



# A review and meta-analysis of the environmental biology of bleak *Alburnus alburnus* in its native and introduced ranges, with reflections on its invasiveness

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**Abstract** The bleak *Alburnus alburnus* is a medium body-size leuciscid fish that is naturally distributed across central European and western Asian fresh waters. However, during the last two decades *A. alburnus* has been widely introduced elsewhere in Europe and in northern Africa, mostly as a forage species for game fishes. Given its relatively recent history of invasion in non-native Eurasian waters, where it can become highly abundant, *A. alburnus* poses a serious risk to native communities where introduced. This study provides a review and

meta-analysis of the biological traits of *A. alburnus* coupled with insights into its invasiveness. In its native range, *A. alburnus* has a moderate lifespan, inhabiting lakes or still waters in medium-to-large rivers, where it feeds mainly on zooplankton. However, non-native *A. alburnus* populations display high phenotypic plasticity in their biological attributes. Thus, growth, reproductive and/or dietary traits have adapted to local environmental conditions, with the species also invading lotic (stream) ecosystems. Feeding changes to benthic invertebrates, plant material and detritus when zooplankton is scarce. Such plasticity, including broad physiological tolerance, is

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likely to facilitate the species' adaptation and invasion of new habitats in the near future.

**Keywords** Distribution · Impacts · Habitat use · Population dynamics · Reproduction · Diet

## Introduction

Biological invasions are considered one of the main threats to global biodiversity, with freshwater ecosystems being particularly sensitive to introduced invasive species (Clavero 2011). Invasive fishes can alter aquatic communities by causing changes in food webs and/or the decline, displacement and disappearance of native species (Cucherousset and Olden 2011), although not all introduced species become invasive (Copp et al. 2005a, 2005b; Gozlan 2008). The establishment and spread of non-native fish can be facilitated by degradation of water quality and hydro-morphological alterations (Moyle and Light 1996; Bunn and Arthington 2002; Kennard et al. 2005; Leprieur et al. 2008), which explains why some fish species, such as the bleak *Alburnus alburnus*, become widespread and exert impacts when introduced outside their native range intentionally and/or unintentionally by humans (Gehrke and Harris 2001; Marchetti and Moyle 2001; Filipe et al. 2004).

The genus *Alburnus* belongs to the Family Leuciscidae, comprising small minnow species of which  $\approx 45$  are recognised for and distributed across a vast geographic range, extending from western Europe to the northern parts of southwest Asia. *Alburnus* species are commonly known as 'bleaks' (Buj et al. 2010), though a group of them is known as 'shemayas' (Özuluğ and

Freyhof 2007). The name 'bleak' originates from the late Middle English name "bleke", which means 'pale'. Historically, the scales of *A. alburnus* were used to produce the "Essence d'Orient"—a coating for artificial pearls (von Wagner et al. 1903; Hugh 1911). Turkey is the centre of the genus' radiation, extending throughout the Palearctic Ecozone (Özuluğ and Freyhof 2007). *Alburnus alburnus* is naturally distributed across Europe and Asia, but during the last decades this species has been introduced to several regions in the south and east of its native range (Froese and Pauly 2021). Although *A. alburnus* is of no interest to the aquarium trade, it is considered a valuable species in recreational fishing for which it is used mainly as bait or as a forage fish that is stocked into waters to promote piscivorous fish populations. For this reason, *A. alburnus* has been introduced widely as a forage fish for piscivores such as the northern pike *Esox lucius*, largemouth (a.k.a. black) bass *Micropterus salmoides*, and pikeperch *Sander lucioperca* (Elvira and Almodóvar 2001). These are the main target species (trophy fishes) of recreational anglers and have consequently led to the rapid invasion by *A. alburnus* of Iberian river catchments (Vinyoles et al. 2007).

The aim of the present study is to review the available literature on the biological traits of *A. alburnus* in its native and introduced distribution ranges, highlighting differences thereof in particular. This review encompasses all aspects of *A. alburnus*' environmental biology, including morphology, distribution, habitat use, population structure and dynamics, ontogeny and growth, reproduction, trophic ecology, physiology, behaviour, pathogens and parasites, and genetic traits. Moreover, a comprehensive overview is provided on the species' potential invasiveness and its adverse impacts on native species and ecosystems in invaded regions, ranging from hybridisation, parasite transmission, resource competition to foodweb changes. Management recommendations are also provided.

## Review

### Morphology

*Alburnus alburnus* has a fusiform body that is laterally compressed. Mean size is 150 mm total length (TL), with maximum length and weight of 250 mm TL and 60 g, respectively (Billard 1997). Body pigmentation

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is green- or blue-tinted with silvery flanks, and yellowish paired anal fins (Keith and Allardi 2001). Sexual dimorphism is said not to occur in *A. alburnus* (Interesova and Chakimov 2015), however, males in a population of the River Ob basin (Siberia, Russia) have been found to have significantly longer anal-fin base, ventral rays and anal fin rays (Interesova and Chakimov 2015). In the Rybinsk Reservoir (Russia), sexual differences were observed in trunk-muscle lipid composition during the pre-spawning period (Khalko 2018). In aggregated samples, lipid content was found to be higher in females than in males, the former demonstrating a bimodal distribution in trunk muscles and the latter a modal distribution (Khalko 2018).

Previous studies have suggested that *A. alburnus* exhibits some phenotypical plasticity due to both ecological and geographical influences (Gašowska 1974; Baruš et al. 1998; Masó et al. 2016). For instance, *A. alburnus* morphology is influenced by waterbody type whereby riverine *A. alburnus* show a deeper body, larger head, shorter caudal peduncle length and a smaller number of lateral line scales than lacustrine *A. alburnus* populations (Gašowska 1974; Golub et al. 2019). Riverine *A. alburnus* populations have longer pelvic and pectoral fins than *A. alburnus* in lakes, probably due to water current. Variability observed in *A. alburnus* meristic characters (e.g. number of scales in the lateral line or number of vertebrae) has also been attributed to habitat type, geography and climatic conditions (Gašowska 1974; Rafikov and Boznak 2021). For instance, lake-dwelling *A. alburnus* were found to have a higher mean number of lateral line scales ( $n=50.7$ ) than riverine *A. alburnus* ( $n=49.3$ ) and estuarine/firth *A. alburnus* ( $n=48.8$ ) (Gašowska 1974). However, despite several descriptive studies that evaluated *A. alburnus* morphological characteristics at a regional scale (e.g. Gašowska 1974; Baruš et al. 1998; Interesova and Chakimov 2015; Rafikov and Boznak 2021), no studies have systematically compared morphological traits among native and introduced populations.

## Geographical distribution

### *Native range*

The oldest Leuciscid fossils have been recovered in central Anatolia and date from around the Oligocene–Miocene boundary (Özuluğ and Freyhof 2007; Perea et al. 2010). The first colonisation of Central

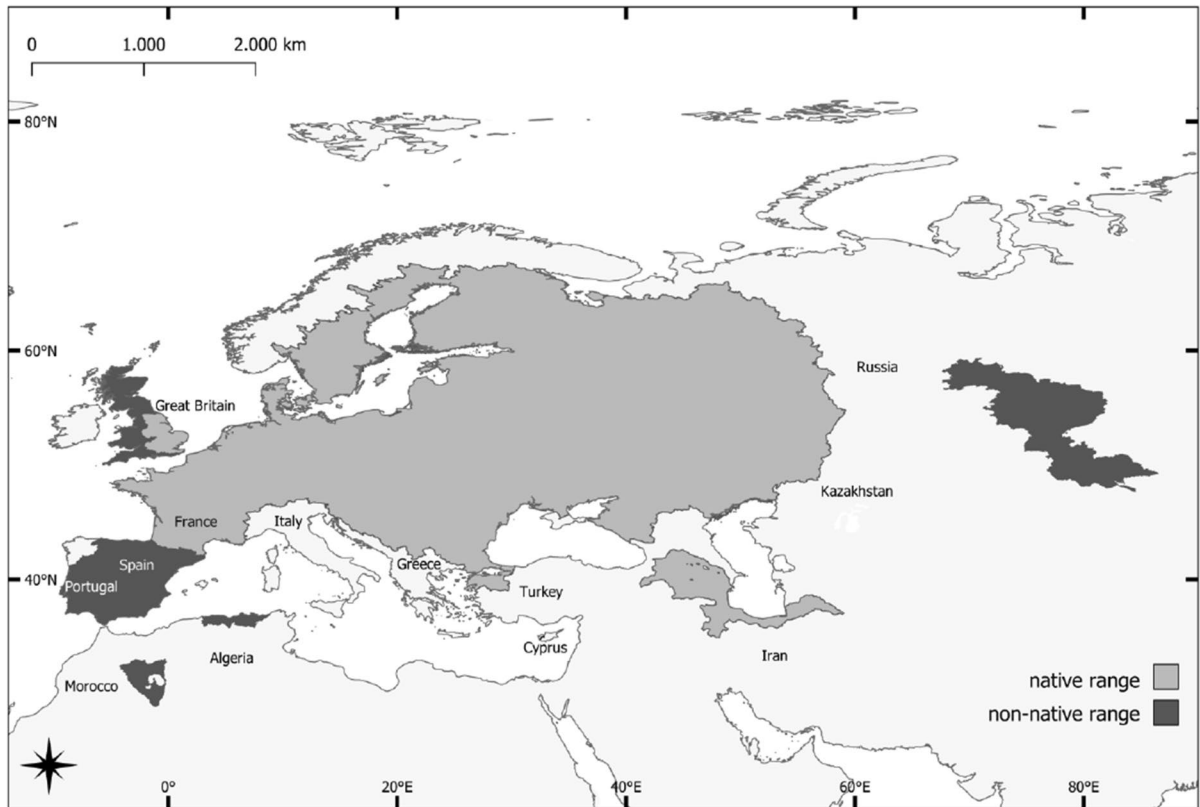
Europe by leuciscids was possible after the connection of Eurasia and Afro-Arabia (20 mya) through the Gomphotherium landbridge (Perea et al. 2010). The first fossils of *Alburnus* sp. in central Europe, which date from about 18–19 mya, were found in Czechia. These paleontological records fit well with the beginning of diversification of *Alburnus* lineages, 19.7 mya (Perea et al. 2010). Alpine orogeny may have also played an important role in isolating Iberian and Italian ichthyofaunas, thereby preventing the arrival of *A. alburnus* to these regions (Zardoya and Doadrio 1999; Levy et al. 2009; Perea et al. 2010).

The native range of *A. alburnus* (Fig. 1) extends from the Ural Mountains in Russia and the River Emba in Kazakhstan in the East (Balzani et al. 2020) to the eastern side of England (Great Britain) in the West (Dodd et al. 2019). The latitudinal distribution of *A. alburnus* extends from 36°N to 65°N (Blanc and Lamoroux 2007), ranging in the north from southern Scandinavia (Rask et al. 2000), southward to the northern slopes of the Pyrénées, across to the Swiss side of the Alps, and continuing uninterrupted to Austria (Gerdeaux et al. 2006). The extent of *A. alburnus* southernmost distribution appears to be the tributary rivers of the southern Caspian Sea in eastern Iran (Kiabi et al. 1999), though translocated populations of *A. alburnus* exist in other parts of Iran (Coad 2006).

### *Non-native range*

From its original distribution range, *A. alburnus* has been introduced in the last decades to several areas in both Europe and Africa, with records of non-native *A. alburnus* extending from Russia (Siberia) to Cyprus (Welcomme 1988; Zogaris et al. 2012) as well as in Portugal and Spain (Vinyoles et al. 2007; Sousa-Santos et al. 2018), Italy (Nocita 2007; Balzani et al. 2020), Algeria (Kara 2012; Attou and Arab 2019) and Morocco (Clavero et al. 2015) (Fig. 1). In Great Britain, *A. alburnus* have been translocated to all other River Basin Districts (sensu European Union 2000) from the species' native distribution in England, which ranges from the River Thames to the Humber Estuary (Wheeler 1977; Dodd et al. 2019).

The non-native distributional range of *A. alburnus* has recently expanded by natural dispersal through the River Ob basin in Russia (Interesova



**Fig. 1** Native and introduced distributional range of the bleak *Alburnus alburnus*

2016; Reshetnikov et al. 2017), where the species was first reported in 1933 (Berg 1933), but whose presence was subsequently questioned (Ioganzen 1947). In the early 1990s, *A. alburnus* was recorded in the River Tobol (Terent'eva and Mukhachev 2006), spreading in the following years throughout rivers of Siberia, mainly the River Tom—a tributary of the Upper Ob basin—by the end of the 1990s (Yurakova and Petlina 2001), the River Ishim by 2000 (Kolomin 2006), and the rivers Om and Miass by 2007 (Zinov'ev and Baklanov 2007). Currently, *A. alburnus* inhabits Novosibirsk Reservoir and most of the rivers and lakes in the upper and middle sections of the River Ob, where the species is highly abundant and still increasing in number and distribution (Yadrenkina 2012; Babkina et al. 2013; Interesova and Chakimov 2015; Romanov et al. 2017; Yevseyeva et al. 2019).

In the Iberian Peninsula, *A. alburnus* have been accidentally or intentionally introduced into reservoirs due to their use as bait by anglers targeting

non-native piscivorous fishes, spreading rapidly to other water bodies by natural dispersal (Elvira and Almodóvar 2001; Amat-Trigo et al. 2019). The first record of *A. alburnus* was in June 1992, for the River Noguera-Ribagorzana (a tributary of the River Ebro) (Elvira 1995), after which the species quickly spread to other river basins in Spain and Portugal (Vinyoles et al. 2007; Maceda-Veiga et al. 2010; Martelo et al. 2021). *Alburnus alburnus* was detected in basins of the Eastern Pyrénées in 1997, in the River Muga in 1999 (Cardona et al. 2002), in the River Tormes (River Duero basin) and in the Campo Maior Reservoir (River Guadiana basin) in 2003 (Pérez-Bote et al. 2004; Velasco et al. 2005), as well as in the basins of the rivers Segura (Andreu-Soler et al. 2004) and Tagus in 2004 (Vinyoles et al. 2007). Expansion of the species' range in the Ebro basin and other Mediterranean rivers (i.e. Jucar, Mijares and Turia) has also been documented (Doadrio 2001). Currently, *A. alburnus* is very abundant and present in all the main river systems of the Iberian Peninsula, particularly

those with nearby reservoirs (Masó et al. 2016; Latorre et al. 2018; Matono et al. 2018; Martelo et al. 2021).

Although *A. alburnus* has been reported for Italy (Nocita 2007; Balzani et al. 2020), the congeneric arborella *Alburnus arborella*, which is endemic to the Padano-Venetian district, has been alternatively considered a sub-species of *A. alburnus* (e.g. Tirelli et al. 2012). In this regard, the scientific name of the congeneric *A. arborella* has been formally validated (Ketmaier et al. 2009). Overall, owing to the similarity between these two congeners and their morphological features, further research is needed to assess whether or not available *A. alburnus* records confirm the species' presence in Italy.

