

A review of growth and life-history traits of native and non-native European populations of black bullhead *Ameiurus melas*

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Abstract North American black bullhead, *Ameiurus melas*, which were introduced to Europe in the nineteenth and twentieth centuries, have received relatively little study. With focus on growth and reproduction, this extensive review, which includes new European data, aims to inform the risk analysis process concerning this non-native species in Europe. Surprisingly, the new data for Europe were more comprehensive than for native populations, with data available mainly from Oklahoma, and North and South Dakota (USA). In terms of relative growth, juvenile

A. melas were found to have a relatively uniform body shape regardless of the population's origin, whereas adults developed different phenotypes depending upon location. Overall growth trajectory was significantly faster for native than for non-native populations. Growth index values decreased significantly with increasing latitude in non-native but not native populations—the latter decreasing weakly with increasing altitude in the populations located at latitudes <40°. Mean general condition (slope 'b'), mean sex ratio and mean egg diameter did not differ significantly between

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native and non-native populations. Absolute fecundity was slightly (but not significantly) higher in non-native than native populations. GSI data, which were very scarce for native populations, suggest gonad production may be slightly higher in native than in non-native populations. Precise data on age at maturity (AaM) are lacking for the native range, where 2–5 years is reported. Whereas, in the introduced range the greatest AaM was 3.5 years, and AaM decreases with increasing juvenile growth (TL at age 3). The populations with fastest juvenile growth tended to be from warmer water bodies where they are considered to be invasive. The great growth and life-history plasticity of black bullhead affords the species great potential to invade and establish viable populations in new areas.

Keywords Non-native species · Illegal releases · Acclimatization · Non-native ornamental fish

Introduction

The introduction to Europe of non-native freshwater fishes from North America has a long history (Copp et al. 2005a), beginning with salmonid and then centrarchid and ictalurid species. Of the latter, the black bullhead *Ameiurus melas* (Rafinesque 1820) is known to have introduced to many European countries, but established self-sustaining populations have only been confirmed for the Belgium Province of Wallonie, and the Netherlands (Verreycken et al. 2010), Austria (Wiesner et al. 2010), Germany (Wolter and Röhr 2010), Czech Republic (Musil et al. 2008), England (Wheeler 1978; this study), France (Copp 1989; Cucherousset et al. 2008), Hungary (Bódis et al. 2012), Italy (Pedicillo et al. 2009), Poland (Nowak et al. 2010a, 2010b), Portugal (Gante and Santos 2002; Ribeiro et al. 2006), Romania (Wilhelm 1998; Gaviloaie and Falka 2006), Serbia (Cvijanović et al. 2005), Slovakia (Koščo et al. 2010) and Spain (Miranda et al. 2010; De Miguel et al. 2014), Switzerland (Wittenberg 2005) and the Ukraine (Movchan et al. 2014). Countries where establishment of *A. melas* is listed (www.fishbase.org), but not recently been confirmed, include Albania (Elvira 2001) and Ireland (Minchin 2007). Until recently, information on the environmental biology of introduced populations of black bullhead had previously

been very limited. Indeed, initial studies focused primarily on the identification and distinction of black bullhead (e.g. Wheeler 1978; Thiero Yatabary 1981) from its close congener, brown bullhead *Ameiurus* (Lesueur 1819), and these comparative studies continue (Movchan et al. 2014). The latter of these two species will be examined in a future study.

Black bullhead is classed as a warm-water species (Hasnain et al. 2010), and in its native range, the species is found in the downstream sections of small-to-medium-sized streams of low gradient, ponds and backwaters of large rivers and silty, soft bottomed areas of lakes and impoundments (Scott and Crossman 1973). Black bullhead are said to be most abundant in smaller water bodies (Campbell and Branson 1978), especially artificial and heavily managed ponds (Jenkins 1959). Such systems were where initial studies of European populations were undertaken, focussing on diet and habitat (Boët 1980; Thiero Yatabary 1981), with some data provided on growth (Boët 1981) and body condition (Thiero Yatabary 1981). More recently, investigations of the species in Europe focused on distribution (Copp 1989) and habitat use (Copp 1993; Carpentier et al. 2004; Cucherousset et al. 2006), growth (Pedicillo et al. 2009), diet (Leunda et al. 2008; Ruiz-Navarro et al. 2015) and body morphology (Novomeská et al. 2010, 2013; Cvijanović et al. 2012; Movchan et al. 2014), with some attention to life-history traits (Novomeská and Kováč 2009) and management options (Cucherousset et al. 2008).

A species tolerant of pollutants (Ribeiro et al. 2008), low dissolved oxygen (3.0 mg L^{-1} ; Stuber 1982), and elevated water temperatures (up to $35 \text{ }^\circ\text{C}$; Scott and Crossman 1973), the black bullhead also has a specialized, nest-guarding, reproductive strategy (Stuber 1982). Many of the introduced fishes in Europe are nest-guarders, which suggests that black bullhead has the potential to be highly invasive (Novomeská and Kováč 2009) and exert impacts to ecosystem function through increased turbidity (Braig and Johnson 2003). Using an invasiveness screening tool for freshwater fishes (FISK; Copp et al. 2009), the black bullhead has been ranked in several European countries/regions as representing a high risk of being invasive, including the Balkan countries, Belgium, Iberia, Turkey and the UK (Verbrugge et al. 2012; Almeida Real et al. 2013; Simonović et al. 2013; Tarkan et al. 2014; Piria et al. 2016), but medium risk

in Finland (Puntila et al. 2013). This invasiveness is demonstrated in some countries, e.g. France (Thiero Yatabary 1981; Copp 1993), where it is among the few freshwater fish listed with a legal status of ‘invasive’ (Guevel 1997). Whereas in the UK, only one of a few reported populations (Wheeler and Maitland 1973; Wheeler 1978; Wheeler et al. 2004) has been confirmed, though the species has nonetheless been the subject of regulation since the 1980s (Copp et al. 2005a). Data on that lone population in England is limited to morphology (Novomeská et al. 2013) and an initial study of gonad development and dietary breadth (Ruiz-Navarro et al. 2015).

Scientific interest over the last two decades in the life-history traits of introduced populations of North American nest-guarding species, in particular the pumpkinseed *Lepomis gibbosus* (see Copp and Fox 2007), and the life-history theory that has underpinned these studies (e.g. Gadgil and Bossert 1970) predicts that age at maturity and reproductive allocation in females will be influenced by pre-maturity growth rates, which determines size at maturity. The conclusions of reviews of research on pumpkinseed introduced to Europe (Copp and Fox 2007) and comparisons with native North American populations (Fox and Copp 2014) provide a template for assessing the factors likely to influence the degree of black bullhead invasiveness in Europe: (1) life history traits, with particular reference to age at maturity and juvenile growth rate, which both depend to a degree on temperature; (2) characteristics of the drainage basin/landscape into which the species was first introduced, with dispersal facilitated by water course and water body connectivity (e.g. Fobert et al. 2013); and (3) human-assisted dispersal such as unauthorized fish movements and releases for angling amenity or religious reasons (Copp et al. 2005b).

Concurrent with this recent work on pumpkinseed, studies of black bullhead life-history traits have become very topical due to the species’ recent arrival and/or expansion in Continental and southern European inland waters (Musil et al. 2008; Novomeská and Kováč 2009; Nowak et al. 2010b; Orrù et al. 2010). Black bullhead has nonetheless been present in Europe for many decades, even very abundant in parts of some European rivers (e.g. Vooren 1971; Thiero Yatabary 1981; Copp 1989, 1993; Gozlan et al. 1998). However, even in its native range, little information is available on the species biology, e.g. “nothing is known of the

biology of this species in Canada” (Scott and Crossman 1973), with length-at-age data and length-weight equations (Carlander 1969; Bister et al. 2000) being virtually the only consistently available type of data. However, closer scrutiny of the grey literature indicates that much unpublished work and lesser known studies exist on the species (e.g. Wallace 1967, 1969; Lohmeyer 1972; Maddux 1985).

The aim of the present investigation was to inform the risk assessment process regarding non-native black bullhead through a thorough review and meta-analysis of existing and new data on the biological traits of this species in its native North American and introduced European ranges. The new data for introduced populations emanated from five European countries (England, France, Italy, Slovakia and Spain) and from native populations in South Dakota (U.S.A.). The specific objectives of the study were to: (1) assess the age-specific growth, growth index and body condition; (2) evaluate reproductive traits (fecundity, egg diameter, length and age at maturity, gonado-somatic index); and (3) examine three of the growth and life-history relationships hypothesized for nest-guarding species by Copp and Fox (2007) and their possible relationships with geographical variables, e.g. latitude as a surrogate of temperature regime (e.g. Cucherousset et al. 2009), and altitude as a possible explanatory factor for extreme variations within a given latitude range (e.g. Ballinger 1979; Miaud et al. 2000).

Because of the similarity in life-history strategies of black bullhead and other North American species successfully introduced to Europe, such as the pumpkinseed (i.e. nest-guarding reproductive strategy, variable age at maturity and TL at age in females; Copp and Fox 2007), we predicted that: (1) juvenile growth rate of black bullhead will decrease with increasing latitude; (2) age at maturity of females bullheads will increase with increasing latitude; and (3) female age and size at maturity of bullheads will be inversely related to juvenile growth rate (as per Fox 1994), with particular reference to whether or not the relationship between female age at maturity and juvenile growth is likely to be useful as a predictor of invasiveness (e.g. Copp and Fox 2007). In view of the limited data on the species, available data on both females and males are included here where possible; this contrasts current work on pumpkinseed, which has mainly been restricted to females because male reproductive indices are poor indicators of population

responses to environmental variability (see Danylchuk and Fox 1994).

Materials and methods

Data acquisition

The review of literature encompassed all available published (peer and grey) documents that could be acquired on the growth and reproductive traits of black bullhead in its native North American and introduced European ranges. Body lengths were mostly given as total length (TL), but in cases where standard length (SL) was given, SL was converted to TL using the mean conversion factor (1.199) calculated from 12 conversion factors (min–max = 1.173–1.227) reported in Carlander (1969).

When geographical coordinates (latitude, longitude and altitude) of the study area were not indicated in a bibliographic source, the coordinates were derived from on-line search engines and map coordinate conversion tools, with representative mean coordinates used when samples were collected over a large area and approximate coordinates (the closest cited inhabitation) when precise locations were not reported and could not be obtained from local sources. Given the diversity of data sources and the lack of detailed information on sampling methods used (etc.), the possibility exists that patterns observed in the data could be due to sampling and/or analytical biases.

Novel population data

To complement existing published data, specimens were collected from 15 locations in five European countries (England, France, Spain, Italy, Slovakia) during the reproductive season (April to early July) between 2006 and 2010 using various sampling methods, and from six lakes in South Dakota (USA) in 2012 (Table 1). In total, 3113 specimens were sampled in Europe and examined for life history and reproductive traits, with age determined for 1148 specimens, and 554 specimens were collected in South Dakota (Table 2).

