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"The giants' feast": predation of the large introduced European catfish on spawning migrating allis shads

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Abstract European catfish *Silurus glanis* is a large non-native opportunistic predator able to develop hunting strategy in response to newly available prey where it has been introduced. Migrating spawning anadromous prey such as allis shad *Alosa alosa* could represent this available and energy-rich food resource. Here, we report an impressive catfish hunting behavior on shad spawning act in one of the main spawning grounds in Europe (Garonne River, Southwest France). Shad spawning act consists of at least one male and one female swimming side by side, trashing the water surface with their tail which, therefore, produces a splashing noise audible from the river bank. The catfish hunting behavior on shad spawning act was studied, at night, during spring months, using both auditory and video survey. Simultaneously, catfish individuals were fishing to analyze their stomach content. Catfish disturbed 12% of the 1024 nocturnal spawning acts we heard, and this proportion increased to 37% among the 129 spawning acts when estimated with low-light camera recording. Stomach content analyses on 251 large catfish individuals (body length > 128 cm) caught in the same river stretch revealed shad represented 88.5% of identified prey items in catfish diet. This work demonstrates that European catfish predation must be considered as a significant factor of mortality of allis shad. In a context of the extension of the European catfish range area in western and southern European freshwaters, this new trophic impact, with other ones previously described for salmon or lamprey, has to be considered in European conservation plans of anadromous species.

Keywords Anadromous fish · Diet · Endangered species · Large non-native apex predator · Mating

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Introduction

Migratory animals in search of food, new habitats or mates, concentrate in time and space, strongly exposing them to predators. The well-known annual migration of wildebeest (*Connochaetes taurinus*) through the Serengeti triggers high densities of adult crocodiles (*Crocodylus niloticus*) when crossing the Mara River (Subalusky et al. 2017). The shoals of migrating sardines (*Sardinops sagax*) along the east coast of South Africa also known as 'sardine runs' concentrate many associated predators such as the common dolphin *(Delphinus capensis*), the cape gannet (*Morus capensis*) or the bottlenose dolphin (*Tursiops aduncus*) (O'Donoghue et al. 2010). In freshwater ecosystems, brown bears (*Ursus arctos*) and black bears (*Ursus americanus*) kill at least half of the returning adult Pacific salmons (*Oncorhynchus* spp.) that spawn in small streams in Alaska (Quinn et al. 2003). In South-Central Connecticut, double-crested cormorant (*Phalacrocorax auritus*) are important predators for alewife (*Alosa pseudoharengus*) (Dalton et al. 2009).

Many fish species migrate between seawater and freshwater to spawn. Most of these anadromous species are protected from fish predation during their upstream migration by their large adult body size. Biological invasions have disrupted this rule, given that introduced predatory fish species are globally larger than native fish species (Blanchet et al. 2010). For instance, the introduced piscivorous blue catfish (*Ictalurus furcatus*) mainly consume *Alosa sp*. during their spawning run in the upper tidal freshwater reaches of the Rappahannock River in Virginia, USA (MacAvoy et al. 2000). In western and southern European freshwaters, the establishment of the large non-native European catfish *Silurus glanis* also exposes adult anadromous fish species to predation by increasing the threshold body size at which prey are invulnerable to predation. The European catfish is among the 20 largest freshwater fish in the world and is the largest in Europe (Stone 2007; Boulêtreau and Santoul 2016). The species can measure up to 2.7 m total length (Boulêtreau and Santoul 2016), with adults being at least twice larger than native predators (e.g., Northern pike *Esox lucius*). The species is native from Eastern Europe. Its native distribution extends from Germany eastward through to Poland, up to Southern Sweden, and down to Southern Turkey and Northern Iran through the Baltic States to Russia and to the Aral Sea of Kazakhstan and Uzbekistan (Copp et al. 2009). Their extremely body size has resulted in making them an increasingly popular target species for recreational anglers in Europe, resulting in their intentional introductions into some Western and Southern European countries, but also in China, Tunisia and more recently in Brazil (Cunico and Vitule 2014; Cucherousset et al. 2018). In Southwestern France, the first introduction likely occurred during the 1980s (Schlumberger et al. 2001).

