



Fish-farming bolsters algal fouling and negatively affects condition and reproduction in European pond turtles (*Emys orbicularis*)

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Received: 30 September 2020 / Revised: 15 January 2021 / Accepted: 2 March 2021
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Abstract

Fish-farming can lead to eutrophication of freshwater environments through the increase in organic matter resulting from food supplementation and fish wastes. Eutrophication can induce an excessive development of plants and algae on various substrates, including living organisms (algal epibiosis). Although algal epibiosis has been shown to reduce mobility by increasing drag in marine species, its consequences on host species in freshwater ecosystems remain poorly known. In this study, we investigated the individual (age and sex) and environmental (extensive versus intensive fish-farming) determinants of epizoic algae presence and abundance on European pond turtles (*Emys orbicularis*). We also explored the potential consequences of algal epibiosis on fitness-related traits of *E. orbicularis*. Based on a large sample size (1112 turtles from 23 ponds), we found that the abundance of algae growing on turtles increased during spring and summer. However, such increase was different across ages and sex; presumably reflecting the influence of thermoregulation (required to increase metabolic rates to sustain growth and reproduction) and thus, periodical drying of the shell, in reducing algal cover. We also found that intensive fish-farming increased algal epibiosis, especially when fish-farming involved food supplementation. Finally, we found that adult female body condition and reproduction of turtles were negatively linked to algal cover, thereby suggesting a potential negative impact of algal fouling on some fitness-related traits of adult female turtles. Future studies should usefully assess the demographic consequences of algal epibiosis induced by fish farming in this long-lived vertebrate.

Keywords Algae · Aquaculture · Biofouling · Epibiosis · Eutrophication · Turtles

Introduction

Aquaculture can negatively impact local ecosystems and the global environment (Strain 2005; Aubin et al. 2009). Fish farming usually involves high densities of fish in relatively restricted areas and thus requires food and medicine supplementation, sometimes leading to high concentrations of antibiotics in the water (Kümmerer 2009) as well as high concentrations of organic matter in the water and thus increased nitrogen and phosphorus concentration (Smith

et al. 1999). Fish farming can also lead to an enrichment of water in organic matter indirectly, i.e. via a high concentration of fish wastes (Khan and Ansari 2005; Strain 2005).

Increased concentrations of nitrogen and phosphorus, but also carbon, contained in organic matter strongly influence the growth of algae and vascular plants (Vollenweider 1968; Goldman et al. 1972; Hecky and Kilham 1988; Nixon 1995; Smith et al. 1999). Eventually, such high concentration of organic matter can lead to eutrophication (Strain 2005; Khan and Ansari 2005), a process defined as ‘an increase in the rate of supply of organic matter to an ecosystem’ (Nixon 1995). Eutrophication is now considered a worldwide problem across aquatic ecosystems (Dolbeth et al. 2010; Gubelit and Berezina 2010).

Consequences of eutrophication can be multiple. For instance, eutrophication is known to influence the physico-chemical composition and the turbidity of water (Candolin et al. 2008). Most of the time, these consequences are mediated by excessive algae growth triggered by the excess in organic matter (Smith et al. 1999). Increased algal biomass

Communicated by: Oliver Hawlitschek

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can generate oxygen deficit (Rosenberg and Loo 1988; Strain 2005) and reduced light levels that prevent the growth of other algae or vascular plants (Khan and Ansari 2005). Cyanobacteria can also proliferate under these conditions and lead to mass mortality events in some species (Nasri et al. 2008) resulting from the production of toxic compounds (Smith et al. 1999).

