Variation in Life-History Traits Between a Newly Established and Long-Established Population of Non-Native Pumpkinseed, *Lepomis gibbosus* (Actinopterygii: Perciformes: Centrarchidae)

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**Background.** The life-history traits of non-native species are believed to change in a predictable manner in relation to time since introduction, with populations in the early stages of establishment predicted to invest more energy into reproduction than long-established populations, mainly due to lower intraspecific competition for resources. In Europe, the range of non-native pumpkinseed, *Lepomis gibbosus* (Linnaeus, 1758), continues to increase. Despite this, the majority of hitherto conducted studies have investigated long-established populations only, very few focusing on newly established populations (<10 years old) or comparisons of life-history traits of new and older populations.

**Material and methods.** In this study, we compared the fecundity, condition, and population structure of a new and a long-established pumpkinseed population (two- and 14-years after introduction, respectively) in two small Central European lakes in order to identify any differences in life-history traits.

**Results.** We confirmed that the established population displayed lower fecundity and poorer overall condition than the new population. Unexpectedly, there was no significant difference in size-at-maturity.

**Conclusion.** While this study confirmed that life-history traits of introduced species appear to change with time since introduction, it also emphasises the possible effect of other factors such as temperature, size of body of water, and relative predator pressure in shaping such traits.

**Keywords:** freshwater fish, alien species, introduced species, date of introduction, size-at-maturity, fecundity

INTRODUCTION

The majority of successful introductions of non-native species pass through three stages: introduction—when the species arrives at a new environment, establishment—in which the species successfully reproduces and rapidly increases in number, and assimilation—when the non-native species integrates into the native ecosystem (Feiner et al. 2012). During each of these stages, life-history strategies employed by the species may vary along an $r$-$K$ continuum (see Fox et al. 2007). Traits typical for the establishment stage (defined by a low density of conspecifics and low competition for resources) include fast individual growth (for juveniles especially), early maturation, and high investment in reproduction. During the assimilation stage, investment into reproduction decreases and growth is limited by higher competition for food resources (Fox et al. 2007).

Successful fish invaders are mostly characterised by having suitable traits for establishment in a new environment, such as: a broad diet spectrum, wide environmental tolerance, and parental care (Garcia-Berthou 2007) or by the ability to shift from $r$-strategy life-history traits, which are suitable for the years immediately after introduction, to $k$-strategy traits, more suitable for established populations (Feiner et al. 2012). The pumpkinseed, *Lepomis gibbosus* (Linnaeus, 1758), is a freshwater fish known for its recent successful establishment and rapid spread in many non-native areas (Fox and Copp 2014). A native of North America, the species was first introduced into European waters: Spain (Rooke and Fox 2014), France and Germany (Przybylski and Zięba 2011) during the late 19th century, since when it has spread to at least 28 European countries (Copp and Fox 2007). The species’ high invasive potential is supported, at least in part, by its ability to survive and successfully establish itself in both lentic and lotic waters under a range of environmental conditions, including low or high water temperatures or hypoxic conditions (Fox and Copp 2014). As a result, the pumpkinseed is presently one of the most-frequently studied invasive fish in Europe. The majority of these studies have focused on differences in life-history traits between the various European populations (e.g., the influence of latitude and thermal regime;

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Tomeček et al. 2007) and shifts in life-history traits between native and non-native ranges (e.g., Fox and Copp 2014).

Despite distribution of pumpkinseed continuing to increase in Europe, the majority of studies have investigated long-established populations only, with very few focusing on characteristics of newly established populations (<10 years; Oliva-Paterna et al. 2005, Diripasko et al. 2007) or comparisons of life-history traits of new and older populations (Fobert et al. 2013).