In England, specimens were collected from a population that has been established for several decades (Lever 1977) in a former clay pit, locally known as Tom's Pond (Table 1), which is located

within agricultural and pasture lands near North Weald Bassett (County of Essex). The fish were killed with an overdose of 2-phenoxyethanol and then cooled to frozen (as per Home Office licensed procedure). This spring-fed pond (mean depth = 2.4 m) has been used for several decades by a private angling club, which had attempted unsuccessfully to extirpate the population through repeated removals of the dense 'balls' of young-of-the-year juveniles that can be seen moving about the pond in early summer (K.J. Wesley, personal communication). More recently, all bullheads in the pond were eradicated by the UK Environment Agency using rotenone (GB Non-native Species Secretariat 2014).

In France, specimens were sampled from five water bodies in northeast France and from a large marshland in northwest France. In the northeast, the five water bodies are situated adjacent to the River Moselle along the French section of its south-to-north, 545-km long course, which begins in the Vosges Mountains (vicinity of Bussang, German-Luxembourg border, altitude 735 m) and flows through France, Luxembourg and Germany to its confluence with the River Rhine. The Canal de Jouy is 6 m wide and has no downstream connection with the River Moselle. The four other sites (Pont-à-Mousson, La Maxe, Mondelange, Sentzich) are groundwater-fed former gravel pits (min–max of maximum depth = 2.6–4.0 m) situated in the river's flood plain. Now managed for recreational purposes, these pits had a mixture of vegetation beds and open water. The Brière Marsh of northwest France is a freshwater wetland system composed of a complex network of permanently-flooded canals and marsh meadows in which 85 % of surface area was occupied by beds of common reed *Phragmites australis* and other grasses (Poaceae), with the remainder being covered by open waters (Cucherousset et al. 2006). The fish were euthanized using either a lethal dose of eugenol or in carbon-dioxide saturated water and then immediately cooled to frozen.

In Slovakia, specimens were captured near the city of Komárno from a floodplain oxbow lake of the River Váh that has been subjected to rehabilitation work to re-establish a more natural shoreline and return water character to a less eutrophic state. The oxbow was dominated by common reed *Phragmites australis*, with the riparian vegetation consisting mainly of deciduous species (e.g. *S. alba*, black poplar *Populus nigra*, Eurasian elm *Ulmus laevis*, narrow-leafed ash

Table 1 Details of new data collected for this meta-analysis, including the country, site name (C. = canal; L. = Lake; R. = River; GP = gravel pit), sampling dates, geographical coordinates, altitude (Alt. in m), surface area (in km²) and fish

capture method (FN = fyke netting; R&L = rod and line; KID = kiddie, a barrier constructed of nets and stakes; EF = electrofishing; GN = gill netting)

Country	Site name	Sampling dates	Latitude	Longitude	Alt.	Area	Method
<i>Introduced range</i>							
England	Tom's Pond	27 Apr 2009	51:42:20:N	00:10:36:E	85	0.003	FN
France	Brière Marsh	28 Jun 2006	47:21:58:N	02:18:45:W	7	90.000	EF
	C. Jouy-aux-Arches	14 Jun 2010, 7 Apr 2011	49:04:38:N	06:05:36:E	169	0.063	EF
	La Maxe GP	15 Jun 2010, 7 Apr 2011	49:10:48:N	06:11:27:E	159	0.053	EF
	Mondelange GP	Mar–Jun 2010	49:16:01:N	06:11:27:E	158	0.033	EF
	Pont-à-Mousson GP	Mar–Jun 2010	48:53:27:N	06:04:19:E	178	0.042	EF
	Sentzich GP	Mar–Jun 2010	49:25:15:N	06:16:00:E	152	0.043	EF
Slovakia	R. Váh	Apr–May, Sep 2006 Mar–Aug 2007	47:48:30:N	18:07:30:E	125	0.140	R&L, KID
	R. Tisa (oxbows)	May–Jun 2002	48:21:40:N	21:48:19:E	118	2.324	EF
	R. Latorica (pits)	Apr 2007	48:50:68:N	21:88:42:E	111	0.021	EF
	Hatalov (pond)	Apr 2007	48:39:37:N	21:53:16:E	98	0.018	EF
	Budkovce (pond)	Sep 2007	48:37:57:N	21:55:45 E	100	0.011	EF
Italy	L. Trasimeno	May–Aug 2009	43:05:21:N	12:09:18:E	257	126.000	FN & GN
Spain	R. Arga (Bidaurreta)	10 May 2007	42:46:01:N	01:49:53:W	369	–	EF
	R. Arga (Artazu)	24 April 2007	42:42:51:N	01:50:32:W	370	–	EF
<i>Native range</i>							
USA	North Buffalo L.	28–30 May 2013	45:37:56:N	97:17:25:W	564	1.620	GN
	South Buffalo L.	11–13 Jun 2013	45:36:55:N	97:17:30:W	561	7.240	GN
	North Drywood L.	28–30 May 2013	45:36:42:N	97:09:55:W	607	4.460	GN
	Opitz L.	18–20 Jun 2013	45:35:53:N	97:30:43:W	553	6.330	GN
	Pickrel L.	18–20 Jun 2013	45:30:17:N	97:16:15:W	564	3.970	GN
	North Rush L.	4–6 Jun 2013	45:21:00:N	97:25:50:W	558	11.360	GN

Fraxinus angustifolia). The fish were killed with an overdose of 2-phenoxyethanol, followed by immediate fixation in 4 % formaldehyde (Novomeská et al. 2010, 2013).

In Italy, specimens were collected from Lake Trasimeno (River Tiber basin), which is of tectonic origin and the fourth largest lake in Italy (mean depth = 4.7 m) and the largest lake in the Italian peninsula (Lorenzoni et al. 2010). The fish were euthanized with an overdose of anaesthetic acetone chloroform, trichloro-ter-butyl alcohol (Pedicillo et al. 2009).

Spanish bullheads were collected from two lentic locations (Artazu and Bidaurreta) along the banks of the regulated, middle section of the River Arga (Province of Navarra), which is a 145-km long tributary of the River Ebro. The Arga flows north-to-

south and drains a catchment area of 2760 km² area composed of cropland, scrubland, deciduous forests and pastures (Table 1). The sampling sites were bordered by emergent reed and bulrushes, with riparian vegetation dominated by deciduous species (e.g. *F. angustifolia*, weeping willow *Salix alba*, black poplar *Populus nigra*, silver poplar *P. alba*, etc.). The fish were killed with an overdose of 2-phenoxyethanol and then cooled to frozen.

The six collection sites in northeast South Dakota, which are located in the counties Day, Marshall and Roberts, are of glacial origin but are now eutrophic and contain both emergent vegetation (e.g. bulrush *Scirpus* spp, cattails *Typha* spp.) and submerged vegetation (coontail *Ceratophyllum demersum* and pondweeds *Potamogeton* spp.). The specimens were captured using gill nets, were found to be dead at

Table 2 Available data from the literature (see footnotes for sources) and the present study (all other sites) for black bullhead populations in various European countries, total number of specimens (n_T) except where a sub-sample number is indicated ([†]), sex ratio (number of males ÷ number females), minimum (Min), maximum (Max) and mean values, number of males (n_M) and females (n_F), mean gonado-somatic index (GSI) for mature fish collected on the dates given in Table 1 unless otherwise indicated, and general condition (slope value ‘ b ’ of the logarithmic weight-total length [TL] relationship) separately by gender, as well as female absolute (AF) fecundity (number of oocytes per female) and relative (RF) fecundity (number of oocytes g^{-1} body weight)—the values for Iowa ponds and for Clear Lake were derived using body mass back-calculated (LogW = $-5.791 + 3.414 \text{ Log TL}$; page 26, Carlander 1969) either from the reported TLs or (values in italics) using the mid-point for the reported size class (see [Materials and methods](#) section)

Country	n_T	Sex Ratio	Total length (mm)			Body weight (g)			Males			Females						
			Min	Max	Mean	Min	Max	Mean	n_M	GSI	n_b	b	n_F	AF	RF	GSI	n_b	b
<i>Introduced range</i>																		
England (Tom’s Pond)	203	0.87	73	216	107.9	4.2	129.7	19.0	60	0.251	64	3.303	66	3095	221.4	1.44	73	3.191
England (Tom’s Pond) ^a	80	1.03	46	208	165.0	–	–	–	–	–	–	–	–	–	–	–	–	–
France (Brière Marsh)	150	0.96	55	216	146.5	2.1	157.2	58.0	53	0.348	69	3.249	49	6083	176.0	5.60	72	3.272
France (Canal de Jouy)	349	0.29	38	181	71.4	0.8	92.4	7.8	–	–	20	3.070	7	5364	84.2	5.93	68	2.993
France (Lac de Créteil) ^b	980	0.98	45–50	305–310	–	–	–	–	426	–	426	3.086	436	–	–	–	436	3.128
France (La Maxe)	334	0.71	48	177	98.7	1.6	81.0	22.7	–	–	20	3.330	13	4328	93.4	6.45	28	2.793
France (Mondelange)	321	1.31	45	170	93.7	1.4	68.1	12.8	–	–	148	3.071	1	–	–	1.61	113	2.925
France (Pont-à-Mousson)	250	0.77	61	244	143.8	2.4	180.8	48.0	–	–	102	2.927	17	7975	116.6	1.79	132	3.062
France (Senzich)	62 [†]	1.17	68	175	129.2	3.8	74.5	33.8	–	–	32	3.117	14	1770	44.7	1.43	29	3.128
France (River Rhône) ^c	210	1.12	–	–	–	–	–	–	–	–	111	3.094	–	–	–	–	99	3.071
Italy (Lake Trasimeno)	441	1.41	35	273	183.9	0.6	383.1	102.9	–	–	222	3.160	103	4976	31.4	6.79 ^d	158	3.077
Italy (Corbara Res.) ^e	313	0.92	99	262	167.1	11.3	267.1	64.8	150	–	150	3.129	15	2802	53.0	8.29	163	3.000
Slovakia (River Váh)	708	0.95	21	214	137.0	0.1	143.3	42.6	–	–	293	2.514	194	3620	75.6	3.79 ^f	307	2.402
Slovakia (Tisa oxbows)	105	1.14	125	169	144.0	35.0	80.0	49.8	–	–	–	–	30	1251	25.1	3.26	49	2.891
Spain (River Arga)	40	0.70	93	177	140.5	8.3	72.0	32.9	14	0.183	14	3.151	20	–	–	1.28 ^g	20	3.101
Means/min–max:		0.93	21	273	129.1	0.1	383.1	40.5	–	0.241	–	3.093	–	4446	99.6	4.04	–	3.001
<i>Native range</i>																		
SD (N. Buffalo Lake)	100	1.04	178	370	241.7	75.0	796.0	227.2	51	0.142	–	2.185	–	–	–	2.85	49	3.257
SD (S. Buffalo Lake)	99	0.65	162	345	248.0	70.0	677.0	278.2	39	0.113	–	2.938	–	–	–	4.08	60	3.109
SD (N. Drywood Lake)	90	0.69	163	350	259.0	69.0	728.0	288.4	35	0.151	–	3.052	–	–	–	2.26	55	3.139
SD (Opitz Lake)	93	1.33	177	421	273.2	80.0	1054.0	393.5	53	0.198	–	3.085	–	–	–	10.40	40	3.072
SD (Pickrel Lake)	88	1.00	123	390	289.5	28.0	1004.0	453.6	44	0.183	–	2.942	–	–	–	5.51	44	3.017
SD (N. Rush Lake)	84	0.87	145	376	280.9	43.0	879.0	404.0	39	0.208	–	3.613	–	–	–	5.13	45	3.235
SD (Big Stone Reservoir) ^h	–	0.64	181	308	–	82.0	518.0	–	50	0.320	–	–	78	5647	18.8	5.74	50	0.210
Iowa ponds ⁱ	–	–	182	193	–	–	–	–	–	–	–	–	3	2155	–	–	–	–
Iowa ponds ^j	–	–	208	211	–	–	–	–	–	–	–	–	3	2734	–	–	–	–