The accumulation of plants and algae on various substrates (i.e. biofouling) resulting from algae blooms can have negative impacts on human activities and structures which have been widely studied (Landoulsi et al. 2011; Fitridge et al. 2012; Nguyen et al. 2012). Biofouling can also involve living organisms, a phenomenon known as ‘epibiosis’ (Wahl 1989). Although epibiosis has been widely studied in marine environments (Shine et al. 2010; Pfaller et al. 2012), the causes and consequences of epibiosis on ‘host’ species in freshwater ecosystems remain poorly understood (Allen et al. 1993; Pedroso Dias et al. 2008; Christiansen et al. 2020). Yet, the consequences of epibiosis on freshwater ‘hosts’ species can be multiple and range from commensalism (e.g. the host only provides a substrate and/or means of dispersal for the epibiont, Edgren et al. 1953; Ziglar and Anderson 2005; Garbary et al. 2007; Burgin and Renshaw 2008; Pedroso Dias et al. 2008) to mutualism (e.g. combining both dispersal for the algae and camouflage for the host, Neil and Allen 1954; Hulse 1976; Barea-Arco et al. 2001) and can even involve amensalism (e.g. when the epibiont induce negative impacts on the host, Neil and Allen 1954; Allen et al. 1993; Burris and Dam 2014).

Freshwater turtles are well suited to investigate the causes and consequences of epibiosis in freshwater ecosystems. The natural occurrence of epizoic algae on freshwater turtles has been documented since the end of the nineteenth century (Peter (1886) in Edgren et al. 1953; Harper 1950; Smith (1882) in Neil and Allen 1954). Many freshwater turtle species have been described to be hosts of epizoic algae, mostly in the Americas (Harper 1950; Edgren et al. 1953; Proctor 1958; Sexton 1965; Gibbons 1968; Ziglar and Anderson 2005; Garbary et al. 2007; Bury et al. 2015; Rodrigues and Silva 2015), but also in Australia (Skinner et al. 2008) and Europe (Ziglar and Anderson 2005; Soylu et al. 2006; Akgul et al. 2014; Fayolle et al. 2016; Vassal et al. 2021); and a remarkable diversity and abundance of algae have been recorded on freshwater turtles (e.g. up to 60–70 different taxa, Ersanli and Gonulol 2015; Fayolle et al. 2016; Bertrand 2018; Vassal et al. 2021).

In this study, we investigated epizoic algae on European pond turtles (*Emys orbicularis*) in one of the largest continental French wetlands: the Brenne region. The goals of our study were threefold. First, we investigated the individual (i.e. sex and age), seasonal and environmental determinants (i.e. type of fish farming) of epizoic algae. We hypothesised (i) that algal cover should increase throughout the spring and the

summer according to increasing photoperiod and water temperature (McQueen and Lean 1987), (ii) that the influence of thermoregulation required to increase metabolic rates to sustain growth in juveniles and vitellogenesis in adult females and thus, periodical drying of the shell, should negatively influence algal cover, and (iii) that increased concentration of nutrients due to intensive fish farming should positively influence algal growth on turtles. In addition, we also investigated the possible impacts of algal fouling on *E. orbicularis*. Increased algal cover could reduce mobility (swimming speed) by increasing drag (Shine et al. 2010) and thus, reduce foraging performance, and we hypothesised that algal cover should negatively influence body condition and reproduction.

Material and methods

Study species and study sites

Our study took place from 2016 to 2018 in the Brenne Natural Park (hereafter ‘Brenne’) which harbours a large population of *E. orbicularis*, a small European freshwater turtle species. Brenne spreads over 1700 km² and is characterised by a matrix of ~4000 artificial ponds created in the Middle Age in order to raise fish (Benarrou 2017). In this area, aquaculture is mainly dedicated to the production of Carp (*Cyprinus carpio*). Production methods differ between extensive aquaculture, where fish are raised under natural conditions, and intensive fish-farming, which involves high carp density and food supplementation (crushed cereal, essentially corn).

Sampling (see below) took place on 23 ponds, located in the vicinity of the Réserve Naturelle Nationale de Chérine (46° 47' 25.23" N, 1° 12' 3.54" E). Sites were sampled from April to August during three consecutive years (2016–2018).

Each site was characterised by the type of fish farming (extensive: $n = 11$ or intensive: $n = 9$), the presence of carp (yes: $n = 9$ or no: $n = 10$) and associated food supplementation (occurring: $n = 7$ or no: $n = 15$). This detailed information was lacking for some study sites. In such cases, data were kept for the analyses dealing with the individual determinants of algal cover solely. Suitable basking sites for the turtles were available at all study sites.

