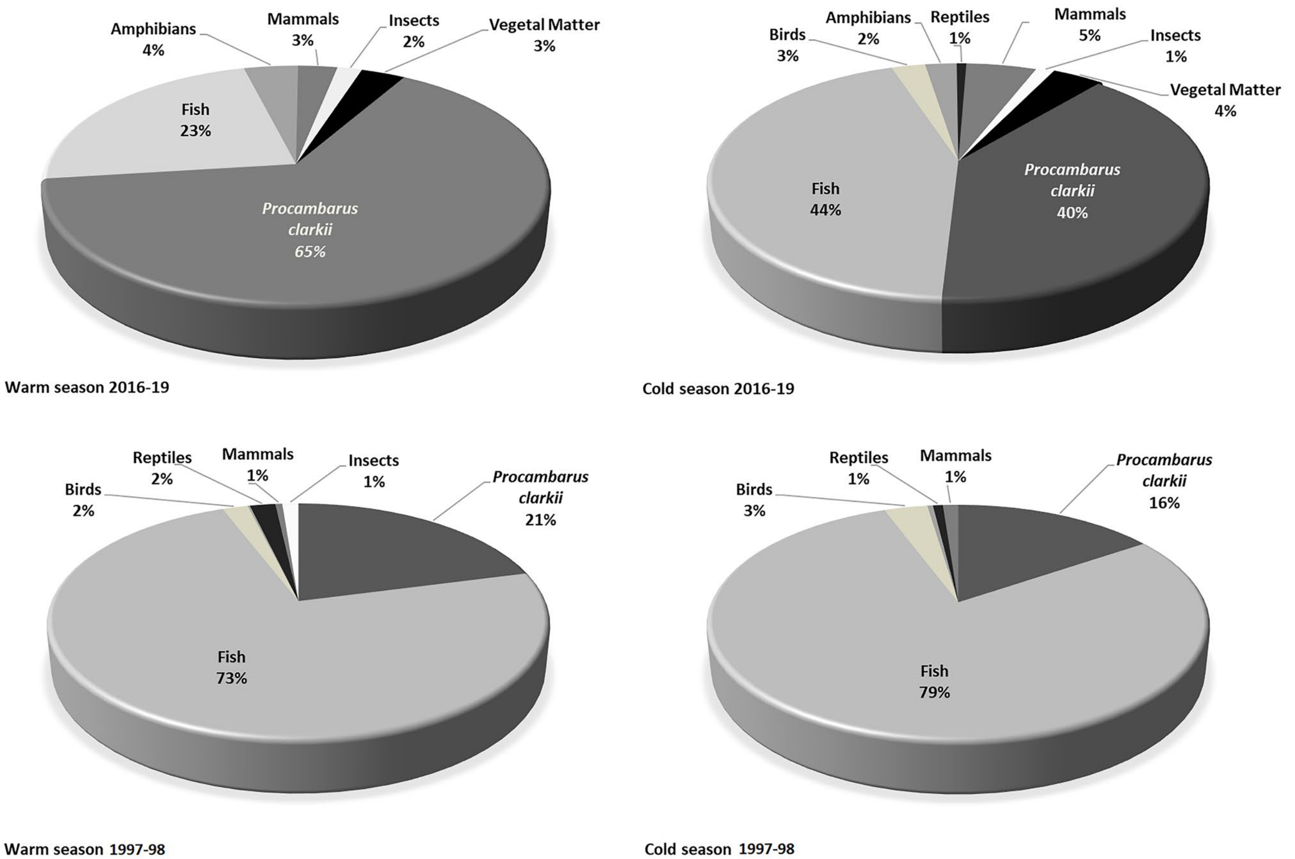


Fig. 2 Seasonal variation in otter diet on the River Segura, as assessed by the analysis of fecal samples collected in 1997–1998 and 2016–2019

crayfish were introduced in the marshes of the River Guadalquivir, southwestern Spain, in 1973, and by the end of the decade spread throughout eastern Spain (Gutiérrez-Yurrita et al. 1999; Oficialdegui et al. 2019). Being highly resistant to adverse conditions, red swamp crayfish are capable to spread through dry land and temporary habitats, coping with large seasonal fluctuations in water levels (Barbaresi and Gherardi 2000), as those occurring in our study area.

In a study carried out between October 2004 and February 2005 by the analysis of 943 spraints (Pastor González 2011), the relative frequencies of occurrence of fish and crayfish in otter diet were intermediate (48% and 38.2%, respectively) to those recorded in 1997–1998 and 2016–2019, suggesting that throughout the study period the importance of crayfish as prey has progressively increased. Although otters can rely on a relatively wide range of aquatic food resources, fish are their preferred prey (Ruiz-Olmo and Palazón 1997; Clavero et al. 2003; Remonti et al. 2008; Smiroldo et al. 2019a), and use by otters of alternative-to-fish prey mainly depends on fish shortage (Remonti et al. 2010; Krawczyk et al. 2016; Smiroldo et al. 2019b).