Table 2 continued

Country	<i>n</i> _T	Sex	Total length (mm)			Body weight (g)			Males			Females							
			Ratio	Min	Max	Mean	Min	Max	Mean	<i>n</i> _M	GSI	<i>n</i> _b	<i>b</i>	<i>n</i> _F	AF	RF	GSI	<i>n</i> _b	<i>b</i>
Iowa ponds ⁱ	-	-	224	-	-	-	-	-	-	-	-	-	1	6820	17.7	-	-	-	-
Iowa (Clear Lake) ^j	-	-	-	-	-	-	-	-	-	-	-	41	2.156	-	-	-	53	2.188	-
Iowa (Clear Lake) ^j	-	-	203	226	-	-	-	-	-	-	-	-	-	19	3283	-	-	-	-
Iowa (Clear Lake) ^j	-	-	229	251	-	-	-	-	-	-	-	-	-	24	3845	-	-	-	-
Iowa (Clear Lake) ^k	-	-	260	260	-	-	-	-	-	-	-	-	-	5	3805	13.4	-	-	-
<220 mm TL ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3012	-	-	-	-
220–229 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	3	2990	17.4	-	-	-
230–239 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	18	2892	14.5	-	-	-
240–249 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	23	3451	15.0	-	-	-
250–259 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	30	3572	13.5	-	-	-
260–269 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	24	3870	12.8	-	-	-
270–279 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	6	4046	11.8	-	-	-
280–289 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5495	14.2	-	-	-
290–299 ^k	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2381	5.5	-	-	-
Streams in Kentucky	224	-	197	240	218	-	-	-	-	-	-	-	-	17	2645	17.0	-	-	-
Wilgreen Lake, KY	50	-	223	264	237	-	-	-	-	-	-	-	-	7	3372	16.3	-	-	-
Ponds in Kentucky	349	-	213	249	228	-	-	-	-	-	-	-	-	23	2552	14.1	-	-	-
Means/min–max:		0.89	123	421	265.4	28	1054	340.8	0.166	2.853	6.01	3609	14.4	6.01	3.002				

^a Tom’s Pond population in May–December 2013 (Ruiz-Navarro et al. 2015), with the mean TL being that of fish used in the stable isotope analysis

^b A lake in the vicinity of Paris (Boët 1981)

^c An abandoned side-channel of the River Rhône (Thiero Yatabary 1981)

^d Mean value for 5, 12 and 19 May as well as 12, 25 and 30 June 2009 combined

^e Corbara Reservoir, Italy (Pedicillo et al. 2009)

^f Mean value for 27 May 2006 and 1 June 2007

^g Mean value for 26 Sept. 2007

^h Maddux (1985), the maximum GSI value is given (see Fig. 3 of this article for monthly values), and male GSI

ⁱ Values for two groups of three females and for a single female from Carlander and Sprugel (1950) cited in Dennison and Bulkley (1972)

^j Forney (1955) from Ventura Marsh, Clear Lake

^k Data for five females of 260 mm TL cited in the text and then data by size class from Table 2 in Dennison and Bulkley (1972)

The bold values indicate Overall mean values

capture, and were immediately placed on ice and then frozen for subsequent laboratory examination.

Laboratory processing

In the laboratory, specimens from European sites were defrosted and individually measured for TL to the nearest mm and weighed (wet) to the nearest 0.1 g. Gonads were removed to determine sex and then weighed (both genders for England, northwest France and Spain populations; ovaries only for populations from Italy, Slovakia and northeast France). The vertebrae (Slovakia population), pectoral spines (five populations from the River Moselle basin, France) and otoliths (for all other populations) were removed for age estimation. Females with ovaries containing non-yolked or indistinguishable eggs were classified as immature, and those with ovaries containing yolked eggs (even those that appeared to be spent) were classified as mature. Males with clearly distinguishable (white) testes were classed as mature. All ovaries were weighed to the nearest 0.1 g and the entire ovary fixed in 99.8 % ethanol, except ovaries of bullheads from Spain and northeast France, which were not retained for further analysis. Native bullheads from South Dakota ($n = 6$) were measured for TL (mm), weighed (g) and sex determined by examination of the gonads. Ovaries and testes were removed and weighed to the nearest 0.01 g before being discarded.

Fecundity analysis for both the French ($n = 6$) and English ($n = 1$) populations was completed by removing a sub-sample of each mature ovary as a transverse section in the middle part of the right ovary and then fixed in Gilson solution (100 mL 60 % ethanol; 15 mL 80 % nitric acid, 18 mL glacial acetic acid, 20 g mercuric chloride, 880 mL water) one month prior to the oocyte count and diameter measurements. The sub-sample weight varied from 10 to 30 % of the total weight of the ovary. Oocyte images (JPEG) were taken under a binocular microscope using a Motic camera and processed using Image J software (count and diameter measurement). Oocytes with a diameter $<200 \mu\text{m}$ (reserve stock) were not considered (Novomeská and Kováč 2009). Oocytes were counted and measured using the method described by Ganiyas et al. (2011): (1) conversion of the image to an 8-bit image type; (2) limitation

(thresholding) of the color spectrum to a region that included all of the oocytes; (3) separation (segmentation) of individual particles; and (4) measurement of egg diameters $\geq 200 \mu\text{m}$ with conversion to area (e.g. a diameter of $200 \mu\text{m} = 125\,600 \mu\text{m}^2$).

Despite the benefit of using Gilson solution to harden the oocytes, while chemically separating them from the ovarian tissue, a major problem with Gilson's is its reported shrinkage of oocytes (15–25 % for immature to mature oocytes, respectively) during the first week in the solution (Witthames and Greer Walker 1987; Stéquert and Ramcharrun 1995). After this period, Gilson solution does not have an effect on oocyte diameter. Subsequently, measured oocyte diameter was corrected using a $\times 1.25$ multiplier. For populations from Slovakia ($n = 194$ specimens) and Italy ($n = 54$ specimens), a gonad sample was removed as a transverse section in the middle part of the ovary; the Corbara Reservoir (Italy) population of bullheads was represented by 15 females only—this was due to problems encountered with formalin preservation, which was used when Gilson solution was not available. Sample weight varied from 10 to 30 % of the total gonad weight.

To assess the annual gonadal and spawning cycles as well as fecundity, the samples were examined using a Leica stereomicroscope and/or a Lambda microscope. The diameter of 50 randomly-chosen oocytes from all females was measured using an ocular micrometer. Absolute fecundity (AF) was estimated gravimetrically for specimens from the pre-spawning period using the formula: $\text{AF} = (\text{Number of oocytes} \times \text{ovary wet weight}^*) \div \text{ovary sub-sample wet weight}^*$ (*after removal from ethanol). Relative fecundity (RF = number of oocytes g^{-1} of female) was calculated using standard conversion with body weight. In the absence of comparable data for RF for the native range, where absolute fecundity values were given for fish TL classes only, estimates of RF were calculated as follows: (1) the mid-point of the minimum and maximum TL was used as an estimate of the mean value for that TL class; (2) body weight was back-calculated from the TL estimate using the formula: $\text{LogW} = -5.791 + 3.414 \text{Log TL}$ (page 26 in Carlander 1969); and (3) the RF estimates for each TL size class were obtained by dividing the reported AF values by the corresponding estimates of body weight.

The individual ages of all bullheads were, in most cases, determined from otoliths as described by Crumpton et al. (1987), which has been shown to be a reliable age estimation method for ictalurid species (e.g. Nash and Irwin 1999; Buckmeier et al. 2002). Also, dorsal spines and vertebrates were used for ageing in some French and Slovak specimens, respectively. This is because the reliable age structure for ageing varies in different populations of the same species (Chilton and Beamish 1982). Otoliths were removed from each individual for age estimation, and after cleaning they were cross-sectioned thinly using a Buehler low-speed saw (Buehler Limited, Low Speed Isomet, Lake Bluff, IL, U.S.A.) fitted with a diamond wafer-cutting blade (10 cm diameter \times 0.3 mm wide). The \approx 0.5 mm thick sections were examined at 40 \times using transmitted light. In the absence of otoliths, pectoral spines and vertebrate were used for ageing. Pectoral spines were disarticulated, extracted (Mayhew 1969), cleaned and stored in scale envelopes until they were examined by cutting multiple cross sections (\approx 75 μ m thick) of several spines with the Buehler low-speed saw.

Similar to otolith ageing, sections of each spine were mounted on microscope slides and viewed through a dissecting microscope at 40 \times magnification (Buckmeier et al. 2002). Age estimations of the Slovak bullheads were determined from photographs of the anterior part of the fifth vertebra, which was examined using an Olympus SZX 7 TR 30 microscope fitted with a MOTICAM 2500 5.0 MPx camera (Motic Image Advanced version 3.0 software). All age estimates were cross-checked by a second independent reader. If there was a discrepancy between the readers, then the structure was aged independently by both readers and the age estimate in further analysis was only used if at least two out of the three age estimates agreed. The total radius of the aged structure and the radius of the annual rings were measured at the smallest distance between the centre and distal edge of the structure (Bagenal and Tesch 1978).

Data analysis

Comparisons of length-at-age data were made for combined sexes only to match the available literature data (Table 3). Linear and non-linear models were fitted to determine which equations best describe the

relationship between TL and hard structure (otolith, pectoral spine and vertebra) radius. For the novel data, the body-hard structure relationship was best described by a power function, so back-calculation of TLs was carried out using the equation $L_i = (S_i/S_c)^b \times L_c$, where L_i is TL at age i , L_c is TL at capture, S_i is the radius of the structure at age i , b is the constant of the equation and S_c the radius of the structure at capture (Bagenal and Tesch 1978). TLs at previous age were back-calculated following two proportional methods: the scale-proportional hypothesis (SPH) and the body-proportional hypothesis (BPH) (Francis 1990). No significant differences were found between the estimates and the observed size (Students' t test, $P > 0.05$) with the BPH, so the BPH approach was used for the novel populations.