Field procedures and sampling

Turtles were captured with baited funnel traps from April to August usually during three 4-day-long capture sessions per site. Funnel traps were visited every day in order to avoid long-term disturbance of captured individuals.

Upon capture, each turtle was individually and permanently marked with notches in the marginal dorsal and marginal ventral scutes. The straight carapace length (SCL) was measured with a calliper (± 0.01 mm) and body mass was

measured with a digital scale (± 1 g). Most individuals were sexed based on the morphology of the plastron (concave in males, Zuffi and Gariboldi 1995). Sexing was not possible in a few juvenile individuals, and these individuals were kept as ‘unsexed’ in our analyses. Individuals were classified as juveniles when a large growth ring was visible on the ventral scutes, while individuals lacking this growth mark were classified as adults (Olivier 2002). Gravidity of adult females was systematically assessed using manual pelvic palpation (Duguay and Baron 1998; Olivier 2002).

Presence or absence of epizoic algae was assessed for each individual regardless of algal cover for both the carapace and the plastron. Abundance of algae was assessed as the percentage covered of both the carapace and the plastron with 25%-increments from 0 (no algae, Fig. 1) to 100% (turtles entirely covered by algae, Fig. 1).

Overall, during 1883 contacts (including recaptures), we sampled carapace and plastron algal cover from 1112 individuals representing 551 females, 515 males and 46 unsexed individuals.

Each individual was released at the location of capture, usually within a few minutes after capture.

Statistical analyses

All data were tested for homogeneity of variance, residues independence and normality. Determinants of algal presence were analysed using Pearson’s χ^2 tests. We used generalised linear mixed models to investigate individual determinants of algal cover for the carapace and for the plastron, with algal cover as the dependent variable and individual characteristics as the factors (sex [female, male], age class [juvenile, adult]). We also used generalised linear mixed models to investigate environmental determinants of algal cover, with algal cover as the dependent variable, and pond



Fig. 1 European pond turtle (*Emys orbicularis*). Pictures of the same individual captured without algal cover (on 15/06/2017, left panel) and subsequently re-captured with a remarkably high algal cover (on 19/07/2017, right panel)

characteristic as the factors. Consequences of algal cover on body condition were investigated using generalised linear mixed models, with the body mass as the dependent variable, algal cover as the factor and carapace length (body size) as the co-factor. Finally, influence of algal cover on gravidity was investigated using Pearson’s χ^2 tests. Because some individuals were represented more than once in our dataset, individual identity was included as a random factor in all analyses to avoid pseudoreplication. All analyses were performed with Statistica 12.

Results

Overall, more individuals had algae on the carapace than on the plastron (82% versus 10%), and the following results focus on the carapace algal cover (a summary of the results for the plastron can be found in Appendix Table 1).

Individual determinants of algal cover

Presence of algae on the carapace was different between age classes, with 83.1% of adults displaying algal cover versus 67.9% in juvenile individuals ($\chi^2 = 16.77$, $df = 1$, $p < 0.0001$). Abundance of algae on the carapace varied according to the month of capture ($F_{4,1873} = 8.39$, $p < 0.0001$, Fig. 2) but not the age class of the turtle ($F_{1,1873} = 3.28$, $p = 0.07$) or their interaction ($F_{4,1873} = 1.14$, $p = 0.33$).