In this study, we compared two pumpkinseed populations in the Czech Republic, one established in 1997 (long-established population) and the other in 2011 (new population). Based on life-history theory (Sakai et al. 2001, Bohn et al. 2004), we hypothesised that newer pumpkinseed populations would mature younger and display increased fecundity compared with long-established populations. Further, low population density would decrease competition for resources and lead to higher body condition per fish (Carol et al. 2009). As increased energy depletion following reproduction may cause increased mortality and/or a shorter life span, however, we further predicted that newer and older populations would differ in population structure, body condition, and reproductive characteristics. We discuss the results in relation to other European pumpkinseed populations.

The goals of this work were to evaluate selected life-history traits of two pumpkinseed populations, one long-established and the other established relatively recently, and to assess such traits change with time since introduction.

**MATERIAL AND METHODS**

**Study sites.** Pumpkinseeds (*Lepomis gibbosus*) for this study were sampled from two lakes in southeast Moravia, Czech Republic: Annin (49°25’20.366″N, 17°17’49.275″E; 0.8 ha) and Rohlik (48°38’57.541″N, 17°17’49.275″E; 119 ha). Annin Lake was created in the 1950s through flooding of a gravel extraction pit. The lake has established itself as one of the few successfully reproducing populations in the Czech Republic.

Rohlik Lake was formed through flooding of a gravel borrow pit in 1983. It has a mean depth of 2 m and the bottom is sand–gravel with a thin layer of organic mud. Despite being shallow, the water levels never dropped below 1 m, even during the driest periods (Janáč et al. 2010). While aquatic vegetation is almost absent, numerous submerged branches and tree stumps provide sufficient shelter for fish. Rohlik’s fish fauna is dominated by bit-tering, *Rhodeus amarus* (Bloch, 1782); common bream, *Abramis brama* (Linnaeus, 1758), and Prussian carp, *Carassius gibelio* (Bloch, 1782); with pike, *Esox lucius*, and wels catfish, *Silurus glanis* Linnaeus, 1758, as predators. Pumpkinseed was first registered there in 2011, following extensive local flooding (P. Jurajda, personal observation). The Dyje River is just 700 m away, suggesting this was the source of the new population.

Though both lakes are situated at the same latitude, differences in depth and surface area could have influenced water temperatures. As temperature range is an important factor for comparing populations across Europe, we monitored the annual temperature range using HOBO 64K data loggers (Onset Computer Corporation, MA, USA) placed at 0.8 m depth at each locality between April and October 2013. Though the data loggers were unavailable for monitoring temperatures at Annin Lake in 2011 (when fish were sampled), we were able to download data for this site from a Czech on-line diving website* for comparison (see Fig. 1).

**Fish collection.** Pumpkinseed were sampled from Annin Lake at the end of May 2011, and from Rohlik Lake at the end of May 2013 (in each case, prior to the predicted start of the spawning season) using a five-metre beach seine and electrofishing equipment (Lena, Bednář Olomouc, Czech Republic). All fish caught were euthanized with an overdose of clove oil, placed in crushed ice, and transported to the laboratory for further analysis.

**Ethical issues.** The presently reported study has been carried out in strict accordance with the Czech Law No. 246/1992 about “Animal welfare”.

**Assessment of size, age, sex, and sexual maturity.** In the laboratory, all fish were measured to the nearest 0.01 mm of total length (TL) and standard length (SL) using digital callipers and weighed to the nearest 0.01 g of total weight ($W_T$). The age of each fish was determined by counting the annuli on scales. Scales were removed from the left side of the body, between the lateral line and dorsal fin, cleaned and placed between two glass slides, and allowed to dry.

* www.stranypotapecske.cz

**Fig. 1.** Water temperature regime for Annin (dashed line) and Rohlik (solid line) lakes in 2013; Individual points indicate separate temperature measurements for Annin in 2011
The scales were examined by two independent observers using a microfiche projector. The fish were then dissected to remove the gonads and gastrointestinal tract to determine the eviscerated weight \( W_{\text{ev}} \) and the gonad weight \( W_{G} \). Sex and maturity of each fish was determined during dissection based on the presence and type of gonads. Fish with no-, indistinguishable-, or very small and clearly immature gonads (according to colour in males; colour and absence of mature or maturing/vitellogenic oocytes in females) were considered as immature juveniles. The proportion of each sex (juveniles excluded) was used to calculate the population sex ratio.