Stable isotope analysis revealed that the diet of some specialized European catfish individuals could reach up to 50% of marine prey in the Garonne River in Southwestern France (Syväranta et al. 2009). More specifically, anadromous fish such as twait shad (*Alosa fallax*), thinlip grey mullet (*Chelon ramada*), sea lamprey (*Petromyzon marinus*) and Atlantic salmon (*Salmo salar*) have been detected by DNA metabarcoding techniques in European catfish feces or stomach contents (Libois et al. 2016; Guillerault et al. 2018; Ferreira et al. 2019). Fishermen have also reported some allis shad (*Alosa alosa*) individuals in European catfish stomach contents. The allis shad (*Alosa alosa*) is a member of the herring family, Clupeidae. This anadromous fish can be historically found along the northeastern Atlantic coast from Morocco to Norway (Baglinière et al. 2003). Adult allis shad occurs mainly in shallow coastal water and estuaries, but, during the spawning migration, adults enter well upstream in some of the largest European rivers, mainly in France, Spain and Portugal (Maitland and Hatton-Ellis 2003). The allis shad is now critically endangered over most of its range due to pollution, overfishing and river fragmentation (Aprahamian et al. 2003). Further, its spawning migration is often limited by obstacles to migration, such as waterfalls and man-made dams and weirs. Moreover, predation-induced mortality in rivers, though to be important, has never been quantified. Here, we report the occurrence of a hunting behavior in the non-native European catfish on spawning allis shad. Additionally, we quantify the impact of European catfish predation on migrating allis shad in one of the main European spawning grounds in Southwestern France.

Methods

Study site

The Garonne basin (Southwestern France) hosted the largest allis shad population in Europe at the end of the twentieth century (Rougier et al. 2012). The 1400 m long studied stretch is located in the tailrace of the Golfech-Malause large-scale hydroelectric complex at about 270 km from the river mouth (Fig. 1b). The stretch is ended upstream by a dam equipped with a fish lift as fishway (44° 6′ 34.17″ N, 0° 51′ 12.58″ E) and a permanent video fish-counting to monitor fish upstream passages (Fig. 1a). The fishway is fit with a fish trap that allows fish collection. In this stretch, the river is channelized and approximately 100 m wide with a mean depth of 6 m. The stretch belongs to the industrial area where passing and angling are prohibited. The studied spawning ground (80 by 100 m around) is located at the downstream part from the stretch (44° 6′ 53.75″ N, 0° 50′ 19.73″ E).

Shad spawning acts

Allis shad spawning occurs at night during spring months (from April to June with a peak at the end of May). The typical spawning act consists of at least one male and one female swimming side by side in circle and thrashing the water surface with their tail (Acolas et al. 2006). The splashing noise (35 dB at one meter) can be heard from the riverbank (Chanseau et al. 2005; Diep et al. 2016). Counting the number of splashes (auditory survey), i.e., the number of spawning acts over the spawning season is classically used to approximate the reproductive potential of allis shad populations (Chanseau et al. 2005).

We observed spawning acts during the night from a bridge located above the spawning ground (Fig. 1a)