In adults, presence of algae on the carapace was different between sexes, with 80.3% of females displaying algal cover versus 85.3% in male individuals ($\chi^2 = 7.98$, $df = 1$, $p = 0.004$). Abundance of algae on the carapace varied according to the month of capture ($F_{4,1760} = 51.44$,

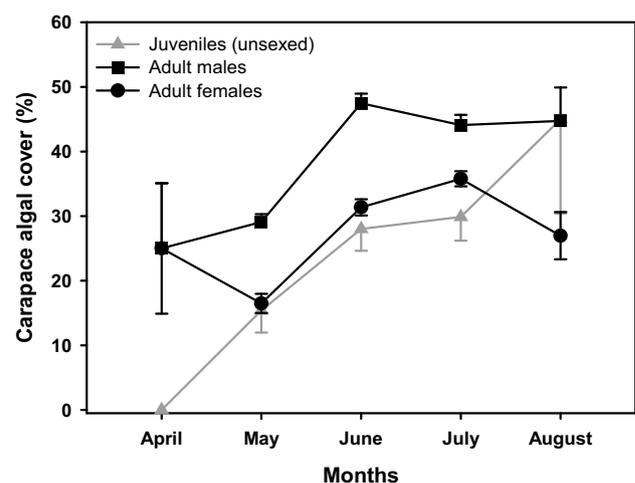


Fig. 2 European pond turtle (*Emys orbicularis*). Evolution of algal abundance (%) on the carapace of female (black circles), male (black squares) and juvenile (grey triangles) turtles during the spring and summer. Data are presented as mean \pm SE

$p < 0.0001$, Fig. 2), the sex ($F_{1,1760} = 11.73$, $p = 0.0006$, Fig. 2) and their interaction ($F_{4,1760} = 2.34$, $p = 0.05$, Fig. 2). Abundance of algae increased throughout the season and this increase was higher in males than in females (Fig. 2).

Environmental determinants of algal cover

Study sites differed strongly in algal presence ($\chi^2 = 165.79$, $df = 23$, $p < 0.0001$, range 63.64–100%).

Abundance of algae on the carapace of turtles was linked to pond usage. Turtles from ponds used for intensive fish-farming had more algae ($F_{1,1719} = 18.48$, $p < 0.0001$, Fig. 3). Similarly, the type of fish-farming (carp-specialised versus generalist fish-farming) influenced turtle algal cover, with turtles from ponds dedicated to carp farming having more algae ($F_{1,1704} = 4.52$, $p = 0.03$). Food supplementation (corn) also affected turtle algal cover both globally ($F_{1,1786} = 15.55$, $p < 0.0001$) or when restricting the analysis on ponds dedicated to carp farming specifically ($F_{1,634} = 21.38$, $p < 0.0001$).

Consequences of algal cover

In males, neither the presence ($F_{1,739} = 0.006$, $p = 0.94$) nor the abundance ($F_{4,732} = 0.62$, $p = 0.64$) of algae affected body condition. The presence of algae negatively affected the body condition of adult females ($F_{1,903} = 8.42$, $p = 0.003$, Fig. 4), but this was not linked to abundance of algae ($F_{4,896} = 1.12$, $p = 0.34$). Algal presence was not linked to the proportion of reproductive females ($\chi^2 = 3.36$, $df = 1$, $p = 0.06$), with 19.72% of the females without algae being reproductive, versus 13.69% in females with algae. The abundance of algae on the carapace was negatively linked to the proportion of reproductive females ($\chi^2 = 7.98$, $df = 3$, $p = 0.04$, Fig. 5).

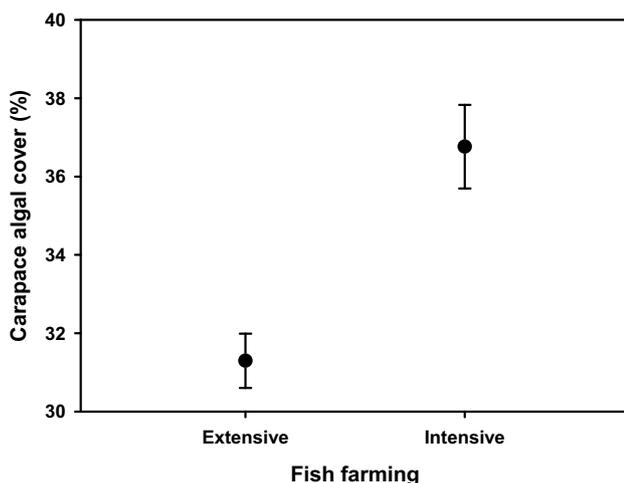


Fig. 3 European pond turtle (*Emys orbicularis*). Influence of fish-farming type (extensive versus intensive) on algal abundance assessed on turtle carapace (%). Data are presented as mean \pm SE