Growth trajectories were compared following the procedure of Hickley and Dexter (1979), which endeavours to identify a true mean for the populations being compared, thus providing a standard growth curve for the species: (1) TL at mean age (n) of all populations is plotted against TL at age ($n + 1$) to obtain a straight line using the Walford (1946) method; (2) the standard TLs at age are obtained using the formula $l_n = L_\infty(1 - k^n)$ where $L_\infty = l_i/(1 - k)$; l_i = intercept; l_n = TL at age n ; k = slope of the Walford plot; (3) mean TLs at age for each year class are expressed as a proportion (%) of the standard TLs; (4) these proportions are then summed; and (5) the resulting mean percentage (the growth index, GI, for each population) is used to determine relative growth for the group of populations in different years. Because of the likely high level of noise in the estimated TLs at age in the literature dataset, only the first six age classes (whenever available) of each population were included in the computations.

The linear relationship for TL vs. weight was determined using data from all fish collected in the spring as per Ricker (1975, 1979). Fish condition was also assessed by Fulton's condition (plumpness) factor ($K = W10^5 \times TL^{-3}$) (Mills and Eloranta 1985) to allow a standard comparison of black bullhead body condition between the present results and those previously published elsewhere. Generalised condition (sensu Pitcher and Hart 1992) was taken as the slope ' b ' value of the log linear relationship of total body weight regressed against TL.

Table 3 Latitude (in PGIS coordinates of °N), back-calculated total lengths (TL in mm) at age (A) for both sexes combined, growth index (GI), Fulltons's condition index (K) for which all SEs were < 0.20 (see Table 2 for the number of specimens included for the introduced populations), mean TL at maturity (LaM) and mean age at maturity (AaM) from various sources for introduced (sources 1–4) and native black bullhead populations (sources 5–10, using abbreviations for states in the USA from Carlander (1969): (1) present study; (2) Boët (1981); (3) Novomeská and Kováč (2009); (4) Thiero Yatabary (1981); (5) derived from raw data summarized in Pedicillo et al. (2009); (6) Carlander (1969); (7) Hanchin et al. (2002); (8) Priegel (1966); (9) Forney (1955); (10) Mork and Bisping (2009); (11) Lohmeyer (1972); (12) Campbell and Branson (1978); (13) Houser and Collins (1962) – all sites attributed to this paper are located in Oklahoma (OK); (14) Elkin (1955)

Water body	Lat.	Mean back-calculated TL at age														Females				Males				Source					
																LaM		AaM		n		LaM			AaM				
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A9	GI	K	n	LaM	AaM	n	LaM	AaM	n	LaM	AaM							
<i>Introduced range</i>																													
Tom's Pond (UK)	51.71	54	82	107	143	187	206																73	89.8	3.52	64	98.2	3.63	(1)
Sentzich (F)	49.25	65	116	145	166																		29	101.3 ^a	2.08	34	129.6	2.79	(1)
Mondelange (F)	49.16	65	115	153	170																		20			45	131.0	2.86	(1)
La Maxe (F)	49.10	59	110	147	168																		27	121.7	2.38	18	120.0 ^b	2.25	(1)
Canal de Jouy (F)	49.04	53	106	133	160	179																	64	51.7 ^c	1.03	20	80.0 ^c	1.00	(1)
Lac de Créteil (F)	48.78	53	129	175	222	232																	436			426			(2)
Pont-à-Mousson (F)	48.53	66	129	153	172	195	214																72	135.3	2.66	70	81.0	2.84	(1)
River Váh (SK)	47.81	63	95	137	158	183	206																307	119.2	3.00	293	119.5	2.91	(3)
Brière Marsh (F)	47.37	80	117	148	173	187	193	204	211														72	102.6	3.22	69	63.3	1.93	(1)
River Rhône (F)	45.80	83	126	172																			79						(4)
Lake Trasimeno (I)	43.09	77	118	149	170	191	215	239	252	269													158	155	3.41	222	134.9	3.61	(1)
River Arga (E)	42.71	80	109	131	152	182																	23	120.0 ^b	3.29 ^d	17	112.5 ^c	3.42	(1)
Corbara Reservoir (I)	42.70	86	126	166	191																		79	1.23	1.40	150	125.3	1.64	(5)
<i>Native range</i>																													
Lake Darling, ND	48.57	66	140	201	257																								(6)
Lake Ashtabula, ND	47.10	61	135	185																									(6)
Heart Butte Lake, ND	46.60	53	122	183	226																								(6)
Clear (Marshall), SD	45.68	90	148	217	248	256																							(7)
Roy, SD	45.68	82	125	176	217	253																							(7)
South Red Iron, SD	45.67	105	153	193	228	256																							(7)
South Buffalo, SD	45.61	112	148	197	232	257	274																						(7)
Molstad, SD	45.57	115	189	254	290	304	310																						(7)
Hiddenwood, SD	45.53	108	176	219	260	291																							(7)
Enemy Swim, SD	45.43	130	190	258	307	335	364																						(7)
Little Lake, WI	45.40	–	198	211	267																								(8)
Cresbard, SD	45.17	114	168	220	263	293	342																						(7)

Table 3 continued

Water body	Lat.	Mean back-calculated TL at age										K	Females		Males		Source			
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10		n	LaM	AaM	n		LaM	AaM	
Kampeska, SD	44.92	106	160	202	238	281	336						103						(7)	
Potts, SD	44.92	146	240	317	341								144						(7)	
Alice, SD	44.87	93	124	170	217	262	326						91						(7)	
Louise, SD	44.62	123	222	296	336	369							133						(7)	
Byron, SD	44.55	99	133	165	200	229							84						(7)	
Spirit, SD	44.48	91	134	188	244	268							91						(7)	
Jones, SD	44.47	89	122	149	172	201	221						76						(7)	
West Oakwood, SD	44.43	82	130	176	204								81						(7)	
Cavour, SD	44.40	91	156	194	213	224							89						(7)	
Hayes, SD	44.35	124	194	234	260	274	291						110						(7)	
Goldsmith, SD	44.33	96	131	170	205	235	280						87						(7)	
Thompson, SD	44.29	88	129	220	265								94						(7)	
East 81 Slough, SD	44.28	100	153	208	241	260	288						97						(7)	
Cutlew, SD	44.23	101	159	194	209	218	223						88						(7)	
Campbell, SD	44.20	103	177	232	255	267	273						103						(7)	
Madison, SD	43.95	118	166	204	229	253	273						99						(7)	
Twin, SD	43.95	84	109	118									68						(7)	
Long, SD	43.94	94	141	183	211	237							87						(7)	
Brant, SD	43.92	109	193	244	267	274							110						(7)	
Diamond, SD	43.83	90	144	175	190	204							82						(7)	
Island, SD	43.78	111	156	198	234	262							98						(7)	
White, SD	43.78	88	124	185	228	252							87						(7)	
Clear (Minnehaha), SD	43.70	89	132	170	201	228	265						85						(7)	
Wall, SD	43.55	99	171	217	254	276	300						102						(7)	
Ethan, SD	43.53	82	123	145	151								71						(7)	
Silver Lake, IA	43.47	86	192	274	307	331	339						116						(9)	
Alvin, SD	43.43	93	148	202	243								93						(7)	
West Okoboji, IA	43.37	71	151	228	265	270	291	324					98						(10)	
Minnewashta Lake, IA	43.35	76	162	247	262								98						(10)	
Swan, SD	43.22	94	147	198	236	264	264						94						(7)	
Clear Lake, IA	43.12												2.50			200.3 ^f			216.0 ^f	(9)

Table 3 continued

Water body	Lat.	Mean back-calculated TL at age										K	Females		Males		Source											
		A1	A2	A3	A4	A5	A6	A7	A8	A9	GI		n	LaM	AaM	n		LaM	AaM									
Clear Creek, KS	38.50	128	164	192	242															1.31							(11) ^s	
Streams in Kentucky	38.03	107	124	154	209	231	233														84							(12)
Wilgreen Lake, KY	37.40	91	123	144	183	238	247														80							(12)
Ponds in Kentucky	37.77	84	152	139	201	203	206														78							(12)
Rush Creek, OK	37.02	66	130	150	185	213															74							(13)
Snow Creek	36.94	97	165	236																	101							(13)
Snedden Ranch Reservoir	36.81	64	112	165	208																73							(13)
Hudson Lake	36.81	112	236	300	323	338															130							(13)
Gt. Salt Plains Reservoir	36.75	91	145																		72							(13)
Sunset Lake	36.68	66	157	213																	86							(13)
Grand Reservoir	36.61	114	188																		72							(13)
Fairfax City Lake	36.61	140	208																		72							(13)
Fort Supply Reservoir	36.57	74	165	218	267																95							(13)
Lower Hominy Lake	36.53	58	150	246	305																96							(13)
Spavinaw Res. Dam	36.38	132	208																		127							(13)
Eucha Reservoir	36.38	180	284	325																	166							(13)
Lake Eucha,	36.35	178	254	315																	158							(6)
Perry Country Club Pond	36.31	94	170	224	297																105							(13)
Perry Lake	36.27	76	132	142																	73							(13)
Canton Reservoir	36.09	99	163	201	211	213															91							(13)
Walton Pond	36.08	79	188																		95							(13)
Sapuipa Lake	36.00	53	84	119	152																55							(13)
Ketchum Lake	36.00	86	165	193																	91							(13)
Illinois River (1953)	35.97	86	127																		81							(13)
Illinois River (1959)	35.97	89	175	234	353																111							(8)
Soldier Creek	35.95	41	102	168																	60							(13)
Boecher Lake	35.94	25	51	102																	34							(13)
Ranger Creek	35.88	89																			89							(13)
Durham Pond	35.84	76																			76							(13)
Guthrie Lake	35.82	99	191	236																	107							(13)
Verdigris River	35.80	61	117	163	206	292															80							(13)

Table 3 continued

Water body	Lat.	Mean back-calculated TL at age											Females		Males		Source									
		A1	A2	A3	A4	A5	A6	A7	A8	A9	GI	K	n	LaM	AaM	n		LaM	AaM							
Fort Gibson Reservoir	35.80	97	183	254	312	356														117					(13)	
(Twin) Bridges (Pond 2)	35.70	69	142	183																	79					(13)
Tenkiller Reservoir	35.59	147	236	307	330																141					(13)
Salt Creek	35.59	127	170	178	234																101					(13)
Hefner Reservoir	35.58	61	114	175																	70					(13)
Belle Isle Lake	35.53	74	140																		78					(13)
Sportsman Weatherford L.	35.50	41	104	137	160																58					(13)
South Canadian River	35.45	41	79	147																	52					(13)
Lake Henryetta	35.42	76																			76					(13)
Wild Mary Sudik Pond	35.41	84	127	155	183																76					(13)
Ellis Pond	35.39	142	257	323	356																147					(13)
Corn Creek	35.34	79	127	175																	79					(13)
Orr (Family Farm) Pond	35.32	117	246	307																	135					(13)
Crystal Lake	35.26	66	178	216	264																95					(13)
Hall Park Lake	35.24	119	185	231	269																111					(13)
Danielson Lake	35.23	94	175	267	328																114					(13)
Golf Course Pond	35.21	124	218	292																	130					(13)
Arkansas River	35.20	86	137	185	193	191															81					(13)
Little River	35.20	94	173	277																	108					(6)
Hobart Lake	35.17	69	137	193	290																89					(13)
Chickasha Reservoir	35.13	124	180																		115					(13)
Purell City Lake	34.99	102	198	282																	117					(13)
Louis Burttschi Lake	34.97	130	216	267																	127					(13)
Watonga Pond	34.94	104	175	246																	107					(13)
Wister Reservoir	34.92	91	226	297																	121					(13)
Tony Creek	34.83	51	112																		59					(13)
Rocket Plant Lake	34.82	137	226	320	345																140					(14) ^h
Williamson Reservoir	34.78	135	221	274	310	348															130					(13)
Pauls Valley Pond	34.77	61	114	160	191																70					(13)
Lakewood Pond	34.75	86	142	213	318																100					(13)
Elmer Thomas Lake	34.73	137	239	290	315	333															133					(13)