In the African continent, the first official record of *A. alburnus* was in 2003 for the River Kebir, Algeria (Oum Toub, Skikda Province)—a tributary of the Guenitra Dam and the River Guebil (Tandjir and Djebar 2010). However, *A. alburnus* bones were found in the spraints of Eurasian otter *Lutra lutra* in east Algeria (El-Kala National Park) in 1997 (Libois et al. 2015). *Alburnus alburnus* was subsequently recorded in the Hamiz Reservoir in 2006 following the species' introduction as a contaminant of carp species (i.e. common carp *Cyprinus carpio*, bighead carp *Aristichthys nobilis*, silver carp *Hypophthalmichthys molitrix*) consignments imported from Hungary (Attou and Arab 2013). Specimens of *Alburnus alburnus* were also collected in Keddara Reservoir in May 2008, which is connected to Hamiz Reservoir by a water transfer canal (Attou and Arab 2013, 2019), in the Sebaou Basin (Great Kabylia) from 2012 to 2013. More recently, *A. alburnus* has been found in Taksebt Reservoir, probably as part of a 2005–2006 introduction of common carp (Lounaci-Daoudi et al. 2016). In Morocco, *A. alburnus* was first recorded in 2013 in the River Ghir basin, probably originating from the Djorf Torba Reservoir, Algeria (Clavero et al. 2015).

#### Habitat use

In both their native and non-native distribution ranges, *A. alburnus* populations are found mainly in lotic and semi-lotic environments (Mann 1996; Wolter and Bischoff 2001; Mehner et al. 2005; Latorre et al. 2016). In its native range, *A. alburnus* inhabits eutrophic and mesotrophic water bodies (Říha et al. 2013) at altitudes of up to 1800 m above

sea level (Stefanov 2007); this reflects the species' wide oxygen tolerance, i.e. ability to inhabit waters in which oxygen concentration can drop periodically down to 1.5–3.0 mg L<sup>-1</sup> (Blanck et al. 2007).

In the native range, established populations of *A. alburnus* can be found in riverine systems, generally adjacent to annexes of the main channel, characterised mainly by semi-lotic habitats that range from artificial (Williams 1965), rehabilitated (Grift et al. 2003) and near-natural side-channels (Copp and Peňáz 1988; Copp 1992; Roux and Copp 1996). In this respect, *A. alburnus* has been identified as a 'functional describer' (in terms of ecological succession) of natural and regulated riverine ecosystems (Copp 1989; Copp et al. 1991). In riverine environments, *A. alburnus* appears to use connected waterways that are subject to periodic inundation for spawning (Hohausová et al. 2003; Penczak et al. 2004; Scharbert and Borcharding 2013). For example, a field study of fish movements between the main channel of the River Morava (Czechia) and a reconnected, rehabilitated former meander reported older *A. alburnus* ( $\geq 1$  + years, i.e. standard lengths (SL) of 100–150 mm), moving in May between dusk and dawn, and exclusively from the former meander to the main channel (Hohausová et al. 2003). The larvae of *A. alburnus* have been found in shallow, still waters, whereas juveniles in shallow, low-velocity habitats (Copp 1992; Grift et al. 2003), such as river side-channels, where lateral movements of young-of-the-year (0+) juveniles have been observed to take place as an anti-predator behavioural response to predator threats (Copp 1992). *Alburnus alburnus* eggs and larvae are carried downstream by river currents (Copp et al. 2002), and from flood plains to their shallow nurseries at the channel banks (Černý et al. 2003; Scharbert and Borcharding 2013). Riverine habitats that contain refuge habitats (i.e. and crevices or submerged roots) are also inhabited by *A. alburnus*, as revealed in a study of a heavily-modified stream tributary of the River Danube that had undergone rehabilitation (Pander and Geist 2010). Specifically, artificial dead-wood fascines (i.e. bank reinforcement with overhanging riparian wood) were found to provide an excellent winter habitat for smaller-bodied fishes, including *A. alburnus* (Pander and Geist 2010). Moreover, in a recently-constructed artificial fishway on the River Segura (southeast



of Iberian Peninsula), *A. alburnus* was the dominant species both in frequency of occurrence and abundance, which exemplifies its ability to adapt to establish in heavily modified waters (Sánchez-Pérez et al. 2022).

In lacustrine habitats, including reservoirs, *A. alburnus* has been found to spawn preferentially in the faster-flowing waters of tributaries before returning to the main water body for foraging (Říha et al. 2013). Still-water populations are found in lakes, reservoirs, river floodplain channels and adjacent water bodies (e.g. oxbow lakes and abandoned side-channels) and marshlands (Bohl 1979; Copp 1989, 1992; Gozlan et al. 1998; Černý et al. 2003; Blanc and Lamoroux 2007; Navodaru et al. 2002; Pehlivanov et al. 2011; Balzani et al. 2020; Martelo et al. 2021). However, *A. alburnus* populations in ponds (sensu Biggs et al. 2005: i.e. from 1 m<sup>2</sup> to 2 ha area) are uncommon, so references to small water bodies generally relate to shallow lakes or small reservoirs that have been mis-labelled as ‘ponds’ (e.g. Baruš et al. 1998).

In Mediterranean rivers, non-native *A. alburnus* populations inhabit high-velocity microhabitats such as run-type sections (Masó et al. 2016; Muñoz-Mas et al. 2019), where the species is able to sustain relatively high swimming speeds (Cano-Barbacid et al. 2020). During summer, *A. alburnus* shoals perform daily horizontal migrations and become abundant in the shallow littoral zone during the day and in the pelagic zone at night where they feed (Bohl 1982; Kratochvíl et al. 2014). In Mediterranean rivers and reservoirs (e.g. River Guadiana, southwestern Iberian Peninsula), ontogenetic shifts in habitat use that partition/segregate *A. alburnus* populations spatially are difficult to identify due to greater variability in the transition amongst mesohabitat types across seasons in rivers relative to reservoirs (Almeida et al. 2017). Nevertheless, young and small *A. alburnus* (cf. juveniles) in Iberian reservoirs appear to be more restricted to the littoral zone than reported for lakes in the species’ native range (Almeida et al. 2017); whereas, older/larger individuals (cf. adults) tend to occupy both littoral and pelagic zones (Bíró and Muskó 1995; Bogack-Kapusta and Kapusta 2007).

## Population structure and dynamics

Information on *A. alburnus* population structure is relatively scarce for both native (Bíró and Muskó 1995) and non-native (Almeida et al. 2014; Amat-Trigo et al. 2019) areas, thus precluding a comprehensive comparison of its population traits. In the native distribution range, size, age structure and population dynamics of *A. alburnus* populations were found to change in response to both biotic and abiotic factors, such as in the shallow waters of Lake Balaton, Hungary (Bíró and Muskó 1995), where the species’ growth, mortality and production rates were particularly influenced by food availability (i.e. zooplankton and benthos) along the littoral zone. Previous studies revealed substantial differences in stock densities especially during the spawning period, where some populations had slower growth rates (Entz and Lukacsovics 1957; Bíró 1980, 1990). These differences probably resulted from density-dependent regulating mechanisms in fish (Elliott 1987) as well as from interspecific competition and predation within the *A. alburnus* populations (Latorre and Almeida 2019).

In terms of sex ratio, *A. alburnus* populations in Iberian waters generally contain a greater proportion of males than native-range populations (Masó et al. 2016; Latorre et al. 2018) (Table 1). A seasonal effect on sex ratio, with a strong bias toward males, both in lotic and lentic environments, was observed in the rivers Segura and Guadiana during spring, although females were found to be more abundant in lotic habitats during autumn (Almeida et al. 2014; Amat-Trigo et al. 2019). This pattern may be due to elevated predation pressure on females in spring, mediated by their higher ambulation rate (Almeida et al. 2014) when searching for spawning sites (Latorre et al. 2018), thus affecting sex ratio in favour of males. Sex ratio of non-native *A. alburnus* in the Keddara Reservoir (Algeria) was reported to be strongly influenced by environmental factors (Fouzia and Abdeslem 2012), whereby oxygen and conductivity favoured females, with males favoured by pH and conductivity.

Seasonal differences in *A. alburnus* size structure have been reported in lacustrine populations of the native range (Bíró and Muskó 1995) as well as in non-native populations between rivers and reservoirs from the southwest of the Iberian Peninsula (Almeida et al. 2017). Size structure in Iberian reservoirs showed a bimodal pattern in autumn and winter, whereas only

**Table 1** Sex ratio (male/female) of bleak *Alburnus alburnus* populations in their native and non-native distribution ranges

Water body	Country	Sex ratio	Sampling date	Reference
<i>Native range</i>				
River Danube	Serbia	2.27	August–October	Lujic et al. (2013)
Çaygören Reservoir	Turkey	0.96	(Not indicated)	Erdoğan and Koç (2017)
River Saône	France	1.53	June	Latorre et al. (2018)
<i>Non-native range</i>				
River Cardener	Spain	1.64	May–June	Masó et al. (2016)
River Fluvia	Spain	1.36	May–June	Masó et al. (2016)
River Foix	Spain	1.97	May–June	Masó et al. (2016)
River Muga	Spain	2.86	May–June	Masó et al. (2016)
River Ebro	Spain	2.08	May	Latorre et al. (2018)
River Guadalquivir	Spain	3.00	May	Latorre et al. (2018)
River Guadiana	Spain	3.35	May–June	Latorre et al. (2018)
River Segura	Spain	0.75	November	Amat-Trigo et al (2019)
River Tagus	Spain	3.17	May	Latorre et al. (2018)

one cohort was observed in spring, probably because of a high winter mortality of larger individuals due to low food resources availability (Almeida et al. 2017). These two cohorts were also observed in the river population in winter although they were less apparent, suggesting an effect of severe environmental conditions (e.g. lower temperatures and higher discharge rates) on the size structure of *A. alburnus* populations (Almeida et al. 2014). In the relatively uniform stream discharges of the River Stour, native *A. alburnus* demonstrated the typical temperate-zone growth pattern, which consists of rapid length and weight increases during summer with virtually no growth in winter, and this is apparent in ages 0+, 1+ and 2+ (Mann 1991).

The dynamics of fish populations in their early stage of invasiveness rely on different life strategies compared with long-established populations (Ribeiro et al. 2008). In south-eastern Iberian populations, greater longevity and larger mature cohorts were found in sites with longer residence time, but still subject to a longitudinal gradient effect, with upstream populations showing higher growth rates and reproductive investment than in downstream populations (Amat-Trigo et al. 2019). Moreover, in the aforementioned study, *A. alburnus* abundance and growth were significantly dependent on ecological variables related to water discharge, such as discharge variability influenced *A. alburnus* abundance in a positive manner. Fast growth rates and high reproductive investment promote a rapid spread along highly

regulated rivers, as reported for the River Segura, where *A. alburnus* colonised about 170 km of the river since its introduction in 2004 (Andreu-Soler et al. 2004; Amat-Trigo et al. 2019). Overall, a suite of factors mediate *A. alburnus* invasions of southern Iberian rivers, including habitat conditions and river discharge regulation along the rivers longitudinal course. This is apparent from variations in *A. alburnus* population structure among invaded rivers of the Iberian Peninsula (Masó et al. 2016; Latorre et al. 2018).

#### Ontogeny and growth

The SL of *A. alburnus* at the end of the free embryo stage (i.e. absorption of the yolk sac) is reported to be  $\approx 6.5$ – $7.0$  mm (Pinder 2001), with larvae being 13 mm (TL  $\approx 16$  mm) at  $\approx 20$  days after fin formation, whereas the SL of 0+ *A. alburnus* towards the end of summer was  $\approx 40$  mm, but with some individuals only measuring 20 mm in the Międzyodrze wetland, Poland (Kompowski 2000). Young-of-the-year *A. alburnus* can represent nearly half of biomass increase (46.2%) in *A. alburnus* populations, such as reported for the River Thames in England (Mann 1991).

In Iberian populations, somatic growth is faster in the first two years of life than after maturity has been achieved, which is characterised by decreased somatic growth, with annual growth increments becoming minimal after 6–7 years (Latorre et al. 2018). There

are no reported differences in growth rate between males and females (Masó et al. 2016; Latorre et al. 2018). As for other cyprinids, ageing of *A. alburnus* specimens is typically based on scale analysis. Although highly variable, growth in *A. alburnus* is generally considered to be slow (e.g. Williams 1967; Bíró and Muskó 1995; Kompowski 2000; Britton 2007). Mean growth increment is around 30 mm SL in the first year,  $\approx 18$  mm between the first and second year, then decreasing to 6 mm between ages eight and nine years, which is the maximum recorded age for this species (Bíró and Muskó 1995). Based on length-at-age data from the native and introduced ranges (Tables 6 and 7; see also Appendix: Age and growth modelling), global growth in body length is asymptotic with an estimated  $SL_{\infty} = 130.4$  mm (Table 2) and is characterised by large variation within year classes (Fig. 2a). *Alburnus alburnus* populations in lotic environments were found to achieve larger sizes than those in lentic environments (Fig. 2b), and a similar pattern was apparent in continental populations compared with those located in temperate climate zones (Fig. 2c). No apparent relation is observed in the length–weight relationships for *A. alburnus* populations along a latitudinal gradient neither between native or non-native populations (Table 3).

## Reproduction

*Alburnus alburnus* is a dioecious species, with external fertilisation. In its native range, size at maturity ranges 85–100 mm TL in males and 120 mm TL in females, with age at maturity being 2–3 years (Politou 1993). Spawning takes place at water temperatures of 14–28 °C (Alabaster and Lloyd 1980), though a lower limit of 17 °C has been reported (Mann 1996). *Alburnus alburnus* is a phyto-lithophilous species, scattering its eggs on submerged aquatic plants, alluvia and ligneous debris (Balon 1975). In *A. alburnus* eggs, yolk mass represents 30% of oocyte volume, with the remainder being perivitelline space (Winnicki and Korzelecka 1997). During egg development, a lateral position is taken pre-hatch by the blastodisc and the subsequent embryo and larva, and *A. alburnus* distinguishes itself from many teleost fishes by the absence of lipid droplets in the yolk mass. Despite their moderate embryonic respiratory organs, *A. alburnus* embryos hatch out late, are photophobic and possess cement glands with which to attach to the spawning substratum to avoid descent to the bottom (Balon 1975, 1990).