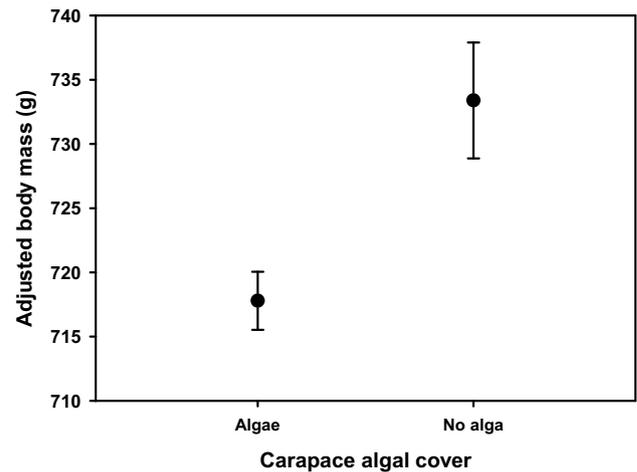


Fig. 4 European pond turtle (*Emys orbicularis*). Influence of algal presence on female body condition (body mass adjusted to body size (g)). Data are presented as mean \pm SE

Discussion

Our results indicate that all sexes and ages of the European pond turtle *E. orbicularis* populations we studied are hosts of visible epizotic algae. According to our hypotheses, we found that algal cover increased throughout the spring and the summer, that algal cover varied according to the age and the sex of individuals and that intensive fish farming positively influenced algal growth on turtle. Importantly, our results allowed to show that algal epibiosis induced by fish farming negatively influenced body condition and reproduction in adult females.

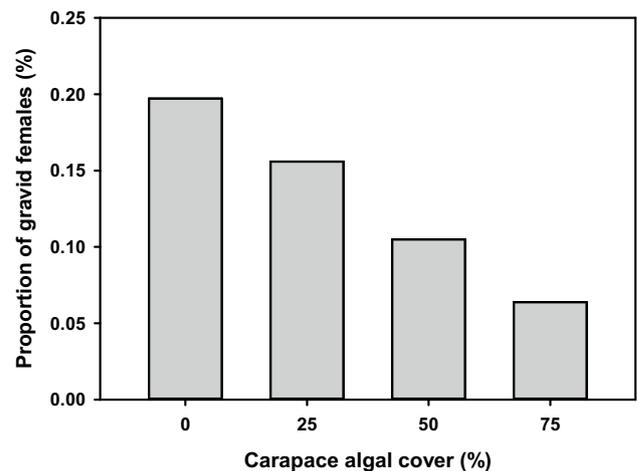


Fig. 5 European pond turtle (*Emys orbicularis*). Proportion of gravid females (%) for each class of carapace algal cover (%)

Individual determinants of algal cover

The European pond turtle is known to harbour a large variety of algal taxa (Akgul et al. 2014; Ersanli and Gonulol 2015; Fayolle et al. 2016; Vassal et al. 2021). In our study, the overall proportion of individuals displaying algal presence on the carapace (~82%) was similar to what has been found in other geographic areas (~77% in Turkey, Akgul et al. 2014). However, research on the individual determinants of algal cover on freshwater turtles lacked to date. We found that juvenile individuals harboured less often algae than adults, a result that is probably linked to the diverging ecologies of these two age-classes (Lefevre and Brooks 1995; Gamble 2006). Juveniles are characterised by relatively high growth rates (Krawchuk and Brooks 1998; Carrière et al. 2008). In order to sustain the energetic demands of growth, juvenile individuals need to frequently thermoregulate in order to reach optimal body temperature. This process occurs through sun-basking in freshwater turtles (Krawchuk and Brooks 1998; Carrière et al. 2008). Frequent periods dedicated to sun-basking may allow the carapace to dry, a process that is likely detrimental to algal survival. The same process may explain the differences between males and females, with lower algal cover found in females. Indeed, reproduction is an energy-demanding process in female turtles (Krawchuk and Brooks 1998; Edwards and Blouin-Demers 2007). Accordingly, females display intense basking behaviour during vitellogenesis (Hammond et al. 1988; Krawchuk and Brooks 1998). Conversely, although males need to bask for spermatogenesis, the associated metabolic costs, and thus thermoregulatory demands are likely lower than in females (Hammond et al. 1988). Overall, it is likely that different thermoregulatory strategies (sun-basking) between age classes and sexes are responsible for the results we found. Accordingly, complementary results on the algal cover of the plastron of turtles strengthen this hypothesis (Appendix Table 1).