**Assessment of body condition and fecundity.** Changes in body condition were expressed using Clark’s condition coefficient \( K_{c} \) (Clark 1928), expressed as

\[
K_{c} = 100 \frac{W_{\text{ev}}}{W_{T}} \cdot \frac{T}{L}^{-1}
\]

where \( W_{\text{ev}} \) represents eviscerated fish weight and \( T \) is total length. Gonad development in females was determined by the gonadosomatic index (GSI) (West 1990), expressed as

\[
\text{GSI} = 100 \frac{W_{G}}{W_{T}} \cdot \frac{T}{L}^{-1}
\]

where \( W_{G} \) represents weight of gonads and \( W_{T} \) is total weight. Fecundity was assessed through a detailed study of the female gonads. Each ovary was removed, opened, and spread thinly on a viewing slide. An image of each opened ovary was obtained using a uEye-1540C digital camera coupled with an Olympus SZX7 binocular microscope (20×, 25×, and 32×). The image was then examined using LUCIA 5 image analysis software (Laboratory Imaging Ltd.) to obtain the number and precise measurements of the oocyte size. Individual oocyte developmental stage was characterised according to Burns (1976), and Santos et al. (2012) as previtellogenic (primary growth), cortical alveoli, vitellogenic, or mature. For each female, absolute fecundity was assessed as the total number of oocytes in the ovaries minus previtellogenic oocytes.

**Data analysis.** The effect of fish size, site, and their interaction on female fecundity, and female GSI was revealed using analysis of covariance (ANCOVA). All data complied with the assumptions of ANCOVA (normality, homoscedasticity) and the validity of the model was confirmed through residual analysis (Shapiro test at α level of 0.05 for normality of residuals; visual check for absence of trend in residuals vs. fitted values). Any significant difference in temperature range between the two sites was assessed using the paired Wilcoxon test as data did not comply with the assumptions of parametric tests (normality, homoscedasticity), effect of site on body condition was revealed using the non-parametric Mann–Whitney test. The effect of fish size, site, and their interaction on size-at-maturity was revealed using a generalised linear model (GLM; binomial distribution of data; model design corresponding to ANCOVA). For each site, GLM was used to estimate the size at which 10%, 50% (size-at-maturity for comparison with literature), and 90% of fish became mature (SL10, SL50, and SL90, respectively).

**RESULTS**

At Annin Lake 198 pumpkinseed were caught (81 females, 90 males, and 27 juveniles) with a random sex ratio of 1 : 1.1. Sixty-four fish were sampled from Rohlik Lake (15 females, 24 males, and 25 juveniles), with a random sex ratio of 1 : 1.6. At both sites, there was no significant deviation from a 1 : 1 sex ratio (Annin, \( \chi^2 = 0.24, P > 0.05 \); Rohlik, \( \chi^2 = 1.04, P > 0.05 \)). Juveniles represented 13% of all pumpkinseed caught at Annin and 39% at Rohlik. Scale reading indicated four age groups in both populations (Fig. 2), though the proportions of each age group differed at each site. More than 70% of fish sampled at both localities were in their second (1+) or third (2+) year of life. In the newly established population at Rohlik, 1+ fish constituted 20% and 2+ fish—50% of the pumpkinseed caught. In the long-established population of Annin 1+ fish represented just 5% of fish caught and 2+ fish—65% (Fig. 2). At both localities, all 1+ fish were juveniles; however, just 10% of 2+ fish at Annin and 19% of 2+ fish at Rohlik were juvenile, indicating that the majority of fish reached maturity in their third year. Whilst the majority of immature 1+ fish and older individu-
uals (4+) could be clearly identified in the length frequency histograms for both localities, there was considerable overlap in 2+ and 3+ fish of 64–80 mm at Annin and for 2+ and 3+ fish of 68–70 mm at Rohlik (Fig. 2).