Reproductive traits show large variability both in the species' native (Rinchard and Kestemont 1996;

**Table 2** Growth of *A. alburnus* as modeled by the von Bertalanffy growth function (VBGF) based on length-at-age data

Parameter	Estimate	SE	LCI	UCI	<i>t</i>	<i>P</i>
Global ( <i>n</i> = 235, <i>N</i> = 51)						
$SL_{\infty}$	130.4	5.5	121.2	143.8	23.80	<b>&lt; 0.001</b>
<i>K</i>	0.54	0.10	0.38	0.79	5.36	<b>&lt; 0.001</b>
<i>t</i> <sub>0</sub>	0.01	0.19	−0.47	0.31	0.01	0.999
Habitat (Lentic: <i>n</i> = 141, <i>N</i> = 27; Lotic: <i>n</i> = 194, <i>N</i> = 24)						
$SL_{\infty\text{Lentic}}$	125.8	5.3	117.1	137.5	23.7	<b>&lt; 0.001</b>
$SL_{\infty\text{Lotic}}$	155.8	16.6	131.3	208.2	9.4	<b>&lt; 0.001</b>
<i>K</i> <sub>Lentic</sub>	0.58	0.11	0.39	0.82	5.03	<b>&lt; 0.001</b>
<i>K</i> <sub>Lotic</sub>	0.36	0.10	0.19	0.57	3.73	<b>&lt; 0.001</b>
<i>t</i> <sub>0</sub>	−0.10	0.21	−0.60	0.23	−0.46	0.649
Climate class (C: <i>n</i> = 171, <i>N</i> = 37; D: <i>n</i> = 54, <i>N</i> = 11)						
$SL_{\infty\text{C}}$	127.9	5.6	118.9	140.4	22.9	127.9
$SL_{\infty\text{D}}$	137.2	6.8	125.5	152.1	20.1	137.2
<i>K</i>	0.55	0.11	0.38	0.76	5.18	0.55
<i>t</i> <sub>0</sub>	−0.01	0.20	−0.47	0.29	−0.05	−0.01

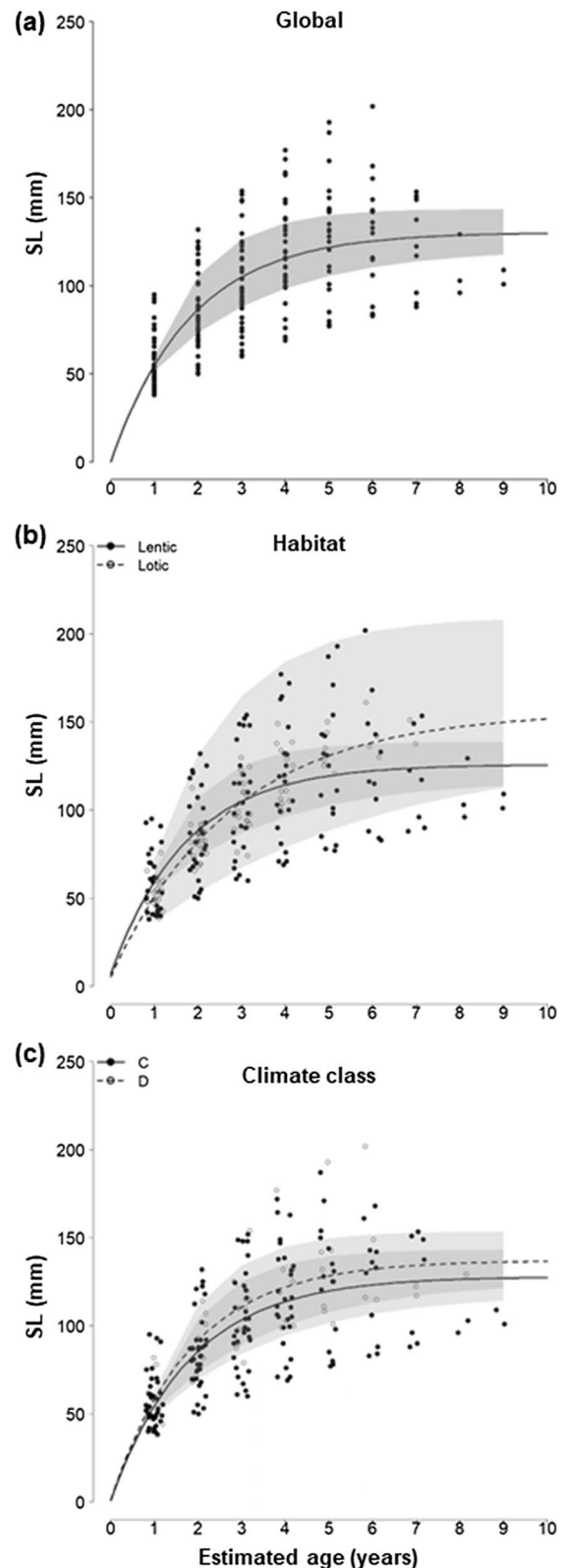
For each 'best-fit' model, the corresponding VBGF parameter estimates are provided including SE (standard errors), 95% lower and upper confidence intervals (LCI and UCI, respectively), *t* value and probability *P* (statistically significant at  $\alpha = 0.05$  in bold). *n* = number of means of LAA (see Table); *N* = number of populations;  $SL_{\infty}$  = asymptotic standard length (mm); *K* = Brody's growth coefficient ( $\text{years}^{-1}$ ); *t*<sub>0</sub> = age of fish at 0 mm SL. Climate class: C = Temperate; D = Continental. See also Fig. 2a–c



**Fig. 2** Growth in length of *A. alburnus*, as described by the von Bertalanffy growth function fitted to: (a) global dataset, (b) habitat, (c) Köppen-Geiger climate class (C=temperate; D=continental). In the scatterplots, each point represents a single mean length-at-age value (see Table 7) and the shaded area for each curve indicates 95% bootstrapped confidence intervals. Points in the scatterplots (except for the global fit) are slightly jittered to improve visibility. Parameters in Table 2

Boniśławska et al. 2001) and non-native ranges and both in small and large rivers (Masó et al. 2016; Latorre et al. 2018). This reproductive variability is expressed mainly in terms of fecundity (Mackay and Mann 1969), oocyte diameter (Boniśławska et al. 2001) and energy investment in reproduction (Rinchar and Kestemont 1996; Amat-Trigo et al. 2019). In small Mediterranean rivers in the northeast of the Iberian Peninsula (Catalonia), a high variability was also observed in traits such as reproductive investment, length at maturity and age at maturity in different *A. alburnus* populations (Masó et al. 2016).

Greater breeding performance has been observed in the non-native range (Latorre et al. 2018), with reproduction rates changing in response to the prevailing environmental conditions. In a comparison of *A. alburnus* in the River Gévara and the Sierra Brava Reservoir (southwestern Spain), the proportion of smaller mature *A. alburnus* individuals was lower in the river than in the reservoir, and both males and females were larger and presented higher body condition and reproductive investment in the river (Almeida et al. 2014). *Alburnus alburnus* fecundity is highly variable in both its native (Politou 1993; Baruš and Prokeš 1993; Raikova-Petrova et al. 2009) and non-native ranges (Latorre et al. 2018), ranging from 1,707 to 12,284 spawned eggs in native populations (Raikova-Petrova et al. 2009) and from 1,829 to 8,069 eggs in non-native populations (Latorre et al. 2018). Relative fecundity by size class is equally variable elsewhere in the native range, ranging in Bulgaria from 104 to 788 in Lake Chepintsi, which is almost 2.1× higher than in the Batak Dam (Table 6). The greatest variability across the species' native range has been reported for the Věstonice Reservoir, Czechia, where seasonal fecundity ranged from 3383 to 15,438 eggs, and relative fecundity reached 102.2–220.4 eggs g<sup>-1</sup> of body weight (Baruš and Prokeš 1993). Fecundity rate in the River Thames (UK) was estimated at ≈6400 eggs in 5-year-old females (Mackay and Mann 1969), which is almost



**Table 3** Length–weight relationship ( $W = aL^b$ ) parameters for *A. alburnus* at various locations

Water body	Country	Length	Measurements	<i>a</i>	<i>b</i>	Reference
Lake Kirkkojärvi	Finland	TL	cm, g	0.006	3.013	Gama and Nyberg (2017)
River Inya	Russia	SL	mm, g	0.0118	3.0548	Interesova and Chakimov (2015)
River Pilica	Poland	SL	cm, g	0.0126	3.0387	Mann and Penczak (1984)
Międzyodrze Wetland	Poland	SL	mm, g	0.0134	2.947	Kompowski (2000)
[Water bodies of Flanders]	Belgium	TL	cm, g	0.0071	3.013	Verreycken et al. (2011)
Lake Balaton (Palóznak bay)	Hungary	SL	cm, g	0.0063	3.0851	Bíró and Muskó (1995)
Lake Balaton (Bozsai bay)	Hungary	SL	cm, g	0.0047	3.2593	Bíró and Muskó (1995)
Lake Balaton (Szigliget bay)	Hungary	SL	cm, g	0.0063	3.1019	Bíró and Muskó (1995)
Lake Balaton (Bala-tongyörök bay)	Hungary	SL	cm, g	0.0052	3.1966	Bíró and Muskó (1995)
Lake Balaton (Keszthely bay)	Hungary	SL	cm, g	0.0081	2.9725	Bíró and Muskó (1995)
River Timiș	Romania	SL	cm, g	0.0087	3.215	Stavrescu-Bedivan et al. (2017)
Lake Chepintsi	Bulgaria	SL	cm, g	0.1499	1.8499	Raikova-Petrova et al. (2009)
Lake Mikri Prespa (males)	Greece	FL	mm, g	0.0000004823	3.641	Crivelli and Dupont (1987)
Lake Mikri Prespa (females)	Greece	FL	mm, g	0.0000003510	3.641	Crivelli and Dupont (1987)
Lake Koronia	Greece	TL	cm, g	0.0038	3.33	Politou (1993)
River Strymon estuary	Greece	TL	cm, g	0.0098	2.790	Koutrakis and Tsikliras (2003)
River Rihios estuary	Greece	TL	cm, g	0.0064	3.098	Koutrakis and Tsikliras (2003)
[Several water bodies]	Slovenia	TL	cm, g	0.0053	3.1366	Marčeta (2014)
River Bosna	Bosnia and Herzegovina	TL	mm, g	0.0001	2.8865	Golub et al. (2019)
[Several water bodies]	Croatia	TL	cm, g	0.0092	2.932	Treer et al. (2008)
Lake Kuş	Turkey	SL	cm, g	0.0145	3.069	Balaban (2010)
Enne Reservoir	Turkey	TL	cm, g	0.0122	3.0552	Koyun and Karadavut (2010)
Çaygören Reservoir	Turkey	TL	cm, g	0.0087	3.26	Erdoğan and Koç (2017)
Lake Estany d'Ivars i Vila-sana*	Spain	FL	cm, g	0.00000601	3.360	Sánchez-González et al. (2020)
River Ebro*	Spain	TL	cm, g	0.0062	3.051	Leunda et al. (2006)
[Water bodies of the Iberian Peninsula]*	Portugal, Spain	TL	cm, g	0.012	2.787	Miranda et al. (2006)

Length: SL = standard length; FL = fork length; TL = total length. For parameter *a* and *b*, values are provided with the original digits from the reference source

\*Non-native populations

double the mean of  $\approx 3800$  eggs estimated in 4-year-old females from the River Sône in France (Latorre et al. 2018). Egg diameter in the species' native range also varies, with a mean diameter of 1.48 mm from various water courses in Poland (Bonisławska

et al. 2001) being greater than the mean ( $\approx 1.20$  mm) observed in the River Sône (Latorre et al. 2018). Outside the species' native range, high variability in fecundity (1829–8069 eggs) and egg diameter (0.95–1.14 mm) was observed across large rivers of

the Iberian Peninsula (Latorre et al. 2018). The high reproductive plasticity reported by Latorre et al. (2018) may be a mechanism for adapting successfully to newly invaded habitats, which can differ greatly in local conditions (e.g. water quality, available habitat) and in landscape character (e.g. topography, rainfall). These patterns suggest that *A. alburnus* in non-native Iberian populations may display greater reproductive capacity (i.e. ovary mass, fecundity and egg size) than in the species' native range; however, this requires further investigation due to the limited data from studies on non-native populations and to differences in the methodological approaches employed therein.

## Trophic ecology

### Prey

*Alburnus alburnus* feed on a wide range of food items, and for this reason it should be regarded as an omnivorous, opportunistic forager (Chappaz et al. 1987). In its native range, *A. alburnus* forages at the surface of open inland waters (preferably lentic habitats), and its diet is based primarily on zooplankton (Herzig 1994; Vinni et al. 2000; Vašek and Kubečka 2004), crustaceans and chironomids (Bíró and Muskó 1995; Latorre et al. 2016) and nektonic invertebrates, but it can include other drifting and terrestrial prey (e.g. flying and terrestrial arthropods that fall onto the water's surface). As with many omnivores, *A. alburnus* are known to adapt their diet in response to food availability (Chappaz et al. 1987; Almeida et al. 2017; Latorre et al. 2018) in both native (Chappaz et al. 1987) and non-native (Latorre et al. 2016, 2018, 2020b; Almeida et al. 2017) populations.

In shallow river stretches, the diet of *A. alburnus* consists of benthic invertebrates including insect nymphs, larvae and snails (Haberlehner 1988; Latorre et al. 2016; Almeida et al. 2017), with detritus and plant material being a frequent component (Vøllestad 1985; Bíró and Muskó 1995). The eggs of other fish species have also been reported in the diet of *A. alburnus* in the Želivka Reservoir (Czechia), where the species may become the dominant egg predator (Šmejkal et al. 2017)—though the effect of *A. alburnus* predation on native threatened or endemic species requires further investigation.

In reservoirs and lakes, *A. alburnus* forage more intensively during the first half of the day, preying on

zooplankton in deeper waters (Politou et al. 1993), whereas night-time diet consists of terrestrial invertebrates that have fallen on the water's surface (Chappaz et al. 1987). The presence of predators can modify the species' feeding strategies, so *A. alburnus* foraging follows a nocturnal pattern when predators are abundant and a diurnal pattern when predators do not represent a threat (Politou et al. 1993). This may explain the mainly diurnal pattern observed for *A. alburnus* larvae in a side-channel of the River Rhine (Schröder 1979; see also Fig. 5 in Copp et al. 2005c) and for 0+juvenile *A. alburnus* in a lentic side-channel of the River Danube. In the latter case, 0+juvenile *A. alburnus* densities were negatively correlated with zooplankton densities, which increased in abundance overnight (Copp et al. 2005c). Additionally, changes in foraging strategy have been observed in relation to water transparency (Ivlev 1960). Similarly, foraging activity depends directly on water temperature, being related to the species' general mobility and seasonal dynamics (Politou et al. 1993). Depending on density, stocking of *A. alburnus* may play an important role for the food web (Bíró and Muskó 1995).

Diet composition in *A. alburnus* is not likely to be influenced by its body size, though there are slight shifts during early ontogeny (Politou et al. 1993; Bíró and Muskó 1995; Almeida et al. 2017), and the diet is primarily zooplankton (e.g. Nunn et al. 2007), with *Bosmina* sp. being the most frequent prey (Garner 1996). The variety of dietary items increases substantially with growth (Bogacka-Kapusta and Kapusta 2007), so adult diet includes insect nymphs, worms and algae. Although *A. alburnus* select higher energy prey items when occurring in habitats with little or scarce competition (Latli et al. 2019), in conditions of higher interspecific competition and lower trophic availability, juvenile individuals can diversify their diet and ingest lower energy resources (i.e. plants or algae). Consumption of algae seems to be secondary and depends on the availability of other food resources, but the energy content of algae is low (Latorre et al. 2016); similar to roach *Rutilus rutilus* (Mann 1997)—this could explain why *A. alburnus* with abundant algal remains in their gut have been observed to demonstrate reduced growth and fecundity (Chappaz et al. 1987).

In lakes and reservoirs, *A. alburnus* forage intensively during summer and at the beginning of

autumn, and foraging activity declines in winter upon a temperature decrease (Politou et al. 1993). Foraging intensity increases from early February, although a decrease occurs in April, coinciding with gonad development (Politou et al. 1993). The relative position of *A. alburnus* in the water column also varies among seasons in response to food availability (Chap-paz et al. 1987). Regarding diet composition, there are seasonal changes that follow zooplankton composition and structure during spring and summer, being substituted by chironomids during autumn (Bíró and Muskó 1995; Bogacka-Kapusta and Kapusta 2007), with food diversity increasing in summer in response to available food resources (Politou et al. 1993; Almeida et al. 2017).