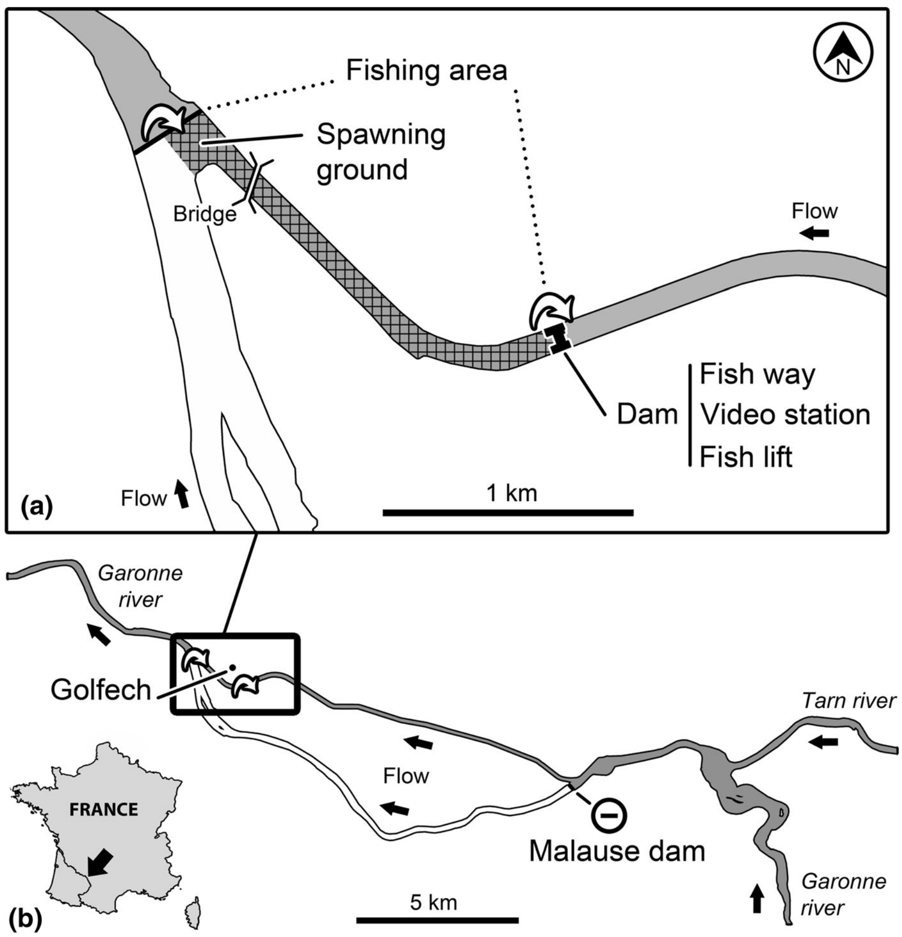

Fig. 1 Maps of the studied river stretch (**a**) inside the Golfech-Malause large-scale hydroelectric complex on the Garonne River (**b**). The studied stretch (striped gray) is located upstream from a dam equipped with a fish lift as fishway and a permanent video fish-counting (**a**)

for 34 nights from May 2 to June 28, 2019. Over the period, we recorded the number of splashes for a total of 59.5 h between midnight and 5 am, for 4 to fifteen 15 min periods per night. We recorded whether spawning acts were disturbed, i.e., attacked by one or several European catfish over every listening 15 min periods (ESM Video 1). We discriminated normal and disturbed splashes by ear (ESM Audio 1). We analyzed the effects of the sampling date, sampling quarter hour (15 min period) and the total spawning act number (explanatory continuous variables) on the disturbed act number (dependent continuous variable) using generalized linear mixed model (GLMM) with log as link function and the number of listening 15 min periods per night as random factor in R software version 3.5.2 (R Development Core Team 2016). Sampling quarter hour was the 15 min period during which we recorded the spawning act (from 1 to 20, as recording was performed between midnight and 5 am). The interaction terms were subsequently removed when not significant.

The spawning ground area is slightly lit at night, allowing to use low-light camera in this site. Therefore, we also filmed spawning acts for ten hours with a low-light camera (Canon EOS 1Dx II, ISO 52 000) for 2 h (from 23:30 to 01:30) during five nights (on May 14, 15, 21, 22 and July 6) to produce images of spawning acts and to describe the potential interactions between European catfish and allis shad (Fig. 2).