Interestingly, we detected a strong effect of the season on algal abundance on turtles, irrespective of the age-class or the sex. This is likely linked to the biological cycle of the algae species that occurred on turtles, which presumably grow throughout the spring and the summer, according to increasing photoperiod and water temperature (McQueen and Lean 1987).

Environmental determinants of algal cover

Previous studies have highlighted large differences of epizoic algae on freshwater turtles between study sites, but these differences remained essentially unexplained (Proctor 1958; Soyulu et al. 2006). Because fish production methods differ between ponds in our study area, our study offers a strong mechanistic basis for explaining such differences. We found a significant impact of pond management on epizoic algae on turtles. Specifically, we found a higher algae abundance on

the carapace of turtles collected at sites where intensive fish-farming took place (as compared to sites of extensive fish-farming), at sites dedicated to carp-specialised fish-farming (as compared to generalist fish-farming) and at sites where food supplementation (i.e. crushed corn) occurred (as compared to sites without food supplementation). These results suggest that fish-farming affects the abundance of epizoic algae, and are consistent with the expected and reported relationships between fish-farming and eutrophication described in the 'Introduction' section. In addition, specialisation of pisciculture on carps is likely to worsen the situation, as carps are a bottom-feeding species which behaviour results in the re-suspension of sediments. In turn, the consequent enrichment in organic matter promotes algal blooms which colonise turtles, sometimes to a remarkably large extent (Fig. 1).

Consequences of algal fouling

We tentatively related algal cover with body condition and the proportion of reproductive females, two indices of turtle fitness relatively straightforward to assess. We found that the body condition of females, but not males, was lower in individuals covered by algae. Three different hypotheses can explain this result. First, females in lower body condition, and thus with lower body reserves, may decrease their propensity to sun-bask to reduce the energy expenditure linked to an elevated metabolism. In turn, because these females stay more frequently immersed in water, they provide optimal conditions for continuous algal growth (i.e. no periodic drying of the carapace, see above). Alternatively, significant algal cover may affect foraging success in individuals covered by algae. For instance, strong algal cover (as pictured in Fig. 1) could potentially reduce mobility (swimming speed) by increasing drag (Shine et al. 2010; see also Frick and Pfaller 2013). Conversely, it is equally plausible that females with important algal cover may voluntarily bask more in order to reduce the costs associated with strong algal cover. Future studies should test for these three diverging hypotheses to assess the putative negative influence of epizoic algae on turtle condition, as well as potential behavioural shifts associated with strong algal cover. We also found that the proportion of gravid female decrease according to the proportion of their carapace covered by algae. As above, this may not be a direct negative consequence of algal growth. For instance, non-reproductive females should bask less frequently than reproductive ones, thereby offering better algal growth conditions. Yet, the gradual decrease in the proportion of gravid females in relation of algal cover we found (see Fig. 5) does not support this hypothesis. On the contrary, such a gradual decrease of the proportion of gravid females with increasing algal suggests a direct negative influence of epizoic algae on reproduction. The specific mechanism that

would link epizoic algae to decreased reproductive success remains complicated to assess, but we contend that it could be linked to reduced mobility and/or behavioural shifts, and thus reduced ability to forage successfully in order to sustain vitellogenesis. Future studies are required to assess the impact of algal cover on the locomotor performances of European freshwater turtles.