### Predators

*Alburnus alburnus* is a common prey for most freshwater piscivorous species throughout its distribution range. Predation of *A. alburnus* begins at an early age, with eggs preyed upon by European eel *Anguilla anguilla* (Mills 1991). Older *A. alburnus* are predated by piscivorous fishes, including *Esox lucius* (Vøllestad et al. 1986; Kangur and Kangur 1998; Měřo 2014) and *Sander lucioperca* (Bíró and Muskó 1995; Peltonen et al. 1996; Kangur and Kangur 1998), but also by *Lutra lutra* (Prigioni et al. 2006) and piscivorous birds such as European kingfisher *Alcedo atthis* (e.g. Reynolds and Hinge 1996; Vilches et al. 2012), grey heron *Ardea cinerea* (e.g. Jakubas and Mioduszevska 2005; Stolbunov et al. 2017) and great cormorant *Phalacrocorax carbo* (e.g. Gagliardi et al. 2007; Čech et al. 2008; Čech and Vejřík 2011; Russell et al. 2022). Use of *A. alburnus* as a prey (forage) species for piscivorous fishes has been the vector for introductions in the Mediterranean region (Vinyoles et al. 2007), such as Spain (Ruiz-Olmo and Jiménez 2009; Vilches et al. 2012; Ribeiro et al. 2021) and Italy (Prigioni et al. 2006; Gagliardi et al. 2007), where *A. alburnus* has been used by recreational anglers as bait.

### Physiology

#### *Ontogeny of swimming performance and metabolism*

In fish and other aquatic organisms, swimming performance is considered to be a principal attribute for

individual survival, reproductive success, and even invasiveness (Cano-Barbacid et al. 2020). Following an initial 8–10 days post-hatch in the substratum's interstices, when the small yolk sac has been absorbed and the swim bladder is functional, the *A. alburnus* larvae initiate swim-up behaviour (El-Fiky et al. 1987). Larval swimming behaviour is dominated by attempts to hold position in the water by undulating their body and fin folds. During this early period of development, young *A. alburnus* larvae demonstrate a relatively high propensity to drift, both in smaller (Copp et al. 2002) and larger water courses (Copp and Cellot 1988; Oesmann 2003; Zitek et al. 2004a, 2004b). The rate (density) of larval drift, and not size, was found to be negatively correlated with light intensity, the mean drift density of *A. alburnus* in the River Morava (Czechia) being more than 6× greater at night than at twilight; this suggests that *A. alburnus* drift is not a passive displacement due to visual disorientation but instead a behavioural decision that is triggered by light levels (Reichard et al. 2002).

Swimming is almost entirely aerobic, being powered by the deep layers of muscle fibres, which exhibit strong activity of aerobic enzymes such as cytochrome oxidase (El-Fiky et al. 1987; El-Fiky and Wieser 1988). The superficial layer of red muscle fibres is the main respiratory organ for newly hatched *A. alburnus*, though gills are not yet functional (El-Fiky and Wieser 1988). Following the onset of exogenous feeding, *A. alburnus* larvae grow, the red layer of muscle fibres diminishes gradually in mass by contracting towards the lateral region of the body, while at the same time gill filaments and secondary lamellae increase rapidly in number (El-Fiky et al. 1987). In *A. alburnus*, the red layer represents about 20% of the total muscle mass after hatching and it is not until 20 days later that it begins to decrease in size (El-Fiky and Wieser 1988). Compared with other cyprinid species (e.g. *Rutilus rutilus*), which begin to swim freely 2–3 days after hatching, completion of the gill structure in *A. alburnus* is delayed due to the longer period of attachment of the larvae to the substratum (El-Fiky et al. 1987). In addition, the activities of the isoenzymes of lactate dehydrogenase, which are characteristic of fast glycolytic muscle fibres, increase more slowly in developing larvae of *A. alburnus* (El-Fiky et al. 1987; El-Fiky and

Wieser 1988). Notably, this delay in development of the enzymes of anaerobic energy metabolism may compromise the ability of fish to sustain ultrafast movements (Wieser 1991).

Critical swimming speed ( $U_{crit}$ ), which represents the maximum aerobic swimming speed that a fish can attain, has been found to increase positively with body length in *A. alburnus* larvae (Abramiuk and Afanasyev 2017) and adults (Rubio-Gracia et al. 2020a). In the former study, however, velocity was gradually increased until larvae were no longer able to withstand the current, whereas the latter study relied on stepwise increases in water velocity (i.e. one body length  $s^{-1}$ ) with a 20 min time interval. In determining swimming speed, the duration of the step-test interval is important because shorter time steps will result in a higher critical swimming speed (Cano-Barbacid et al. 2020). As such, methodological differences between the above two studies would explain why some larvae exhibited higher critical swimming speed than small-bodied adults. Also, comparative studies have shown that not only can *A. alburnus* larvae and adults swim faster than other fish species of similar size, like Eurasian perch *Perca fluviatilis* (Abramiuk and Afanasyev 2017; Cano-Barbacid et al. 2020), but they can also exhibit lower mass-specific cost of transport (Rubio-Gracia et al. 2020a). This improved swimming performance and efficiency is consistent with the species' active exploratory behaviour throughout the water column during early ontogeny (da Silva et al. 2019).

Like swimming capacity, maximum metabolic rate (i.e. the highest rate of oxygen consumption) and standard metabolic rate (i.e. the basal metabolism of an animal to sustain basic life functions) are positively related with body size (measured as fresh weight) in *A. alburnus*. It has been shown that *A. alburnus* adults have lower standard metabolic rate at a comparable temperature than do other freshwater fish species, including some other cyprinids, centrarchids (e.g. pumpkinseed *Lepomis gibbosus*) and salmonids (e.g. Arctic char *Salvelinus alpinus*) (Rubio-Gracia et al. 2020a; Voutilainen et al. 2011).

The critical swimming speed of *A. alburnus* adults is enhanced by their more streamlined body, including a head shape adapted to reduce friction when swimming against the current (Gąsowska 1974), relatively low drag coefficient (Sagnes and Sfgatzner 2009), estimated as fineness ratio

(measured as SL/maximum body depth) and by the thickness of the caudal peduncle (estimated as caudal peduncle depth factor)—the latter being considered a key morphological trait to generate thrust (e.g. Fisher and Hogan 2007; Rubio-Gracia et al. 2020b). Moreover, the species' standard metabolic rate is also influenced by body shape (Table 4). Similarly, deep-bodied fish have been found to attain lower standard metabolic rate than shallow-bodied fish (Pettersson and Brönmark 1999; Latorre et al. 2020a). Propulsive ratio (measured as propulsive body area/total body area), which represents the proportion of the fish's body able to be used for swimming (Fisher and Hogan 2007), can also increase markedly the variation in standard metabolic rate (Table 4). Therefore, elevated standard metabolic rate in *A. alburnus* can be largely based on the development of muscles and other features related to locomotion, as reported for other fishes (e.g. Nanami 2007).

#### Energy acquisition and allocation

The energy acquisition and allocation is particularly relevant to understand fish survival when facing novel environments, such as newly invaded areas, but also

**Table 4** Simple and multiple regression models to predict critical swimming speed ( $U_{crit}$ :  $cm s^{-1}$ ), maximum metabolic rate (MMR:  $mgO_2 h^{-1}$ ), and standard metabolic rate (SMR,  $mgO_2 h^{-1}$ ) in *A. alburnus* using body size and some morphological ratios

Model	<i>N</i>	<i>k</i>	$R^2_{adj}$
$\log U_{crit} = 1.76 \log(SL) + 0.46$	1	3	0.50
$\log U_{crit} = 1.20 \log(SL) + 0.23FR - 42.15CP - Df + 41.49CPDf^2 + 10.90$	3	6	0.65
$\log MMR = 1.27 \log(W) - 1.08$	1	3	0.51
$\log MMR = 1.47 \log(W) - 0.025FR^2 - 0.73$	2	4	0.52
$\log SMR = 0.92 \log(W) - 2.41$	1	3	0.29

*N* refers to the number of unique variables included in the model, and *k* refers to the total number of parameters (including intercept and error term). SL=standard length (cm); W=body mass (g; measured as fresh weight); FR=fineness ratio (SL/maximum body depth); CPDf, caudal peduncle depth factor. Data extracted from Rubio-Gracia et al. (2020a)

Statistical procedures were conducted following Fisher and Hogan (2007). Because body shape is not necessarily linearly related to swimming performance, the squares of morphological variables were also used. The Bayesian information criterion was used to select the 'best' models



when coping with environmental change, e.g. resulting from global warming. Preferential allocation of energy to somatic growth is an essential feature of larvae since rapid growth rates favour survival and predator avoidance (Wieser 1991). However, only a few studies have attempted to determine the partitioning of ingested energy during the development of *A. alburnus* by measuring rates of food consumption, routine metabolism and growth (Keckeis and Schiemer 1990, 1992). Overall, consistent with the foraging patterns described here above, the pattern of energy partitioning depends on food availability. During the early ontogeny of *A. alburnus*, when food is unlimited, daily food consumption increases with age, e.g. at 22 days daily consumption was 0.60 mg day<sup>-1</sup> and at 61 days 3.85 mg day<sup>-1</sup> (Keckeis and Schiemer 1990). The relationship between daily food consumption rates ( $C$ , J day<sup>-1</sup> ind<sup>-1</sup>) and body size ( $W$ , mg dry weight) in *A. alburnus* also varies, being dependent on the amount of food ingested. At high and low food levels, the allometric relationships were  $C = 18.32 (\pm 1.28) W^{0.81 (\pm 0.02)}$  and  $C = 5.07 (\pm 1.32) W^{1.04 (\pm 0.03)}$ , respectively (Keckeis and Schiemer 1992). The slope of the allometric relationship between respiration ( $R$ ), i.e. without incorporating the slope due to food searching and specific dynamic action, and body weight ( $R = 0.11 [\pm 1.86] W^{0.87 (\pm 0.02)}$ ) was found to be higher at high-food availability than that of the above-mentioned relationship between food consumption and body weight. This indicates that metabolic expenditure increases faster with body size than energy uptake rates, causing a decrease in the growth rate of *A. alburnus* with increasing size at higher food availability. Growth rates ranged from 5 to 8% day<sup>-1</sup> at higher food levels, but at lower food availability they ranged from 3 to 5% day<sup>-1</sup>, which can occur independent of body size (Keckeis and Schiemer 1992).

In a comparison of growth rates over 90 days in recently hatched *A. alburnus* and *Rutilus rutilus* larvae at different levels of food supply (Keckeis and Schiemer 1990), production efficiency [ $PE = P / (P + R) \times 100$ ] was found to decrease with increasing weight in the two species. However, despite the similar energy intake and routine metabolism of the two species, *A. alburnus* grew slower than *R. rutilus* at the same age and under high food availability (Keckeis and Schiemer 1990, 1992). This interspecific difference in growth patterns can be directly

attributed to differences in assimilation efficiency [ $AE = (P + R) \times C^{-1} \times 100$ ], which correlates with the relative gut length of the species (Keckeis and Schiemer 1990). Because of its shorter gut length, *A. alburnus* is much less efficient in the conversion of consumed energy into body mass, likely due to lower power of digestion (Hofer and Nasir Uddin 1985). However, both species had similar growth when food was more restricted (Keckeis and Schiemer 1992). This finding, together with higher prey detection capacities (Wanzenböck and Schiemer 1989), indicates that *A. alburnus* may be well adapted to low-nutrition environments. These differences in energetic performance between the two species point to mechanisms leading to trophic-niche differentiation in their early-life history. In addition to food availability, temperature is also known to affect *A. alburnus* growth (Wieser et al. 1988b). Thus, the relative growth rate (% fresh weight d<sup>-1</sup>) of *A. alburnus* increases proportionally with temperature and decreases with increasing fish size, using *R. rutilus* as a model species (Wieser et al. 1988a). Understanding these energy allocation metrics is essential specially to understand *A. alburnus* adapting capacity given that most of the invaded range is located in southern latitudes, generally with warmer environments.

## Behaviour

### *Activities and social patterns*

Categorised as a ‘compulsory schooling’ species (Karst 1968) and an ‘obligate schooler’ (Haberlehner 1988), *A. alburnus* occurs almost exclusively in shoals, which commonly consist of 30–50 individuals (Holubová et al. 2020) and move through the surface layer of the water column, usually at a depth not exceeding 1.5 m (Vašek et al. 2009). Underwater observations demonstrated that adult *A. alburnus* shoals move rapidly (Karst 1968), positioned near the water’s surface (Karst 1968; Vinyoles et al. 2008), and that high swimming speeds preclude other species (e.g. *Rutilus rutilus*) from joining *A. alburnus* shoals (Haberlehner 1988). However, *A. alburnus* larvae and 0+ juveniles have been observed as part of mixed shoals in various river systems within the native range, consisting of other 0+ cyprinids such as *R. rutilus*, chub *Squalius cephalus*, rudd *Scardinius erythrophthalmus* (Copp 1992, 1993; Gozlan et al.

1998) and *Perca fluviatilis* (Copp et al. 1994), with a preference for locations close to littoral areas (Černý et al. 2003).

Shoal formation acts as a predation-avoidance strategy of a small-bodied species, so *A. alburnus* demonstrates a preference to forming dense shoals, as observed in natural lakes (Tischler et al. 2000) but also in reservoirs (Říha 2012). The effect of fish density on shoaling formation has been investigated in the epipelagic habitat of the Římov Reservoir, Czechia (Holubová et al. 2019), where the most abundant species of the pelagic habitat corresponded to those species with the strongest shoaling behaviour (Říha 2012). The origin of these aggregations, which were mainly composed of species such as *A. alburnus*, may be driven by the absence of refuges in the pelagic habitat (Magurran and Pitcher 1983). Moreover, the formation of shoals has been observed to be a function of fish density in the habitat (Holubová et al. 2019). Fish aggregations tend to attract more individuals, especially when they are feeding, thus shoal size increases in a linear relationship with fish density, supporting that shoaling behaviour is partly driven by fish density in open water habitats (see experimental data in da Silva et al. 2019). Such shoaling behaviour was found to emerge at a ‘critical density’ of 20–30 individuals within 10 m distance (Makris et al. 2009; Maury 2017).

In both the native and introduced ranges, *A. alburnus* shoal movements are generally similar, with shoals consisting of medium- to large-sized individuals, which move in a wedge-shaped configuration to improve hydrodynamics under more slightly lotic conditions (Haberlehner 1988). Shoals were observed to swim in one direction in the centre of the river channel, whereas along the river banks circles or loop-shaped patterns of several meters in diameter were formed (Haberlehner 1988; da Silva et al. 2019). Within a shoal, *A. alburnus* position was highly variable, with inter-individual distances ranging from a single body length at the front of the shoal to  $\approx 2$  m separation towards the back of the shoal. Moreover, solitary adult individuals may be occasionally found together with juveniles (Hohausová et al. 2003). Nevertheless, solitary individuals can increase swimming activity to join new schools rapidly, including other species’ aggregations, such as those of chubs (Genus *Leuciscus*), until a group of *A. alburnus* is found (Haberlehner 1988).