No significant difference in daily temperature range was observed between the two sites (Wilcoxon paired test, V = 6883, n = 348, P = 0.273; Fig. 1). The GLM model (Fig. 3) showed no significant effect for both site and size–site interaction (effect of site, df = 1 and 255, P = 0.241, effect of size–site interaction, df = 1 and 255, P = 0.175), thereby indicating no significant difference in size-at-maturity between the two sites. Based on the GLM model, SL<sub>50</sub> at Annin was slightly lower than that at Rohlik (51.1 mm compared to 55.0 mm; SL<sub>10</sub> – SL<sub>90</sub> range = 40.7–61.5 for Annin and 48.3–61.8 for Rohlik; Fig. 3).

There was no significant difference in female GSI between Rohlik and Annin (ANCOVA, effect of site, F<sub>1,43</sub> = 0.45, P = 0.506; Fig. 4). There was, however, a significant difference in the relation between GSI and fish size between the two sites (ANCOVA, effect of site–size interaction, F<sub>1,43</sub> = 13.28, P < 0.001; Fig. 4), with GSI increasing significantly more with fish size at Rohlik (linear regression, F<sub>1,13</sub> = 18.81, P < 0.001) but not at Annin, where high variability in GSI was observed (linear regression, F<sub>1,79</sub> = 3.23, P = 0.076; Fig. 4).

Absolute fecundity for pumpkinseed from Rohlik (62–92 mm) was significantly higher (ANCOVA, effect of site, F<sub>1,43</sub> = 89.23, P < 0.001; Fig. 5) than that for Annin pumpkinseed (58–92 mm), with fecundity ranging from just 907 to 4097 oocytes at Annin and 1235–15 650 oocytes at Rohlik. In addition, fecundity increased significantly more with fish size at Rohlik (ANCOVA, effect of site–size interaction, F<sub>1,43</sub> = 49.17, P < 0.001; Fig. 5).

Body condition of juveniles, males and females was significantly higher at Rohlik than Annin (Mann–Whitney test; juvenile: W = 10, n = 52, P < 0.001; male: W = 14, n = 113, P = 0.001; female: W = 52, n = 96, P < 0.001; Fig. 6), with coefficients approximately 30% higher for all three categories (average condition of male = 1.5 vs. 2.1; female = 1.5 vs. 1.9; juvenile = 1.4 vs. 1.9; Fig. 6).
DISCUSSION

According to Fox et al. (2007), life-history traits of introduced and successfully established species are predicted to shift along a continuum between $r$ and $K$ strategies, depending upon the time that has passed since introduction. The extent of this shift can be influenced by a range of biotic and abiotic factors. During the first years following the introduction, fish populations typically display high investment into reproduction, thereby aiding successful establishment in the new environment. This is reflected in a lowered age-at-maturity and higher fecundity (Bøhn et al. 2004). On the other hand, newly colonised areas typically have a low density of conspecifics, resulting in lowered intra-specific competition, faster growth, and improved body condition (Feiner et al. 2012).

In this study, we compared life-history traits and population characteristics of two pumpkinseed populations, one still in the early phase of establishment (Rohlik; sampled two years after its introduction in 2011) and the other an established population introduced in 1997 (Annin; sampled 14 years after introduction). We predicted that our ‘new’ and ‘old’ populations would differ in population size structure, body condition and reproductive characteristics.