Table 3 continued

Water body	Lat.	Mean back-calculated TL at age										K	Females		Males		Source					
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10		n	LaM	AaM	n		LaM	AaM			
Altus Reservoir	34.66	53	107	147	198														66			(13)
Hell Roaring Creek	34.65	91	147	198	226	236													90			(13)
Humphreys Reservoir	34.59	69	130	244	307														96			(13)
Canyon Creek	34.59	89	145	191															88			(13)
Satterfield Lake	34.59	99	211	267															116			(13)
Veterans Lake	34.49	122	168	282															118			(13)
Stringtown Lake	34.47	119	244	312	361														139			(13)
Classen Lake	34.46	89	193	282	320														116			(13)
Atoka Reservoir	34.44	71	180	231	254	269	351												102			(13)
Boktuklo Creek	34.39	64	112																65			(13)
Mountain Lake	34.37	198	259	366															174			(13)
Little Pine Creek	34.32	117	203																119			(13)
Goddard Oil Creek Lake	34.30	99	216	295	351														127			(13)
Goddard Ranch Lake	34.30	86	183	282	338	345													118			(13)
Ardmore Club Lake	34.25	84	160	203	251	323	335												102			(13)
Darbonne (Pond 1)	34.25	51	114																59			(13)
Noble Lakes (Pond 8)	34.24	135	226																134			(13)
Noble Lakes (Pond 10)	34.24	79	168	229	269														99			(13)
Ardmore City Lake	34.22	119	152	196	300	335													109			(13)
Rod & Gun Club Lake	34.22	109	203	244	302	328	366												120		1.66–1.77	(6) ^h
South Rod & Gun Lake	34.22	114	208	259	330	345	366												125		1.30	(13)
Colverts (Pond 1)	34.21	69	89																61			(13)
Colverts (Pond 2)	34.21	114	140																98			(13)
Chickasaw Club Lake	34.20	137	279																151			(13)
Henderson Pond	34.19	81	188	264	295														109			(13)
West Pine Creek	34.18	109	178																107			(13)
Rock Creek	34.11	58	114																63			(13)
Madill City Lake	34.09	58	157																75			(13)
Feamster Cutoff	34.02	117	234	318															135			(13)
Lake Texoma Reservoir	33.99	89																	89			(13)
Big Pine Creek	33.87	64	132	236															84			(13)

Table 3 continued

Water body	Lat.	Mean back-calculated TL at age											Females		Males		Source													
		A1	A2	A3	A4	A5	A6	A7	A8	A9	GI	K	n	LaM	AaM	n		LaM	AaM											
Gladney Lake	33.77	46	94	132	206															62										(13)
Cookeys Pond	-	152	236	279	318	368															138									(13)
Gunnery Range Pond	-	41	91	152																	55									(13)
Krob Pond	-	89	145	188	213	241															88									(13)
Lee Pond	-	119	183	244	292																115									(13)
Waggoners Pond	-	122	211	320	371	437															142									(13)
Wylie Pond	-	130	206	287	330	356															131									(13)
Odum Lake	-	168	264																		162									(13)

^a No fish < 90 mm TL were captured, so LaM value assumes that 50 % of fish of 90–99 mm TL were mature (i.e. the mid-point between 0 % and 100 % mature)

^b No fish < 110 mm TL were captured, so LaM value given in italics assumes that 50 % of fish of 100–109 mm TL were mature (i.e. the mid-point between 0 % and 100 % mature)

^c No females of < 50 mm TL and no males of < 80 mm TL were captured, so LaM values assume, respectively, that 50 % of females of 40–49 mm TL and 50 % of males of 70–79 mm TL were mature (i.e. the mid-point between 0 % and 100 % mature)

^d No fish of age < 2 and > 4 were captured, so AaM value given in italics assumes that 100 % of fish of age ≥ 5 were mature

^e No fish were captured in size classes 100–109, 120–129 and 130–139 mm TL, for LaM value given in italics assumes that 50 % of fish of 100–109 mm TL and that 100 % of fish in the subsequent size classes were mature

^f Mean values based on single smallest mature females (n = 3) and males (n = 2) cited in the reference

^g Mean total lengths at capture (10 August 1971 – 26 November 1971), so not included in analyses using back-calculated TL at age

^h The same data values are given in reference '14'

Egg diameters were compared using analysis of variance (ANOVA) in conjunction with the Fisher probable least significant difference (PLSD) test. Mean age at maturity was calculated from the percentage of mature females in each age-class using the formula of DeMaster (1978):

$$\alpha = \sum_{x=0}^w (x) [f(x) - f(x-1)]$$

where α is the mean age of maturity (AaM), x is the age in years, $f(x)$ is the proportion of fish mature at age x , and w is the maximum age in the sample. A modified version of this formula (10 mm TL intervals in place of age-classes; Trippel and Harvey 1987) was used to calculate mean TL at maturity (LaM). The gonadosomatic index ((GSI : $100 \times (\text{gonad weight} \div \text{total body weight})$) was calculated for ripe, mature males and females only. In the case of specimens from the Corbara Reservoir (Italy), male gonads were not weighed.

Because invasiveness in nest-guarding species appears to be a function of growth and life-history traits (see Copp and Fox 2007), which are influenced by temperature, biological traits (AaM, LaM, GI, GSI) were regressed linearly against latitude (in numerical GPS coordinates), which is a surrogate of temperature regime (Cucherousset et al. 2009). To assess extreme variation in GI within relatively narrow latitudinal ranges, GI was regressed against altitude in the following latitude ranges (all European sites, USA sites of 33–39°N, USA sites of 43–49°N). To assess the potential use of the relationship between mean AaM and juvenile growth (Fox 1994) as a predictive model for determining invasiveness potential (Copp and Fox 2007; Cucherousset et al. 2009; Fobert et al. 2013; Masson et al. 2015), AaM was regressed against juvenile growth (as per Fox 1994), which in black bullhead was defined as mean TL at age 3 ($TL_{AGE\ 3}$), given that mean AaM of both males and females in non-native populations was 2.7 years and that age 3 is reported as the age at maturity for the native range (Carlander 1969; Stuber 1982). Differences among mean TLs at age between native and introduced populations were tested using analysis of variance (ANOVA), which was also used to test for differences among Fulton's condition (K) values and egg diameters of introduced populations. When significant differences among the study sites were detected

($P < 0.05$ was accepted as the level of significance), Tukey's honestly significant difference (HSD) test was used to determine which study sites were different. The Mann–Whitney U test was used to test the differences between native and introduced populations for mean GSI values, relative fecundities and general condition (slope ' b '). This test was also used for determining the significant differences between habitat types for mean ' b '.

Population traits

Sex ratio, body size and condition

Mean sex ratio (males \div females) was virtually identical in the non-native and native populations for which data are available (Table 2), with the greatest deviations from unity in Europe being for Canal de Jouy (female dominated) and Lake Tasimeno (male dominated), and in North America for South Buffalo Lake (female dominated) and Opitz Lake (male dominated).

Body lengths and weights varied greatly, though the overall size (TL and weight) of bullheads from the native range was greater than observed in the European populations (Table 2). General condition (slope ' b ') showed slightly greater variability in native than non-native populations (Table 4), but the means for these two population groupings (introduced = 3.03, native = 3.06) did not differ significantly (Mann–Whitney U test, $P = 0.84$). Comparisons of b values by habitat type in Thiero Yatabary (1981) showed bullheads in <25 % *Phragmites australis* to be slightly plumper (mean $b = 3.06$) than those in >40 % *P. australis* (mean $b = 2.86$), though this was not significant (Mann–Whitney U test, $P = 0.074$). This suggests that benthic foraging in areas more densely populated by *P. australis* may be less energetically advantageous than in more open waters.

Relative condition (K) values showed that black bullhead in Slovakia were significantly plumper than those in the other non-native populations (Tukey HSD test, $P < 0.001$, Table 3). There was no significant difference between the populations in Italy and France ($P > 0.05$, Table 3), however they had higher relative condition values than observed in the English population ($P < 0.001$, Table 3). The Spanish black

Table 4 Number (*n*) and generalised condition index (i.e. total length–weight regression slope ‘*b*’ for both sexes combined) of black bullhead, with comparable data from various non-native and native populations (all but one of the introduced populations are in Europe; all native populations are in the USA.). Data from Thiero Yatabary (1981) for the ‘Lône des Pêcheurs’,

a ‘parapotamon’ side-channel of the River Rhône flood plain (for further explanation, see Copp 1989) in upstream-to-downstream order and grouped by reproductive (March–June) and post-reproductive (November–December) periods in 1978–1979 (relative abundance of common reed *Phragmites australis* was derived from the thesis’ site map)