In the open and shallow waters of Rybinsk Reservoir (Russia), the highest number of 0+ juvenile *A. alburnus* was recorded during the day, whereas the number of older larvae recorded during darkness was much lower (Stolbunov and Kuzmina 2018). Further, the weights of older larvae at different stages of development differed significantly throughout the day, decreasing as darkness approached, thus indicating diurnal migrations and redistribution of older larvae along the reservoir. A similar diel pattern was reported for *A. alburnus* juveniles in a side-channel of the River Danube (Copp et al. 2005c), where relative densities of *A. alburnus* decreased at night but size (mean SL  $\pm$  SE) increased at night (60.4 mm  $\pm$  12.17) compared with day-time size (20.8 mm  $\pm$  0.73). Presumably, a circadian cycle may also be involved in the movement of individuals that migrate between pelagic and littoral habitats. Thus, in a stratified European reservoir, larger individuals were caught in greater proportion during the day, whereas the proportion of smaller fish increased during the afternoon and night (Vašek et al. 2009).

In experiments to assess the effect of predator (*Esox lucius*) presence on *A. alburnus* behaviour, feeding and growth under two treatments, *A. alburnus* feeding rates were reduced by 35% and 20% when exposed to the scent of freshly-fed and starved pike, respectively (Jachner 1997). This reduction resulted from a decrease in time spent feeding, which was followed by a decrease in individual growth rates, thus supporting the hypothesis that an alarm substance, and not simply the predator’s odour, is the trigger for predator-avoidance responses (Jachner 1997). In the absence of the ‘recently-fed’ scent, *A. alburnus* moved calmly, either in groups or individually, and without any preference between open water and vegetation, but in its presence *A. alburnus* preferred to move in groups and quickly towards vegetation in search of refuge and remained hidden until it needed to feed (Jachner 1996).

#### *Migrations and movements*

Although *A. alburnus* has been classified as non-migratory (Wheeler 1977), perhaps because more sedentary populations have been reported in some lakes and reservoirs, this potamodromous fish is known to migrate from reservoirs and medium-to-large rivers upstream into small tributaries to spawn

(e.g. Lelek and Libosvárský 1960; Peterka et al. 2004; Meulenbroek et al. 2018), such as reported in the native range for the Rímov Reservoir (Czechia) into its main tributary (Hladík and Kubečka 2003). Migrations up tributaries of several reservoirs have also been reported to occur in the species' non-native range, where reservoirs act as a stepping-stone from which *A. alburnus* invade upstream areas (Matono et al. 2018). In African rivers, such upstream migrations by *A. alburnus* occur in desert streams close to reservoirs and in lentic and stable habitats generated by dams (Attou and Arab 2013; Clavero et al. 2015).

Changes in *A. alburnus* migration rates are generally related to fluctuations in water quality (e.g. physical and chemical variables: Santos et al. 2002; Lilja et al. 2003; Kotusz et al. 2006; Brodersen et al. 2008; Taylor and Cooke 2012; Benitez et al. 2015). In the case of Rímov Reservoir (Czechia), the frequency of *A. alburnus* moving upstream into the tributary was related to an increase in water temperature, which is an important regulatory factor in *A. alburnus* spawning migrations (Hladík and Kubečka 2003). During upstream migrations in the River Tundzha (Bulgaria) during April and May (spawning period), *A. alburnus* migration intensity was highest in mid-afternoon (14:00) at temperatures of 11–14 °C (Angelov et al. 2020). A telemetry study of four radio-tagged *A. alburnus* in the River Elbe during July–September 2007 documented a mean home-range area of  $0.197 \pm 0.125$  km<sup>2</sup>, with diurnal movements of  $827 \pm 580$  m, which was seemingly influenced by abiotic factors, mainly turbidity, water temperature and discharge (Josefovičová 2019).

During winter, many fish species move downstream to find refuge and avoid being displaced by high water velocities (Lucas et al. 1998), such as reported for the use of pools by *A. alburnus* in a fish pass on the River Danube (Meulenbroek et al. 2018). By using automated, passive-integrated-transponder tags, fish behaviour was examined over a wide range of sizes and species in a narrow fish pass located in Northeast England. Tagged *A. alburnus* were detected in the fish pass by the downstream end of the antennae, indicating a much higher level of activity from fish entering and trying to use the pass than from those successfully ascending it (Lucas et al. 1999). Most of the records compiled by downstream antennae were by the antenna closest to the downstream end of the pass, suggesting that most fish were more

active where velocity (and effort) was lowest in the water column. However, the efficiencies of coarse fish passage were low, possibly because cyprinids were impeded by the high levels of turbulence and the complex spatial environment (Lucas et al. 1999). Extensive use of fish passes by *A. alburnus* has also been reported elsewhere, such as in the rivers Meuse in Belgium (Baras et al. 1994), Elbe in Czechia (Prchalová et al. 2011), Odra in Poland (Kotusz et al. 2006) and Danube in Austria (Schmutz et al. 1998). *Alburnus alburnus* have been reported to use the lower extent of the Danube fish pass as a winter refuge habitat (Meulenbroek et al. 2018). More recently, high *A. alburnus* abundances were reported in different fish passages in the River Segura in southeastern Spain, where *A. alburnus* moved along the river but also used these passages as seasonal refugia (Sánchez-Pérez et al. 2022).

Migrations of juvenile *A. alburnus* against the water current can be related to either foraging (Prchalová et al. 2004) or the search for winter refuges (Prignon et al. 1998; Lucas and Baras 2000; Prchalová et al. 2004, 2006), such as observed from September to November in the delta of the River Volga (Tryapitsyna 1965; Podolyako et al. 2017). *Alburnus alburnus* migrations upstream, dominated by 1+ and 2+ juveniles, occur in a broadly-dispersed pattern (between 10–15 m) along the left and right margins of the river sections, beginning around 06:00, peaking between 12:00–15:00 and continuing until 20:00–21:00 (Pavlov et al. 2019).

The invasion by *A. alburnus* of the Iberian Peninsula has been facilitated by human-induced alterations to river channel morphology and hydrology, such as river impoundment for water retention. As a result, *A. alburnus* displays seasonal migrations along the tributaries of various reservoirs. A study of *A. alburnus* in the River Guadiana (Portugal) reported size-related seasonal migrations (Matono et al. 2018). In summer, *A. alburnus* of up to 60 mm TL were found mostly upstream, whereas those between 120–150 mm were found downstream, and individuals between 60–120 mm were equally dispersed along the entire river (Matono et al. 2018). These findings suggest an upstream recruitment of juvenile individuals during summer and autumn, and a higher proportion of reproductive individuals downstream in spring and summer.

## Pathogens and parasites

*Alburnus alburnus* has been found to host more than 40 species of pathogens and parasites that belong to the groups Acanthocephala, Cestoda, Crustacea, Hirudinea, Monogenea, Myxosporea, Nematoda and Protista (Borowik 1968; Baska and Molnár 1988; Koyun and Altunel 2007; Molnár et al. 2009; Koyun 2011). Bacterial (e.g. *Bacillus* spp.) and fungal (e.g. *Branchiomyces* spp.) diseases in *A. alburnus* have been also detected (Table 8). Whilst viral diseases in *A. alburnus* have received relatively little attention compared with its parasites, experimental trials have revealed that *A. alburnus* is a potential healthy host of the carp edema virus (CEV), i.e. no clinical signs or mortality have yet to be reported (Matras et al. 2019). Shorter periods (only 12 h) of exposure to *A. alburnus* in cohabitation studies were sufficient for CEV to be transmitted to other host species, thus confirming the species' potential role in virus dispersal (Way et al. 2017).

Myxosporean parasites can also infect *A. alburnus*, and they have been recorded in the internal organs of *A. alburnus* in Hungary, where plasmodia of *Myxobolus shaharomae* were apparent in blood vessels of the kidney, liver, testes and intestinal wall—though in most cases the plasmodia did not elicit a host reaction (Molnár et al. 2009). A three-year study carried out in Hungary on *A. alburnus* from Lake Balaton and from the River Danube revealed the species to be a host of four *Myxobolus* species, with a prevalence up to 16% (Molnár 2000).

Based on 165 specimens of *A. alburnus* in a broader eco-parasitological study (Chunchukova et al. 2019a), helminth community structure in *A. alburnus* from the River Danube comprised seven species of parasites (see Table 8), including Trematoda (four species:  $n=971$ ), Nematoda ( $n=7$ ), Cestoda ( $n=4$ ), and Acanthocephala ( $n=2$ ). In Lake Kortowskie (Poland), 14 parasite species were found in *A. alburnus*, including seven monogeneans (Dzika et al. 2008). Infections by helminth parasites are common in *A. alburnus* populations, with *Ligula intestinalis* and *Pomphorhynchus laevis* considered as important intestinal parasites and found in several populations at relatively high prevalence levels (e.g. Kirin 2001; Chunchukova et al. 2019a, 2019b). Thus, *P. laevis* was a core parasite species of *A. alburnus* in the Bulgarian section of the River Danube, where prevalence

levels were highest in summer and autumn (Chunchukova et al. 2019a). In the River Marista (Bulgaria), helminth parasites were recorded in 83% of the *A. alburnus* individuals examined and included both *L. intestinalis* and *P. laevis* (Chunchukova et al. 2019b). Five helminth parasites were recorded in *A. alburnus* from two other rivers in Bulgaria, with the nematode *Rhabdochoata* having the highest prevalence, but no record of either *L. intestinalis* or *P. laevis* (Kirin 2001). Conversely, in Great Britain, *L. intestinalis* was the only helminth detected in a review of helminth parasites of freshwater fishes in Great Britain (Price and Clancy 1983), with helminth prevalence in the River Thames varying seasonally and peaking in summer (Harris and Wheeler 1974). A similar pattern was observed in Lake Enne, Turkey (Koyun et al. 2007).

A feature of cestode parasites is their accumulation of heavy metals relative to their host species and environment (Sures and Siddall 1999; Sures et al. 1999). Accumulations in *A. alburnus* infected with *Pomphorhynchus* spp. (*P. laevis*, *P. tereticollis*) has been found to be significantly higher, with regard to arsenic, nickel and lead, in the parasite than in the host tissues and organs (Chunchukova et al. 2017; Chunchukova 2018; Chunchukova and Kuzmanova 2017).

Amongst the monogenean parasites that infect *A. alburnus* populations, *Dactylogyrus* spp. are common, with two species recorded as infecting two lacustrine populations in two Adriatic river basins (lakes Prespa and Ohrid, Macedonia), together with two monogenean parasites, and with overall prevalence levels at 45% (see Table 8, Stojanovski et al. 2009). A previous study of *A. alburnus* from Lake Prespa revealed a similar monogenean fauna, with 41% of *A. alburnus* infected with at least one of these parasites and with the highest prevalence (22%) for *Dactylogyrus alatus* (Stojanovski et al. 2003), whereas in Lake Dojran (Macedonia) prevalence was lower, with 2% of *A. alburnus* infected with *Ligophorus* sp. (Stojanovski et al. 2008). In the River Porsuk (Turkey), monthly *A. alburnus* samples indicated infection by three *Dactylogyrus* species (see Table 8), with prevalence levels, abundance, and mean intensity always highest for *D. fraternus*, with a prevalence of 50%, 5.2% and 2.6%, respectively (Koyun 2011). Studies on the molecular phylogeny of *Dactylogyrus* parasites have revealed the presence of three lineages, with *A. alburnus*



populations infected by a single lineage that also infects other leuciscids (European minnows) as well as the European common barbel *Barbus barbus* (Šimková et al. 2004). Finally, two species of *Gyrodactylus* parasites have been recorded for *A. alburnus*: *G. bliccensis* (Matejusová et al. 2001) and *G. gracilihamatus* (Zietara and Lumme 2002).

Regarding digenean parasites, the majority of *A. alburnus* examined from Lake Dabie (Poland) were parasitised in muscle tissues by the metacercariae of either *Paracoenogonimus ovatus* or *Posthodiplostomum cuticola*, but with a low proportion, and with an intensity of infection up to 34 metacercariae (Ostrowska et al. 2019). In 22 host fish species from Lake Modrac (Bosnia), the metacercaria of *P. cuticola* was commonly encountered, but with the lowest prevalence recorded in *A. alburnus* (Adrović et al. 2011). Among others, the Opisthorchiidae and Heterophyidae Families include genera that cause fish zoonoses; however, owing to the small size of their metacercaria, these parasites cannot be visually detected in fishes. Through the application of multiple PCR methods, the Genus *Metagonimus* (Heterophyidae), which is one of the main potentially zoonotic trematodes present in Europe, was identified in *A. alburnus* specimens (Caffara et al. 2020). In addition, the most important species of zoonotic flukes transmitted in fresh waters is *Opisthorchis felineus* (Cech et al. 2021), which has been observed at a prevalence of 74% in *A. alburnus* from German fresh waters (Hering-Hagenbeck and Schuster 1996).

Ergasilid parasites tend to infect the gills of their fish hosts, with *Paraergasilus longidigitus* recorded in the branchial filaments of *A. alburnus* in Lake Enne (Turkey) at an overall prevalence of 57%, but with a peak in autumn at 74%, and with prevalence increasing with fish size (Koyun and Altunel 2007). *Lernaea cyprinacea* (also known as ‘anchor worm’) feeds on the host’s blood and tissue was recorded in *A. alburnus* from Iran, where 68% of the fish examined were infected, but with the extent of the pathological damage not reported (Raissy et al. 2013).

#### Genetic traits

The genetic character of *A. alburnus* is characterised by a diploid karyotype that consists of 50

chromosomes: 14 metacentric, 14 sub-metacentric, 14 sub-telocentric and 8 telocentric (Ziegler et al. 2003). In addition, there are two giant super-numerary chromosomes of two different sizes, which can extend the possible karyotypes to  $2n=51$  and  $2n=52$ , respectively. This remarkable genetic trait has been reported for 11% of individuals possessing one or two giant supernumerary *B* chromosomes of different size (Ziegler et al. 2003; Schmid et al. 2006). Detailed DNA sequencing of the *B* chromosomes determined this trait to be of retro-transposable origin, as a strong homology was found with the long-terminal-repeat retro-transposon from the medaka fish *Oryzias latipes*. Overall, these findings suggest a possible interspecific origin for the *A. alburnus* supernumerary chromosomes (Camacho et al. 2000; Ziegler et al. 2003).

As in other species, an important factor that influences genetic diversity in *A. alburnus* is its elevated capacity for hybridisation. The introduction of closely related fish species, along with habitat disturbance, has increased the incidence of interspecific hybridization and establishment of hybrid zones (Costedoat et al. 2005). *Alburnus alburnus* can hybridise with other cyprinid genera, including *Abramis*, *Blicca*, *Leuciscus*, *Rutilus* and *Squalius* (Wheeler 1978; Blachuta and Witkowski 1984; Crivelli and Dupont 1987; Berrebi et al. 1989; Maceda-Veiga et al. 2010; García-Berthou et al. 2015; Witkowski et al. 2015). However, detailed information on long-term viability and reproductive performance of hybrid individuals is still lacking.