While we were able to sample 198 fish from the long-established and abundant population in Annin, only 64 fish were obtained from the lower-density population in Rohlik, despite an order-of-magnitude higher sampling effort. We found no evidence, however, that differences observed in life-history traits (or lack of them) were related to the number of fish caught. Furthermore, as the Dyje River is a main tributary of the Morava River, joining close to the Morava’s confluence with the Danube, and the Danube and lower (Slovakian) stretch of the Morava is believed to be the source for pumpkinseed in the Dyje (Hanel and Lusk 2005), it is highly likely that the fish from Annin and Rohlik both came from a common source population, i.e., the Danube, effectively ruling out genetics as a cause of differing life-history traits.

Both populations comprised four age groups (1+ through 4+), with the oldest fish at Rohlik probably representing individuals from the founder population. Population structure at the two sites differed only in the proportion of 1+ fish at each site, the relatively weak 1+ class observed at Annin in 2011 probably being caused by exceptional flooding in 2010 (there was no severe flooding prior to sampling at Rohlik). Both populations showed a high degree of overlap between the 2+ and 3+ size classes, almost certainly related to the pumpkinseed’s ability to produce multiple clutches each breeding season (Ribeiro and Collares-Pereira 2010).

While pumpkinseed can live for up to eight years and measure up to 162 mm TL (Lake of Banyoles, Spain; Villa-Gispert and Moreno-Amich 2000), Lake Kerkini, Greece (Neophitou and Giapis 1994), Mrtva Tisa, Serbia (Maletin et al. 1989), all of which displayed a similar water temperature range during summer to that at Annin (unfortunately, we were unable to find any information on pumpkinseed fecundity at higher or lower temperature ranges). In comparison, female fecundity at Rohlik was extremely high, which appears to confirm our prediction of a higher investment into reproduction at the newly established site. Investment into reproduction, however, is not only measured by fecundity (i.e., the number of possible offspring) but also by GSI. Surprisingly, despite the higher fecundity of fish in the newly established population, we found no significant difference in GSI, probably due to the unexpectedly high GSI of some 2+ fish in the long-established population (Fig. 4) and a relatively low number of females sampled from the new population. GSI is strongly affected by both total num-

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Pumpkinseed fecundity in the established population at Annin was comparable with that at several other established populations in Europe such as those of: Lake of Banyoles, Spain (Villa Gispert and Moreno Amich 2000), Lake Kerkini, Greece (Neophitou and Giapis 1994), Mrtva Tisa, Serbia (Maletin et al. 1989). Unlike populations in larger bodies of water in Spain and Greece, which may reach 8+ (Vila-Gispert and Moreno-Amich 2000, Villeneuve et al. 2005), the majority of European populations display a much shorter life-span, with the 4+ maximum observed in our study being typical. This is most likely linked to temperature differences between the study regions, with most (non-Mediterranean) European waters showing high annual variation in temperature, resulting in rapid heating during summer and ice-cover during winter in the small bodies of water typically inhabited by pumpkinseed (as observed at both our study sites). Cold winter weather could lead to higher fish mortality in smaller bodies of water, and especially for smaller fish such as pumpkinseed (Uzunova et al. 2008).

Pumpkinseed show great plasticity in age- and size-at-maturity, both in their native and non-native range. In Europe, fish from southerly populations (e.g., Spain) can reach maturity as early as their second year (1+); however, the majority of populations in the rest of Europe tend to mature in their third year (2+; Przybylski and Zięba 2011). Both our study populations confirm this trend, with most fish maturing at age 2+ and immature individuals representing a very small proportion.