Conclusion

Overall, our results indicate that epizoic algal is largely mediated by anthropogenic activities (fish-farming) and that it affects age classes and sexes differently according to their different biological characteristics. The presence and abundance of algal cover seem to be largely mediated by behavioural thermoregulation (sun-basking) that may allow turtles to limit algal growth on their carapace. We also detected a potential negative impact of algal cover on some fitness-related traits of adult female turtles (i.e. on body condition and reproduction). Despite the need to further testing the mechanistic bases of the correlations we found, such negative influence are a major phenomenon to investigate owing to its potential critical impacts on reproduction and thus persistence of populations in this long-lived vertebrate.

Appendix

Table 1 European pond turtle (*Emys orbicularis*). Summary of the results of algal presence and abundance on turtle plastron

Variable	Factor	Test	Statistical results	Result
Presence	Age	χ^2	$\chi^2 = 6.62$, $df = 1$, $p = 0.01$	Adult = 8.8% Juvenile = 16.1%
Abundance	Age Month Interaction	glm	$F_{1, 1873} = 3.7322$, $p = 0.05$ $F_{4, 1873} = 10.988$, $p < 0.0001$ $F_{4, 1873} = 1.7480$, $p = 0.13$	Juvenile > adult Increase over time
Presence	Sex	χ^2	$\chi^2 = 28.9$, $df = 1$, $p < 0.0001$	Female = 5.8% Male = 13.1%
Abundance	Sex Month Interaction	glm	$F_{1, 1760} = 7.6026$, $p = 0.005$ $F_{4, 1760} = 36.852$, $p < 0.0001$ $F_{4, 1760} = 8.6573$, $p < 0.0001$	Male > female Increase over time
Presence	Pond	χ^2	$\chi^2 = 229.59$, $df = 23$, $p < 0.0001$	Range 0 to 41.46%
Abundance	Month Pond	glm	$F_{4, 1855} = 31.388$, $p < 0.0001$ $F_{23, 1855} = 11.533$, $p < 0.0001$	Increase over time
Abundance	Type of fish farming		$F_{1, 1719} = 16.226$, $p < 0.0001$	Intensive > extensive
Abundance	Presence of carp		$F_{1, 1704} = 4.3393$, $p = 0.03$	Carp > non carp
Abundance	Feeding		$F_{1, 1786} = 19.455$, $p < 0.0001$	Yes > no
Presence	Female body condition	glm	$F_{1, 903} = 0.2267$, $p = 0.63$	
Abundance	Female body condition	glm	$F_{4, 900} = 1.7263$, $p = 0.14$	
Presence	Male body condition	glm	$F_{1, 739} = 5.7016$, $p = 0.017$	With > without
Abundance	Male body condition	glm	$F_{4, 736} = 1.6056$, $p = 0.17$	

Acknowledgements We thank all the volunteers and the staff from the Réserve Naturelle Nationale de Chérine for their help during field work and especially J. Lemaire, J. Morgnieux and N. Delmas. Two anonymous reviewers as well as the editor provided insightful comments that improved a previous version of this manuscript.

Author contribution F.Br. and F.Be. conceived and designed the study; F.Be. collected the data; F.Be. and F.Br. conducted the analyses, interpreted the data, designed the figures and wrote the manuscript.

Funding Funding was provided by the Agence de l'Eau Loire-Bretagne, the WWF (World Wide Fund), the Réserve Naturelle Nationale de Chérine and the Centre National de la Recherche Scientifique (CNRS).

Data availability Data will be made available upon reasonable request.

Code availability N/A

Declarations

Ethics approval This work was approved by the French authorities (DDT-Indre # 36–2018-05–16-003).

Consent to participate All authors accepted to participate.

Consent for publication All authors approved the final version of the manuscript.

Conflict of interest The authors declare no competing interests.

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