To improve knowledge on the extent of hybridisation impact in Iberian freshwaters, the genetic profile of *A. alburnus* was identified for *cyt b* and beta-actin genes, together with Iberian endemic leuciscids, namely Spanish minnowcarp *Anaocypris hispanica*, Iberian roach *Squalius alburnoides* and Southern Iberian chub *Squalius pyrenaicus* (Almodóvar et al. 2012; Sousa-Santos et al. 2018). Sequencing of the mitochondrial *cyt b* gene yielded four haplotypes that differed by 1–5 mutations, accounting for 0.10 to 0.50% of pairwise divergence among sequences. A phylogenetic tree based on these analysed sequences revealed *A. alburnus* to be more closely related to *A. hispanica* than to the sympatric *Squalius* species. One *A. alburnus* haplotype from the River Guadiana was shared with specimens from the River Jarama (a tributary of the River Tagus in central Spain) and, together



with one haplotype from Czechia, formed a well-supported clade different from the clade conformed by individuals from Croatia, Greece and Russia. On the other hand, sequencing of the nuclear beta-actin gene revealed the presence of 12 haplotypes among specimens from the River Guadiana and Croatia, with only three of them being found in homozygosity. Mitochondrial and nuclear molecular analyses were also conducted in *A. alburnus* specimens from the River Jarama to establish the pattern of introgression of *A. alburnus* with the genus *Squalius* (Almodóvar et al. 2012). Mitochondrial DNA analyses (cyt *b* and 16S) in hybrids were of *A. alburnus* maternal origin. Since the Internal Transcribed Spacer 1 sequences showed the same results, these regions were deemed to be of maternal type as well (Slyenko and Stolbunova 2010). Regarding the beta-actin gene, the results showed that all hybrid sequences had a double peak generated by two different parental sequences, namely *A. alburnus* and *Squalius*. However, the hybrids were different in terms of the direction of gene introgression, with one hybrid proving to be of *A. alburnus* paternal origin and the other two hybrids proving to be of maternal *A. alburnus* origin (Sousa-Santos et al. 2018). More recently, a single direction on hybridisation from male *A. alburnus* towards females of northern Iberian chub *Squalius carolitertii* has been identified (Curto et al. 2022). Because there is increasing evidence supporting the theory that hybridisation can lead to adaptation through the establishment of new and optimised genotypes and morphologies (Rieseberg et al. 1999), the findings described here above indicate that introduced *A. alburnus*, which are widespread in the Iberia Peninsula (see Curto et al. 2022), have the potential to produce irreversible genetic swamping of rare endemic species.

### Invasiveness and ecological impacts

Introduced populations of *A. alburnus* exhibit large and sudden increases in abundance, which is characteristic of invasive fishes (Copp et al. 2005a; Fox et al. 2011; Britton and Gozlan 2013), and this is one reason that introduced *A. alburnus* populations have dispersed widely in the Iberian Peninsula. The life-history traits that enabled *A. alburnus* to invade drainage basins of the Iberian Peninsula will vary depending on invasion stage (Ribeiro et al. 2008). In fact,

small body size, an elevated capacity to adapt to local conditions and high fecundity rates have all been demonstrated to be important in population establishment (Ribeiro et al. 2008). The species dispersal between and within drainages is mostly related with its interest for recreational fisheries (Ribeiro et al. 2008), with propagule pressure (i.e. frequency and quantity of fish releases) being a key factor in the rate of spread. *Alburnus alburnus* is listed amongst the most frequently introduced species in both Spain and Portugal due to its common use as live bait by anglers (Banha et al. 2017). These bait bucket releases generally involve small numbers of fish (<30 specimens), but the frequency of these releases is high (25% of anglers), representing a considerable propagule pressure (Banha et al. 2017). This elevated propagule pressure is exacerbated by demonstrated plasticity in life-history traits (Table 5) (e.g. high reproduction, see below), which may increase the establishment and spread success (Lockwood et al. 2005). The ability of *A. alburnus* to cope with long term environmental variability on Iberian waters (invasion stage: integration) appears to be associated with the species' dietary traits as well as the similarity in environmental conditions of the *A. alburnus*' native and non-native ranges and their proximity (Ribeiro et al. 2008).

Not surprisingly, *A. alburnus* was the second most captured fish species in basins of the Catalonia Region (northeastern Spain), where native fish populations were reduced on average by 60% relative to the period prior to invasion by *A. alburnus*. Local extinctions of the endemic 'bermejuela' *Achondrostoma arcasii* have coincided with the arrival of *A. alburnus* (Maceda-Veiga et al. 2010). *Alburnus alburnus* is also known to threaten species of the genus *Parachondrostoma*, such as *P. arrigonis* and *P. turiense*, through competition for food and habitat resources (Doadrio et al. 2011; Latorre and Almeida 2019). In the Keddara Dam (Algeria), the accidental introduction of *A. alburnus* has been linked to the decline of native Algerian barb *Barbus setivimensis* (Attou and Arab 2013). Introduced *A. alburnus* populations have also been linked to the decline of other endemic fishes in Spain, including the Ebro nase *Parachondrostoma miegii* (Almeida and Grossman 2012), and to cause a substantial shift in the behavioural patterns of this Iberian nase species (Vinyoles et al. 2009; Almeida and Grossman 2012) as well as on the endangered minnow *Anaocypris hispanica* (da Silva et al. 2019).

**Table 5** Biological traits of *A. alburnus* in populations both in the native and in the non-native range pertaining to potential invasiveness. Description of main findings for each trait with respective reference. Note that information for some traits in non-native regions is still scarce or absent

Native range	Non-native range
<i>Morphology</i>	
High morphological plasticity related to ecology and geography	High morphological plasticity related to habitat No studies comparing morphological traits between native and introduced populations
<i>Habitat use</i>	
Present in natural riverine and lacustrine ecosystems (e.g. river side-channels, marshlands) and in altered riverine ecosystems (e.g. artificial dead-wood fascines, artificial fishways, reservoirs)	Present in both natural riverine and lacustrine system including high-velocity microhabitats and reservoirs (lentic habitats)
<i>Population structure and dynamics</i>	
Size, age structure and population dynamics respond to abiotic factors, food availability and competition	Larger proportion of males documented in Spain compared to the native range Greater longevity and larger mature cohorts found in reservoirs with longer residence time Upstream populations showing higher growth rates than downstream populations
<i>Ontogeny and growth</i>	
Standard length at the end of the free embryo stage $\approx$ 6.5–7.0 mm, with larvae $\approx$ 13 mm	No studies available
Somatic growth faster in the first two years of life	
No reported differences in growth rate between males and females	
No apparent patterns observed along a latitudinal gradient	
<i>Reproduction</i>	
Variability in reproductive traits such as fecundity, egg size and energy investment	High plasticity in reproductive traits Greater breeding performance and reproductive investment Comparative studies between native and non-native needed to evaluate putative differences
<i>Trophic ecology</i>	
Omnivorous, opportunistic forager (forages at the surface of open waters and its diet is mainly based on zooplankton, macroinvertebrates, fish eggs and plant material)	High plasticity, adapts diet according to food availability and habitat type
Adapts diet according to food availability and presence of other predators	
Common prey for majority of piscivorous species	
<i>Physiology</i>	
Greater swimming performance but lower standard metabolic rate than in other freshwater fish species	No study comparing physiological traits between native and introduced populations
<i>Behaviour</i>	
Schooling species (30–50 fish), at larval and 0+ juvenile stage observed as part of mixed shoals	Shoal movements generally similar to those of native populations
Shoals formed by medium- to large-sized individuals moving in a wedge-shaped configuration	Seasonal movements along tributaries of various reservoirs
Despite having more sedentary populations that inhabit lakes and reservoirs, it is known to migrate from reservoirs and medium-to-large rivers upstream into small tributaries to spawn	
<i>Pathogens and parasites</i>	
Populations can develop diseases caused by more than 40 species of pathogens and parasites	The species is a disease vector by acting as a host of the cestode <i>Ligula intestinalis</i>

**Table 5** (continued)

Native range	Non-native range
<i>Genetic traits</i>	
Diploid karyotype consisting of 50 chromosomes: 14 metacentric, 14 sub-metacentric, 14 sub-telocentric and 8 telocentric High capacity for hybridisation	Hybridisation with native Iberian species such as <i>Squalius</i> spp.

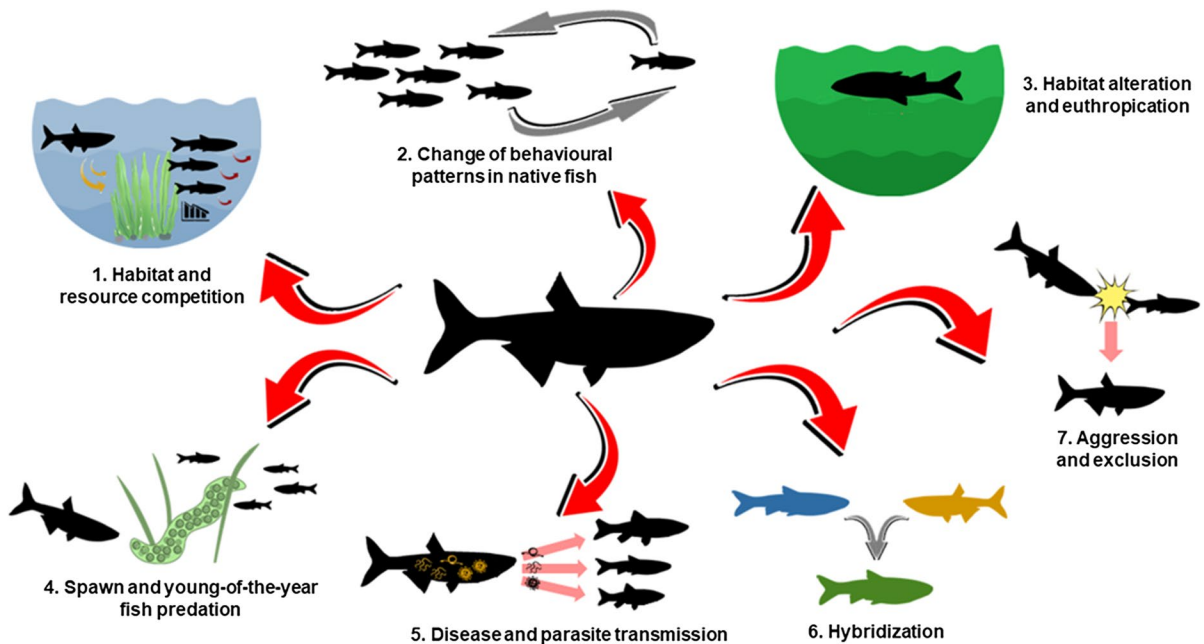
Specifically, the change in behaviour has led to higher metabolic expense, reduced shelter use, and increased predation risk in *A. hispanica* (da Silva et al. 2019).

The role of hydrological disturbances as a facilitator of invasions by *A. alburnus* of temporary Mediterranean streams has examined the species' dispersal process within the River Guadiana basin (Portugal) at three different levels (Matono et al. 2018): (i) upstream and downstream movements along river sections, (ii) invasion of interconnected river sections from passive movements through upstream dams, and (iii) dispersal related to human intervention or deliberate introductions—the only factor that explains movement through large dams. Accordingly, the expansion of *A. alburnus* was found to be clearly associated with dam-regulated river systems (Matono et al. 2018), where *A. alburnus* spread appears to be related to hydrological alterations (Vinyoles et al. 2007). The lentic conditions created by water retention structures have likely facilitated the establishment of *A. alburnus* and its dispersal both by active movement and through passive larval dispersal (Reichard et al. 2002). *Alburnus alburnus* is considered by many to be an eurytopic fish species (Copp 1989, 1992; Wolter and Vilcinskis 1997; Aarts and Nienhuis 2003; Fladung et al. 2003; Zitek et al. 2004a; Lasne et al. 2007) and a good swimmer due to its low drag coefficient (Sagnes and Statzner 2009), thus enabling the species to sustain prolonged swimming performance and efficiency (Rubio-Gracia et al. 2020a). Consequently, *A. alburnus* can achieve high densities in a variety of freshwater environments (Masó et al. 2016), including the highly variable hydrological regimes of natural Mediterranean temporary streams (Almeida et al. 2014; Amat-Trigo et al. 2019). *Alburnus alburnus* have demonstrated their ability to move large distances from the rivers and reservoirs where the species was first introduced (Almeida et al. 2014). This mobility is complemented by plasticity of several biological traits that facilitate

adaptation and invasion to new environments, such as high fecundity, an omnivorous diet, and a broad temperature tolerance (Fig. 3) (Chappaz et al. 1987; Latorre et al. 2016, 2018, 2020a). Indeed, temperature tolerances of *A. alburnus* (Kuttel et al. 2002) indicate that eggs are able to withstand water temperatures of 14–31 °C (Alabaster and Lloyd 1980), with optimal embryonic development at 21–27 °C (Alabaster and Lloyd 1980). For adults, temperatures > 20 °C are critical, with a CT<sub>Max</sub> of 38 °C reported for *A. alburnus* in a heated lake (Alabaster and Lloyd 1980).

As an omnivorous planktivore, *A. alburnus* occupies a relatively-low trophic position (Almeida et al. 2014; Latorre et al. 2016, 2018, 2020a), which can afford a fish species greater efficiency in obtaining energy from basal trophic groups (Gido and Franssen 2007). During the early stages of *A. alburnus* invasions, different life traits are important along the invasion stage, from recently introduced to well-established populations (Ribeiro et al. 2008). For example, faster growth rates have been found during the initial stages of invasion compared with sites where fish populations are in the establishment phase (e.g. Bøhn et al. 2004; Fobert et al. 2013; Copp et al. 2017). A similar pattern has been suggested for reproductive effort (Copp and Fox 2007). Overall, phenotypic and habitat plasticity of *A. alburnus* in both the native and introduced populations appears to be an important factor in its invasiveness, such as throughout highly regulated, Mediterranean-type rivers (Almeida et al. 2014; Masó et al. 2016; Matono et al. 2018; Amat-Trigo et al. 2019).

Elevated abundances of *A. alburnus* in reservoirs and rivers do not seem to be controlled by the region's predators, such as *Lutra lutra*, which is known to be an opportunistic predator. However, despite the high abundance of introduced fish species, the diet of *L. lutra* has been found to contain limited occurrence (Miranda et al. 2006) or no evidence (Bedmar et al. 2022) of the invading species. With specific reference



**Fig. 3** Schematic representation of demonstrated and potential major ecological impacts reported for *A. alburnus* in invaded regions. YOY: young-of-the-year

to *A. alburnus* in Iberia, no evidence was found of otter predation on *A. alburnus* at a large reservoir in the River Guadiana from spraint samples collected before 2001 and in 2003 as well as in 2018, despite the high *A. alburnus* abundance in this last period (Bedmar et al. 2022). Similarly, the efficient non-native piscivorous *Sander lucioperca* was not found to reduce high abundance of *A. alburnus* in a study of 14 different populations across Portuguese drainage basins (Ribeiro et al. 2021).

Whenever native and non-native fishes display similar ecological traits and life histories, the risk of developing ‘strong interactions’ (sensu Schumann et al. 2015) with native species increases, as demonstrated by the European cyprinid sunbleak *Leucaspis delineatus* in England, where it is not native (Beyer et al. 2010). Thus, in the absence of an evolutionary history of coexistence, which promotes segregation of ecological niches, interactions between *A. alburnus* and *Anaocypris hispanica* may be expected due to their close phylogenetic relationship (Sousa-Santos et al. 2018). However, these two species currently do not live in sympatry, despite there being evidence of a high overlap in their ecological niches (da Silva et al. 2019). Behavioural interference and aggression seems

to be one of the main causes of native fish exclusion due to the dominance of an invasive species (Blanco-Garrido et al. 2009; Leunda 2010; Almeida et al. 2014). Some of these mechanisms may be related to indirect competition for space and food as well as changes in feeding behaviour (i.e. prey preference or feeding rate) and activity (Keller and Brown 2008; Schumann et al. 2015). Under laboratory conditions, *A. alburnus* presence was found to be responsible for changes in the behavioural patterns of *A. hispanica*, these being related mainly to an increase in the activity rate of individual fish and a decrease in their time spent within a refuge; this suggests a potential dominance of *A. alburnus* when coexisting in the wild with its highly endangered congener (da Silva et al. 2019). Although no direct competition was observed in the above study between these two species, their possible coexistence in the future may have a negative effect on the general behaviour pattern of *A. hispanica*.