As predicted, pumpkinseed from Rohlik displayed the increased body condition typical for fish populations in the early stage of settlement (Carol et al. 2009), presumably due to lower inter- (absence of perch) and intra-specific competition for food resources at this site. Despite the slight shift toward smaller size-at-maturity evident in the newly established population at Rohlik (55 mm compared to 51 mm at Annin), the difference between two sites was not significant. Size-at-maturity at these two sites was comparable to that at other sites at similar latitudes, e.g., Grand-Lieu Lake in France (Cucherousset et al. 2009) and Tanyard Lake in England (Villeneuve et al. 2005).
number of oocytes and stage of maturation (i.e., the readiness of females to spawn; Jons and Miranda 1997). Given the lower number of oocytes in 2+ fish from Annin, the higher GSI in these fish could have been caused by an increase in the number of mature oocytes (confirmed by direct observation; in fact 2+ fish from Annin had a higher number of mature oocytes than 4+ fish), suggesting that we caught a group of females just prior to spawning (older/larger females tend to spawn earlier in the season). The unexpectedly high GSI in 2+ Annin females was only observed in eight of 46 individuals; hence, if the scales from these fish had been read incorrectly and the fish were actually older, this could also have introduced bias. On the other hand, scale readings were undertaken independently by two experienced observers, suggesting this was not an issue. In some pumpkinseed populations (e.g., rivers Ardilla and Degebe; Ribeiro and Collares-Pereira 2010) GSI can show considerable variation, both at the beginning of spawning and during the spawning season. During August sampling at Annin, several 4+ females were caught with high GSI and mature oocytes. While this could suggest either a protracted spawning season or a later start and end to the spawning season for larger individuals, we have no definitive evidence for this (and other bias factors) and suggest that further long-term studies of life-history traits over the spawning studies are needed to help shed light on factors affecting GSI at these, and other, sites.

Further development of the two populations remains uncertain. While the long-established population at Annin appears to be stable, the newer population at Rohlík may yet fail due to the relatively small surface area of the body of water (0.8 ha), which could prove limiting for further population growth due to the potential risk of high intra-specific competition and predator pressure. On the other hand, the overall carrying capacity at Rohlík is enhanced by its relatively high nutrient content. More importantly, several other ‘new’ populations were observed at adjacent sites in autumn 2014 (Jurajda, personal observation), strongly suggesting that regular spring flooding both maintains and increases connectivity between pumpkinseed meta-populations and decreases the overall risk of local extinction, even in small water bodies.

To summarise, pumpkinseed at Rohlík displayed life-history traits typical for a newly established population, i.e., they invested more energy into reproduction (high fecundity) and had a relatively high condition factor, presumably as a low density of conspecifics resulted in lower competition for food. On the other hand, pumpkinseed at Annin displayed a mixture of features typical for populations at an early stage of establishment (i.e., a relatively short life-span and relatively low size-at-maturity) and of more established populations (i.e., lowered body condition and lowered fecundity). The preservation of features typical for newly established populations at Annin was probably caused by the typically central European temperature regime; with low temperatures and ice cover in winter increasing overwinter mortality, resulting in a relatively short lifespan. In addition, these temperature conditions appear to have reduced age-at-maturity in these Czech populations to 2+ (compared to 4+ in warmer Mediterranean waters), even in newly established populations.

It should be noted that these results were based on just two sites and one year’s monitoring and, as such, should be considered a pilot study for future research. In order to confirm our results, and perhaps reveal further factors influencing life history traits in such populations, we suggest more frequent sampling before, during and after the spawning season with more detailed measurement of biotic and abiotic factors at the sites. In this study, we focused on time since establishment; however, the factors contributing to the differences observed in our two populations (e.g., temperature, size of the body of water, and relative predator pressure; see Fox and Copp 2014) may yet prove to be more complex.