Location	<i>n</i>	<i>b</i>	Source
<i>Introduced range</i>			
England (Tom’s Pond)	203	3.245	Present study
France (Senzich)	62	3.100	Present study
France (Mondelange)	289	2.988	Present study
France (La Maxe)	100	3.139	Present study
France (Canal de Jouy)	346	3.036	Present study
France (Lac de Créteil)	980	3.087	Boët (1981)
France (Pont-à-Mousson)	346	3.032	Present study
France (Brière Marsh)	150	3.272	Present study
France (River Rhône)			
Aulnes (April 1979) – <i>Ph. australis</i> absent	124	3.107	Thiero Yatabary (1981)
Touradons (April 1979) – <i>Ph. australis</i> throughout	255	2.969	Thiero Yatabary (1981)
Gué (upstream end) (June 1979) – <i>Ph. australis</i> ≈ 50 % cover	98	3.200	Thiero Yatabary (1981)
Gué (downstream end) (March 1978) – <i>Ph. australis</i> ≈ 25 % cover	18	3.068	Thiero Yatabary (1981)
Gué (downstream end) (May 1979) "	153	2.767	Thiero Yatabary (1981)
Gué (downstream end) (June 1979) "	16	2.921	Thiero Yatabary (1981)
Gué (downstream end) (July 1979) "	61	3.214	Thiero Yatabary (1981)
Pics (March 1979) – <i>Ph. australis</i> ≈ 50 % cover	105	2.681	Thiero Yatabary (1981)
Coude (March 1979) – <i>Ph. australis</i> ≈ 40 % cover	31	2.949	Thiero Yatabary (1981)
Coude (June 1979) "	34	2.889	Thiero Yatabary (1981)
Ferrande right bank (June 1979) – <i>Ph. australis</i> < 25 % cover	38	3.146	Thiero Yatabary (1981)
Ferrande left bank (June 1979) "	92	2.997	Thiero Yatabary (1981)
Aulnes (November 1979) – <i>Ph. australis</i> absent	120	3.174	Thiero Yatabary (1981)
Gué (upstream end) (January 1979) – <i>Ph. australis</i> ≈ 50 % cover	9	2.323	Thiero Yatabary (1981)
Gué (downstream end) (October 1979) – <i>Ph. australis</i> ≈ 25 % cover	80	3.263	Thiero Yatabary (1981)
Gué (downstream end) (November 1979) "	29	3.163	Thiero Yatabary (1981)
Pics (December 1979) – <i>Ph. australis</i> ≈ 50 % cover	135	3.050	Thiero Yatabary (1981)
Coude (November 1978) – <i>Ph. australis</i> ≈ 40 % cover	35	2.562	Thiero Yatabary (1981)
Coude (December 1979) "	19	3.101	Thiero Yatabary (1981)
Ferrande (December 1978) – <i>Ph. australis</i> < 25 % cover	37	2.850	Thiero Yatabary (1981)
Italy (Lake Trasimeno)	441	3.002	Present study
Italy (Lake Corbara)	3260	3.071	Pedicillo et al. (2009)
Slovakia (River Váh)	708	3.041	Present study
Spain (River Arga)	40	3.177	Present study
Canada, British Columbia (Kootenay River flood plain)	500	3.289	Forbes and Flook (1985)
<i>Native range</i>			
Alabama	2049	3.140	Carlander (1969)
Wisconsin (Lake Butte des Morts)	–	2.924	Carlander (1969)
Iowa (Clear Lake) 1950	66	2.860	Forney (1955)
Iowa (Clear Lake) 1951	559	2.801	Forney (1955)
Iowa (Clear Lake) 1952	257	2.285	Forney (1955)

Table 4 continued

Location	<i>n</i>	<i>b</i>	Source
Iowa (Clear Lake – western end) 1952	56	2.620	Forney (1955)
Iowa (Little Wall Lake)	441	2.935	Carlander (1969)
Iowa (Williams Lake)	123	3.326	Carlander (1969)
Iowa (various ponds; 76–254 mm TL)	244	3.414	Carlander (1969)
Iowa (various ponds; 102–229 mm TL)	55	3.326	Carlander (1969)
Iowa (various ponds; 76–279 mm TL)	243	3.060	Carlander (1969)
Kansas (Clear Creek)	79	3.797	Lohmeyer (1972)
South Dakota (Drywood)	90	3.140	Forbes and Flook (1985)
South Dakota (Rush)	84	3.370	Forbes and Flook (1985)
South Dakota (North Buffalo)	100	3.077	Forbes and Flook (1985)
South Dakota (South Buffalo)	99	3.033	Forbes and Flook (1985)
South Dakota (Pickerel)	88	2.980	Forbes and Flook (1985)
South Dakota (Opitz)	93	3.137	Forbes and Flook (1985)
South Dakota (Fort Randall)	–	2.887	Carlander (1969)
Oklahoma (Canton Lake)	802	2.892	Carlander (1969)
Oklahoma (from lakes, ponds and streams during 1950–1961)	1173	3.180	Houser and Collins (1962)
Kentucky (streams)	100	1.999	Campbell and Branson (1978)
Kentucky (Wilgreen Lake)	45	4.181	Campbell and Branson (1978)
Kentucky (ponds)	167	3.114	Campbell and Branson (1978)

bullhead population was significantly less plump (lower condition value) than the other study populations ($P < 0.001$, Table 3). Mean K did not differ between introduced (mean = 1.37, $n = 11$) and native (mean = 1.62, $n = 5$) populations (Mann–Whitney U test; $P > 0.5$).

Lengths at age and growth trajectories

Data on mean back-calculated TLs at age (LaA) were obtained for 13 non-native populations in Europe (nine original data, four from the literature) and 142 native North American populations from nine bibliographic sources (Table 3) and six novel populations from South Dakota (Table 1). The smallest and largest mean LaA values emanated from the same area (Oklahoma) of the native range: age-1 fish from Boecher Lake and age-6 fish from the Rod and Gun Club lakes, respectively. The maximum recorded age in the non-native range was of 9 years (Lake Trasimeno, Italy) and 7 years in the native range (West Okoboji, Iowa). The shortest-lived population in the non-native range was 3 years (River Rhône, France), whereas data for the native range suggests several

populations of very short life span (1–2 years), though these may be sampling artifacts rather than true life spans (Table 3).

The overall growth trajectories revealed that native black bullhead populations grew significantly faster than introduced populations at all comparable ages (Table 3, Fig. 1; ANOVA, $P < 0.01$). Indeed, juvenile growth (TL at age 3) was significantly lower ($F = 21.66$, $df = 129$, $P < 0.001$) in non-native (mean = 145.1, $SE = 9.35$, $n = 12$) than in native populations (mean = 220.1, $SE = 5.12$, $n = 119$).

In terms of overall black bullhead growth in Europe, GI was highest in the Italian populations and in the River Rhone population (France), followed by the other French, Slovak and Spanish populations. The English population had the lowest growth index, which was remarkably lower relative to the other populations (Table 3). The populations in France, Spain and Italy grew faster in younger ages relative to Slovak and English populations but had similar TLs at age in older ages (Table 3). Similar to juvenile growth, overall growth (GI) was significantly lower ($F = 15.74$, $df = 152$, $P < 0.001$) in the non-native bullhead (mean = 69.0, $SE = 1.82$, $n = 12$) than in

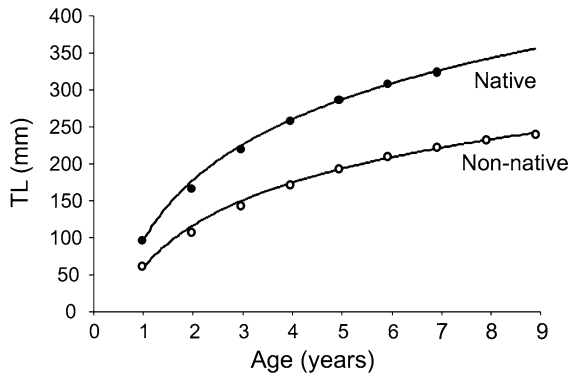


Fig. 1 Growth curves based on back-calculated total lengths (TL) of black bullhead, using the Walford (1946) method together with calculated growth indices (Hickley and Dexter 1979), for native North American (filled circles) and introduced non-native European (open circles) populations (see Table 2 for details)

the native populations (mean = 98.6, SE = 2.16, $n = 142$) (Fig. 1).

In terms of geographical location, juvenile growth ($TL_{AGE\ 3}$) in non-native populations (Table 3) showed no relationship with latitude (linear regression: $P = 0.135$), but overall growth index decreased in a nearly significant manner ($GI = -1.197Lat + 126.162$, $r^2 = 0.29$; $F = 4.499$, $df = 11$, $P = 0.0575$) with increasing latitude (Fig. 2). Whereas the opposite was observed in the native populations, which showed no significant relationship between growth index and latitude, but juvenile growth decreased significantly with increasing latitude ($TL_{AGE\ 3} = -2.879Lat + 330.852$, $r^2 = 0.058$; $F = 6.783$, $df = 110$, $P = 0.0105$). However, the available data on native black bullheads represents two latitudinal groupings, clumped around 33–39°N and 43–49°N (see Fig. 2), which showed great variation in GI values. The great variation in the GI values for native populations at a similar latitude (Fig. 2) suggests a possible influence of altitude, which is well known to affect growth in both plants (e.g. Coomes and Allen 2007) and animals (e.g. Frisnacho and Baker 1970). A weakly significant linear (solid line) relationship ($GI = -0.059Alt + 115.82$; $F = 3.728$, $df = 63$, $r^2 = 0.056$, $P = 0.058$) was found for USA sites located at 33–39°N but not for those located at 43–49°N nor in the non-native European populations.

A principal constraint in these analyses was the relatively low number of populations for which data were available in Europe and the limited comparable

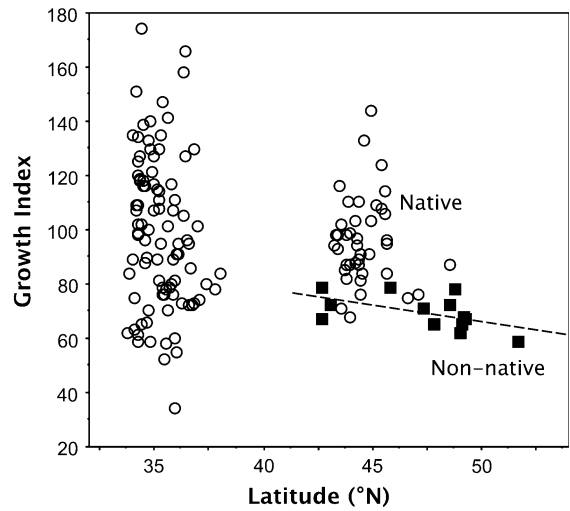


Fig. 2 Growth index versus latitude of native North American and non-native European black bullhead populations

data on reproductive traits of black bullhead populations in the native range. A relatively greater amount of information was available for body condition (plumpness; Tables 2 and 4), though Fulton’s condition index values emanate from different populations than those for which TLs at age were available. The summary values for condition in the native range (Carlander 1969) provide a mean and range (1.38, $n = 18$; SE = 0.029; min–max: 1.11–1.66) that are notably greater than those (mean = 0.96, $n = 5$, SE = 0.049) observed in introduced populations (Table 3). However, this was not replicated in the generalised condition (b) values (Table 4).

Considerable data on the growth of native black bullhead populations was available for comparison with non-native populations, and this revealed faster growth, in terms of overall growth trajectories as well as growth index, in the native range than those in the non-native populations (Fig. 1). Growth and condition (Tables 3 and 4) generally reflect local environmental conditions (e.g. temperature, food and habitat availability and quality, predation and/or competition pressure), and non-native populations of freshwater fish seem to perform less well than native populations (e.g. Copp et al. 2004; Rypel 2013), though this may be apparent in adults but not juveniles (Fox and Copp 2014). Growth differences were also apparent within the introduced range of the species and lifespans of the introduced populations are indicative of slower growth compared to the populations in the native range (Table 3).