European catfish stomach contents

A total of 329 European catfish (mean ± SD body size = 163 ± 42 cm, ranging from 59 to 243 cm) was collected from May 2 to June 28, 2019 to analyze stomach content and to quantify the contribution of allis shad to European catfish's diet. Twenty-seven European catfish were trapped and collected inside the fishway (Fig. 1a). Fish trap was checked every morning to collect catfish trapped at night. Three hundred and two individuals were fishing by commercial inland fishermen using 16 hoop nets (12 m total length; 0.82 m opening size; 40 mm mesh size) installed along the studied stretch (fishing area, Fig. 1a). Fishermen put up and checked the 16 hoop nets every morning from 8 to 10 am. All European catfish were euthanatized by professional fishermen to be commercialized for food, according to an ongoing catfish control plan. Stomach content was identified, and European catfish body size was measured. Diet composition from stomach content analysis was expressed as percentage of prey abundance. We tested the effects of sampling date and European catfish body size on allis shad proportion in non-empty stomach contents of largest European catfish (body size > 128 cm) using a GLM with binomial distribution (lme4 R package). The smallest European catfish to have had allis shad in stomach content was 129 cm in length. Therefore, we assumed that only European catfish whose body size was higher than 128 cm had the required gape size to consume adult allis shad.

Predation pressure estimate

We estimated the number of shads the European catfish caught in the studied stretch could have consumed over the 58 days studied period (from May 2 to June 28, 2019). We also assumed here that only largest European catfish (body size > 128 cm) consumed adult allis shad and we excluded the smallest 78 catfish from the subsequent estimation.

We calculated shad abundance consumed based on three assumptions. First, we considered that each European catfish daily consumed 1.32% of its body weight, ranging from 0.43 to 4.09% according to Boulêtreau et al. (2011). This large range produced a high confidence interval on calculated shad abundance consumed. Second, we assumed that allis shad abundance ratio consumed by European catfish was 88.5%, from previous stomach content composition (Fig. 3) and the contribution was consistent over the 58-days period for every European catfish. Finally, we also assumed that adult allis shad weight averages 1.46 kg in French rivers (Keith et al. 2001). Each European catfish body weight was computed assuming the length–weight relationships established for individuals from Garonne River (n = 154) (ESM Fig. 1): $y = 2.10^{-5}\,x^{2.7636}$, with x is body length (cm) and y is body weight (kg).

We compared allis shad abundance consumed with (1) the number of allis shads that passed inside the fishway in front of the fish-counting station to join spawning grounds located upstream and with (2) allis shad spawner number inside the stretch over the same period. We estimated spawner number from previous counts on allis shad spawning acts. First, we assumed that night spawning period lasted 5 h (from midnight