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REFERENCES

Bohn T., Sandlund O.T., Amundsen P.-A., Primicerio R. 2004. Rapidly changing life history during invasion. Oikos 106 (1): 138–150. DOI: 10.1111/j.0030-1299.2004.13022.x
Burns J.R. 1976. The reproductive cycle and its environmental control in the pumpkinseed, Lepomis gibbosus (Pisces: Centrarchidae), Copeia 1976 (3): 449–455. DOI: 10.2307/1443358
Carol J., Benejam L., Benito J., García-Berthou E. 2004. Life-time growth patterns of the pumpkinseed, Lepomis gibbosus (Pisces: Centrarchidae). Copeia 2004 (3): 289–306. DOI: 10.1111/j.0030-1299.2004.13022.x
Clark F.N. 1928. The weight–length relationship of the California sardine (Sardina pilisus) at San Pedro. Fishery Bulletin No. 12: 1–59.
Copp G.H., Fox M.G. 2007. [Chapter fifteen] Growth and life history traits of introduced pumpkinseed (Lepomis gibbosus) in Europe and the relevance to its potential invasiveness. Pp. 289–306. DOI: 10.1007/978-1-4020-6029-8
Cucheroisset J., Copp G.H., Fox M.G., Sterud E., van Kleef H.H., Verreycken H., Záhorská E. 2009. Life-history traits and potential invasiveness of intro-
duced pumpkinseed *Lepomis gibbosus* populations in northwestern Europe. Biological Invasions 11 (9): 2171–2180.

DOI: 10.1007/s10530-009-9493-5

Diripasko O.A., Demčenko N.A. [Demchenko N.A.], Kulik P.V., Zabroda T.A. 2008. Razširenie arealas solnečnogo okunâ *Lepomis gibbosus* (Centrarchidae, Perciformes), na vostok Ukrainy. ["An expansion of the pumpkinseed, *Lepomis gibbosus* (Centrarchidae, Perciformes) area of distribution into the east of Ukraine."] Vestnik zoologii 42 (3): 269–273.

Feiner Z.S., Aday D.D., Rice J.A. 2012. Phenotypic shifts in white perch life-history strategy across stages of invasion. Biological Invasions 14 (11): 2315–2329.

DOI: 10.1007/s10530-012-0231-z

Fobert E., Zięba G., Vilizzi L., Godard M.J., Fox M.G., Stakénas S., Copp G.H. 2013. Predicting non-native fish dispersal under conditions of climate change: Case study in England of dispersal and establishment of pumpkinseed *Lepomis gibbosus* in a floodplain pond. Ecology of Freshwater Fish 22 (1): 106–116.

DOI: 10.1111/eff.12008

Fox M.G., Copp G.H. 2014. Old world versus new world: Life-history alterations in a successful invader introduced across Europe. Oecologia 174 (2): 435–446.

DOI: 10.1007/s00442-013-2776-7

Fox M.G., Vila-Gispert A., Copp G.H. 2007. Life-history traits of introduced Iberian pumpkinseed *Lepomis gibbosus* relative to native populations. Can differences explain colonization success? Journal of Fish Biology 71 (Suppl. D): 56–69.

DOI: 10.1111/j.1095-8649.2007.01683.x

Garcia-Berthou E. 2007. The characteristics of invasive fishes: What has been learned so far? Journal of Fish Biology 71 (Suppl. D): 33–55.

DOI: 10.1111/j.1095-8649.2007.01668.x

Hanel L., Lusk S. 2005. Ryby a mihule České Republiky. [Fish and lampreys of the Czech Republic.] Český svaz ochránce přírody, Vlašim, Czech Republic. [In Czech.]

Janáč M., Ondračková M., Jurajda P., Valová Z., Reichard M. 2010. Flood duration determines the reproduction success of fish in artificial oxbows in a floodplain of a potamal river. Ecology of Freshwater Fish 19 (4): 644–655.

DOI: 10.1111/j.1600-0633.2010.00449.x

Jons G.D., Miranda L.E. 1997. Ovarian weight as an index of fecundity, maturity, and spawning periodicity. Journal of Fish Biology 50 (1): 150–156.

DOI: 10.1111/j.1095-8649.1997.tb01347.x

Maletin S., Dukić N., Kostić D. 1989. The growth and fecundity of *Lepomis gibbosus* (Pisces: Centrarchidae) in the Tisa dead-arm (Curug–Biserno Ostrvo). Tiscia 24: 103–106.