Relative growth (external morphology)

One of the presumed attributes of successful invasive fish species was found to be their great morphological variability (Tomeček et al. 2005; Záhorská et al. 2009), as body shape is influenced by the ambient environmental conditions (Norton et al. 1995). These attributes result from the developmental plasticity of a species, and thus emerge during ontogeny as the individual grows. Relative growth of body proportions of black bullhead has not been examined in native populations, but it has in four non-native European populations: England, France, Italy and Slovakia (Novomeská et al. 2013).

In general, three basic models can reflect the patterns of relative growth: (1) isometric (the growth rate of a character is identical to the body growth rate throughout the life), (2) allometric (the growth rate of a character is higher or lower than the body growth rate), and (3) isometric with an abrupt change (the initial isometric growth of a character is interrupted by a period of allometric growth and then followed by another period of isometric growth). The latter model is expressed by a breakpoint between two limbs of otherwise linear regressions, and it can indicate thresholds in the life history of a species (Kováč et al. 1999).

In all black bullhead populations examined, breakpoints were recorded only in adult specimens and in most cases quite late in ontogeny. This means that black bullhead attains its definitive phenotype early in ontogeny and no substantial body shape changes appear later, which suggests relatively uniform ecological requirements of black bullhead throughout its ontogeny from early juvenile to adult periods (Novomeská et al. 2013).

Furthermore, no statistically significant differences were found among juveniles when all four non-native populations were compared. Continuous developmental changes in these populations, however, resulted in increased variation between adult individuals of the same population, as well as between populations (Novomeská et al. 2013). The geometric-shape analysis (allometric form-space PCA) also confirmed that adults in all four populations had a significantly different body shape than juveniles (Fig. 3). Nevertheless, even if the direction of the developmental changes was identical in all populations (changes related to the longitudinal axis of body), their intensity in the developmental trajectories was not. As a result,

developmental changes associated with growth led to different overall phenotypes among populations (Novomeská et al. 2013). In other words, juvenile *A. melas* were found to have a relatively uniform body shape regardless of the population's origin, whereas adults developed different phenotypes depending upon location. In the Slovak population, both juveniles and adults showed very limited morphological variation between individuals (Novomeská et al. 2010). Such intra-population uniformity may reflect a possible founder effect and low phenotypic plasticity.

Life-history traits

Black bullhead is described as a batch spawning species, with reproduction initiated when waters reach ≈ 21 °C (Stuber 1982; Scott and Crossman 1973) and usually taking place in a nest that has been excavated in or near moderate-to-dense beds of submerged vegetation (Scott and Crossman 1973), beneath logs or other submerged objects (Stuber 1982).

Egg size and fecundity

Egg diameter in the native range has been reported to range from 2 to 3 mm (Simon and Wallus 2004), and this seems consistent with the introduced European populations, where mean diameters ranged from 1.52 to 2.72 mm. The most comprehensive information on black bullhead egg size from the native range was provided for a population in a cooling water reservoir in South Dakota (Maddux 1985), where egg diameter distributions increased with increasing GSI class to a maximum diameter of 2.62 mm (Table 5). In Europe, egg diameter data are available for four populations: Tom's Pond (England), Brière Marsh (France), Lake Trasimeno (Italy), and River Váh (Slovakia). Significant differences (ANOVA, $F = 6.66$, $P = 0.0005$) were observed in the mean egg diameters, with eggs in the River Váh population (mean = 1.52; SE = 0.119, $n = 36$) being significantly smaller (Fisher PLSD at $P = 0.05$) than eggs from Brière Marsh (mean = 2.72 mm; SE = 0.193, $n = 5$) and Tom's Pond (mean = 2.68 mm; SE = 0.062, $n = 68$), and eggs from Tom's Pond were significantly bigger than eggs from Lake Trasimeno (mean = 2.29 mm; SE = 0.091, $n = 52$), eggs from Lake Trasimeno and Marsh were significantly bigger than eggs from the River Váh

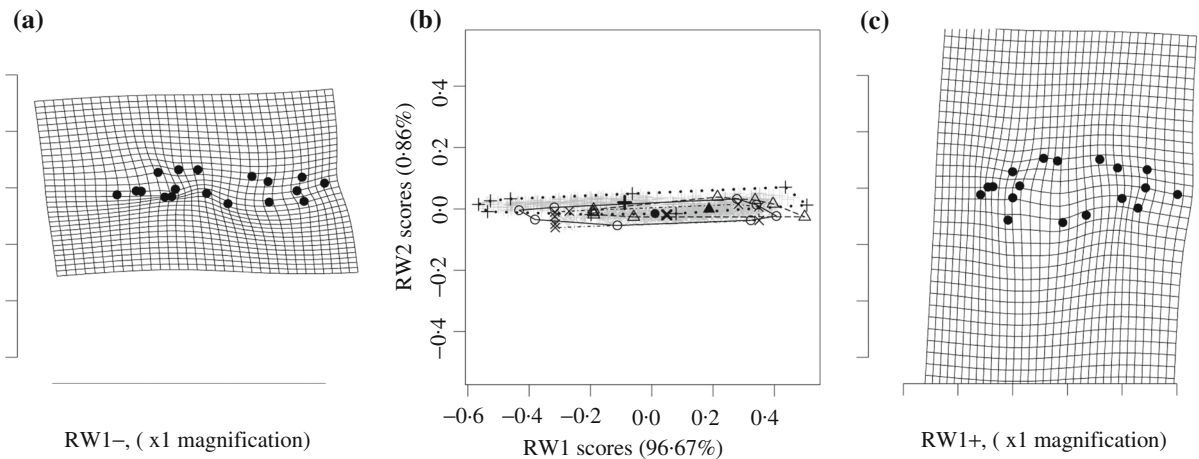


Fig. 3 Form-space Principal Components (PC) analysis (size-and-shape space PC analysis, relative warps analysis; RWA, 96.67 %) and *thin-plate spline* (TPS) grids for illustrating changes in the relative growth during black bullhead ontogeny (form-space PCA [RWA] explains 97.53 % of the variability). **a** The body shape of juvenile specimens. **b** The development of body proportions (the relative growth during ontogeny) in all

four non-native populations of black bullhead (UK, *black filled circle*; France, *black filled triangle*; Italy, *plus*; Slovakia, *times*) appeared equal and parallel. **c** The body shape of adult specimens (both ‘a’ and ‘c’ are in the direction of RW1). (Figure 4 from Novomeská et al. 2013, used with permission from the publisher)

bullheads. Overall, egg diameter appears to be largely similar in the native and introduced ranges of this species.

From the available data, absolute fecundity (AF) appears to be slightly (but not significantly: ANOVA, $F_{1,23} = 1.223$, $P = 0.28$) higher in the non-native than the native range (Table 2). The earliest comparable data on the species’ fecundity comes from the native range (Carlander and Sprugel 1950), where

mean numbers of eggs were reported for seven females, but only the minimum and maximum for the body weights and TLs were given. This form of data presentation is common to all of the available documents, whether from the peer-reviewed or grey literature, and therefore exact values for relative fecundity were only possible to calculate in cases where the studies mentioned body length and AF of individual fish. For example, using the length-weight

Table 5 Egg diameter distributions by gonado-somatic index (GSI) class for black bullhead (from Maddux 1985)

GSI	Egg diameter (mm)														
	0.49	0.65	0.8	0.95	1.1	1.25	1.41	1.56	1.71	1.86	2.01	2.17	2.32	2.47	2.62
0–0.99	2	15	54	16	7	3	3	1							
1–1.99	20	38	33	10											
2–2.99		4	8	23	32	23	10	1	1						
3–3.99		1	5	13	23	27	22	7	1						
4–4.99				2	6	15	18	21	19	13	6	1			
5–5.99				3	6	14	16	20	23	15	3	1			
6–6.99					1	4	5	12	17	25	15	11	7	3	1
7–7.99							1	4	4	15	21	16	16	14	9
8–8.99								3	2	4	10	19	27	24	11
9–9.99										6	8	21	30	17	10
10–10.99								1		1	5	8	10	24	36

relationship in Carlander (1969), data from Carlander and Sprugel (1950) and from Dennison and Bulkeley (1972) provide the estimates in Table 2 for those populations.

Estimated RF values for various size classes of black bullheads in Iowa ponds (Maddux 1985) ranged from 5.5 to 18.8 eggs g^{-1} female (Table 2), and the overall mean for non-native Europe populations was significantly higher (Mann–Whitney U test: $Z = -3.761$, $n = 19$; $P < 0.0002$) than that based on the estimated values for the native range (Table 2). This suggests that on a weight-for-weight basis, females in the introduced populations are producing more mature eggs than their native counterparts.

Reproductive allocation

Prior to the present study, GSI data for the native range were very scarce and the available information suggested that gonad production was higher in native than in non-native populations. The discovery of data for Big Stone Reservoir, South Dakota (Fig. 4; redrawn from Maddux 1985) and new data acquired for this review (Table 2) corroborate this assumption, though the difference is not statistically significant (Mann–Whitney U : $Z = -0.679$, $P = 0.5$).

Mean gonad weight and GSI for mature bullheads varied greatly (Table 2), but did not differ between native and non-native populations for females or males. Mean female GSI was variable in both the non-native and native populations, but less so in males for which data were mainly from the native range (Table 2). Data on absolute and relative fecundity were lacking for the native range. Note that estimates of LaM and AaM (given in italics in Table 3) were unreliable for the River Arga population (Spain) due to the limited age and size spread of captured specimens.

Age and length at maturity

Female age at maturity (AaM) in the native range has been reported to span 2–5 years (Carlander 1969; Stuber 1982; Jenkins and Burkhead 1993), but in the introduced range the greatest AaM was 3.5 years (Table 3). The only available detailed information on female maturity in the native range comes from the Mississippi River in Illinois, where bullhead females were reported to mature at 254 mm TL and age 3 (Barnickol and Starrett 1951), and Clear Lake, Iowa,

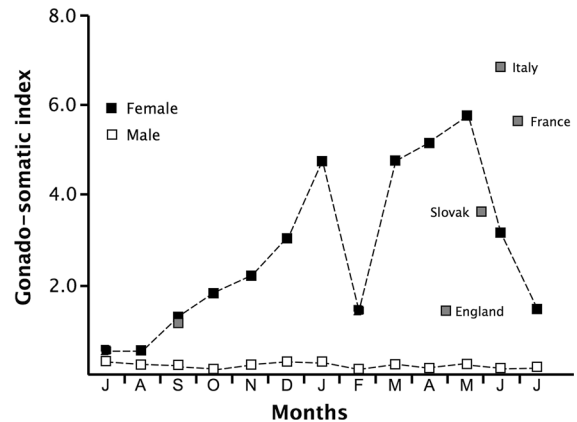


Fig. 4 Mean gonado-somatic index values for males (*open squares*) and female (*filled squares*) from a native population of black bullhead in a cooling water reservoir (South Dakota, USA) over months in 1982–1983 (redrawn from Maddux 1985) with individual values (new data) from European populations (*grey-filled squares*) positioned approximately according to the month of sampling (see Table 1; Slovak and Italian data points given at the mid-point in their respective sampling periods)

where females matured at 200.3 mm TL and males at 216 mm TL (Forney 1955).