Additional risk factors associated with *A. alburnus* include disease transmission, habitat and foodweb alteration and genetic contamination. *Alburnus alburnus* is a host of *Ligula intestinalis* in many European countries (see Section “Pathogens and parasites”). In the Iberian Peninsula, this cestode was detected in *A.*

*alburnus* collected from the River Guadiana basin, including both tributaries and reservoirs (Sánchez and Alarcón-Elbal 2014), indicating that *A. alburnus* can carry this parasite throughout Iberian waters and affect other native fishes (Latorre and Almeida 2019). Regarding habitat alteration, *A. alburnus* can affect food web structure, and thus water quality, by feeding on cladocerans, copepods, and other small invertebrates (see Section “Trophic ecology”) that play an important role in freshwater ecosystems as zooplankton (Maceda-Veiga et al. 2010; Adamczuk 2016). This aspect consequently increases productivity and biomass of algae, thereby promoting eutrophication events (Horppila and Kairesalo 1992). In terms of genetic ‘contamination’, *A. alburnus* has been able to affect native leuciscid species through hybridisation (Blachuta and Wikowski 1984; Crivelli and Dupont 1987; Maceda-Veiga et al. 2010; see also Section “Genetic traits”). For instance, in the River Jarama an event of hybridisation has been documented with *Squalius alburnoides* complex and *S. pyrenaicus*, resulting in a certain degree of introgression (Almodóvar et al. 2012). More recently, *A. alburnus* hybridisation was observed with *S. carolitertii* in northern Portugal, expanding the hybridisation concerns to other local *Squalius* endemics (e.g. Malaga chub *Squalius malacitanus* or Torgal chub *Squalius torgalensis*), which present very restricted distributions (Curto et al. 2022). The aforementioned study also described wide hybridisation across several Portuguese river basins, encompassing different *Squalius* species, but the authors acknowledged that this impact has been poorly studied and largely overlooked (Curto et al. 2022).

In summary, the ‘broad plasticity and capacity of *A. alburnus* to adapt to different environmental conditions when invading new habitats makes this species a potentially successful global invader (Masó et al. 2016; Latorre et al. 2018; Attou and Arab 2019). Using the Fish Invasiveness Screening Kit (Copp et al. 2009) in Iberia, *A. alburnus* was found to pose a medium risk of being invasive in Catalonia (Andreu et al. 2011), but a high risk in the Iberian Peninsula as a whole (Almeida et al. 2013). More recent screenings that used the Aquatic Species Invasiveness Screening Kit (Copp et al. 2016, 2021), which

includes predictions of how future climate conditions could affect a species’ invasiveness, *A. alburnus* was classified as posing a high-risk of being invasive in Turkey (Tarkan et al. 2017b), in non-native parts of Great Britain (Dodd et al. 2019), and in both Croatia and Slovenia (Radočaj et al. 2021) under current and future climate conditions. Whereas, a medium-risk ranking was attributed to *A. alburnus* for the River Ob basin in Russia (Interesova et al. 2020), and a low risk ranking for Lake Marmara in Turkey (Tarkan et al. 2017a), and in both cases the risk rank was the same under current and future climate conditions. However, future climate conditions are expected to facilitate expansion of the *A. alburnus*’ invasive range (Lehtonen 1996). Indeed, the available data suggest that the high phenotypic plasticity shown by *A. alburnus* outside its native range (Masó et al. 2016; Latorre et al. 2018) could favour its invasion process, colonisation, and establishment outside its natural distribution area, and in particular Iberia.

## Management

Management options to control *A. alburnus* are highly dependent on the extent of its invaded range. In the Iberian Peninsula, it is unfeasible to eradicate *A. alburnus* from large water bodies, particularly given its life-history traits described here above. In areas where the species is spatially restricted to smaller, isolated reservoirs, containment options could be feasible, such as the installation of physical barriers that would reduce dispersal rates from reservoirs to lotic systems (e.g. Rischbieter 2000). However, barrier construction is not only context dependent but also runs contrary to European efforts to reconnect rivers. Currently, the legal framework in Portugal and Spain aims for local and national administrations to develop specific management plans to control and eradicate *A. alburnus* in those areas where it has been introduced. *Alburnus alburnus* is included in both Spanish (RD 630/2013) and Portuguese (DL 92/2019) catalogues (i.e. regulation lists) of invasive species. Under both legislative acts, the introduction of *A. alburnus* to the natural environment (usually as ‘forage’ fish) for culture,



transport or trade is completely forbidden. In fact, Spanish legislation also provides management strategies for this species. However, for more than five years since its implementation, these management plans have clearly failed to control the spread of *A. alburnus* in Iberia (Latorre and Almeida 2019; Martelo et al. 2021). As illegal *A. alburnus* introductions (and possibly translocations) are likely to continue, this propagule pressure will most likely lead to further spread of the species. Since no viable eradication or control measures are known for *A. alburnus*, management must focus on campaigns to educate anglers about the risks posed by *A. alburnus* and other non-native fishes in order to prevent their translocation, enhance compliance of the existing regulations, and to increase their enforcement. These are the only preventive actions that could reduce the species spread. Moreover, monitoring programmes for invasive alien species should be conducted across the Iberia to permit evaluation of *A. alburnus* population trends. At the local level, particularly for riverine systems high ecological value or threatened native fish species, where *A. alburnus* impacts could potentially be greater, culling campaigns should be considered (Salvador Vilariño 2015).

Future research on non-native *A. alburnus* populations could best focus on the species' ontogeny, growth, trophic impacts, behaviour and physiology to inform impact assessments and to implement more efficient control measures. For instance, a better understanding of *A. alburnus*' adverse impacts on food webs using stable isotope analysis (SIA) can be particularly useful as an integrative tool to assess long-term dietary traits (e.g. Cucherousset et al. 2007, 2012). Assessing hybridisation impacts, particularly looking at genetic introgression, is a priority because of the strong evidence of *A. alburnus* hybridisation with native fish species. The role of *A. alburnus* on disease transmission to other fish species is also an important area for future research due to the severe impacts that some novel parasites and diseases can impose on naïve native species. Finally, for population control, research is needed to understand *A. alburnus* reproductive behaviour in order to determine whether or not there are chemical cues that could be used in bait traps, similar to what has been developed for invasive sea lampreys in the Great Lakes region (Miehls et al. 2020).

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## Appendix

### Age and growth modelling

Data on *A. alburnus* growth were retrieved from both primary and secondary (cf. *vide*) literature sources. A necessary condition for inclusion of a literature source was that it provided mean length-at-age (LAA) values for the population under study. Whenever mean LAA values were provided for only one or a few age classes (e.g. as representative of the population from which fish were sampled), these were still included into the global database for the sake of completeness (cf. Vilizzi and Copp 2017). For these analyses (and in other relevant parts of the present study), LAA data originally given as total length (TL, mm) were converted to standard length (SL, mm) using the formula  $SL = 0.875 \times TL$  ([www.fishbase.org](http://www.fishbase.org)).

The latitude and longitude of the water body where each *A. alburnus* population was sampled were recorded, except for those ‘large’ rivers for which no specific indication was provided of the sampling location(s). Sections of rivers or sampling locations therein were considered as separate water bodies (cf. *A. alburnus* populations). For each water body, the corresponding habitat was labelled as either ‘lentic’ (i.e. natural lakes and man-made reservoirs) or ‘lotic’ (water courses). Based on the waterbody latitude and longitude, the corresponding Köppen-Geiger climate class and type (Peel et al. 2007) were identified with reference to a regular 0.5 degree latitude/longitude grid for the period 1951–2000 (Kottek et al. 2006: <http://koeppen-geiger.vu-wien.ac.at/data/Koeppen-Geiger-ASCII.zip>).

Growth models were based on the Beverton-Holt parameterisation of the von Bertalanffy growth function (VBGF; Ricker 1975):

$$SL = SL_{\infty} (1 - e^{-K(age - t_0)})$$

where  $SL_{\infty}$  is the asymptotic SL,  $K$  the instantaneous growth rate or Brody’s growth coefficient ( $\text{years}^{-1}$ ), and  $t_0$  the age of the fish at 0 mm SL. Following Vilizzi and Copp (2017), VBGF-based comparisons in growth of ide populations between ranges, habitats,

climates classes and climate D types (see Table) were made by fitting eight models in total: i) a general model with separate parameter estimates for each population; ii) three models with one parameter in common amongst populations; iii) three models with two parameters in common amongst populations; and iv) one common model with the same parameter estimates for all populations. Both the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) were computed to select the best-fitting model, with preference given to BIC in case of major disparity of outcomes for reasons of model parsimony (i.e. fewer parameters), otherwise to AIC for ‘biological meaningfulness’ (Burnham and Anderson 2003). Fitting of growth models was in R×64 v3.6.3 (R Development Core Team 2021) using packages FSA and nlstools (Ogle 2016) with 1000 bootstrap confidence interval estimates of the parameters (and with additional code written by LV). Note that growth models based on the *A. alburnus*’ range of distribution (i.e. native vs non-native) could not be fitted because of the low number of populations (hence, LAA data points) from the non-native range (see Table).

See Tables 6, 7, 8

**Table 6** Water bodies for which length-at-age data for *A. alburnus* were retrieved

Water body	Country	Lat	Lon	Range	Habitat	Class
20 lakes (North Germany)	Germany	52°69’N	09°57’E	Native	Lentic	C
Batak Reservoir	Bulgaria	41°58’N	24°11’E	Native	Lentic	D
Brno Reservoir	Czechia	49°14’N	16°30’E	Native	Lentic	C
Danube Delta (Somova)	Romania	45°11’N	28°40’E	Native	Lentic	C
Gorni Dubnik Reservoir	Bulgaria	43°21’N	24°18’E	Native	Lentic	C
Lake Bacău	Romania	46°35’N	26°55’E	Native	Lentic	D
Lake Balaton	Hungary	46°51’N	17°43’E	Native	Lentic	C
Lake Balaton (B. györök)	Hungary	46°51’N	17°43’E	Native	Lentic	C
Lake Balaton (Bozsai)	Hungary	46°51’N	17°43’E	Native	Lentic	C
Lake Balaton (Keszthely)	Hungary	46°51’N	17°43’E	Native	Lentic	C
Lake Balaton (Palóznak)	Hungary	46°51’N	17°43’E	Native	Lentic	C
Lake Balaton (Szigliget)	Hungary	46°51’N	17°43’E	Native	Lentic	C
Lake Bicaz	Romania	47°02’N	26°05’E	Native	Lentic	D
Lake Chepintsi	Bulgaria	42°44’N	23°25’E	Native	Lentic	D
Lake Ilmen	Russia	58°16’N	31°17’E	Native	Lentic	D
Lake Legińskie	Poland	53°58’N	21°08’E	Native	Lentic	D
Lake of Sainte-Croix	France	43°45’N	06°11’E	Native	Lentic	C
Lake Øyeren	Norway	59°51’N	11°09’E	Native	Lentic	D

**Table 6** (continued)

Water body	Country	Lat	Lon	Range	Habitat	Class
Lake Pângărați	Romania	48°56'N	26°09'E	Native	Lentic	D
Lake Tuusula	Finland	60°26'N	25°03'E	Native	Lentic	D
Lipno Reservoir	Czechia	48°42'N	14°04'E	Native	Lentic	C
Międzyodrze Wetland	Poland	53°40'N	14°57'E	Native	Lentic	C
Piasuchnik Reservoir	Bulgaria	42°40'N	24°56'E	Native	Lentic	C
River Beek	Germany	53°13'N	08°52'E	Native	Lotic	C
River Danube	Slovakia	–	–	Native	Lotic	–
River Danube (Rusovce)	Slovakia	48°08'N	17°07'E	Native	Lotic	C
River Danube (Vlčie hrdlo)	Slovakia	48°07'N	17°10'E	Native	Lotic	C
River Danube (Žofín)	Czechia	50°88'N	14°56'E	Native	Lotic	C
River Daugava	Belarus	–	–	Native	Lotic	–
River Ebro	Spain	41°47'N	01°05'W	Non-native	Lotic	C
River Guadalquivir	Spain	37°37'N	05°35'W	Non-native	Lotic	C
River Guadiana	Spain	38°59'N	05°51'W	Non-native	Lotic	C
River Laben (Děčín)	Czechia	50°46'N	14°11'E	Native	Lotic	C
River Ohře (Karlovy-Vary)	Czechia	50°13'N	12°52'E	Native	Lotic	C
River Pilica	Poland	51°51'N	21°16'E	Native	Lotic	C
River Prokhladnaya	Russia	54°61'N	20°24'E	Native	Lotic	C
River Saône	France	45°43'N	04°49'E	Native	Lotic	C
River Segura	Spain	38°06'N	01°17'W	Non-native	Lotic	B
River Tagus	Spain	39°49'N	04°20'W	Non-native	Lotic	C
River Thames (Reading)	United Kingdom	51°27'N	00°58'W	Native	Lotic	C
River Vltava (Méchenice)	Czechia	49°54'N	14°23'E	Native	Lotic	C
River Vltava (Podbaba)	Belarus	54°46'N	27°30'E	Native	Lotic	D
Slapi Reservoir	Czechia	49°49'N	14°26'E	Native	Lentic	C
River Cardener	Spain	42°10'N	01°35'E	Non-native	Lotic	C
River Fluvià	Spain	42°12'N	03°06'E	Non-native	Lotic	C
River Foix	Spain	41°25'N	01°33'E	Non-native	Lotic	C
River Muga	Spain	42°18'N	02°55'E	Non-native	Lotic	C
River Stropnice	Czechia	48°68'N	14°71'E	Native	Lotic	C
Vranov Reservoir	Czechia	48°91'N	15°81'E	Native	Lentic	C

For each water body, the country, latitude, longitude, species' distributional range, habitat and Köppen-Geiger climate class and type are provided (after Peel et al. 2007). Climate class: C = Temperate; D = Continental