Maletin S., Giapis A.J. 1994. A Study of the biology of pumpkinseed (*Lepomis gibbosus* (L.)) in Lake Kerkini (Greece). Journal of Applied Ichthyology 10 (2–3): 123–133.

DOI: 10.1111/j.1439-0426.1994.tb00151.x

Oliva-Patena F.J., Andreu A., Verdiell D., Torralva M. 2005. First occurrence of *Lepomis gibbosus* (L., 1758) in the Segura River basin (SE, Spain). Limnnetica 24 (3–4): 199–202.

Przybylski M., Zięba G. 2011. NOBANIS—Invasive Alien Species Fact Sheet; *Lepomis gibbosus*. Online Database of the European Network on Invasive Alien Species; NOBANIS www.nobanis.org

Ribeiro F., Collares-Pereira M.J. 2010. Life-history variability of non-native centrarchids in regulated river systems of the lower River Guadiana drainage (south-west Iberian Peninsula). Journal of Fish Biology 76 (3): 522–537.

DOI: 10.1111/j.1095-8649.2009.02506.x

Rooke A.C., Fox M.G. 2014. Living a century in warm thermal conditions: Introduced populations of pumpkinseed (*Lepomis gibbosus*) inhabiting the Iberian Peninsula (Spain) show reduced adaptation to North American winter conditions. Aquatic Sciences 76 (4): 497–509.

DOI: 10.1007/s00027-014-0349-4

Sakai A.K., Allendorf F.W., Holt J.S., Lodge D.M., Molofsky J., With K.A., Baughman S., Cabin R.J., Cohen J.E., Ellstrand N.C., McCauley D.E., O’Neil P., Parker I.M., Thompson J.N., Weller S.G. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305–332.

DOI: 10.1146/annurev.ecolsys.32.081501.114037

Santos R.E., Silva T.P., Chehayeb I.V., de Magalhães A.L.B. 2012. Reproduction of the non-native fish *Lepomis gibbosus* (Perciformes: Centrarchidae) in Brazil. Revista de Biologia Tropical 60 (3): 1327–1334.

Tomeček J., Kovalč V., Katina S. 2007. [Chapter sixteen] The biological flexibility of the pumpkinseed: A successful colonizer throughout Europe.

DOI: 10.1007/978-1-4020-6029-8_16. Pp. 307–336.

In: Gherardi F. (ed.) Biological invaders in inland waters: Profiles distribution and threats. Springer, Berlin.

DOI: 10.1007/978-1-4020-6029-8

Uzunova E., Georgieva M., Nikolova S., Studenkov S., Traykov V. 2010. Pumpkinseed (*Lepomis gibbosus*) distribution and abundance in littoral zones of sandpit lakes. Bulgarian Journal of Agricultural Science 16 (3): 275–283.

Uzunova E., Velkov B., Studenkov S., Georgieva M., Nikolova M., Pehlivonov L., Parvanov D. 2008. Growth, age and size structure of the introduced pumpkinseed (*Lepomis gibbosus*) population from small ponds along the Vit River (Bulgaria). Bulgarian Journal of Agricultural Science 14 (2): 227–234.

Vila-Gispert A., Moreno-Amich R. 2000. Fecundity of pumpkinseed (*Lepomis gibbosus*) inhabiting the Elder River in northwestern Europe. Oecologia 24: 123–133.

DOI: 10.1007/s100270050004

Villeneuve E., Copp G.H., Fox M.G., Stakénas S. 2005. Interpopulation variation in growth and life-history traits of the introduced sunfish, pumpkinseed *Lepomis gibbosus* (Perciformes: Centrarchidae) in Brazil.
*gibbosus*, in southern England. Journal of Applied Ichthyology 21 (4): 275–281.
DOI: 10.1111/j.1439-0426.2005.00679.x

West G. 1990. Methods of assessing ovarian development in fishes: A review. Australian Journal of Marine and Freshwater Research 41 (2): 199–222.
DOI: 10.1071/MF9900199

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