Thus, the recorded trend may indicate the progressive decline of native fish, which may have been worsened by either competition with non-native fish or human-altered flow regimes (Lytle and Poff 2004). Particularly, growth, age structure, body condition, and population abundance of Andalusian barbels have been demonstrated to be affected by waterflow regulation in the River Segura catchment (Torralva et al. 1997; Oliva-Paterna et al. 2003, 2019). The smaller size of preyed barbels recorded in 2016–2019 with respect to the late 1990s, together with their lower contribution to otter diet, is consistent with a decline in barbel profitability for otters, which may have forced the mustelid to switch to alien crayfish, particularly in the warm season, when large crayfish are most abundant and native fish availability is the lowest (Beja 1996; Kruuk 2006).

Our results stress the dichotomous role played by red swamp crayfish in introduction areas, as they both alter freshwater food webs and prey on fingerlings (Geiger et al. 2005; Loureiro et al. 2015; Souty-Grosset et al. 2016), affecting fish communities and food availability to otters and, at the same time, provide a major alternative food resource for several predators in man-altered freshwater ecosystems (Correia 2001; Tablado et al. 2010; Musseau et al. 2015), possibly contributing to otter ongoing recolonization of Iberian catchments (see Beja 1996), particularly in peri-urban

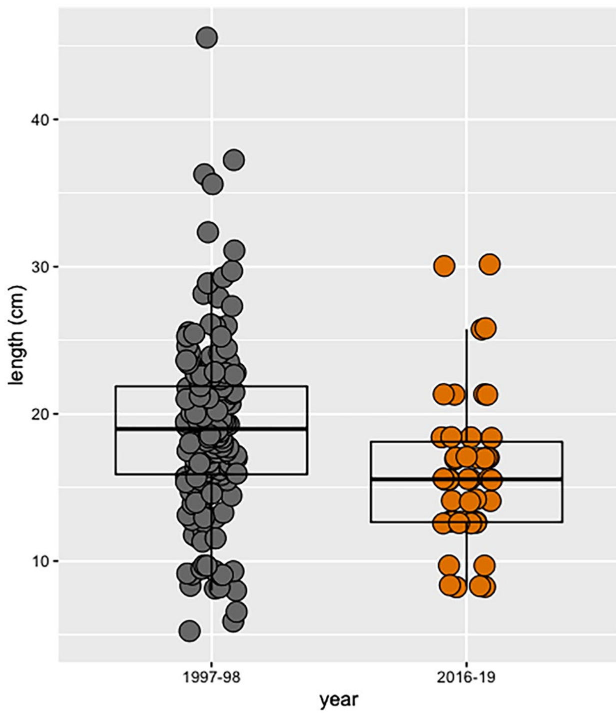


Fig. 3 Box-plot diagram showing variation in the mean length of barbels preyed on by otters in 1997–1998 and 2016–2019

and agricultural land, where native fish are often replaced by non-native species (Dettori et al. 2021). On the other hand, crayfish can store large amounts of xenobiotic substances, such as heavy metals (Alcorlo and Baltanás 2013), with serious risks for otter health and recovery (Rodríguez-Estival et al. 2020).

As climate warming is expected to increase water deficit, with direct and indirect consequences for cyprinid populations (Beja 1995; Ilheu et al. 2007), information on the ability of semi-aquatic species to face the expansion of arid areas is pivotal for implementing conservation actions (Harms et al. 2008). The spread of invasive aquatic species, interacting with climate change (Burgiel and Muir 2010; Capdevila-Arguelles et al. 2011), will pose additional threats on the whole trophic web of semiarid rivers. In the Iberian Peninsula, strategies aimed at otter conservation should focus on the restoration of freshwater habitats, which have been demonstrated to improve both habitat quality and otter abundance (Bruno et al. 2019; Dettori et al. 2019, 2021). Specific actions should be directed at improving native fish species through site-specific measures (Santos et al. 2018), whereas invasive crayfish are difficult to eradicate. In addition, the design of flows that mimic natural flow regime patterns may provide more suitable environmental conditions for native fish species (Sánchez-Perez et al. 2020). The Eurasian otter should be regarded as a useful indicator of the effectiveness of such actions, as already demonstrated with respect to both the recovery of fish in depleted rivers (Narváez et al. 2020) and contaminant accumulation (Rodríguez-Estival et al. 2020).

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Author contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by EED, AB, and SP. The first draft of the manuscript was written by EED and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and material The datasets generated during and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Research involving human and animal participants The study did not involve humans or animals.

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