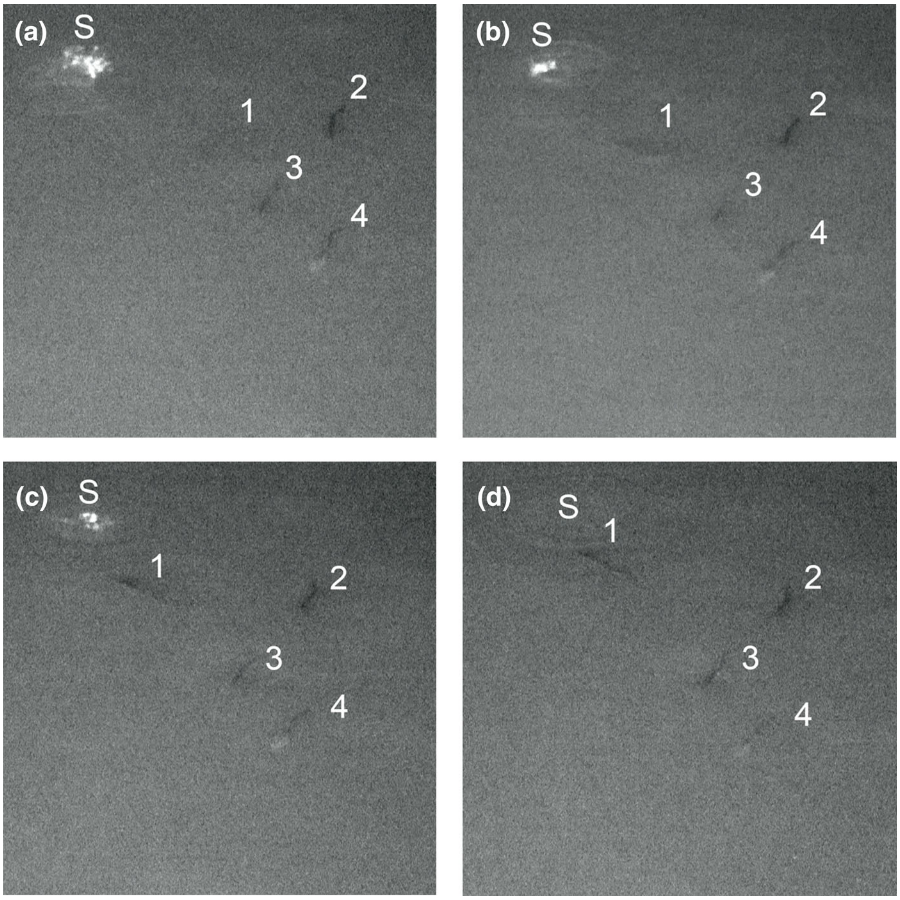

Fig. 2 Nocturnal scene of one allis shad spawning act (S), showing four European catfish individuals (#1–4) and one catfish (#1) coming close to the spawning act (panels **a**, **b** and **c**) to attack it (panel **d**)

to 5 am) and the total number of spawning acts over the 58 days studied period is proportional to the total number of spawning acts (even disturbed) we heard for 59.5 h. We also considered each spawning act involved one female and one male and allis shad females spawn six times over the period (average between 5 and 7) (Baglinière and Elie 2000).

Results

Shad spawning acts

We recorded a total of 1024 splashes during the 59.5 h of survey (i.e., 86 spawning acts per night) from May 2 to June 28, 2019. We detected by ear that 119 acts were disturbed by European catfish, i.e., 12% of the heard spawning acts. The number of disturbed spawning acts significantly increased with the total number of heard spawning acts ($p < 0.001$, Table 1) and significantly decreased with sampling date ($p < 0.01$, Table 1).

We filmed 129 spawning acts for 10 h. Forty-eight of them (i.e., 37%) have been disturbed by catfish. Video pictures also showed many European catfish from 10 to 44 individuals swimming at the river surface during the survey (ESM Video 1). Video use turned out to be very efficient here to observe allis shad spawning acts and to differentiate normal from disturbed splashes.

European catfish stomach contents

We observed that 266 individuals had an empty stomach, i.e., 80% of the 329 caught European catfish individuals. In fully stomach contents, we found 69

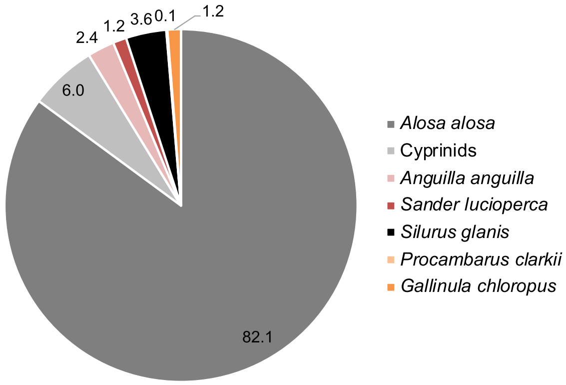

Fig. 3 Diet composition (in % of each identified prey item) of European catfish based on stomach contents divided into seven food sources. Allis shad was the main prey of European catfish. Apart from allis shad, European catfish had consumed other fish species such as common bream *Abramis brama*, common barbel *Barbus barbus*, eel *Anguilla anguilla*, pike-perch *Sander lucioperca* and European catfish *Silurus glanis*. We also detected items from crayfish species *Procambarus clarkii*, and an aquatic bird, the common moorhen *Gallinula chloropus*, confirming the known large dietary spectrum of the European catfish (Cucherousset et al. 2018)