**Table 7** Mean length-at-age (standard length: SL, mm) values for *A. alburnus*. Source references in footnote

Population	Estimated age (years)									Reference
	1	2	3	4	5	6	7	8	9	
20 lakes (North Germany)	42	66	90	116	125	133	149	–	–	(7)
Batak Reservoir (1974)	82	101	110	119	132	–	–	–	–	(27)
Batak Reservoir (1971/1972)	78	107	120	–	–	–	–	–	–	(27)
Brno Reservoir	70	122	149	165	171	–	–	–	–	(25)
Danube Delta (Somova)	68	78	91	105	–	–	–	–	–	(22)
Gorni Dubnik Reservoir	95	102	–	–	–	–	–	–	–	(13)
Lake Bacău	44	72	90	103	111	–	–	–	–	(3)
Lake Balaton	43	60	71	81	98	106	–	–	–	(4)
Lake Balaton (B. györök)	54	70	82	90	–	–	–	–	–	(5)
Lake Balaton (Bozsai)	42	55	67	76	85	–	–	–	–	(5)
Lake Balaton (Keszthely)	40	51	61	71	80	88	96	103	109	(5)
Lake Balaton (Palóznak)	40	53	63	71	78	83	88	–	–	(5)
Lake Balaton (Szigliget)	40	50	60	69	77	84	90	96	101	(5)
Lake Biczaz	41	87	115	132	142	149	–	–	–	(2)
Lake Chepintsi	53	80	98	–	–	–	–	–	–	(23)
Lake Ilmen	62	93	125	132	143	–	–	–	–	(12)
Lake Legińskie	–	76	79	99	101	116	117	–	–	(20)
Lake of Sainte-Croix	46	75	104	120	131	143	153	–	–	(9)
Lake Øyeren	38	68	87	100	108	115	123	129	–	(1)
Lake Pângărați	50	114	154	177	193	202	–	–	–	(2)
Lake Tuusula	40	82	115	125	–	–	–	–	–	(8)
Lipno Reservoir	93	132	148	–	–	–	–	–	–	(21)
Międzyodrze wetland	59	89	116	132	–	–	–	–	–	(14)
Piasuchnik Reservoir	61	87	98	–	–	–	–	–	–	(6)
River Beek	48	92	124	138	–	–	–	–	–	(16)
River Danube	60	83	–	–	–	–	–	–	–	(21)
River Danube (Rusovce)	49	74	–	–	–	–	–	–	–	(15)
River Danube (Vlčie hrdlo)	62	87	108	129	144	–	–	–	–	(15)
River Danube (Žofín)	60	81	99	111	125	136	–	–	–	(11)
River Daugava	40	82	115	125	–	–	–	–	–	(26)
River Ebro	55	83	97	99	–	–	–	–	–	(17)
River Guadalquivir	49	80	94	104	–	–	–	–	–	(17)
River Guadiana	61	87	104	106	–	–	–	–	–	(17)
River Laben (Děčín)	48	75	96	115	128	142	151	–	–	(10)
River Ohře (Karlovy-Vary)	50	83	–	–	–	–	–	–	–	(10)
River Pilica	55	92	120	139	150	–	–	–	–	(18)
River Prokhladnaya	47	92	123	134	–	–	–	–	–	(16)
River Saône	58	88	98	99	–	–	–	–	–	(17)
River Segura	43	65	89	102	–	–	–	–	–	(17)
River Tagus	76	112	130	149	–	–	–	–	–	(17)
River Thames (Reading)	39	70	92	111	121	130	138	–	–	(24)
River Vltava (Méchenice)	52	78	94	105	135	161	–	–	–	(10)
River Vltava (Podbaba)	54	87	110	–	–	–	–	–	–	(10)
Slapi Reservoir (1957)	75	121	148	163	154	168	–	–	–	(21)
Slapi Reservoir (1959)	91	125	152	172	187	–	–	–	–	(21)

**Table 7** (continued)

Population	Estimated age (years)									Reference
	1	2	3	4	5	6	7	8	9	
River Cardener	66	88	–	–	–	–	–	–	–	(19)
River Fluvià	51	86	110	–	–	–	–	–	–	(19)
River Foix	53	69	76	–	–	–	–	–	–	(19)
River Muga	42	75	–	–	–	–	–	–	–	(19)
River Stropnice	49	68	74	–	–	–	–	–	–	(10)
Vranov Reservoir	70	118	140	147	–	–	–	–	–	(21)

References: <sup>1</sup>Backe-Hansen (1982) *vide* Kompowski (2000); <sup>2</sup>Battes (1974) *vide* Battes and Palaghiță (1999); <sup>3</sup>Battes and Palaghiță (1999); <sup>4</sup>Bíró (1975) *vide* Kompowski (2000); <sup>5</sup>Bíró and Muskó (1995); <sup>6</sup>Boiadjiev (1969) *vide* Raikova-Petrova et al. (2009); <sup>7</sup>Buch (1955) *vide* Battes and Palaghiță (1999); <sup>8</sup>Carnefeld (1936) *vide* Battes and Palaghiță (1999); <sup>9</sup>Chappaz et al. (1987); <sup>10</sup>Chitravadivelu (1971) *vide* Kompowski (2000); <sup>11</sup>Chitravadivelu (1974); <sup>12</sup>Damracev (1926) *vide* Battes and Palaghiță (1999); <sup>13</sup>Ivanov (1991) *vide* Raikova-Petrova et al. (2009); <sup>14</sup>Kompowski (2000); <sup>15</sup>Krupka (1972) *vide* Chitravadivelu (1974); <sup>16</sup>Kugel (1942) *vide* Kompowski (2000); <sup>17</sup>Latorre et al. (2018); <sup>18</sup>Mann and Penczak (1984); <sup>19</sup>Masó et al. (2016); <sup>20</sup>Młyniec (1986) *vide* Kompowski (2000); <sup>21</sup>Oliva et al. (1968) *vide* Raikova-Petrova et al. (2009); <sup>22</sup>Papadopol (1970) *vide* Chitravadivelu (1974); <sup>23</sup>Raikova-Petrova et al. (2009); <sup>24</sup>Williams (1967); <sup>25</sup>Wohlgemuth (1979) *vide* Kompowski (2000); <sup>26</sup>Zhukov (1965) *vide* Raikova-Petrova et al. (2009); <sup>27</sup>Zivkov (1974)



**Table 8** Bacterial and eukaryotic pathogens/parasites of *A. alburnus*

Taxonomic group/species	Family	Geographical distribution	Reference(s)
<b>Bacteria</b>			
Phylum: Actinobacteria			
Class: Actinobacteria			
<i>Gordonia</i> sp.	Gordoniaceae	Lake Mogan (Turkey)	(33)
<i>Kocuria</i> sp.	Micrococcaceae	Lake Mogan (Turkey)	(33)
<i>Microbacterium</i> sp.	Microbacteriaceae	Lake Mogan (Turkey)	(33)
<i>Rhodococcus</i> sp.	Corinebacteriaceae	Lake Mogan (Turkey)	(33)
Phylum: Firmicutes			
Class: Bacilli			
<i>Bacillus</i> sp.	Bacillaceae	Lake Mogan (Turkey)	(33)
<i>Staphylococcus</i> sp.	Staphylococcaceae	Lake Mogan (Turkey)	(33)
Phylum: Proteobacteria			
Class: Alphaproteobacteria			
<i>Brevundimonas</i> sp.	Caulobacteriaceae	Lake Mogan (Turkey)	(33)
Class: Gammaproteobacteria			
<i>Acinetobacter</i> sp.	Moraxellaceae	Lake Mogan (Turkey)	(33)
<i>Aeromonas</i> sp.	Aeromonadaceae	Lake Mogan (Turkey)	(33)
<i>Pseudomonas</i> sp.	Pseudomonaceae	Lake Mogan (Turkey)	(33)
<b>Protista</b>			
Phylum: Apicomplexa			
Class: Conoidasida			
<i>Eimeria cylindrospora</i>	Eimeriidae	Lake Balaton (Hungary)	(35)
<i>Eimeria nemethi</i>	Eimeriidae	Rivers and lakes (Hungary)	(35, 38)
<i>Eimeria</i> sp.	Eimeriidae	Rivers and lakes (Bulgaria)	(10, 12)
<i>Goussia alburni</i>	Barrouxiidae	Lake Dospat (Bulgaria)	(10, 12)
Phylum: Ciliophora			
Class: Oligohymenophorea			
<i>Ichthyophthirius multifiliis</i>	Ichthyophthiriidae	River Sava (Bosnia and Herzegovina)	(31)
<i>Trichodina</i> sp.	Trichodinidae	Lake Prespa (Macedonia)	(14, 15)
Class: Phyllopharyngea			
<i>Chilodonella cyprini</i>	Chilodonellidae	River Sava (Bosnia and Herzegovina)	(31)
<b>Fungi</b>			
Phylum: Oomycota			
Class: Peronosporae			
<i>Branchiomyces</i> sp.	Saprolegniaceae	Rivers and lakes (Italy)	(11)
<b>Metazoa</b>			
Phylum: Cnidaria			
Class: Myxosporae			
<i>Henneguya cutanea</i>	Myxobolidae	Lake Syamozero (Russia)	(32)
<i>Myxobolus alburni</i>	Myxobolidae	River Danube and Lake Balaton (Hungary)	(28)
<i>Myxobolus improvisus</i>	Myxobolidae	Lake Syamozero (Russia)	(32)
<i>Myxobolus margitae</i>	Myxobolidae	River Danube and Lake Balaton (Hungary)	(28)
<i>Myxobolus obesus</i>	Myxobolidae	River Danube and Lake Balaton (Hungary)	(28)
<i>Myxobolus pseudodispar</i>	Myxobolidae	Lake Mogan (Turkey)	(9, 29)
<i>Myxobolus shaharomae</i>	Myxobolidae	Rivers and lakes (Hungary)	(30)
Phylum: Platyhelminthes			
Class: Cestoda			
<i>Caryophyllaeides femica</i>	Lytocestidae	River Tundzha (Bulgaria)	(17)
<i>Ligula intestinalis</i>	Diphyllobothriidae	Rivers and lakes (Czechia, France, Serbia, Spain, Ukraine)	(3, 36, 8)
<i>Schyzocotyle acheilognathi</i>	Bothriocephalidae	Outdoor pond (Norway)	(13)
Class: Monogenea			
<i>Dactylogyrus alatus</i>	Dactylogyridae	River Tundzha (Bulgaria) and River Porsuk (Turkey)	(17, 22)

**Table 8** (continued)

Taxonomic group/species	Family	Geographical distribution	Reference(s)
<i>Dactylogyrus fraternus</i>	Dactylogyridae	River Tundzha (Bulgaria) and River Porsuk (Turkey)	(17, 22)
<i>Dactylogyrus minor</i>	Dactylogyridae	River Tundzha (Bulgaria)	(17)
<i>Dactylogyrus minutus</i>	Dactylogyridae	River Porsuk (Turkey)	(22)
<i>Dactylogyrus tissensis</i>	Dactylogyridae	River Tundzha (Bulgaria)	(17)
<i>Dactylogyrus vistulae</i>	Dactylogyridae	River Tundzha (Bulgaria)	(17)
<i>Gyrodactylus gracilihamatus</i>	Gyrodactylidae	River Tundzha (Bulgaria)	(17)
<i>Gyrodactylus hronosus</i>	Gyrodactylidae	River Tundzha (Bulgaria)	(17)
<i>Gyrodactylus laevis</i>	Gyrodactylidae	River Tundzha (Bulgaria)	(17)
<i>Paradiplozoon homoion</i>	Diplozoidae	River Tundzha (Bulgaria) and River Porsuk (Turkey)	(17, 23)
<i>Octomacrum europaeum</i>	Octomacridae	Rivers and lakes (Europe)	(26)
Class: Trematoda			
<i>Allocreadium album</i>	Allocreadiidae	Rivers and lakes (Ukraine)	(21)
<i>Allocreadium dogieli</i>	Allocreadiidae	Rivers and lakes (Russia and Ukraine)	(21)
<i>Diplostomum mergi</i>	Diplostomidae	River Danube (Czechia)	(27)
<i>Nicolla skrjabini</i>	Opecoelidae	River Danube (Bulgaria)	(7)
Phylum: Nematoda			
Class: Chromadorea			
<i>Rhabdochona denudata</i>	Rhabdochonidae	Rivers Arda, Marista and Tundzha, and Lake Kardzhali (Bulgaria)	(17, 18, 19, 20)
<i>Rhaphidascaris acus</i>	Rhaphidascarididae	River Danube and Lake Srebarna (Bulgaria)	(6, 37)
Class: Secernentea			
<i>Contraecum microcephalum</i>	Anisakidae	River Danube (Bulgaria)	(7)
Phylum: Acanthocephala			
Class: Palaecanthocephala			
<i>Acanthocephalus anguillae</i>	Echinorhynchidae	River Tundzha (Bulgaria)	(5)
<i>Acanthocephalus lucii</i>	Echinorhynchidae	River Danube (Bulgaria)	(7)
<i>Pomphorhynchus laevis</i>	Pomphorhynchidae	River Tundzha (Bulgaria)	(17)
Phylum: Annelida			
Class: Clitellata			
SubClass: Hirudinea			
<i>Piscicola geometra</i>	Piscicolidae	Lake Zegrzyński (Poland)	(2)
Phylum: Arthropoda			
SubPhylum: Crustacea			
Class: Hexanauplia			
<i>Lernaea cyprinacea</i>	Lernaeidae	Rivers and lakes (Iran)	(1, 4, 16, 34)
<i>Paraergasilus longidigitus</i>	Ergasilidae	Lake Enne (Turkey)	(25)
Class: Maxillopoda			
<i>Argulus foliaceus</i>	Argulidae	Lake Porsuk (Turkey)	(24)

Taxonomy follows the World Register of Marine Species (WoRMS: <https://www.marinespecies.org/>) database, except for Crustacea taxonomy, which follows the World of Copepods database ([www.marinespecies.org/copepoda/](http://www.marinespecies.org/copepoda/)). Some taxa have been revised, so valid and verified species names are used in the list that may be different from the original record. Subgenera are not given. Source references in footnote

<sup>1</sup>Barzegar and Jalali (2009); <sup>2</sup>Borowik (1968); <sup>3</sup>Bouزيد et al. (2008); <sup>4</sup>Bozorgnia et al. (2018); <sup>5</sup>Chunchukova and Kirin (2020); <sup>6</sup>Chunchukova et al. (2017); <sup>7</sup>Chunchukova et al. (2019a); <sup>8</sup>Djikanovic et al. (2012); <sup>9</sup>Forró and Eszterbauer (2016); <sup>10</sup>Golemansky (2017); <sup>11</sup>Grimaldi (1971); <sup>12</sup>Grupcheva et al. (2006); <sup>13</sup>Hansen and Alarcón (2019); <sup>14</sup>Hristovski et al. (2006); <sup>15</sup>Hristovski et al. (2012); <sup>16</sup>Jalali (1998); <sup>17</sup>Kakacheva-Avramova (1972); <sup>18</sup>Kirin (2001); <sup>19</sup>Kirin (2003); <sup>20</sup>Kirin et al. (2002); <sup>21</sup>Koval (1950); <sup>22</sup>Koyun (2011); <sup>23</sup>Koyun and Altunel (2007); <sup>24</sup>Koyun et al. (1997); <sup>25</sup>Koyun et al. (2007); <sup>26</sup>Kuchta et al. (2020); <sup>27</sup>Kudlai et al. (2017); <sup>28</sup>Molnár (2000); <sup>29</sup>Molnár et al. (2002); <sup>30</sup>Molnár et al. (2009); <sup>31</sup>Nedić et al. (2018); <sup>32</sup>Novokhatskaya and Ieshko (2010); <sup>33</sup>Ozaktas et al. (2012); <sup>34</sup>Pazooki and Masoumian (2012); <sup>35</sup>Rosenthal et al. (2016); <sup>36</sup>Sánchez and Alarcón-Elbal (2014); <sup>37</sup>Shukerova et al. (2010); <sup>38</sup>Xavier et al. (2018)

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