The onset of sexual maturity of non-native black bullhead was observed in some age-1 females and males (Table 3), though this was mainly restricted to two populations: Corbara Reservoir (Italy); and the Canal de Jouy (France), the latter population being dominated by females. As such, females of non-native populations had considerably lower mean TLs at maturity (90–155 mm TL) but largely similar mean ages at maturity (3.0–3.5). Our review of the available data fails to support the conclusion in Novomeská and Kováč (2009), that non-native females black bullhead in Slovakia mature earlier than native populations. Black bullhead are effectively maturing at similar ages in the native and introduced ranges, so the smaller size (TL) at maturity observed in non-native relative to native females (Table 3; also Novomeská and Kováč 2009), is simply a consequence of a slower growth rate, which results in smaller TL at age values (Fig. 1).

Age at maturity (AaM) in non-native black bullhead populations (Fig. 5), which resembles that of both native North American (Fox 1994) and introduced European (Copp and Fox 2007) pumpkinseed, decreases with increasing juvenile growth (TL at age 3). In this model, the proposed physiological transition phase between non-invasive and invasive black bullhead populations is hypothesized as the zone

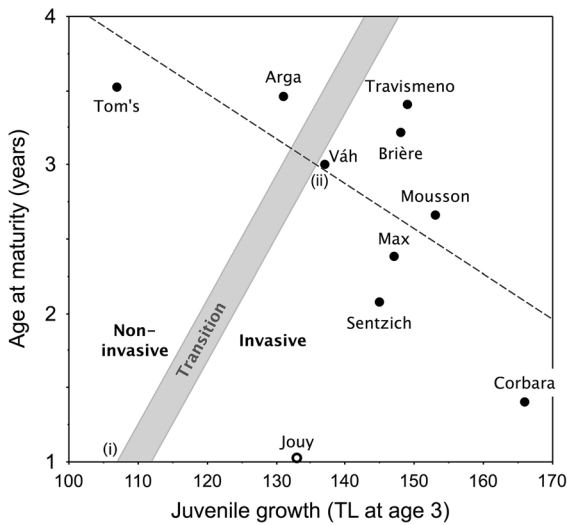


Fig. 5 Proposed model for predicting invasiveness in non-native black bullhead (adapted from the model proposed for pumpkinseed by Copp and Fox 2007), which is based on the mean female age at maturity (AaM, in years) as a function of mean juvenile growth ($TL_{AGE\ 3}$) for introduced black bullhead in European inland waters. Ignoring the extreme outlier (Canal de Jouy, open circle), the relationship is significant at $P = 0.0405$ ($AaM = -0.03TL_{AGE\ 3} + 7.102$, $r^2 = 0.473$, $F = 6.294$, $df = 7$). The proposed physiological transition phase is explained in the [Materials and methods](#) section

delineated by the minimum observed TL at maturity (at ‘i’ in Fig. 5) and the end of juvenile growth (which for most black bullhead populations is age 3); thus, a line was traced from age 0 on the y axis to the intercept of the regression line with age 3 (at ‘ii’ in Fig. 5), then a line was traced from ‘i’ to the regression line, maintaining an equal distance between the two parallel lines (Fig. 5). The area between these two lines represents the transition zone between the proposed non-invasive and invasive populations.

However, unlike pumpkinseed (Copp and Fox 2007), no relationship was found ($P_s > 0.5$) between age at maturity and latitude in either males or females. But similar to European pumpkinseed, non-native black bullhead with the fastest juvenile growth appear to be the most abundant, i.e. invasive (Table 2, Fig. 5). This relationship, which could not be tested for native bullhead populations due to a lack of data (Table 1), was found to be significant when the outlier population (Canal de Jouy) was ignored in the analysis. The resulting relationship revealed age at maturity to decrease significantly ($r^2 = 0.473$, $F = 6.294$, $df = 7$, 2.22 , $P = 0.0405$) with increasing juvenile

growth (Fig. 5) in European bullhead populations ($AaM = -0.03TL_{AGE\ 3} + 7.102$). Removal of this population value was justifiable because of the extreme dominance of females (Table 2). Outliers such as this have been observed in this relationship for other freshwater fishes (Alm 1959, Leggett and Power 1969) as well as in both native and non-native populations of “stunted” pumpkinseed (Crivelli and Mestre 1988; Fox 1994), the native pumpkinseed populations being characterised by low adult survival. A similar outlier has also been observed more recently in a ‘stunted’ population of the European cyprinid, crucian carp *Carassius carassius*, which like the bullhead population in Canal de Jouy was also heavily dominated by females (Tarkan et al. 2016). The dominance of females in the Canal de Jouy may be related to the elevated biomass of large predators in that canal (G. Masson, personal observation; P. Carlin, personal communication), but why predation would be biased towards male black bullheads remains unknown.

Reflections on the species’ potential invasiveness

Detailed comparisons of growth and reproduction features of black bullhead obtained from a comprehensive literature review and field work in Europe suggest that introduced European populations demonstrate slower growth and ultimate TLs (Fig. 1, Table 2) as well as lower reproductive allocation (GSI; Table 2), but greater reproductive effort (higher relative fecundity), than native North American populations. Furthermore, observed slower growth in the first years of life were reflected in the smaller size and greater age at maturity in introduced populations, which cannot be compared with native range of the species due to lack of the relevant data. This is probably the result of an energetic trade-off between reproduction and growth for the species when the species colonises a novel ecosystem (e.g. Grabowska et al. 2011).

The decline of brown bullhead in some European countries, e.g. Belgium (Verreycken et al. 2007), Czech Republic (Lusk et al. 2010) and Poland (Grabowska et al. 2010), has coincided with an increase in the distribution and abundance of black bullhead in Central and Eastern Europe (Nowak et al. 2010b); these contrasting patterns have led to suggestions that black bullhead is displacing brown bullhead.

However, the two species have overlapping native distributions (see species fact sheets at: www.usgs.org), so this may simply be coincidental. However, further study is needed to determine whether or not this is artifact or indicative of black bullhead displacing brown bullhead.

The morphological ontogenetic trajectories (relative growth) in the four introduced European populations of *A. melas* were found to be parallel (Fig. 1), and the overall morphological differences between populations were emerging during ontogeny, to be expressed in larger adult individuals (Fig. 3). On the other hand, it has been demonstrated that black bullhead from these European populations have some potential to alter their body shape both within and between populations, depending on environmental conditions. For example, the thermal conditions associated with lower latitudes are likely to be responsible for the distinct patterns in the morphology of the Italian population, as the water temperature in Lake Trasimeno often exceeds 30 °C in summer (Lorenzoni et al. 2010) and thus differs considerably from the other sites where *A. melas* were sampled (Novomeská et al. 2013).

In terms of relative growth, the phenotypic plasticity of *A. melas*, however, was not found to be as significant as in other invasive fish species, e.g. topmouth gudgeon *Pseudorasbora parva* or pumpkinseed. In topmouth gudgeon, for example, the phenotypic plasticity was expressed not only in the formation of different definite phenotypes but also in the manner by which the phenotypes are achieved (Záhorská et al. 2009). Novomeská et al. (2013) demonstrated that the morphological variability itself is not necessarily essential for invasive success. The invasiveness of black bullhead is therefore probably favoured by variations in its life-history traits and reproduction variables, together with some behavioural traits, e.g. generalist/opportunistic feeding, parental care (Scott and Crossman 1973; Ribeiro et al. 2008) rather than by phenotypic plasticity expressed in external morphology.

Non-native fishes have been shown to modify their life history traits during the invasion process when variable environments are encountered (Fox et al. 2007; Ribeiro and Collares-Pereira 2010; Tarkan et al. 2012). These changes in invading species have been associated with epigenetic mechanisms, suggesting that invading populations show phenotypic plasticity

and more adaptable character than those populations in their native range. This has been reported for several invading species, for Ponto–Caspian gobies: bighead goby *Neogobius kessleri* and round goby *N. melanostomus* (Lavrínčiková and Kováč 2007; Kováč et al. 2009), topmouth gudgeon (Záhorská and Kováč 2009) and gibel carp *Carassius gibelio* (Tarkan et al. 2012). Whereas, recent comparisons of morphological and phenotypic plasticity in studies of native Canadian and repatriated Spanish pumpkinseed revealed that the repatriated (invasive) fish were less plastic than native populations with respect to locomotion (Yavno et al. 2013), competition with bluegill sunfish *Lepomis macrochirus* (Yavno et al. 2014), responses to sustained water velocities (Yavno and Fox 2013) and to habitat type (Yavno and Fox 2014).

In black bullhead, large-scale comparisons between its native and introduced populations provide results consistent with the proposed mechanism (i.e. elevated juvenile growth and reproductive effort leading to early maturation and decreased adult growth rates for successful colonization). Indeed, several advantageous reproductive features of black bullhead, such as multiple spawning associated with a prolonged spawning period and parental care, have been previously noted (Scott and Crossman 1973), increasing the likelihood of establishment success of the species in new areas (Grabowska 2005). Following this strategy, which maximizes colonizing capacity through early maturity and elevated reproductive effort in new environments, such as suggested for non-native pumpkinseed populations (e.g. Copp and Fox 2007), black bullhead can be placed in the ‘opportunistic strategy’ of the three-point life history continuum model proposed by Winemiller and Rose (1992).

Previous research on black bullhead suggests that it is highly tolerant to environmental degradation and is capable of living with poor water quality conditions (Ribeiro et al. 2008). Usually foraging on the most abundant and available prey (Leunda et al. 2008), black bullhead is considered to be a generalist species. It is also a vector of some non-native parasites (Scholz and Cappellaro 1993; Uzunova and Zlatanova 2007). One of the greatest concerns is that black bullhead is associated with degraded or impacted ecosystems, which are considered more susceptible to invasion (Moyle 1986). This facilitates invasions by species such as the black bullhead (Hanchin et al. 2002), which have been found to benefit in growth terms from

increasing eutrophication through a positive correlation ($r = 0.65$, $df = 16$, $P = 0.004$) between $TL_{AGE\ 3}$ and total phosphorous concentration (Phelps et al. 2005). Indeed, all of these factors contribute to the black bullhead's potential as a successful invader (e.g. Gante and Santos 2002; Koščo et al. 2004; Dextrase and Mandrak 2006). In European waters, the black bullhead's dispersal mechanism is not clear but is likely to be associated with accidental and illegal introductions, followed by natural spread between neighbouring countries via natural and manmade water courses (Nowak et al. 2010b). The results of the present study lend support to the belief that black bullhead has a great potential to invade and establish viable populations in new areas, and this is facilitated by life-history plasticity. However, the risk posed by black bullhead will vary according to local environmental conditions, and this is apparent in the FISK rankings of this warm-water species, which is perceived in the north of Europe (Finland) as posing a lower risk of becoming invasive than in countries of intermediate or lower latitudes (cf. Introduction). In view of the continued reports of non-native range expansions by the species in Europe, it is highly likely that the distribution and impact to native communities and ecosystem services of the species will increase.

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