allis shad over the 91 food items, i.e., 76% of total prey abundance, and 82% of total identified prey abundance (Fig. 3). These proportions slightly increased (to 88.5% of identified prey abundance) when considered only large European catfish able to prey allis shads (body size > 128 cm). We observed up to six shad individuals in catfish stomach content. Allis shad proportion in stomach content did not significantly depend on European catfish body size ($p = 0.631$, Table 2), neither on sampling date ($p = 0.067$, Table 2).

Predation pressure estimate

We estimated that the largest 251 European catfish (body size > 128 cm) sampled in the stretch could have consumed between 1401 and 13,328 individuals, depending on the assumed daily prey consumed by catfish, from May 2 to June 28, 2019. During the same period, 1620 migrating allis shad were recorded passing inside the fishway in front of the video fish-counting. We also estimated, from the 1024 spawning acts we recorded, that there were 1664 allis shad spawners inside the spawning ground over the same period.

Discussion

Allis shad are very exposed to European catfish attack during spawning acts in May–June in the studied spawning ground. Indeed, video movies reveal high concentration of catfish swimming at the river surface inside the spawning ground at night. European catfish have attacked in average 12% of spawning acts over the observation period, and this proportion reaches 37% when estimated by video-counting, but over a six-times-lesser time period. The risk for the spawning allis shad to be attacked decreased with sampling date over the migration period but increased with the total heard spawning act number, i.e., when feeding opportunity for the European catfish increased. This confirmed that the European catfish is an opportunistic predator able to rapidly develop a hunting strategy in response to newly available and energy-rich food resources (Cucherousset et al. 2018). It is possible that European catfish individuals were voluntary waiting for allis shad, as it was previously observed on Atlantic salmon inside the fishway of the present study area

Table 1 Effects of sampling hour, date and the number of heard allis shad spawning acts on the number of acts disturbed by the European catfish tested using generalized linear mixed models

Variable	Parameters	Estimate ± SE	DF	*z*-value	*p* value	R^2
Number of attacks	Intercept	− 0.49 ± 0.32		− 1.50	0.133	0.49
	Sampling hour	0.02 ± 0.02	173	0.74	0.459	
	Sampling date	− 0.02 ± 0.01	172	− 2.82	0.005	
	Number of spawning acts	0.07 ± 0.01	171	8.75	< 0.001	

Table 2 Effects of sampling date and catfish body size on allis shad proportion in catfish stomach contents, tested using generalized linear models

Variable	Parameters	Estimate ± SE	DF	*t*-value	*p* value	R^2
Proportion of shads	Intercept	3.61 ± 2.62		1.37	0.175	0.07
	Sampling date	− 0.04 ± 0.02	53	− 1.87	0.067	
	Catfish size	− 0.01 ± 0.01	52	− 0.48	0.631	

(Boulêtreau et al. 2018). Further research using radio-telemetry could help us to test such hypothesis.

Several features could explain why the spawning allis shad is an easy prey for the European catfish. The first reason could be river stretch-dependent and associated with the proximity with a dam, as fish aggregation downstream dams increase high predation pressure by making predator–prey encounter easier (e.g., Agostinho et al. 2012). The conspicuous display that allis shad perform during spawning act may attract predators. European catfish detect more easily a moving prey than a static prey and their hearing is exceptionally sensitive to extra-aquatic sounds (Copp et al. 2009). Risk perception is generally lower for all animals during reproduction (Magnhagen 1991), and is likely to be higher, for 'naïve' species that have not developed antipredator strategies by adapting to (or coevolving with) a newly introduced predatory species.

We observed that European catfish consumed some spawning allis shad without quantifying whether catfish attacks were successful. Results from stomach content analyses we performed on 329 European catfish over the same period showed allis shad was their preferential prey during the migration period. These results suggested high allis shad mortality during spawning, although we cannot exclude that catfish consumed post-spawning dead individuals, as allis shad individuals die four days after their last spawning act on average (Tentelier et al. 2018). The catfish stomach vacuity of 80% (266 over 329) is in accordance with previous observations on the European catfish (Copp et al. 2009; Vejřík et al. 2017) and common observations on nocturnal and piscivorous fishes that consume prey whole (Arrington et al. 2002, Vinson and Angradi 2011). In fully stomach contents, allis shad represented the main prey, reaching 82% of identified prey abundance and 88.5% of identified prey abundance when considered only large European catfish able to prey allis shads (body size > 128 cm).

By consuming allis shad, the European catfish directly affects allis shad reproductive success. Predator can also induce stress, affect individual fitness and therefore population dynamics through non-consumptive effects. For example, elk (*Cervus elaphus*) has lower progesterone concentrations that appear to reduce reproductive output in the presence of risk from wolves (Creel et al. 2007). Predation stress caused *Gambusia holbrooki* to reduce clutch size by 43% and to produce larger and heavier offspring (Mukherjee et al. 2014). Attacks on allis shad spawning could have non-consumptive impact on allis shad mating, offspring production and consequently population dynamics. This impact on reproduction is critical for the population as the species reproduces only once during its lifecycle. Further studies are needed to quantify exactly the lethal consequences of European catfish hunting behavior on shad during spawning to help understanding the implications of European catfish attack-derived stress on allis shad reproductive success and population survival.

The dramatic decline in allis shad catches observed during the first decade of the 21 century led to the Garonne basin's diadromous fish management committee implementing a total moratorium in 2008 to forbid allis shad commercial and recreational fisheries in the estuary and lower section of the river. The collapse of allis shad population could be due to high estuarine mortalities (fishery) in an initial phase combined with juvenile mortality and difficulties for allis shad to find a mate that hamper stock recovery (Rougier et al. 2012). Rougier et al. (2012) also mentioned predation by the European catfish as a potential adult mortality factor in freshwater. Our results show that this factor is substantial in the studied river stretch. Indeed, we estimated the largest 251 European catfish sampled inside the stretch could have consumed a total ranging from 1401 to 13,328 allis shads in May–June, 2019. This corresponds to a high abundance compared to the 1620 migrating allis shad that were recorded passing inside the fishway to join other spawning grounds located upstream, and the 1664 allis shad spawners we estimated inside the spawning ground over the same period. Predation on spawning or migrating allis shad is far from anecdotal and could partly explain allis shad observed decline in the former largest allis shad European population. This new factor could be considered in European conservation plans of allis shad. Total European catfish eradication is impossible in large ecosystems such as the Garonne basin, where the species is yet well-established. Preventing new introductions must be a priority of fish management strategies. In areas where the risk of prey–predator encounter is high (e.g., anthropized systems), management practices such as long-term control of large individuals should be deployed and accompanied by an efficient evaluation of the potential impacts of the non-native predator species on native prey species of particular conservation concern.

Conclusion

This work provides a new example of the potential impact of introduced large apex predator on biodiversity. It enlarges the list of adult anadromous fish species the European catfish could impact. Like Atlantic salmon (Boulêtreau et al. 2018) and sea lamprey (Boulêtreau et al. 2020), allis shad is particularly exposed to catfish predation during its freshwater migration. There is no doubt that European catfish predation must be considered as a factor of allis shad mortality in the Garonne basin where fisheries and fragmentation had already led these species to ecological extinction.

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Author contributions SB, WB, TF and FS conceived and designed the experiments. FA, ML, RD, WB and FS led the monitoring of spawning acts. TF led the European catfish stomach content analyses. SB and FS analyzed the data and wrote the first draft of the manuscript. All authors gave final approval for publication.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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